Wildlife Technical Bulletin 14, ADF&G/DWC/WTB-2012-14

Fortymile Caribou Herd: Increasing Numbers, Declining Nutrition, and Expanding Range

Rodney D. Boertje
Craig L. Gardner
Kalin A. Kellie
Brian D. Taras

2012

Alaska Department of Fish and Game
Division of Wildlife Conservation

Wildlife Technical Bulletin 14, ADF&G/DWC/WTB-2012-14

Fortymile Caribou Herd: Increasing Numbers, Declining Nutrition, and Expanding Range

RODNEY D. BOERTJE, Wildlife Biologist, 1300 College Road, Fairbanks, AK 99701-1551, rod.boertje@alaska.gov, 907-459-7237
CRAIG L. GARDNER, Wildlife Biologist, 1300 College Road, Fairbanks, AK 99701-1551, craig.gardner@alaska.gov, 907-459-7329
KALIN A. KELLIE, Wildlife Biologist, 1300 College Road, Fairbanks, AK 99701-1551, kalin.seaton@alaska.gov, 907-459-7235
BRIAN D. TARAS, Biometrician, 1300 College Road, Fairbanks, AK 99701-1551, brian.taras@alaska.gov, 907-459-7278

PREPARED BY:

Alaska Department of Fish and Game
Division of Wildlife Conservation
1300 College Road
Fairbanks, AK 99701-1551

This research was supported by Pittman-Robertson funds from the Federal Aid in Wildlife Restoration program. Monies come from a manufacturer's excise tax from the sales of handguns, sporting rifles, shotguns, ammunition, and archery equipment. State matching funds were provided from the Fish and Game general fund. Additional funding for fieldwork and creation of maps was received from Bureau of Land Management, Office of Subsistence Management, and the National Park Service. Funding does not imply approval of the contents of this report.

Wildlife Technical Bulletins provide thorough review and analysis of data and other information available regarding a particular topic. They may incorporate data obtained from one or more original research projects undertaken by agency staff as well as data and information obtained from other sources. These reports are professionally reviewed by research staff in the Division of Wildlife Conservation. These bulletins are numbered for internal tracking purposes. Wildlife Technical Bulletins have been produced since 1971 and are numbered sequentially within the series regardless of year produced. In 2012, a new numbering system was implemented that maintains sequential numbering within the series but also incorporates the year the bulletin was produced.

This Wildlife Technical Bulletin was approved for publication by Scott M. Brainerd, Research Coordinator in Region III for the Division of Wildlife Conservation.

This and other reports are available from the Alaska Department of Fish and Game's Division of Wildlife Conservation, PO Box 115526, Juneau, Alaska 99811-5526; telephone (907) 465-4190; email: dfg.dwc.publications@alaska.gov; website: www.adfg.alaska.gov. The report may also be accessed through most libraries, via interlibrary loan from the Alaska State Library or the Alaska Resources Library and Information Service (www.arlis.org).

This document should be cited as:

BOERTJE, R. D., C. L. GARDNER, K. A. KELLIE, AND B. D. TARAS. 2012. Fortymile caribou herd: Increasing numbers, declining nutrition, and expanding range. Alaska Department of Fish and Game, Wildlife Technical Bulletin 14, ADF&G/DWC/WTB-2012-14. Juneau, Alaska.

Cover Photo: Photo of Fortymile caribou by Robert R. Gingue/Tok ©2012 ADF&G.

Executive Summary

Historically, the Fortymile caribou (*Rangifer tarandus*) herd is most noted for its extreme decline in numbers and accompanying decline in range size. We estimated herd numbers declined from about 260,000 caribou in the early 1920s to 6,000 in 1973 (Murie 1935, Valkenburg and Davis 1989, this paper). When herd size was near minimum levels, about 90% of the historic range was abandoned, including most of the accessible range along the Steese Highway north of Fairbanks.

We surmised from recent and historic literature that at least 3 factors likely contributed to the decline in Fortymile herd numbers. These 3 factors were 1) reduced caribou nutrition resulting from overabundance; 2) heightened wolf (*Canis lupus*) predation, both because wolves were recovering from a low point and because caribou were likely experiencing reduced nutrition; and 3) excessive harvest of caribou during the early 1970s (Valkenburg et al. 1994). From studies elsewhere, we know that 1) peak caribou numbers are most often short-term occurrences; 2) before peak numbers are attained, caribou experience lowered birth rates; and 3) widespread overgrazing of the calving and summer range is the single factor most likely to cause a pronounced and often prolonged decline in caribou herd nutrition and numbers (Manseau et al. 1996, Mahoney and Schaefer 2002, Bergerud et al. 2008).

An equally intriguing question is how did Fortymile caribou reach relatively high peak numbers in the 1920s? A unique factor in the early 1920s was the unusual scarcity of wolves. For example, Murie (1944) did not find wolf tracks during winter 1922–1923, despite extensive travels by dog sled across Interior Alaska, including a trip through the primary Fortymile winter range. This unusual scarcity of wolves may have resulted in part from canine disease(s) introduced through sled dogs that accompanied the pioneer mining industry (Murie 1944:14–16).

If wolves had been common in the early 1920s, it is probable that the Fortymile herd would have remained well below the historic highs. For example, an absence of wolves for several years could have allowed the herd to at least double in size and peak well above sustainable levels. Indeed, with effective wolf control (1975–1982), the adjacent Delta caribou herd doubled in size in 5 years ($\lambda = 1.16$; Boertje et al. 1996). Similarly, we found wolf predation was the major factor limiting Fortymile herd numbers during 1994–2003, despite adequate caribou nutrition and an active nonlethal wolf control program during 1997–2001 (Boertje and Gardner 2000*a*, Boertje et al. 2008).

To encourage recovery of Fortymile caribou numbers from an estimated 6,000 caribou in 1973, the Alaska Board of Game adopted 1) continuous conservative harvest rates (≤2% of herd size annually) since 1973; and 2) various measures that reduced wolf numbers on various portions of the herd's range during 1997–2011 (Boertje and Gardner 2000*a*; Boertje et al. 2008; Gross 2009*a*, *b*; this paper). Most recently, a coalition of stakeholders wrote, and the Board of Game approved, the *Fortymile Caribou Herd Harvest Plan 2012–2018*[1]. This plan directs a harvest rate of 2% of herd size for hunters in Alaska and continued wolf control. Representatives from the Yukon resolved that Yukon hunters would continue to largely forego their allowable harvest of 1%. However, if herd size reached 70,000 caribou, the combined Alaska and Yukon harvest rate would effectively increase to 4% total.

---

[1] http://www.adfg.alaska.gov/index.cfm?adfg=wildlifeplanning.main

Using photocensuses, we documented a nearly 9-fold increase in Fortymile herd size during 1973–2010 from 6,000 to almost 52,000. During 1995–2009, the herd took 14 years to double in numbers.

This substantial and prolonged increase in caribou numbers, and the potential for overgrazing, led us to evaluate whether nutritional indices were changing. We examined 2 long-term nutritional indices and both declined significantly: 1) 36-month-old parturition rates during 1994–2010, and 2) October calf weights during 1990–2010. Most strikingly, these nutritional indices were lowest during summers 2008 and 2009. However, both indices showed modest improvement through May 2012.

These declines in caribou nutritional indices motivated us to evaluate how we would quantitatively identify a cautionary signal or biological threshold to indicate notably lowered caribou nutritional status. Reduced nutritional status was previously implicated when 36-month-old parturition rates fell below 55%, particularly in the Denali, Delta, and Nelchina herd case histories (Adams and Dale 1998, Valkenburg et al. 2003). Also, recent herd recovery in the Mulchatna herd was linked to a substantial rise in 36-month-old parturition rates from 0–50% to 67–83% (Woolington 2009; J. D. Woolington, ADF&G unpublished data, Dillingham). We found the best indices to explain variability in parturition rates were the 3 prior years of average October calf weights. We presumed that October calf weights integrated a variety of factors largely related to the quality of the previous summer's weather and range condition. We concluded that selected weather variables alone did not adequately explain the variability in caribou parturition rates, calf weights, or calf:cow ratios. However, to help explain the variability in parturition rates, we combined weather variables and October calf weights as covariates in a modeling exercise. Parturition rates were not well predicted by seasonal caribou densities or annual herd size.

Based on all Alaska data collected to date (9 caribou herds), we proposed the following indicator of low nutritional status: a decline below 55% in the 5-year moving weighted average of 36-month-old parturition rates. This threshold of <55% previously signaled prolonged periods of low nutrition in the Delta, Nelchina, and Mulchatna caribou herds, and did not trigger a management concern in any other case (except in the Fortymile herd in 2012). We proposed that this threshold would signal potential overgrazing and possible justification for more liberal harvests.

We caution that this low nutritional threshold could occasionally result from extended adverse weather rather than overgrazing, in which case a liberalized harvest would likely be unjustified. Furthermore, we caution that this "more liberal" harvest is justifiable only when a caribou herd is increasing, so simultaneous data on both nutritional status and herd trajectory are necessary to justify more liberal harvests. For example, the Delta herd's 5-year threshold dropped below 55% in 1991, when the herd was already declining (Valkenburg et al. 2003).

Longer term data are needed to test the utility of the threshold to warn managers of impending declines in herd numbers. Until then, we are recommending the threshold be used as a cautionary signal to notably reduced nutritional status that has been linked to immediate or imminent herd decline. Each management scenario will likely have a unique set of circumstances.

In the case of the Fortymile herd, the 5-year moving weighted average parturition rate in 2012 was 54%, similar to the cautionary threshold of 55%. We recommend managers use this triggering to warn stakeholders of a potentially significant decline in herd nutritional status. If the 5-year rate remains <55% through May 2014, the Board of Game should be prepared to support stabilizing herd numbers in autumn 2014, particularly given that larger sample sizes (n = >15 collared 36-month-olds) are expected beginning in 2013. Stabilizing herd numbers may require a more liberal harvest of up to 3,000 caribou (up from 1,000). Forewarning stakeholders of such a change is essential to maintaining public support. If Fortymile caribou begin calving or summering in new upland areas simultaneous to triggering the threshold, managers may consider waiting a year or 2 to see if the herd benefits from the new calving and summer range. However, in general, when the threshold is triggered, we would recommend against waiting for a herd to change movements.

We surmised from distribution data that the Fortymile herd overgrazed its core upland tundra during this study. For example, summer (1 July–15 August) Fortymile movements off the core upland tundra (about 7,000 km^2 of subalpine and alpine tundra) into surrounding spruce-moss taiga, particularly in 2008, was a possible causative factor for the reduced 36-month-old parturition rates by 2009. Most migratory caribou herds use mostly tundra in the summer in contrast to mostly taiga in the winter. Taiga provides a relatively poor summer diet (Boertje 1984, 1990). Departure from the isolated core uplands during summer may have resulted from local overgrazing given 1) the 9-fold increase in herd size over 37 years; 2) year-round use of the core uplands; 3) the low percentage of upland habitat (17%) above 1,060 m in the current year-round range; and 4) the cumulative effect of high and increasing calving densities in the core uplands, particularly during 2000–2008 when caribou ceased periodic use of the upper Salcha River calving area. To remedy effects of high, prolonged densities on the core uplands, summering caribou could regain use of the historic subalpine and alpine summer range in the White Mountains, just west of the Steese Highway.

During 17 years of radiotracking (1992–2008), we observed an unpredicted, rapid expansion in range size during summer and autumn, with accompanying declines in summer density. This rapid expansion may have been an indicator of localized overgrazing of the core upland tundra. In contrast, we observed an expected, slow expansion of the early winter (1 October–30 November), winter (1 December–31 March), and precalving (1 April–10 May) ranges.

Experience with the adjacent Nelchina herd indicated that a caribou herd can be managed below former peak densities, at a relatively stable level, while ultimately providing relatively stable and high harvests (Tobey and Schwanke 2009). The Nelchina herd sustained the highest reported harvest rate of caribou in Interior Alaska ($\bar{x}$ = 5.8% of herd size annually, 1997–2009) with herd size stable (λ = 1.002; Tobey 2003, Alaska Department of Fish and Game 2009, Tobey and Schwanke 2009). This contrasted with a total estimated average annual harvest rate of 1.6% of herd size in the increasing Fortymile herd (λ = 1.045, 1997–2010). The Nelchina strategy of managing for stability appears to have lessened the chance of the herd declining from malnourishment.

The Nelchina herd management strategy may be achievable in the Fortymile herd, because demand for harvesting caribou far exceeds the sustainable supply. Thousands of hunters can be mobilized near roadside crossings. We estimated the potential sustainable harvest rate was 6.1%

for the Fortymile herd with mostly moderate and declining nutrition (1997–2010), which was similar to the 6.0% potential sustainable harvest rate for the Nelchina herd with mostly lower and improving nutrition (1997–2009). However, intensive predator harvests and wolf control are central to managing the Nelchina herd. High predator take on the Nelchina calving and summer ranges are particularly unique in Interior Alaska, primarily because of high accessibility and relative close proximity to high human populations. This take of predators has enhanced Nelchina calf recruitment (35 calves:100 cows in October 1997–2009) and allowed for the reallocation of caribou from predators to people. In contrast, the Fortymile current calving and summer range is remote and much of the area is in the federally-protected Yukon-Charley Rivers National Preserve. Thus, because of relatively high year-round wolf predation, Fortymile calf recruitment may decline more readily as nutrition declines.

Monitoring trends in caribou numbers and nutritional status are key components of prudent management of the increasing Fortymile herd. To monitor trend in caribou numbers, we recommend continued annual June photocensuses and October surveys to estimate calf:cow ratios. To monitor nutritional limitation annually, we recommend 1) weighing of 15–20 female 4-month-old calves, 2) estimating parturition rates of ≥14 females 36 months of age, 3) estimating parturition rates of females ≥48 months of age, and 4) seasonal mapping of range use to assist with explaining how, when, and where overgrazing may adversely affect nutrition. We recommend radiocollaring 10–15 short yearlings to ultimately secure a sufficient sample (n = 14) of radiocollared, known-age 36-month-old females, because overwinter mortality of 4-month-old calves and the subsequent mortality of yearlings and 2-year-olds has often resulted in minimal sample sizes in prior years.

◆ ◆ ◆

Table of Contents

List of Figures

List of Tables

◆◆◆

Introduction

The range size of a caribou (*Rangifer tarandus*) herd typically constricts as herd size decreases and expands as herd size increases (Skoog 1968, Davis 1980, Bergerud et al. 2008). Constriction of the Fortymile herd range, which occurred simultaneous to the herd's extreme decline during 1920–1973, was particularly well documented (Murie 1935, Skoog 1956, Valkenburg et al. 1994). For example, Valkenburg and Davis (1986) illustrated historical and recent variations in the size and location of Fortymile calving and annual ranges during 1900–1985.

After 1963, it was noteworthy that caribou with young calves no longer crossed the Steese Highway. Furthermore, the Fortymile herd ceased all crossings of the Steese Highway during 1967–1990, when herd size ranged from only 6,000–23,000 (Valkenburg et al. 1994). These constricted movements eventually resulted in the 'Steese-Fortymile' herd being renamed the 'Fortymile' herd (Valkenburg and Davis 1986, Valkenburg et al. 1994). The herd also ceased using all winter ranges to the east in Yukon, Canada by the early 1970s (McDonald and Cooley 2004).

Stakeholders were inspired to advocate for a recovery of the herd, and particularly for a return of the herd to vast landscapes left devoid of caribou as herd size declined. These visionaries largely determined recent management practices (Urquhart and Farnell 1986, Valkenburg et al. 1994, Gronquist et al. 2005). Unpublished, detailed management plans are available from the Alaska Department of Fish and Game's website[2] and include the *Fortymile Caribou Herd Management Plan 1995* and the *Fortymile Caribou Herd Harvest Plans 2001–2006*, *2006–2012*, and *2012–2018*. All 4 plans were approved by the Alaska Board of Game.

The harvest plan for 2012–2018 was authored by an advisory coalition that represented a majority of stakeholders. This harvest plan proposed a harvest rate of 2% of herd size for hunters in Alaska and continued wolf (*Canis lupus*) control. Representatives from Yukon resolved that Yukon hunters would continue to largely forego their allowable harvest of 1%. However, if herd size reached 70,000 caribou, the combined Alaska and Yukon harvest rate would effectively increase to 4% total.

Yet, future management of the herd remains controversial. A few stakeholders are advocating for immediate management actions aimed at stabilizing or decreasing the Fortymile herd. In contrast, some stakeholders remain convinced that the herd should be managed for peak distribution.

We wrote this technical bulletin to provide an impartial biological foundation to guide current and future management planning. This bulletin is timely because it was drafted with input from the advisory coalition and to answer queries from the coalition. Overall, we sought to contribute to a management strategy based on current knowledge of the ecology of the Fortymile herd and other Alaska herds. Our specific objectives were as follows:

1. Review and evaluate the herd's history to gain realistic expectations of herd demography and to avoid repeating past management mistakes;

---

[2] http://www.adfg.alaska.gov/index.cfm?adfg=wildlifeplanning.main

2. Document changes in herd size and trend during 1973–2010 and the associated harvest rates;
3. Document changes in Fortymile parturition rates since data collection began in the early 1990s;
4. Model the effects of covariates (October calf weights and selected weather variables) on parturition rates to evaluate mechanisms that might explain the variability in parturition rates;
5. Compare caribou parturition rates throughout Alaska;
6. Propose and discuss a cautionary signal signifying sufficient caribou nutritional stress to warrant increasing harvests to slow or halt Fortymile herd growth;
7. Document changes in Fortymile October calf weights and calf:cow ratios and evaluate through modeling how well certain weather variables explain those weights and ratios;
8. Illustrate the Fortymile herd's seasonal ranges during 1992–2008, document changes in seasonal movements and distribution, and discuss the potential implications of changing movements;
9. Evaluate responses of Fortymile and Nelchina caribou to the large, widespread 2004 and 2005 wildfires;
10. Estimate historic herd size of the Fortymile herd (in the1920s and 1950s) by extrapolating from an empirical, linear relationship between range and herd sizes since 1980; and
11. Discuss management implications of findings and provide management recommendations.

Without a nutritional threshold signaling the need to stabilize herd size, we could inadvertently stockpile or accumulate too many caribou, precipitating another rapid decline in herd size. For example, a common socially-driven objective is to allow growth of ungulate herds, largely to allow stakeholders to encounter more animals. Strictly adhering to this socially-driven approach can eventually result in nutrition-related steep declines in caribou abundance and long periods of recovery. During these long periods of recovery, stakeholders are unsatisfied and managers fail to meet harvest and population objectives. Also, managers fail to meet mandates for managing a caribou herd "near maximum sustained yield" (Alaska Fish and Game Laws and Regulations:949).

We previously summarized factors limiting herd growth and efforts to increase herd growth during 1992–2008 (Boertje and Gardner 2000*a*,*b*; Boertje et al. 2008). We also contributed 7 maps of seasonal Fortymile distribution (1991–2000) to a report written by the Fortymile Planning Team (Fortymile Caribou Herd Planning Team 2000, *Habitat Management Needs Assessment for the Fortymile Caribou Herd*, Alaska Department of Fish and Game, Fairbanks). Gronquist et al. (2005) summarized the unique planning process to rebuild the Fortymile herd during 1996–2001.

The Fortymile caribou herd is the most economically important herd in the road-accessible portions of Interior Alaska north of the Alaska Range. The herd's range encompasses highly mineralized, wild lands managed virtually entirely by government agencies and private Native entities. In Alaska, land managers included the Alaska Department of Natural Resources, National Park Service, Bureau of Land Management, Fish and Wildlife Service, and the U.S. Air Force, as well as the Doyon Native Corporation. In Yukon, land managers included the Government of Yukon and the Tr'ondëk Hwëch'in Government. These land managers, as well as mining advocates and particularly the advisory coalition, provided the stimulus for this bulletin.

Methods

DATA COLLECTION

We followed methods described by Boertje and Gardner (2000*a*) for radiocollaring caribou and for estimating Fortymile caribou numbers, harvest, calf:cow ratios, and calf weights. We radiocollared only female caribou during this study. We annually weighed 14–18 calves using a calibrated spring or electronic scale during 24 September–9 October, 1990–2010.

To estimate parturition rates, we began by observing radiocollared females ≥24 months of age once during 11–13 May via small, fixed-wing aircraft. We documented the presence or absence of a calf, hard antlers, and a distended udder; ≥1 of these characteristics provided evidence that a female was parturient (Whitten 1995). Some antlerless females eventually develop udders and give birth, so to confirm that a female was not parturient, we repeated observations at least twice during 15–31 May. During 1992–2002, we observed parturient females daily until they gave birth, with observations beginning 11 or 12 May each year.

DATA ANALYSIS: HERD GROWTH RATES, PARTURITION RATES, CALF WEIGHTS, AND CALF:COW RATIOS

We estimated herd growth rate for several herds and time periods. We calculated herd growth rate (λ) by regressing the natural log (ln) of population estimates over the survey years to estimate the slope (m) of the line, and calculated $\lambda = e^m$.

To test for trend in parturition rates of 36-month-old and older caribou, we fit generalized linear models with a logit link function in Program R (R Core Development Team 2011). Essentially, we used the maximum likelihood version of the classic logistic regression model to test for trend.

To evaluate possible mechanisms that might explain the variability in Fortymile parturition rates, we modeled the effects of covariates (October average calf weights and/or weather variables) on parturition rates. We considered October average calf weights during the 3 years preceding a 36-month-old parturition rate to be metrics that might explain variability in parturition rates. For example, we presumed that each average October calf weight integrated a variety of factors largely related to the quality of the previous summer's weather and range condition. In addition, Valkenburg et al. (1994) tested the effects of a multitude of weather variables on calf:cow ratios and the percentage of calves in the Fortymile herd in October. They described the important weather variables as follows: average July temperature (C), total July rainfall (mm), and a snow index prior to parturition equivalent to the sum of the monthly maximum snow depths (in) from November (year $t-1$) through April (year t). We used these weather variables in our modeling, as well as the number of days with snow depth <2.54 cm, hereafter referred to as snow-free days

(Boertje et al. 1996). We also used a snow index (calculated as indicated above) prior to conception. We used weather data from Eagle, Alaska (National Weather Service 2011). We did not include interactions among weather and calf weight variables. To simplify the modeling exercise, we focused on adding weather covariates to the top 5 models that resulted from using only calf weights as covariates. We compared 146 models for the Fortymile herd. We ran similar models for the Delta and Nelchina herds using only calf weights as covariates. We also used logistic regression models to investigate the relationship between parturition rates and seasonal caribou densities as well as annual caribou numbers.

We summarized caribou parturition rate data throughout Alaska to provide insights into herd nutritional status. We used simple linear regression to describe the relationship between herd growth rates and average parturition rates of caribou 36 months of age. We used chi-square tests (Agresti 2007) to identify differences in the parturition rates of Fortymile and Nelchina caribou. We examined a new method for monitoring the nutritional status of caribou herds that entailed comparing, to a threshold value of 55%, a 5-year moving weighted average of parturition rates of 36-month-old caribou. For year *t*, we estimated a 5-year moving average of parturition rates weighted by annual sample sizes as:

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

where:

$\hat{p}_i$ is the annual estimated parturition rate and n_i is the annual sample size. For example, the 5-year moving weighted average for year $t = 2010$ is:

$$\hat{\hat{p}}_{2010} = \frac{\sum_{i=2010}^{2010-4} n_i \hat{p}_i}{\sum_{i=2010}^{2010-4} n_i} = \frac{n_{2010}\hat{p}_{2010} + n_{2009}\hat{p}_{2009} + n_{2008}\hat{p}_{2008} + n_{2007}\hat{p}_{2007} + n_{2006}\hat{p}_{2006}}{n_{2010} + n_{2009} + n_{2008} + n_{2007} + n_{2006}}$$

We evaluated the performance of this method by calculating the above moving weighted averages for each herd. We compared the results against the relevant population and nutritional status of these herds. We also performed simulations using Program R to evaluate the effect of sample size on the power of the moving weighted average to trigger a management concern (i.e., moving weighted average <55%) for various combinations of parturition rates. Through simulation we tested the method on parturition rates exhibiting increasing and decreasing trend, as well as parturition rates exhibiting bimodal variability. For each scenario of changing parturition rates, 5 annual samples of the desired size were randomly generated from binomial distributions with the probability of success set equal to the appropriate parturition rate. The value of the moving weighted average was then calculated and stored. These steps were repeated 5,000 times resulting in a sampling distribution for the estimated moving weighted average from which the probability of triggering a management concern could be calculated. For example, for a particular scenario having a mean parturition rate (given by the mean of the 5,000 repetitions) <55% and where 4,000 of the 5,000 repetitions resulted in a moving weighted average <55%, the power to trigger a management concern would be 4,000/5,000 = 0.80 or 80%. We also evaluated the probability of falsely triggering a management concern. For example, for a scenario with a mean parturition rate >55% and where 900 of the 5,000 repetitions resulted in a moving weighted average <55%, the probability of falsely triggering a management concern would be 900/5,000 = 0.18 or 18%. Our approach was a fixed-effects approach, rather than the random-effects approach used by Fleiss et al. (2003) to estimate the marginal mean proportion. We chose a fixed-effects approach because we were only concerned about, and not inferring beyond, the 5 years contributing to the moving weighted average.

To test for trend in weights of 4-month-old female calves, we used a linear mixed effects model (Zhang et al. 1998, McCulloch and Searle 2001, DeLong and Taras 2009). To test for the effects of the weather variables on 4-month-old calf weights, we used multiple linear regression models in Program R. To test for the effects of weather variables on calf:cow ratios, as previously explored by Valkenburg et al. (1994), we used generalized linear models with a logit link function in Program R.

We evaluated parsimony of models in our candidate set using AIC for small sample sizes (AICc; Sugiura 1978, Hurvich and Tsai 1989) or, for generalized linear models, the quasi-likelihood alternative (QAICc; Burnham and Anderson 2002). When using QAICc, the fit of the global model was evaluated using the Pearson statistic. We also used R^2 values to assess the predictive capability of a model. R^2 values for the generalized linear models were calculated as (null deviance–residual deviance)/null deviance.

FORTYMILE RANGE USE, BURNS, AND HISTORIC HERD SIZE

We monitored the distribution of Fortymile caribou using radiocollared females for 17 years (Table 1). For organizational purposes, we began the caribou's annual cycle with winter data (1 December–31 March) and terminated with early winter data (1 October–30 November); for example, we defined winter 1992 as 1 December 1991–31 March 1992. We differentiated seasons based, in part, on seasons described by Boertje (1984, 1990), as well as time periods of maximum range size, minimum range size, and the intervening periods of range expansion and contraction. Numbers of caribou radiotracked varied by season and year, as did the number of telemetry surveys (Table 1). We sampled at a similar intensity throughout the study, except that sampling intensity was lowest in 1991–1992.

During all seasons, except the calving season, we delineated ranges based on approximate locations of radiocollared caribou from telemetry surveys. During each telemetry survey (1–3 days of flying), we located aggregations of radiocollared caribou and recorded the portion of the drainage where we heard the signals. Locations of aggregations were accurate to within approximately 15 km. We based this estimate on results of flights when we practiced listening for radio collars and subsequently verified the location of the respective radio collars. Practice flights occurred at least monthly, as we investigated caribou mortalities and conducted calving flights, photocensuses, and autumn composition counts (Boertje and Gardner 2000*a*). We similarly recorded locations of individual radiocollared caribou that formed the periphery of the respective distribution. Locations of scattered individuals within the survey perimeter were accurate to within 25 km, because we did not approach these individuals as closely as the aggregations. To sample animals as socially independent as possible, we used only 1 location per radiocollared cow-calf pair. After plotting the points from all the surveys for a particular season on a range map (1 cm = 12.5 km), we smoothed a line by hand around the peripheral survey points approximately 10 km outside peripheral points to compensate for inaccuracies and imprecision in the locations. In 3 cases, 1–3 points were widely separated ≥40 km from other points; these outliers had minor influences on the results and were excluded from the range perimeter to conservatively estimate range size. We entered points and range perimeters into ArcGIS® 9.3.1 (ESRI, Redlands, California) to combine and contrast seasonal ranges among years. For example, we plotted postcalving density estimates by year based on delineated seasonal polygons rather than kernel methods.

We sampled during the calving season by mapping (latitude and longitude) the birth sites of radiocollared caribou. We used fixed kernels to estimate annual utilization distributions (Silverman 1986, Worton 1989) using program KERNELHR (Seaman et al. 1998). To estimate annual calving range size, we used automatic grid cell size selection and least-squares cross validation to estimate smoothing parameters (Seaman and Powell 1996). To be consistently conservative in estimating range size, we used 90% volume contours to estimate annual calving range sizes.

To estimate calving ranges for the periods 1992–2000, 2001–2008, and 1992–2008, we averaged annual utilization distributions. Averaging annual estimates served to 1) avoid the issue of unequal annual sample sizes having undue influence within pooled datasets, 2) allow uncertainty in annual distributions to be propagated, and 3) allow accurate estimates of modes of high probability of use. To generate averages, we used a common grid cell size (12.96 km^2) determined using the rounded mean grid cell size from the initial estimates of annual distribution and selected annual smoothing parameters using least-squares cross validation. Kernel densities at each grid cell intersection were summed and divided by the number of annual estimates to generate averaged utilization distributions. Utilization distributions were converted to the estimated percentage of birth sites per km^2 by multiplying by 100 to convert to a percentage, and dividing the output by 12.96 km^2 to convert to 1 km^2. The 50% and 95% volume contours were generated for display using Hawth's Geospatial Modeling Environment (Version 0.5.5 Beta).

We used ArcGIS to calculate the proportional use of specific, similarly-sized drainages by radiocollared caribou for the calving and early winter seasons for all years. To correct for differences in sample size among years, we first counted the number of points by drainage for a particular year (numerator) and divided counts by the total number of locations for that year (denominator); fractions totaled 1.0 for each year and were converted to percentages. To calculate the percent use by drainage for all years, we summed the percentages by drainage for all years, and divided by the number of years.

We also used ArcGIS to calculate the percentage of the maximum Fortymile caribou range (1991–2008) that was above the approximate visual treeline (about 1,067 m) and to depict areas burned in 2004 and 2005 (Alaska Interagency Coordination Center 2011, Government of Yukon 2011). Finally, we used ArcGIS to calculate multi-year range sizes from 3 recent 5- or 6-year study periods since 1992 and 4 previously published 4- to 7-year study periods. The basis for these 4 previously published range sizes were original figures (Skoog 1956:8, Valkenburg and Davis 1986:316, Valkenburg et al. 1994:12) or a combination of original figures and descriptions of caribou movements in the Fortymile area in the 1920s (Murie 1935:51, 57, 70–73; McDonald and Cooley 2004). We then developed a relationship between average herd size and multi-year range size using a simple linear regression model in Program R to estimate historic herd size.

Results

FORTYMILE HERD SIZE AND TREND, 1973–2010

During 1973–2010, herd size increased nearly 9-fold from 6,000 to almost 52,000 (Fig. 1) with a moderate rate of growth ($\lambda = 1.06$; Fig. 2). However, herd growth was not continuous. Rather, we documented 3 intervals of growth during 1973–2010. During the first 17-year interval of this 37-year history, herd numbers increased at a moderate rate ($\lambda = 1.08$). This increase began coincidental with favorable weather and the initiation of conservative annual harvests ($\bar{x} = 1.6\%$ during 1973–2010, Table 2). However, despite conservative harvests, herd numbers remained stable during 1990–1996 ($\lambda = 1.00$).

Consequently, intensive herd research and novel management planning efforts began in 1994, which in 1997 led to the initiation of various degrees of wolf control on various portions of the herd's range (Boertje and Gardner 2000*a*, Boertje et al. 2008, Gross 2009*a*). Coincidental to initial wolf control efforts and minimal harvesting of caribou (1996–2000, Table 2), herd numbers again increased at a moderate rate ($\lambda = 1.09$, 1996–2003).

We assumed herd numbers stabilized during 2003–2006, based on calf:cow ratios (Table 2). The 2003 and 2005 calf:cow ratios were among the 3 lowest ever measured in the Fortymile herd, indicating herd numbers stabilized or declined. This potential 4-year period of stability or decline was not verified by a complete photocensus (Table 2, Fig. 1). If we assume herd size was stable during 2003–2006, then herd size increased at a slow rate ($\lambda = 1.04$) during 2006–2010 (Fig. 1).

PARTURITION RATES

The substantial and prolonged increase in Fortymile caribou numbers, coupled with reduced growth rates since 2003, led us to examine whether herd nutritional status was declining, as indicated by first age of reproduction. Parturition among 24-month-old females was rare. Only 4 (5%) of 73 24-month-old females were parturient in the Fortymile herd during 1992–2002; 3 subsequently gave birth and 1 succumbed to wolf predation.

We deemed focusing on parturition rates of caribou 36 months of age most relevant to evaluating nutritional status, because parturition was common among 36-month-old females yet less common than among prime-age females (48–72 months of age). During 1993–2010, 110 (74%) of 150 36-month-old Fortymile caribou were parturient. Parturition at 36 months of age did not adversely affect the parturition rate at 48 months of age. Of 97 parturient and 34 nonparturient 36-month-olds observed at 48 months of age, 85% and 82% were parturient, respectively. During 1994–2011, parturition rates of Fortymile caribou 48, 60, and 72 months of age averaged 84% ($n = 135$), 86% ($n = 109$), and 89% ($n = 84$), respectively.

Annual parturition rates of 36-month-old Fortymile caribou declined significantly during 1994–2010 (slope on the logit scale = −0.17 [SE = 0.048], $P = 0.0003$, $R^2 = 0.39$, Fig. 3), as did parturition rates of older Fortymile caribou (slope on the logit scale = −0.04 [SE = 0.022], $P = 0.046$, $R^2 = 0.098$, Fig. 4). These trend models left a substantial amount of the variability in parturition rate unexplained, so we included covariates in subsequent modeling of parturition rates of 36-month-old caribou.

Substantially more of the variability in parturition rates of 36-month-old caribou was explained by adding October average calf weights as covariates (Table 3) than by the trend model alone. However, no model using covariates was clearly superior. Five models had delta QAICc values <2.0 and QAICc weights between 0.11 and 0.22 for a cumulative QAICc weight of 0.84 (Table 3). Of these 5, the top model for predicting Fortymile 36-month-old parturition rates (i.e., the model with the highest R^2, model 12) included the 3 prior years of average October calf weights and an interaction between the first and third year's average calf weights; this model had $R^2 = 0.69$ and a delta QAICc = 1.41 (Table 3). The second best model for prediction was similar to the top model, except that this model lacked the second year average calf weight as a covariate. This model (model 9) had $R^2 = 0.59$ and the lowest QAICc (i.e., the most parsimonious model). All 5 models included average calf weight in year $t-1$ as a covariate, and most included average calf weight in year $t-3$ (Table 3). All 5 models associated increasing parturition rates with increasing calf weights. For the top predictive model (model 12), each kilogram increase in calf weights for years $t-1$, $t-2$, and $t-3$ corresponded to maximum increases in parturition rate of 5.9%, 4.3% and 5.3%, respectively, when the other covariates were fixed at the respective average levels and the probability of parturition was near 0.5. The interaction term indicated that, within the range of the bulk of the data, an increase in weight at $t-1$ resulted in an increased positive effect due to the $t-3$ covariate, and vice versa. For this top model, the estimated parturition rate was 76% with all covariates set at their average, versus 74% based on the observed average with $n = 150$.

Applying the top Fortymile herd predictive model in Table 3 to the Delta herd (1994–2005) and Nelchina herd (1998–2005) resulted in $R^2 = 0.53$ and 0.41, respectively. For both the Delta and Nelchina herds, the model with the lowest QAICc had the first year average calf weight as the only covariate and resulted in $R^2 = 0.34$ and 0.21, respectively.

Models with only weather variables as covariates explained little of the variability in Fortymile herd parturition rates and performed poorly (delta QAICc > 15.8; Table 4). However, when certain weather variables were added as covariates along with average calf weights, model parsimony and predictive capability improved (Table 4). Seven of the 9 models with delta QAICc values <2.0 included at least 1 weather covariate (6 models included the number of snow-free days, 3 included average July temperature, and 2 included the snow index). Model improvement was greater for the top calf-weight models with only additive terms (models 1, 4, and 5) compared to calf-weight models with an interaction term (models 9 and 12). The R^2 of models 1, 4, and 5 were increased by 0.15, 0.12, and 0.12 when the number of snow-free days was added and increased by up to 0.34 with additional weather variables. QAICc values were also reduced.

Although weather variables led to some improvement in model parsimony and predictive capability, the importance of specific weather variables remains unclear. Even more so than for the calf-weight-only models (Table 3), none of the top 9 models with differing weather covariates was clearly superior, demonstrated by 7 models with QAICc <1 and low QAICc weights (0.04–0.08). In addition, the top 9 models include the top predictive (model 12) and the most parsimonious (model 9) of the calf-weight-only models (Table 3). Finally, the R^2 of only one model, the new top model, was larger than that for model 12 and the increase was due to an interaction term that was highly dependent on data from only 2 years, 1992 and 1998, which were the 2 extremes for number of snow-free days (Table 5). All 9 models included calf weight in year *t*−1.

Assessing whether or not the interaction term and the related increase in R^2 (0.81 vs. 0.69) in the top model was spurious will require more data; however, the possibility that it is valid motivated an examination of effect sizes. This top model included the number of snow-free days, average July temperature, interactions between these parameters, as well as average calf weight in years *t*−1 and *t*−2. According to this model, each kilogram increase in calf weights for years *t*−1 and *t*−2 corresponded to maximum increases in parturition rate of 7.2% and 6.9%, respectively, when the other covariates were fixed at the respective average levels and with the probability of parturition near 0.5. The model also indicated that an increase of 1 snow-free day corresponded to a maximum 2.2% increase in parturition rate, and an increase in 1 degree in average July temperature (17–18°C) corresponded to a maximum decrease in parturition rate of 21%. At the other end of the average July temperature scale, an increase from 14 to 15°C corresponded to a decrease in parturition rate of 4%. The interaction term indicated that when the number of snow-free days was near or above average (171 days), an increase in average July temperature decreased a relatively high parturition rate. However, when the number of snow-free days was below average, an increase in average July temperature increased a relatively low parturition rate.

Finally, in a subsequent modeling exercise, we tested for an effect of snow on parturition rates when the snow index came from the winter preceding conception, rather than the winter preceding parturition. In this modeling exercise, the top group of models with delta QAICc <2 remained the same as in Table 4, with the exception of the 2 models with the snow index preceding parturition. A new model with the snow index preceding conception became the top model. This model had a lower R^2 (0.62 vs. 0.81) and a slightly lower QAICc (61.27 vs. 61.35) than the top model in Table 4. Average calf weight in year *t−1*and the number of snow-free days remained as covariates. Neither of the snow indices was correlated with snow-free days, as Pearson correlation coefficients were 0.14 (preceding conception) and −0.18 (preceding parturition).

We found little of the variability in Fortymile parturition rates to be predicted by seasonal densities or annual caribou numbers, as indicated by R^2 values ≤0.17. For example, 36-month-old caribou parturition rates (1993–2009) were negatively correlated with densities (1992–2008) during calving ($P = 0.016$, $R^2 = 0.16$) and postcalving ($P = 0.015$, $R^2 = 0.17$) and positively correlated with densities during summer ($P = 0.04$, $R^2 = 0.14$). Also, 36-month-old parturition rates (1993–2009) were not correlated with densities during winter (1992–2008, $P = 0.58$, $R^2 = 0.01$), and were negatively correlated with annual caribou numbers (1993–2009, $P = 0.015$, $R^2 = 0.15$).

After summarizing parturition data for 36-month-old caribou throughout Alaska (Table 6), we found that herd growth rates were positively related to average parturition rates ($R^2 = 0.57$, $P = 0.005$, Fig. 5). Herd growth rates were negative when average parturition rates were <40%. A wider range of herd growth rates occurred when average parturition rates were >60%, presumably the result of varying calf survival related in part to different predation regimes.

After illustrating average 36-month-old parturition rates for individual herds during periods with generally consistent population trend (Fig. 6), we concluded that average parturition rates fit into 3 categories; low (<55%), moderate (55–80%), and high (>80%). Average parturition rates in the Fortymile herd were moderate (74%) during the recent period of largely increasing trend (λ = 1.05, 1995–2011, Fig. 1).

Using the same 3 categories to compare annual 36-month-old parturition rates, Fortymile rates ranked moderate to high, except in 1993, 2005, 2009, and 2010 (Table 6). During 1997–2003 (except 2002), 36-month-old parturition rates were significantly greater among Fortymile caribou than adjacent Nelchina caribou ($\chi^2 \geq 4.00$, $P \leq 0.046$; Fig. 7). During 2004–2010, Fortymile rates mostly declined and Nelchina rates mostly increased (Fig. 7, Table 6). Consequently, Fortymile and Nelchina parturition rates did not differ during 2004–2010 ($\chi^2 \leq 2.22$, $P \geq 0.14$). The Denali herd had the highest parturition rates in Alaska, and the Denali and Fortymile rates were nearly identical during the early years of study, 1993–2001, with 9-year averages of 83% and 82%, respectively (Table 6).

Parturition rates of caribou aged ≥48 months were less valuable in distinguishing nutritional status, in part because these older females displayed less annual variation than females 36 months of age (Figs. 7 and 8). Annual parturition rates of Fortymile caribou aged ≥48 months ranked high in 13 (72%) of 18 cases and moderate in 5 (28%) of 18 cases. These rates did not differ among Fortymile and Nelchina caribou during 2002–2009 ($\chi^2 \leq 2.45$, $P \geq 0.12$). However, Fortymile rates were significantly greater than Nelchina rates in 1999 ($\chi^2 = 5.79$, $P = 0.016$) and 2000 ($\chi^2 = 11.36$, $P = 0.0008$) and marginally greater in 2001 ($\chi^2 = 3.00$, $P = 0.083$; Fig. 8). In 2010, Nelchina rates were marginally greater than Fortymile rates ($\chi^2 = 3.55$, $P = 0.059$).

The 5-year moving weighted averages of 36-month-old parturition rates declined below our 55% cautionary signal in 3 cases, the Delta herd (1991–1997), Nelchina herd (2001–2008), and Mulchatna herd (2005–2011; Table 6). Except for these 3 cases and the 2012 value for the Fortymile herd, the 5-year moving weighted average has not fallen below 55% in Alaska (Table 6).

We investigated the annual sample sizes required to correctly trigger the 5-year moving weighted average. From simulations (Fig. 9), samples sizes of 14/yr over 5 years (70 total) provided a high probability (85% for the bimodal example and 82% for the trend example) of detecting a true decline to 50%, and provided a reasonable balance between ensuring triggering when true moving weighted average < 0.55 and not triggering when true moving weighted average > 0.55. The probability of correctly triggering was greatest when the parturition rates declined in a rapid, bimodal manner rather than with a slowly declining trend (Fig. 9). These examples along with additional simulations (e.g., very slowly declining rates from 85% to 20% over 27 years) led us to recommend a sample size of 14/yr. Smaller sample sizes generally led to relatively high rates of triggering when the true moving weighted average was >55%, which risked an unnecessary action. Smaller sample sizes also generally led to relatively low rates of triggering when the true moving weighted average was <55%, which risked a delayed intervention.

FORTYMILE CALF WEIGHTS AND CALF:COW RATIOS

Four-month-old calf weights declined 0.22 kg/yr ($P = 0.02$, $R^2 = 0.24$, 1990–2010; Fig. 10). To explore the effect of weather on average calf weights (Table 5), we first replaced the continuous covariate year (i.e., trend) with the 4 weather variables, which resulted in less parsimonious models but a modest improvement in R^2. The clear top weather-only model (second model had delta AICc = 2.3) included total July rainfall, the snow index, and their interaction as covariates. This top model was slightly less parsimonious (AICc higher by ~0.1) than the trend model, and had an $R^2 = 0.44$. The same interaction term was included in the second and third models as well. All additive models had delta AICc ≥4.5 and explained little variability ($R^2 < 0.13$).

When we considered the 4 weather covariates along with the year covariate (i.e., trend), the clear top model contained the same weather variables as the top weather-only model. This model had an AICc weight = 0.66 and a larger $R^2 = 0.62$; the next closest model had a delta AICc = 3.84. This model showed that when the other covariates were fixed at their average levels, an increase in 10 mm in July precipitation corresponded to an increase in calf weight of 0.37 kg, an increase in 25.4 cm of accumulated snow corresponded to an increase in calf weight of only 0.07 kg, and calf weights declined by 0.20 kg/yr rather than by 0.22 kg/yr, as in the model without weather variables. The July rainfall:snow index interaction term indicated that a strong positive gradient existed in calf weights with increasing July precipitation in years of above-average snow, and this gradient was substantially weaker in years of below-average snow.

Correlations between average calf weights and the 4 weather variables were low (between −0.23 and 0.22). These low correlations were consistent with the relatively poor explanatory power of weather variables when modeling average calf weights.

Little of the variability in calf:cow ratios (1970–2010, Table 2) was explained by population trend with or without the 3 weather variables identified by Valkenburg et al. (1994); average July temperature, total July rainfall, and snow index. The trend model without weather covariates had $R^2 = 0.08$, and the trend model including all weather covariates had $R^2 = 0.12$. After including all 2-way weather interactions, R^2 increased to 0.28. Including the 3-way interaction resulted in an additional increase in R^2 of <0.01.

CHANGES IN FORTYMILE HERD MOVEMENTS, RANGES, AND DENSITIES

Because weather variables did not adequately explain the low nutrition in 2008 and 2009 (Figs. 7 and 10), we explored changes in herd movements and distribution that might be indicative of localized overgrazing and nutritional stress. However, we monitored seasonal distribution only during 1992–2008. During these years, sampling intensity was similar enough to detect differences in range size over time (Table 1).

We found supporting evidence that localized overgrazing occurred on the core upland tundra habitat (7,000 km^2). For example, a year-round distribution of seasonal areas used by caribou clearly illustrated high use of the isolated, core upland tundra (blue areas in Fig. 11 with 71–100% use). The surrounding areas were predominately taiga. The core uplands were used most extensively from precalving (1 April–10 May) through early winter (1 October–30 November).

In contrast, during winter (1 December–31 March) these core uplands were largely an area of overlap among adjacent winter ranges dominated by taiga.

Of all the seasonal ranges, summer range size (1 July–15 August) increased most during this study (Fig. 12), possibly indicating summer nutritional stress. For example, as herd size increased, summering caribou were spacing away from the core upland tundra into surrounding lower spruce-moss taiga, which provided less optimal summer range. The summer expansion was most apparent in 2008 (Fig. 12), when summer nutrition was particularly low (Figs. 7 and 10).

Data during calving (11 May–27 May) added support to the overgrazing hypothesis. Virtually all calving occurred on portions of the core upland tundra, and calving densities increased during this study. For example, the average size of the calving area (Fig. 12) declined 28%, when comparing the first 9 years of data (Fig. 13) with the last 8 years (Fig. 14). This restriction occurred largely because calving caribou ceased periodic use of the upper Salcha River after 2000. Calving caribou used on average only 2,904 km^2 (41%) of the core uplands during the last 8 years (Fig. 14) with densities (bulls excluded) averaging 17 caribou/km^2 and reaching 42 caribou/km^2 in 2008 (Fig. 15). Also, during the last 8 years, postcalving caribou (28 May–30 June) used virtually all of the core uplands, with densities averaging 6 caribou/km^2 (Fig. 15).

Over all years, birth sites were most concentrated in the alpine and subalpine tundra near Mount Harper and Glacier Mountain and in the subalpine areas southwest of Glacier Mountain (Figs. 16 and 17). When lingering snow covered a high proportion of the upland tundra, calving was more concentrated at or slightly below treeline. Lingering snow was particularly apparent in 1992 and 2000.

After caribou left the relatively densely-populated calving range, a regular pattern of gradual range expansion occurred seasonally until midwinter (Fig. 12). For example, the postcalving ranges (Fig. 18) were larger than the calving ranges each year, except in 1995. The postcalving ranges were generally above treeline on and near the calving ranges, except in 2005 when considerable movements occurred below treeline. Postcalving range sizes increased little during the study (Fig. 12), as movements were usually restricted to the core uplands.

The summer range size (Fig. 19) increased consistently throughout the study period, and the rate of increase was the greatest for any season, followed closely by the rate of increase in autumn (Fig. 12). Summer range sizes were similar to the postcalving range sizes only during the initial 2 years of this study (Fig. 12). During summer 2008 (final year of summer data) the herd expanded its range both east and west and crossed both the Steese and Taylor highways. The autumn ranges (Fig. 20) were larger than summer ranges each year, except 2000, 2005, and 2006 (Fig. 12). Autumn range reached maximum size during 2003 and 2007 (final year of data). Summer foods senesced during early autumn, and caribou transitioned to a winter diet more readily available in the more expansive lower elevations.

During early winter (Fig. 21), range sizes were larger than autumn ranges every year, except 2002, and range sizes increased gradually during the study (Fig. 12). Caribou in early winter distributed themselves uniformly among years (Fig. 22), so all portions of the range received nearly equal grazing pressure. Maximum eastward expansion during these 17 years occurred in early winter 2002, and maximum westward expansion occurred in early winters 2007 and 2008 (Fig. 23). However, annual maximum seasonal range size occurred during winter (Fig. 24) in 13 of 17 years (Fig. 12). Each April, female caribou and calves began a withdrawal from the most expansive winter or early winter range (Figs. 23 and 24) to the most constricted calving range (Fig. 12). Thus, the precalving season (Fig. 25) was a dynamic time characterized by movement generally from the lower forested areas of winter habitat towards the higher core upland tundra.

The expansion in summer range led to a declining summer density, while the slower expansion in winter range led to an increasing winter density (Figs. 26 and 27). For example, as herd size increased, summer density declined from 3.4 caribou/km^2 in 1995 to 1.9 caribou/km^2 in 2008, and winter density increased from 1.0 caribou/km^2 to 1.6 caribou/km^2.

We found no sudden changes in seasonal range sizes after the large and widespread 2004 and 2005 wildfires (Fig. 12). These burns (Fig. 28) covered only small proportions of the recent winter ranges and smaller proportions of the summer and autumn ranges.

Finally, average herd size mostly increased with multi-year range size (Fig. 29, Table 7). Using an extrapolation of the recent relationship between average herd size and multi-year range size, we derived 2 new estimates of historical herd size and the 90% prediction intervals: 55,102 during 1952–1955 and 261,202 during 1918–1924 (Fig. 30).

Discussion

FORTYMILE HERD TREND, HARVESTS, AND WOLVES

The recent 9-fold increase in the Fortymile herd ($\lambda = 1.06$, 1973–2010; Fig. 2) is exceptional among Interior Alaska caribou herds. Indeed, Interior herds without wolf control have remained at low numbers in recent times (Table 8), despite low harvest rates similar to those in the Fortymile herd (Table 2, Alaska Department of Fish and Game 2009). Given that the Fortymile herd's increase during 1996–2003 ($\lambda = 1.09$) was unique in Interior Alaska and occurred concurrent with nonlethal wolf control on a portion of the herd's range, we have circumstantial evidence that nonlethal wolf control promoted herd growth (Boertje et al. 2008). Alternatively, history suggests the Fortymile herd may simply be recovering from its low point in 1973, and the herd may have increased with favorable weather and without wolf control, as during 1973–1990 ($\lambda = 1.08$). In contrast, the adjacent Delta caribou herd increased at an unusually rapid rate for Interior Alaska caribou ($\lambda = 1.16$, 1975–1982) concurrent with the only well-documented experiment that used substantial wolf control in Interior Alaska (55–80% reduction in wolves from precontrol numbers, $\bar{x}$ = 69%; Boertje et al. 1996). Thus, we have relatively convincing evidence that substantial wolf control throughout a herd's range can promote growth of Interior Alaska caribou herds. We have less evidence that a lower level of wolf control can promote herd growth. The Delta herd subsequently declined after a 5-fold increase, partly in response to the adverse winters of 1990–1993, and has remained at low levels in the absence of renewed wolf control (Boertje et al. 1996, Seaton 2009).

Boertje and Gardner (2000*a*, *b*) and Boertje et al. (2008) provided direct evidence that wolf predation was the dominant factor affecting Fortymile herd numbers. These studies of Fortymile caribou births and deaths (1994–2003) showed wolf predation was the dominant factor influencing herd trend in years preceding, during, and after nonlethal wolf control on a portion of the herd's range. Also, O. Murie (1935) documented that Fortymile herd numbers peaked during a relatively short period (1916–1925) when wolves were scarce throughout Interior Alaska. A. Murie (1944:14–16) indicated this wolf scarcity resulted from newly arrived epizootic canine disease, as evidenced by widespread and acute disease that killed entire sled dog teams. In contrast, present-day Alaska wolf populations have largely acquired immunity to such diseases, and disease is a minor factor affecting wolf numbers in Alaska, except for occasional rabies epidemics along the north and west coastal areas (Ballard et al. 1997, Mech et al. 1998, Adams et al. 2008).

The reported scarcity of wolves in the early 1920s was likely a major factor contributing to the historic high numbers of Fortymile caribou. For example, the reported scarcity of wolves could have allowed the herd to at least double in size and peak well above sustainable levels. For example, with effective wolf control (1975–1982), the adjacent Delta caribou herd doubled in size in 5 years ($\lambda = 1.16$; Boertje et al. 1996). The same doubling result can be derived by substantially reducing wolf-caused caribou deaths in empirical models of Fortymile caribou births, deaths, and total numbers (Boertje and Gardner 2000*a*).

We inferred that recovery of the Fortymile herd to historic levels of >100,000 caribou in the next decade is unlikely, unless some unforeseen factors cause a renewed scarcity of wolves for a protracted period. For example, a complete lack of wolves could result in a doubling of herd size in 4 or 5 years (Boertje et al. 1996, Boertje and Gardner 2000*a*). Such a scenario is highly unrealistic. Instead, with recent wolf control programs, we recorded a doubling of herd size in 14 years (1996–2010, Table 2).

We learned valuable lessons from the herd's rapid decline in the early 1970s. For example, ill-timed liberal harvests during 1970–1972 (Table 2), when the herd was already declining, were partly to blame for the severe decline to 6,000 that disenfranchised most users of the herd. Valkenburg et al. (1994) concluded that if harvest had been curtailed in 1970 instead of 1973 (Table 2), the herd could probably have been stabilized at a low point of 10,000–12,000 caribou with a potential recovery to >33,000 by 1990 (Fig. 1). Instead, excessive harvests during 1970–1972 accelerated the decline, and those harvests were a major factor contributing to the low point of about 6,000 caribou (Table 2).

CARIBOU NUTRITIONAL STATUS, INDICES, AND WEATHER

The Fortymile herd's 9-fold increase stimulated us to explore whether increasing herd size was potentially causing low nutritional status. Studies elsewhere have shown that high or peak caribou densities are often associated with substantially reduced nutritional status (Bergerud et al. 2008).

We measured only 2 long-term nutritional indices in the Fortymile herd and both declined significantly: 36-month-old parturition rates during 1994–2010 (Fig. 3) and October calf weights during 1990–2010 (Fig. 10). Most strikingly, nutritional status was lowest during summers 2008 and 2009, as indicated by low calf weights in those years and low 36-month-old parturition rates in subsequent years. However, nutritional status was moderate during more recent years, 2010–2012. Average parturition rates of 36-month-old caribou appeared to offer a useful index to interand intra-herd nutritional status of Alaska caribou (Figs. 5 and 6, Table 6). Adams and Dale (1998) concluded that each annual 36-month-old parturition rate was a cumulative index of the 3 prior years' nutrition, because caribou that calved for the first time had reached a particular herd-specific weight. Similarly, we found the best predictors of 36-month-old parturition rates in the Fortymile herd to be the prior 3 years of October calf weights. The same relationship explained a substantial portion of the variability in 36-month-old parturition rates for both the Delta and Nelchina herds. Although weather variables led to improvements in model parsimony and predictive capability, the importance of specific weather variables in determining Fortymile parturition rates remains unclear. The only model that stood out from the calf-weight-only models in terms of R^2 did so because of an interaction term that was highly dependent on data from only 2 years, 1992 and 1998. While this interaction term was biologically sensible and predictions for low parturition rate years were improved, the reliance on only 2 years of data kept us from endorsing the model. We concluded that longer term data is required to verify the significance of weather to the Fortymile herd, as well as to further develop our understanding of the relationship between average calf weights and 36-month-old parturition rates.

Data from the Denali herd supported using parturition rates of 36-month-old caribou as an index to herd nutritional status. Caribou generally first give birth at 36 months of age; seldom do they give birth at 24 months of age. However, those individuals that give birth at 24 months of age regularly give birth again at 36 months of age (Davis et al. 1991, Adams and Dale 1998, and this study). Thus, the value of the index is preserved as caribou nutrition improves. For example, the Denali herd had both the highest parturition rate among 24-month-old (27%) and 36-month-old caribou (88%) in Alaska (Table 6, Fig. 6; Adams and Dale 1998). Nutritional status was not an important factor limiting the Denali herd; rather the herd was maintained at low densities by predation, primarily predation on calves (Adams et al. 1995).

Reduced nutritional status was previously implicated when 36-month-old parturition rates fell below 55%, particularly in the Denali, Delta, and Nelchina herd case histories (Table 6; Adams and Dale 1998, Valkenburg et al. 2003). The lowest parturition rates in Interior Alaska (Table 6) were related to the most extreme snowfalls (winters 1990–1991 and 1992–1993) and corresponding short summers (Boertje et al. 1996). In particular, caribou birth rates were low across the continent in 1993 in response to the short, cold summer of 1992 caused by the eruption of Mount Pinatubo in the Philippines in June 1991 (Table 6; Bergerud et al. 2008:298–299). Boertje et al. (1996) detailed the corresponding weather-induced declines in calf:cow ratios in the Delta, Denali, and Macomb herds from 30–36:100 (1988–1989) to 4–18:100 (1990–1993); these herds reside south and southwest of the current Fortymile herd range and primarily on the north slopes of the Alaska Range. In contrast, Fortymile weather variables and calf weights were not unusual in 1992 (except for the low number of snow-free days, Table 5) and calf:cow ratios and herd numbers did not decline in 1993 (Table 2), presumably due to the relatively hot and dry, continental climate of the Fortymile range. However, Fortymile 36-month-old parturition rates averaged only 44% in 1993 (n = 9, Fig. 7), and herd numbers ceased increasing and stabilized during 1990–1995 (Table 2).

We searched for a specific high caribou density that might cause low parturition rates in Interior Alaska, but no well-documented cases exist where Interior Alaska herds declined largely from density-dependent causes. The highest well-documented peak density among non-insular Alaska herds was reached in the Western Arctic herd in 2003 ($\geq$1.3 caribou/km^2; Valkenburg et al. 1996, Dau 2009). In contrast, the Fortymile herd's recent density (0.88 caribou/km^2, Table 7) is high for Interior Alaska and similar to the Delta herd's peak density in 1989 (0.89/km^2), when adverse weather initiated a strong decline in Delta caribou numbers and density (Boertje et al. 1996, Valkenburg et al. 1996).

Unlike the consistently low 1993 parturition rates among 36-month-old caribou in the Denali, Delta, and Fortymile herds, the low 2009–2010 Fortymile parturition rates were unique among the herds studied (Table 6). Thus we were stimulated to define a cautionary signal to low nutritional status among caribou, particularly among Interior Alaska caribou. Establishing a cautionary signal or threshold appeared timely and proactive. We proposed using a 5-year moving weighted average of 36-month-old parturition rates below 55% to signal low nutritional status, potential overgrazing, and possible justification for more liberal harvests. This biological threshold signaled the initiation of lengthy periods of nutritional stress in 3 of 3 prior cases, and did not trigger a management concern in any other case (except in the case of the Fortymile herd in 2012; Table 6). In 2 of the cases (Delta and Mulchatna herds), the lengthy periods of nutritional stress were temporary and concurrent with rapid declines in herd numbers (Valkenburg et al. 2003, Woolington 2009). In the third case (Nelchina herd), reduced nutritional status was noted but several factors acted to enhance caribou survival (Valkenburg et al. 1994, 2003) and harvest rates were elevated to stabilize herd numbers (Tobey and Schwanke 2009). In the Denali herd, the 5-year moving weighted average has consistently remained well above the threshold of 55% (range = 75–97%, $\bar{x}$ = 88%, 1991–2011), as expected given the herd's relatively high nutritional status (Adams et al. 1995).

We also found several other reasons to support using a 5-year period for averaging parturition rates. First, most stakeholders support continued herd growth and do not want to overreact to short-term declines in nutrition by increasing harvest prematurely. For example, a 3- or 4-year moving average could be unduly influenced by 1 or 2 years of severe weather or local overgrazing. Second, we believe most stakeholders would choose to attempt to manage below peak unsustainable densities. A 5-year moving average could enable managers to increase harvest in response to the initial 3 years of overabundance (Table 6). After periods of overabundance >3 years in duration, herd trend is more likely to be decreasing, even in the absence of harvest. Finally, cost is another factor for recommending a 5-year moving weighted average. We estimated that sample sizes of 14 caribou per year for 5 years (n = 70) provided a relatively cost-effective, yet statistically robust, index to herd nutritional status (Fig. 9). However, sample sizes other than 14 may be justifiable depending on herd-specific circumstances and the manager's tolerance for risk, as evaluated using power analyses.

Without this nutritional threshold, we could inadvertently accumulate too many caribou until the herd rapidly declines again, or we could reach an elevated density where the herd will not sustain the minimum desired harvest. We caution that this low nutritional threshold could also be a result of extended adverse weather, so managers should agree that overgrazing is the most likely cause for low nutrition before advocating for liberalized harvest. Caribou may also move to new areas after overgrazing a particular area, so monitoring of movements can be useful to explain changes in parturition rates.

We caution that simultaneous data on both nutritional status (e.g., Figs. 3 and 10) and herd trajectory (e.g., Fig. 1) are necessary to prudently manage caribou harvest. For example, the

Fortymile herd may eventually decline in numbers nearly simultaneous to a decline in 36-month-old parturition rates, as occurred in the Delta herd during 1989–1993 (Valkenburg et al. 2003). Under those circumstances, increased harvest, ostensibly to improve nutrition, could accelerate a decline to lower numbers.

Studies of other herds show changes in 36-month-old parturition rates also coincided with or followed changes in herd trajectory. For example, 36-month-old parturition rates in the Mulchatna herd increased substantially (Fig. 6) simultaneous to herd recovery (Woolington, unpublished data). Also, low 36-month-old parturition rates existed during rapid declines of the Mulchatna and Northern Alaska Peninsula herds; no data were collected during initial declines in these herds (Fig. 6; Butler 2009, Woolington 2009).

Declining nutritional status in the Fortymile herd was also indicated by the significant decline in October calf weights ($P = 0.02$, $R^2 = 0.24$, 1990–2010). Attempts to explain the variability in calf weights with only weather variables largely failed. The top model had $R^2 = 0.44$ with nearly all of the variability explained by a snow index:July precipitation interaction term. This interaction term was not biologically or mechanistically clear. For example, July precipitation should be equally or more important to calves in years of below-average snowfall compared with years of above-average snowfall. Therefore, we concluded that this relationship was likely spurious, and we found no evidence for a strong weather effect.

Valkenburg et al. (1994) investigated the effects of a multitude of weather variables on Fortymile calf percentages in early winter and identified 3 weather variables as potentially important: average July temperature, total July rainfall, and the snow index from the previous winter. However, we found no corroborating evidence to support a relationship between calf:cow ratios in early winter and weather variables. Even complex models yielded limited explanatory strength and were not mechanistically helpful in explaining the variation in calf:cow ratios. We acknowledge that weather patterns in the vast, remote Fortymile herd range were inadequately measured. Also, the interactions of favorable and unfavorable weather are ill-defined as they relate to caribou calf:cow ratios, particularly in the Fortymile herd where predation has a dominating effect on early calf survival (Boertje and Gardner 2000*a*).

FORTYMILE HERD MOVEMENTS, RANGES, AND DENSITIES

If, as it appears, weather was a minor factor adversely affecting herd nutrition in summers 2008 and 2009, causative factors could have been localized overgrazing, widespread overgrazing, or other unidentified factors. We surmised from herd movements that, in 2008, summer expansion outward from the isolated, core upland tundra (7,000 km^2) into surrounding spruce-moss taiga was at least one of the factors causing low calf weights in October 2008 and reduced 36-month-old parturition rates in 2009. Most migratory caribou herds in Alaska and Canada use mostly tundra in the summer and mostly taiga in the winter (Davis 1980, Bergerud et al. 2008). Taiga provides a relatively poor summer diet (Boertje 1984, 1990). Also, during the 17 years of radiotracking (1992–2008), we observed an unpredicted, marked expansion in range size during summer and autumn (Fig. 12), with accompanying declines in summer density (Fig. 27). This may have been an indicator of localized overgrazing of the core upland tundra. In contrast, we observed an expected, slow expansion of the early winter, winter, and precalving ranges (Fig. 12).

We found supporting documentation that summer range can be an important factor limiting caribou at peak numbers. Bergerud et al. (2008) concluded that 1) depleted summer range was a major factor in causing density-dependent declines in several large migratory caribou herds, and 2) summer range affected herd trajectory by affecting fecundity. Mahoney and Schaefer (2002) surmised that 8-week earlier caribou movements off a summer range in Newfoundland reflected heightened competition for summer forage, because these movements occurred simultaneous to declines in parturition and survival when caribou numbers were high and increasing. Also, Manseau et al. (1996) documented degradation of the George River herd's calving and summer habitat concurrent with increasing herd size and diminished body size, birth rates, and survival (Crete et al. 1996). Later, after herd size declined, caribou remained on the summer range 3 weeks longer (Mahoney and Schaefer 2002, Bergerud et al. 2008).

Fortymile calving and postcalving densities on the core uplands reached and exceeded the high thresholds (5–10 caribou/km^2) described by Bergerud et al. (2008), where density-dependent nutrition limitation might be expected and cause for concern. For example, calving densities were 25 caribou/km^2 in 2001, 23 in 2007, and 42 in 2008 (Fig. 15). These high densities largely resulted from increased herd size (Fig. 1) simultaneous to decreased size of the calving area (Fig. 12). For example, after 2000, the herd largely abandoned the upper Salcha River during calving (Figs. 13 and 14). We surmised that these high densities, and continued almost year-round use of the uplands (Fig. 11), ultimately triggered early summer departure from the Fortymile herd's core uplands and potentially adversely affected nutrition in 2008 and 2009 (Table 6).

The Fortymile herd's high tolerance for elevated density during calving (relative to other seasons) may have been a trade-off between lessened predation and localized overgrazing. For example, elevated calving density has previously been described as a common strategy among large caribou herds to reduce predation risk on highly vulnerable young calves, particularly if calving can occur in areas with less predation (Bergerud et al. 2008). The general strategy is to greatly outnumber the local predators and to avoid a more expansive and consequently larger predator base.

Given the almost 9-fold increase in herd size (Fig. 1), we expected the slow increase in winter density (Fig. 27). However, we did not expect a slow decline in summer density (Fig. 27), which we hypothesized to be an indicator of stress. Likewise, we did not expect to find an extrapolation of the data that indicated the size of the summer range may eventually exceed the size of the winter range (Fig. 26). Elsewhere, summer ranges of large migratory herds are consistently smaller than winter ranges. We inferred that the relatively rapid expansion in summer range may simply be temporary and possibly a result of discontinuous upland tundra in the current Fortymile range and overgrazing on the core uplands. More specifically, we expect the summer range expansion rate may slow considerably after the herd regains use of the historic and expansive summer range in the White Mountains just west of the Steese Highway.

CARIBOU RESPONSE TO RECENT BURNS

An alternative explanation for the relatively rapid expansion of the summer range (Fig. 12) is that caribou were simply expanding summer movements into the large 2004 and 2005 burns (Figs. 19 and 28). These burns would have provided an improved summer diet compared to unburned spruce forests dominated by a moss ground cover (Boertje 1984, 1990). However, summer range expansion began prior to the large 2004 and 2005 burns (Fig. 12). Thus, caribou did not appear to be responding concurrent to the large burns in summer. Nevertheless, some of these burns were utilized by Fortymile caribou in summer 2008.

No clear test exists for evaluating whether burns affected Fortymile winter movements at the scale we measured. For example, caribou avoid burns in winter (Joly et al. 2003), so herd movements might be expanded or contracted in response to burns. However, the slow increase in winter range throughout this study (1992–2008; Fig. 12) indicated little or no expansion or contraction in response to the large burns on the winter ranges during 2004 and 2005 (Fig. 28). Factors contributing to high adaptability of Fortymile caribou to the burns in winter include the low proportion of total range burned in the last 50 years; relatively high winter mobility (Fig. 12); relatively low winter density (Fig. 27); probable high lichen quantity and quality on current winter range (Boertje and Gardner 2000*a*, Collins 2006); and the ability of wintering caribou to avoid burns <50 years old (Thomas et al. 1996) and choose unburned inclusions and perimeters of burns (Joly et al. 2003). Dunford (2003) reported caribou avoidance of burns decreased with increased wildfires. Fortymile caribou annual range is fairly unique in Interior Alaska in having a preponderance of mature spruce stands dominated by a moss-lichen ground cover, suitable primarily for winter habitat (Boertje 1984, 1990).

High winter use in and around the large burns immediately north of Tok (Fig. 28) by the Nelchina herd added a competing factor for winter forage in this area, as well as a better test for the effect of the 2004 and 2005 burns on caribou nutrition. This burned area and adjacent areas included the primary wintering range of the Nelchina herd since winter 1994–1995 and contained a large area burned in the mid-1960s (Joly et al. 2003). Nelchina caribou were known to feed largely on the perimeter of the 1960s burns and in unburned inclusions prior to the 2004 and 2005 burns, so Nelchina caribou were already restricted to relatively small areas for feeding while traveling through the burns (Joly et al. 2003). Given that a major portion of the Nelchina's primary wintering area north of Tok burned twice in 40 years, we would have expected Nelchina parturition rates to decline if the 2004 and 2005 burns were major factors controlling caribou parturition rates. However, the Nelchina herd's parturition rates were mostly low during 1997–2005 and increased during 2006–2010 (Fig. 7, Table 6). Thus we concluded that the 2004 and 2005 burns did not reduce the Nelchina herd's nutrition. Apparently Nelchina caribou found adequate winter forage in adjacent areas, suggesting the Fortymile winter range was not overgrazed.

Long-term studies have consistently indicated little or no impact of fire on population dynamics of caribou (Scotter 1967, Skoog 1968, Bergerud 1974, Johnson and Rowe 1975, Miller 2000, Dunford 2003, Payette et al. 2004, this paper). The earliest studies suggested that large burns had negative effects on caribou (Leopold and Darling 1953, Scotter 1965). This theory was largely based on the propensity of fire to destroy slow-growing lichens, which provide a unique source of highly digestible energy and are the preferred winter forage of caribou (Boertje 1984, 1990). However, Alaska caribou numbers have recently increased at high rates on the North Slope with very low lichen consumption (Boertje et al. 1985, Alaska Department of Fish and Game 2009). Bergerud (1996) reported that caribou do not require lichens.

CURRENT ESTIMATES OF HISTORIC FORTYMILE HERD NUMBERS

Herd management is somewhat based on past peak numbers, so stakeholders desired a critical review of reported peak numbers. Murie (1935:6) reported that caribou crossed 100 km of gravel road (the original Steese Highway) traveling only one direction for 20 consecutive days, day and night, in autumn. Based on some daily crude counts, Murie extrapolated to an estimate of 568,000 roadside caribou. An accurate estimate would have required multiple vehicles and continuous travel, because most of the road was surrounded by forest, and only a few kilometers of the road were visible from any single vantage point. Yet Murie (1935) did not mention the number of observers, transportation mode used, or number of daylight and nighttime hours spent traveling. Thus, there are many reasons to question the accuracy of Murie’s estimate. In contrast, we trust that Murie’s (1935:51) mapping and descriptions of herd movements were relatively reliable (Fig. 29), because movement data were based on conversations with people who relied on the herd and who were distributed throughout the herd’s range. Also, McDonald and Cooley (2004) corroborated Murie’s reports of Fortymile herd movements in the Yukon.

To hypothetically fill this historic range with caribou, we regressed herd size over range size (Fig. 30) during 5 periods when average Fortymile herd size increased from 11,796 to 43,481 (Table 7). Bergerud et al. (2008:327) provided a comparative fill rate for the George River herd, where an additional 740 km^2 was required for each 1,000 caribou, as herd size increased from 180,000 to 600,000 caribou. To compare our results, we reversed the dependent and independent variables of our regression. The slope of this reversed relationship indicated the Fortymile herd used an additional 548 km^2 for each 1,000 caribou. Differences in fill rates could result from differences in habitat quality, for example more area would be required for each 1,000 caribou when habitat quality is relatively low. We expect future studies will improve estimates of fill rates. We currently had only 5 points to derive our regression, and we extrapolated to 261,202 caribou with a range size 5-fold greater than the current range size. Also, we assumed the relationship remained linear (Fig. 30).

Management Implications and Recommendations

USER OPPORTUNITY AND INTEREST

As a minimum, most users want the opportunity to view or harvest Fortymile caribou, in most autumns or winters, along the Steese and Taylor highways and near the Yukon border. Given recent history, this opportunity is most likely to be satisfied when herd numbers exceed 35,000, and particularly when herd numbers exceed 45,000.

Proponents for a larger Fortymile herd argue that broad interest in the herd will approach historic levels when the herd once again frequents the Steese Highway during calving and summer. At approximately the same time, expansive eastward winter migrations should largely return to Dawson, Yukon Territory and beyond (McDonald and Cooley 2004). During 1900–1963, the herd regularly calved west of the Steese Highway (Valkenburg and Davis 1986). Also, the herd regularly crossed to upland areas northwest of the Steese Highway and southeast of the Taylor Highway in spring, summer, and autumn. Given past history, resumption of these movements will likely occur regularly after herd numbers exceed 60,000 (Table 7, Fig. 29).

MANAGING WITH REGARD TO WOLVES

Desires for elevated Fortymile caribou numbers should be tempered with the realization that previous rapid increases in herd size occurred during 2 periods of greatly reduced wolf numbers, unlike any recent periods. The first period was during and shortly after epidemics of diseases that killed sled dogs and probably wolves (1916–1925; Murie 1944:14–16). Murie (1944) found no wolf tracks during winter 1922–1923, despite extensive travels by dog sled across Interior Alaska, including a trip through the main Fortymile winter range. The second period was during federal aerial wolf control that included air-dropping poison baits and deploying cyanide guns, especially along the Steese and Taylor highways (1950s, Valkenburg et al. 1994). In contrast, Fortymile caribou regularly live with average wolf densities of 7 wolves/1,000 km^2, except during localized wolf control (Boertje and Gardner 2000*a*). Predation by wolves has been the dominant factor limiting Fortymile herd size in recent decades (Boertje and Gardner 2000*a*, Boertje et al. 2008). Most other large North American herds (>50,000 caribou) have a long history of spring migrations north of the arctic treeline to space newborn calves away from moderate wolf densities. Also, rabies epizootics have been known to reduce wolf numbers in coastal areas of northern and western Alaska and northern Canada, where the largest caribou herds reside (Ballard et al. 1997). To our knowledge, Fortymile wolves have not contracted rabies.

The highly accessible Nelchina herd is the only Alaska herd actively and successfully managed to keep herd size stable, and intensive management of predators plays a key role. Predator harvest and particularly wolf control have proved more challenging and less successful on the more remote, more forested, and more federally-protected Fortymile range (particularly the calving range) than on the Nelchina calving and summer ranges. Therefore, we do not know whether we can successfully reallocate caribou from predators to people in the Fortymile herd, particularly when Fortymile herd parturition rates regularly decline below 55%. For example, calf:cow ratios could decline with lower parturition rates, which would likely result in lower sustainable harvest rates.

MANAGING WITH REGARD TO RANGE/NUTRITIONAL STATUS

Desires for elevated Fortymile caribou numbers should be tempered with the realization that additional spring and summer upland tundra may be of key importance to realizing continued herd growth. Compared with other large migratory caribou herds (Bergerud et al. 2008:179–181), the Fortymile herd's current annual range (Fig. 11) has a low proportion of range above treeline (17%), so taiga predominates over upland tundra. Based on historical movements, the most likely path to greatly increased upland spring and summer range will include crossing the Steese Highway and returning to the White Mountains and adjacent uplands.

From studies elsewhere, we know that peak caribou numbers are temporary, lowered birth rates will occur before peak numbers are attained, and widespread overgrazing of the summer range is likely to be the single factor most likely to ultimately cause a pronounced and often prolonged decline in caribou herd nutrition and numbers (Bergerud et al. 2008). Thus, in the future, Fortymile managers must compromise between 1) growing the herd large enough to expand into key portions of the former range, and 2) growing the herd too large for its nutritional well being. However, winter icing events, deep snow, short summers, and concurrent increased predation can strongly elevate mortality temporarily, and cause reductions in herd size independent of summer range conditions and density (Boertje et al. 1996). Also, predation, particularly predation on calves, is the chief factor maintaining caribou at low densities in Interior Alaska (Adams et al. 1995, Boertje et al. 1996, Boertje and Gardner 2000*a*, Valkenburg et al. 2004). Thus, caribou in Interior Alaska are well nourished during most years (Table 6, Fig. 6). A notable exception was the Nelchina herd during 1997–2005. One explanatory hypothesis is that the Nelchina calving and summer ranges may have been compromised by caribou overabundance in the mid-1960s and mid-1990s, and may only recently be recovering (Tobey and Schwanke 2009; R. Schwanke, Wildlife Biologist, ADF&G, Glennallen, personal communication).

If nutritional status appears compromised by widespread overgrazing, we recommend conforming to a management scenario proven successful for the adjacent Nelchina caribou herd (Tobey and Schwanke 2009) and Tanana Flats moose (*Alces alces*) population (Boertje et al. 2007, 2009). In the Nelchina herd case history, a decision was made in 1995 to substantially increase harvest and stabilize the herd at 35,000–40,000 caribou from a herd size near 50,000. Alternatively, the Nelchina herd could have been allowed to regain the mid-1960s level of 70,000 caribou and probably experience another rapid decline. At 35,000–40,000 caribou, the Nelchina herd sustained the highest reported harvest rate for caribou herds in Interior Alaska ($\bar{x}$ = 5.8% of herd size annually, 1997–2009) with herd size stable ($\lambda = 1.002$; Tobey 2003, Alaska Department of Fish and Game 2009, Tobey and Schwanke 2009). This contrasted with a total estimated average annual harvest rate of 1.6% of herd size in the Fortymile herd (1997–2010) while allowing herd size to grow 4.5% each year. Thus, the potential sustainable harvest rate was 6.1% for the Fortymile herd with moderate and declining nutrition (Table 6), which was similar to the 6.0% potential sustainable harvest rate for the Nelchina herd with mostly lower and increasing nutrition (Table 6) yet uncompromised calf survival. Calf:cow ratios averaged 35:100 in the Nelchina herd versus 32:100 in the Fortymile herd during 1997–2009. The highest sustained harvest rates for moose in Interior Alaska also occurred where moose had the lowest nutritional status (Boertje et al. 2007) yet uncompromised calf survival (Boertje et al. 2009). Low nutritional status has been instrumental in justifying harvests aimed at stabilizing ungulate numbers (Boertje et al. 2010).

Longer term data are needed to test the utility of the 55% threshold to warn managers of impending declines in herd numbers. Until then, we are recommending the threshold be used as a cautionary signal to notably reduced nutritional status that has been linked to immediate or imminent herd decline. Each management scenario will likely have a unique set of circumstances.

In the case of the Fortymile herd, the 5-year moving weighted average parturition rate in 2012 was 54%, similar to the cautionary threshold of 55% (Table 6). We recommend managers use this triggering to warn stakeholders of a potentially significant decline in herd nutritional status. If the 5-year rate remains <55% through May 2014, the Board of Game should be prepared to support stabilizing herd numbers in autumn 2014, particularly given that larger sample sizes (*n* = >15 collared 36-month-olds) are expected beginning in 2013. Stabilizing herd numbers may require a more liberal harvest of up to 3,000 caribou (up from 1,000). Forewarning stakeholders of such a change is essential to maintaining public support. If Fortymile caribou begin calving or summering in new upland areas simultaneous to triggering the threshold, managers may consider waiting a year or 2 to see if the herd benefits from the new calving and summer range. However, in general, when the threshold is triggered, we would recommend against waiting for a herd to change movements.

To prudently manage the Fortymile herd, we recommend continued annual monitoring of trends in herd numbers and nutritional status. To monitor trend in herd numbers, we recommend continued annual June photocensuses and October surveys to estimate calf:cow ratios. To monitor nutritional status, we recommend annual: 1) weighing of 15–20 4-month-old females; 2) estimating parturition rates of ≥14 36-month-old females (Fig. 9); 3) estimating parturition rates of all known-age females ≥48 months of age; and 4) mapping of seasonal range use to assist with explaining how, when, and where overgrazing may adversely affect nutrition. Calf weights provide a within-herd index to nutritional status, and long-term data are needed to further test the predictive relationship between weights and 36-month-old parturition rates. To achieve a known-age, radiocollared sample of 14 36-month-old females, we recommend radiocollaring 10–15 females as short yearlings in late April or early May to supplement the sample of calves remaining post-winter and to allow for mortality between 12 and 36 months of age. We have no recommendations for monitoring range use using vegetative sampling.

We recommend costs be considered when deciding how to monitor year-round range use because costs may outweigh benefits, and the priority is to adequately estimate parturition rates of 36-month-old females. One exception is that monitoring expansion of the calving, postcalving, and summer ranges by the Fortymile herd may be extremely relevant; for example, if the herd begins reestablishing use of the White Mountains or other upland areas.

MANAGEMENT OBJECTIVES

We propose that a biologically-sound objective for the Fortymile herd is to eventually stabilize herd size. Specifically, we propose intentionally stabilizing herd size when the 5-year moving weighted average of 36-month-old parturition rates declines below 55% and overgrazing, not adverse weather, is the most likely cause for the low nutrition. This management scenario would fulfill current mandates for the Fortymile herd to be managed for “near maximum sustained yield” (Alaska Fish and Game Laws and Regulations:949). For example, given recent studies, maximum sustained yield (in absolute numbers of caribou harvested) may well be attained near some elevated herd size when we first observe a sustained period of nutrition limitation. In contrast, current intensive management objectives simply specify the Fortymile herd be managed for a population of 50,000–100,000 caribou with an annual harvest of 1,000–15,000.

Acknowledgments

Most of our understanding of the Fortymile caribou herd has been made possible due to research and survey and inventory projects that began in 1992 and have continued to the present which have been funded with money made available to the State of Alaska through the Federal Aid in Wildlife Restoration program. Major federal aid-funded research projects on the Fortymile caribou herd have included 1) grants W-24-1 through W-24-5, project 3.38, “Factors limiting the Fortymile caribou herd;” 2) grants W-27-2 through W-27-5 and W-33-1, project 3.43, “Reducing mortality on the Fortymile caribou herd;” 3) grants W-33-2 through W-33-6, project 3.48, “Monitoring of Fortymile ungulates and wolves following wolf sterilization and translocation;”

and 4) grants W-33-7 through W-33-11, project 3.50, "Analysis and summary of data from the Fortymile caribou range."

Skilled piloting and note taking by Paul Zaczkowski were essential to this work. In recent years, Jeff Gross, Torsten Bentzen, Al Keech, and Bob Gingue collared and weighed calves, monitored harvest, and assisted with photocensuses. We also thank Cortney Pylant and Cameron Carroll for their assistance with GIS data entry and cartography, and Tom Paragi for assisting with mapping of burns. Lincoln Parrett ably assisted with the analysis of calving areas. We also acknowledge Jim Herriges and Ruth Gronquist, both of the Bureau of Land Management, for partially funding fieldwork and map preparation. We thank Layne Adams, Scott Brainerd, Bruce Dale, Jim Herriges, David James, Doreen Parker McNeill, Lincoln Parrett, Becky Schwanke, and Rita St Louis for editing earlier drafts of this manuscript. We are particularly indebted to Laura McCarthy for her skills and graciousness in formatting, editing, and ultimately preparing this bulletin in all regards for publication.

References

ADAMS, L. G., AND B. W. DALE. 1998. Reproductive performance of female Alaska caribou. Journal of Wildlife Management 62:1184–1195.

ADAMS, L. G., F. J. SINGER, AND B. W. DALE. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59:584–594.

ADAMS, L. G., R. O. STEPHENSON, B. W. DALE, R. T. AHGOOK, AND D. J. DEMMA. 2008. Population dynamics and harvest characteristics of wolves in the central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

AGRESTI, A. 2007. An introduction to categorical data analysis, 2nd edition. Wiley series in probability and statistics. John Wiley and Sons, Inc., New York.

ALASKA DEPARTMENT OF FISH AND GAME. 2009. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. P. Harper, editor. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

ALASKA FISH AND GAME LAWS AND REGULATIONS ANNOTATED, 2010–2011 EDITION. 2010. LexisNexis Matthew Bender, Charlottesville, Virginia.

ALASKA INTERAGENCY COORDINATION CENTER. 2011. Alaska Fire Service. Fire Perimeter Shape Files for 2004 and 2005. Fort Wainwright, Alaska. http://fire.ak.blm.gov/predsvcs/maps.php (Accessed 10 May 2012).

BALLARD, W. B., L. A. AYERS, P. A. KRAUSMAN, D. J. REED, AND S. G. FANCY. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. Wildlife Monographs 135.

BERGERUD, A. T. 1974. Decline of caribou in North America following settlement. Journal of Wildlife Management 38:757–770.

BERGERUD, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Rangifer, Special Issue 9:95–115.

BERGERUD, A. T., S. N. LUTTICH, AND L. CAMPS. 2008. The return of caribou to Ungava. McGill-Queen's University Press, Montreal, Canada.

BOERTJE, R. D. 1984. Seasonal diets of the Denali caribou herd, Alaska. Arctic 37:161–165.

BOERTJE, R. D. 1990. Diet quality and intake requirements of adult female caribou of the Denali Herd, Alaska. Journal of Applied Ecology 27:420–434.

BOERTJE, R. D., J. L. DAVIS, AND P. VALKENBURG. 1985. Uses and limitations of fecal analyses in *Rangifer* studies. Pages 307–316 *in* T. C. Meredith and A. M. Martell, editors. Proceedings second North American caribou workshop. Val Morin, Canada. McGill Subarctic Research Station. Paper No. 40. Schefferville, Quebec, Canada.

BOERTJE, R. D., AND C. L. GARDNER. 2000*a*. The Fortymile caribou herd: Novel proposed management and relevant biology, 1992–1997. Rangifer, Special Issue 12:17–37.

BOERTJE, R. D., AND C. L. GARDNER. 2000*b*. Reducing mortality on the Fortymile caribou herd. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Research Performance Report 1 July 1999–30 June 2000, Study 3.43, Juneau, Alaska. http://www.adfg.alaska.gov/static/home/about/management/wildlifemanagement/intensivemanagement/pdfs/refs/3.43_00.pdf (Accessed 29 May 2012).

BOERTJE, R. D., C. L. GARDNER, AND J. A. GROSS. 2008. Monitoring of Fortymile ungulates and wolves following wolf sterilization and translocation. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Research Final Performance Report 1 July 2007–30 June 2008, Study 3.48, Juneau, Alaska. http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/research_pdfs/ca-40mi08final.pdf (Accessed 29 May 2012).

BOERTJE, R. D., M. A. KEECH, AND T. F. PARAGI. 2010. Science and values influencing predator control for Alaska moose management. Journal of Wildlife Management 74:917–928.

BOERTJE, R. D., M. A. KEECH, D. D. YOUNG, K. A. KELLIE, AND C. T. SEATON. 2009. Managing for elevated yield of moose in Interior Alaska. Journal of Wildlife Management 73:314–327.

BOERTJE, R. D., K. A. KELLIE, C. T. SEATON, M. A. KEECH, D. D. YOUNG, B. W. DALE, L. A. ADAMS, AND A. W. ADERMAN. 2007. Ranking Alaska moose nutrition: Signals to begin liberal antlerless harvests. Journal of Wildlife Management 71:1494–1506.

BOERTJE, R. D., P. VALKENBURG, AND M. E. MCNAY. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management 60:474–489.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag, New York, New York.

BUTLER, L. 2009. Units 9C and 9E caribou. Pages 32–42 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

CAIKOSKI, J. R. 2009. Units 25A, 25B, 25D, and 26C caribou. Pages 240–258 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

COLLINS, W. B. 2006. Habitat use, foraging behavior, and nutritional ecology of Nelchina caribou. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Research Final Performance Report 1 July 2001–30 June 2006, Project 3.47, Juneau, Alaska. http://www.adfg.alaska.gov/static/home/library/pdfs/wildlife/research_pdfs/ca-habnelchina06.pdf (Accessed 29 May 2012).

CRETE, M., S. COUTURIER, B. J. HEARN, AND T. E. CHUBBS. 1996. Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George caribou herd. Rangifer Special Issue 9:27–36.

DAU, J. 2009. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24, and 26A caribou. Pages 176–239 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

DAVIS, J. L. 1980. Status of *Rangifer* in the USA. Pages 793–797 *in* E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings Second International Reindeer/Caribou Symposium, Røros, Norway, Direktoratet for vilt og ferskvannsfisk, Trondheim.

DAVIS, J. L., L. G. ADAMS, P. VALKENBURG, AND D. J. REED. 1991. Relationships between body weight, early puberty, and reproductive histories in central Alaskan caribou. Pages 115–142 *in* C. E. Butler and S. P. Mahoney, editors. Proceedings Fourth North American Caribou Workshop. St. John's, Newfoundland.

DELONG, R. A., AND B. D TARAS. 2009. Moose trend analysis user's guide. Alaska Department of Fish and Game, Fairbanks, Alaska.

DUNFORD, J. S. 2003. Woodland caribou–fire relationships in northern Alberta. Master's Thesis, University of Alberta, Edmonton, Canada.

FLEISS, J. L, B. LEVIN, AND M. C. PAIK. 2003. Statistical methods for rates and proportions, Third Edition. John Wiley and Sons, Inc., Hoboken, New Jersey.

GARDNER, C. L. 2003. Units 20 and 25 caribou. Pages 160–189 *in* C. Healy, editor. Caribou management report of survey and inventory activities 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

GOVERNMENT OF YUKON. 2011. Department of Community Services, Wildland Fire Management Data, Maps and Bulletins Archive. 2004 and 2005 Yukon Wildland Fire Maps. Whitehorse, Yukon, Canada. http://www.community.gov.yk.ca/firemanagement/wfarchives.html (Accessed 10 May 2012).

GRONQUIST, R. M., T. L. HAYNES, AND C. L. GARDNER. 2005. Rebuilding the Fortymile caribou herd: A model of cooperative management planning. Rangifer, Special Issue 16:163–175.

GROSS, J. A. 2009*a*. Units 20E wolf. Pages 185–196 *in* P. Harper, editor. Wolf management report of survey and inventory activities 1 July 2005–30 June 2008. Alaska Department of Fish and Game, Project 14.0, Juneau, Alaska.

GROSS, J. A. 2009*b*. Units 20B, 20C, 20D, 20E, and 25C caribou. Pages 136–158 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

HURVICH, C. M., AND C. L. TSAI. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

JOHNSON, E. A., AND J. S. ROWE. 1975. Fire in the subarctic wintering ground of the Beverley caribou herd. American Midland Naturalist 94(1):1–14.

JOLY, K., B. W. DALE, W. B. COLLINS, AND L. G. ADAMS. 2003. Winter habitat use by female caribou in relation to wildland fires in Interior Alaska. Canadian Journal of Zoology 81:1192–1201.

LENART, E. A. 2009. Units 26B and 26C caribou. Pages 299–235 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

LEOPOLD, A. S., AND F. F. DARLING. 1953. Wildlife in Alaska: An Ecological Reconnaissance. Ronald Press, New York.

MAHONEY, S. P., AND J. A. SCHAEFER. 2002. Long-term changes in demography and migration of Newfoundland caribou. Journal of Mammalogy 83:957–963.

MANSEAU, M., J. HUOT, AND M. CRETE. 1996. Effects of summer grazing by caribou on consumption and productivity of vegetation: community and landscape level. Journal of Ecology 84:503–513.

MCCULLOCH, C. E., AND S. R. SEARLE. 2001. Generalized, linear, and mixed models. Wiley series in probability and statistics. John Wiley and Sons, Inc. New York.

MCDONALD, J., AND D. COOLEY. 2004. The historical annual range use patterns of the Fortymile caribou herd in Yukon. Yukon Fish and Wildlife Branch Report MRC-10-01. Whitehorse, Yukon.

MECH, L. D., L. G. ADAMS, T. J. MEIER, J. W. BURCH, AND B. W. DALE. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis.

MILLER, D. R. 2000. Lichens, wildfire, and caribou on the taiga ecosystem of northcentral Canada. Rangifer, Special Issue 12:197–207.

MURIE, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States, Fauna Series No. 5. U.S. Government Printing Office, Washington, D.C.

MURIE, O. J. 1935. Alaska-Yukon caribou. U.S. Department of Agriculture, Bureau of Biological Survey, North American Fauna Series 54.

NATIONAL WEATHER SERVICE. 2011. Climatological data, Alaska. National Climatic Data Center, Asheville, North Carolina, USA. http://cdo.ncdc.noaa.gov/pls/plclimprod/poemain.cdobystn?dataset=DS3220&StnList=NNNNNN26422,502607NNNNN,50260726422 (Accessed 29 May 2012).

PAYETTE, S., S. BOUDREAU, C. MORNEAU, AND N. PITRE. 2004. Long–term interactions between migratory caribou, wildfires and Nunavik hunters inferred from tree rings. Ambio 33:482–486.

R CORE DEVELOPMENT TEAM. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.r-project.org (Accessed 29 May 2012).

SCOTTER, G. W. 1965. Studies of the winter range of barren-ground caribou with special reference to the effects of forest fires. Canadian Wildlife Service Progress Report 3. Ottawa: Canadian Wildlife Service.

SCOTTER, G. W. 1967. Effects of fire on barren-ground caribou and their forest habitat in northern Canada. Transactions of the North American Wildlife Conference 32:243–254.

SEAMAN, D. E., B. GRIFFITH, AND R. A. POWELL. 1998. KERNELHR: A program for estimating animal home ranges. Wildlife Society Bulletin 26:95–100.

SEAMAN, D. E., AND R. A. POWELL. 1996. An evaluation of the accuracy of kernel density estimators for home range. Ecology 77:2075–2085.

SEATON, C. T. 2009. Unit 20A caribou. Pages 122–135 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska, USA.

SILVERMAN, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, United Kingdom.

SKOOG, R. O. 1956. Range, movements, population, and food habits of the Steese-Fortymile caribou herd. Master's Thesis, University of Alaska Fairbanks.

SKOOG, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Dissertation, University of California, Berkeley.

SUGIURA, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Communications in Statistics, Theory, and Methods 7:13–26.

THOMAS, D. C., S. J. BARRY, AND G. ALAIE. 1996. Fire-caribou-winter rang relationships in northern Canada. Rangifer 16:57–67.

TOBEY, B. 2001. Units 13 and 14B caribou. Pages 90–105 *in* C. Healy, editor. Caribou management report of survey and inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

TOBEY, B. 2003. Units 13 and 14B caribou. Pages 108–124 *in* C. Healy, editor. Caribou management report of survey and inventory activities 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

TOBEY, B. 2005. Units 13 and 14B caribou. Pages 89–104 *in* C. Brown, editor. Caribou management report of survey and inventory activities 1 July 2002–30 June 2004. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

TOBEY, B., AND R. SCHWANKE. 2009. Units 13 and 14B caribou. Pages 83–98 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

URQUHART, D., AND R. FARNELL. 1986. The Fortymile caribou herd on the comeback trail to the Yukon. Yukon Renewable Resources, Whitehorse, Canada.

VALKENBURG, P., AND J. L. DAVIS. 1986. Calving distribution of Alaska's Steese–Fortymile caribou herd: A case of infidelity? Rangifer, Special Issue 1:315–324.

VALKENBURG, P., AND J. L. DAVIS. 1989. Status, movements, range use patterns, and limiting factors of the Fortymile caribou herd. Alaska Department of Fish and Game, Federal Aid in Wildlife Restoration, Research Final Report 1 July 1984–30 June 1988, Study 3.32, Juneau, Alaska.

VALKENBURG, P., J. L. DAVIS, J. M. VER HOEF, R. D. BOERTJE, M. E. MCNAY, R. M. EAGAN, D. J. REED, C. L. GARDNER, AND R. W. TOBEY. 1996. Population decline in the Delta caribou herd with reference to other Alaskan herds. Rangifer, Special Issue 9:53–62.

VALKENBURG, P., D. G. KELLEYHOUSE, J. L. DAVIS, AND J. M. VER HOEF. 1994. Case history of the Fortymile caribou herd, 1920–90. Rangifer 14:11–22.

VALKENBURG, P., M. E. MCNAY, AND B. W. DALE. 2004. Calf mortality and population growth in the Delta caribou herd after wolf control. Wildlife Society Bulletin 32:746–756.

VALKENBURG, P., R. W. TOBEY, B.W. DALE, B. D. SCOTTON, AND J. M. VER HOEF. 2003. Body size of female calves and natality rates of known-age females in two adjacent Alaskan caribou herds, and implications for management. Rangifer, Special Issue 14:203–209.

WHITTEN, K. R. 1995. Antler loss and udder distention in relation to parturition in caribou. Journal of Wildlife Management 59:273–277.

WOOLINGTON, J. D. 2009. Mulchatna caribou, Units 9B, 17, 18 south, 19A, and 19B. Pages 11–31 *in* P. Harper, editor. Caribou management report of survey and inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Project 3.0, Juneau, Alaska.

WORTON, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168.

ZHANG, D., X. LIN, J. RAZ, AND M. SOWERS. 1998. Semiparametric stochastic mixed models for longitudinal data. Journal of the American Statistical Association 93:710–719.

◆ ◆ ◆

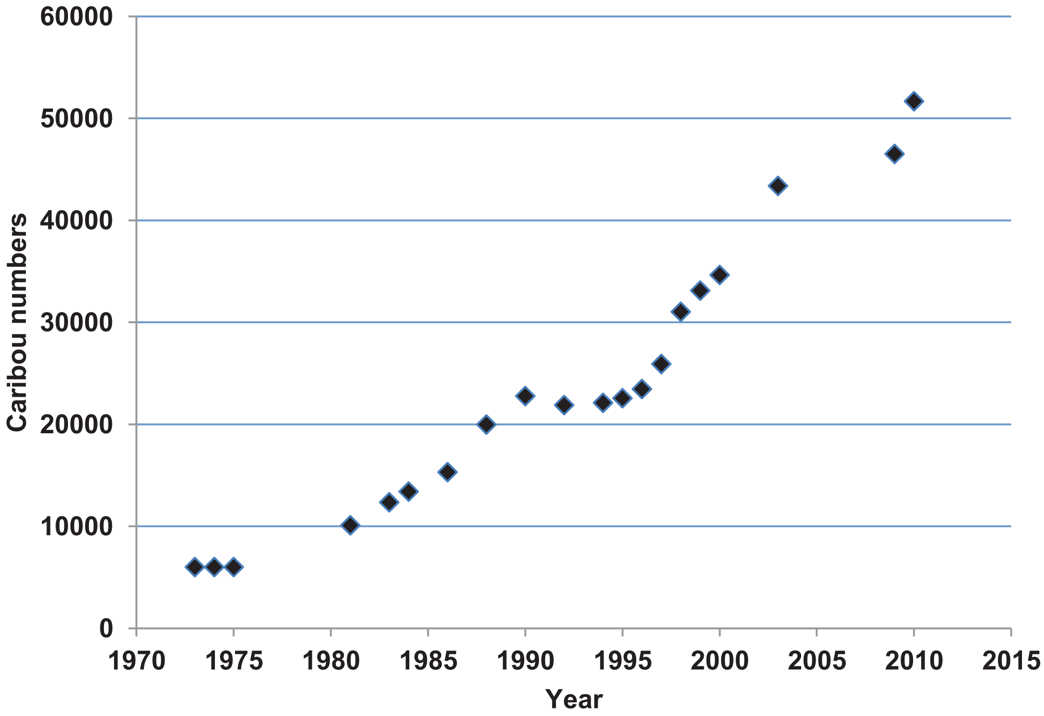


FIGURE 1. Fortymile caribou numbers from photocensuses, 1973–2010, Interior Alaska. Valkenburg and Davis (1989) analyzed somewhat incomplete data from the 1973–1975 photocensuses to derive a constant minimum value of about 6,000 caribou.

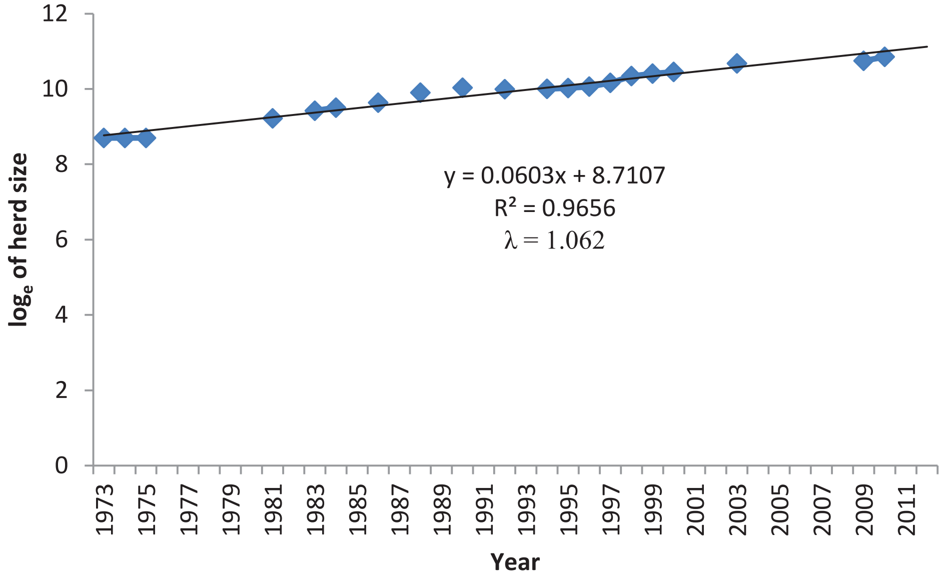


FIGURE 2. Growth of the Fortymile caribou herd based on photocensuses,1973–2010, Interior Alaska.

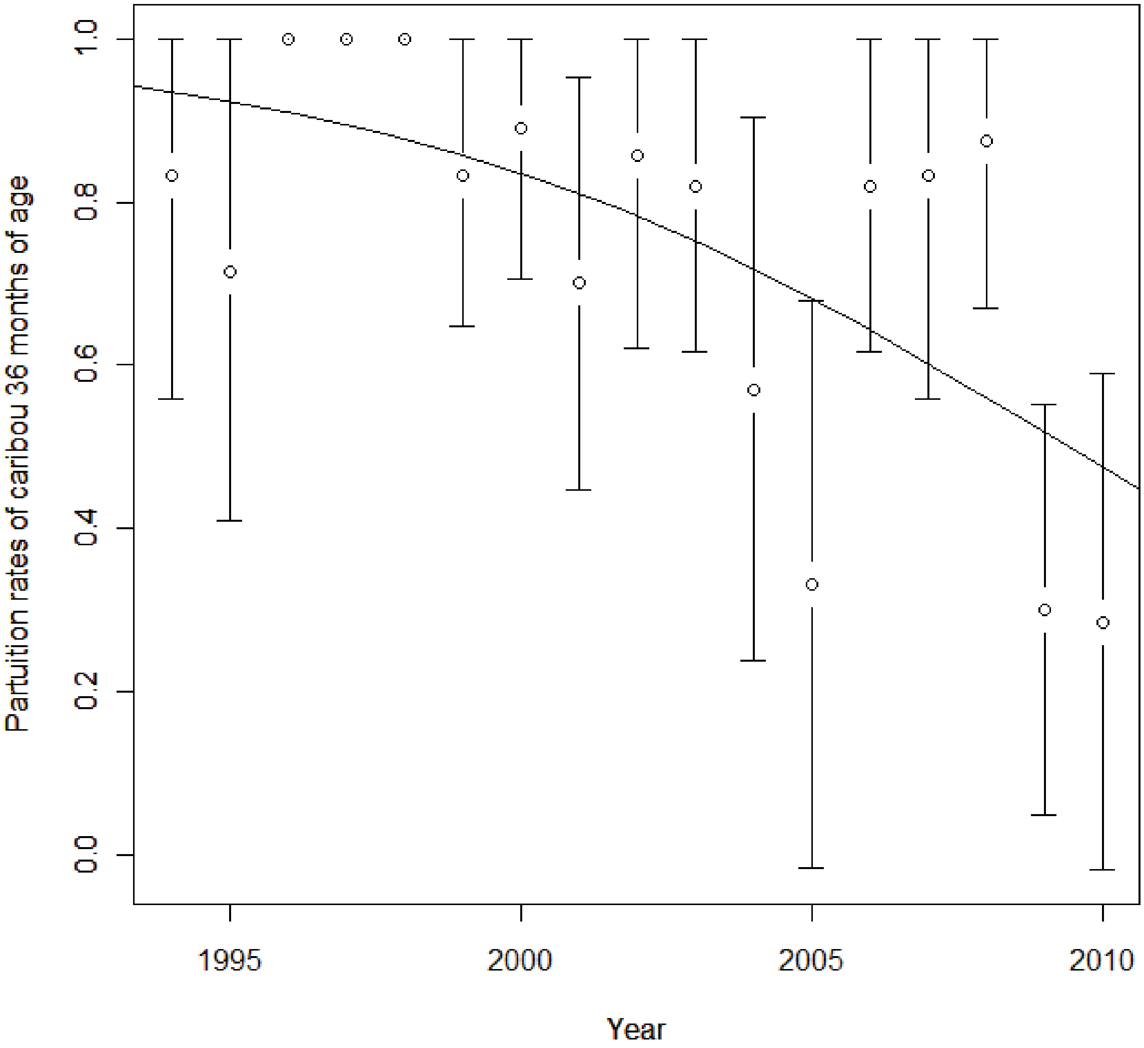


FIGURE 3. Parturition rates and 90% binomial CIs (truncated at 1.0 in 9 cases) among radiocollared 36-month-old caribou in the Fortymile herd, 1994–2010. The low parturition rates in 2004, 2005, 2009, and 2010 caused a significant decline in trend based on using annual data and logistic regression (generalized linear model) in Program R (slope on the logit scale = −0.17 [SE = 0.048], $P = 0.0003$, $R^2 = 0.390$). Annual sample sizes ranged from 6 to 12 ($\bar{x} = 8$).

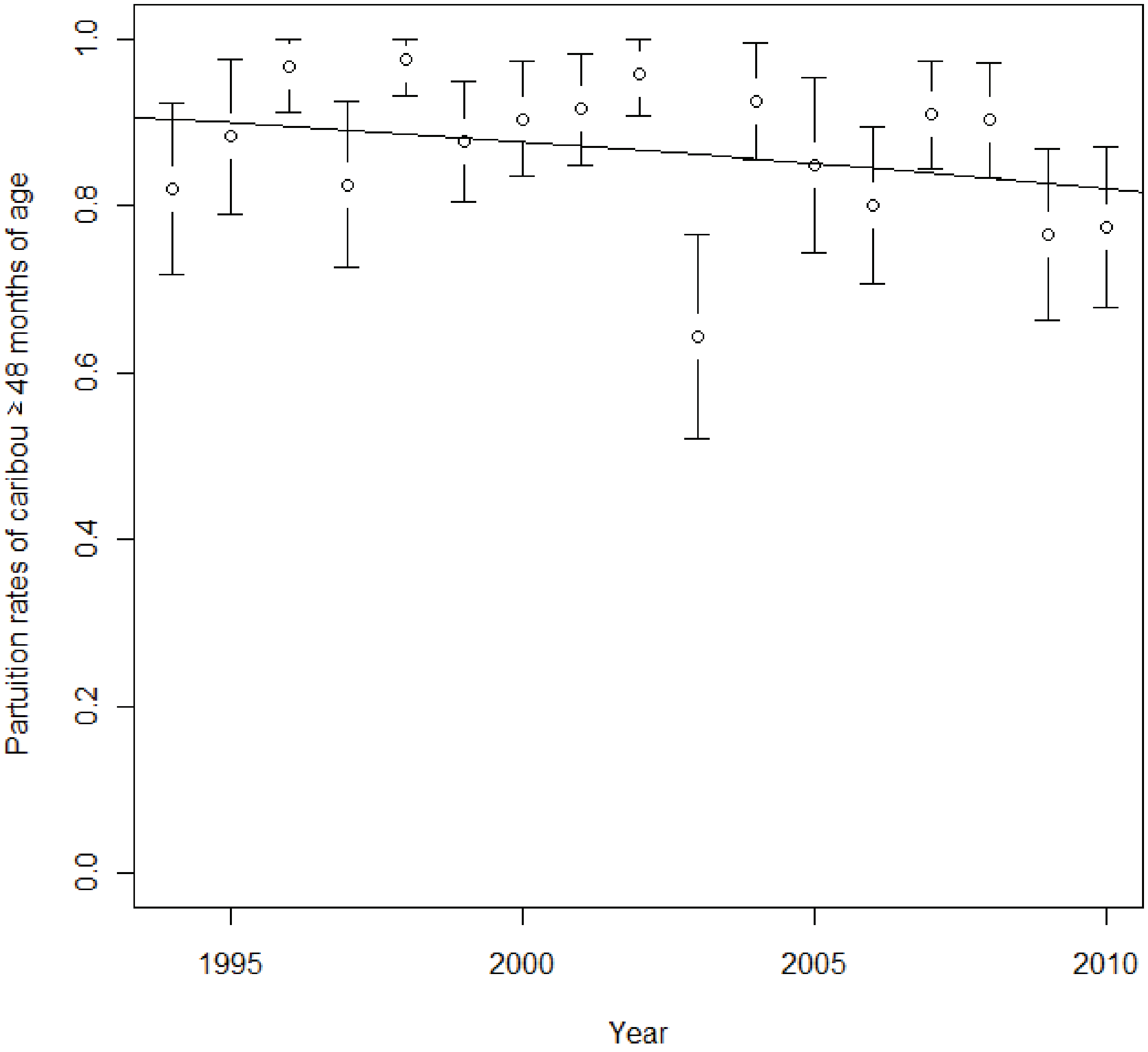


FIGURE 4. Parturition rates and 90% binomial CIs (truncated at 1.0 in 3 cases) among radiocollared caribou ≥48 months of age in the Fortymile herd, 1994–2010. The low parturition rates in 2003, 2009, and 2010 caused a significant decline in trend based on using annual data and logistic regression (generalized linear model) in Program R (slope on the logit scale = −0.04 [SE = 0.022], $P = 0.046$, $R^2 = 0.098$). Annual sample sizes ranged from 33 to 57 ($\bar{x} = 48$).

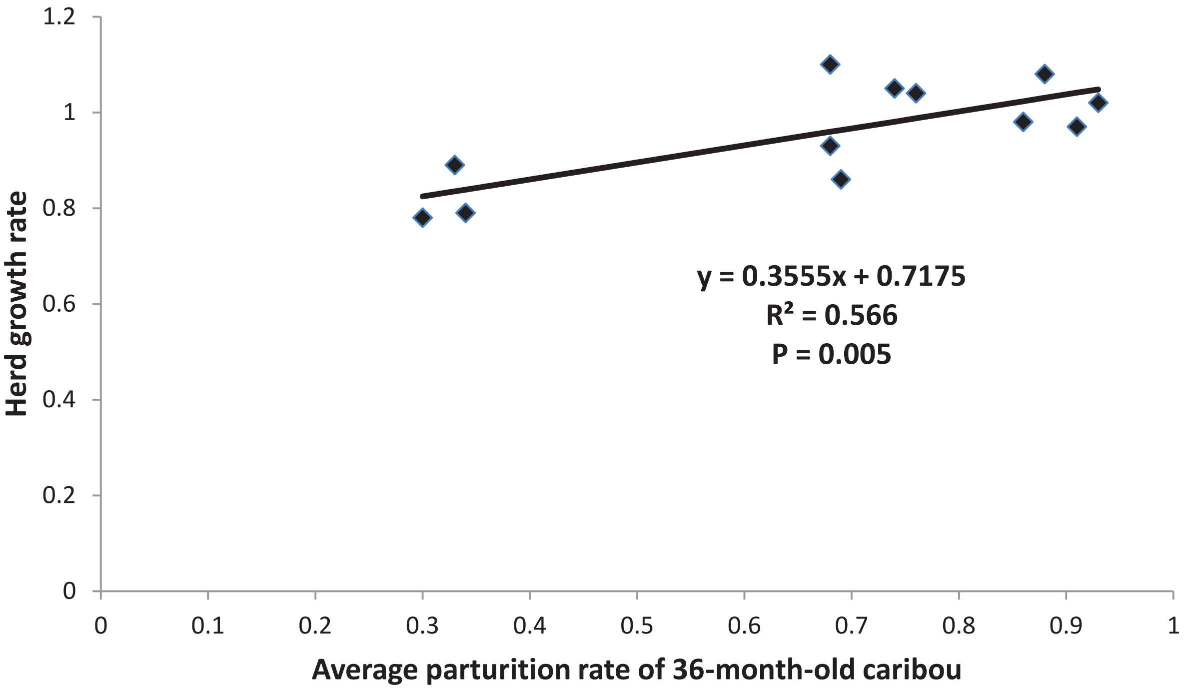


FIGURE 5. Relationship between herd growth rate (λ) and average parturition rate of 36-month-old female caribou during 12 study periods using simple linear regression, 1981–2011, Alaska. Data are from 8 different herds as detailed in Figure 6. We excluded data from the Nelchina herd because managers acted to increase predator take and simultaneously implemented high harvest rates of caribou to stabilize herd growth.

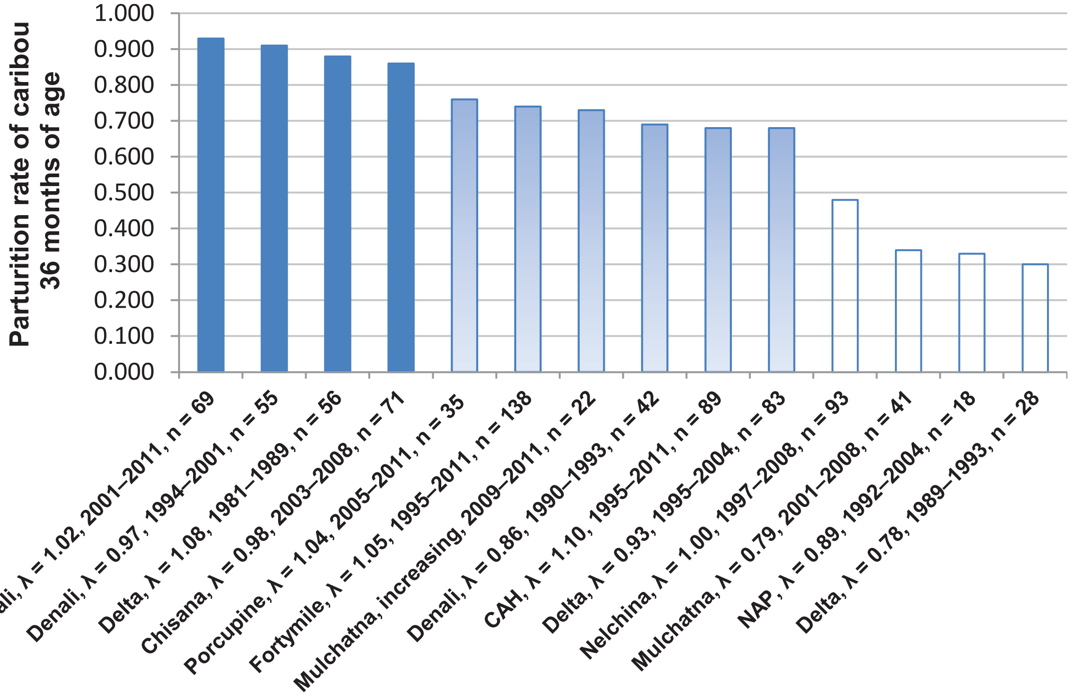


FIGURE 6. Average annual parturition rates of radiocollared 36-month-old caribou and trends in herd size from 4 studies (solid bars) when caribou exhibited relatively high reproductive rates (>80%), 6 studies (gradient bars) when caribou exhibited moderate rates (55–80%), and 4 studies (open bars) when caribou exhibited low rates (<55%), Alaska. We chose study periods based on years when herd trend was relatively consistent. All caribou were radiocollared as calves. The total number of 36-month-old caribou sampled during the respective study years is given by *n*. References include L. Adams, USGS, unpublished data for Denali and Chisana herds; Boertje et al. (1996) and Seaton (2009; C. T. Seaton, ADF&G unpublished data, Fairbanks) for Delta herd; Caikoski (2009; J. R. Caikoski, ADF&G unpublished data, Fairbanks) for Porcupine herd; this paper for Fortymile herd; Woolington (2009; J. D. Woolington, ADF&G unpublished data, Dillingham) for Mulchatna herd; Lenart (2009; E. A. Lenart, ADF&G unpublished data, Fairbanks) for CAH (Central Arctic herd); Tobey (2001), Tobey (2005), and Tobey and Schwanke (2009; R. Tobey and B. A. Schwanke, ADF&G unpublished data, Glennallen) for Nelchina herd; and Butler (2009) for NAP (Northern Alaska Peninsula).

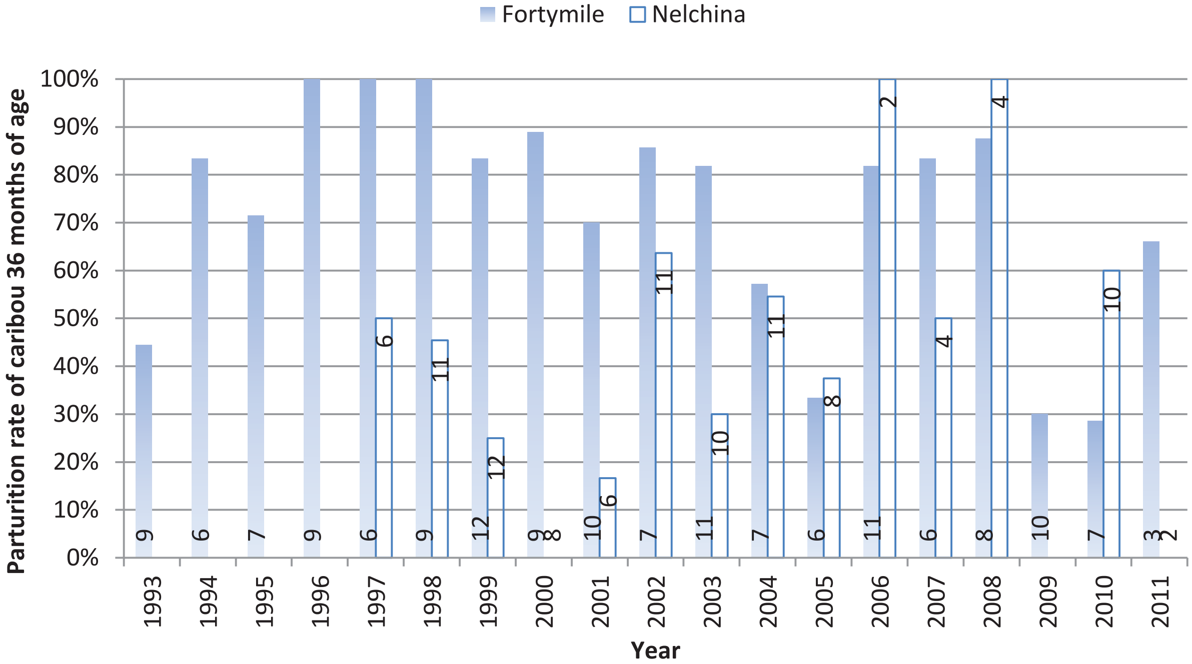


FIGURE 7. Parturition rates of radiocollared caribou 36 months of age, Fortymile and Nelchina herds, 1993–2011, Alaska. Data labels are sample sizes, ranging from 2 to 12 per herd/yr.

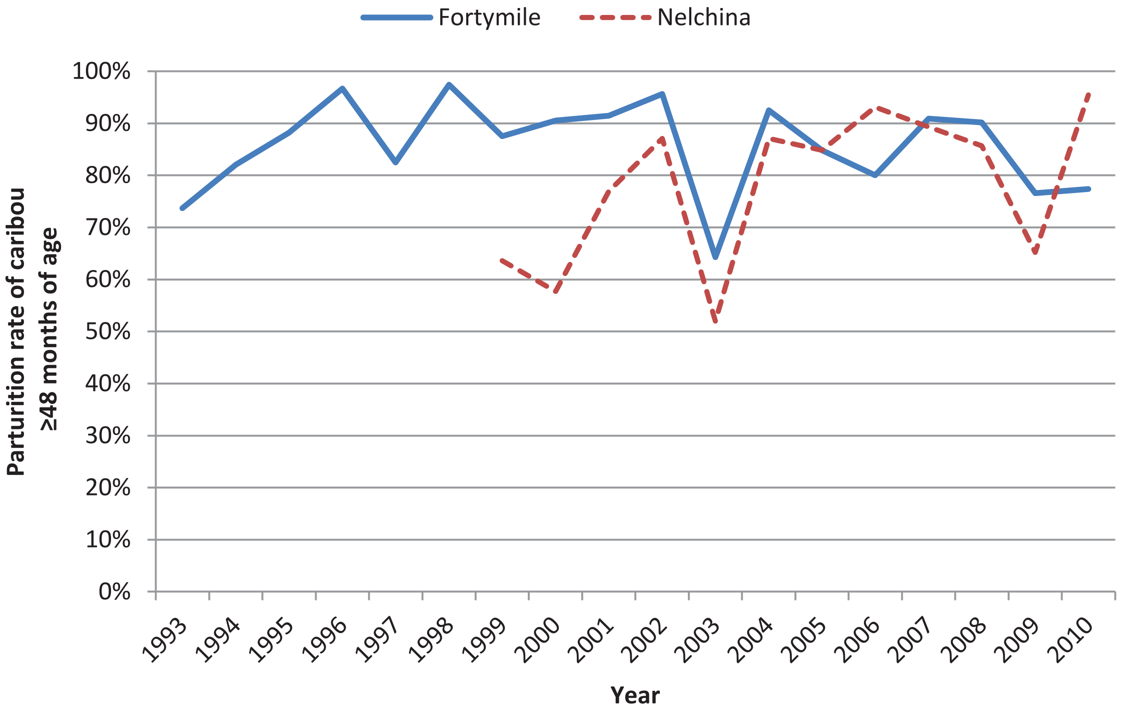
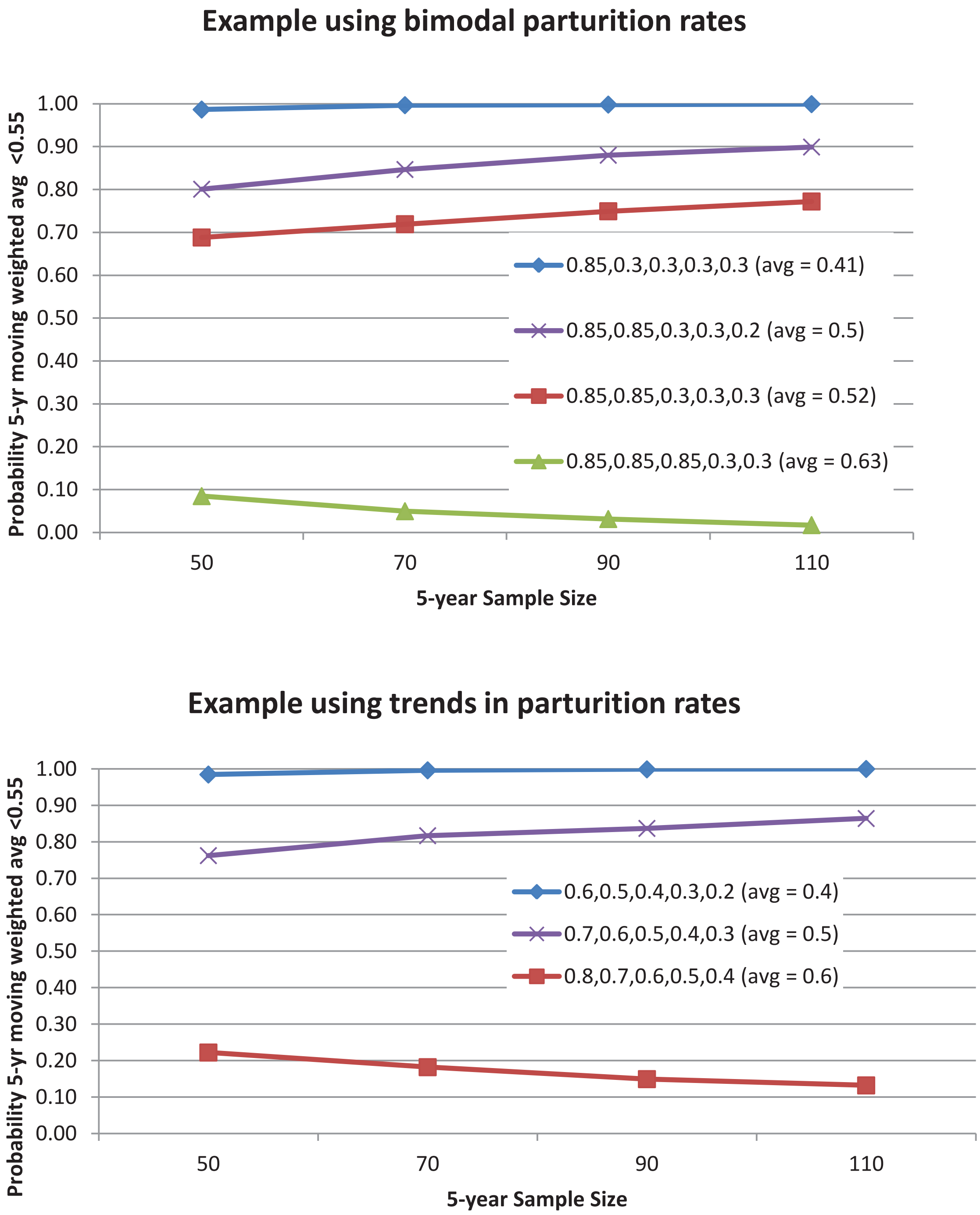


FIGURE 8. Parturition rates of radiocollared caribou ≥48 months of age in the Fortymile and Nelchina herds, 1993–2010, Alaska. Annual sample sizes ranged from 33 to 57 ($\bar{x}$ = 48) in the Fortymile herd and 22 to 33 ($\bar{x}$ = 27) in the Nelchina herd.


Example using bimodal parturition rates

Example using trends in parturition rates

FIGURE 9. Examples showing the probability that the moving weighted average will fall below the 55% threshold given various patterns of true parturition rates and different sample sizes. We considered constant annual and 5-year (in parentheses) sample sizes of 10 (50), 14 (70), 18 (90), or 22 (110) and true parturition rates distributed either bimodally or with constant trend, although the ordering of the rates was inconsequential to the results. The figures demonstrated the power of the moving weighted average to trigger a response (decline below 0.55) under a variety of scenarios.

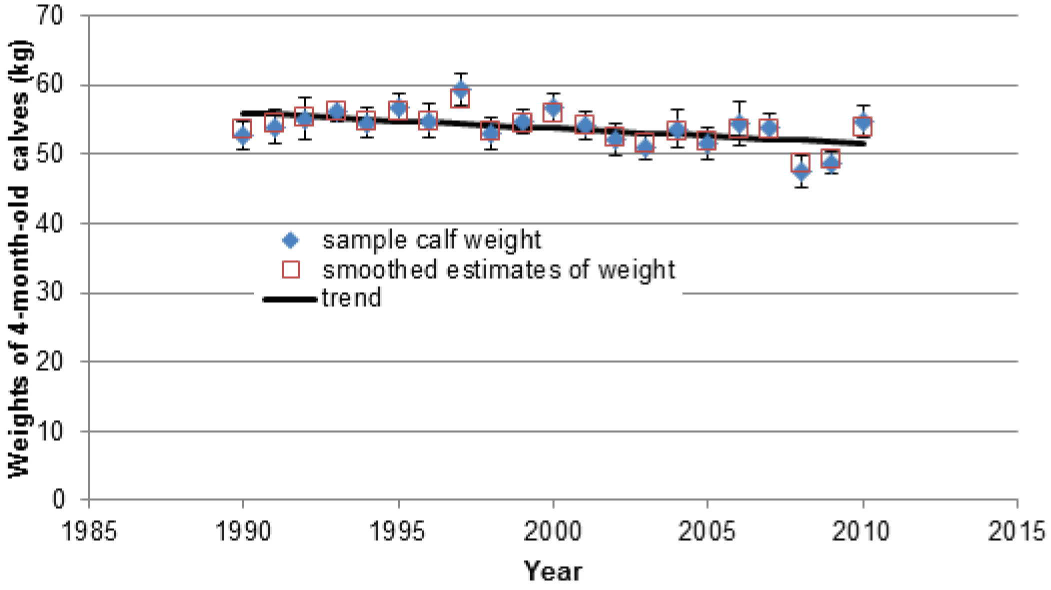


FIGURE 10. Trend analysis on female calf weights at 4 months of age in the Fortymile caribou herd, 1990–2010, Interior Alaska. Annual sample sizes ranged from 14 to 18. The linear mixed effects model indicated a significant linear decrease of 0.22 kg/yr (*P* = 0.02). We provided 95% CIs for sample estimates.

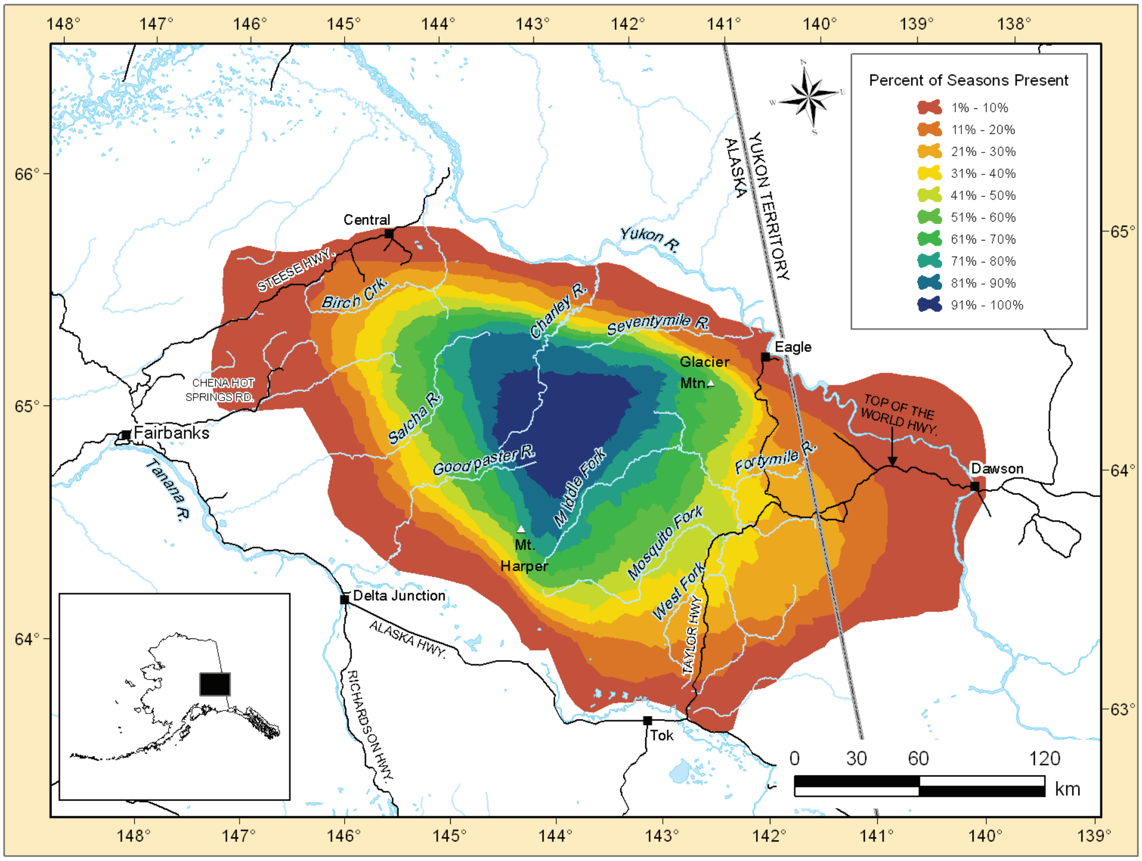


FIGURE 11. Fortymile caribou herd distribution based on percentages of 99 independent seasonal boundaries, 1991–2008, Interior Alaska and adjacent Yukon. The maximum number of seasons that overlapped was 94. The blue areas, representing 71–100% of the seasons, largely encompass the area referred to in text as the core uplands or core upland tundra (7,000 km^2).

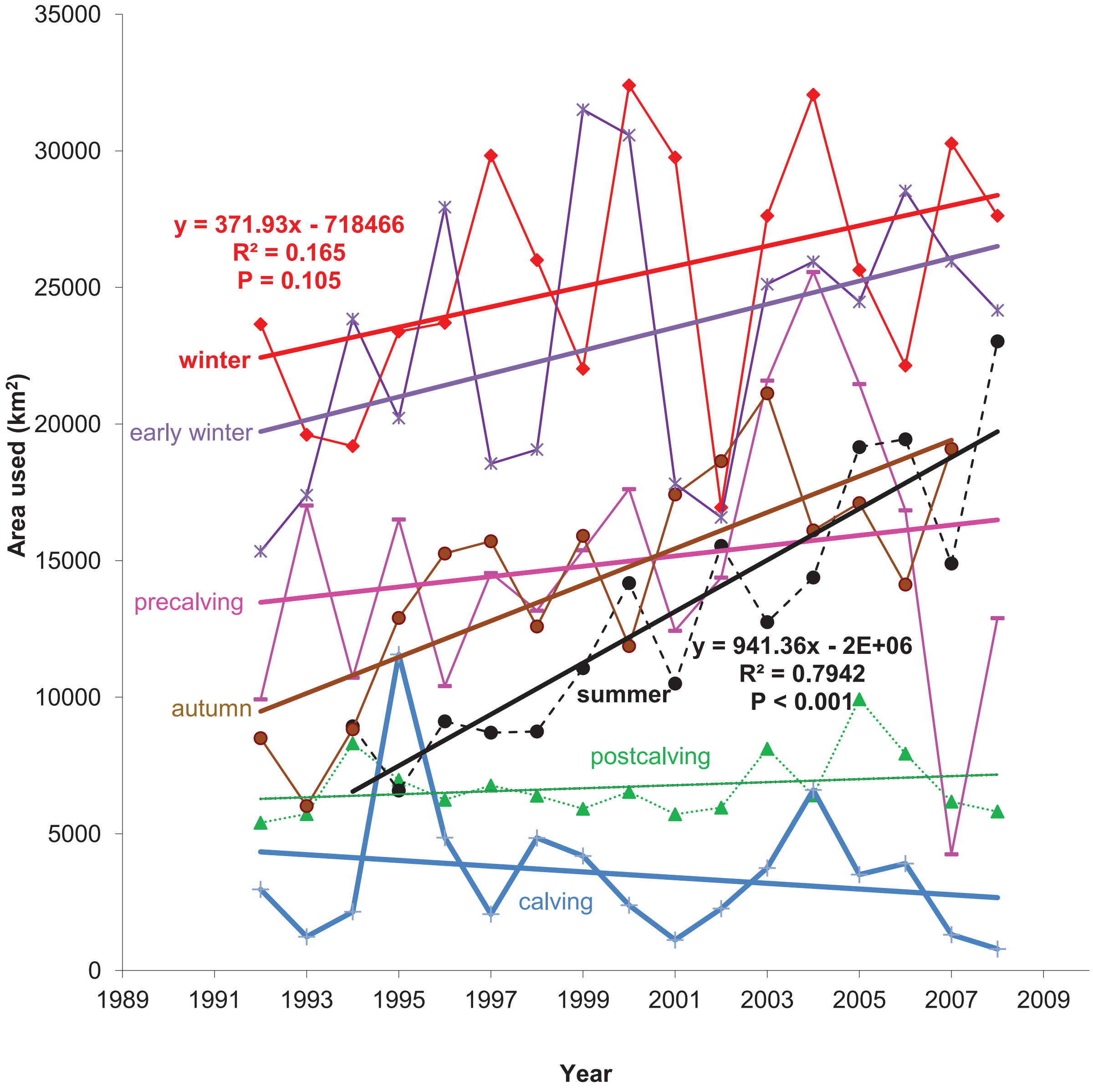


FIGURE 12. Range sizes (km^2) during each of 7 seasons over a 17-year study period when herd size doubled, Fortymile caribou herd, 1991–2008, Interior Alaska and adjacent Yukon. We used simple linear regression to describe the trend in seasonal range sizes during the study period. For summer and winter seasons, we provided equations for the trend lines and the associated R^2 and P values.

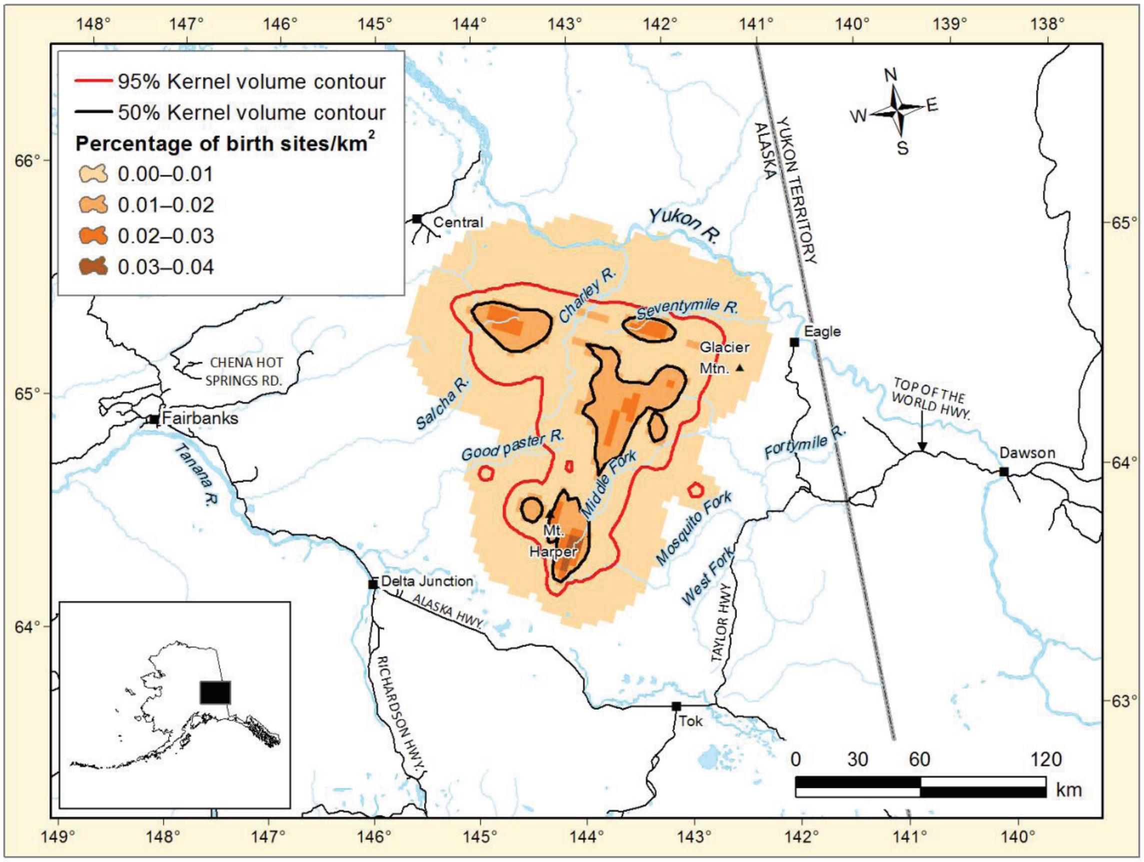


FIGURE 13. Estimated mean Fortymile calving site density generated using averaged fixed kernel utilization distributions, 1992–2000, Interior Alaska (*n* = 9 years, 341 birth sites of collared caribou). We present the percentage of calving sites of collared caribou, rather than density of the herd's calving sites, which would require incorporating the herd size and parturition rate. Calving use of the upper Salcha River was periodic, not continuous, during 1992–2000.

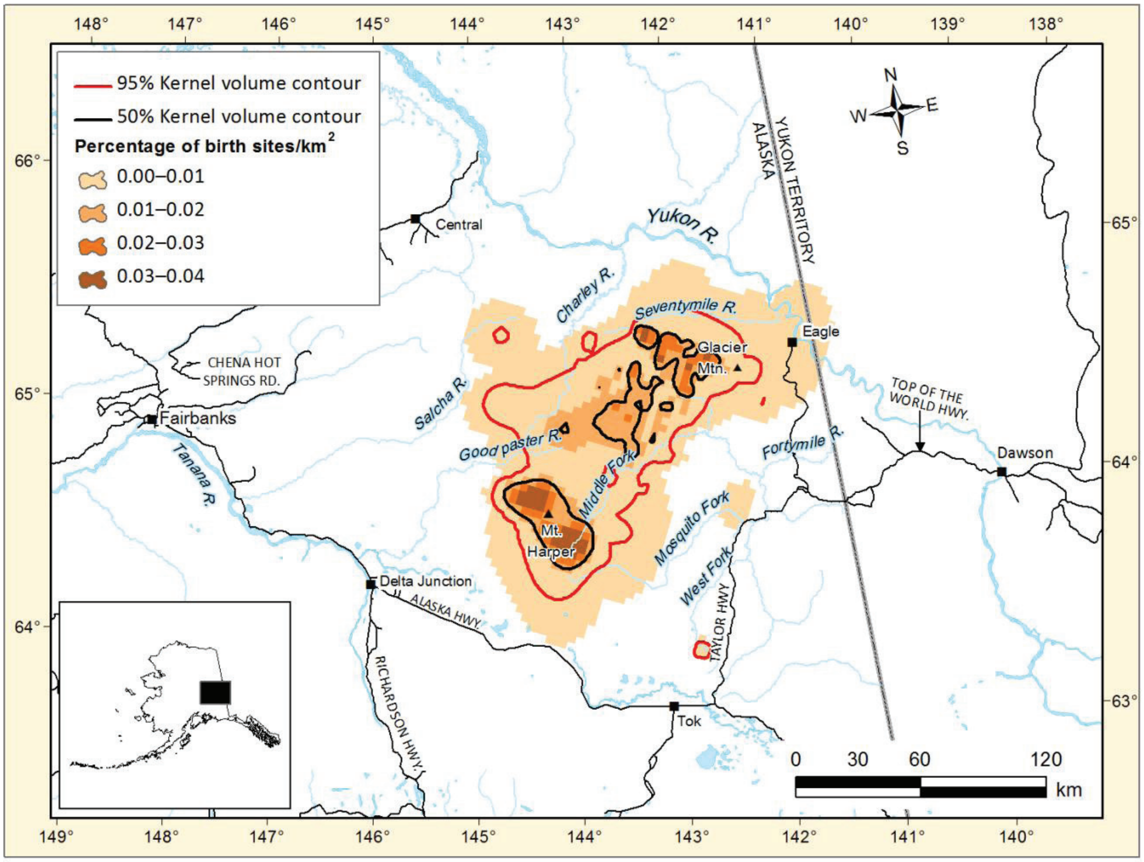


FIGURE 14. Estimated mean Fortymile calving site density generated using averaged fixed kernel utilization distributions, 2001–2008, Interior Alaska (*n* = 8 years, 270 birth sites of collared caribou). We present the percentage of calving sites of collared caribou, rather than density of the herd's calving sites, which would require incorporating the herd size and parturition rate.

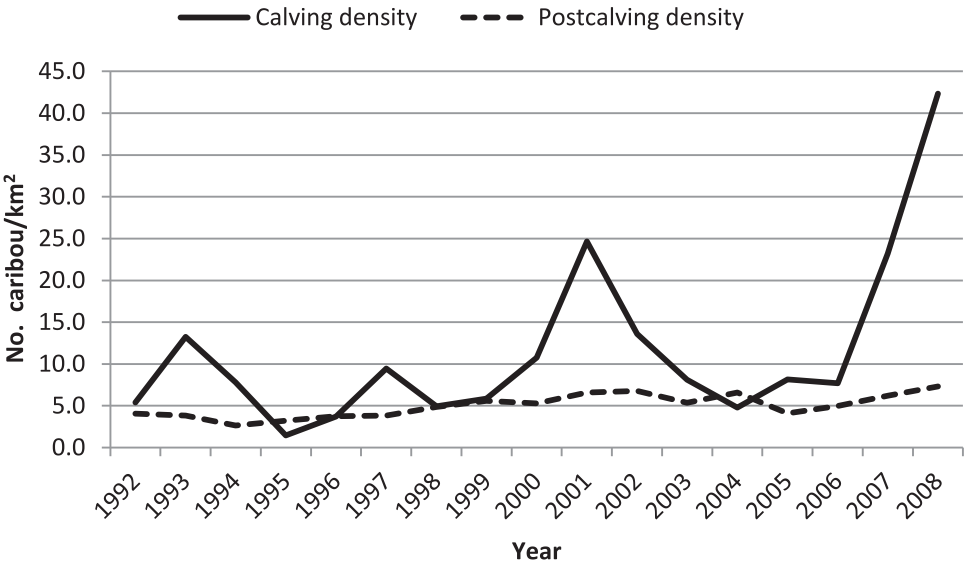


FIGURE 15. Caribou density during calving (11 May–27 May, bulls excluded) and postcalving (28 May–30 June, bulls included), Fortymile herd, 1992–2008, Interior Alaska.

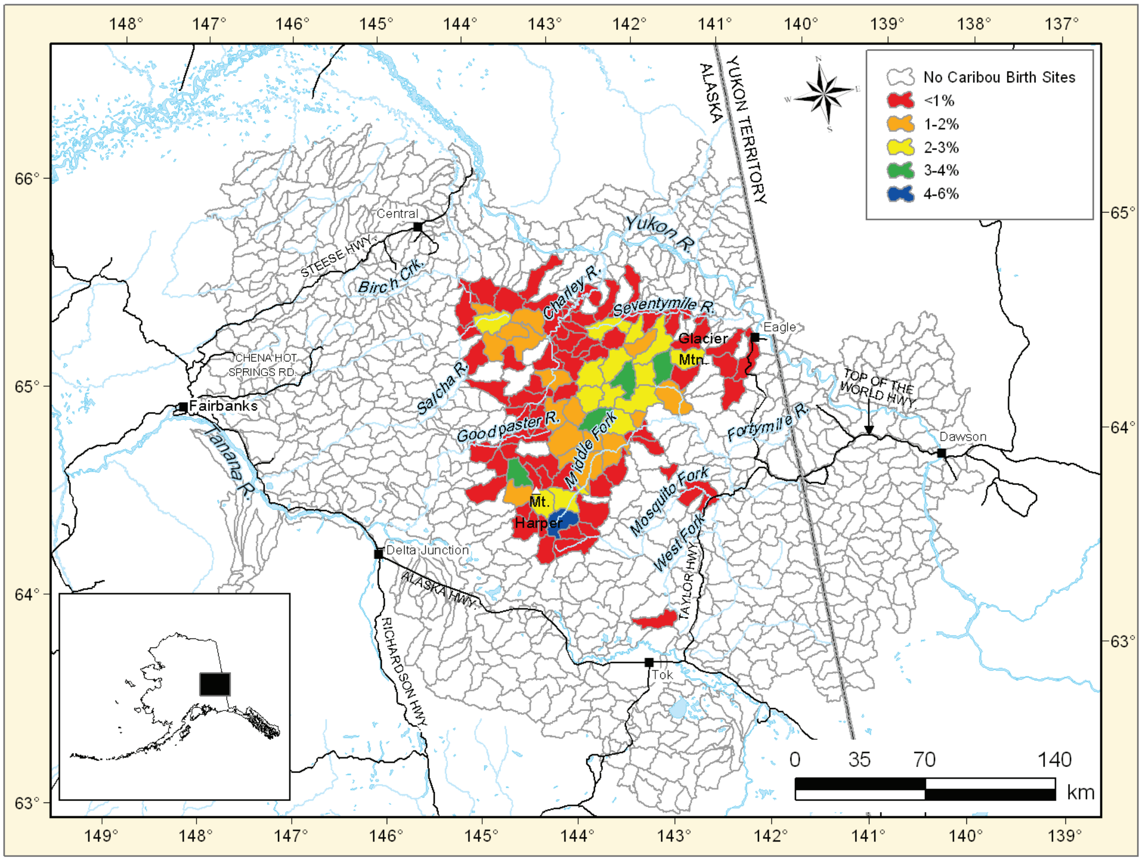


FIGURE 16. Percentage of 611 birth sites of radiocollared female caribou in portions of drainages, Fortymile caribou herd, 1992–2008, Interior Alaska.

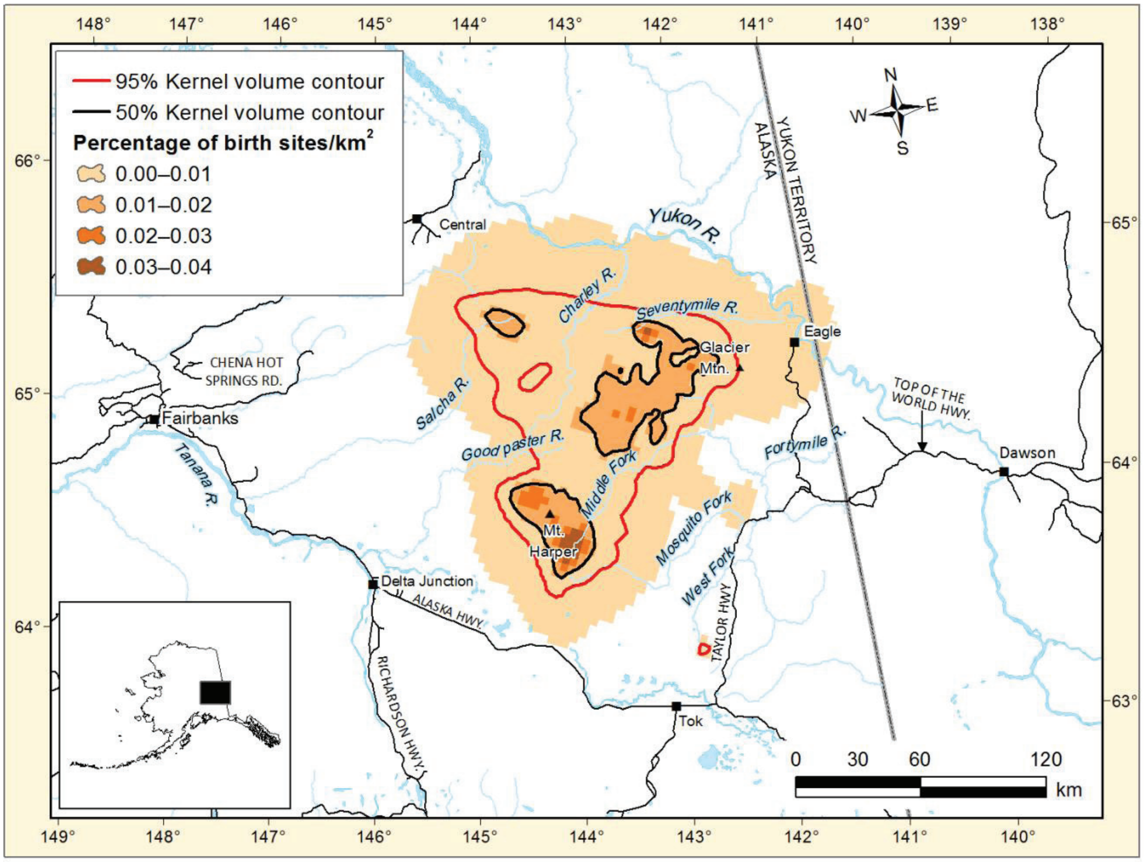


FIGURE 17. Estimated mean Fortymile calving site density generated using averaged fixed kernel utilization distributions, 1992–2008, Interior Alaska (*n* = 17 years, 611 birth sites of collared caribou). We present the percentage of calving sites of collared caribou, rather than density of the herd's calving sites, which would require incorporating the herd size and parturition rate.

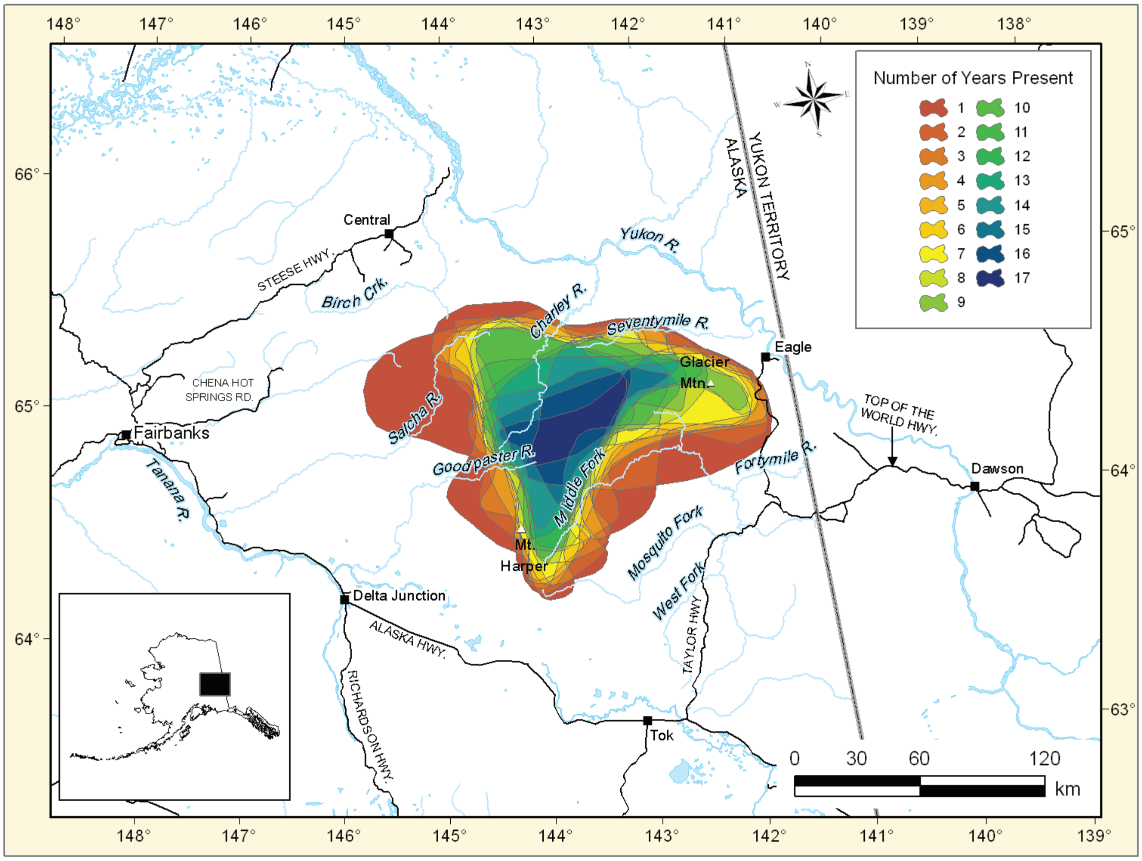


FIGURE 18. Overlap among 17 years of postcalving (28 May–30 June) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1992–2008, Interior Alaska. The area depicted (excluding red) largely encompassed the area we refer to in text as the core uplands or core upland tundra (7,000 km^2).

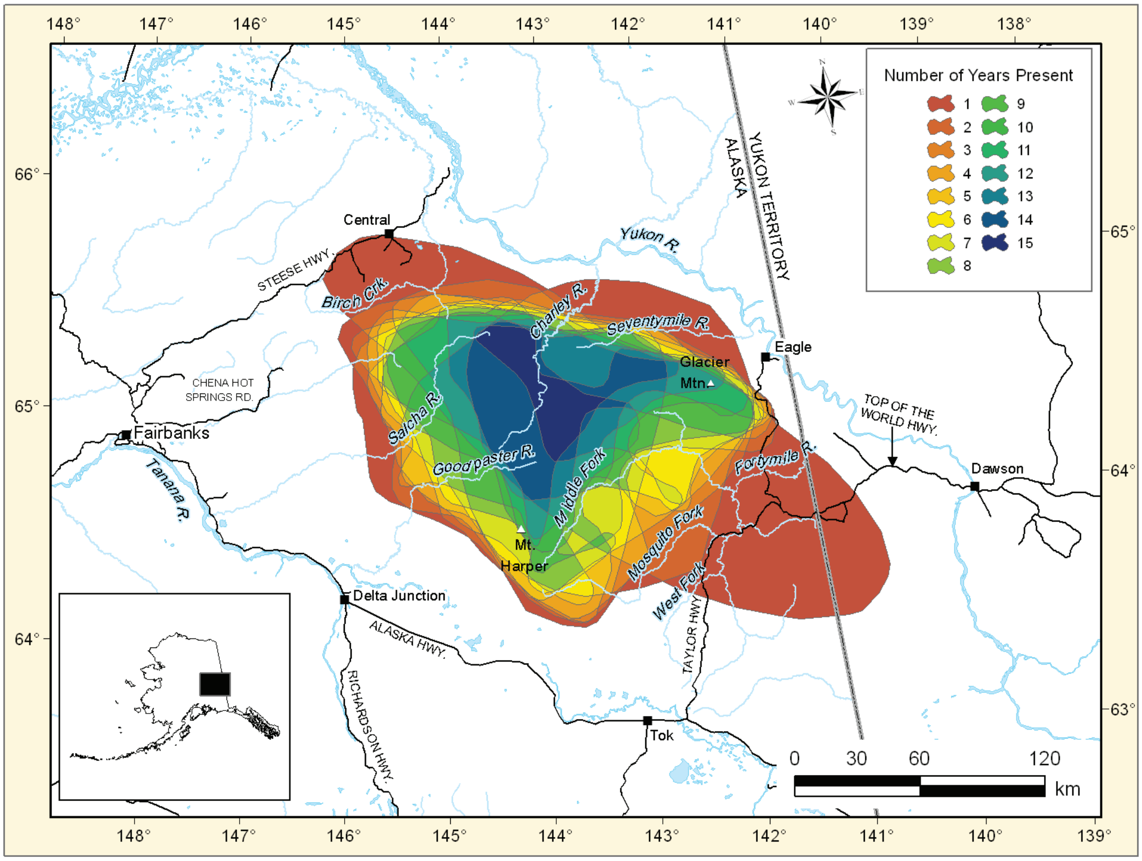


Figure 19. Overlap among 15 years of summer (1 July–15 August) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1994–2008, Interior Alaska and adjacent Yukon.

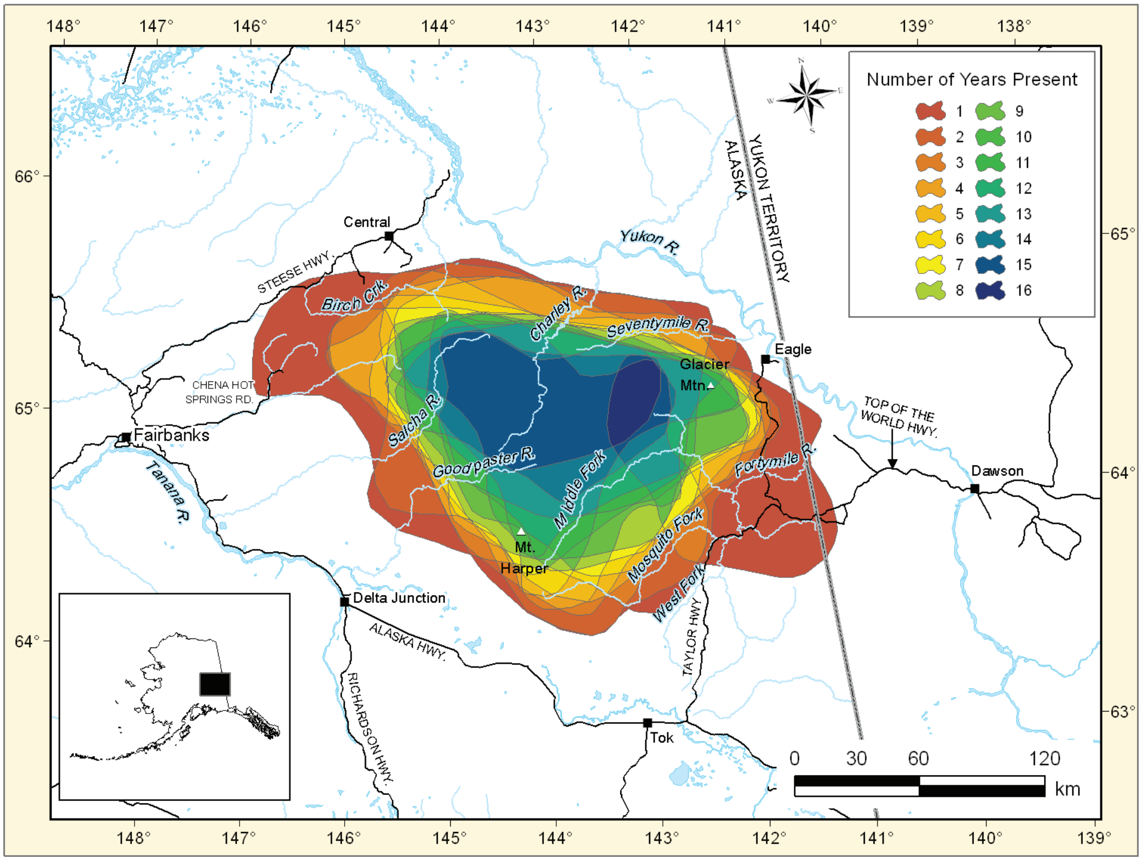


FIGURE 20. Overlap among 16 years of autumn (16 August–30 September) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1992–2007, Interior Alaska and adjacent Yukon.

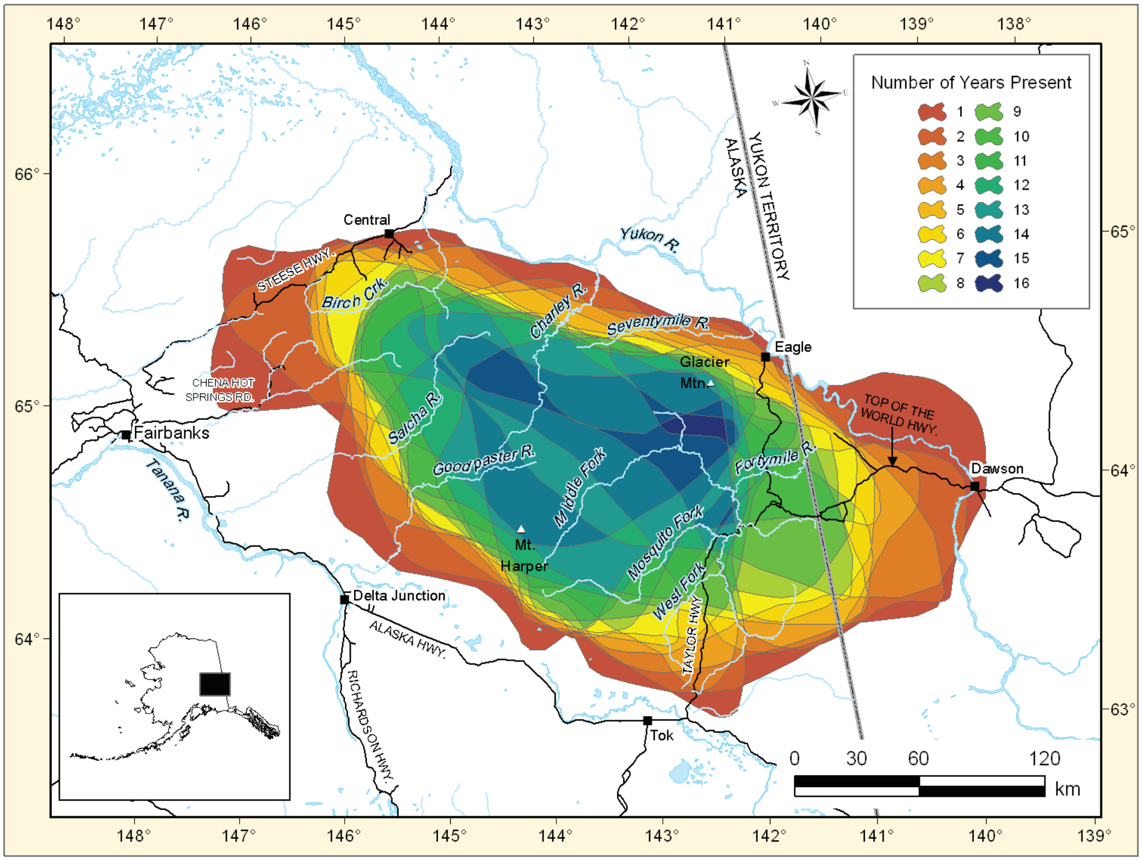


FIGURE 21. Overlap among 16 years of early winter (1 October–30 November) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1992–2008, Interior Alaska and adjacent Yukon. Sample size would have been 17 years, except that no overlap existed between 2 winters when caribou were separated onto extreme eastern or western ranges.

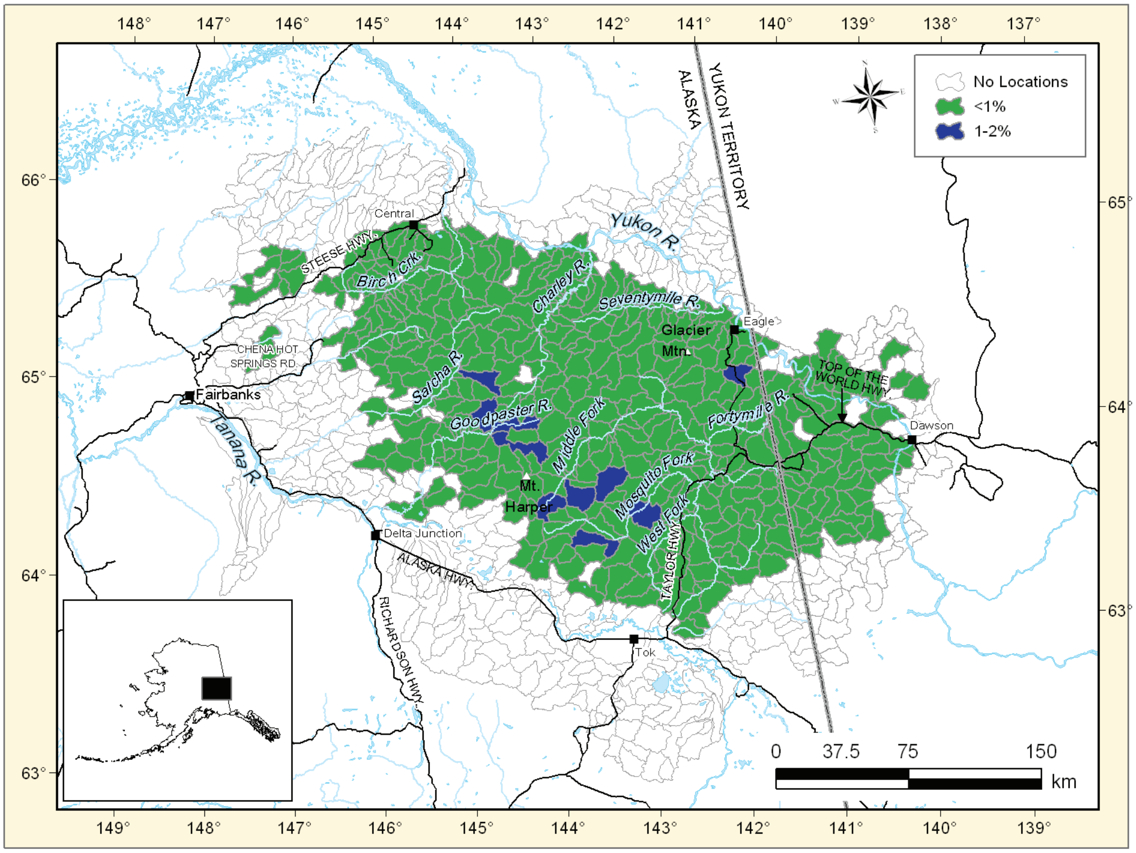


FIGURE 22. Percentage of 3,452 approximate locations of radiocollared female caribou among portions of drainages during early winter (1 October–30 November) corrected for annual sample sizes, Fortymile caribou herd, 1992–2007, Interior Alaska and adjacent Yukon.

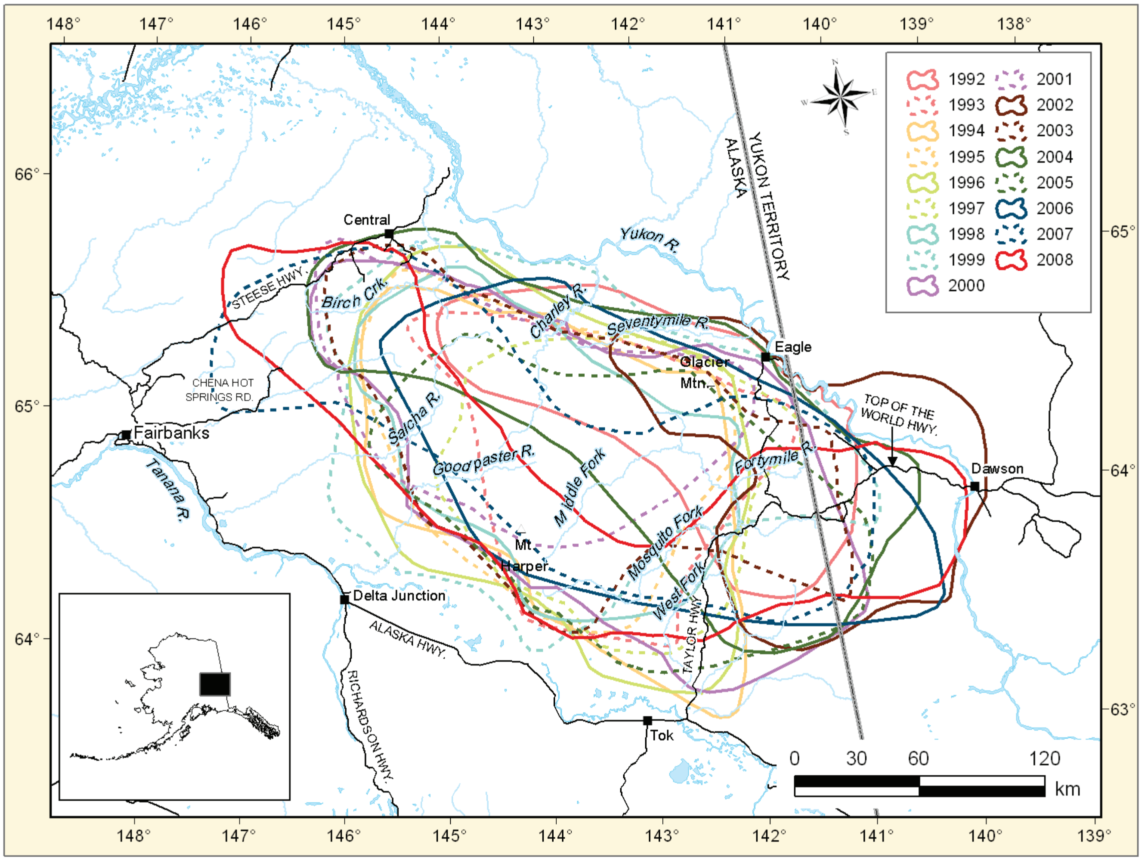


FIGURE 23. Outer boundaries of 17 years of early winter (1 October–30 November) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1992–2008, Interior Alaska and adjacent Yukon.

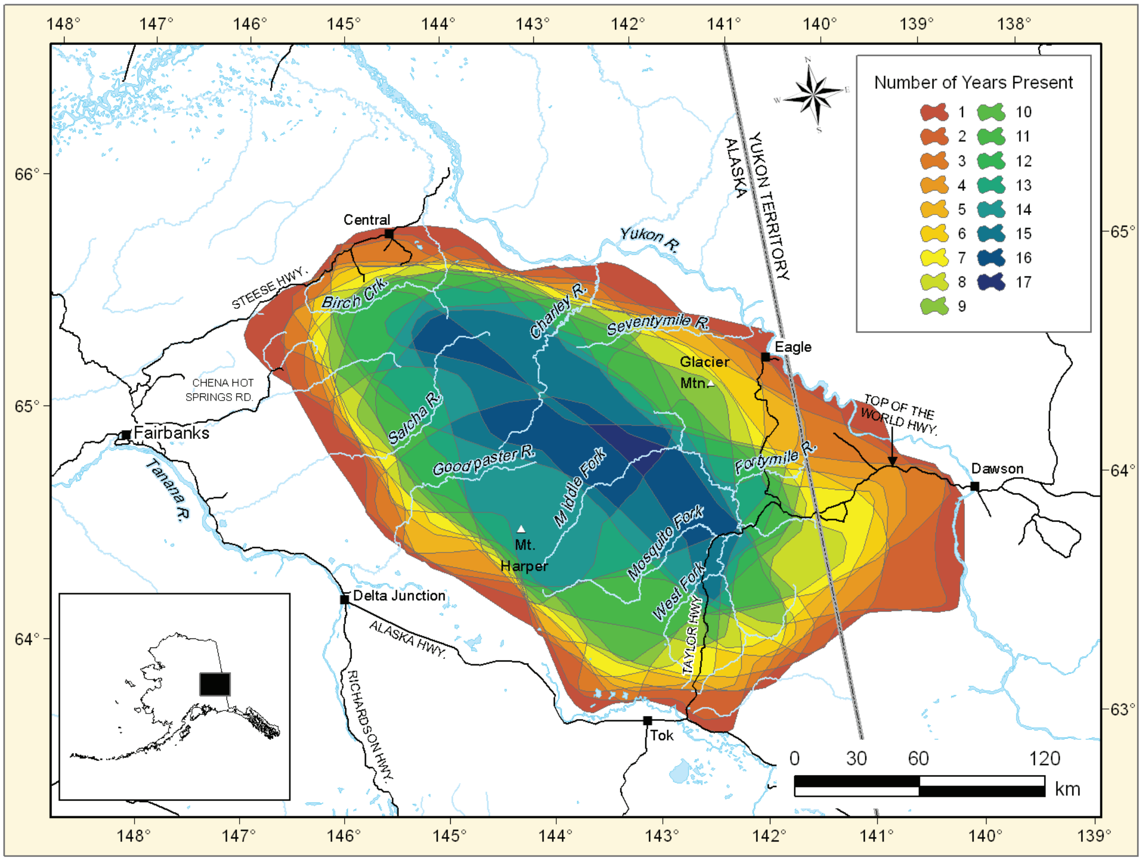


FIGURE 24. Overlap among 17 years of winter (1 December–31 March) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1991–2008, Interior Alaska and adjacent Yukon.

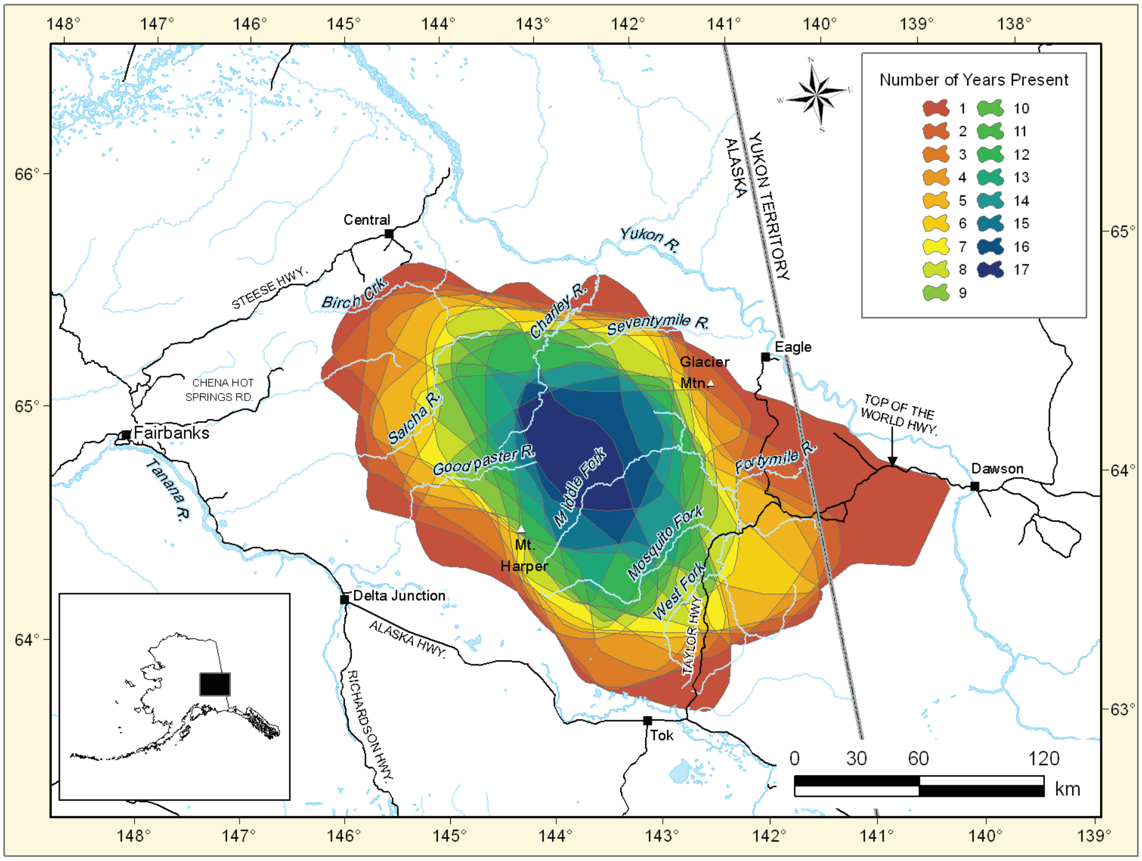


FIGURE 25. Overlap among 17 years of precalving (1 April–10 May) ranges based on locations of radiocollared, female caribou, Fortymile caribou herd, 1992–2008, Interior Alaska and adjacent Yukon.

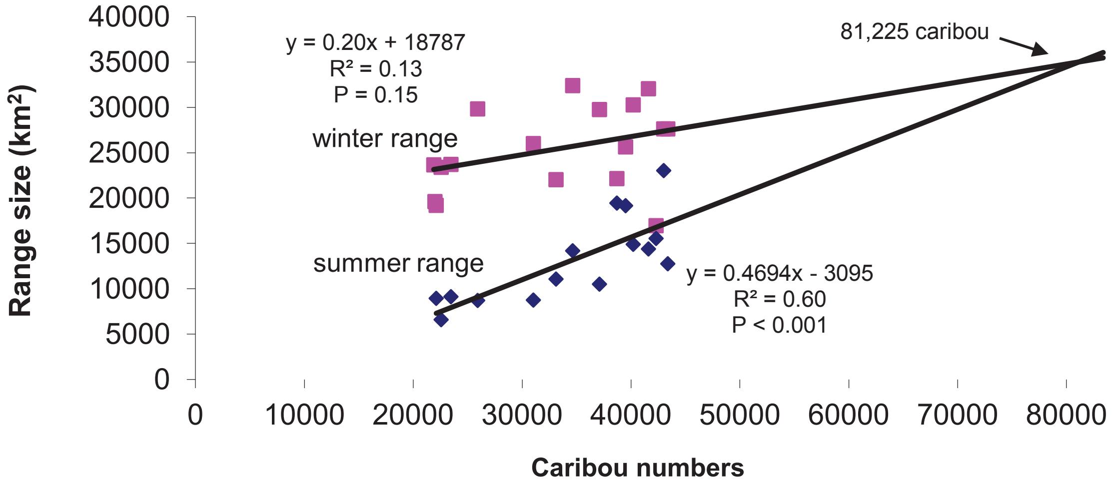


FIGURE 26. Relationships between seasonal range size, during winter (1 December–31 March) and summer (1 July–15 August), and caribou numbers for a 17-year period when herd size doubled, Fortymile caribou herd, 1992–2008, Interior Alaska and adjacent Yukon. Based on extrapolation of the results of simple linear regression, we might predict winter and summer range sizes will be similar when herd numbers reach 81,225. However, in other herds, winter range sizes are larger than summer range sizes (Bergerud et al. 2008). We surmised that the relatively rapid increase in summer range size may be indicative of stress and possibly a temporary phenomenon.

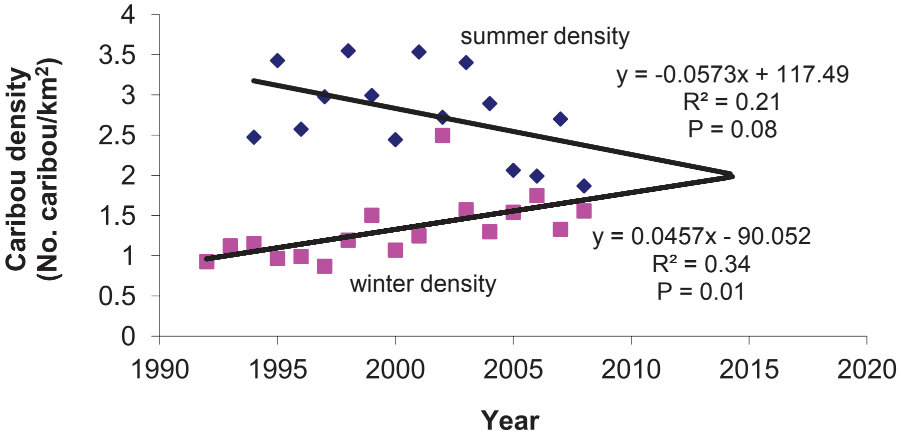


FIGURE 27. Relationships between seasonal caribou density, during summer (1 July–15 August) and winter (1 December–31 March), over a 17-year study period, Fortymile caribou herd, 1992–2008, Interior Alaska and adjacent Yukon. Based on extrapolation of the results of simple linear regression, we might predict that summer and winter densities may be similar in about 2015. However, in other herds, winter caribou densities are lower than summer densities (Bergerud et al. 2008). We surmised that the decline in summer density may be indicative of stress and possibly a temporary phenomenon.

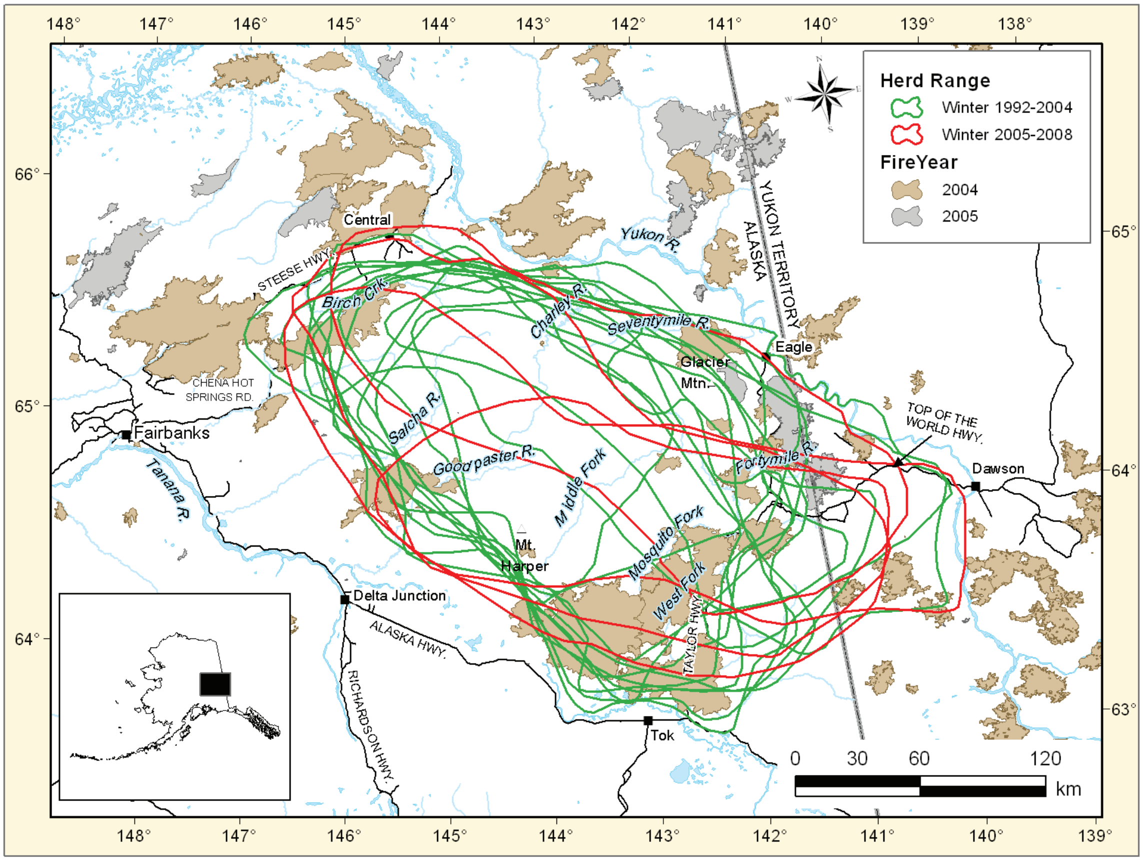


FIGURE 28. Outline of wildfires in 2004 and 2005 and Fortymile caribou winter ranges pre- and post-wildfires, 1992–2008, Interior Alaska and adjacent Yukon.

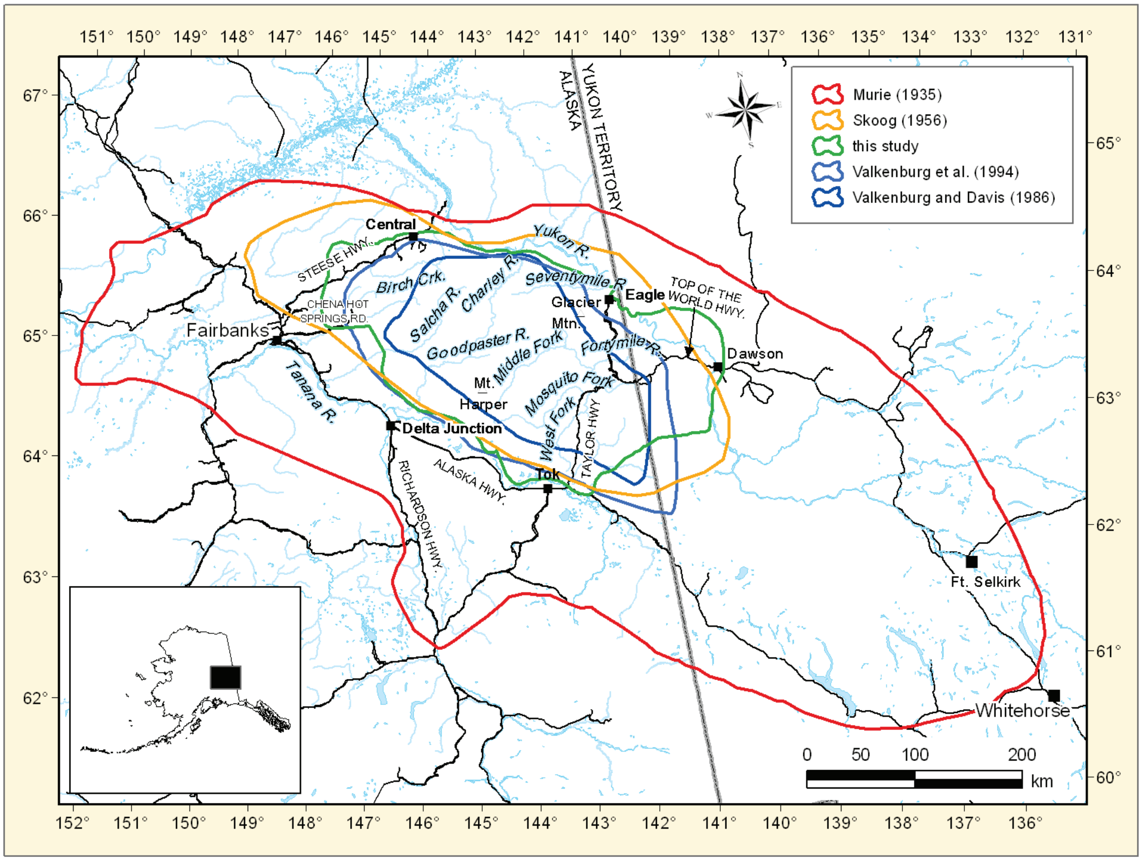


FIGURE 29. Cumulative multi-year Fortymile caribou herd distribution delineated during 5 study periods from largest to smallest range size, 1918–1924 (Murie 1935), 1952–1955 (Skoog 1956), 1992–2008 (this study), 1986–1990 (Valkenburg et al. 1994), and 1980–1985 (Valkenburg and Davis 1986), Interior Alaska and adjacent Yukon.

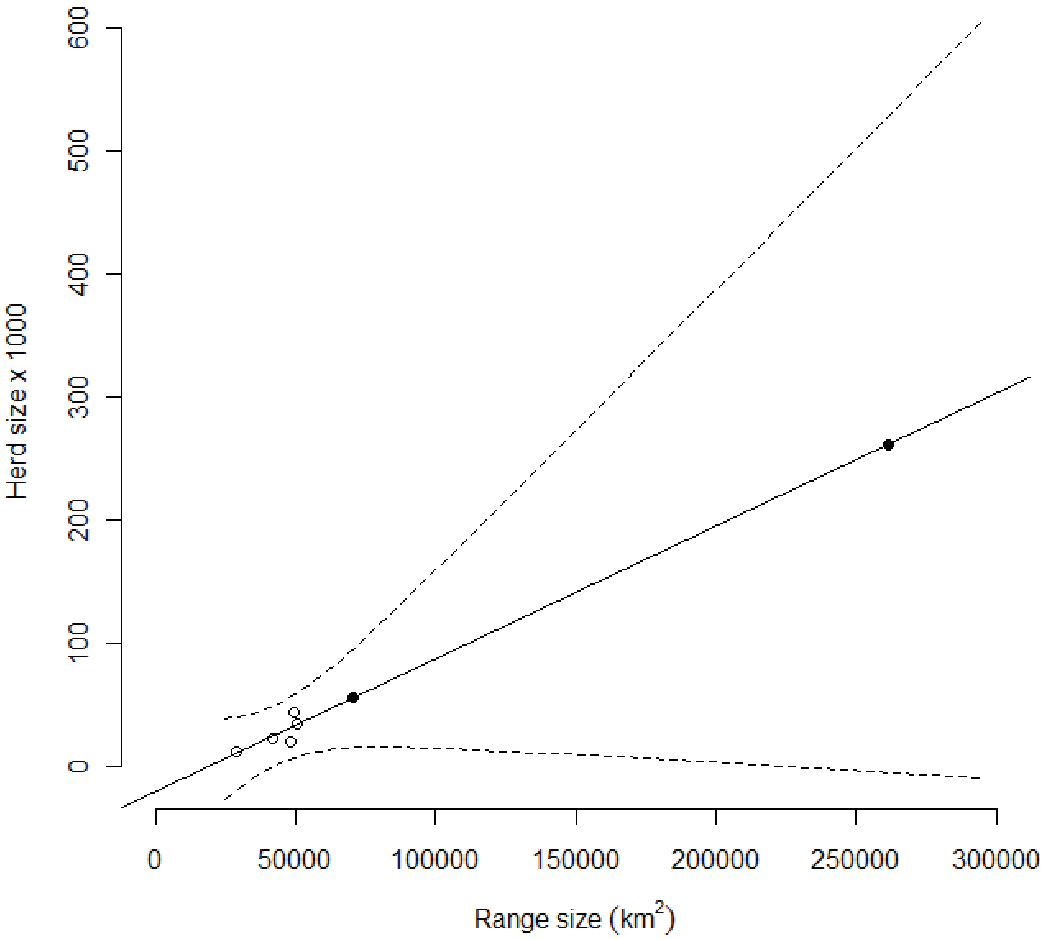


FIGURE 30. Relationship between average herd size and total multi-year range size during 5 study periods, each 5 or 6 years in duration (open circles), Fortymile caribou herd, Interior Alaska and adjacent Yukon. The solid line and solid circles depict the results of linear regression in Program R used to estimate average herd size during 1952–1955 (55,102 caribou) and 1918–1924 (261,202 caribou), when range size was estimated but no reliable methods were available for estimating herd size (slope = 1.080 [SE = 0.518], intercept = −21,120, $P = 0.128$, $R^2 = 0.59$). The dashed lines are the 90% prediction intervals.

TABLE 1. Average annual number of independent caribou, telemetry surveys, and points used to depict Fortymile caribou herd range use, 1992–2008, Interior Alaska and adjacent Yukon.

	No. of independent caribou[a]			No. of complete telemetry surveys			No. of points		
Season and years	Mean	SE	Range	Mean	SE	Range	Mean	SE	Range
Winter (1 Dec–31 Mar) 17 yr, 1992–2008	66.6	3.39	41–90	4.1	0.31	3–8	271.2	24.00	105–510
Precalving (1 Apr–10 May) 17 yr, 1992–2008	64.0	4.62	35–103	2.2	0.13	1–3	135.8	9.83	52–206
Calving[a] (11 May–27 May) 17 yr, 1992–2008	35.9	3.50	15–64	10.6	1.42	3–17	35.9	3.50	15–64
Postcalving migration (28 May–30 Jun) 17 yr, 1992–2008	52.4	4.95	20–98	7.5	1.17	2–16	357.5	58.30	99–990
Summer (1 Jul–15 Aug) 15 yr, 1994–2008	52.1	3.05	37–74	4.1	0.41	2–7	212.7	23.03	88–430
Autumn migration (16 Aug–30 Sep) 16 yr, 1992–2007	61.2	3.56	39–95	4.3	0.43	1–7	271.3	34.13	50–568
Rut/Early winter (1 Oct–30 Nov) 17 yr, 1992–2008	67.4	4.21	43–98	3.1	0.16	2–4	203.1	15.08	111–339

[a] Calving distribution was defined by birth sites of radiocollared females. All other seasons were defined by approximate locations of independent radiocollared caribou.

TABLE 2. Estimated number of Fortymile caribou harvested, percent of herd size harvested, and number of calves:100 females ≥1 year old, 1970–2010, Interior Alaska and adjacent Yukon.

	Estimated harvest[a]					
Year	M	F	Estimate of herd numbers[b] or interpolations[c]	Percent of herd harvested	No. of F ≥ 1 yr old sampled in Sep or Oct[d]	No. of calves:100 F ≥ 1 yr old in Sep or Oct[d]
1970	956	430	15,000	9.2	no data	
1971	1,298	1,062	11,000[c]	21.5	no data	
1972	638	692	7,500[c]	17.7	484	21
1973	61	14	6,000	1.3	2,292	16
1974	41	4	6,000	0.8	1,078	20
1975	49	26	6,000	1.3	no data	
1976	44	8	6,667[c]	0.8	476	34
1977	87	8	7,333[c]	1.3	543	45
1978	19	11	8,000[c]	0.4	417	26
1979	30	0	8,666[c]	0.3	no data	
1980	50	0	9,333[c]	0.5	no data	
1981	100	0	10,093	1.0	547	31
1982	200	0	11,200[c]	1.8	901	27
1983	294	0	12,350	2.4	1,058	33
1984	430	20	13,402	3.4	no data	
1985	421	20	14,400[c]	3.1	574	36
1986	360	20	15,303	2.5	842	28
1987	229	20	17,600[c]	1.4	1,274	37
1988	645	150	19,975	4.0	770	30
1989	401	100	21,400[c]	2.3	1,182	24
1990	321	22	22,766	1.5	1,002	29
1991	495	10	22,325[c]	2.3	931	16
1992	432	35	21,884	2.1	1,417	30
1993	335	11	21,994[c]	1.6	2,095	29
1994	313	15	22,104	1.5	1,710	27
1995	203	22	22,558	1.0	1,879	32
1996	145	5	23,458	0.6	2,601	36
1997	143	8	25,910	0.6	3,313	41
1998	151	4	31,029	0.5	2,433	38
1999	142	13	33,110	0.5	2,347	37
2000	142	8	34,640	0.4	3,780	27
2001	493	215	37,552[c]	1.9	3,645	38
2002	694	193	40,463[c]	2.2	3,347	39
2003	636	188	43,375	1.9	3,777	17
2004	615	253	43,000[e]	2.0	2,445	28
2005	569	186	43,000[e]	1.8	1,391	18
2006	620	254	43,000[e]	2.0	2,839	34
2007	771	271	43,837[c]	2.4	3,031	37
2008	705	227	44,673[c]	2.1	2,164	32
2009	892	222	46,510	2.4	2,036	33

Year	Estimated harvest[a]		Estimate of herd numbers[b] or interpolations[c]	Percent of herd harvested	No. of F ≥ 1 yr old sampled in Sep or Oct[d]	No. of calves:100 F ≥ 1 yr old in Sep or Oct[d]
	M	F				
2010	514	57	51,675	1.1	4,146	32

[a] Harvest was from Valkenburg et al. (1994) for 1970–1983, Boertje and Gardner (2000*a*) for 1984–1997, Gardner (2003) for 1998–2001, and Gross (2009*b*) for 2002–2007.

[b] Estimates of herd size are from Valkenburg et al. (1994) for 1970–1990 and Gross (2009*b*) for 1992–2007. The 1970 estimate was a crude estimate, whereas the remaining estimates originated from photocensuses. Valkenburg and Davis (1989) reevaluated the 1973–1975 photocensuses and, based partly on low calf:cow ratios, concluded that herd size was likely stable between 5,740 and 8,610 caribou during 1973–1975. We chose an estimate of 6,000 as the low point in herd size. After 1982, we conducted photocensuses with the benefit of radiocollared caribou, which greatly enhanced the efficiency of locating the largest groups of caribou.

[c] Average interpolations of herd size are provided, because herd size was not estimated.

[d] Estimates of numbers of calves:100 F ≥ 1 yr old are from Valkenburg et al. (1994) for 1972–1984 and Gross (2009*b*) for 1985–2008.

[e] Herd size was likely nearly stable during 2003–2006 based on low calf:cow ratios.

TABLE 3. Model selection results for predicting parturition rates of 36-month-old caribou from prior 3 years of October calf weights, Fortymile caribou herd, 1993–2010. The “*” symbol equates to additive effects and an interaction between parameters, and the colon refers to only an interaction between the parameters.

Model	Covariates	Parameters	QAICc[a]	Delta_QAICc	QAICcWt	Cum. Wt	Quasi.LL	R^2
mod 9	calfwt$_{t-1}$*calfwt$_{t-3}$	5	57.51	0.00	0.22	0.22	−21.25	0.594
mod 1	calfwt$_{t-1}$	3	57.68	0.17	0.21	0.43	−24.98	0.384
mod 4	calfwt$_{t-1}$+calfwt$_{t-2}$	4	57.87	0.36	0.19	0.61	−23.39	0.473
mod 5	calfwt$_{t-1}$+calfwt$_{t-3}$	4	58.84	1.34	0.11	0.73	−23.88	0.446
mod 12	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$	6	58.91	1.41	0.11	0.84	−19.64	0.685
mod 7	calfwt$_{t-1}$+calfwt$_{t-2}$+calfwt$_{t-3}$	5	60.11	2.61	0.06	0.9	−22.56	0.521
mod 8	calfwt$_{t-1}$*calfwt$_{t-2}$	5	61.73	4.22	0.03	0.93	−23.36	0.475
mod 2	calfwt$_{t-2}$	3	62.14	4.63	0.02	0.95	−27.21	0.259
mod 6	calfwt$_{t-2}$+calfwt$_{t-3}$	4	62.77	5.27	0.02	0.97	−25.85	0.335
mod 16	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+ calfwt$_{t-2}$:calfwt$_{t-3}$	7	63.98	6.48	0.01	0.97	−19.39	0.699
mod 13	calfwt$_{t-2}$*calfwt$_{t-3}$+calfwt$_{t-1}$	6	64.29	6.79	0.01	0.98	−22.33	0.534
mod 14	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+ calfwt$_{t-1}$:calfwt$_{t-3}$	7	64.47	6.97	0.01	0.99	−19.64	0.685
mod 11	calfwtyrminus1*calfwtyrminus2 +calfwtyrminus3	6	64.73	7.22	0.01	0.99	−22.55	0.521
mod 10	calfwt$_{t-2}$*calfwt$_{t-3}$	5	66.34	8.84	0.00	1.00	−25.67	0.345
mod 3	calfwt$_{t-3}$	3	67.04	9.53	0.00	1.00	−29.66	0.121
mod 15	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+ calfwt$_{t-2}$:calfwt$_{t-3}$	7	69.81	12.30	0.00	1.00	−22.30	0.535
mod 17	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+ calfwt$_{t-1}$:calfwt$_{t-3}$+calfwt$_{t-2}$: calfwt$_{t-3}$	8	70.78	13.27	0.00	1.00	−19.39	0.699
mod 18	calfwt$_{t-1}$*calfwt$_{t-2}$*calfwt$_{t-3}$	9	79.09	21.58	0.00	1.00	−19.29	0.704

[a] Calculated using = 1.20 from model 18.

TABLE 4. Model selection results for predicting parturition rates of 36-month-old caribou from prior 3 years of October calf weights and 4 weather parameters, Fortymile caribou herd, 1993–2010. The “*” symbol equates to additive effects and an interaction between the parameters, and the colon refers to only an interaction between the parameters. “SF” equates to the number of days with <2.54 cm of snow prior to the early winter of conception. “SI” equates to the snow index during the winter prior to parturition. “Temp” equates to the average July temperature prior to conception. “PPT” equates to the total July rainfall prior to conception.

Model	Covariates	Parameters	QAICc^{a}	Delta_QAICc	QAICcWt	Cum. Wt	Quasi.LL	R^2
mod 102	calfwt$_{t-1}$+calfwt$_{t-2}$+SF*Temp	6	61.35	0.00	0.08	0.08	−20.86	0.813
mod 70	calfwt$_{t-1}$+SF+Temp	4	61.50	0.15	0.07	0.15	−25.21	0.609
mod 64	calfwt$_{t-1}$+SF	3	61.53	0.18	0.07	0.22	−26.91	0.530
mod 42	calfwt$_{t-1}$*calfwt$_{t-2}$+SI	5	62.04	0.68	0.06	0.28	−23.52	0.689
mod 9	calfwt$_{t-1}$*calfwt$_{t-3}$	4	62.14	0.79	0.05	0.33	−25.53	0.594
mod 12	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$	5	62.19	0.83	0.05	0.38	−23.59	0.685
mod 85	calfwt$_{t-1}$+calfwt$_{t-2}$+SF	4	62.25	0.90	0.05	0.43	−25.59	0.592
mod 81	calfwt$_{t-1}$+SF*Temp	5	62.62	1.26	0.04	0.48	−23.81	0.675
mod 80	calfwt$_{t-1}$+SF*SI	5	62.85	1.50	0.04	0.51	−23.93	0.669
mod 106	calfwt$_{t-1}$+calfwt$_{t-3}$+SF	4	63.49	2.14	0.03	0.54	−26.21	0.563
mod 43	calfwt$_{t-1}$*calfwt$_{t-3}$+SF	5	63.68	2.33	0.02	0.56	−24.34	0.650
mod 69	calfwt$_{t-1}$+SF+SI	4	63.71	2.36	0.02	0.59	−26.32	0.557
mod 73	calfwt$_{t-1}$+SF+SI+Temp	5	63.78	2.42	0.02	0.61	−24.39	0.648
mod 4	calfwt$_{t-1}$+calfwt$_{t-2}$	3	63.93	2.58	0.02	0.63	−28.11	0.473
mod 91	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+Temp	5	64.13	2.78	0.02	0.65	−24.57	0.639
mod 72	calfwt$_{t-1}$+SF+PPT+Temp	5	64.38	3.03	0.02	0.67	−24.69	0.634
mod 1	calfwt$_{t-1}$	2	64.83	3.47	0.01	0.68	−30.01	0.384
mod 126	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SI	6	64.86	3.50	0.01	0.70	−22.61	0.731
mod 68	calfwt$_{t-1}$+SF+PPT	4	64.88	3.52	0.01	0.71	−26.90	0.530
mod 101	calfwt$_{t-1}$+calfwt$_{t-2}$+SF*SI	6	64.99	3.64	0.01	0.72	−22.68	0.728
mod 5	calfwt$_{t-1}$+calfwt$_{t-3}$	3	65.10	3.75	0.01	0.74	−28.70	0.446
mod 7	calfwt$_{t-1}$+calfwt$_{t-2}$+calfwt$_{t-3}$	4	65.28	3.93	0.01	0.75	−27.10	0.521
mod 127	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF	6	65.33	3.97	0.01	0.76	−22.84	0.720
mod 112	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+Temp	5	65.38	4.03	0.01	0.77	−25.19	0.610
mod 63	calfwt$_{t-1}$+SI	3	65.45	4.09	0.01	0.78	−28.87	0.438
mod 48	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+SI	6	65.64	4.29	0.01	0.79	−23.00	0.713
mod 90	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+SI	5	65.68	4.33	0.01	0.80	−25.34	0.603
mod 124	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+PPT	6	65.68	4.33	0.01	0.81	−23.02	0.712
mod 40	calfwt$_{t-1}$*calfwt$_{t-3}$+PPT	5	65.77	4.42	0.01	0.81	−25.39	0.601
mod 82	calfwt$_{t-1}$+calfwt$_{t-2}$+PPT	4	65.81	4.46	0.01	0.82	−27.37	0.508
mod 105	calfwt$_{t-1}$+calfwt$_{t-3}$+SI	4	65.95	4.60	0.01	0.83	−27.44	0.505
mod 89	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+PPT	5	65.95	4.60	0.01	0.84	−25.48	0.597
mod 111	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+SI	5	66.01	4.66	0.01	0.85	−25.51	0.595
mod 41	calfwt$_{t-1}$*calfwt$_{t-3}$+Temp	5	66.07	4.71	0.01	0.85	−25.53	0.594

Model	Covariates	Parameters	QAICc[a]	Delta_QAICc	QAICcWt	Cum. Wt	Quasi.LL	R^2
mod 16	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+calfwt$_{t-2}$:calfwt$_{t-3}$	6	66.23	4.88	0.01	0.86	−23.30	0.699
mod 122	calfwt$_{t-1}$+calfwt$_{t-3}$+SF*SI	6	66.34	4.99	0.01	0.87	−23.35	0.696
mod 46	calfwt$_{t-1}$*calfwt$_{t-3}$+SI+Temp	6	66.45	5.10	0.01	0.87	−23.41	0.694
mod 84	calfwt$_{t-1}$+calfwt$_{t-2}$+SI	4	66.53	5.18	0.01	0.88	−27.73	0.491
mod 45	calfwt$_{t-1}$*calfwt$_{t-3}$+SI+PPT	6	66.67	5.32	0.01	0.88	−23.52	0.689
mod 125	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+Temp	6	66.78	5.43	0.01	0.89	−23.57	0.686
mod 14	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+calfwt$_{t-1}$:calfwt$_{t-3}$	6	66.82	5.47	0.01	0.89	−23.59	0.685
mod 93	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+PPT+Temp	6	66.99	5.64	0.00	0.90	−23.68	0.681
mod 83	calfwt$_{t-1}$+calfwt$_{t-2}$+Temp	4	67.11	5.76	0.00	0.90	−28.02	0.478
mod 8	calfwt$_{t-1}$*calfwt$_{t-2}$	4	67.21	5.86	0.00	0.91	−28.07	0.475
mod 103	calfwt$_{t-1}$+calfwt$_{t-3}$+PPT	4	67.22	5.87	0.00	0.91	−28.07	0.475
mod 123	calfwt$_{t-1}$+calfwt$_{t-3}$+SF*Temp	6	67.23	5.87	0.00	0.92	−23.79	0.676
mod 61	calfwt$_{t-1}$+PPT	3	67.23	5.88	0.00	0.92	−29.76	0.396
mod 49	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+Temp	6	67.27	5.92	0.00	0.92	−23.82	0.675
mod 62	calfwt$_{t-1}$+Temp	3	67.35	6.00	0.00	0.93	−29.82	0.393
mod 110	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+PPT	5	67.37	6.01	0.00	0.93	−26.18	0.564
mod 59	calfwt$_{t-1}$*calfwt$_{t-3}$+SF*SI	7	67.56	6.20	0.00	0.94	−21.18	0.798
mod 74	calfwt$_{t-1}$+SF+SI+PPT	5	67.58	6.23	0.00	0.94	−26.29	0.559
mod 75	calfwt$_{t-1}$+SF+SI+PPT+Temp	6	67.60	6.25	0.00	0.94	−23.98	0.667
mod 94	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+SI+Temp	6	67.80	6.45	0.00	0.95	−24.08	0.662
mod 86	calfwt$_{t-1}$+calfwt$_{t-2}$+PPT+Temp	5	67.86	6.51	0.00	0.95	−26.43	0.552
mod 79	calfwt$_{t-1}$+SF*PPT	5	67.98	6.63	0.00	0.95	−26.49	0.549
mod 67	calfwt$_{t-1}$+SI+Temp	4	68.04	6.69	0.00	0.95	−28.48	0.456
mod 47	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+PPT	6	68.32	6.97	0.00	0.96	−24.34	0.650
mod 115	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+SI+Temp	6	68.33	6.98	0.00	0.96	−24.35	0.650
mod 104	calfwt$_{t-1}$+calfwt$_{t-3}$+Temp	4	68.47	7.11	0.00	0.96	−28.70	0.446
mod 66	calfwt$_{t-1}$+SI+PPT	4	68.55	7.20	0.00	0.96	−28.74	0.444
mod 13	calfwt$_{t-2}$*calfwt$_{t-3}$+calfwt$_{t-1}$	5	68.65	7.30	0.00	0.97	−26.83	0.534
mod 65	calfwt$_{t-1}$+PPT+Temp	4	68.84	7.48	0.00	0.97	−28.88	0.437
mod 114	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+PPT+Temp	6	68.96	7.61	0.00	0.97	−24.66	0.635
mod 108	calfwt$_{t-1}$+calfwt$_{t-3}$+SI+PPT	5	69.09	7.74	0.00	0.97	−27.04	0.523
mod 11	calfwtyrminus1*calfwtyrminus2+calfwtyrminus3	5	69.18	7.82	0.00	0.97	−27.09	0.521
mod 87	calfwt$_{t-1}$+calfwt$_{t-2}$+SI+PPT	5	69.37	8.02	0.00	0.97	−27.19	0.517
mod 132	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+SI	7	69.46	8.11	0.00	0.98	−22.13	0.754
mod 109	calfwt$_{t-1}$+calfwt$_{t-3}$+SI+Temp	5	69.79	8.44	0.00	0.98	−27.40	0.507
mod 6	calfwt$_{t-2}$+calfwt$_{t-3}$	3	69.82	8.47	0.00	0.98	−31.05	0.335
mod 52	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+SI+Temp	7	69.89	8.54	0.00	0.98	−22.35	0.743
mod 100	calfwt$_{t-1}$+calfwt$_{t-2}$+SF*PPT	6	69.98	8.62	0.00	0.98	−25.17	0.611
mod 129	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SI+PPT	7	70.01	8.66	0.00	0.98	−22.40	0.741
mod 57	calfwt$_{t-1}$*calfwt$_{t-3}$+SI*Temp	7	70.08	8.72	0.00	0.98	−22.44	0.739

Model	Covariates	Parameters	QAICc[a]	Delta_QAICc	QAICcWt	Cum. Wt	Quasi.LL	R^2
mod 88	calfwt$_{t-1}$+calfwt$_{t-2}$+SI+Temp	5	70.10	8.75	0.00	0.98	−27.55	0.500
mod 2	calfwt$_{t-2}$	2	70.19	8.84	0.00	0.98	−32.69	0.259
mod 95	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+SI+PPT	6	70.21	8.86	0.00	0.99	−25.29	0.606
mod 44	calfwt$_{t-1}$*calfwt$_{t-3}$+PPT+Temp	6	70.23	8.88	0.00	0.99	−25.30	0.605
mod 130	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SI+Temp	7	70.39	9.04	0.00	0.99	−22.60	0.732
mod 71	calfwt$_{t-1}$+SI+PPT+Temp	5	70.46	9.11	0.00	0.99	−27.73	0.491
mod 107	calfwt$_{t-1}$+calfwt$_{t-3}$+PPT+Temp	5	70.46	9.11	0.00	0.99	−27.73	0.491
mod 131	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+PPT	7	70.48	9.13	0.00	0.99	−22.64	0.730
mod 133	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+Temp	7	70.58	9.23	0.00	0.99	−22.69	0.727
mod 116	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+SI+PPT	6	70.63	9.28	0.00	0.99	−25.50	0.596
mod 128	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+PPT+Temp	7	70.88	9.53	0.00	0.99	−22.84	0.720
mod 53	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+SI+PPT	7	71.15	9.79	0.00	0.99	−22.97	0.714
mod 78	calfwt$_{t-1}$+SI*Temp	5	71.23	9.87	0.00	0.99	−28.11	0.473
mod 121	calfwt$_{t-1}$+calfwt$_{t-3}$+SF*PPT	6	71.40	10.05	0.00	0.99	−25.88	0.578
mod 143	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF*SI	8	71.66	10.31	0.00	0.99	−19.83	0.861
mod 17	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+calfwt$_{t-1}$:calfwt$_{t-3}$+calfwt$_{t-2}$:calfwt$_{t-3}$	7	71.79	10.44	0.00	0.99	−23.30	0.699
mod 50	calfwt$_{t-1}$*calfwt$_{t-3}$+SI+PPT+Temp	7	71.81	10.46	0.00	0.99	−23.31	0.698
mod 60	calfwt$_{t-1}$*calfwt$_{t-3}$+SF*Temp	7	71.83	10.48	0.00	0.99	−23.32	0.698
mod 96	calfwt$_{t-1}$+calfwt$_{t-2}$+SF+SI+PPT+Temp	7	72.02	10.67	0.00	1.00	−23.41	0.694
mod 56	calfwt$_{t-1}$*calfwt$_{t-3}$+SI*PPT	7	72.09	10.74	0.00	1.00	−23.44	0.692
mod 92	calfwt$_{t-1}$+calfwt$_{t-2}$+SI+PPT+Temp	6	72.11	10.76	0.00	1.00	−26.24	0.561
mod 77	calfwt$_{t-1}$+SI*PPT	5	72.22	10.87	0.00	1.00	−28.61	0.450
mod 97	calfwt$_{t-1}$+calfwt$_{t-2}$+PPT*Temp	6	72.35	11.00	0.00	1.00	−26.36	0.556
mod 51	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+PPT+Temp	7	72.36	11.00	0.00	1.00	−23.58	0.686
mod 76	calfwt$_{t-1}$+PPT*Temp	5	72.70	11.35	0.00	1.00	−28.85	0.439
mod 10	calfwt$_{t-2}$*calfwt$_{t-3}$	4	72.76	11.41	0.00	1.00	−30.84	0.345
mod 113	calfwt$_{t-1}$+calfwt$_{t-3}$+SI+PPT+Temp	6	72.81	11.46	0.00	1.00	−26.59	0.545
mod 117	calfwt$_{t-1}$+calfwt$_{t-3}$+SF+SI+PPT+Temp	7	73.06	11.71	0.00	1.00	−23.93	0.669
mod 144	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF*Temp	8	73.09	11.74	0.00	1.00	−20.54	0.828
mod 120	calfwt$_{t-1}$+calfwt$_{t-3}$+SI*Temp	6	73.17	11.82	0.00	1.00	−26.77	0.536
mod 15	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+calfwt$_{t-2}$:calfwt$_{t-3}$	6	73.23	11.88	0.00	1.00	−26.80	0.535
mod 119	calfwt$_{t-1}$+calfwt$_{t-3}$+SI*PPT	6	73.59	12.24	0.00	1.00	−26.98	0.526
mod 58	calfwt$_{t-1}$*calfwt$_{t-3}$+SF*PPT	7	73.62	12.27	0.00	1.00	−24.21	0.656
mod 98	calfwt$_{t-1}$+calfwt$_{t-2}$+SI*PPT	6	73.99	12.64	0.00	1.00	−27.18	0.517
mod 99	calfwt$_{t-1}$+calfwt$_{t-2}$+SI*Temp	6	74.04	12.69	0.00	1.00	−27.20	0.516
mod 118	calfwt$_{t-1}$+calfwt$_{t-3}$+PPT*Temp	6	74.94	13.59	0.00	1.00	−27.65	0.495
mod 55	calfwt$_{t-1}$*calfwt$_{t-3}$+PPT*Temp	7	75.03	13.68	0.00	1.00	−24.92	0.623
mod 136	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+SI+Temp	8	75.66	14.31	0.00	1.00	−21.83	0.768

Model	Covariates	Parameters	QAICc[a]	Delta_QAICc	QAICcWt	Cum. Wt	Quasi.LL	R^2
mod 141	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SI*Temp	8	75.73	14.38	0.00	1.00	−21.87	0.766
mod 3	calfwt$_{t-3}$	2	76.07	14.72	0.00	1.00	−35.64	0.121
mod 137	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+SI+PPT	8	76.15	14.80	0.00	1.00	−22.08	0.756
mod 135	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+PPT+Temp	8	76.20	14.84	0.00	1.00	−22.10	0.755
mod 140	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SI*PPT	8	76.35	14.99	0.00	1.00	−22.17	0.752
mod 134	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SI+PPT+Temp	8	76.36	15.01	0.00	1.00	−22.18	0.751
mod 54	calfwt$_{t-1}$*calfwt$_{t-3}$+SF+SI+PPT+Temp	8	76.48	15.13	0.00	1.00	−22.24	0.748
mod 142	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF*PPT	8	77.16	15.81	0.00	1.00	−22.58	0.733
mod 38	SF*PPT	4	77.17	15.81	0.00	1.00	−33.04	0.242
mod 139	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+PPT*Temp	8	77.61	16.26	0.00	1.00	−22.81	0.722
mod 18	calfwt$_{t-1}$*calfwt$_{t-2}$*calfwt$_{t-3}$	8	78.36	17.01	0.00	1.00	−23.18	0.704
mod 22	SF	2	78.71	17.36	0.00	1.00	−36.95	0.059
mod 19	PPT	2	79.46	18.10	0.00	1.00	−37.33	0.041
mod 21	SI	2	80.45	19.09	0.00	1.00	−37.82	0.018
mod 27	SF+PPT	3	80.75	19.40	0.00	1.00	−36.52	0.079
mod 20	Temp	2	80.87	19.52	0.00	1.00	−38.04	0.008
mod 26	SF+SI	3	81.31	19.96	0.00	1.00	−36.80	0.066
mod 34	PPT*Temp	4	81.46	20.11	0.00	1.00	−35.19	0.142
mod 28	SF+Temp	3	81.62	20.26	0.00	1.00	−36.95	0.059
mod 24	PPT+SI	3	81.80	20.45	0.00	1.00	−37.04	0.055
mod 23	PPT+Temp	3	82.27	20.91	0.00	1.00	−37.28	0.044
mod 25	Temp+SI	3	83.05	21.69	0.00	1.00	−37.67	0.026
mod 39	SF*Temp	4	83.14	21.78	0.00	1.00	−36.03	0.102
mod 138	calfwt$_{t-1}$*calfwt$_{t-3}$+calfwt$_{t-2}$+SF+SI+PPT+Temp	9	83.51	22.16	0.00	1.00	−21.50	0.783
mod 37	SF*SI	4	83.52	22.16	0.00	1.00	−36.22	0.093
mod 30	PPT+Temp+SF	4	83.73	22.38	0.00	1.00	−36.33	0.088
mod 32	PPT+SI+SF	4	83.83	22.48	0.00	1.00	−36.38	0.086
mod 35	PPT*SI	4	84.64	23.29	0.00	1.00	−36.78	0.067
mod 31	SI+Temp+SF	4	84.66	23.31	0.00	1.00	−36.79	0.067
mod 29	PPT+SI+Temp	4	85.09	23.73	0.00	1.00	−37.00	0.057
mod 36	Temp*SI	4	86.35	25.00	0.00	1.00	−37.64	0.027
mod 33	PPT+SI+Temp+SF	5	87.43	26.08	0.00	1.00	−36.21	0.094
mod 145	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+calfwt$_{t-1}$:calfwt$_{t-3}$+calfwt$_{t-2}$:calfwt$_{t-3}$+SF+SI+PPT+Temp+SF:PPT+SI:PPT+SF:SI	14	204.54	143.18	0.00	1.00	−18.27	0.935
mod 146	calfwt$_{t-1}$*calfwt$_{t-2}$+calfwt$_{t-3}$+calfwt$_{t-1}$:calfwt$_{t-3}$+calfwt$_{t-2}$:calfwt$_{t-3}$+SF+SI+PPT+Temp+SF:PPT+SI:PPT+SF:SI+SF:Temp+SI:Temp	16	611.37	550.01	0.00	1.00	−17.68	0.962

[a] Calculated using = 1.0 from model 145, which had < 1.0 (= 0.97).

TABLE 5. Average female weights at 4 months of age in the Fortymile caribou herd and weather variables, 1990–2011. Weather variables were from Valkenburg et al. (1994) and Boertje et al. (1996).

Year	Average 4-month-old weight (kg)[a]	SE	Total July rainfall (mm)	Average July temperature (C)	Snow index (in)[b]	No. days snow <2.54 cm
1990	52.75	1.155	34	17.3	155	163
1991	53.93	1.372	22	14.9	136	164
1992	55.12	1.679	39	16.2	120	138
1993	56.14	0.857	47	16.4	108	165
1994	54.45	1.232	19	16.9	106	172
1995	56.69	1.183	85	15.4	116	175
1996	54.74	1.404	31	15.9	82	178
1997	59.31	1.288	75	16.6	113	173
1998	53.01	1.313	37	16.8	139	208
1999	54.67	0.974	56	14.8	72	166
2000	56.70	1.140	98	14.7	111	158
2001	54.13	1.128	120	14.6	106	162
2002	52.03	1.312	37	14.9	84	168
2003	51.06	1.019	75	16.2	99	185
2004	53.68	1.624	65	16.8	143	163
2005	51.44	1.315	21	15.3	128	171
2006	54.36	1.827	33	16.2	108	174
2007	53.89	1.059	19	17.8	100	169
2008	47.45	1.273	153	14.2	59	162
2009	48.76	0.973	8	16.3	99	188
2010	54.73	1.296	113	15.3	89	179
2011	50.63	0.956	93	15.7	111	–[c]
Average	53.62		58	15.9	108	171

[a] Sample sizes were 14–18, except in 2011 ($n = 26$).

[b] Snow index was the sum of the Eagle monthly maximum snow depths (in) for November, December, January, February, March, and April (e.g., for 1990, November and December 1989 was combined with January, February, March, and April 1990).

[c] Data not yet available.

TABLE 6. Proportions of radiocollared caribou 36 months of age observed parturient during respective calving seasons in 9 herds[a], Alaska, 1981–2012. We provided annual proportions and sample sizes, as well as 5-year moving weighted averages. When a herd's data stream lapsed for a year, we provided 4-year moving weighted averages. Moving weighted averages are color coded as Green = >55%, Red = <55%, and Blue = 55–60%. All caribou were radiocollared as calves. Sources are listed in Figure 6.

	Denali			Chisana			Porcupine			Fortymile			Central Arctic			Delta			Mulchatna			Nelchina		
Year	%	*n*	5-yr[b]	%	*n*	5-yr[b]	%	*n*	5-yr[b]	%	*n*	5-yr[b]	%	*n*	5-yr[b]	%	*n*	5-yr[b]	%	*n*	5-yr[b]	%	*n*	5-yr[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	30	10	63.5	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	62.1	60	5	71.3[d]				69	13	52.8[e]	60	10	70.0[f]
2011	100	8	94.1					0		67	3	56.1	50	4	66.7[d]				67	3	53.9	0	2	60.0[f]
2012	100	10	93.9					0		62	13	54.0	71	7	61.8[d]				75	15	66.4	25	8	50.0[f]
	89			86			76			72			68			66			48			44		

[a] Data on the Northern Alaska Peninsula herd were gathered only during 1998 and 1999 (= 33%, *n* = 18; Butler 2009).

[b] Column headers labeled "5-yr ” contain 5-year moving weighted averages, except as indicated below.

[c] Delta herd 4-year moving weighted averages are provided during 1987–1991, as *n* = 0 in 1987.

[d] Central Arctic herd 4-year moving weighted averages are provided during 1999, 2000, and 2003–2012, as *n* = 0 in 1996, 2003, and 2008.

[e] Mulchatna herd 4-year moving weighted averages are provided during 2006–2010, as *n* = 0 in 2006.

[f] Nelchina herd 4-year moving weighted averages are provided during 2009–2012, as *n* = 0 in 2009.

TABLE 7. Cumulative multi-year range size, average estimated herd size, and respective caribou densities for 7 study periods, Fortymile caribou herd, 1918–2008, Interior Alaska and adjacent Yukon.

Study period	Range size (km^2)	Herd size	Respective density (caribou/km^2)	Reference
2003–2008	49,593	43,481, average of 6 estimates from Table 2	0.88	This study
1997–2002	50,337	33,784, average of 6 estimates from Table 2	0.67	This study
1992–1996	42,033	22,400, average of 5 estimates from Table 2	0.53	This study
1986–1990	47,940	19,409, average of 5 estimates from Table 2	0.40	Valkenburg et al. (1994)
1980–1985	28,971	11,796, average of 6 estimates from Table 2	0.41	Valkenburg and Davis (1986)
1952–1955	70,551	55,102 derived from Figure 29	0.78	Skoog (1968) for range size only
1918–1924	261,321	261,202 derived from Figure 29	1.00	Murie (1935) for range size only

TABLE 8. Numbers of caribou in 18 Interior Alaska herds during 3 inventories by the Alaska Department of Fish and Game, 1993–2011. Herd numbers were not estimated annually, but each inventory contained the most recent herd estimates.

Interior herds	1993	2002	2011
Beaver Mountains	649	125	70
Chisana	850	300	700
Delta	3,661	2,800	2,985
Denali	1,890	1,900	2,100
Farewell-Big River	750	750	750
Fortymile	21,884	45,000	52,000
Fox River	75	70	75
Galena Mountain	275	400	100
Hodzana	No estimate	No estimate	780
Macomb	500	600	1,300
Mentasta	880	300	350
Nelchina	40,361	35,000	40,233
Rainy Pass	750	1,800	1,500
Ray Mountains	700	2,000	1,370
Sunshine Mountains	800	150	370
Tonzona	800	700	1,000
White Mountains	1,000	750	650
Wolf Mountain	650	600	450

©1996 ADF&G – *Photo by Rodney D. Boertje*. Mounted antenna used to radiotrack collared Fortymile caribou.

©2009 ADF&G – *Photo by Rodney D. Boertje*. Radiotracking flight in June to look for caribou grouping above the treeline, in this case on snowbanks.