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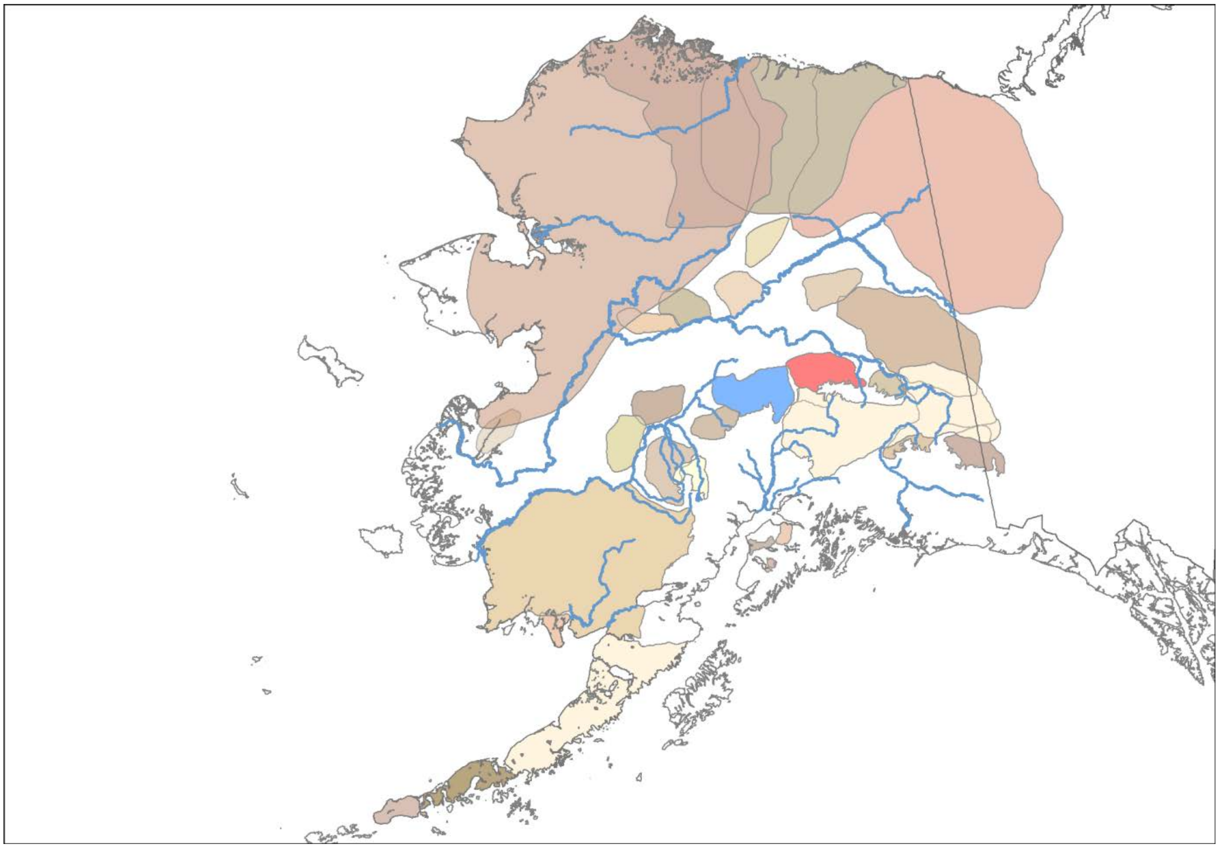

2016

Alaska Department of Fish and Game Division of Wildlife Conservation

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Monitoring caribou herds in Alaska, 1970–2008, with focus on the Delta caribou herd, 1979–2007

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This research was primarily supported by Pittman-Robertson funds from the Federal Aid in Wildlife Restoration program and ADF&G’s Fish and Game Fund. Other funding, including logistical support, came from U.S. Fish and Wildlife Service.

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This wildlife technical bulletin was approved for publication by Scott M. Brainerd, Regional Research Coordinator in Region III for the Division of Wildlife Conservation.

Wildlife technical bulletins are available from Alaska Department of Fish and Game, Division of Wildlife Conservation, PO Box 115526, Juneau, Alaska 99811-5526; phone (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).

Suggested citation:

Valkenburg, P., B. W. Dale, J. L. Davis, M. M. Ellis, R. D. Boertje, M. A. Keech, D. D. Young Jr., R. M. Eagan, R. W. Tobey, C. L. Gardner, R. A. Sellers, L. G. Butler, J. D. Woolington, B. D. Scotton, T. H. Spraker, M. E. McNay, A. R. Aderman, and M. J. Warren. 2016. Monitoring caribou herds in Alaska, 1970–2008, with focus on the Delta caribou herd, 1979–2007. Alaska Department of Fish and Game, Wildlife Technical Bulletin ADF&G/DWC/WTB-2016-16, Juneau.

Cover Photo: Alaska’s caribou herd ranges, with some herds extending into Canada. Delta herd range shown in red.

Preface

The intended audience for this Alaska Department of Fish and Game (ADF&G) wildlife technical bulletin is caribou management biologists, research biologists, policymakers, the Alaska Board of Game, and the Federal Subsistence Board. Most of the funding for the Delta herd studies from 1978 to 2007 came from Federal Aid in Wildlife Restoration with matching funds from Alaska's Fish and Game Fund. The major thrust of the caribou research program at ADF&G has a practical and management-related focus. Although this document is rather technical in nature, portions of it should also be of interest to hunters and people with a general interest in caribou.

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Executive Summary

INTRODUCTION

Following recommendations from a November 1977 international workshop convened to review existing knowledge of caribou (*Rangifer tarandus granti*) ecology, we conducted an intensive long-term monitoring program on the Delta caribou herd in the Central Alaska Range from 1979 to 2007. During the 1980s and 1990s, we subsequently expanded the study with less intensive cooperative monitoring of many other Alaska caribou herds. Cooperating agencies included Alaska Department of Fish and Game, U.S. Fish and Wildlife Service, National Park Service, U.S. Geological Survey, North Slope Borough, and U.S. Department of Defense. In this technical bulletin, we have reviewed data from the Delta caribou herd and other Alaska caribou herds from 1970 to 2008 to help answer central questions identified at the 1977 caribou workshop and other questions about the ecology of Alaska caribou in general.

ORIGINAL STUDY GOALS AND RESEARCH QUESTIONS

Goals for the long-term research project on the Delta caribou herd were to determine the ultimate and proximate causes of population fluctuations in the Delta herd over a relatively long period of time (compared with typical 5-year study plans) by addressing 4 basic questions. Those questions were:

1. Can caribou “herds” be considered “populations” for management purposes, or do mass shifts of caribou from one herd to another influence herd size and management?
2. Are periodically observed low calf numbers (i.e., poor recruitment) in caribou herds most likely the result of low natality rates in females (i.e., resulting from nutritional, density dependent factors, or disease)?
3. What are the major causes of mortality in adult and calf caribou?
4. Is predation on caribou a major limiting factor that can be managed?

METHODS

In the Delta herd, we radiocollared cohorts of female calves in almost every year of the study, measured environmental variables, and closely monitored survival and natality rates, population size, fall calf:cow ratios, and bull:cow ratios. We also conducted similar but less intensive monitoring of many other Alaska herds and we collected (i.e., shot) samples of calves in some larger herds. In the early years of the study, we improved methods for conducting caribou censuses and composition counts statewide and incorporated the improved counts into routine management programs. We also identified some useful indices of individual and herd nutrition in caribou, including estimating proportion of lichens in winter diets and tallying trophy caribou represented in Boone and Crockett records.

Through regression modeling of survival, natality, calf:cow ratio, and body weights of female calves in the Delta herd, we also gained insight about weather variables that may influence caribou population performance.

RESULTS AND CONCLUSIONS

Causes of Population Change in Caribou Herds

We concluded that a high and unsustainable population size (~10,700) and a preponderance of older-aged females in the Delta herd predisposed it to a major decline when 5 severe winters occurred beginning in 1989. The herd was particularly affected by an early and unusually severe winter storm in September 1992. After the severe winters ended in 1994, caribou in the Delta herd were slow to recover their body condition probably because of lingering effects of overgrazing during the population high in the late 1980s.

We identified recruitment of calves as the most variable factor affecting population growth in the Delta caribou herd and other Interior Alaska caribou herds. We found some evidence for some synchrony in population growth and decline in Alaska caribou herds that is likely caused by regional weather patterns, but most weather parameters likely to be significant for caribou proved to be difficult to measure at a scale meaningful for caribou. Even snow depth, a variable that has been widely associated with population performance in ungulates, is difficult to measure in Alaska where climate stations or snow measuring sites are far apart and not necessarily representative of conditions experienced by animals like caribou that move in response to weather conditions.

Grazing pressure on winter and summer ranges, and predation, especially in smaller-sized herds, seemed to act independently or synergistically with weather to modify population growth. We found evidence from Alaska and other areas of arctic North America (particularly Quebec) that natural overgrazing can be a major factor affecting population change in caribou.

Mortality and Survival

In Interior caribou herds, predation by wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and golden eagles (*Aquila chrysaetos*) was the leading cause of low fall calf:cow ratios, but there is strong evidence that environmental factors (either working alone or in concert with density-related factors) predisposed caribou calves to mortality. We also found evidence that pneumonia and hoofrot could have played a role in determining population growth patterns when body condition declined from heavy grazing in the Mulchatna herd. Pneumonia was also recorded in the Northern Alaska Peninsula herd when caribou were in poor condition and body weights of calves were low. Significant outbreaks of hoofrot were also noted in the Western Arctic herd but did not appear likely to have affected population growth.

In Interior caribou herds, predation by wolves was the leading cause of death of adult caribou but age of caribou was a major factor affecting caribou survival. We found that predation, particularly predation by wolves, can potentially be managed to increase harvest in caribou herds, but not all wolf management programs in Alaska have been successful because of political and biological reasons. The biological circumstances under which predator management programs can be successful for caribou are still under investigation and most programs should be considered experimental.

Survival rates proved to be difficult to document in Alaska caribou with the use of VHF radio collars because of the intensity of monitoring required to determine timing and detect cause of death. Often, samples of radiocollared females were too small and radiocollared caribou were not likely to be representative of the age structure.

Patterns of mortality in small- to medium-sized Interior herds appeared to be quite different than mortality patterns in herds in Southwest Alaska and the large Arctic herds. In general, Interior herds experienced high neonatal calf mortality from predation by wolves, grizzly bears, and golden eagles, and had relatively low fall calf:cow ratios when herds were stable (15–30 calves:100 cows). In contrast, during periods of relative stability, herds in Southwest Alaska (Northern Alaska and Southern Alaska Peninsula herds particularly) tended to have low neonatal calf mortality but calf mortality continued at moderate levels throughout the summer, and fall calf:cow ratios in fall were moderate (30–40 calves:100 cows). In the Porcupine herd, neonatal mortality of calves was relatively high and golden eagles were primary predators.

In the Delta herd, regression models identified age and initial weight (calf weight at 4 months of age) as the main covariates affecting survival of radiocollared females. The effects of initial weight continued to influence survival of female caribou up to 40 months of age. For adult females, once age was considered, no other covariates were significant in regression models, but the radiocollared sample of Delta herd females was biased toward younger age classes, and our ability to discern interactions of age and environmental factors was compromised. During the severe winters of the early 1990s, almost all females older than 10 died. The importance of age as a factor affecting survival suggests that “population inertia” must be considered by managers. In other words, periods of caribou population increase with strong cohorts will be followed in later years by periods of high mortality as females from strong cohorts reach and exceed 10 years of age, especially during periods with deep snow winters.

Natality

Intensive radiotracking (particularly in the Delta, Denali, Fortymile, and Nelchina herds during the calving period) has allowed biologists to draw firm conclusions about some aspects of natality in caribou that were previously subject to considerable debate. At least for these Interior caribou, low natality rates were rare, once females reached 4 years of age they consistently produced calves (except in 1993 in the Delta herd following a very unusual year of weather) and there appeared to be no reproductive cost to early reproduction. If Delta caribou produced calves at 24 months of age, they were more likely to keep producing calves in subsequent years than encounter a breeding pause at 36 months of age.

Evidence from large Arctic herds in Canada, wild reindeer herds in Norway, and Alaska caribou indicates there are a variety of factors that cause low calf numbers in fall and these factors act either singly or in various combinations with or without density-dependent factors. If late winter conditions are severe (either from weather conditions like snow or icing and/or overgrazed winter ranges), calves tend to be born later, their birth weights are light, and neonatal survival is relatively poor (primarily because of predation in Interior Alaska herds), resulting in lower fall calf:cow ratios. Similarly, if summer conditions are poor (either from climate, weather, and/or overgrazing combined with the demands of lactation), cows will have lower body weight in fall and a lower probability of becoming pregnant. Lower body weights in fall then reduce the likelihood of reproduction. At extremely high summer densities ($>10/\text{km}^2$), even natality of adults can be severely reduced, but these high densities are most likely in large Arctic herds. It also appears that either summer or winter ranges (or both) can be overgrazed and once overgrazing becomes severe, both natality and calf survival (with or without predation) are affected.

In regression models of natality of radiocollared known-aged Delta herd females that included age and previous pregnancy as fixed effects, various environmental variables (including snow depth, summer rainfall, summer temperature, and 4- or 10-month-old calf weight) explained about 50% of the annual variation in natality rate. Natality did not vary greatly (except in 1993), models were not strongly supported, and many weather variables did a roughly equivalent (and poor) job of explaining variation in natality rates.

Movements, Distribution, Emigration, and Immigration

During the 30+ years of long-term research on the Delta herd and the enhanced monitoring program for caribou statewide, we found no evidence that permanent mass shifts occurred from one herd’s range, or from one region, to another, despite the fact that many herds reached historic high population sizes. We did find evidence for dispersal of small numbers of caribou and we also found that fidelity to calving areas can occasionally break down. At least over the short term (i.e., decades), caribou herds in Alaska can be considered populations and the current management model based on this framework continues to be an appropriate model.

Indices of Nutrition in Caribou

We found that the best indices for monitoring nutritional condition in caribou were 1) measuring live weights of caribou calves at 4 and 10 months of age; 2) measuring natality rates of known-aged young female caribou with radio collars (2-, 3-, and 4-year olds); 3) measuring live weights of newborn calves; and 4) documenting shifts in peak calving dates, although they can be difficult to measure. Some or all of these condition indices should be used in combination with data on calf recruitment (preferably fall calf:cow ratios). To be most useful for managers, techniques for monitoring nutritional condition need to be repeatable and affordable so that data gaps are avoided and data sets are as continuous as possible. The best combination of nutritional indices selected for management purposes will depend on the economic importance of the herd, logistical considerations, cost, and whether the herd is likely to be most limited by winter or summer range. ADF&G has already gradually incorporated much of this information into caribou management programs.

Ecological Differences Across Herd Ranges

During the intensive study and monitoring of the Delta herd and the extensive monitoring of the many other Alaska caribou herds, we noted major ecological differences between caribou herds. This was true across regions and within regions. These herd-specific and regional differences make it difficult to generalize about limiting and/or regulating factors that might apply to all caribou in general, or to all caribou in Alaska. We found evidence that in some herds winter range appeared to be most limiting (Delta and probably Northern Alaska Peninsula), while in other herds (e.g., Nelchina and perhaps Fortymile) weights of calves in fall and natality rates indicated that summer range was most limiting. Other differences we observed included the lack of lichens, absence of golden eagles, and volcanic ash falls (that can increase tooth wear) on the Alaska Peninsula. Rabies that can reduce wolf numbers in coastal areas also has the potential to influence survival of caribou in these areas. We found evidence that some caribou summer ranges are inherently better than others. For example, the summer range of the Fortymile herd is relatively low in elevation, has relatively little alpine, and includes areas of spruce forest and spruce woodland. The herd is likely subject to more insect harassment, may be nutritionally limited in summer, and produces proportionally fewer trophy caribou than most other Interior herds.

Information Needed for Management Decisions

Our understanding of caribou ecology and management options is now sufficiently advanced that informed decisions can be made about management programs that are intended to restore depleted caribou herds or improve caribou harvests. In many cases the information needed to make management decisions (population size, fall composition counts, harvest, and indices of nutritional status) are affordable and can be gathered in a timely manner (a few years) if the information is not already available from ongoing studies.

Optimum Population Size for Caribou Herds

With the improved techniques developed over the last 30+ years for monitoring population parameters and nutritional condition of caribou, it is now possible for managers to make educated guesses about what might constitute an "optimum" sustainable population size for some caribou herds. "Optimum" as used in this context means a population size that can be sustained over the long term with most caribou in reasonably good physical condition, and where harvests will be relatively high, predictable, and sustainable. In most cases, however, actually managing a herd for an "optimum" population size will be difficult because most herds in Alaska are remote and inaccessible and harvest will seldom be sufficient to restrain herd growth in the large, economically important herds (e.g., Mulchatna, Western Arctic, Central Arctic, Porcupine). In the range of the Delta herd, management goals for moose (*Alces alces*) will make it difficult to manage the herd at its optimum size (e.g., Delta). To date in Alaska, only one caribou herd (Nelchina) has been successfully managed at its estimated "optimum" population size. Other economically important herds that in future might practically and advantageously be managed at an "optimum" population size include the Northern Alaska Peninsula, Southern Alaska Peninsula, and Fortymile herds. However, caribou managers should recognize that a strategy of restraining herd growth and maintaining "optimum" population sizes has potential costs. For example, gene flow might be constrained and users living outside normal caribou range may never benefit from occasional irruptions that would allow occasional temporary increases in harvest.

Answers to the Four Original Research Questions

1. For management purposes, caribou herds in Alaska can be considered "populations," but there is a low level of population and genetic exchange between adjacent herds and with enough mixing on seasonal ranges, fidelity to calving areas can occasionally be lost, and large herds can assimilate smaller herds.

2. Low calf numbers were generally caused by poor calf survival as a result of predation in Interior Alaska herds rather than by low natality rates, but natality rate was a factor that had some influence on fall calf:cow ratios.

3. Major causes of mortality of calves in Interior caribou herds were predation by wolves, grizzly bears, and golden eagles, and mortality was concentrated around the neonatal period within 2–3 weeks of birth. In Southwest Alaska, early calf mortality rates were lower but mortality continued to be significant through August. In the Porcupine herd, nonpredation neonatal mortality of calves was considerable in some years and golden eagles were the most important predator of calves. In adult female caribou in the Delta herd, wolf predation was the major cause of death of radiocollared females, but there was a strong interaction with age, and survival declined steadily with age. By age 14 the modeled annual survival rate of females declined to ~50%.

4. Predation on caribou is a major limiting factor, at least in Interior Alaska caribou herds, and predation can be managed to increase harvest of caribou in some circumstances. Not all predator control programs have been successful at increasing harvests and most programs should still be considered experimental.

RECOMMENDATIONS FOR CONTINUED RESEARCH

We recommend continued and new research in the following areas of caribou ecology and management: 1) ecology and movements of male caribou; 2) compensatory hunting mortality in male caribou; 3) regional patterns in population change that result from weather and climate on caribou; 4) genetics of caribou, male-mediated gene flow, and investigation of genetically based morphological differences among caribou in Alaska; 5) the influence of age structure on population change in caribou herds and “population inertia;” 6) the influence of herd mixing on seasonal ranges and dispersal of individual caribou on herd dynamics; and 7) determining rates of wounding loss during caribou hunting, especially in northwest Alaska where motorized vehicles are used to pursue caribou for harvest.

Key Words: Adak, adult mortality, age structure, Alaska, Andreafsky, Beaver Mountains, Big River, calf mortality, calf weight, *Canis lupus*, caribou, caribou regions, Central Arctic, checkstations, Chisana, climate change, compensatory mortality, Delta, Denali, density dependent, disease, fecal pellets, Fortymile, Fox River, Galena Mountain, genetics, Hodzana Hills, hoofrot, hunting, illegal hunting, Kenai Lowlands, Kenai Mountains, Kilbuck, Killey River, lynx, *Lynx canadensis*, Macomb, McKinley, Mentasta, mortality, Mulchatna, natality, Nelchina, North Pacific Oscillation, Northern Alaska Peninsula, Nushagak Peninsula, nutritional condition, Pacific Decadal Oscillation, plant fragments, pneumonia, population growth, population inertia, Porcupine, predation, Rainy Pass, *Rangifer tarandus granti*, Ray Mountains, snow depth, Southern Alaska Peninsula, Sunshine Mountains, survival, Teshekpuk, Tonzona, Unimak, unreported harvest, volcanic ash, weather, Western Arctic, White Mountains, wolf, Wolf Mountain.

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Introduction

CIRCUMSTANCES IN THE 1970S LEADING TO LONG-TERM RESEARCH AND INCREASED MONITORING OF CARIBOU HERDS IN ALASKA

During the early to mid-1970s in Alaska, widespread declines in caribou (*Rangifer tarandus*) numbers resulted in considerable social upheaval as state regulatory authorities (Alaska Department of Fish and Game [ADF&G] and Fish and Game Board [later called Board of Game]) restricted harvest to prevent further population declines, particularly in the Nelchina, Fortymile, Denali (formerly McKinley), Delta, and Western Arctic caribou herds (Fig. 1; Davis 1976a, Davis et al. 1976, Davis and Valkenburg 1978, Davis et al. 1980). It was unclear what had caused caribou declines or if declines were phases of natural fluctuations, and there was considerable debate among biologists (Banfield 1954; Bergerud 1967, 1978; Kelsall 1968; Parker 1972; Miller 1974; Bos 1975; LeResche 1975; Brewer 1976; Dauphiné 1976). Similar caribou declines were reported in the Northwest Territories of Canada for many years (c.f. Banfield 1954; Harper 1955; Kelsall 1960, 1968; Miller 1978); however, hunters, local residents, and even some biologists questioned whether declines in Alaska caribou populations were real, thus compelling biologists in Alaska to conduct more surveys (Davis 1976b). Excessive and wasteful harvest in Canada and Alaska (particularly in the Nelchina, Fortymile, and Western Arctic herds) were found to be a principal factor in the later stages of accelerating caribou declines in some areas and this fact greatly increased the level of controversy (see section *Fieldwork Photos*:photographs 1 and 2) (Banfield 1954; Kelsall 1968; Bos 1975; Davis 1976a; Grauvogel and Pegau 1976:37; Klein 1976; Davis and Valkenburg 1978; Davis et al. 1978; Doerr and Shea 1979).

To promote information exchange, summarize existing knowledge, and help plan for future research, professors D. R. Klein and R. G. White of the Cooperative Wildlife Research Unit and Institute of Arctic Biology at the University of Alaska Fairbanks agreed to organize a symposium and workshop at the University of Alaska in November 1977. This symposium focused on 3 key areas of caribou ecology: 1) nutrition, disease, parasites, and population dynamics; 2) plant-animal relations; and 3) population dynamics and predation (Klein and White 1978). Funding for the symposium and workshop was provided by the Federal-State Land Use Planning Commission, United States Fish and Wildlife Service (USFWS), National Park Service (NPS), and Institute of Arctic Biology (Klein and White 1978). Biologists from Alaska, Canada, and Scandinavia reviewed and discussed existing information and agreed that explanations for caribou population fluctuations were largely speculative and that existing research efforts were inadequate and unlikely to answer critical questions about recruitment, mortality, natality, predation, nutrition, and dispersal (Klein and White 1978). Although there was as much disagreement as there was agreement over priorities for research, a consensus opinion from the workshop was that, in addition to extensive monitoring of basic population parameters in as many herds as possible over the long term (>10 years), intensive research projects were needed on one or more Alaska caribou herds (Klein and White 1978:42–43). Subsequent discussion led to the suggestion of picking one relatively large herd and one smaller herd for intensive long-term research. The herds chosen for these studies were the relatively small and accessible Delta caribou herd in central Alaska and the larger Porcupine caribou herd in northeastern Alaska and adjacent Yukon Territory, Canada (Fig. 1). For other reasons (i.e., to mitigate the effects of

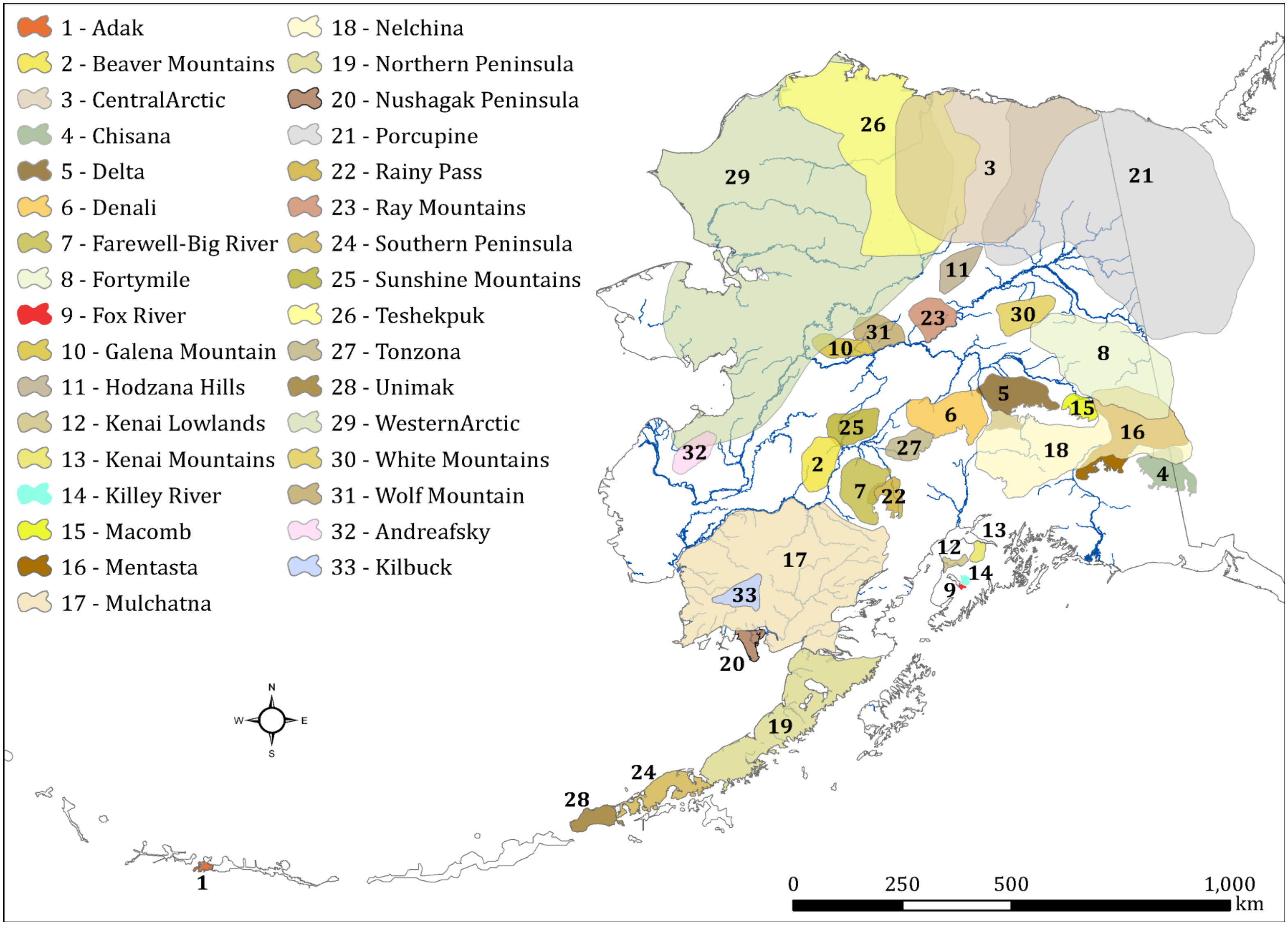


Figure 1. Location map and names of Alaska caribou herds used in this document. The “Yanert” herd is not shown but was entirely within the western portion of the range of the Delta herd.

industrial development), intensive research had already begun on the Central Arctic caribou herd (Fig. 1) (c.f. Cameron and Whitten 1976, Cameron et al. 1986).

Although ADF&G had already begun expanding its caribou research program in response to declining caribou herds, increasing industrial development, and planned federal lands legislation (i.e., Alaska National Interest Lands Conservation Act), ADF&G biologists and policymakers largely agreed with the recommendations for new research from the 1977 workshop, especially in the areas of population dynamics, predation, improving techniques for measuring population parameters, and increasing monitoring of all caribou herds (c.f. Davis and Valkenburg 1978, 1979; Davis et al. 1978, Davis et al. 1982, Davis et al. 1988). ADF&G leadership also agreed on the need for long-term research in response to caribou declines. Therefore, in early 1978, immediately following the 1977 conference and workshop, ADF&G embarked on a major effort to improve techniques for monitoring population size, population identity, recruitment, and mortality in all of Alaska's caribou herds with an intensive focus on the Delta herd (Davis and Preston 1980, Davis and Valkenburg 1981, Valkenburg et al. 1985, Davis and Valkenburg 1985b). The intensive research on the Delta herd began in January 1979 when radio collars were first deployed in the herd. Other similar long-term and short-term intensive research projects were eventually initiated jointly by ADF&G and USFWS on the Porcupine caribou herd as proposals for oil development provided funding for research (c.f. Fancy and Whitten 1991; Whitten et al. 1992; Fancy et al. 1994; Whitten 1995a,b) and by NPS and U.S. Geological Survey (USGS) on the Denali, Tonzona, and Mentasta caribou herds in the early 1980s and 1990s (c.f. Adams et al. 1995a, 1995b, 1998a, 1998b; Del Vecchio et al. 1995; Barten et al. 2001; Jenkins and Barten 2005). By 1979 the northern region (i.e., Region III) of ADF&G had 6 staff positions dedicated to caribou research and there was close collaboration with all area management biologists within the region. In addition to the Delta herd project, ADF&G also initiated a separate intensive monitoring study and then a 9-year series of calf mortality studies on the Fortymile herd (Valkenburg and Davis 1986; Valkenburg et al. 1994; Valkenburg 1997; Boertje and Gardner 1999, 2000a, 2001). ADF&G, NPS, and USGS biologists also collaborated with professors at the University of Alaska–Institute of Arctic Biology and Cooperative Wildlife Research Unit (primarily R. G. White, D. R. Klein, and R. T. Bowyer) and with many graduate students in studying various aspects of caribou ecology, including winter feeding behavior of Western Arctic caribou (Thing 1977, Shea 1979), nutritional ecology of the Denali herd (Boertje 1981), patterns of activity of migrating caribou (Duquette 1984), energy budgets of caribou (Fancy 1986), winter range use of the Delta herd (Fleischman 1990), nutrient partitioning in caribou and reindeer (Allaye-Chan 1991), influence of weather on movements and migration of caribou (Eastland 1991), nutritional and reproductive ecology (Gerhart 1995), foraging ecology and social dynamics (Post 1995), effects of weather and parasitic insects on behavior of caribou in the Central Arctic and Delta herds (Dau 1986, Mörschel 1996, Mörschel and Klein 1997), habitat use by female caribou in the Mentasta herd (Barten et al. 2001, Jenkins and Barten 2005), habitat selection by calving caribou in the Western Arctic and Teshekpuk herds (Kelleyhouse 2001), and effects of summer weather on the Chisana herd (Lenart 1997, Lenart et al. 2002).

Collaborative efforts among research and management biologists in ADF&G were eventually expanded outside the Interior region to include the Western Arctic caribou herd in 1992 (previously the subject of intensive study during 1976–1982; Davis and Valkenburg 1978, Davis et al. 1980, Davis et al. 1985a, Valkenburg et al. 1996b); Nelchina herd in 1994; the 5 recognized caribou herds in Southwest Alaska in 1995 (Kilbuck was no longer recognized) (Valkenburg et al. 2002, Keech and Valkenburg 2007); and caribou herds on the Kenai Peninsula in 1996 (Spraker 2001) (Appendices A and B). Other projects to monitor individual caribou herds were initiated by several USFWS refuges in Alaska in cooperation with ADF&G (Mulchatna and Kilbuck – Hinkes 1989, Hinkes and Van Daele 1996, Hinkes et al. 2005; Galena Mountain – Saperstein 1997; Northern Alaska Peninsula, Southern Alaska Peninsula, and Unimak – Sellers et al. 1998a, 1998b, 1999, 2003; Nushagak – Aderman and Woolington 2001) and also with the Bureau of Land Management (BLM) in cooperation with ADF&G on the Teshekpuk (P. Reynolds, BLM files, Fairbanks), Fortymile, and White Mountains herds (Robinson 1985, Durtsche and Hobgood 1990).

We report here the results of intensive population monitoring of the dynamics of the Delta caribou herd from 1979 to 2007, and the similar but less intensive monitoring of other Alaska caribou herds by ADF&G and cooperators from 1970 to 2008. Although data from other Alaska herds may not be immediately relevant to the Delta herd, much of these data are certainly relevant to the larger subject of why and how caribou numbers fluctuate. As this technical bulletin was being written (2014–2016), we realized that there have been many interesting changes in movements and distribution, as well as mixing and dispersal of caribou (notably in the Central Arctic, Delta, Fortymile, Porcupine, and Teshekpuk herds) between 2008 and the present. These new developments present an opportunity for biologists to further our collective knowledge of caribou ecology and their findings, and will certainly help to test, support, or perhaps refute some of our conclusions and hypotheses. We have tried to include, as much as possible, results of all of the collaborative efforts of research and management biologists from many agencies to coordinate data collection on caribou demographics and nutrition throughout Alaska during 1980–2008. Synchronous population data from other Alaska caribou herds proved useful in interpreting results of the intensive study of the Delta herd. Further, we believe that caribou biologists in general would benefit from the synthesis of historical data and data gathered for routine management programs and unpublished agency studies from other Alaska caribou herds. Much of these data were scattered in a variety of sources using different formats and were difficult to obtain. During the 1970s and 1980s, management reports were extremely brief and much valuable information remained in office files and internal memos and some reports have since been lost (e.g., in an office fire in McGrath). Since ~1990, the biennial ADF&G management reports have become a valuable and much more reliable source of information.

WHAT BIOLOGISTS KNEW ABOUT CARIBOU POPULATION DYNAMICS IN THE MID-1970S

Because caribou are distributed across vast roadless areas of the circumpolar north, studying movements, distribution, and abundance effectively was difficult until the use of aircraft became widespread in the north following World War II (Scott et al. 1950, Banfield 1954, Skoog 1956, Watson and Scott 1956, Siniff and Skoog 1964, Skoog 1968, Valkenburg 2001). Even during the late 1960s, more than 20 years after aircraft became commonly used for wildlife surveys, the delineation of caribou populations (i.e., herds) was rudimentary and many herds that existed were not recognized (Skoog 1968, Hemming 1971). Biologists still lacked the ability to follow individual animals and to accurately estimate caribou numbers, and money for research and monitoring was scarce, particularly for remote herds (Skoog 1968, Klein and White 1978, Valkenburg 2001). For example, immediately after the State of Alaska assumed responsibility for managing wildlife (except migratory birds) in 1960, funding was limited and the increasing human population along the road system shifted management focus from remote caribou herds to more accessible moose (*Alces alces*) populations (Valkenburg 2001). For approximately 12 years (1963–1974) there was relatively little research and monitoring done on caribou in Alaska. Thus, when the major Alaska caribou declines occurred during the early 1970s, biologists' understanding of population dynamics remained largely conjectural.

During the mid-1970s there were major disagreements among biologists over the definition of a caribou "population." Some biologists believed that mass movements of caribou from one herd's range to another (including calving ranges) could be expected, especially when populations were high. Therefore, they believed the term "population" should be reserved to describe all caribou in Alaska, rather than "population" being used to describe individual herds (i.e., groups of caribou that shared a common and exclusive calving area) (c.f. Skoog 1968, Hemming 1971, LeResche 1975, Burch 2012).

Another major area of debate concerned the role of nutrition versus predation, especially in determining the upper limits of herd size (Bergerud 1978, Klein and White 1978, Valkenburg 2001). Further, most biologists agreed that mechanisms of population regulation and limitation could vary between small primarily sedentary herds and large migratory herds.

A major step forward in understanding caribou population dynamics was the development of an accurate method of counting caribou using aerial photography (Hemming and Glenn 1968). However, it was relatively expensive and logistically difficult to conduct on more than one major herd per year because it required the use of BLM or contracted photography aircraft, and there were remaining questions about the underlying assumptions of the extrapolations used to derive the final estimate after photography was completed (Davis et al. 1979, Valkenburg et al. 1985). Additionally, the continuing problem of not being able to follow individual animals also needed to be addressed. Therefore, ADF&G biologists decided to conduct long-term research on at least one small herd and at least one large herd, ultimately leading to research on the Delta herd that began in 1978.

GOALS AND DEVELOPMENT OF THE LONG-TERM RESEARCH PROJECT ON THE DELTA CARIBOU HERD

The goals for the long-term research project on the Delta caribou herd were to determine the ultimate and proximate causes of population fluctuations in the Delta herd over a relatively long period of time (compared with typical 5-year study plans) by addressing 4 basic questions. These were 1) can caribou "herds" be considered "populations" for management purposes, or do mass shifts of caribou from one herd to another influence herd size and management; 2) are periodically observed low calf numbers (i.e., poor recruitment) in caribou herds most likely the result of low natality rates in females (i.e., resulting from nutritional, or density-dependent factors, including disease); 3) what are the major causes of mortality in adult and calf caribou; and 4) is predation a major limiting factor on caribou that can be managed? To answer these questions we planned to evaluate the influence of weather, density, food limitation, hunting, predation, and emigration and immigration on the population dynamics of the Delta herd. We also realized that to accomplish these goals it would be necessary to develop reliable radio collars and to establish an annual program of radiocollaring and population monitoring in the Delta herd and surrounding herds.

An important consideration in designing the new long-term research program on the Delta herd was that all of Alaska's caribou herds were near historic lows during the mid-1970s and would likely take many years before studying population processes in herds at high density would be possible. We also realized that a long-term view was needed and that conclusions drawn early in the studies on one caribou herd might not be applicable to other herds. Although the focus of the research was to be on the Delta herd, we also wanted to collect relevant comparative data from other caribou herds to help interpret data from the Delta herd and more efficiently find answers to basic research questions that might not be forthcoming in the Delta herd alone.

We realized that developing a reliable radio collar with a life of at least 3 years and a range of at least 10 miles would be critical to the success of long-term Delta caribou research. We worked with Telonics, Inc. (Mesa, Arizona) to develop a suitable radio collar. The first improved radio collar design became available in January 1979.

We did not have a set study duration in mind in 1978, but hoped to continue the intensive research long enough to address the 4 major questions listed above. To be effective, the research would extend longer than the career of a single principal investigator and we envisioned and established an apprenticeship program that would help maintain focus and continuity.

The development of long-term research on the Delta herd (including other herds) was an "adaptive" process with changing priorities, budget requests, and geographic areas of interest. However, annual monitoring of basic population parameters in the Delta herd and other herds was consistent and we used the improved population monitoring methods developed after 1980. These basic parameters included population size, recruitment, age-specific natality, and mortality rates of radiocollared females, as well as harvest, distribution, and dispersal of radiocollared caribou. Part of the "adaptive" process also included incorporating new techniques and new knowledge as they became available.

Blood collections, which included blood serum, blood clots, and whole blood collected by ADF&G, USFWS, USGS, NPS, and BLM, were coordinated by R. Zarnke (1978–2002) and K. Beckmen (2002–2008) through the Fairbanks office of ADF&G. These collections provided material for disease screening and research and genetic research as well (c.f. Røed and Whitten 1986; Cronin et al. 1995, 2005, 2006; Zarnke 1996, 2000; Zittlau et al. 2000; Zittlau 2004; Beckmen 2014; Colson et al. 2014; Mager et al. 2014).

With all long-term research, deciding when to summarize work is always a concern and it is tempting to gather "just a few more years" of data before writing up the study. Technically speaking, the originally envisioned long-term research project on the Delta herd formally ended with the completion of a detailed final research report and the retirement of the senior author (and second principal investigator) in 2003 (Valkenburg et al. 2002). However, after 2003, much of the same data continued to be collected under a separate research project that included several caribou herds in Interior and Southwest Alaska (Keech and Valkenburg 2007, Harper 2011). In addition, sampling protocols developed during the 1990s were incorporated into routine caribou management activities and continued to provide data useful in testing hypotheses and answering questions that were goals of the original long-term Delta herd research (Healy 2003; Brown 2005; Harper 2009, 2011). Thus, we decided to include the entire period from 1970 through 2008 in this wildlife technical bulletin, and we also present historical data from as early as 1970. After 2007, the research and monitoring effort on the Delta herd declined due to shifting priorities.

We elected to publish the results of these 30 years of research and monitoring on the Delta herd and other caribou herds in the form of an ADF&G wildlife technical bulletin so that we could include as much detailed information on Alaska caribou as possible. We were particularly interested in making detailed information available in the form of large tables and appendices that might not otherwise be accepted in technical journals or monographs. We believe these detailed data will be most useful as a reference for Alaska caribou managers, hunters, ethnohistorians, and others who have contributed so much over the years to caribou ecology, conservation, and management.

THE DELTA CARIBOU HERD PRIOR TO 1978

Currently, the Delta herd is one of Alaska's 33 recognized caribou herds (Fig. 1). Caribou in this area of the central Alaska Range were first recognized by biologists as possibly being a separate herd in the late 1940s and their winter numbers were initially estimated at 300 caribou in 1949 (Scott et al. 1950). Subsequently, Olson (1957) estimated caribou numbers on the "north slopes of the Alaska Range" in winter at 1,000–1,500. However, Siniff and Skoog (1964) demonstrated that initial winter estimates were likely biased low. Both Skoog (1968:285) and Hemming (1971) speculated that the Delta herd was a "remnant" or "relic" population left from autumn movements of the Fortymile herd between 1918 and 1932 when that herd was large and ranged over much of eastern Interior Alaska and western Yukon. The origin of the Delta herd is actually unknown and it appears just as likely that a population of sedentary caribou resided in the area prior to the increase of the Fortymile herd. Frank Glazer, for example, reported that caribou were "resident" in the vicinity of Black Rapids during his market hunting days prior to the completion of the Alaska Railroad in 1923 (Rearden 1998). Confusion about the identity and ranges of caribou herds in the central and eastern Alaska Range continued until the early 1970s. For example, Hemming (1971) used a different description for the ranges of the Delta and Mentasta herds than Skoog (1968), and neither recognized the existence of the Macomb caribou herd between the Richardson Highway and the Robertson River (Fig. 2).

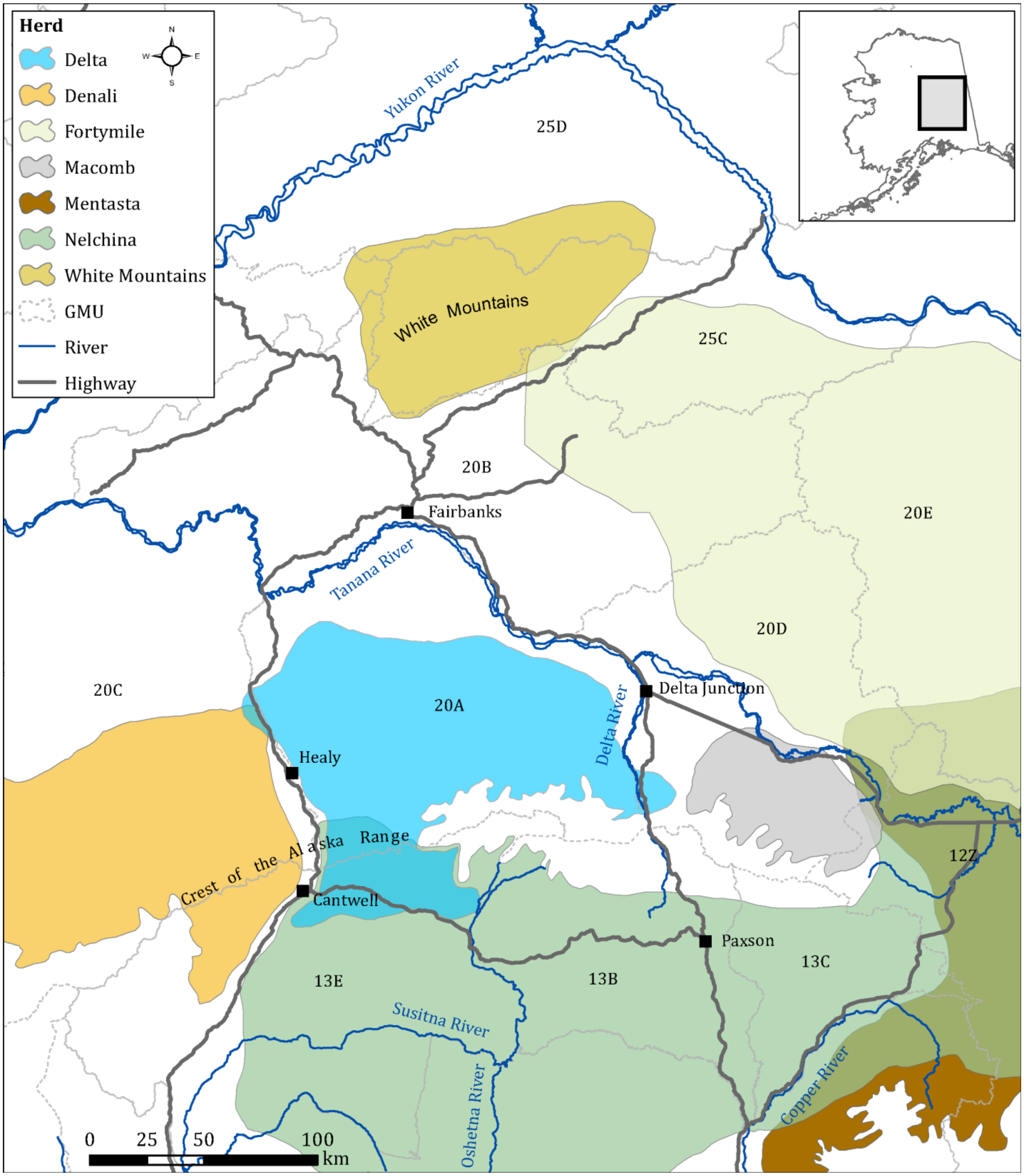


Figure 2. Map of the location of the Delta caribou herd, Alaska, and its nearest neighbors.

ADF&G biologists first counted the Delta herd in 1973 using the new aerial photo-direct count-extrapolation (APDCE) technique (Hemming and Glenn 1968, Buchholtz 1974), and autumn composition counts on the Delta caribou were conducted annually from 1969 through 1977 (except in 1975) (Table 1). In addition, between October 1966 and March 1968, 205 Delta herd caribou were captured and marked with metal ear tags and plastic ear streamers in a cooperative study with the University of Oklahoma and U.S. Army (Army Project 1577) (Hemming 1971). Many marked caribou were subsequently observed by biologists and hunters but none were ever reported outside the “normal” range of the Delta herd (i.e., east of the Delta River, west of the Nenana River, north of the foothills of the Alaska Range, or south of the Alaska Range; Hemming 1971).

The Delta herd likely increased during the late 1950s and early 1960s. Skoog (1968) speculated that much of this increase may have been the result of “ingress” from either the Denali herd or the Nelchina herd into the Yanert River drainage (Fig. 2). In addition, poisoning and aerial shooting of wolves (*Canis lupus*) occurred from 1954 through 1960 and may have resulted in increased caribou numbers; however, no data were collected to assess the effects of this wolf control (Gasaway et al. 1983b, National Research Council 1997). By the time of the first rigorous summer population estimate in 1963 there were ~5,000 adult caribou (probably about 7,000 caribou, including calves) in the central Alaska Range between the Alaska Railroad and the Robertson River (i.e., within the present day ranges of the Delta and Macomb herds; Skoog 1968). From 1963 to 1970 the Delta herd likely remained stable (Skoog 1968, Gasaway et al. 1983b). The Delta herd declined rapidly during the early 1970s based on both the first APDCE estimate of 2,800 caribou (including calves) in July 1973 and autumn composition counts (Table 1). Herds in most other parts of Alaska also declined rapidly during this period (Davis 1978, Gasaway et al. 1983b).

Although purported caribou declines in Alaska continued to be debated by the public and the possible causes of documented declines continued to be debated by biologists, results of the 1973 census of the Delta herd left no doubt that there were several thousand fewer caribou in the central Alaska Range than there had been in 1963. Calf numbers seen during fall composition counts also indicated that recruitment was low and that the decline was continuing (Table 1). Debate among biologists then centered on whether the cause of continuing low calf numbers was poor calf production (i.e., low natality) or high calf mortality from birth through September. This debate was seemingly resolved (at least temporarily) when biologists conducted surveys for distended udders (Bergerud 1964) and found that a high proportion of females in the Delta herd were parturient during late May 1974 and 1975 (J. L. Davis, Wildlife Biologist, ADF&G personal observations), indicating that low calf:cow ratios in fall were not caused by low natality.

After a short delay because of litigation, wolf control, primarily to benefit the concurrently declining moose population, was implemented within the range of the Delta herd in winter 1975–1976 and both moose and caribou numbers increased rapidly thereafter (Gasaway et al. 1983b, Harbo and Dean 1983, Boertje et al. 1996, National Research Council 1997). Therefore, the Delta caribou herd was at a relatively low size but increasing rapidly at the beginning of this study in 1978 while all of the surrounding herds were at relatively low sizes and stable (Davis 1978, Gasaway et al. 1983b).

Table 1. Results of fall composition counts and estimates of population size in the Delta caribou herd, Alaska, 1969–2007.

Approximate survey date	Bulls:100 Cows	Running 3-YearBull:100	Calves: 100 Cows	Calves %	Cows %	Small bulls % of bulls	Medium bulls % of bulls	Large bulls % of bulls	Total bulls %	Composition sample size	Count of herd size[a]	Sampling fraction (%)
13–15 Oct 1969	40	49	28	15	53				21	777		
21–23 Oct 1970	77	46	34	14	43				33	896		
29–31 Oct 1971	29	30	15	10	65				19	1,139		
27–31 Oct 1972	33	30	11	7	67				22	1,185		
23–24 Oct 1973	29	32	10	7	70				20	1,050	2,804	
23–25 Oct 1974	28	33	2	1	76				21	1,141		
1975[b]												
29–31 Oct 1976	38	49	45	24	54				21	1,055		
26–31 Oct 1977	33	49	42	23	55				18	1,365		
26 Oct 1978	75	66	39	17	45				33	725	3,200	23
7 Dec 1979	39	57	65	32	49				19	361	4,191	9
25 Oct 1980	85	58	49	21	43				36	1,369	4,478	31
2 Oct 1981	46	41	41	22	53	47	3	50	25	1,451	4,962	29
8 Oct 1982	42	40	31	18	58	48	4	48	24	1,565	7,335	21
4 Oct 1983	35	42	46	25	55	59	6	36	20	1,208	6,969	17
17 Oct 1984	42	44	36	20	56	28	32	40	24	1,093	6,260	17
9–12 Oct 1985	49	41	36	20	54	57	24	19	26	1,164	8,083	14
22 Oct 1986	41	35	29	17	59	49	30	21	24	1,934	7,804[c]	25
5 Oct 1987	32	31	31	19	61	53	23	24	20	1,682	8,380	20
14 Oct 1988	33	33	35	21	60	50	38	12	20	3,003	8,535	35
10 Oct 1989	27	31	36	22	62	64	28	7	16	1,965	10,690	18
4 Oct 1990	38	31	17	11	65	45	39	16	24	2,411	8,700	28
1 Oct 1991	29	30	8	6	73	55	29	16	21	1,705	5,755	30
28 Sep 1992	25	29	11	8	74	46	43	11	19	1,240	5,877	21
25 Sep 1993	36	28	5	3	72	45	33	22	25	1,525	3,661	42
3–4 Oct 1994	25	26	23	16	68	33	29	39	17	2,131	4,341	49
3 Oct 1995	24	27	20	14	69	41	19	40	17	1,567	4,646	34
3 Oct 1996	30	34	21	14	66	51	20	29	20	1,532	4,019	38
27 Sep 1997	27	38	18	13	69	48	20	32	18	1,598	3,699	43
1 Oct 1998	44	45	16	10	62	31	49	20	27	1,519	3,829	40
1 Oct 1999	44	43	19	11	62	37	40	23	27	674	3,227	21
3–4 Oct 2000	46	45	11	7	64	41	37	22	30	1,010	3,227	31
30 Sep 2001	39	42	13	8	66	46	30	24	26	1,378	2,950	47
28 Sep 2002	50	49	25	14	57	43	23	34	29	924		

Approximate survey date	Bulls:100 Cows	Running 3-YearBull:100	Calves: 100 Cows	Calves %	Cows %	Small bulls % of bulls	Medium bulls % of bulls	Large bulls % of bulls	Total bulls %	Composition sample size	Count of herd size[a]	Sampling fraction (%)
6–7 Oct 2003	37	45	20	13	64	32	39	29	23	1,023	2,581	40
29 Sep 2004	49	45	35	19	54	29	42	29	27	1,267	2,211	57
26 Sep 2005	50	46	33	18	55	28	49	23	27	1,182		
5, 15 Oct 2006	40	42	27	16	60	45	36	19	24	1,022		
8 Oct 2007	35		24	15	63	21	48	30	22	719	2,985	24

[a] All counts presented here of the Delta herd were summer (late June-early July) censuses (complete counts) without extrapolation, except the 1973 count which was a fall estimate that included extrapolation for missing bulls and summer calf survival (i.e., an APDCE estimate based on the summer census. All counts of the Delta herd include the “Yanert” herd.

[b] No survey.

[c] Yanert herd no longer distinguishable from 1986 onwards.

Study Area for the Delta Herd

Between 1978 and 2007, the Delta caribou herd ranged over an 8,000–14,000 km^2 area in the central Alaska Range and adjacent Tanana Flats, including most of Game Management Unit (GMU) 20A, western GMU 20D, and northern GMU 13E (Fig. 3). The area is physiographically diverse and includes lowlands dominated by white and black spruce (*Picea glauca* and *Picea mariana*), western larch (*Larix laricina*), paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*) from 200 m to 500 m in elevation. The foothills of the Alaska Range are dominated by low shrubs (*Alnus crispa*, *Betula nana*, *Betula glandulosa*, *Vaccinium* spp., and *Salix* spp.) at elevations of 500–1,000 m, and areas of mountain tundra dominated by sedges (primarily *Eriophorum vaginatum*), mountain avens (*Dryas* spp.), lowbush cranberry (lingonberry) (*Vaccinium vitis-idaea*), and bearberry (*Arctostaphylos* spp.) at elevations of 1,000–1,500 m. Snow depth varied considerably among years and caribou winter ranges within the study area, but maximum snow depth during winter in most areas was <1.5 m. Winter (1 October–30 April) temperatures were rarely above freezing but only occasionally were <−40°C. Summer (1 June–31 August) temperatures were rarely below freezing during the day and seldom >25°C.

The range of the Delta herd is adjacent to the ranges of 3 other currently recognized caribou herds; including Denali to the west, Nelchina to the south, and Macomb to the east (Fig. 1). In addition, the Delta herd is separated by a distance of ~100 km from the White Mountains herd to the north and by ~50 km from the Fortymile herd to the northeast (Fig. 2). Two other groups of caribou existed as discreet populations (herds) for short periods of time within or adjacent to the range of the Delta herd. We discuss these caribou groups and herds and how they interacted with the Delta herd in the section *Emigration-Immigration*.

Methods

OVERVIEW

The major focus of the study was to collect detailed information on the Delta herd. Specifically, this included monitoring basic population parameters: population size, recruitment and sex ratio, emigration-immigration, and harvest. We also focused on detailed studies of mortality and natality. In addition, we documented population distribution annually during the calving, summer, and winter periods, and we gathered available information collected by other biologists on wolf and moose numbers within the range of the Delta herd.

We realized the importance of monitoring herd size and movements of those herds surrounding the Delta herd and the greater benefits to management that would accrue from monitoring population size and trend and recruitment in as many Alaska caribou herds as possible. These objectives coincided with a general realization that all of the economically important caribou herds in Alaska needed more attention for adequate harvest management. We therefore worked closely with most ADF&G area biologists (who had responsibility for managing caribou herds) as well as biologists in other agencies. In many respects, the study became essentially statewide in nature and included almost all of the caribou herds in Alaska. Many of the authors of this technical bulletin were also involved in separate caribou research projects on the Denali, Central

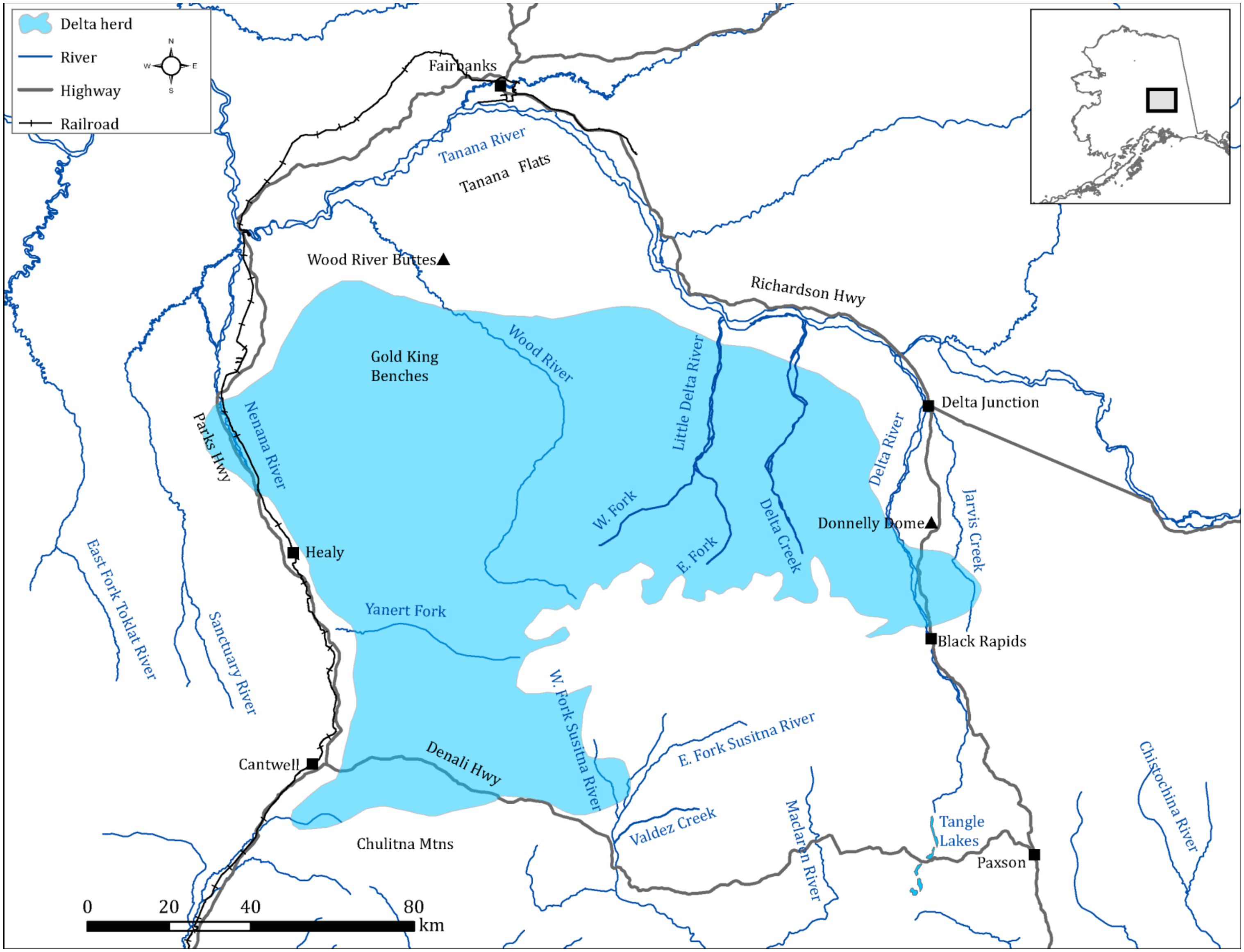


Figure 3. Detail of maximum extent of range of the Delta caribou herd, Alaska, 1970–2008 (except for 1992–1993).

Arctic, and Porcupine herds. Obviously, some caribou herds received more attention than others, depending on their management and research importance, ease of access, and available funding.

To facilitate accurate measurement of population parameters and population distribution in the Delta herd, we realized the need for radiocollared caribou, especially females. We deployed the first batch of radio collars on 8- and 10-month-old male and female calves in January and March 1979. It was apparent that caribou calf survival was high, likely because of the ongoing wolf control program (Davis and Valkenburg 1981, Gasaway et al. 1983b). Based on the success of collaring female calves in 1979, the discovery that females of that age could safely carry a relatively large radio collar (Telonics Model 500), and our desire to obtain age-specific birth and death rates, we refined the collaring protocol and began collaring cohorts of female calves in early April, annually starting in 1981. We also decided at that point to try to maintain collars on the known-aged females for as much of their lives as possible so that we could gather information on age-specific survival and birth rates.

Over the course of the study, as information accrued and better techniques were developed, the study became very much an “adaptive” research project. A good example of this occurred in 1991, when we realized that 4-month-old calves were capable of carrying an adult-sized collar (Telonics Model 600), thus enabling us to radiocollar female calves at both 4 months of age as well as at 10 months of age. This change in approach was implemented because, by weighing cohorts of calves at both 4 months and 10 months of age, we could get information on survival and weight loss (or gain) of calves over their first winter. We also wanted a more direct measure of how nutrition during a calf’s first summer of life affected its subsequent survival and reproduction. We also were beginning to realize how difficult it was to directly measure range conditions or determine the influence of environmental variables on survival and reproduction. It was becoming apparent that weights of calves at 10 months of age had the potential to integrate many environmental variables and we hoped that weights of calves at 4 months of age would provide even more information in this regard.

DEMOGRAPHIC MONITORING

Population Size in the Delta Herd and Other Caribou Herds

We counted the number of caribou within the range of the Delta herd annually during 12 June–17 July from 1979 through 2007, except 2002, 2005, and 2006, when no censuses were completed. In April 1981 we collared 8 caribou in the Yanert drainage and we were able to document that 7 of the 8 calved in the Yanert or upper Wood River drainages, indicating the possibility that 2 separate caribou herds occupied GMU 20A. During late June 1981 the Yanert River drainage was included in the annual caribou census for the first time. In 1982 we again made a concerted effort to find and count all of the caribou in the Yanert drainage and this was the first complete census of caribou in the drainage. In 1983 the Delta and Yanert caribou again spent the calving and postcalving periods apart and were counted separately during the census in late June. During the late June censuses in 1984 through 1986, the distribution of Yanert and Delta radios partially or wholly overlapped and it was not possible to accurately estimate each herd separately. In 1987 the June–July distribution of the Yanert and Delta radios overlapped again and the 2 herds were also mixed during the rut. Population counts and estimates for the

Delta herd that were used for demographic analyses and modeling include all caribou found within the greater range of the Delta herd, including “Yanert” herd caribou.

We conducted all caribou censuses in the Delta herd from 1979 through 2007 using aerial photography of larger groups (>200 caribou) with no extrapolation for caribou missing from postcalving aggregations. Beginning in 1976 in the Central Arctic herd and 1979–1982 in several herds, radiocollared caribou (primarily cows) were used to find major aggregations during late June or early July once conditions became suitable (warm, calm weather with high insect numbers). Once the major aggregations were photographed, we used from 3 to 6 aircraft to search all of the treeless areas of the Delta herd's range for smaller groups of caribou that were not with the main aggregations. We did not search forested areas because radiocollared caribou from the Delta herd or other herds monitored in Alaska were seldom found in forested areas during summer. All aircraft were equipped with radiotracking gear and we tried to account for all radiocollared caribou that had been alive during the calving period or had been located during pre-census reconnaissance flights. At least 95% of all radiocollared caribou were located in censuses. In most instances, radiocollared caribou that were not located were later found to be dead, confirmed to have failed transmitters, or were errors on radiotracking forms. In a few cases (<6 total over 30 years), radiocollared caribou were found to have dispersed away from the herd. Most of the photography was done with 35 mm handheld cameras using color print film, but in some years we used ADF&G's de Havilland Beaver with belly-mounted Fairchild T-11 (1978–1991) or Zeiss RMK-A (1992–2008) aerial mapping cameras with 9-inch black and white film (Davis et al. 1979, Valkenburg et al. 1985). Experience eventually allowed us to develop a rule-of-thumb for the Delta herd that if the temperature at 5,000 ft elevation was ≥50°F (10°C), the caribou would typically be ready to census. This guideline helped observers judge when conditions were right and likely helped save flying and personnel time in conducting pre-census reconnaissance flights.

Depending on weather conditions and if the census was conducted in June or later (sometimes as late as mid-July), some censuses were likely better than others. If there were many small aggregations rather than a few large ones, some groups could have been missed. Also, quality of the photographs varied, so that on some photographs caribou could be obscured behind other caribou or were hard to distinguish from the tundra background. Our experience over years of conducting censuses indicated that these problems were minor in small, thoroughly monitored herds like the Delta (with >50 radio collars per herd), but in some years census results were higher or lower than expected from population models (see section *Deterministic Population Model of the Delta Caribou Herd*).

We observed patterns of population growth in herds surrounding the Delta herd to determine whether the Delta herd followed a regional pattern in common with its neighbors or with other regions. We also used these comparisons to determine if emigration-immigration from herd to herd was likely. The authors were largely responsible for censuses in most caribou herds in Alaska and major herds were censused using aerial photography usually every 2–3 years (Appendix A). NPS and/or USGS staff counted the Denali herd sporadically before 1987 and then every year from 1987 to 2008. Some censuses (notably Porcupine, Nushagak, Mentasta, and Chisana) were cooperative efforts with USFWS or NPS staff, and USFWS staff counted the Adak herd.

Estimating Recruitment of Calves in the Delta Herd and Other Alaska Caribou Herds

We conducted fall composition counts and obtained estimates of recruitment of calves to fall (i.e., calf:cow ratio) over a 27-year period from 1981 to 2007 in the Delta caribou herd. In all but 3 years during 1981–2007 (1999, 2002, 2007), we sampled at least 1,000 caribou in the herd and the sampling fraction (composition sample as a proportion of estimated herd size in late June) averaged 31% (range 14–57%; Table 1). After 1980, as radiocollared caribou (primarily females) became available in the Delta herd and in other herds, we began allocating composition samples approximately according to the distribution of these radio collars. We recognized there were at least 2 poorly tested assumptions inherent in using fall calf:cow ratios as estimates of recruitment, even if distribution of the sample was based on radio collars. The first assumption was that mortality of calves was similar to that of adults after 4 months of age. Based on the initial radiocollaring work in the Delta herd, we suspected that the first assumption would be generally true in years when the herd was increasing during periods of mild winter weather (Davis and Valkenburg 1981). Partly to test this assumption and partly to get the best possible estimates of recruitment in the Delta caribou herd, from 1983 to 1991 we also conducted spring (April) composition counts (Table 2; Valkenburg 1997). Results of these counts were variable and in some years (e.g., 1984–1986) April calf:cow ratios were substantially higher than the calf:cow ratio from the previous fall (Valkenburg 1997). Also, the April counts introduced another untested assumption—that distribution of male and female calves is similar to that of radiocollared females in April. We discontinued these April counts after 1991 because we were not confident of their accuracy, could not test the distribution assumption, and had begun radiocollaring female calves in fall and thus could obtain an independent estimate of overwinter calf mortality. As data accrued on the survival rate of calves from 4 to 16 months of age (especially after 1992), we confirmed that mortality of calves after 4 months of age can be substantially greater than mortality of cows in some years, and in those years the observed fall calf:100 cow ratio was likely to be an overestimate of recruitment (Valkenburg et al. 1996a, Mech et al. 1998). We did not resume the April counts but we did realize that if we could adequately test the distribution assumptions (both in fall and spring counts) we might be able to improve our estimates of recruitment.

The second untested assumption in using fall calf:cow ratio as an estimator of recruitment was that male and female calves were still largely associated with their mothers in fall. Partially to test this assumption, we radiocollared a sample of 10 male calves (whose mothers were also collared) with expandable collars during 26–27 September 2003. We subsequently determined whether they had remained with their mothers in early October, early March, and early April, and determined whether they were within 2 miles of a radiocollared female (including females who were not their mother). Then, during 1996 and 1997 we monitored the April distribution of the remaining (10-month-old) male and female calves with collared mothers from the calf mortality studies done in the previous 2 years (Valkenburg et al. 2004). In early April, we determined that 41% (28/68) of female calves were >2 miles from a radiocollared female and that 24% (8/34) of male calves were >2 miles from a radiocollared female (Valkenburg 1997).

Table 2. Spring sex and age composition counts of Delta herd caribou, Alaska, 1983–1991.

Date	Bulls:100 Cows	Calves:100 Cows	Calves %	Number of calves	Cows %	Number of cows	Bulls %	Number of bulls	Total caribou counted
20 Apr 1983	23	29	19	205	66	708	15	166	1,079
10 Apr 1984	10	49	31	194	63	396	6	38	628
20 Apr 1986	21	29	19	302	67	694	14	145	1,141
6 Apr 1988	22	29	19	285	66	976	14	212	1,473
18 Apr 1990	15	17	13	129	76	781	11	116	1,026
18 Apr 1991	20	8	7	96	78	1,074	16	217	1,387

Based on these data, we concluded there was a high potential for bias in April composition counts and we did not resume doing them. Also, from work done previously in the Western Arctic herd, we realized that by April there was considerable segregation of calves and adult females, at least in the migratory herds where it is common to see large numbers of calves associated with bulls on winter ranges after most cows have already begun migrating back to their calving areas (Davis and Valkenburg 1985a).

Fall calf:100 cow ratio estimates derived from late September–early October composition counts therefore became our primary method of estimating recruitment each year in all Interior and Southwest Alaska caribou herds (Appendix B). However, for practical, economic, and logistical reasons, some biologists conducting fall surveys in the Arctic herds continued to use fixed-wing aircraft and to express recruitment of calves to fall as percent calves rather than calves:100 cows (Appendix B).

During 1976–1985 we conducted composition counts from the ground using a spotting scope and 2 observers in some of the largest caribou herds (e.g., Western Arctic and Porcupine). One person observed through the scope while the other recorded cows, calves, and bulls with a 5-place tally counter. The main reason for conducting counts from the ground rather than from the helicopter was that it was much less disturbing to large groups, therefore less chance of injuring caribou. At that time we used turbine helicopters (Bell Jet Ranger) exclusively and they were louder and more disturbing than the piston helicopters (Robinson R-22 and R-44) used in later years. Also, in the northern herds in early October there can be a considerable amount of glare ice on lakes, so if caribou are pressed to run across ice they can easily dislocate or break their legs. After 1985 all counts were conducted from the helicopter (Bell Jet Ranger until 1992 then Robinson R-22 or R-44). The most critical factors in accurately classifying cow and calf caribou to obtain sex ratio data is to ensure that observers focus on the rear end of animals and can recognize the vulva quickly. Some caribou run with their tail down causing visual difficulties for the observer. The primary criterion for recognizing a calf is that they have a noticeably short head compared with yearlings and older animals, so observers must learn to glance at the head of any animal that superficially appears to be a calf. In this way, confusion between calves and yearlings is minimized.

Estimating Sex Ratio of Adults in the Delta Herd and Other Alaska Caribou Herds

Caribou have a polygamous breeding system and herd sex ratio is therefore an important parameter that influences potential population growth rate. Also, most harvest management programs in Alaska are designed to select for bulls and there are circumstances where herd bull:cow ratios could theoretically be reduced below the point where all estrus cows are bred. We were therefore interested in annually obtaining reliable data on sex ratio of adult caribou in the Delta herd and as many other herds as possible. Further, we realized that monitoring sex ratio of the population would provide a way to also estimate mortality rates of males through population modeling provided we could collect accurate information on sex ratio.

We estimated sex ratio (i.e., bull:cow) simultaneously with calf:cow ratio in the Delta herd and in other herds each year by counting caribou during the rut in late September and early October. We assumed that adult males and females would be most evenly mixed during or just prior to the rut. We estimated the timing of the rut by subtracting the number of days of the average reported gestation period for caribou (227–229 days) from the approximate date of peak calving (20 May in the Delta herd) (Bergerud 1974:84). We distributed the composition sample according to the herd distribution, which was typically determined by locating radiocollared caribou with fixed-wing aircraft. All caribou were classified into 1 of 3 categories: cows, calves, or bulls. Cows and bulls were classified based on genitalia and calves were classified based on their size relative to cows, particularly the length of their head.

Beginning in 1980, we segregated bulls into age classes during fall composition counts in several caribou herds (Appendix B) with the hope that small bull:cow ratios might provide a better index to recruitment than fall calf:cow because we expected that most "small" bulls would be yearlings. Also, in some herds and in some years we suspected that calf mortality over winter was high and thus fall calf:cow could overestimate recruitment of calves into the breeding population. We classified bulls into 3 size classes: large, medium, and small so that we could obtain another index to recruitment (i.e., small bulls:100 cows). This also enabled us to better track the effects of hunting and recruitment pauses on the proportion of mature bulls in caribou herds. Bulls were classified as follows (Eagan 1993):

- Small Bulls: Cow-sized animals or somewhat larger, with antlers nearly indistinguishable from adults cows; uniformly white rump below anus; tail often has cottontail appearance; penis sheath occasionally visible from the side. This category was thought to include all yearling and many 2-year-old bulls.

- Medium Bulls: Antlers clearly larger than small bulls or cows; uniformly white rump below anus; as in small bulls, tail may appear fuller than in cows. This category was thought to include some 2-year olds, all 3-year olds, and some 4-year olds.

- Large Bulls: Large-bodied, white-maned bulls, fully mature antlers that probably would not undergo significantly greater development in antler spread, beam length, or weight in subsequent years. This category was thought to include many 4-year olds, and most older bulls.

Classifying bulls into these categories was somewhat subjective and we were not sure how antler growth in individuals might change from year or with changes in nutrition over time. We speculated that determining the proportion of small bulls in populations could aid in estimating recruitment, while determining proportions of large bulls could help managers judge when hunting was excessive or act as a possible nutritional indicator.

We expected most bulls classified as "small" bulls would be yearlings (Valkenburg 1997). To test this assumption and determine whether there was a predictable relationship between calf:cow ratio in fall and small bull:cow ratio in future years we analyzed data from many Interior herds using linear regression. We also performed an analysis of previous year's fall calf:cow and previous 2 year's calf:cow multiplied by modeled mean calf survival rates as predictors of subsequent year's small bull:cow also using linear regression.

ESTIMATING HARVEST BY HUNTERS IN THE DELTA CARIBOU HERD

We estimated harvest by hunters annually within the range of the Delta herd during regulatory years (RY) 1980 through RY04 (regulatory year begins 1 July and ends 30 June, e.g., RY80 = 1 July 1980–30 June 1981). The hunting season was closed during RY78 and RY79 as well as RY92–RY95. Hunting was allowed by drawing permit, registration permit, or both during RY80–RY82, RY91, and RY96–RY04. Harvest reporting was mandatory under both registration and drawing permit hunts and we believed that reported harvest under these permit types was an accurate reflection of actual harvest (not including wounding loss) because enforcement of reporting was rigorous. Hunters that did not report within 10 days of the close of the season (20 September) were sent reminder letters or received a telephone call. Hunters who did not report were ineligible to enter drawing hunts the following year. In all other years (i.e., RY83–RY90) at least some hunting occurred under a general open season. Although harvest reporting was technically required through the harvest report card system during general seasons, enforcement of general season reporting was lacking and reminder letters were not sent. We suspected that reported harvest was low in these years and therefore derived a correction factor for the reported general season harvest.

During RY86 and RY87 there was no advertising effort to remind hunters to report, but in RY88 there was an advertising campaign to get hunters to report (McNay 1990). During 3 fall hunting seasons (RY87–RY89) we interviewed hunters in the field during the first 2 weeks of September at checkstations operated on the Parks Highway near the Yanert River or at hunting camps we accessed using aircraft. Hunter names, permit numbers, and success were recorded for determining whether they reported later. Hunters were not told the purpose of these interviews and reminder letters were not sent. The hunter interviews and harvest data collected later from harvest report cards were treated as a mark-recapture sample to estimate total hunter numbers and harvest. Data from hunters interviewed in the field composed the marked sample and data from the harvest report cards composed the recapture sample. Total hunters were reported from the following minimum bias mark-recapture formula:

$$N = \frac{\left((n_1 + 1)(n_2 + 1)\right)}{M_2 + 1} - 1$$

Total hunters were calculated using n_{1t} = interviewed hunters (i.e., marked sample), n_{2t} = total harvest reports returned, and M_{2t} = interviewed hunters who also returned harvest report cards (i.e., recaptured markers). Similarly, the number of successful hunters (i.e., harvest) was calculated using n_{1s} = interviewed successful hunters, n_{2s} = total successful harvest report cards returned, and M_{2s} = successful interviewed hunters who also returned harvest report cards. Reporting rates for successful hunters and total hunters were calculated simply as M_{2s}/n_{1s} and m_{2t}/n_{1t}, respectively. Confidence limits were calculated from the binomial distribution. If desired, variance in the number of hunters (N) could be calculated using the minimum bias formula:

$$Var\ (N) = \frac{(n_1 + 1)(n_2 + 1)(n_1 - n_2)(n_1 - M_2)(n_2 - M_2)}{\left((M_2 + 1)(M_2 + 1)(M_2 + 2)\right)}$$

Except for monitoring radiocollared caribou, we did not attempt to estimate illegal (i.e., out of season) harvest because we suspected it was low. There were no roads in GMU 20A, and access was confined to aircraft, off-road vehicles, and snowmobiles. Other than a small subdivision with about 150 people immediately adjacent to Denali National Park, fewer than 20 people lived within the range of the Delta herd.

CAPTURING, RADIOCOLLARING, AND MONITORING WEIGHT, SIZE, AND NUTRITIONAL CONDITION OF CARIBOU

Capture Techniques

Capture techniques for caribou evolved over the years of the study. Initially, for adults, we used 3–7 cc Cap-Chur® (Palmer Chemical and Equipment Company, Douglasville, Georgia) darts with 2–3 cm barbed needles with etorphine (M-99®, D-M Pharmaceuticals, Rockville, Maryland or Lemmon Company, Sellersville, Pennsylvania) and either xylazine (Haver-Lockhart, Shawnee, Kansas) or acepromazine (Ayerst Laboratories, New York, New York) as adjunct tranquilizers (Valkenburg et al. 1983a). The etorphine was reversed with diprenorphine (M50-50®, D-M Pharmaceuticals or Lemmon Company). These drug combinations were not available in the United States in a sufficiently concentrated form and required that a larger than optimum volume be injected rapidly from the relatively large darts (Valkenburg et al. 1983a). Darts routinely did not stay attached to the caribou and most were lost. Also, the completeness of the injection was always in question and downtimes were variable. We therefore began experimenting with shoulder-held and skid-mounted net guns. Although darting with etorphine, in combination with xylazine or acepromazine, and using net guns worked reasonably well and each method had its advantages, we were never satisfied with either the injury rate or the efficacy and efficiency of these capture techniques (Valkenburg et al. 1983a). With net guns, it was particularly difficult to capture specific individuals (especially calves) within groups. Starting in autumn 1985, we switched to using Wildnil® (4.46 mg/ml carfentanil citrate—equivalent to 3 mg/ml carfentanil; Wildlife Pharmaceuticals, Windsor, Colorado) as the primary immobilizing drug. For calves (the majority of all captures), we eventually settled on a dose of 0.33 ml Wildnil in combination with 0.66 ml Cervizine® (100 mg/ml xylazine hydrochloride, Wildlife Pharmaceuticals; Adams et al. 1988). For adult caribou (primarily >3-year-old females whose radio collar batteries were nearing the end of their projected life) we used 1.0–1.33 ml Wildnil and 0.75–1.25 ml Cervizine depending on the condition and sex of the animal and the season in which the handling was done (Adams et al. 1988). Lower doses were generally used in spring when animals were often in poorer condition. We continued using Palmer Cap-Chur rifles but were able to use 1 cc darts for calves and 3 cc darts for adults. After the mid-1980s we used only 2 cm barbed needles on the Cap-Chur darts for all caribou regardless of sex, age, or season. Initially, we used naloxone (naloxone hydrochloride, Wildlife Pharmaceuticals) to reverse the Wildnil, but from the early 1990s on we used Trexonil® (naltrexone hydrochloride, Wildlife Pharmaceuticals). Once yohimbine hydrochloride (Antagonil®, Wildlife Pharmaceuticals) became available as an antagonist for xylazine in the early 1990s we used it as reversal agent as well. Standard doses of antagonist that were used from 1999 on were 2 ml Trexonil (naltrexone hydrochloride 50 mg/ml) with 200 mg Tolazine® (100 mg/ml tolazoline hydrochloride, Wildlife Pharmaceuticals).

Although capture-related mortality rates of caribou calves were reasonably low (~5%), during the mid-1990s we realized that use of powdered charged Cap-Chur rifles was the cause of most of the injuries and deaths of caribou (calves and adults). We changed to using a Cap-Chur CO_2 pistol. This change in capture technique reduced capture mortality from ~5% to <1% (Valkenburg et al. 1999). We also subsequently reduced the dose of Cervizine to 0.33 ml for calves because some of the smaller calves appeared too deeply sedated and could not maintain sternal recumbency. Between 1998 and 2002 we handled hundreds of female caribou calves throughout Alaska with the revised regimen and had very low mortality rates (~1%). However, in spring 2002 we experienced relatively high (10–60%) and unexplained capture mortality rates with 10-month-old female calves and adult females in several caribou herds. We cooperated with veterinarians and the drug manufacturer (Wildlife Pharmaceuticals) and had existing drug batches assayed but we never conclusively determined the cause of the unexpected high mortality rates in 2002. However, for several years we subsequently monitored blood oxygen levels with a pulse oxymeter and administered antagonists as needed if blood oxygen levels or respiration declined below acceptable levels or if an animal appeared too deeply sedated. Generally, we monitored radiocollared caribou within 2 weeks of collaring to determine if they survived handling procedures. We assumed that mortalities of collared caribou occurring <2 weeks after capture were capture-related.

Radio Collar Specifications

From 1979 to 1992 we used Telonics radio collars (model 500 or 505—approximately 500–550 g or 600 or 605 series—approximately 800–850 g). Initially, we found most model 600 or 605 series collars lasted at least 5 years. When collared caribou reached 3–5 years of age, we recaptured them and replaced collars. Prior to 1994 we also recaptured collared caribou when they reached 8–10 years of age. Beginning in 1994 we let collars expire on these older caribou because most died before reaching 12 years of age and collar life increased to 6–8 years. Additionally we felt that older females (those >10) were less likely to survive immobilization and recollaring. In hindsight, the decision not to radiocollar older females may have reduced our ability to detect interactions of age and environmental covariates on mortality and natality rates (L. G. Adams, Wildlife Biologist, U.S. Geological Survey, personal communication). During the early 1990s we deployed some ATS (Advanced Telemetry Systems, Isanti, Minnesota) radio collars on adult caribou (model 9-6 vc—approximately 860 g). After 1997 we used Telonics collars exclusively. All radio collars deployed transmitted signals within the 150–154 MHz range with a pulse rate of 30–55 beats per minute. All collars were equipped with a mortality sensor that doubled the pulse rate if the collar remained stationary for 4 hours.

We recorded greatly increased calf mortality during the early 1990s and switched from model 600 Telonics collars to model 500 collars to determine if the heavier radio collars were contributing to calf mortality. We found no obvious differences in mortality with the lighter collars, and after 1995, we returned to using model 600 collars.

Handling of Captured and Collected Caribou

For each caribou captured or collected, we took various morphometric measurements (Appendix C) and collected blood samples (~25 ml). We used standardized data cards, assigned all caribou unique identification numbers, and trained participating biologists to take measurements in a consistent manner. Capture cards were archived in the Fairbanks office of ADF&G. Mandible and metatarsus measurements were taken to the nearest millimeter using tree-measuring calipers (Haglöf, Inc., Stockholm, Sweden). Girth, hind foot, and total length were measured to the nearest centimeter with a flexible tape. (We found that mandible and metatarsus measurements taken with tape measures were more variable than those taken with calipers, thus we only present caliper measurements here). Blood samples were used for disease screening and to examine genetic relationships within and between herds (Røed and Whitten 1986; Cronin et al. 1995, 2003, 2005, 2006; Zarnke 2000; Zittlau et al. 2000; Valkenburg et al. 2003a; Mager et al. 2014). Prior to 1985 we typically only saved blood serum, thereafter, we also collected ~6 ml of whole blood from each caribou in an EDTA vial.

Each animal was weighed and care was exercised to ensure that scales were calibrated annually. Weights were obtained with a load cell or a 160 lb (Hanson, Inc., Northbrook, Illinois) spring scale. Until the late 1980s, we weighed calves by suspending them from a 2-meter long pole held aloft by 2 people. We weighed adults either by lifting them with a helicopter or with a tripod and winch. After the late 1980s, D. Grangaard (ADF&G Technician, Tok, Alaska) developed a simple weighing pole (see section *Fieldwork Photos*:photograph 3) that enabled a single person to weigh caribou (or other animals) of up to 135 kg (300 lb) on level ground or on steep slopes.

Prior to 1990 we extracted and sent teeth (I_1) away for aging (Matson's Laboratory, Milltown, Montana) from most adult caribou handled in all caribou herds. After the early 1990s we abandoned tooth extraction because >50% of known-aged teeth from the Delta herd were at least 1 year in error and because the procedure seemed unnecessarily invasive compared with the value of the data provided.

During the 1990s in the Nelchina, Mulchatna, and Northern Alaska Peninsula caribou herds, we collected samples of 10–15 female caribou calves to assess condition and monitor herds for the prevalence of disease. We shot calves in the upper neck and head from a helicopter with a 12 ga. shotgun with double-aught buckshot. We then collected blood directly from the heart with a syringe and 1.5 inch 18 ga. needle. Collected calves were weighed both whole (i.e., live weight) and then again with the gastrointestinal tract, lungs, heart, and liver removed (i.e., carcass weight or gutted weight). We compared live weight and carcass weight with linear regression. We also examined lungs, liver, mandibles and other tissues for indications of disease or parasites (Neiland et al. 1968, Neiland and Dukeminier 1972, Doerr and Dieterich 1979).

Capturing and Radiocollaring 4- and 10-Month-Old Calves in the Delta Caribou Herd

From 1981 to 1990 we captured cohorts of female calves and radiocollared them during early April–early May, when they were approximately 10 months of age. During 1991–2005 we also captured and radiocollared calves at 4–5 months of age (late September–early November). This provided us information on winter mortality of calves and also allowed us to investigate whether autumn calf weights could be a sensitive predictor of summer nutrition or natality rates of females during the following calving season. During years when calves were radiocollared at 4–5 months of age, we also sampled 10–20 10-month-old female calves and radiocollared enough of these to ensure that ≥10 radiocollared calves were recruited into the population at 1 year-of-age. This facilitated calculation of age-specific natality and mortality rates and provided enough radiocollared caribou to monitor movements and herd location during censuses and fall composition counts.

We had little trouble distinguishing calves from adults during capture attempts. Most calves were noticeably smaller than older animals, usually were following a female, and had noticeably short heads compared with older animals. However, we did occasionally have trouble deciding between calves (<1 year) and yearlings (>1 year). In these cases, we caught the animal if possible and determined the age by tooth eruption. During this study we captured 23 yearlings while sampling calves. We processed yearlings the same as calves and typically affixed radio collars to them. In a few cases (<5), weights and measurements of the largest calves were found to overlap those of the smallest yearlings. Although few in number, we recognized that the inclusion of these females in survival and natality analyses may have introduced some bias because these animals were likely smaller than average.

Capturing Adult Female and Adult Male Caribou in Range of the Delta Caribou Herd

During 17–18 April 1981 we captured and radiocollared 8 adult female caribou in Dean Creek (Yanert River drainage) to determine if caribou in the Yanert River drainage had a separate calving area from those in the Delta herd. We also captured, collared, and released 1 adult female Delta caribou that was caught in a volleyball net in Goldstream Valley in late September 1992. We captured and radiocollared 23 adult male caribou, 28 male calves, and 1 male yearling in the Delta herd during 1979–1993 to determine causes and timing of mortality, movement patterns, and duration of calf-dam bonding for males. Four of these adult males were specifically captured in the Yanert River drainage to determine if they remained isolated from other caribou in the Delta herd. In addition, we also recaptured most collared female caribou to replace aging radio collars.

Monitoring Nutritional Condition of Individual Caribou

As the Delta herd continued to grow in the early 1980s, we realized that density-dependent feedback mechanisms would likely begin to influence population growth by potentially reducing natality and increasing mortality. We therefore began exploring techniques to measure condition of caribou using 4- and 10-month-old calves as indicators of herd nutrition. We continued to use previously developed techniques and tried to develop additional techniques that would be most applicable to field situations in Alaska (e.g., Riney 1955, 1960; Langvatn 1977; Kistner et al. 1980; Allaye-Chan 1991; Gerhart 1995).

During the first few years of the study, all indications were that the Delta herd and surrounding herds were well below levels where food limitation was likely to affect population growth. Some 2-year-old females in the Delta herd were producing calves (an indication of very good nutrition in caribou) and the herd was below its historic population size measured in the 1960s (Skoog 1968, Hemming 1971). Existing techniques for measuring physical condition in caribou (e.g., Langvatn 1977) and deer (*Odocoileus* spp.) (e.g., Kistner et al. 1980), although potentially useful in some caribou herds in some years, were of limited value in a statewide program because of the difficulty for biologists to obtain sufficient samples of dead animals in remote areas. We wanted to develop techniques that could be incorporated into routine collaring operations without greatly adding to existing workloads. Body weights and certain morphometric measurements of 10-

month-old female calves in the Delta herd appeared to have the greatest potential as sensitive indicators of body condition.

Beginning in 1989, using information collected in the Delta herd on female calves, we began developing a method for monitoring caribou body condition and nutrition that could be used in a statewide program. After reviewing the literature and analyzing weight and morphometric data from nearly 100 female calves collected (i.e., killed) in the early 1990s in the Western Arctic, Nelchina, and Northern Alaska Peninsula herds, and from several hundred live calves handled in various herds, we settled on a program of weighing and measuring samples of 4-month-old or 10-month-old calves. Although we found there were some advantages to collecting calves (*Fieldwork Photos*:photograph 4) because we could take direct measurements of fat deposits, femur marrow fat content, and carcass weight, we concluded that measuring the weight and size of live calves provided an adequate assessment of condition which could be more widely applied. Carcass weight, although theoretically a better measure of condition than live weight (c.f. Langvatn 1977, Allaye–Chan 1991, Gerhart 1995) and potentially available from hunter-killed animals, was not found to be a better measure in practice. For example, we found variations in the way carcasses were handled by different people (including biologists). Also, hunters seldom shot calves and we concluded that calves were the most sensitive indicators of annual nutrition. Opportunistic samples of adults typically taken by hunters were tempting to use as indicators of animal condition, but were difficult to deal with in practice. The samples also tended to be biased (e.g., large bulls killed because they appear fat) and required large numbers of animals to be sampled. Samples must be partitioned by age and sex because there are large differences in weight, body measurements, and marrow fat among various sex and age classes. In some herds (e.g., Western Arctic and Mulchatna) where caribou were abundant but the areas were remote, and we were not also conducting collaring operations, it was more efficient to collect female calves by shooting them from the ground or from a helicopter. In these cases, all the same measurements were taken as if caribou calves were being handled for collaring. In a separate project on the Western Arctic herd from 1991 to 1995 we were able to obtain useful data sets from caribou by training selected individual hunters to collect and weigh female calves (Valkenburg et al. 1996b). Also, during 1977–1983 we obtained long bones from 75 caribou in the Delta and Western Arctic herds and examined marrow depletion patterns (Davis et al. 1987). In 4 other herds (Nelchina, Mulchatna, Northern Alaska Peninsula, and Nushagak) we collected 192 female calves to screen for disease and nutritional condition, and we obtained ancillary data on carcass weight, condition indices, femur and mandible marrow fat content, and number of warble fly larvae (Neiland 1970, Gerhart 1995). Using linear regression analyses, we compared live weight and gutted weight, femur marrow fat and live weight, and number of warbles and marrow fat of calves. Our objectives were to determine if measures of condition that were available from collected calves could significantly improve information gathered from live body weights of calves.

Body weight of 4- and 10-month-old caribou calves appeared to have good potential as an indicator of nutrition for caribou statewide, and we initially assumed that all caribou in Alaska should have the same potential body weight and size because they were all classified as the same subspecies (i.e., barren-ground caribou, *Rangifer tarandus granti*). However, as we began to accumulate data from several caribou herds, especially those in Southwest Alaska and the Western Arctic herd, it appeared that caribou from those regions of the state were smaller, even when they were in good condition. We then began to explore weight:metatarsus ratio as a potential indicator of nutrition in calves with the idea that by including a scaler for body size (i.e., metatarsus length) we might arrive at a better index to nutrition for within and between herd comparisons of body condition. We also investigated the relationship between weight and girth to determine if girth was a useful surrogate for weight.

In the Delta herd we had been gathering information on weight and size of 10-month-old female calves since 1979 (c.f. Davis et al. 1991). We expanded the program in 1991 to include sampling of 4-month-old females. We then began monitoring mean weights of cohorts of 4- and 10-month-old calves in some other herds to compare with our samples from the Delta herd. We had primarily hoped that these collections would provide relative information for caribou managers and researchers about the quality of summer and winter ranges of various herds, whether there were morphological differences in body size and weight of caribou from different herds and regions, and whether some herds might be overgrazing their ranges. We intended this information to be primarily for proposing hypotheses rather than definitively testing hypotheses and we present analyses of this information through 2002.

In the Nelchina herd, we began sampling 10-month-old females in 1992 and subsequently expanded the program to obtain annual samples of 4-month-old females in 1995. In the Fortymile herd, we began collecting data on 4-month-old calves in 1990 and on newborn calves in 1994. Work in the Fortymile herd was then expanded into a separate major research project which included 9 years of calf mortality studies (Boertje and Gardner 1999; Boertje et al. 2012; Boertje et al., *In press*). In other herds (particularly Macomb, White Mountains, Ray Mountains, and Chisana), beginning in 1991, we collected data on an opportunistic basis when caribou were collared for other management purposes. We also collected and/or collared caribou from herds in Southwest Alaska and the Kenai Peninsula starting in 1995, particularly to assess body condition and to monitor parasite loads and prevalence of disease. During this study (during 1979–2007 in the Delta herd and 1987–2002 in other herds), we were able to obtain weights of 1,888 4- and 10-month-old female caribou calves in 145 cohorts from 20 of Alaska's 32 or 33 recognized caribou herds. Of these, 508 calves in 38 cohorts were from the Delta herd. Some of the data, particularly from the Nelchina and Fortymile caribou herds have been analyzed and published in other papers (Valkenburg et al. 2003b, Dale et al. 2008, Boertje et al. 2012). Some composition and weight data from several Arctic, Interior, and Southwest Alaska caribou herds have been presented in published and unpublished formats previously (Adams et al. 1989; Pitcher 1991; Lieb et al. 1994; Whitten 1995a; Lenart 1997; Saperstein 1997; Sellers et al. 1998a, 1998b; Collins et al. 2003; Aderman and Woolington 2001; Sellers et al. 2003).

We caught and weighed 8–40 male and female newborn (0–2 days old) caribou calves for 7 years in the Delta herd (1995–2001), and for 6 years in the Nelchina herd (1996–2001). We also caught and weighed samples of newborn calves during 1997–1999 in the Northern Alaska Peninsula and Southern Alaska Peninsula herds. Comparable unpublished or published data were available for other herds (Pitcher 1991; Whitten et al. 1992; Adams et al. 1995b; Whitten 1995a; L. Parrett, Wildlife Biologist, ADF&G, unpublished data). To catch calves, we used Robinson R-22 or R-44 helicopters and all calves were caught by hand after landing nearby. Detailed descriptions of capture techniques have been previously published (Adams et al. 1988, 1998b; Whitten et al. 1992; Mech et al. 1998:144; Sellers et al. 1998a, 2003; Valkenburg et al. 2004).

We measured lengths of mandibles of 4- and 10-month-old female calves we collected in the Nelchina, Mulchatna, Northern Alaska Peninsula, and Western Arctic herds to determine if mandibles would show differences in body size between regions and herds, determine if skeletal structure of caribou increased over winter, and to see if mandible length might be an additional indicator of body condition. Mandibles were removed whole from calves we collected, dried for 3–10 days, and then measured with a steel ruler (Langvatn 1977). We also determined fat content of marrow in mandibles (Neiland 1972). We used Student's *t*-tests to determine if differences in mandible length were significant between regions and herds.

With the resumption of hunting in the Delta caribou herd after the 1992–1996 closure, we required successful Delta herd hunters to return the entire mandible of harvested caribou (all hunts from 1996 to 2008 were for bulls only) to ADF&G. We received 160 mandibles over 7 years (1996–2002). We first examined mandibles for evidence of disease (Doerr and Dieterich 1979). We then assigned an eruption-wear class to each mandible after examining patterns of tooth eruption, replacement, and wear (Miller 1974) and comparison to mandibles of known-aged caribou (radiocollared caribou that had died in the Delta herd). We used a steel ruler and measured the diastema (base of incisors to anterior opening of the tooth row), and mandible length (i.e., ramus length from the base of the incisors to rearmost point of the ramus) in millimeters (Langvatn 1977). We also measured the tooth row length (anterior opening to posterior opening of tooth row).

We used hunter-collected mandibles to determine how many older-aged males had survived the period of deep snow from 1989 to 1993, if growth of mandibles slowed as the Delta herd reached its population high in 1989, and to construct a mandible length-wear class curve for Delta herd males (Ver Hoef et al. 2001). We used *t*-tests in Microsoft® Excel to compare mean mandible length over birth year periods. We then fitted polynomial (third order) curves (Microsoft Excel) and asymptotic nonlinear regression curves (R Development Core Team 2007) to the mandible length and diastema length data sets over all years.

Monitoring Other Indices of Herd Nutrition

We examined entries (n = 890) for barren-ground caribou in Boone and Crockett (2011) records and segregated records by herd. In most cases, the location given allowed us to determine the herd the individual was harvested from. In some cases (14), the location was too general (e.g., Alaska Range) to allow designation of a specific herd. In other cases (32), locations could not be determined because the locality of take was listed as "unknown," or the place name was unknown to us and not listed in the *Dictionary of Alaska Place Names* (Orth 1967), or there were too many possibilities (e.g., Boulder Creek, Moose Creek, Caribou Creek, etc.). We recognize that there are several potential sources of bias in the Boone and Crockett records. These include differences in logistics of herd access (areas of easier access being overrepresented, especially in older records), time (areas with a longer monitored hunting history might be overrepresented), and motivation for the hunters in an area (e.g., clients of guides were probably more likely to enter caribou into the record books than residents of Alaska who were hunting for meat). Despite bias in the data, we believe the Boone and Crockett records provide valuable information on a broad scale and indicate which herds have the best potential to produce large antlers.

We collected fecal samples to determine relative lichen content of the winter diet of caribou (Dearden et al. 1975, Boertje 1981). We suspected that a diet high in preferred lichens (a good source of energy, i.e., carbohydrate) would likely result in little or no weight loss over winter (Holleman and Luick 1977, Holleman et al. 1979, Boertje 1981). During 1985–1999 we collected 34 samples of fecal pellets from various winter ranges of the Delta herd (Valkenburg et al. 2002:Table 11). These samples were in addition to a much larger number of fecal pellet samples collected by Fleischman (1990) on winter ranges of the Delta herd during the late 1980s. We also collected 27 fecal pellet samples from the winter ranges of 8 other Alaska caribou herds (Valkenburg et al. 2002:Table 12). A fecal pellet sample was composed of 1 fecal pellet from each of 20 different pellet groups dispersed over a feeding area. Samples of fecal pellets were usually collected opportunistically during other winter fieldwork, but we occasionally made special trips by snowmobile or Piper PA-18 Super Cub aircraft to collect fecal pellets from Interior caribou herds. Detailed methodology of using fecal pellet samples for diet analysis are discussed by Dearden et al. (1975), Davitt (1979), Boertje (1981, 1984), and Fleischman (1990).

MORTALITY AND SURVIVAL IN THE DELTA HERD

Females

We radiocollared 343 female caribou that could be used for monitoring mortality and survival. Of these, 320 were captured as 4-month-old (*n* = 218) or 10-month-old (*n* = 102) calves. An additional 23 putative calves turned out to be yearlings (8 captured in fall, 15 captured in spring). They were captured as yearlings (8 aged 16 months and 15 aged 22 months) because they were mistaken for calves (we recognized that these were likely small yearlings and could have introduced some bias in future analyses).

Males

We collected data on causes and timing of mortality for 43 radiocollared males. Twenty-three (23) of these were captured as 4- to 10-month-old calves, and 20 were captured as adults. Because sample sizes were small and collars on males failed at a high rate, data obtained from radiocollared male caribou were not suitable for calculating survival rates or for modeling with covariates. We present only some descriptive analyses based on these animals.

Determining Fate and Cause of Death of Radiocollared Caribou

We monitored collar signals and/or obtained visual observations from aircraft (Bellanca Scout, PA-18 Super Cub, and Cessna 185) to determine fate of radiocollared caribou. The number of monitoring flights varied by season and often depended on objectives of the research. In all years, we attempted to locate all radiocollared caribou during the last week of September or first week of October to determine how many individuals had functioning collars at the end of the normal fall hunting season (also the start of the mortality year, 1 October) and to determine the distribution of radiocollared caribou for fall sex and age composition counts. Monitoring flights also occurred in late November or early December, in early February, and in March or April.

Radiocollared female caribou were located 2–4 times during 15–25 May to determine parturition rates and determine survival. All radiocollared caribou >4 months old were located (but not necessarily observed) 1–6 times during the 2 weeks prior to censuses that were conducted annually between 12 June and 16 July. Radiocollared caribou were relocated in early August, just prior to the hunting season, to assess harvest-related mortality. We usually did not locate caribou during the hunting season (usually 10 August–20 September) to avoid conflicts with hunters. We tried to account for missing collars by flying peripheral ranges and the ranges of adjacent caribou herds up to 160 km away (i.e., radiocollared caribou that could have emigrated from the Delta herd) at least once per year. Frequencies of missing caribou were provided to biologists working on adjacent herds so they could also listen for missing Delta herd caribou.

Because the primary purpose of the study was to monitor births, deaths, and emigration, we did not obtain exact locations on each tracking flight. Caribou were typically tracked until the signal indicated that the caribou was approximately under the aircraft, at which point the frequency was deleted and location recorded. Locations of collared caribou were likely accurate only to the nearest kilometer. Thus, the majority of the relocation data was not suitable for determining habitat use but was suitable for delineating major seasonal ranges used by caribou. We did however obtain accurate locations or visual observation during the calving period (May and early June), during composition counts conducted with the helicopter in early October, and during collar changes (usually in early October or in April).

When a mortality signal was detected, we tracked it to the animal, its carcass, or its radio collar. If possible, we landed the aircraft as close to the location as possible and inspected the area from the ground. However, in most cases we returned to the site by helicopter as soon as possible (usually 1–4 weeks after the caribou died, but sometimes longer in midwinter when daylight was short) and tried to confirm the mortality and determine the most likely cause of death. Likely cause of death could often be determined for caribou that died during winter from evidence of hemorrhaging in snow or tracks of predators. Likely cause of death of caribou that died during summer often could not be determined because evidence (particularly, evidence of hemorrhaging, tracks of predators, etc.) was typically lacking. Kill sites were generally not investigated until at least a week after death occurred.

Analyses of Mortality and Survival Data

Data for estimating mortality and survival rates consisted of fate records for radiocollared female caribou collared as calves (320) and yearlings (23), and fate records of radiocollared male caribou collared as calves (23) and adults (20). Although we could not determine the date of death exactly in most cases, mortality dates could be estimated to the nearest month and unambiguously assigned to year. Furthermore, due to search effort, nondetections for radio collars were uncommon (<5%), which allowed us to treat these data as known fate records. We analyzed the mortality and survival of radiocollared females in 3 ways. First, we summarized the deaths of all radiocollared females annually by probable cause, age class (calves, yearlings, or adults), and month of death. Second, we calculated annual survival rates of female radiocollared caribou by age class (calves 4–16 months of age, yearlings 16–28 months of age, and adults >28 months of age), and third, we modeled survival using logistic regression with potential explanatory covariates. Age in years (at death) was included as a covariate in survival analyses and modeling for adult females. For the males, we tabulated and summarized causes and timing of death and present our qualitative assessment of survival information.

Causes and Timing of Deaths of Radiocollared Female Caribou

We tabulated causes of death of radiocollared caribou by age class and by mortality year. We defined the mortality year as 1 October–30 September. We used this period because most female caribou calves (particularly after 1991) were radiocollared from the last week of September through early November (considered as 4-months old). It was also the approximate time of the annual fall composition counts, it included a full winter and summer in each survival year, and it was the transition from the snow-free period to the period of complete snow cover.

Mortality year for calves does not include mortality within their first 4 months (birth–October). Based on calf mortality studies on the Delta herd during 1995–1997 and in the adjacent Fortymile and Denali herds we expected that substantial mortality occurred in the Delta herd during this time (Adams et al. 1995a,b; Boertje et al., *In press*). For the Delta herd, this early mortality was included in estimates of recruitment derived from fall calf:cow ratio data obtained from composition counts. The decision to include 4–16 months as the calf mortality year was to include a full winter and summer in each survival year and because the most thorough tracking flights, collaring, and accounting for individuals occurred in early October of each year.

We estimated annual survival rates of radiocollared female caribou between early January 1979 and 30 September 2007 using mixed logistic regression with the lme4 package in R (version 3.0.0; Bates et al. 2014). Separate models were fitted for calves, yearlings, and adults. Each model included a random effect for year that accounted for variability among years (σ^2_{yr}). To account for staggered entry of calves, the calf survival model included the number of unobserved days (difference between capture date and 30 September of the birth year) as a covariate in the fixed effect terms of the model. The adult model included age as a fixed covariate.

Estimating survival rates for calves presented some significant challenges. Before 1992 most calves were radiocollared as 10-month olds in April, so they only had a month or so of winter and a 6 month potential period of survival before they advanced to the yearling cohort. After 1991, most calves were radiocollared as 4-month olds (late September to early November) and the survival period for these animals was 11–12 months and included an entire winter and summer before they advanced to the yearling cohort. Because many deaths occurred over the first winter of an animal’s life, there was likely to be bias in the survival rates calculated before 1992. By using a staggered entry design, we used data from both spring and fall captures to account for the different exposure times represented in these 2 periods. However, an implicit assumption with this approach is that conditions were the same during the 2 periods, which was likely not true, at least during 1989–1993 when winters were severe. The staggered entry design also had implications for using individual measures (body mass, skeletal size, etc.) as potential explanatory variables in the subsequent logistic regression analyses because smaller calves could have been more prone to dying over the first winter and thus were not represented in the population of calves captured in April. Preliminary analyses, using data from calves captured in the fall during 1992–2003, showed that capture weight in the fall had a strong effect on the overwinter survival of calves ($\beta = 0.56$, SE = 0.18, $z = 3.04$, $P = 0.002$). Smaller calves were more prone to die over the first winter and were not represented in the population of calves captured in April. Due to this bias in availability, fall and spring capture weights are not comparable.

Estimating annual survival of yearlings and adults (Bates et al. 2014) was more straightforward because a staggered entry design was not needed as the animals automatically advanced to the next age class if they survived their time in the previous age class. We did not include the 9 adult caribou in the Yanert drainage in 1980 and the 1 adult caught in the volleyball net in Fairbanks in 1992 in the survival analyses because they were of unknown age.

Modeling Survival of Radiocollared Female Caribou and Effects of Covariates on Survival

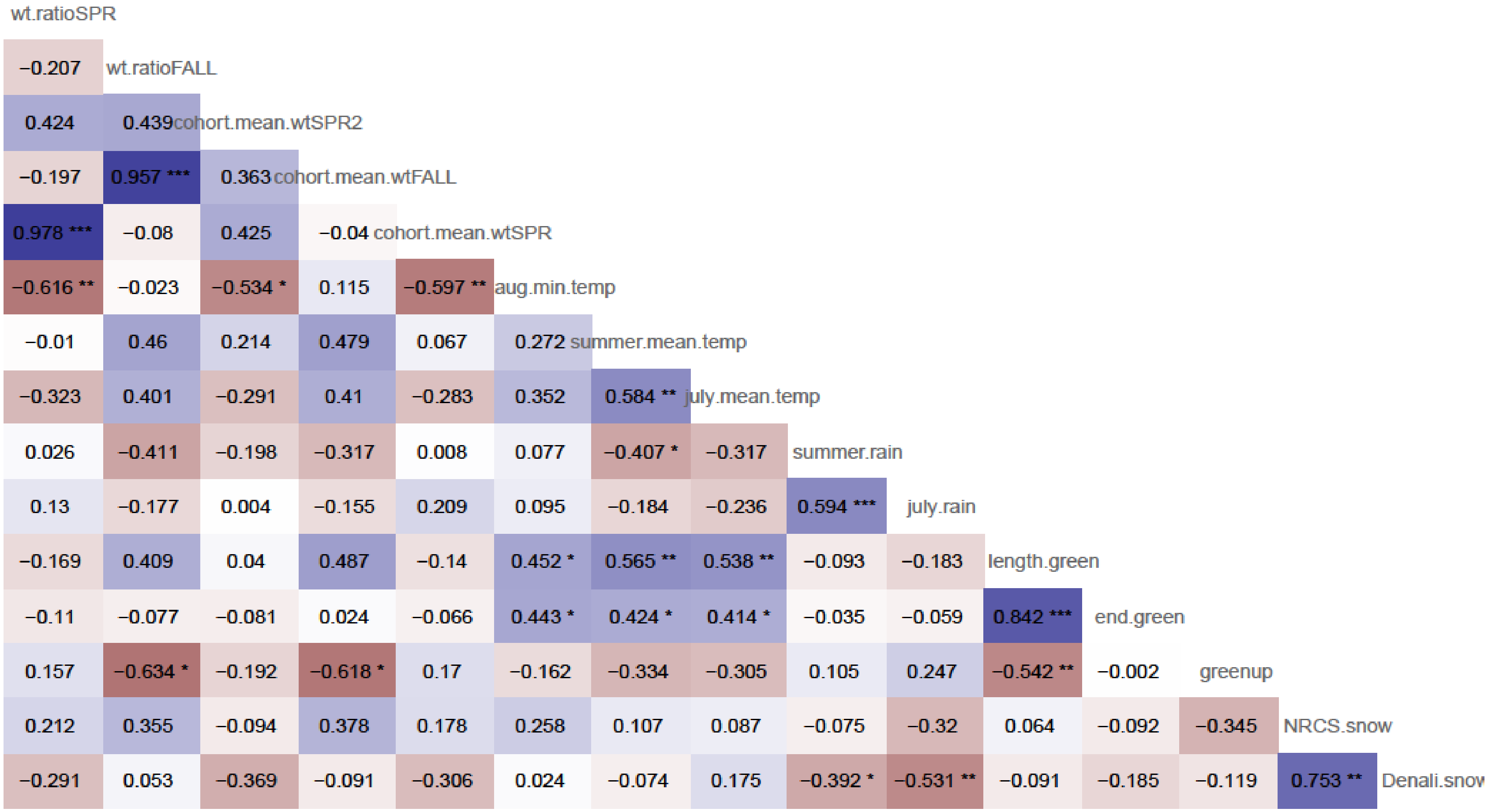
Our goal was to develop a model that would link annual variation in caribou survival to variables including weather conditions (Appendices D and E), measures of caribou cohort health, caribou population size, and wolf and moose numbers (Tables 3 and 4; Appendix F). We constructed a correlation matrix for weather and calf cohort mean weight to aid in visualizing potential relationships among variables (Fig. 4). Because of the large number of potential weather covariates in the analyses, prior to Akaike's information criterion (AIC) model selection, we removed variables we deemed redundant for describing the overall weather patterns. Covariates were grouped according to the underlying weather covariate. For the analysis we only used measures that gave the strongest univariate relationship with survival (Table 5).

Table 3. Description of survival and individual animal variables and covariates used in logistic regression models of survival rates, Delta caribou herd, Alaska, 1979–2008. Variable names are in italics.

Variable	Name given to variable	Description
Accession Number	*Acc.No*	Unique identification number given to each individual caribou
Year	*NominalYear*	The second calendar year in the mortality year from 1 Oct to 30 Sep. For example: for the mortality year 2001–2002, NominalYear = 2002
Survival	*SURV*	Binary indicator of whether the animal survived through 30 Sep of NominalYear
Starting date	*Start.date*	Collaring date or start date of mortality year
Days exposed	*Days.exposed*	Period (in days) during which an radiocollared individual was exposed to mortality during the mortality year
Age	*Age.at.MortYr*	Age at the start of the mortality year (0 = 4–16 months, 1= 6–28 months, 2 = 28–40 months, 3 = 40–52 months, etc.)
Initial weight	*initial.weight*	Weight at capture (kg) (only fall capture weights were used in models)
Girth	*girth*	Circumference of chest just behind the forelegs and hump (cm) at capture
Weight:Metatarsus ratio	*wt.ratio*	Ratio of initial weight (kg):metatarsus length (cm, measured with caliper) at capture

Table 4. Description of environmental, calf weight, and wolf and moose covariates used in logistic regression models of survival rates, Delta caribou herd, Alaska, 1979–2008. Variable names are in italics.

Weather variables	Variable name	Description of variable	Timing of application
Summer rainfall	*summer.rain*	Total rainfall during Jun, Jul, and Aug (cm)	Year-1
Jul rainfall	*july.rain*	Total rainfall in Jul of the nominal year	Year-1
Mean summer temperature	*summer.mean.temp*	Average of monthly mean temperatures (C) for Jun, Jul, and Aug	Year-1
Minimum temperature in Aug	*aug.min.temp*	Minimum temperature (C) recorded in Aug of the nominal year	Year-1
Jul mean temperature	*July.mean.temp*	Mean temperature (C) in the month of Jul of the nominal year	Year-1
Snow depth at Denali Park	*Denali.snow*	Sum of snow depth measurements (cm) for 1 Feb, 1 Mar, 1 Apr at Denali climate station (dog kennels)	Year
Snow depth in GMU 20A	*NRCS.snow*	Sum of snow depth measurements (cm) for 1 Feb, 1 Mar, 1 Apr	Year
Estimated beginning of growing season	*greenup*	Index value for ordinal date of flush of green leaves recorded by the National Weather Service on the south slopes of Chena Ridge in Fairbanks	Year-1
Estimated end of growing season	*end.green*	First day (ordinal date) in autumn that the temperature fell to −2°C at Denali Park climate station	Year-1
Estimated length of growing season	*lengthgreen*	*end.green* minus *greenup*	Year-1
<u>Calf weight indices:</u>			
Mean weight of previous year's cohort	*cohort.mean.wt1*	Mean weight of the previous year's cohort of 10-month-old calves	
Mean weight of current year's cohort	*cohort.mean.wt2*	Mean weight of current year's cohort of 4-month-old female calves	Year-1
Mean weight of current year's cohort	*cohort.mean.wt3*	Mean weight of current year's cohort of 10-month-old calves	
<u>Population indices based on year</u>:			
Caribou herd size	*n.caribou*	Number of caribou counted in the Delta herd in late Jun	Year
Number of moose in GMU 20A	*n.moose*	Number of moose estimated in GMU 20 in Nov	Year
Number of wolves in GMU 20A	*wolf.index*	A categorical variable of estimated wolf numbers (1 = <100, 2 = 100–149, 3 = 150–199, 4 = >200)	Year



wt.ratioSPR														
−0.207	wt.ratioFALL													
0.424	0.439	cohort.mean.wtSPR2												
−0.197	0.957 ***	0.363	cohort.mean.wtFALL											
0.978 ***	−0.08	0.425	−0.04	cohort.mean.wtSPR										
−0.616 **	−0.023	−0.534 *	0.115	−0.597 **	aug.min.temp									
−0.01	0.46	0.214	0.479	0.067	0.272	summer.mean.temp								
−0.323	0.401	−0.291	0.41	−0.283	0.352	0.584 **	july.mean.temp							
0.026	−0.411	−0.198	−0.317	0.008	0.077	−0.407 *	−0.317	summer.rain						
0.13	−0.177	0.004	−0.155	0.209	0.095	−0.184	−0.236	0.594 ***	july.rain					
−0.169	0.409	0.04	0.487	−0.14	0.452 *	0.565 **	0.538 **	−0.093	−0.183	length.green				
−0.11	−0.077	−0.081	0.024	−0.066	0.443 *	0.424 *	0.414 *	−0.035	−0.059	0.842 ***	end.green			
0.157	−0.634 *	−0.192	−0.618 *	0.17	−0.162	−0.334	−0.305	0.105	0.247	−0.542 **	−0.002	greenup		
0.212	0.355	−0.094	0.378	0.178	0.258	0.107	0.087	−0.075	−0.32	0.064	−0.092	−0.345	NRCS.snow	
−0.291	0.053	−0.369	−0.091	−0.306	0.024	−0.074	0.175	−0.392 *	−0.531 **	−0.091	−0.185	−0.119	0.753 **	Denali.snov

Figure 4. Correlation matrix of coefficients (R) for weather variables and calf weight indices used in logistic regression modeling of survival, natality, calf weights, and calf:cow ratios in the Delta caribou herd, Alaska, 1979–2007. Color and shade indicates direction and strength of relationship (blue = positive correlation, red = negative correlation), stars indicate strength of evidence (significance) level (*P*-values: **P*<0.05>0.01, ***P*<0.01>0.001, ****P*<0.001>0.000).

Table 5. Rationale for preliminary variable reduction of weather variable used in modeling survival and its potential covariates in the Delta caribou herd, Alaska, 1979–2008. Asterisk indicates variables retained for the main analysis.

Underlying variable or index	Variable name	Rationale
Winter severity	**Denali.snow* *NRCS.snow*	Both indices were highly correlated. *Denali.snow* had a stronger univariate relationship with survival and data were more complete.
Summer weather conditions	*July.rain* **summer.rain*	*July.rain* and *summer.rain* were about equally correlated with calf survival.
	July.mean.temp **summer.mean.temp*	*Summer.mean.temperature* had a stronger univariate relationship with survival than *July.mean.temperature*.
Growing season length	*greenup* *end.green* **length.green*	Although *greenup* and *end.green* appear to impart different types of information, both were strongly correlated with *length.green*. Neither had strong univariate relationships with survival.
	**Aug.min.temp*	*Aug.min.temp* was related to *length.green* but was left in the analysis to retain some information on the end of the growing season.

Both *NRCS.snow* and *cohort.mean.wt2* had large gaps (period prior to 1992) which prohibited their use in some analyses. For small data gaps, we used multiple imputation to estimate covariate values in missing years based on correlations among all observed covariates (Yuan 2010, Josse et al. 2011; Fig. 5). Although the method has been shown to work well for filling in single missing values in a time series, it can introduce bias if there are large gaps of missing data because correlations among covariates may be overemphasized (Josse et al. 2011). This was a potential problem we decided to accept without attempting to mitigate it, except that in the final models long strings of missing data >3 years (e.g., fall weights and measurements of calves, Natural Resources Conservation Service [NRCS] snow index, etc.) were not used.

After preliminary analyses were completed, we used mixed logistic regression of observed fates to model survival with respect to environmental covariates. Covariates were standardized according to their mean and variance to facilitate comparison of effect size. Incorporating capture weight (*initial.weight)* presented problems for the calf and yearling age classes because of the shift from spring to fall captures in 1992 and because *initial.weight* (measured in spring before 1992, and in fall from 1992 on) appeared to influence survival of calves and yearlings. For the calf and yearling age class models, we therefore limited the first round of analyses to the period from 1991–1992 to 2006–2007, where *initial.weight* refers to weight of individual calves at 4 months of age only. We continued to use *days.exposed* as a covariate in the calf survival models (because of the staggered entry of individuals), but we expected it to drop out because exposure time should have been controlled by limiting the analysis to fall captures. Covariate effects on survival prior to 4 months of age cannot be inferred from this analysis.

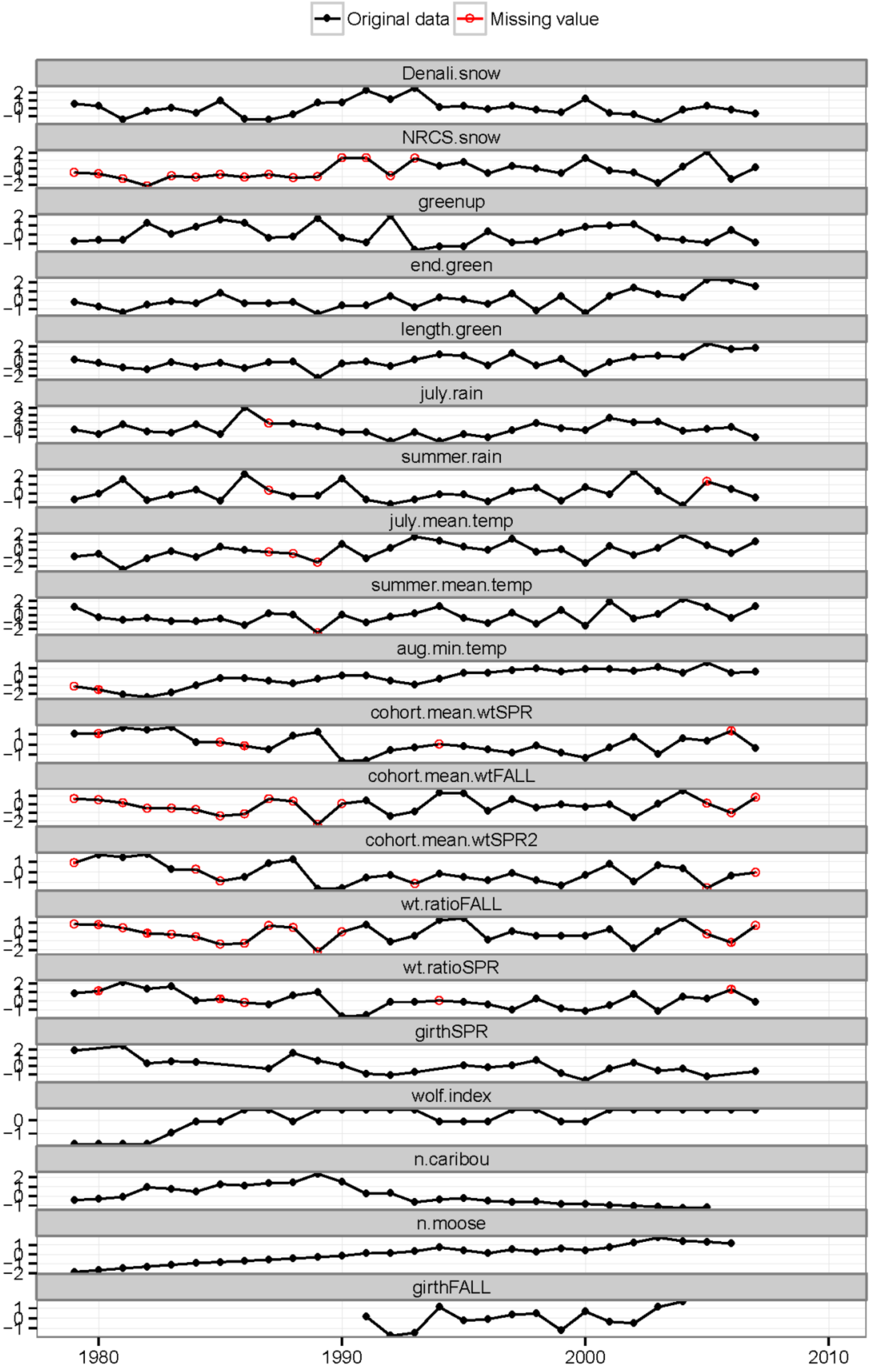


Figure 5. Potential covariates available for logistic regression modeling of the Delta caribou herd, Alaska, 1979–2007. Missing data provided by multiple imputation, but long strings (>3 years) of missing data were not used in modeling.

We used AIC based model selection with a small sample size correction (AICc) to compare among competing models (Burnham and Anderson 2002). The sample size correction used a penalty term based on the number of years of data in the sample. Both deviance ratios (Menard 2000, Ver Hoef 2012) and latent variable methods (Nakagawa and Schielzeth 2013) were used as measures of goodness of fit. Due to the potentially large number of covariates in each analysis, we used a stepwise algorithm to test and compare models for each age group (calves, yearlings, adults). We defined the largest model of interest (global model), including all variables and interactions that were thought to be biologically plausible although excluding redundancies addressed previously. Then, starting with an intercept model in the algorithm (i.e., the smallest model), we separately added each term from the global model to develop a set of competing models (the adult models age was always included as a fixed effect). Any new models in the competing set that met model selection criteria (ΔAIC<2) were also expanded with each term from the global model. This stepwise algorithm allowed us to develop a set of competing models that spanned the possible covariate set. Upon inspection, if it appeared that some covariates or covariate combinations had not been tested, we restarted the algorithm using the additional covariates to ensure their inclusion in the model set. For these comparisons, a generally accepted rule of thumb is that models with delta ΔAICc <2 are considered to have “substantial” support from the data and cannot necessarily be differentiated based on the data (Burnham and Anderson 2002). Models with delta ΔAICc<7 have “some” support. Because there were a large number of models that fell within these cutoffs, we focused only on patterns in the top set of models, rather than on a single best model. Assuming the “true” model is in the candidate set, we interpret AIC weights as the probability that a given model is actually the best model.

Weather Variables

We modeled potential influences of winter and summer weather on survival, natality, calf:cow ratios and body weights of calves in the Delta herd (Fig. 5; Appendices D and E). We selected variables based on literature review of potential effects on caribou and other ungulates as well, choosing variables that were possible to consistently measure. We anticipated that deep snow would increase mortality of caribou over the winter, and could be negatively associated with weights of 10-month-old calves in April, newborn calves in May, and 4-month-old calves the following October (Mech et al. 1998). We also expected that deep snow could reduce calf:cow ratio in fall and natality rate the following year if caribou were unable to regain condition over the summer (Skogland 1984, Adams and Dale 1998b, Mech et al. 1998, Dale et al. 2008). Increased rainfall in summer would be expected to result in greater forage biomass, an extended period of plant growth, and possibly increased protein levels in forage plants as well (Chapin and Shaver 1985, Lenart 1997), as well as possibly greater relief from biting and parasitic insects in summer. Late greenups, hard freezes during August–September, and short growing seasons would also be expected to reduce 4-month-old calf weights and natality rates the following May (Lenart 1997, Valkenburg et al. 2002). We further anticipated that summer precipitation might be positively associated with 4-month-old calf weights and higher natality rates the following May (Lenart 1997, Valkenburg et al. 2002). We anticipated that cloudy summers (measured by reduced summer temperatures) might prolong the period in which vegetation is most nutritious and thus be positively associated with 4-month-old calf weights (Klein 1990, Bo and Hjeljord 1991). Thus, we selected snow depth (*Denali.snow* and *NRCS.snow*), date of spring leaf flush (*greenup*) (National Weather Service [NWS] 2012), end of the growing season in fall (first hard freeze; *end.green*), length of the growing season (first hard freeze minus date of spring leaf flush;

length.green), total July rainfall (*july.rain*), total summer rainfall (1 July–31 August; *summer.rain*), July mean temperature (*july.mean.temp*), summer mean temperature (*summer.mean.temp*), and August minimum temperature (*aug.min.temp*) as preliminary variables that might have biological significance for caribou (Table 4). We obtained snow data (*NRCS.snow*) directly from NRCS and NWS (2011). All other data used to calculate indices were obtained from the Arctic Climate Research Center at the Geophysical Institute at the University of Alaska Fairbanks.

Snow Indices

We were able to construct snow indices (*Denali.snow* and *NRCS.snow*) from data on snow depth from 2 sources. First, snow depth was reliably recorded at NWS's Denali Park (N63°43.02′, W148°58.02′) climate station during the entire period of the study (1978–2007). Second, in summer 1993 we established 4 snow depth measurement stakes in the range of the Delta caribou herd in cooperation with NRCS. These snow stakes were located at Gold King airport (N64°11.77′, W147°55.02′), Ptarmigan Creek airstrip on Delta Creek (N63°48.18′, W146°28.25′), Edgar Creek in the Yanert River drainage (N63°35.65′, W148°01.41′), upper Wood River (N63°45.65′, W147°57.20′), and provided data during 1994–2007.

To construct the *Denali.snow* index, we summed snow depth readings (cm) from 1 February, 1 March, and 1 April. When snow depth measurements were not collected on the first of the month (<10 occasions), we used measurements for the nearest date. To construct the *NRCS.snow* index we averaged snow depth readings (cm) from the 4 snow stations on the first day of February, March, and April during 1994–2007 (14 years). On 7 occasions we failed to obtain readings for an individual station and used the reading of the next closest station as a substitute to construct the index. In 2006 no readings were recorded for 1 February, therefore the index value for 2006 excluded February data.

Greenup Date and Growing Season Length

As an index to the beginning of the growing season (*greenup*) for the Delta herd's range, we used an estimate made by NWS personnel (i.e., "Anderson/Fathauer Index") for the first date (ordinal day) that a green flush of leaves is noticeable on the south side of Chena Ridge (near the University of Alaska Fairbanks; NWS 2012). These estimates began in 1974 and were available each year for the entire study period (1978–2007). We realized that greenup on Chena Ridge was earlier than greenup in the Alaska Range but believed the index at least represented relative greenup date in the Alaska Range from year to year. We defined the end of the growing season (*end.green*) to be the date (ordinal day) when the temperature at the Denali Park climate station first declined to −2°C or lower. We estimated that a temperature of −2°C would have ended the period when green willow leaves are available and relatively nutritious (Boertje 1981). We calculated length of the growing season in days (*length.green*) by subtracting *greenup* from *end.green*.

Rainfall Indices

We defined total July rainfall (*july.rain*) as total rainfall (mm) measured during the month of July at the Denali Park climate station. Summer rainfall (*summer.rain*) was defined as total rainfall (mm) for June, July, and August measured at the Denali Park climate station.

Temperature Indices

We defined July mean temperature (july.mean.temp) as the mean daily temperature (C) for the month of July measured at the Denali Park climate station. Summer mean temperature (summer.mean.temp) was defined as the average of the monthly mean temperatures (C) for June, July, and August measured at the Denali Park airport climate station. August minimum temperature (aug.min.temp) was defined as the minimum temperature (C) recorded in August at the Denali Park climate station.

Monitoring Wolf and Moose Numbers

For purposes of modeling caribou survival rates, we used annual estimates of wolf numbers either as a numeric variable or as a categorized variable (*wolf.index*). We used numbers from March (after most harvest occurred) estimates of total wolves within the range of the Delta herd. Categories were as follows: 1-very low (<100), 2-low (>100<150), 3-moderate (>150<200) or 4-high (>200) (Appendix F). These estimates are based on estimates of wolf numbers derived from aerial track counting techniques combined with radiocollared individuals (Mech 1973; Gasaway et al. 1983b, 1992; McNay 1993; Boertje et al. 1996; Gardner and Pamperin 2014). Concurrent with our study, there were ongoing research programs on wolves or periodic estimates of wolf numbers for management activities throughout the range of the Delta caribou herd (McNay 1998, 2000).

We used the estimated moose population (*n.moose*) in GMU 20A for calculations in Delta herd caribou modeling. During our study the moose population in GMU 20A was estimated on an annual basis by ADF&G management biologists and was the subject of extensive research (Boertje et al. 1996, 2007, 2009; Keech et al. 2000; Young 2010). Moose numbers were low in the late 1970s when the caribou study began, but increased steadily until late 1994 when the population size was constrained by harvests of increasing numbers of cows (Boertje et al. 2009, Young and Boertje 2011; Table 4). Accuracy of wolf and moose estimates was thoroughly evaluated in publications above. However, in most years and on most local winter ranges, the number of wolves that preyed on caribou each winter was unknown. In most years wolf numbers were relatively high, except during the control years 1976–1982 and 1994–1995, but as the moose population increased during the study, and as range use by the Delta herd changed, wolves may have preyed on moose more and caribou less (see section *Discussion*).

NATALITY IN THE DELTA HERD

Determining Natality Rate

We measured natality (also referred to as birth or parturition) rates of Delta herd caribou annually during 1980–2006 (Fig. 6) by observing radiocollared females during the last 2 weeks of May and determining if cows had hard antlers, distended udders, or calves at heel (Bergerud 1964, Whitten 1995b). For observation we used fixed-wing aircraft (primarily 2-place aircraft with tandem seating, Bellanca Scout or Piper Super Cub) and helicopters (primarily Robinson R-22 and R-44 models). We found Robinson helicopters were more efficient, safer, and less disturbing to caribou, especially after groups of caribou began to coalesce as calving progressed. Fixed-wing aircraft often required multiple passes over groups to determine whether radiocollared females were parturient. We hoped to achieve 4 goals with this parturition data. These were to 1) describe and summarize natality rates in the Delta herd from 1980 to 2006; 2) characterize changes in natality rates with age, especially in 2-, 3-, and 4-year-old females; 3) establish an indicator measure of natality to link with environmental indices; and 4) identify possible influences of individual animal attributes and environmental indices on patterns of natality.

Influence of Age on Natality Rate

We used mixed logistic regression (generalized linear mixed model with binomial error and a logit link function) with the lme4 package in R to estimate annual natality rates in the Delta herd (Bates et al. 2014). We included fixed effects with age (2, 3, 4, 5+) as a categorical variable and previous pregnancy status as a binary variable. Because of declines in sample size after age 6, we combined females aged 5 and older into a single age group. Although this approach does not allow for natality rates to be affected by senescence, initial analyses indicated that variation in natality rate declined sharply after age 3 and did not appear to decline in the range of ages that were represented in our data. As with mortality analyses, our decision not to recollar older females likely reduced our ability to detect interactions of natality and its covariates which were more likely in older females (L. G. Adams, personal communication). To account for variability among years, we included a random effect for year on the intercept of the regression. This approach constrains the annual estimates such that they are normally distributed around a mean value. We believed this to be a reasonable assumption because year effects appeared to be consistent across ages and evenly distributed. One important consideration was that natality rates in 1993 were extremely low and well outside the range of variation of the other years in the data set. The approach we used here to estimate annual natality rates would act to pull this extreme year back towards the mean and thus underemphasize this unusual and stochastic event caused by the extreme fall and winter of 1992–1993.

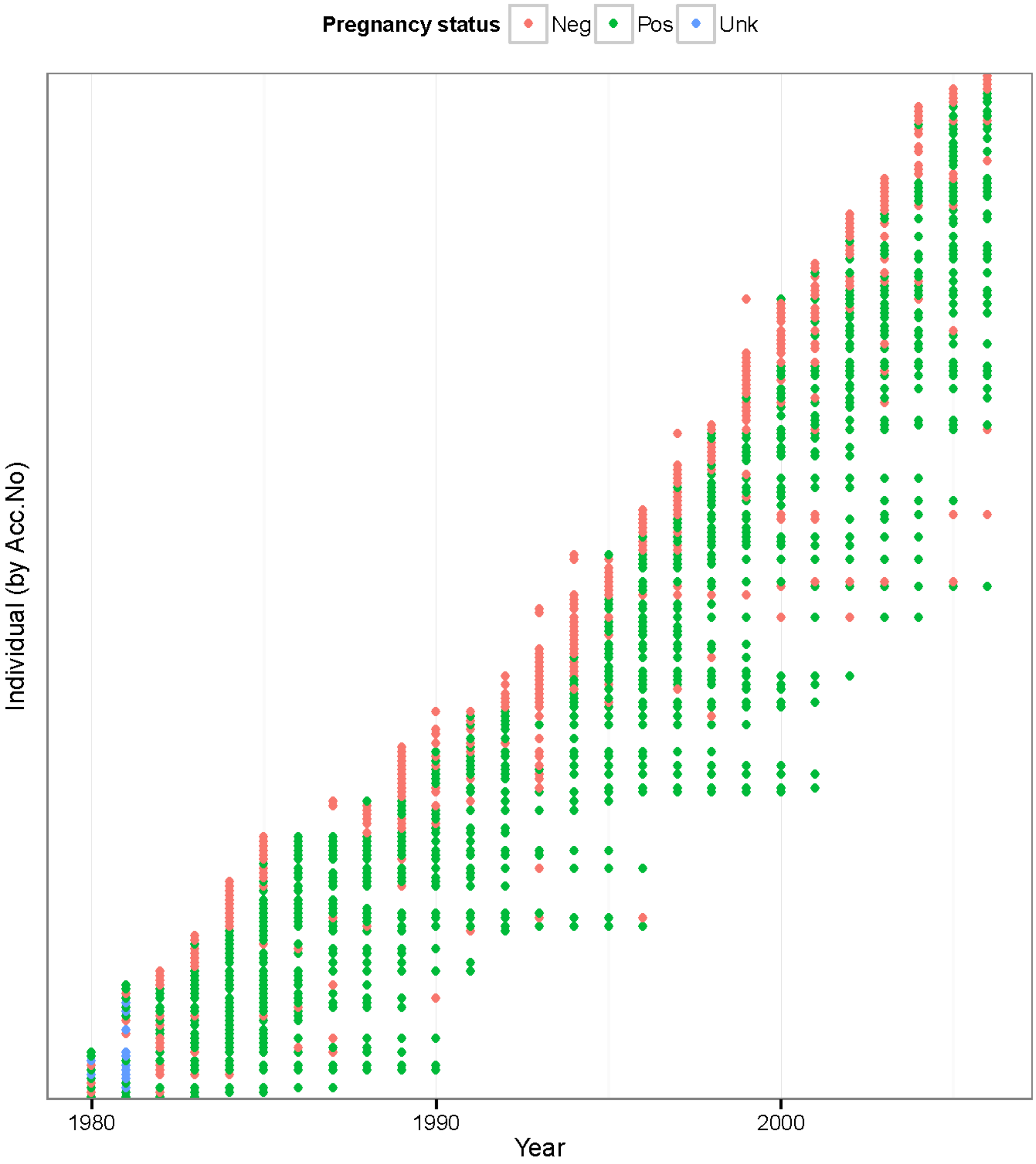


Figure 6. Natality (i.e., pregnancy or parturition) status by individual by year for radiocollared Delta caribou herd females, Alaska, 1980–2007. Blank spaces mean the individual was not located or died. *N* = 220 individuals with 1,077 potential possible calving events.

We used best unbiased linear predictors with corresponding 95% prediction intervals from the random effects model to produce estimated natality rates by age and previous pregnancy status for each year. We included goodness-of-fit measures (R^2; Menard 2000, Nakagawa and Schielzeth 2013) to demonstrate that the model provided a reasonable description of the data. Analyses were restricted to the years 1981–2006. Although data collection began in 1980, only 2-year olds were available for observation in the initial year of the study, so 1980 could not be included in the model as specified above. However, it is important to note that the natality rate for 2-year olds was also unusually high in 1980, and well outside of the range of values observed during the remaining years of the study. Thus, this omission was influential on the results from subsequent analyses on natality.

Modeling Potential Effects of Covariates on Natality

To develop hypotheses for whether or how individual animal and environmental covariates (Tables 6 and 7) were likely to affect natality rates in the Delta herd, we applied an AIC model selection approach using methods similar to those described in the section on modeling survival of radiocollared females. Based on the basic logistic-based natality model described above, we developed a set of candidate models using a stepwise algorithm that incrementally added or removed a single covariate to sample the entire range of possible models. The most comprehensive model we considered contained all environmental covariates, an effect for previous pregnancy status (0, 1), and age as a categorical variable (2, 3, 4, ≥5). Preliminary analysis showed that when environmental covariates were included, these variables could generally account for all the yearly variation found via the mixed modeling approach used previously ($\sigma^2_{yr} = 0$). Therefore, our final analysis was based on logistic regression models with no random terms. We again evaluated goodness of fit of these models using both deviance ratios (Menard 2000) and latent variable methods (Nakagawa and Schielzeth 2013).

Our decision not to recollar females >age 8 resulted in likely underrepresentation of females in age classes older than 14. Although older females would usually have comprised only a small minority of all females in the Delta herd, natality in these females would have been more likely to be influenced by environmental covariates.

EFFECTS OF ENVIRONMENTAL COVARIATES ON CALF WEIGHT AND CALF:COW RATIOS IN THE DELTA HERD

Modeling Calf Weight

We decided to explore possible relationships between mean weight of cohorts of calves and environmental variables (Figs. 4 and 5) by modeling mean weight of calves at 4 months (*cohort.mean.wt2*; available for 1991–2007) and mean weight of calves at 10 months (*cohort.mean.wt3*; available for 1979–2007) as response variables. There was evidence from the preliminary data analysis and from survival and natality modeling that weight of individual calves (i.e., *initial.weight*) continued to have an influence on survival of radiocollared Delta herd females through 40 months of age and on natality of radiocollared females as well (see sections above on modeling survival and natality of radiocollared caribou). Also, there is abundant

Table 6. Individual animal variables used in logistic regression models of natality rates, Delta caribou herd, Alaska, 1980–2007. Variable names are in italics.

Variable	Variable name	Description
Accession number	*Acc.No*	Unique identification number given to each individual caribou
Year	*NominalYear*	Year in which a birth (or lack thereof) occurred
Age	*Age.at.MortYr*	Age in May of the year (0 = birth year, 1 = yearling, etc.)
Initial weight	*initial.weight*	Weight at capture (kg) (4 or 10 months old)
Girth	*girth*	Circumference of chest just behind the forelegs and hump (cm) at capture
Weight:Metatarsus ratio	*wt.ratio*	Ratio of initial weight (kg):metatarsus length (cm, measured with caliper) at capture
Pregnancy/natality status	*preg*	Indicator variable (0 = not pregnant, 1 = pregnant) of status in May
Previous pregnancy	*Prev.preg*	Indicator variable (0 = not pregnant, 1 = pregnant) of status in previous May

Table 7. Description of environmental covariates used in logistic regression models of natality rates, Delta caribou herd, Alaska, 1980–2007. Variable names are in italics.

Variable	Variable name	Description	Timing
Summer rainfall	*summer.rain*	Total rainfall during Jun, Jul, and Aug (cm)	NominalYear-1
Mean summer temperature	*summer.mean.temp*	Average of monthly mean temperatures for Jun, Jul, and Aug	NominalYear-1
Snow depth	*snow.yr*	Sum of snow depth measurements (cm) for 1 Feb, 1 Mar, 1 Apr at Denali Park climate station	NominalYear-1
Snow depth	*snow.yr*	Sum of snow depth measurements (cm) for 1 Feb, 1 Mar, 1 Apr at Denali Park climate station	NominalYear-2
Current year snow depth	*Curr.snow.year*	Sum of snow depth measurements (cm) for 1 Feb, 1 Mar, 1 Apr at Denali Park climate station	NominalYear
Caribou herd size	*n.caribou*	Number of caribou counted in the Delta caribou herd in late Jun	NominalYear-1
4-month cohort mean weight	*4.mo.mean.wt*	Mean weight of 4-month-old calves	Nominal Year-1
10-month cohort mean weight	*10.mo.mean.wt*	Mean weight of 10-month-old calves	Nominal Year

literature on northern cervids that suggests mean weights of cohorts of calves could integrate a suite of complex weather and environmental variables (c.f. Reimers et al. 1983; Skogland 1984, 1990; Valkenburg et al. 2003b; Dale et al. 2008). Cohort mean weights by year were modeled using linear regression with covariates representing environmental conditions in each year. We developed sets of candidate models using the same AIC model selection algorithm as in previous sections and the same global model for both response variables. However, compared with the survival models, we added potential interactions with *cohort.mean.wt1* (the previous cohort's mean 10-month weight) to account for multiyear effects. We also added *Denali.snow.lag1* to look for potential cumulative effects of severe winters on calf weight. Again, the smallest model tested was a model with the intercept only. The largest (global) models contained the following covariates: *summer.rain, summer.mean.temp, aug.min.temp, length.green, cohort.mean.wt1, wolf.index*n.caribou, n.caribou*Denali.snow, wolf.index*Denali.snow, cohort.mean.wt1*n.caribou, cohort.mean.wt1*wolf.index, n.caribou*Denali.snow.lag1, wolf.index*Denali.snow.lag1, and cohort.mean.wt1*Denali.snow.lag1*).

Modeling Calf:Cow Ratios

From examination of the Delta caribou herd data set it was apparent that recruitment of calves to fall (i.e., fall calf:cow ratio) was likely the major factor determining population change in the Delta herd. Also, the fact that natality rates of caribou ≥4 years were generally high with little variability indicated that calf survival over the summer would likely be the primary factor that influenced fall calf:cow ratio. Postcalving survival of caribou calves has also been closely linked with newborn calf weights; newborn calf weights have been associated with previous winter snow and late snowmelt (Adams et al. 1995a,b; Mech et al. 1998), and could also be influenced by their weight gain over summer which would vary with weather conditions. We modeled the effects of a suite of potentially explanatory covariates on fall calf:cow ratio to develop hypotheses about factors that have the greatest influence on this variable. Because individual caribou cows produce only 1 calf per year, we treated calf:cow ratios as grouped binary responses rather than count-based response. We again used mixed logistic regression to model the calf:cow ratio as the percent of cows producing calves (generalized linear mixed model with binomial error and a logit link function; Bates et al. 2014). The smallest model tested was a model with the intercept only, and the largest (global) model contained the following covariates: *cohort.mean.wtSPR* (mean weight of 10-month cohorts), *Denali.snow, length.green, n.caribou, part* (predicted year effect for parturition rate), *summer.mean.temp, end.green, greenup, july.rain, wolf.index,* and *summer.rain.*

We were particularly interested in whether observed spring natality rates had a strong influence on fall calf:cow ratios. A key approach in modeling fall calf:cow ratio was that we developed an additional potential explanatory variable (*part*) that summarized annual herd natality across all age classes. We realized that there was likely some bias in the variable "*part*" because our sample of radiocollared underrepresented older females and older females may have been less likely to be pregnant. We obtained the annual estimates for *part* from the previous descriptive modeling of natality which included effects of age, previous pregnancy, and a random intercept for each year but with no other external explanatory variables. We used the estimated year effect from the best unbiased linear predictors as an index of the natality rate across ages and previous pregnancy status across years. While we followed the same model selection procedure as in previous sections, we also took particular care in interpreting the coefficient for *part* in the analyses. As with previous modeling of survival and natality, associations among explanatory variables complicated model selection and interpretation of results.

MONITORING SEASONAL DISTRIBUTION AND DETECTING EMIGRATION-IMMIGRATION IN THE DELTA CARIBOU HERD

Seasonal Movements

To estimate seasonal range use occurring during calving, summer, rut, and winter, we segregated pooled location data into 4 time periods: 1979–1985, 1986–1991, 1994–2000, and 2001–2007. We used locations collected during 1 June–15 August for summer, 15 September–15 October for rut, and 15 November–30 March for winter. We mapped locations obtained during the rut in 1992 and winter range for 1992–1993 separately because of the unusual movements of the Delta herd that was triggered by the storm event of September 1992 (see sections on *Movements and Distribution of Caribou During "The Perfect Storm"* and *Movements and Evidence for Dispersal of Radiocollared Caribou in the Delta, Denali, and White Mountains Herds After "The Perfect Storm"*). We generated utilization distributions for the pooled intervals using the reference bandwidth and mapped the 90% volume contour. The Parks Highway was used as a physical boundary during the rut, following the methods of Benhamou and Cornelis (2010). Because no caribou (collared or uncollared) were ever observed west of the highway during this season and without using a physical boundary, the 90% volume contour falsely projected occupation west of this boundary. To delineate annually used calving areas, we selected a single location for each radiocollared female caribou (24-months old or older) that we judged was closest to the site where her calf was born that year. For females that were judged not pregnant or of unknown status, we used the location that was temporally nearest to the date of peak calving during 15–30 May. Unlike the other seasonal ranges, calving ranges were generated separately for each year; locations were not pooled across years. All analyses were performed in R using the adehabitatHR package (R Development Core Team 2007, Calenge 2011).

Emigration-Immigration

We defined emigration (or dispersal) from the Delta herd as a case where an individual caribou that was radiocollared as a calf within the normally used range of the Delta herd left the range of the Delta herd and calved outside of the known range. These dispersals could have occurred either through mixing with groups of caribou from adjacent herds or wandering by lone individuals. We defined immigration as an event where a radiocollared caribou documented to have calved on a calving area of one of the surrounding herds, moved to and calved within the Delta herd's range. We placed radiocollared caribou that died outside the known range of the Delta herd without having calved there in a separate category. We also distinguished "dispersals" from the range expansions that occurred several times within the 29-year period of the study. In addition, we increased the frequency of radiotracking flights beginning in late September 1992, to thoroughly document the unusual movements of caribou that occurred following the "perfect storm" of September 1992 (Cole et al. 1999, Adams et al. 2005). This weather event resulted from a combination of reduced regional temperatures (partly from global cooling from the eruption of Mount Pinatubo in the Philippines on 15 June 1991; Self et al. 1996), and a powerful early winter storm that tracked into central Alaska from the northwest during 12–15 September 1992 and became stalled over the central Alaska Range. Precipitation for September was 330%

of normal for Denali Park and the September monthly temperature was 8.4°C below normal, so almost all the precipitation for the month fell as snow (Cole et al. 1999, Adams et al. 2005). By the end of the storm, snow depths in most areas of Interior Alaska (including Fairbanks) were >50 cm. The storm triggered unusual caribou movements, particularly for the Denali and Delta caribou herds. These caribou movements were unusual, interesting, and rare, and it was the first time that biologists had been able to document these kinds of apparently stochastic and unusual movements with radio collars. As these movements began to occur, we realized that they had the potential to provide historical context for previously documented and possibly similar unusual movements of caribou documented by Skoog (1968) that were previously considered to be evidence of mass dispersal.

DETERMINISTIC POPULATION MODELS OF THE DELTA CARIBOU HERD

During the 1980s, as desktop computers and spreadsheet software programs (e.g., IBM® Lotus 1-2-3, Microsoft Excel, etc.) became available, management biologists became interested in these technologies as an aid in calculating annual harvestable surpluses and predicting the size of caribou herds in years when censuses were not conducted. To help with this effort, during the late 1980s, we constructed a deterministic spreadsheet model of the Delta herd that could be adapted for use in all caribou herds. We started with an initial population of 3,000 cows and used the 1969 calf:100 cow (28:100) and bull:100 cow (40:100) ratios (Table 1) as a starting point. We chose 1969 for the starting year because we wanted to go as far back in history as possible while having enough data for inputs (i.e., calf:cow and bull:cow ratio data). We estimated starting population size (1969) based on the 1964 estimate of 6,250 caribou and projected a continuous decline toward the first reliable (APDCE photocensus) estimate from 1973. Then, by manipulating female and male survival rates by trial and error, and using the observed fall calf:cow ratio (with occasional adjustment if needed) for recruitment, we made the modeled population (calculated at the end of the hunting season) track the observed fall bull:cow ratio and arrive at the 1973 summer estimate of 2,804 caribou in late June 1973. By continuing to adjust male and female survival rates and using the observed calf:cow ratios as inputs, we continued to make the model track summer census results and the bull:cow ratios observed in fall composition counts. While this approach produced a crude population model that averaged survival rates over all age classes regardless of age structure, we believe this approach was better than trying to construct a more complex model with many more age classes and more untested assumptions.

We then used the spreadsheet model to compare survival rates needed as inputs to make the model track with those calculated from radiocollared caribou. To calculate survival rates comparable to those needed for the spreadsheet model inputs, we used all radiocollared females older than 4 months and calculated a crude survival rate for them annually. One problem with this approach was that the spreadsheet model considered all females older than 4 months as adults, so it was not directly comparable to survival calculations from regression modeling which separated calves, yearling, and adults. Also there were varying numbers of calves and yearlings in the radiocollared sample each year and, before 1990, calves were generally collared at 10 months of age rather than 4 months of age. The major reason we attempted this comparison was that the spreadsheet model was found to be useful (and became widely used) by ADF&G staff to track caribou population size in years when censuses were not conducted and to calculate potential harvestable surpluses of bulls and cows. In herds where sufficient numbers of radiocollared caribou were also available, biologists have also used them to annually estimate survival of caribou for management purposes. So, even though the above comparison had shortcomings, we considered it a useful exercise with which to further explore the utility and pitfalls of the spreadsheet modeling approach as an aid in caribou management.

Results

MONITORING CHANGES IN CARIBOU HERD SIZES

Delta and Denali

From 1970 to 2007, APDCE or total count censuses were successful in 1973, in all years from 1979 through 2004, and in 2007 in the range of the Delta herd. The "Yanert herd," which was recognized from 1979 to 1984 and numbered up to 600, was included in all estimates for the Delta herd (Fig. 7; Appendix A).

From 1978 to 2007 the Delta caribou herd went through 4 growth phases. From 1978 to 1982 it grew rapidly (λ~1.20) (Fig. 7). However, there were few radio collars on caribou then and the censuses may have lacked the accuracy of later censuses because the radiocollared caribou provided a better idea of herd distribution. During 1982–1989 the Delta herd grew at a more moderate rate (λ~1.05–1.07), and reached a peak population size of 10,690 in 1989. Between 1989 and 1993 the Delta caribou herd declined rapidly (λ~0.80) to about 3,600 in 1993. After a slow increase during a few years in the mid-1990s, the herd then slowly declined again before stabilizing at 2,500–3,000 during 2001–2007.

Regular monitoring of herd size and fall composition in the Denali herd began in 1986; prior to 1986 only the 1976, 1978, and 1984 censuses were considered to be reliable estimates (L. G. Adams, personal communication). The Denali herd generally followed a growth pattern that was similar to the pattern in the Delta herd, but population changes in the unmanaged and essentially unharvested Denali herd were much less pronounced and the herd was essentially stable from 1993 to 2008 (Fig. 7).

Other Alaska Caribou Herds

After the increased emphasis on caribou research and management in the late 1970s, most caribou herds in Alaska were counted every 2–5 years (Figs. 8–12, Appendix A). During the late 1970s and early 1980s, most caribou herds in Alaska grew during mild winters and they recovered from the statewide low population levels of the early to mid-1970s. However, population trajectories of individual herds varied widely. By the late 1980s, many Interior caribou herds peaked in population size (e.g., Chisana, Delta, Denali, Macomb, Mentasta, and probably Beaver Mountains and Sunshine Mountains) while other Interior herds continued to grow (e.g., Fortymile, Nelchina, Ray Mountains, and White Mountains) (Figs. 8 and 9). In the Delta and Nelchina herds, harvest influenced herd growth. The Southwest Alaska caribou herds and the Arctic herds (except Porcupine) did not follow the same general pattern of growth as the Interior herds (Figs. 8–10). The Southern Alaska Peninsula herd peaked in 1983 followed 2 years

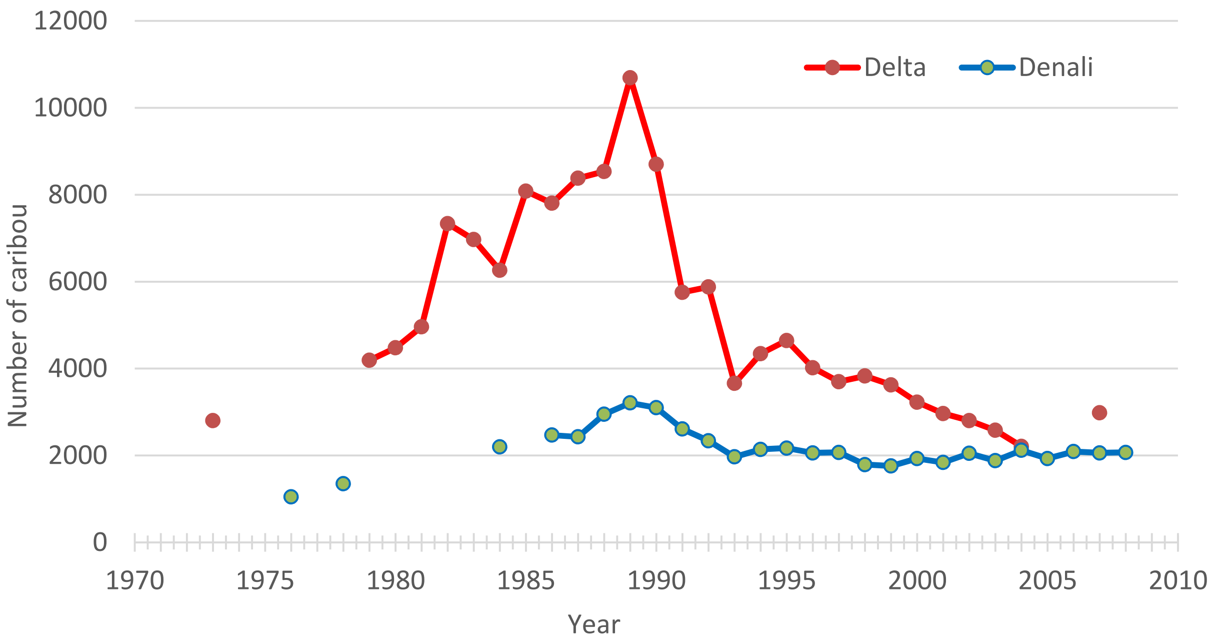


Figure 7. Population size and trend in the Delta and Denali caribou herds, Alaska, 1970–2008.

later by the Northern Alaska Peninsula herd, while the Mulchatna herd continued growing through 1997. By the mid-1990s, 2 of the state's largest caribou herds were reaching historic highs (i.e., Mulchatna and Western Arctic) (Fig. 10). The high population size of these herds combined with the relatively high populations in the Central Arctic, Nelchina, Northern Alaska Peninsula, and Teshekpuk herds resulted in the highest documented caribou population (approximately 930,000) in Alaska from ~1995 through ~2003. After 2003, declines in the 2 largest herds (Western Arctic and Mulchatna) more than offset the continuing rapid growth of the Central Arctic and Teshekpuk herds, and statewide caribou numbers declined.

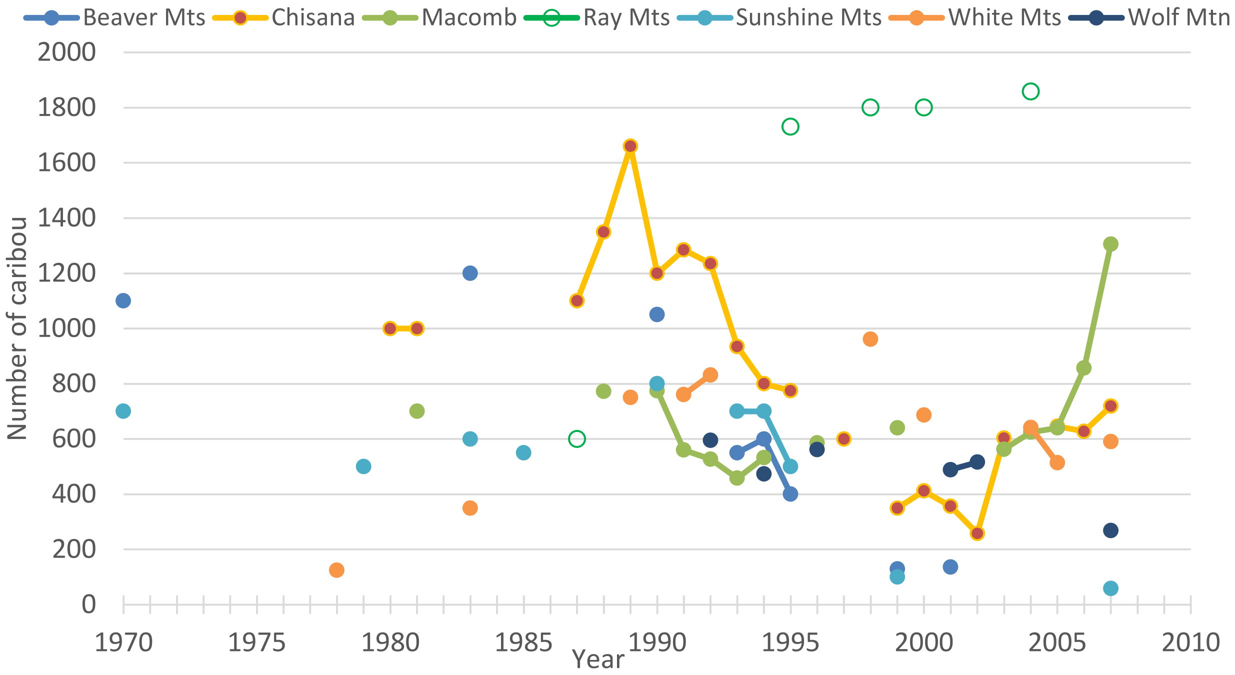


Figure 8. Size of 8 small (maximum<2,000) Interior Alaska caribou herds, 1979–2007.

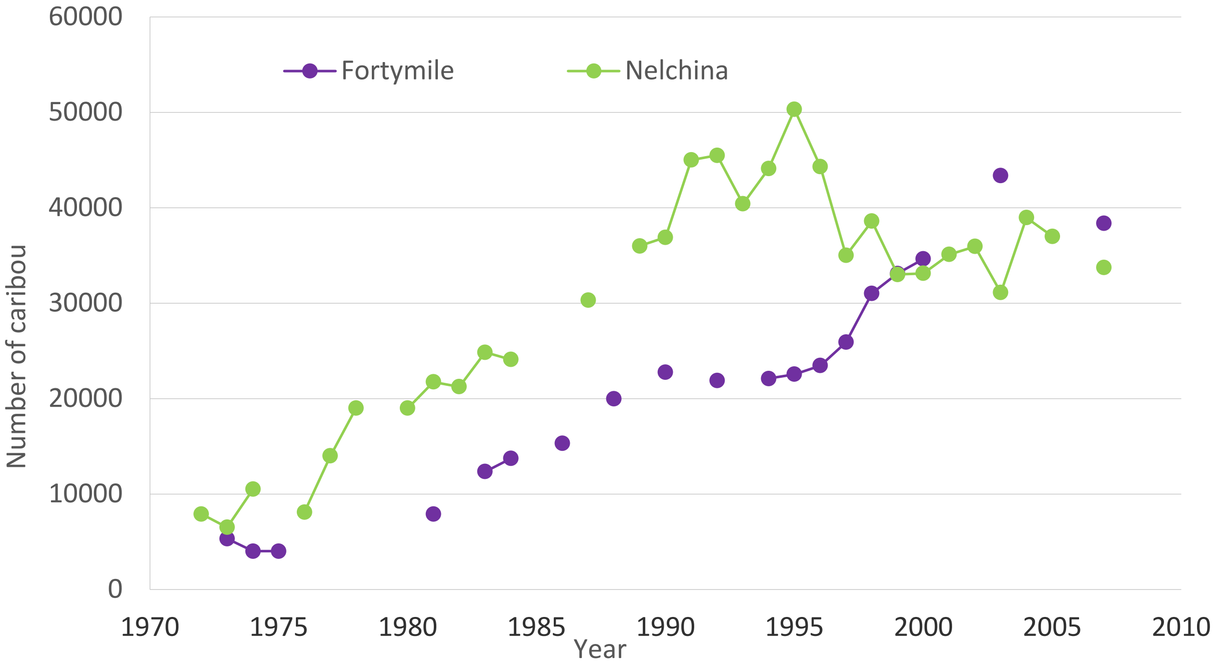


Figure 9. Size of the Fortymile and Nelchina caribou herds in Interior and Southcentral Alaska, 1970–2008. Nelchina size restrained by harvest after 1995.

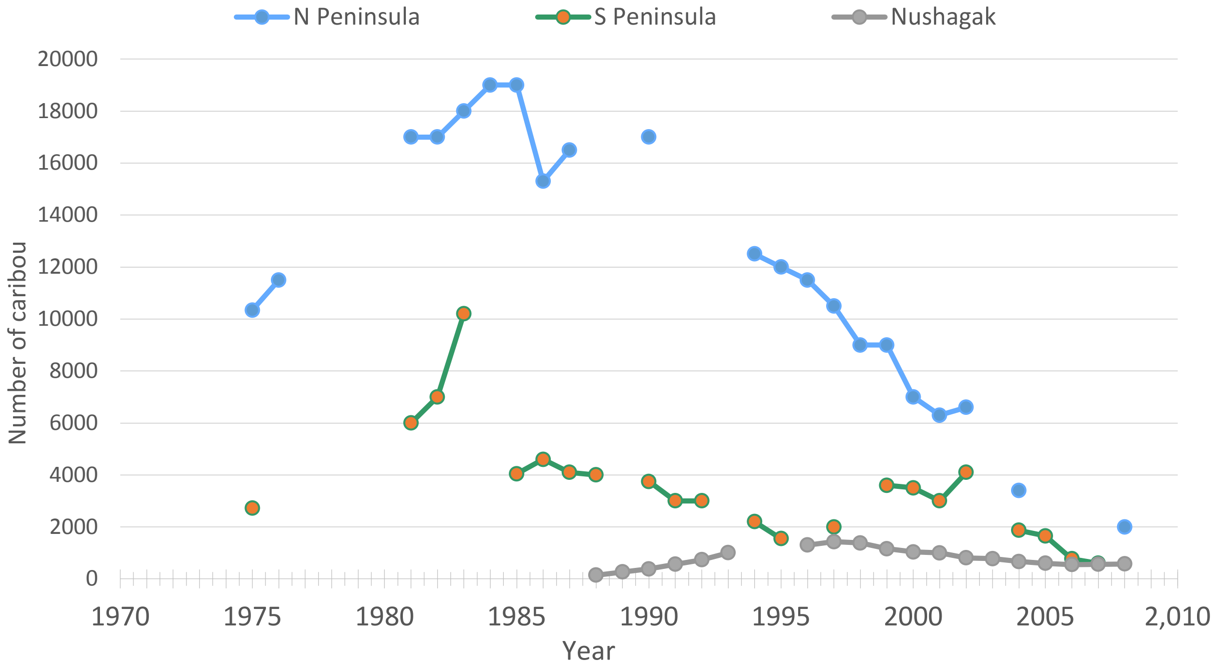


Figure 10. Size of 3 small- to medium-sized caribou herds in Southwest Alaska, 1980–2008. The 1983 peak size of the Southern Alaska Peninsula herd may represent an overestimate.

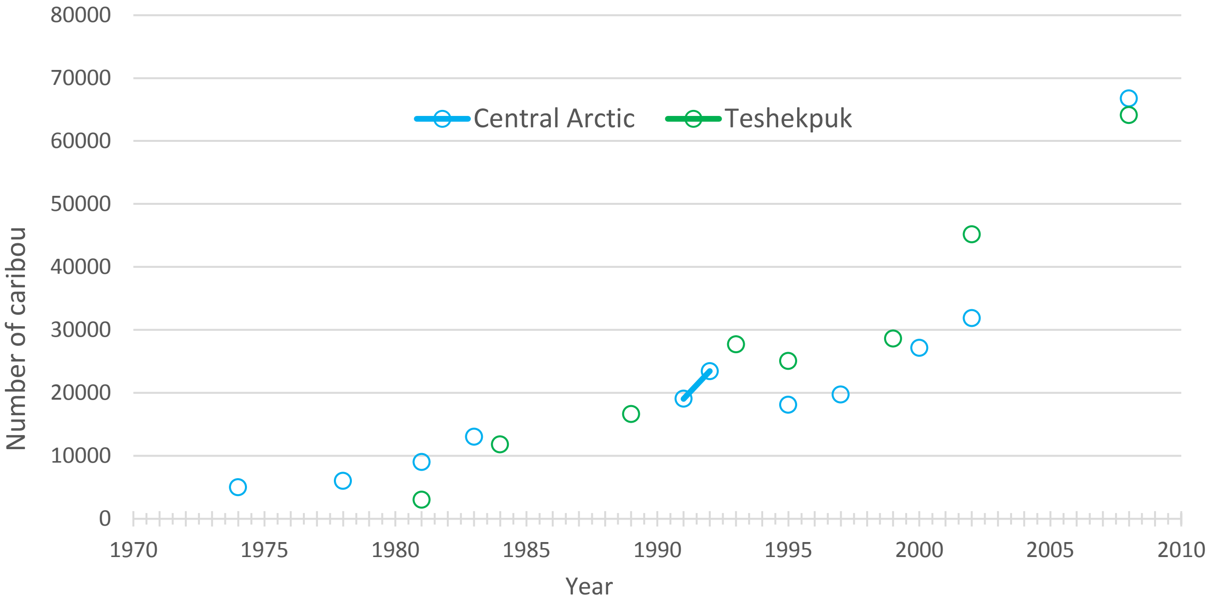


Figure 11. Size of 2 medium-sized but increasing Arctic caribou herds, Alaska, 1974–2008.

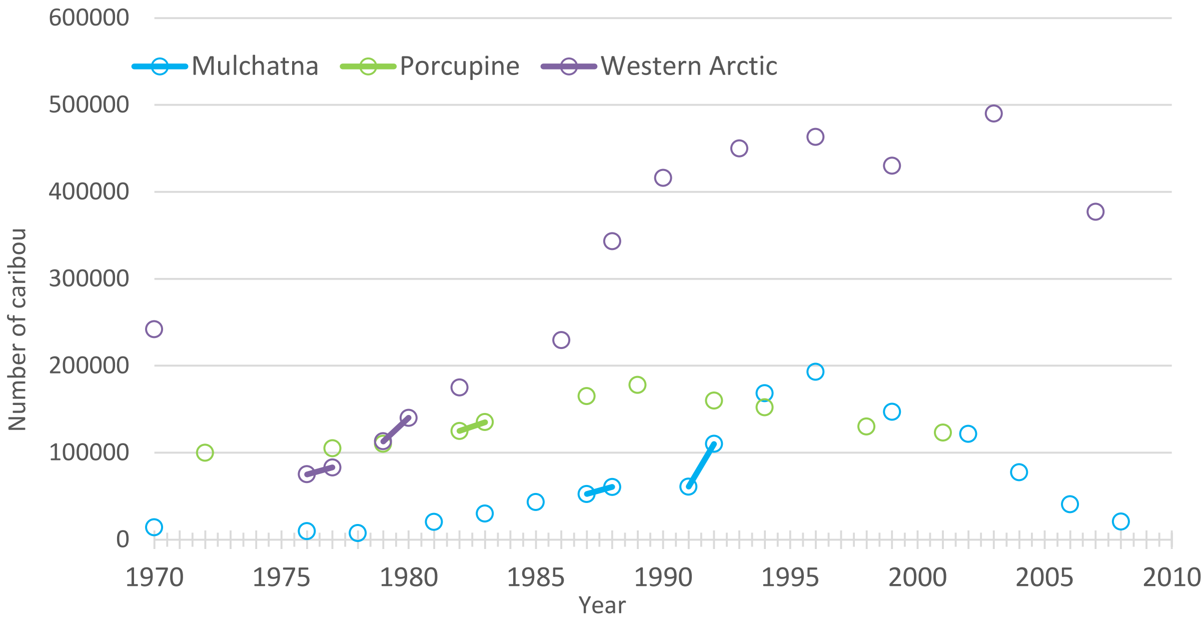


Figure 12. Size of very large (maximum >100,000) Alaska caribou herds, 1970–2008.

CALF:COW RATIOS

Observed calf:cow ratios in the Delta herd varied annually, from about 2 in 1974 to about 65 in 1979 (Fig. 13, Table 1). The lowest ratios observed were coincident with periods of deep snow winters and high wolf numbers in the early 1970s and early 1990s (Gasaway et al. 1992, National Research Council 1997; Fig. 13). The highest ratios observed were in the late 1970s and early 1980s during a period of low wolf numbers and low snowfall.

As in the Delta herd, we found that recruitment of calves to fall (expressed as calves:100 cows or percent calves) varied considerably in other caribou herds as well, and we also found that recruitment was more variable and generally lower in the smaller caribou herds than in the larger herds (Figs. 14–19). The timing of periods of poorer recruitment in many Interior herds was often similar. Although data were relatively incomplete for the Arctic herds, calf:cow ratios (or proportions of calves) were generally higher and less variable than in the Interior and Southwest Alaska herds (Figs. 14–19; Appendix B). In some small herds (e.g., Delta, Chisana, Galena Mountain, Mentasta, Southern Alaska Peninsula, and Unimak) total or near total recruitment failures (i.e., calf:cow ratios <5:100) occurred. These kinds of near total recruitment failures were not observed in the Arctic herds.

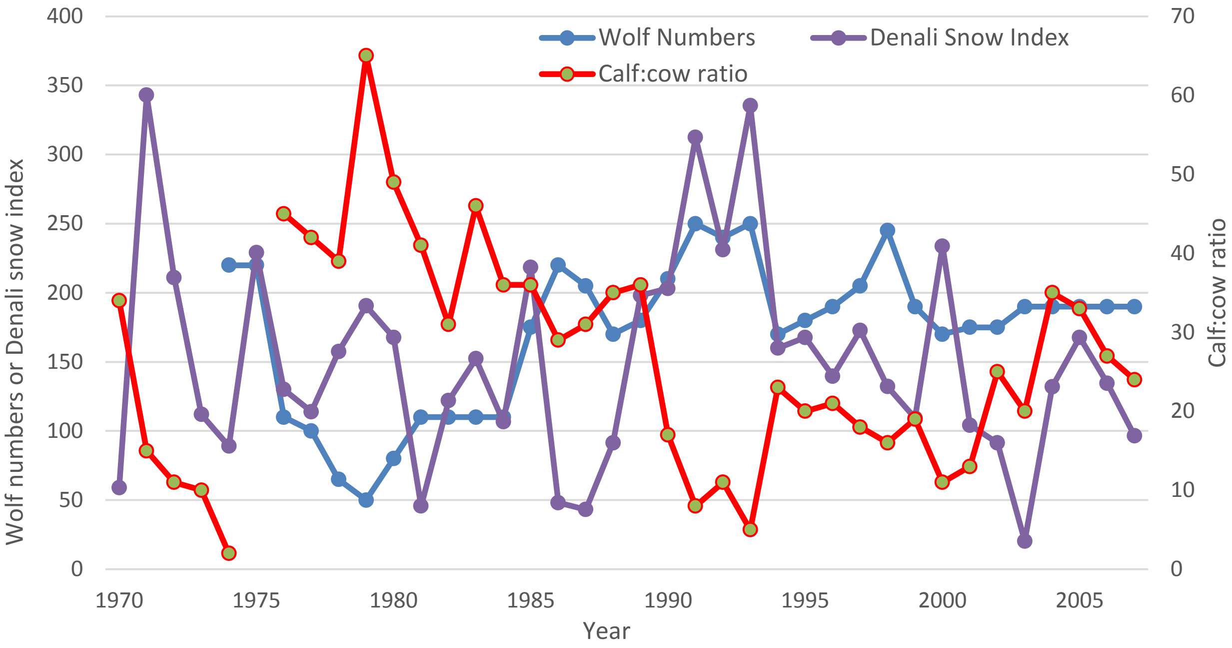


Figure 13. Fall calf:100 cow ratios in the Delta caribou herd, Denali snow index, and estimated wolf numbers within the range of the Delta herd, Alaska, 1970–2007. Denali Snow Index is the sum of 1 February, 1 March, and 1 April snow-on-ground readings converted to centimeters. Average for 1970–2008 = 151.

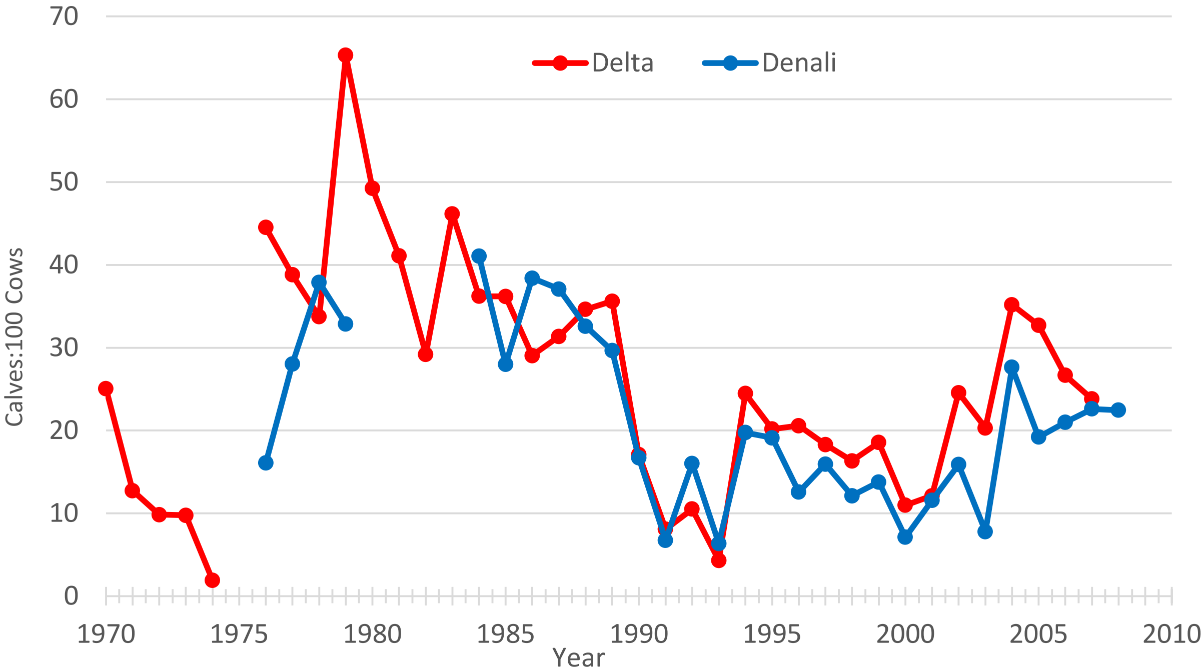


Figure 14. Fall calf:cow ratios in the Delta and Denali caribou herds, Alaska, 1970–2008.

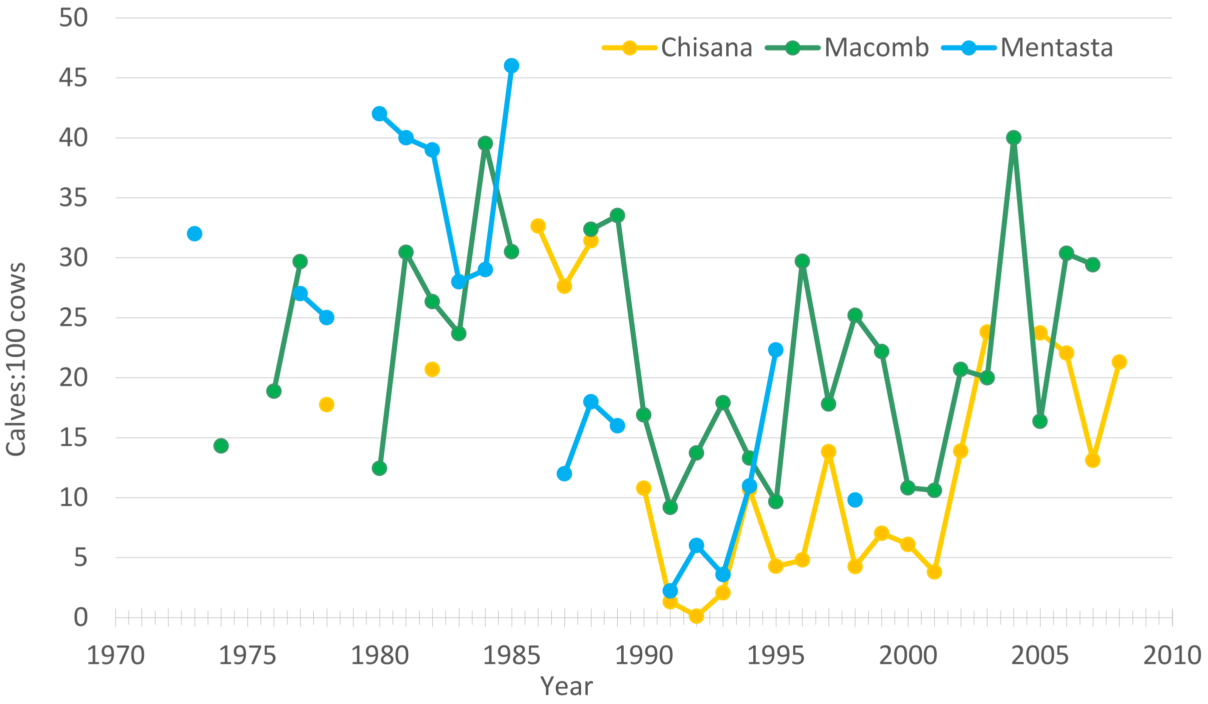


Figure 15. Fall calf:cow ratios in the 3 small (<2,000) eastern Interior-Southcentral Alaska caribou herds, 1970–2008.

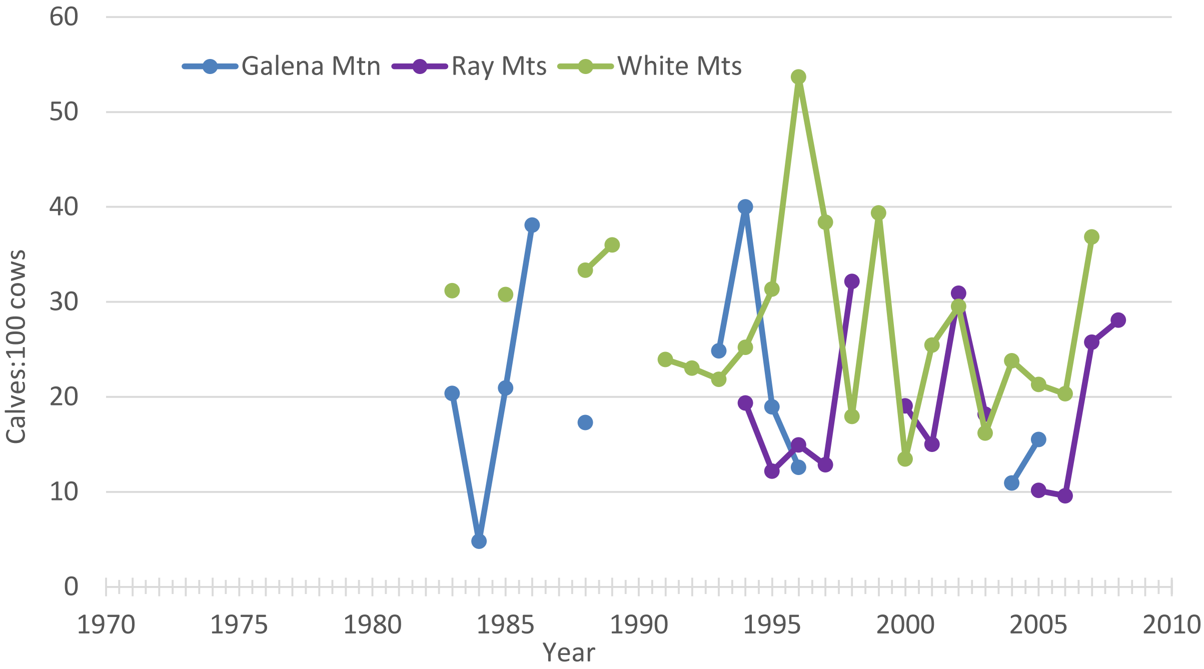


Figure 16. Fall calf:cow ratios in 3 small (<2,000) Western Interior Alaska caribou herds, Alaska, 1970–2008.

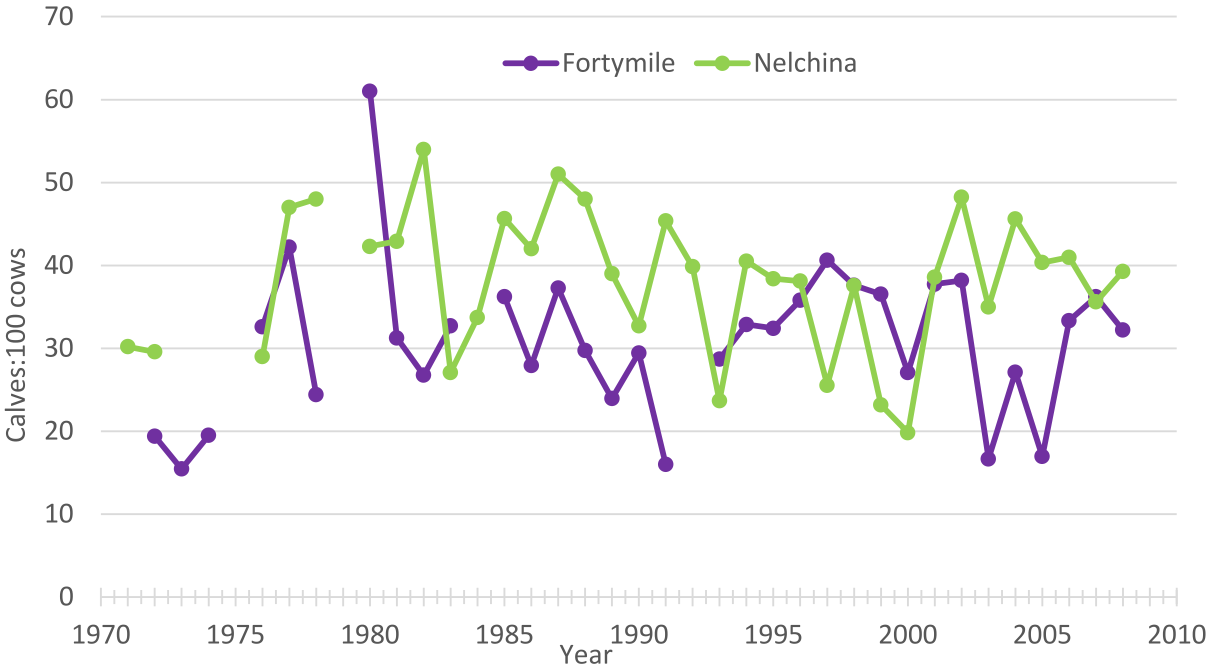


Figure 17. Fall calf:cow ratios in the Fortymile and Nelchina caribou herds, Alaska, 1970–2010.

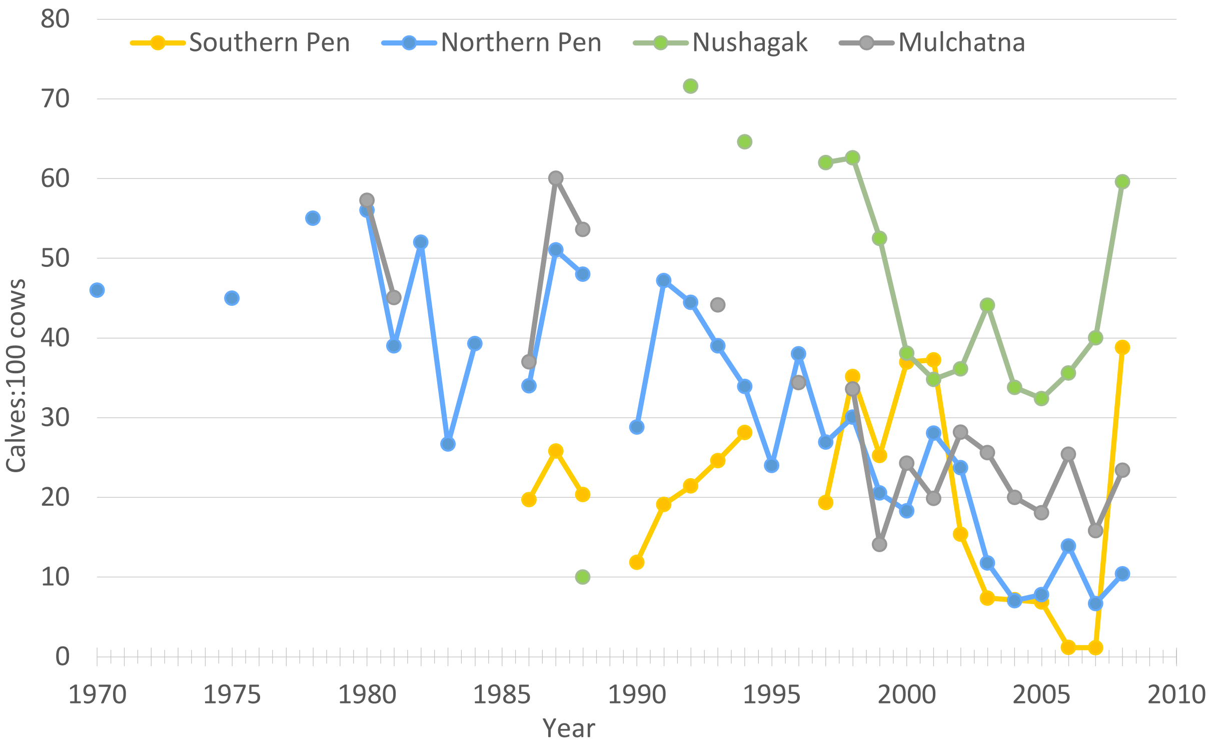


Figure 18. Fall calf:cow ratio in 4 Southwest Alaska caribou herds, 1970–2008.

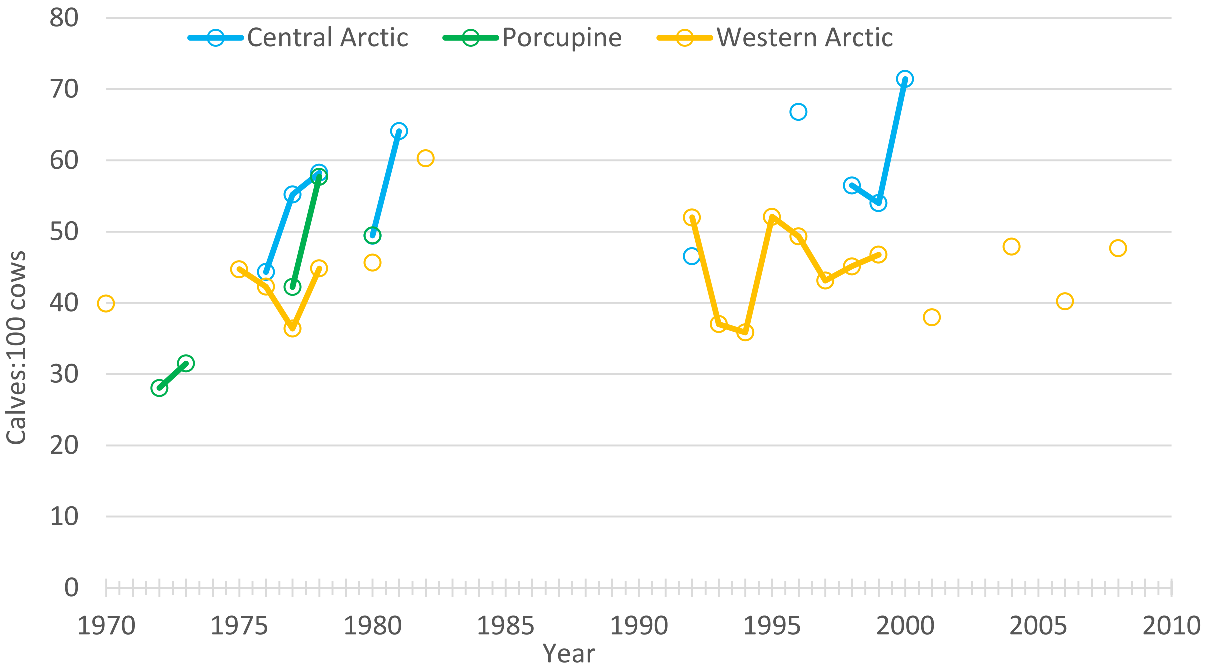


Figure 19. Calf:cow ratios in fall in 3 Arctic Alaska caribou herds, 1970–2008.

BULL:COW RATIOS

During 1981–2007 (years with the most reliable estimates), observed bull:cow ratio in the Delta herd ranged from a low of about 22:100 to over 80:100 with the lowest ratios occurring during and after periods with low calf:cow ratios (Figs. 14 and 20; Table 1). During the mid-1990s, following the period of low recruitment in the Delta herd and most other Interior caribou herds, bull:cow ratios were low and similar in both the Delta (which had been hunted) and the adjacent Denali herd, which was essentially unhunted (Fig. 20; L. G. Adams, personal communication). After 1997, bull:cow ratios were generally higher in the Delta herd than in the Denali herd, despite continued hunting in the Delta and no hunting in the Denali.

Bull:cow ratio varied from a low of ~10 bulls:100 cows to a high of ~85 bulls:100 cows in caribou herds other than the Delta herd, and reached lowest levels in herds in Southwest Alaska (Figs. 21–24). In the Western Arctic herd (the only Arctic herd for which sex ratio data were routinely collected), fall bull:cow ratios remained consistently higher than in Interior and Southwest caribou herds, despite relatively heavy harvests that were focused on bulls in fall, especially during the fall Kobuk River crossing (Fig. 24; Appendix B; Dau 2009). As in the Delta-Denali comparison, we observed low bull:cow ratios in caribou herds during and after periods of low calf recruitment whether herds were being hunted or not (Figs. 21–24; Appendix B; Butler 2009a,b). Bull:cow ratios in the Central Arctic herd occasionally exceeded 100 bulls:100 cows, probably indicating that bulls from other Arctic herds were included in surveys of the Central Arctic herd in fall (Fig. 24; Appendix B; Valkenburg 1992).

Small Bull:Cow Ratios

We examined small bull:cow ratios in 3 Interior herds with relatively complete and continuous data to determine how well these ratios compared with the current year and previous 1-, 2-, and 3-year fall calf:cow ratios (Figs. 25–30). As expected, small bull:cow ratios roughly lagged fall calf:cow ratios in the 3 herds and they were much less variable (Figs. 25–27). From these analyses, it was apparent that the category “small bulls” includes more age classes than yearling and 2-year-old bulls. Relationships between small bull:cow ratios and previous calf:cow ratios generally continued to improve with the addition of more cohorts from previous years (Figs. 28–30). In the Delta herd, the relationship between fall calf:cow and subsequent small bull:cow was not improved by including a factor for modeled mean calf survival with 1- and 2-year lags in the Delta herd (Fig. 31). We did observe a somewhat stronger relationship between fall calf:cow ratios and subsequent small bull:cow ratios in the Denali herd which was unhunted and where composition counts were conducted continuously by the same observer (L. G. Adams, personal communication; Fig. 30).

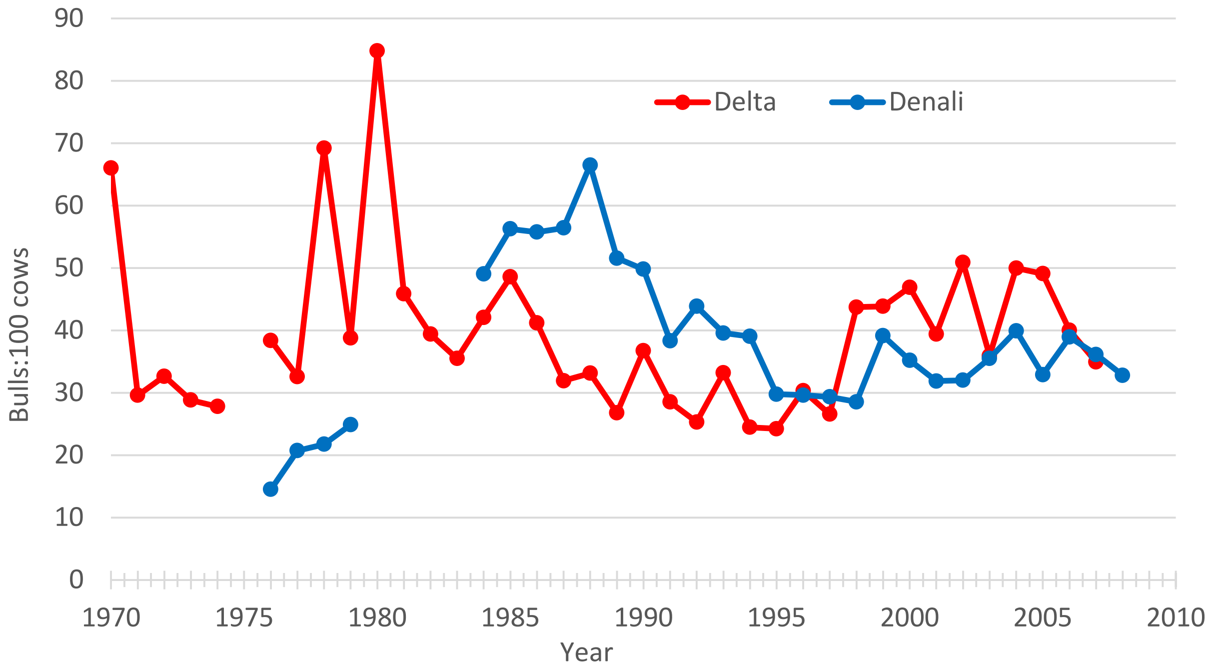


Figure 20. Bull:cow ratios in Delta and Denali caribou herds, Alaska, 1970–2008.

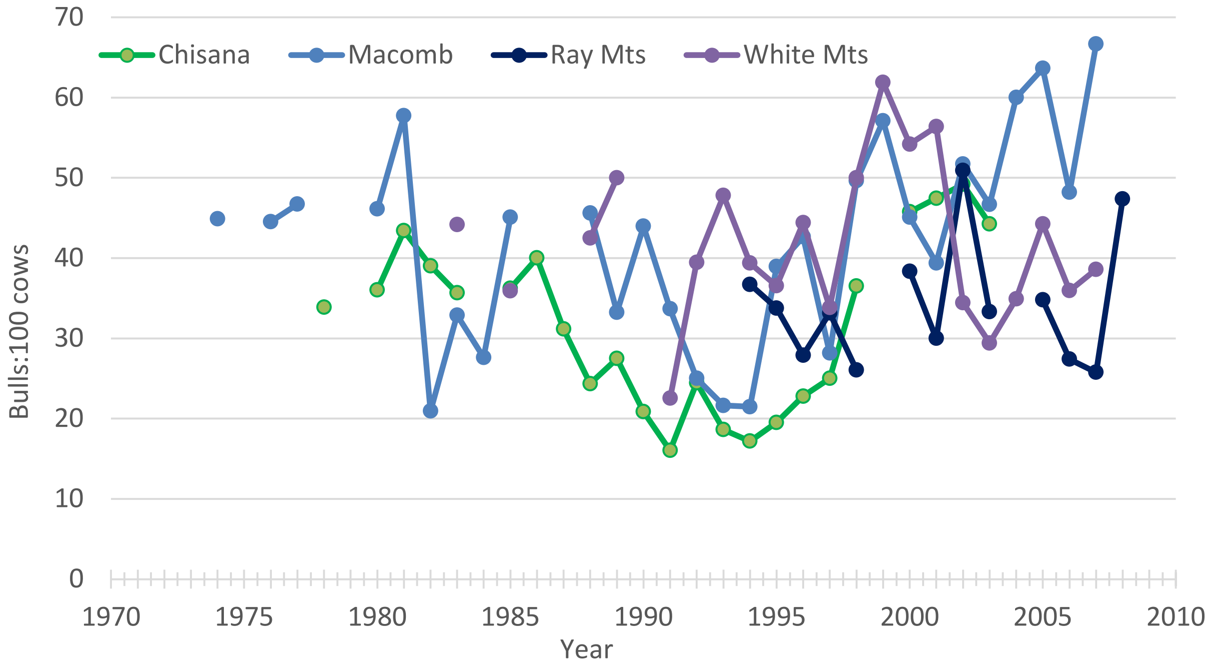


Figure 21. Bull:cow ratios in the Chisana, Macomb, Ray Mountains, and White Mountains caribou herds, Alaska, 1970–2008.

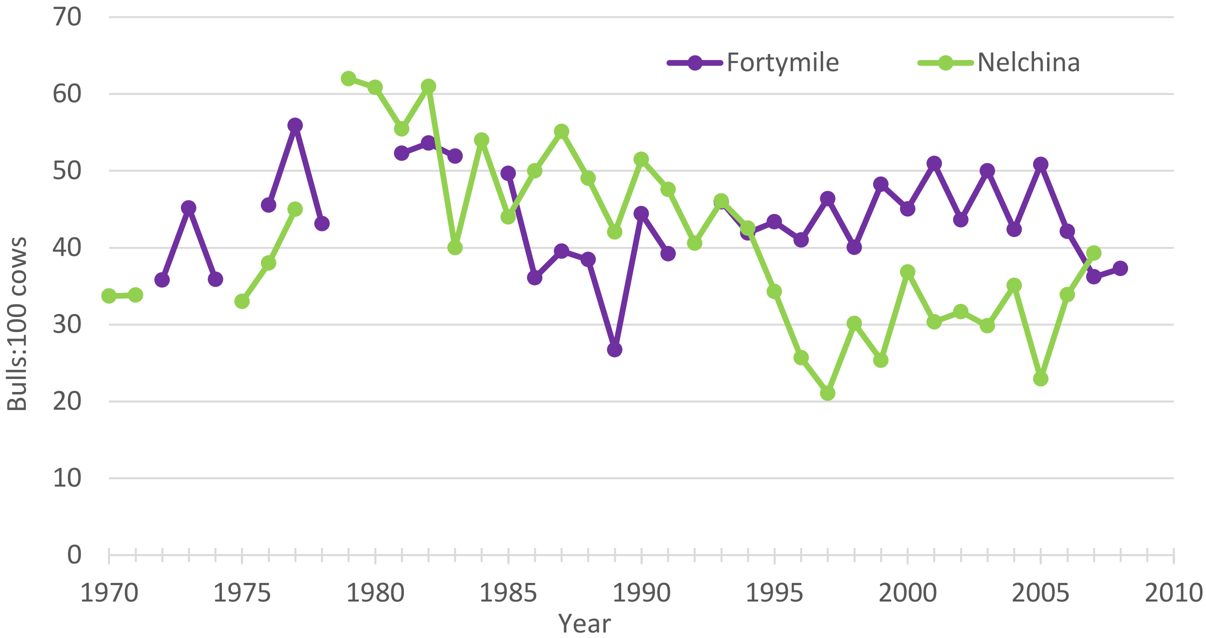


Figure 22. Bull:cow ratios in Fortymile and Nelchina caribou herds, Alaska, 1970–2008.

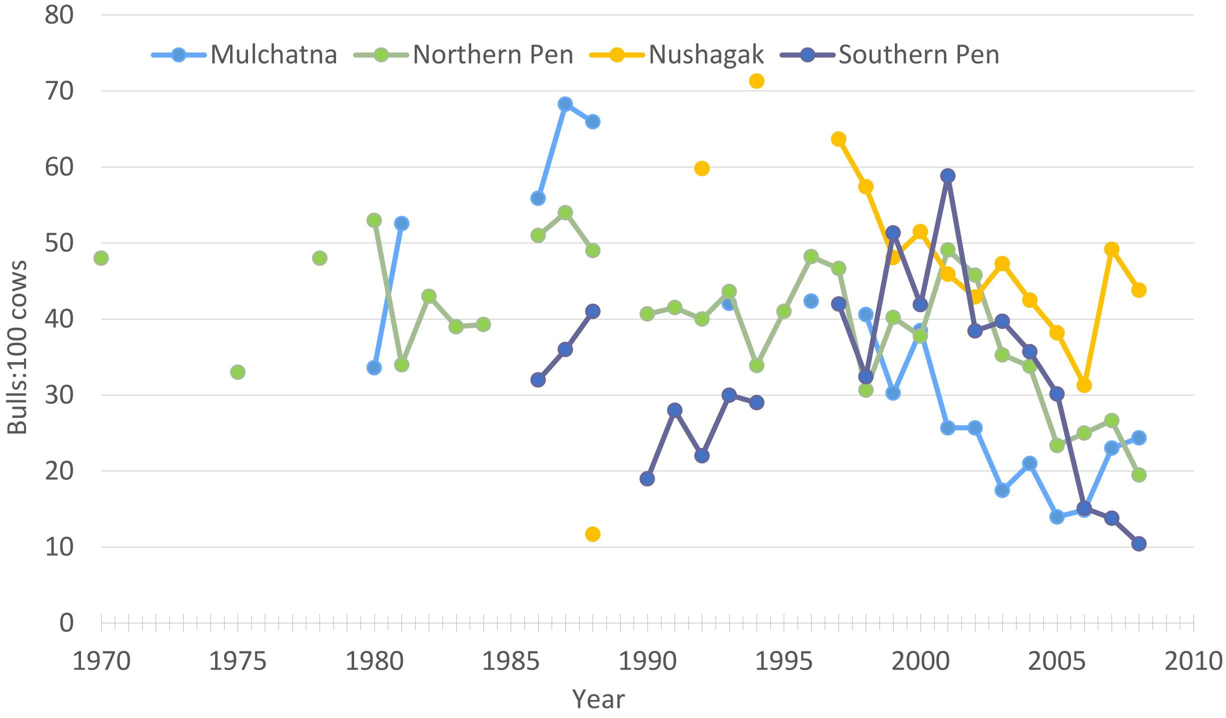


Figure 23. Bull:cow ratios in 4 Southwest Alaska caribou herds, 1970–2008.

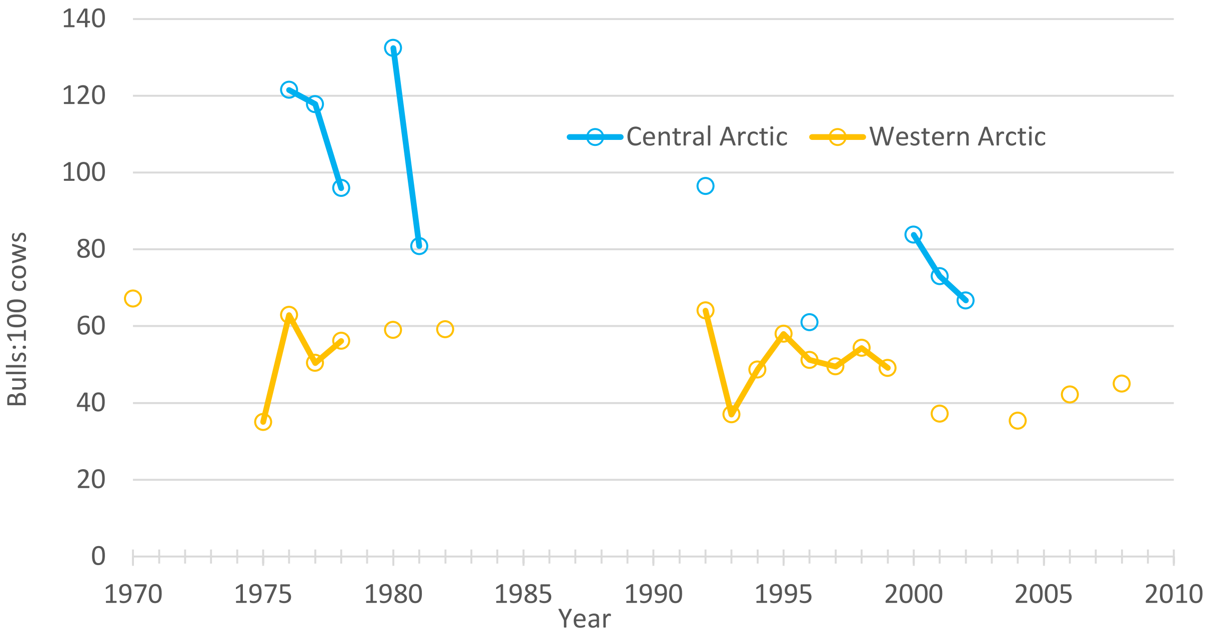


Figure 24. Bull:cow ratios in the Western Arctic and Central Arctic caribou herds, Alaska, 1970–2008.

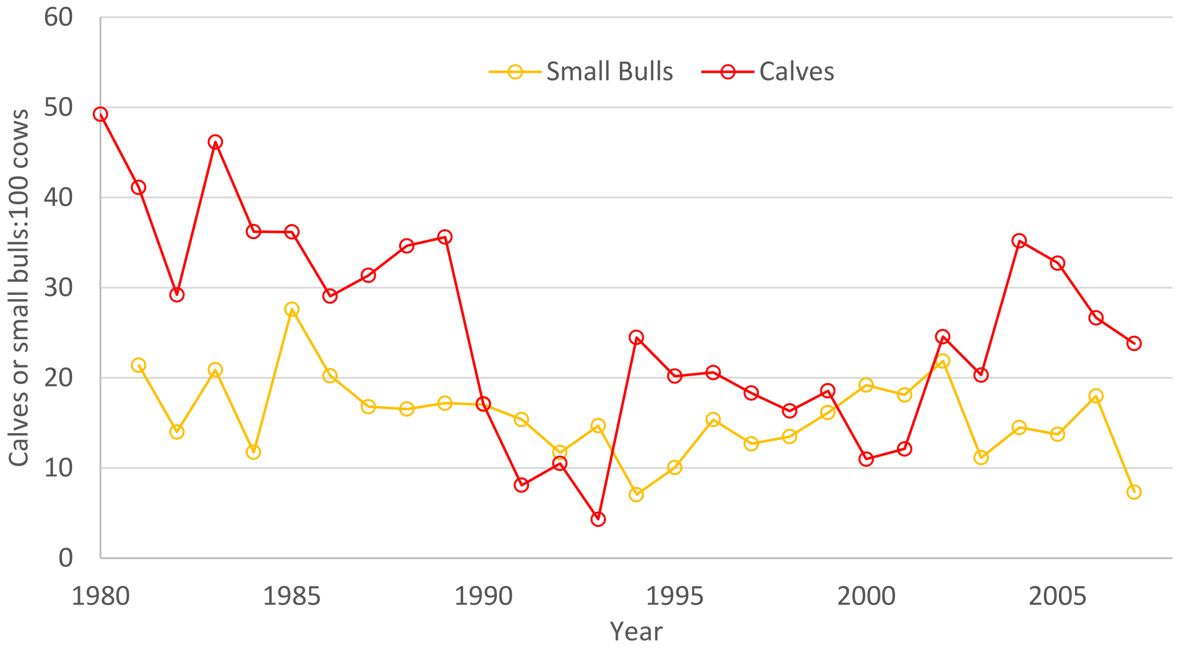


Figure 25. Comparisons of trends in calf:cow and small bull:cow ratios in the Delta herd, Alaska, 1980–2007.

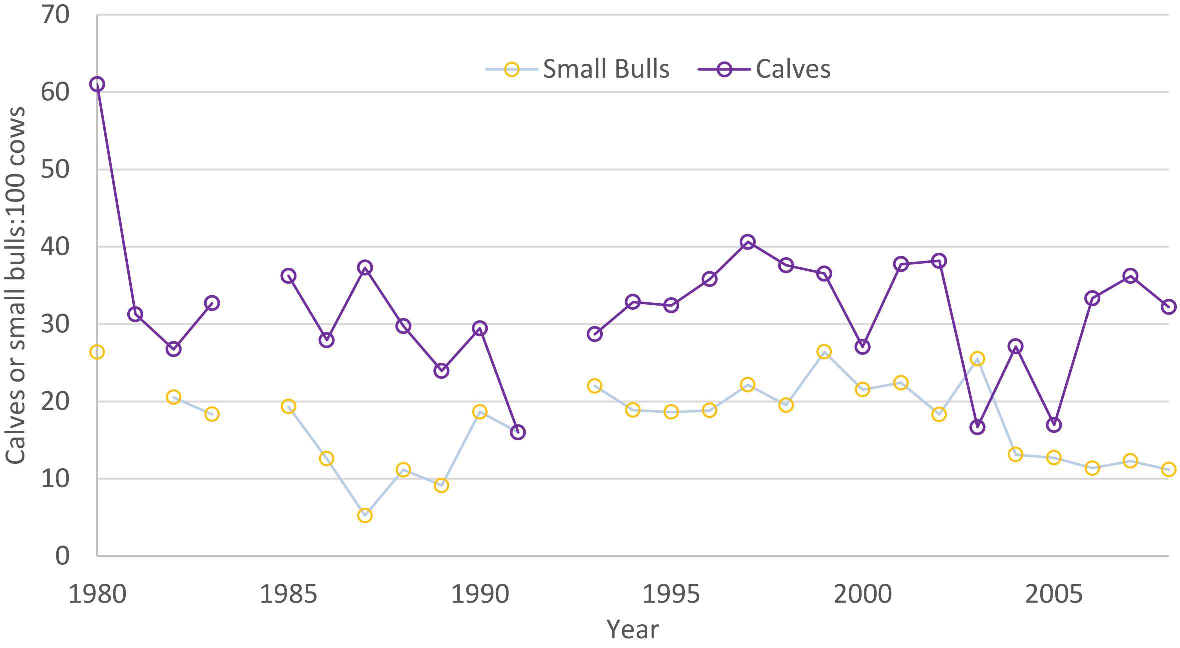


Figure 26. Comparisons of trends in calf:cow and small bull:cow ratios in the Fortymile herd, Alaska, 1980–2008

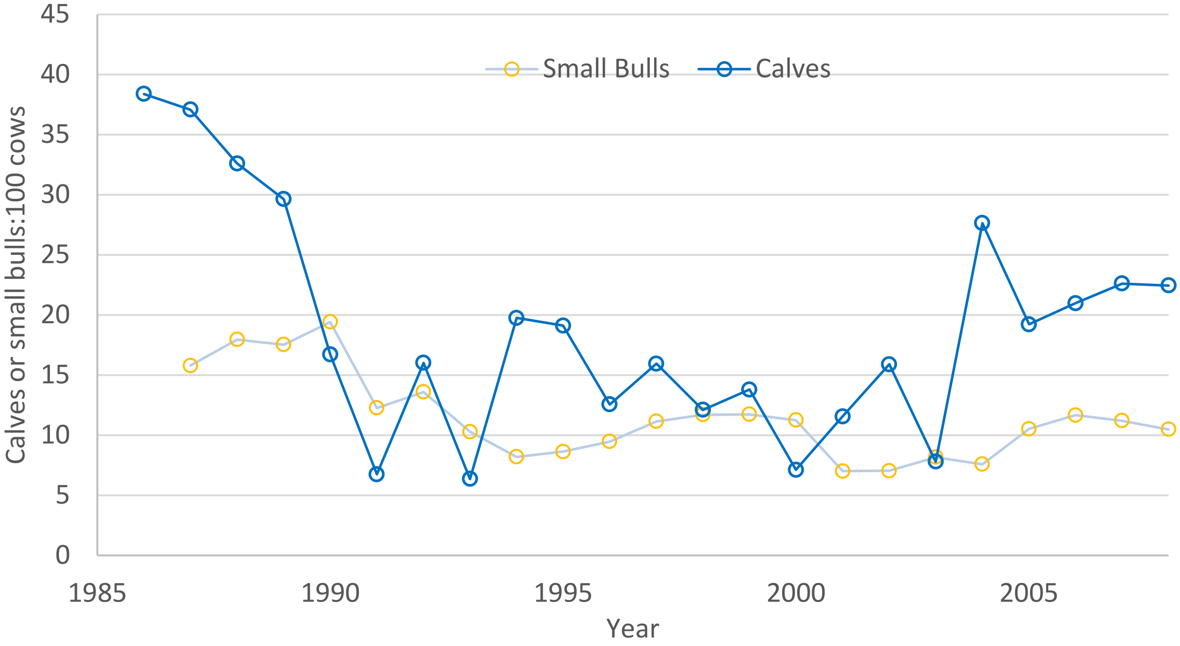


Figure 27. Comparisons of trends in calf:cow and small bull:cow ratios in the Denali herd, Alaska, 1987–2008.

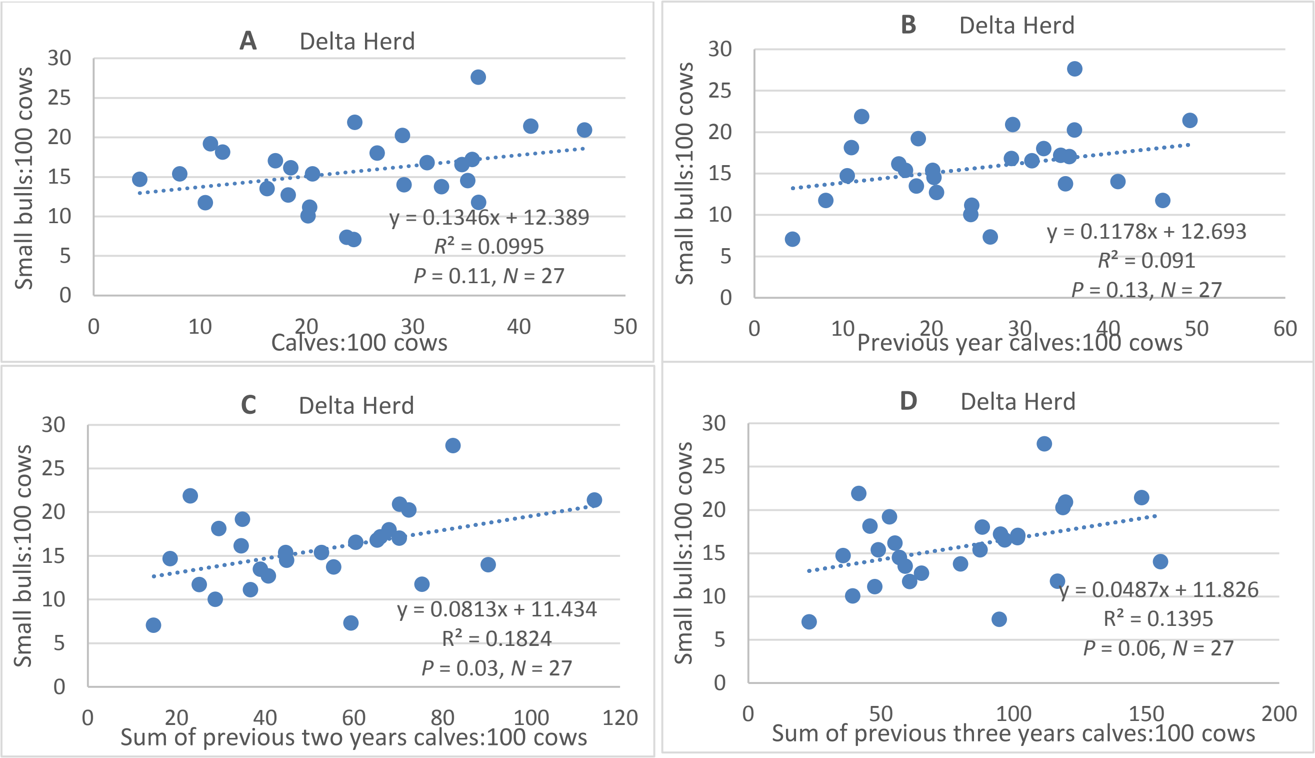


Figure 28. Calves:100 cow ratios as predictors of small bull:cow ratios in the Delta herd, Alaska, 1981–2007.

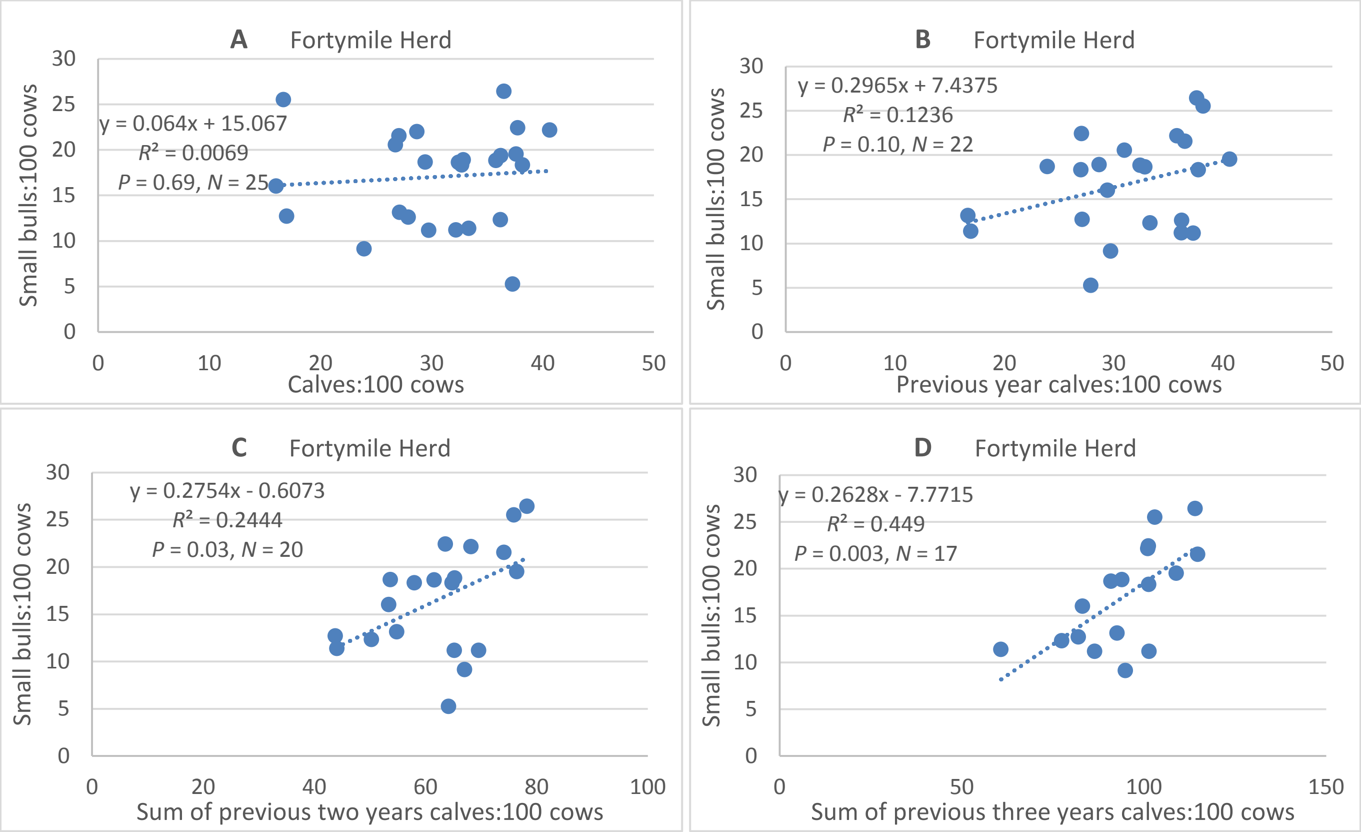


Figure 29. Calves:100 cow ratios as predictors of small bull:cow ratios in the Fortymile herd, Alaska, 1982–2008.

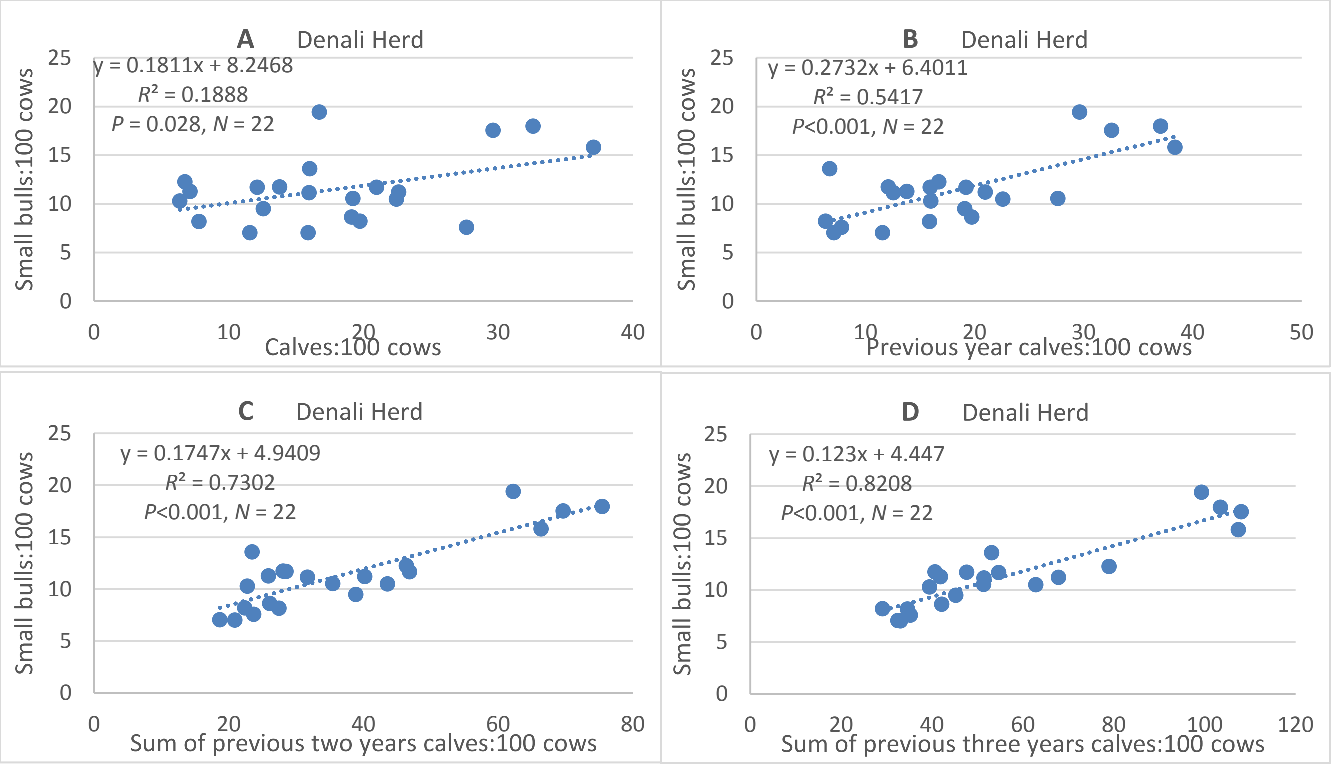


Figure 30. Calves:100 cow ratios as predictors of small bull:cow ratios in the Denali herd, Alaska, 1987–2008.

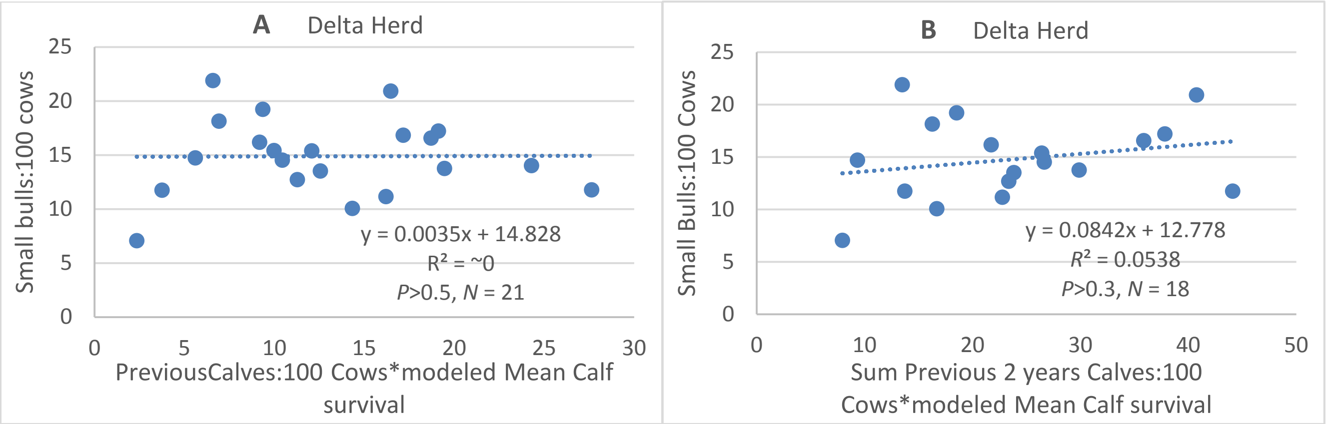


Figure 31. Previous year and previous 2-year calf:cow*modeled mean calf survival as predictors of small bull:cow ratios in the Delta caribou herd, Alaska, 1981–2007.

Trends in Medium and Large Bull Ratios

After many years of experience in gathering data on medium and large bulls, we concluded that classification of bulls involves a great deal of subjectivity and is of limited management utility. We therefore did not conduct extensive data analysis on medium and large bull data but we do discuss some possible advantages of continuing to collect these data in some herds. Existing data appear in Appendix B.

HARVEST IN THE DELTA HERD AND DENALI HERD

Hunting seasons and harvest of caribou in the Delta herd varied considerably during 1970–2008 (Fig. 32, Appendices G and H). Prior to 1969, harvest in the Delta herd was generally low and was not a management concern, although ADF&G managers realized there was a gradually increasing interest in the herd, especially among hunters using aircraft for caribou hunting (O. E. Burris, Wildlife Biologist, ADF&G, personal communication). From 1969 through 1972, harvest increased substantially, and along with other factors, it became a major factor in an unexpected decline in herd size. Hunting was closed in the Delta herd from 1974 through 1979 to allow the herd to recover. Limited harvest was reopened in 1980. In 1983, harvest was greatly expanded in accordance with a management plan designed to keep the herd stable at about 4,000, while providing a continuing high level of harvest (ADF&G, Game Division, 1983 unpublished document, Fairbanks). However, the management plan was rescinded by order of the Director of Division of Game in 1987 and the herd rapidly increased to its population high of 10,690 in 1989. By 1992, harvest again had to be eliminated because herd size and recruitment declined. The hunting season was closed from 1992 to 1995. From 1996 to 2007, harvest was low, relatively stable, and restricted to bulls only (Fig. 32, Appendix G).

The Denali herd sustained a largely unknown level of harvest prior to 1974. Some caribou wintered in the vicinity of Healy and Otto Lake during the 1960s and early 1970s when there was an either-sex season from 10 August through 31 March (Appendix G). The human population in the area was low and travel from Fairbanks to Healy was often difficult because the highway was not paved and poorly maintained. It was never clear if wintering caribou in the area were from the Delta or Denali herds. There was likely a substantial harvest (relative to herd sizes) in 1970–1971 through 1972–1973 because the highway was improved and hundreds of caribou wintered in the area during these 3 winters (R. D. Guthrie, Zoologist, University of Alaska Fairbanks, personal communication). Some of the caribou harvested may have been from the Denali herd. All caribou hunting seasons in the area were closed in 1974 (Appendix G). From 1974 through the mid-1990s the Denali herd was closed to hunting, partly because ADF&G and NPS wanted to have an unhunted herd for study and partly because harvest opportunities would have been very limited. From the late 1990s through 2008, there was a federal hunt open to “federally qualified rural residents” in GMU 13E but no hunting was allowed north of the Alaska Range. Of 178 radiocollared bulls in the range of the Denali herd during 2007–2014, 2 were taken by hunters in the federal hunt (L. G. Adams, personal communication). During the period of intensive study of the Delta herd and the main comparison period with the Denali herd (1987–2008), we believe that harvest in the Denali herd was insignificant.

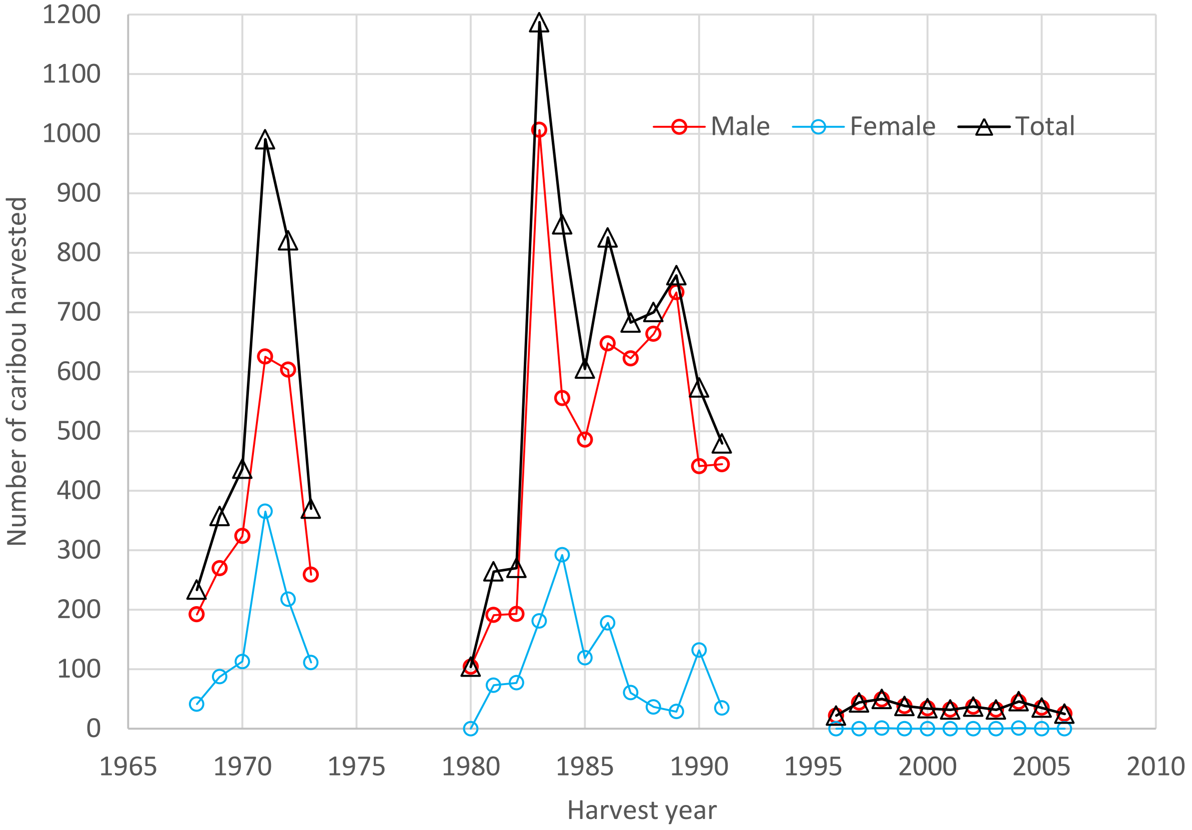


Figure 32. Estimated harvest of Delta caribou herd, Alaska, 1968–2006. Includes correction for nonreporting (reported harvest/0.63) during 1968–1991. In some years, harvest also occurred after 31 December of the harvest year, so harvest year 1968 = harvest during regulatory year 1 July 1968–30 June 1969.

WEIGHT, SIZE, AND NUTRITIONAL CONDITION OF CALVES

Body Weight of Cohorts of 4- and 10-Month-Old Calves

Delta Herd and Delta-Denali Comparison

We caught and weighed samples of 10-month-old female caribou calves in most years in the Delta herd during 1979 through 2007 and mean weights of these cohorts declined slightly over time ($P = 0.02$) (cohort birth years 1978–2006) (Fig. 33; Table 8). During the earlier part of the study (the first 11 years from birth years 1978–1988) or the later part of the study (the last 13 years) there were no significant trends in mean weights of 10-month-old calves (Figs. 34 and 35, Table 8). The 2 lowest mean cohort weights (birth years 1989 and 1990) were recorded during or immediately after the population high that occurred in 1989 and the onset of severe winters.

There were no obvious linear trends in mean weight of cohorts of 4-month-old calves from 1991 to 2004 ($P = 0.78$) (Fig. 36, Table 8). During this period, variability in mean cohort weight was relatively low from year to year and no annual mean was more than 2 standard errors above or below the long-term mean of 57.1 kg (Table 8). The mean 4-month cohort weights were consistently about 1.5 kg above the mean 10-month cohort weights during 1991–2004 (birth years) (Table 8).

Mean weight of cohorts of calves at 4 months of age was not a reliable predictor of weight at 10 months of age (Fig. 36). Similarly, during the early to mid-1980s, although weight of individual calves at 10 months of age was positively correlated with their weight at 46 months of age, there was a considerable amount of unexplained variation ($R^2 = 0.41$, $P<0.01$, $n = 17$).

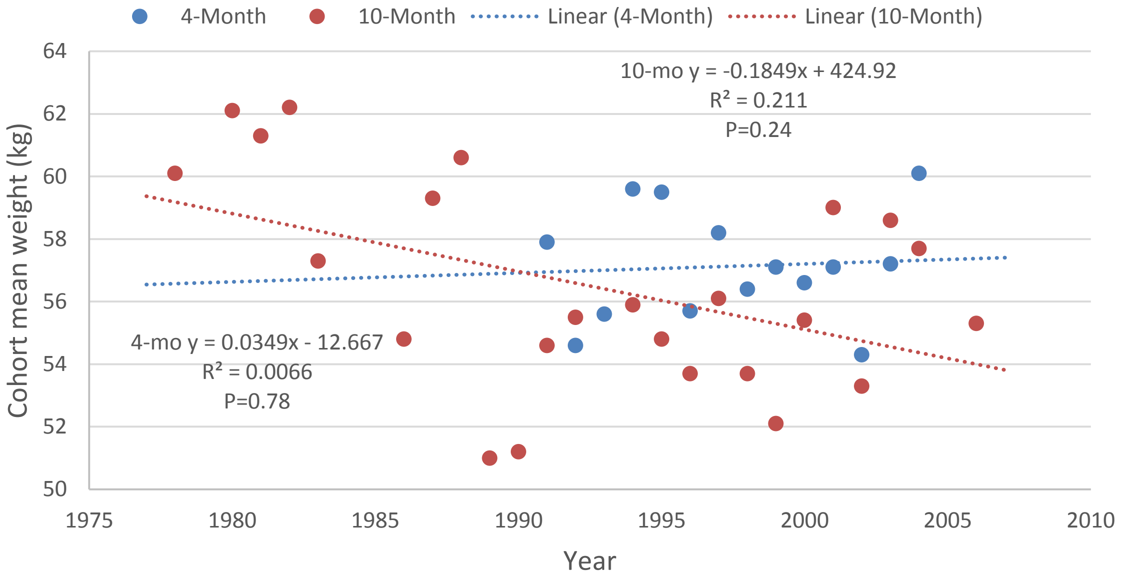


Figure 33. Trends in weights of cohorts of female calves in the Delta caribou herd by birth year, Alaska, 1978–2006.

Table 8. Mean weight of samples of 4- and 10-month-old female calves from the Delta caribou herd, by year of birth, Alaska, 1978–2006.

	Caribou					
Birth	4-months old			10-months old		
year	$\bar{x}$ (kg)	$s_{\bar{x}}$ (kg)	*n*	$\bar{x}$ (kg)	$s_{\bar{x}}$ (kg)	*n*
1978				60.1	1.1	11
1979						
1980				62.1	3.4	5
1981				61.3	1.7	11
1982				62.2	1.5	13
1983				57.3	0.6	12
1984						
1985						
1986				54.8	1.3	9
1987				59.3	1.0	16
1988				60.6	1.2	9
1989				51.0	1.3	14
1990				51.2	1.1	10
1991	57.9	1.2	14	54.6	1.3	16
1992	54.6	1.4	14	55.5	1.3	12
1993[a]	55.6	1.4	14			
1994	59.6	1.3	15	55.9	1.2	15
1995	59.5	1.3	13	54.8	1.5	15
1996	55.7	1.4	14	53.7	1.1	14
1997	58.2	1.0	20	56.1	1.4	12
1998	56.4	1.2	16	53.7	1.3	14
1999	57.1	1.3	14	52.1	1.2	12
2000	56.6	1.8	14	55.4	1.4	11
2001	57.1	1.1	14	59.0	0.9	15
2001	54.3	1.5	15	53.3	1.6	15
2002	57.2	0.9	16	58.6	1.7	14
2003	60.1	1.3	15	57.7	1.7	14
2004	57.9	1.2	14			
2005				55.3	1.6	11
2006				60.1	1.1	11

[a] Too few caribou calves survived from the 1993 cohort to obtain a sample of 10-month-old weights.

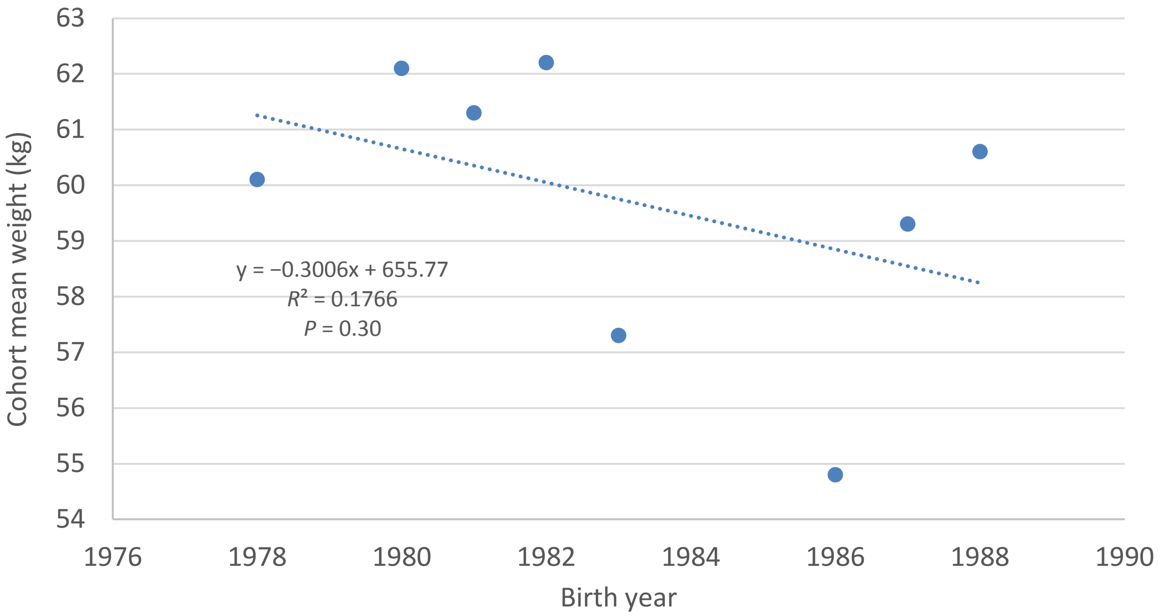


Figure 34. Trend in mean weight of cohorts of 10-month-old calves in the Delta herd, Alaska, 1978–1988. There was no significant trend in calf weights as the grew in size before the bad winters (1989–1993) began. Slight downward slope is largely driven by the low 1986 weights.

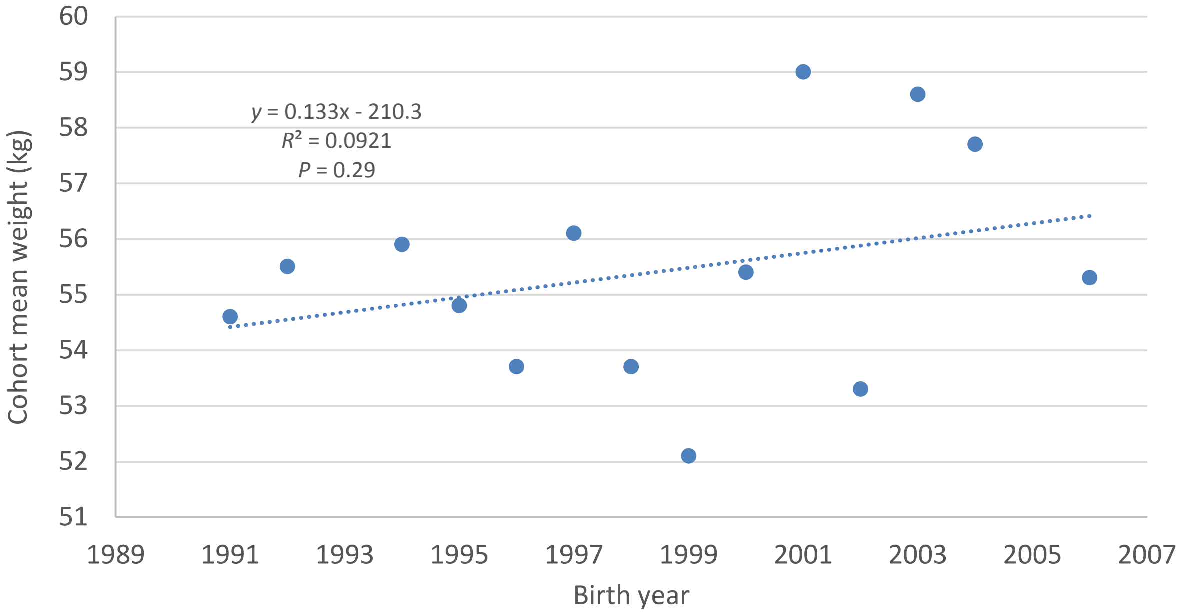


Figure 35. Trend in mean weights of cohorts of 10-month-old calves in the Delta herd, Alaska, 1991–2006. No significant trend is apparent although values for 2001, 2003, and 2004 cause a slight upward slope.

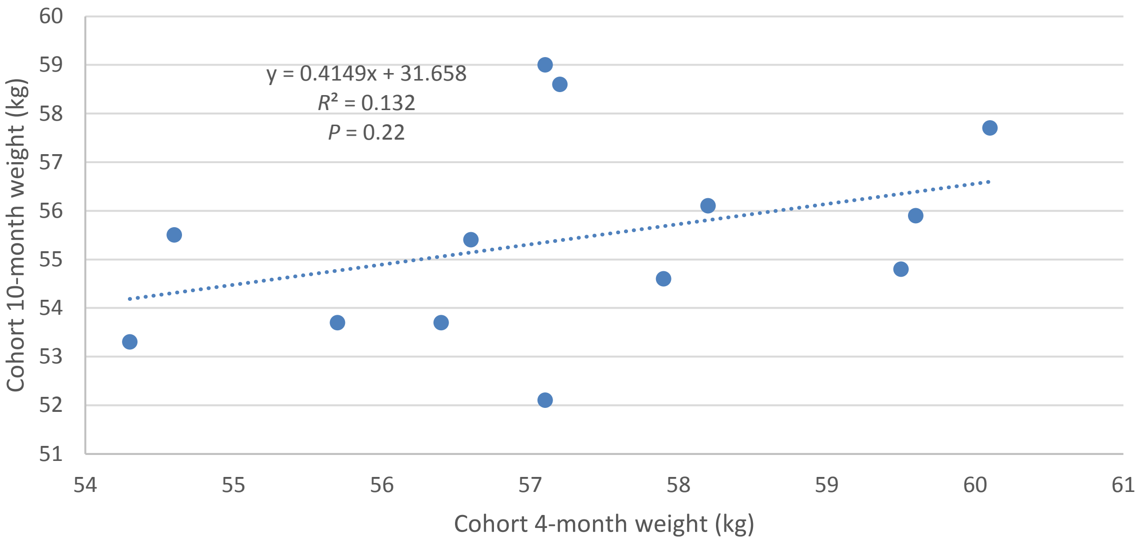


Figure 36. Mean weight of 4-month-old female calves as predictor of mean weight of 10-month-old calves in the same cohort year, Alaska, 1991–2004. Although weight of calves at 4 months of age was not a reliable predictor of weights of 10-month-old calves, the lightest calves were more likely to die over winter, causing bias.

Besides being a direct indicator of nutrition in the Delta herd, we were also interested to see if calf weights could be used as a predictor of population performance. We therefore explored using mean cohort weight of 10-month-old calves as an indicator of expected fall calf:cow ratios because Valkenburg et al. (2002:55) found a reasonably good correlation (1979–2001, $R^2 = 0.59$, $P < 0.01$) between these variables. With additional data covering the entire period and removing the questionable data from 1979 (unrepresentative composition count), the close correlation between 10-month weight and fall calf:cow remained similar (1981–2007, $R^2 = 0.56$, $P < 0.001$) and the slopes of the regression lines were similar (2.74 vs. 3.12) (Fig. 37A). We found no significant relationship between 10-month calf weight and fall calf:cow ratio in the Denali herd during 1987–1997 (Fig. 37B). Data were insufficient to determine if a relationship existed between 10-month weight and fall calf:cow in other herds.

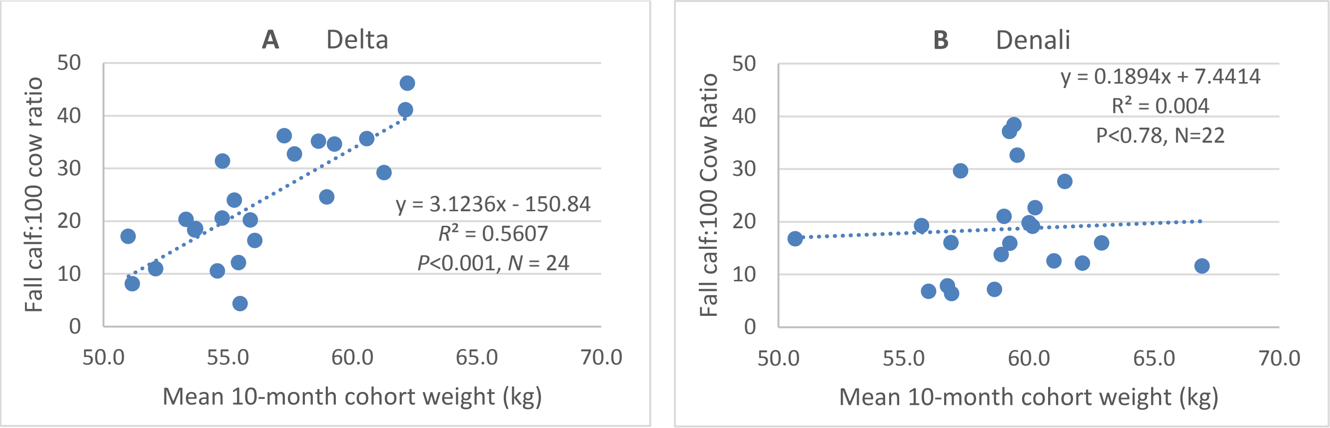


Figure 37. Relationship between mean cohort 10-month weight and fall calf:cow in the Delta (1981–2007) and Denali (1987–1997) herds, Alaska.

Other Herds

Mean weights of cohorts of 4- and 10-month-old caribou varied considerably among Alaska caribou herds and among years, from 32 kg in the Western Arctic herd in 1994 to 66 kg in the Galena Mountain and Killey River herds in 1994 and 1995 respectively (Figs. 38–41; Appendix C). Differences in cohort mean weights of ~5 kg would usually be statistically significant given the observed variance within samples (SE ranged from 0.6 kg to 2.6 kg in samples of ≥10 calves) (Appendix C). Heavy mean weights (60–65 kg) of cohorts of calves were seen in many Interior and Kenai herds, including the Chisana, Delta, Denali, Galena Mountain, Kenai Mountains, Killey River, Macomb, Rainy Pass, White Mountains, and Wolf Mountain. Mean weights of cohorts of 4- and 10-month-old calves were consistently ~5–10 kg smaller in the 5 caribou herds in Southwest Alaska than in Interior Alaska, but most herds in Southwest Alaska were at high population size or declining in size (Figs. 8–11; Appendices A and C). The heaviest mean weights of cohorts of calves in Southwest Alaska occurred in the Nushagak and Unimak herds. Cohorts of Western Arctic herd calves were by far the smallest we encountered and averaged ~20 kg smaller than cohorts from Interior herds and 10–15 kg smaller than the 5 Southwest Alaska herds. Weights of 10-month-old calves in the Central Arctic herd were intermediate between calves from southwestern herds and the Western Arctic herd. Within cohorts, it was more common for mean cohort weight to decline over winter than to increase (Fig. 42).

Delta-Denali Herd Comparison

Although sample sizes in both the Delta and Denali herds were small in some years, we were able to compare 10-month-old calf weights in the 2 herds over the 20-year period from 1987 to 2008 (birth years 1986–2007) (Fig. 40). In 1987 and 1988, before the population high in the Delta herd and prior to the onset of deep snow winters, 10-month calf weights in both herds appeared similar. With the onset of bad winters, calf weights appeared to decline in both herds with some recovery beginning in 1991. Calf weights continued to recover to pre-1989 levels (>60 kg) in the Denali herd but stayed ~55kg in the Delta herd. It was not until 2001 that calf weights appeared to recover in the Delta herd.

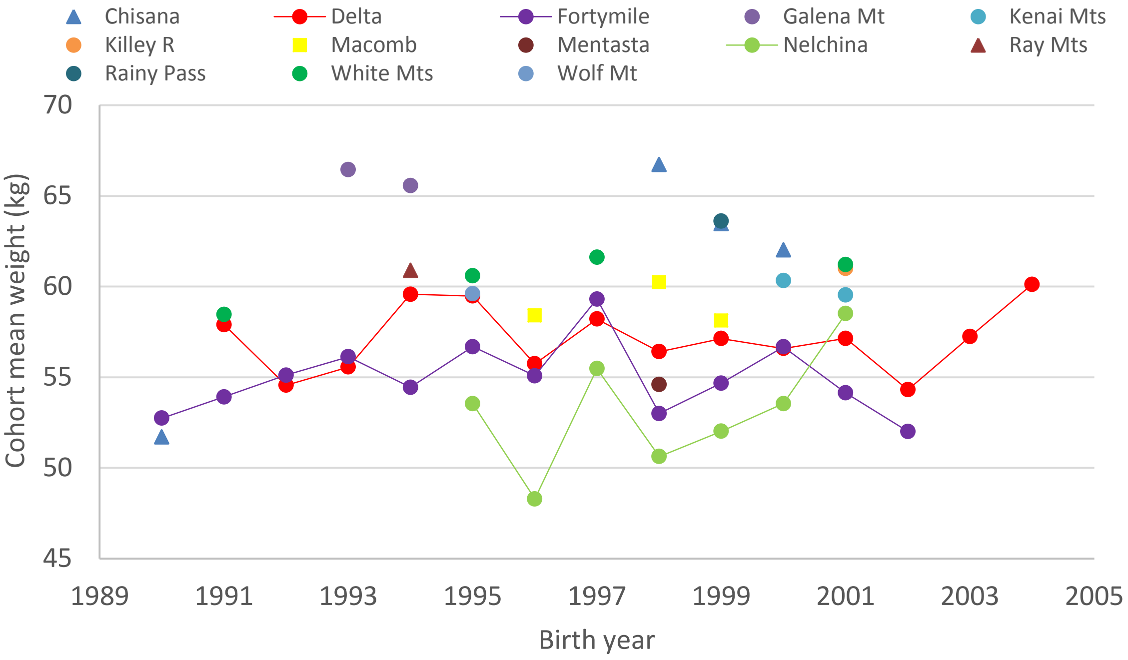


Figure 38. Mean weights of cohorts of 4-month-old female calves from 10 small Southcentral and Interior Alaska caribou herds compared with Delta, Nelchina, and Fortymile, 1990–2004.

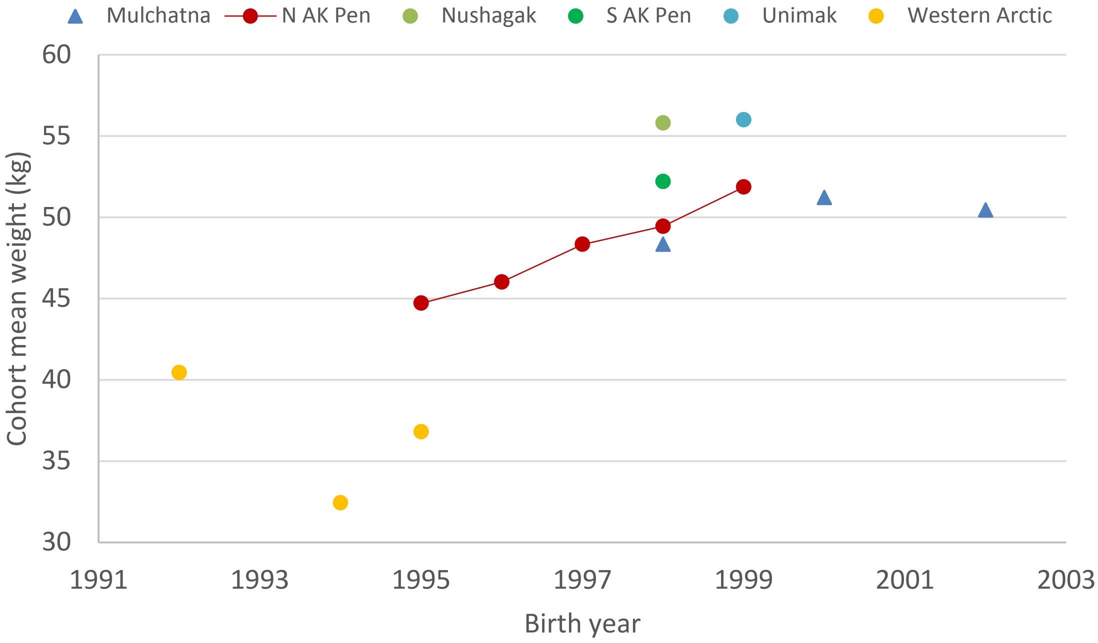


Figure 39. Mean weights of cohorts of 4-month-old female caribou calves from 5 Southwest Alaska herds and the Western Arctic herd, 1992–2002.

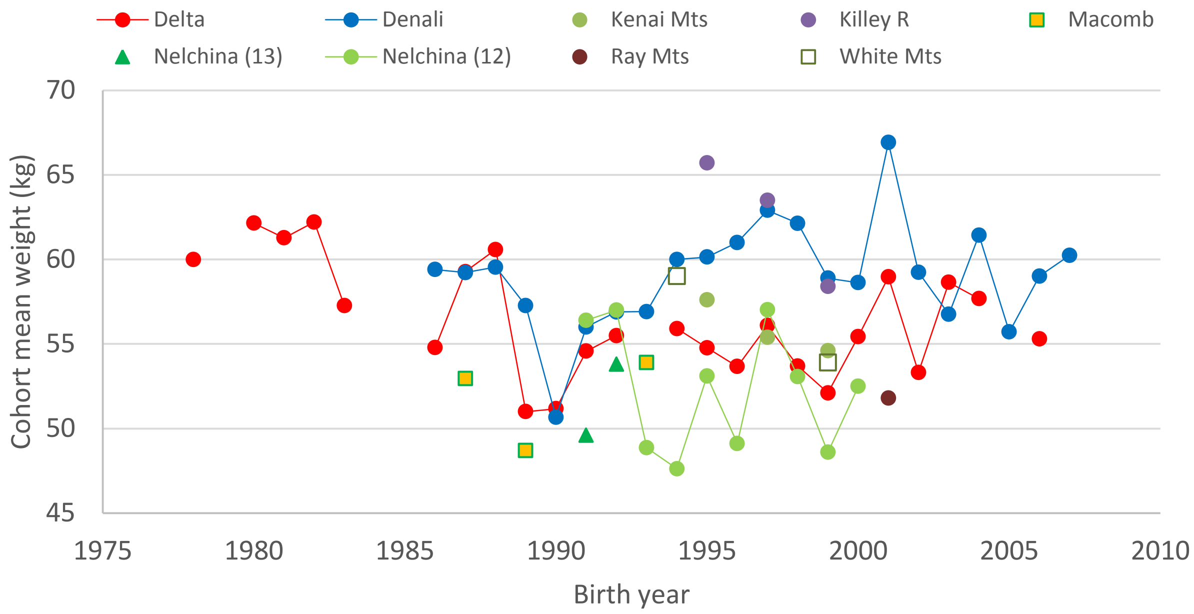


Figure 40. Mean weights of cohorts of 10-month-old female calves from 9 small Interior and Southcentral Alaska caribou herds, compared with Delta, Denali, and Nelchina, 1978–2006. Nelchina herd had 2 wintering areas in 1991 and 1992 (GMU 12 and GMU 13).

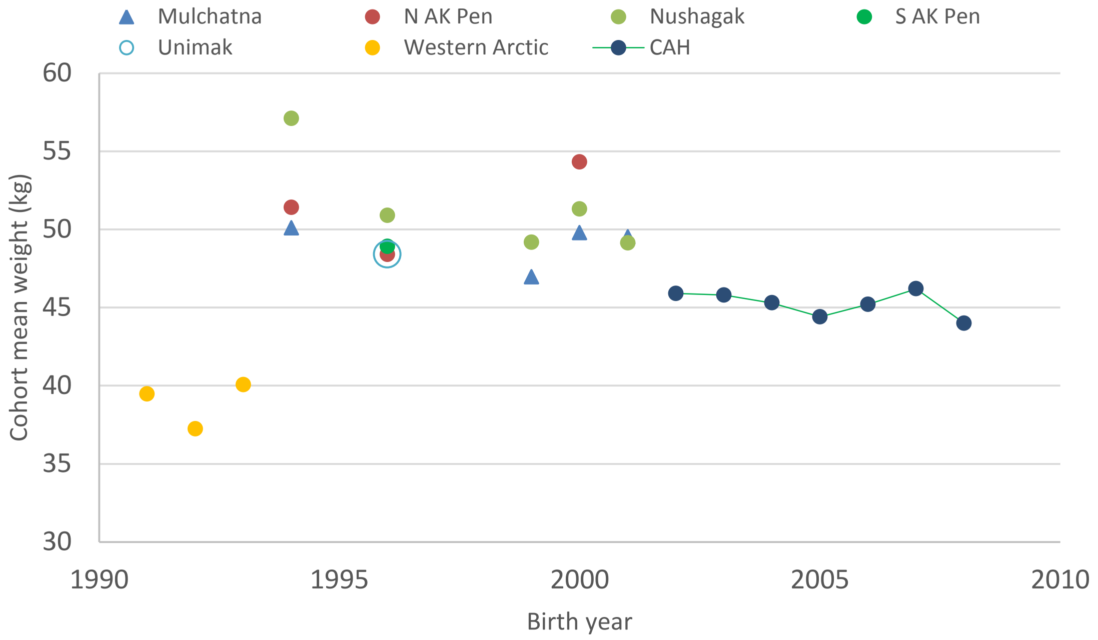


Figure 41. Mean weights of cohorts of 10-month-old female calves from 5 Southwest Alaska caribou herds, and the Central Arctic and Western Arctic herds, 1991–2008.

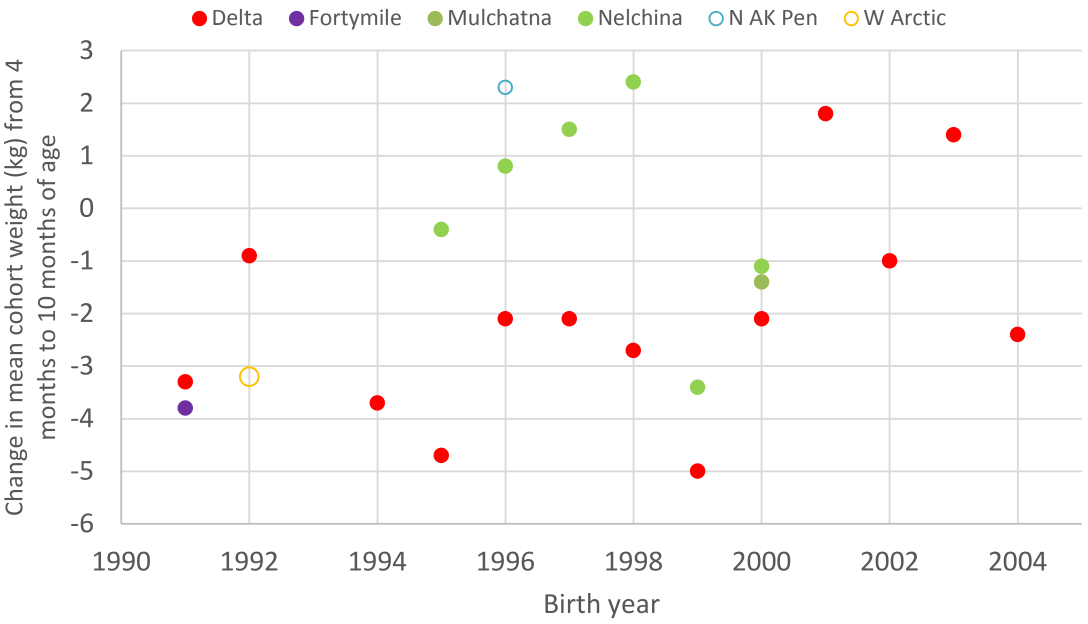


Figure 42. Change in mean cohort weight from 4 months to 10 months of age in 6 Alaska caribou herds, 1991–2004.

Metatarsus Length and Relationship Between Weight and Metatarsus Length in the Delta Herd and Other Caribou Herds

In the longest, most continuous data set available (i.e., data for 10-month-old calves in the Delta herd), mean metatarsus length appeared to follow a pattern similar to mean weight, where both were higher during the late 1970s and early 1980s and lower after the population high in 1989 (Fig. 43). The greatest divergence in the relationship occurred in 1990 and 1991, immediately following the population high in 1989 and the onset of severe winters.

In the Delta herd and in other herds, mean cohort metatarsus length was consistently greater in 10-month-old caribou calves than in 4-month-old calves indicating possible continued growth of long bones over winter (Figs. 44–46, Appendix C). In linear regression of 4- and 10-month-old metatarsus length versus weight in individual caribou, we found that metatarsus length explained about one-third of the variation in a calf's weight in both fall and spring and correlation coefficients between the 2 seasons were similar (mean fall $R^2 = 0.36$, $n = 12$ herds including 822 individuals; mean spring $R^2 = 0.29$, $n = 11$ herds and 790 individuals; $P = 0.37$) (Figs. 47 and 48). Consistent with continued growth of the metatarsus over winter, mean slope of the prediction equations were steeper in the fall data sets than in the spring data sets (fall = 3.19, spring = 2.28, *t*-test $P = 0.09$) (Figs. 47 and 48).

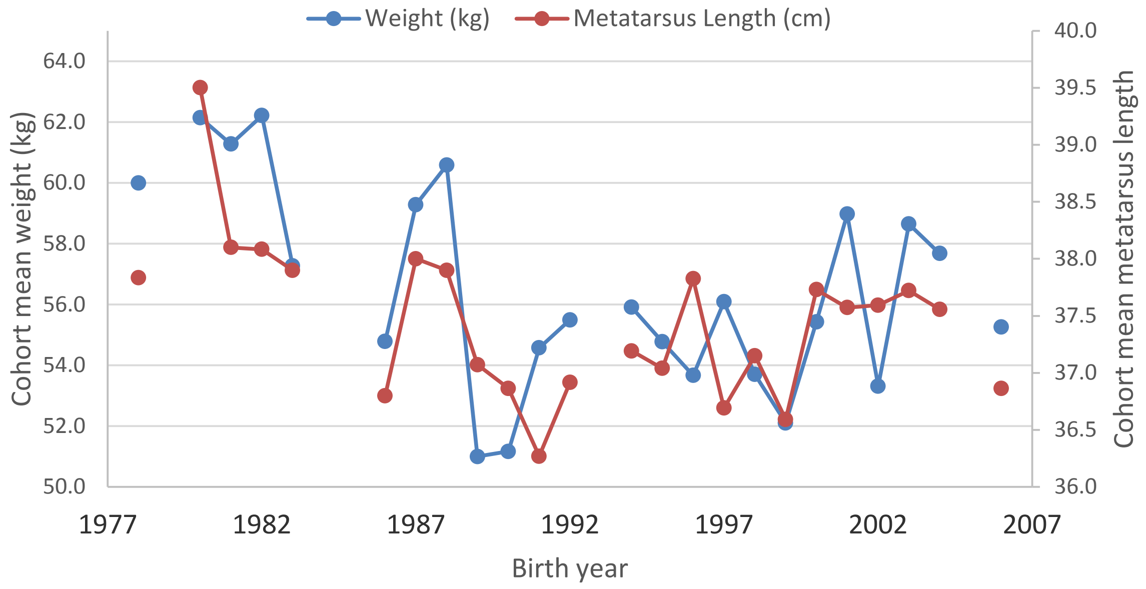


Figure 43. Mean weight and mean metatarsus length of cohorts of 10-month-old female caribou calves in the Delta caribou herd, Alaska, 1978–2006.

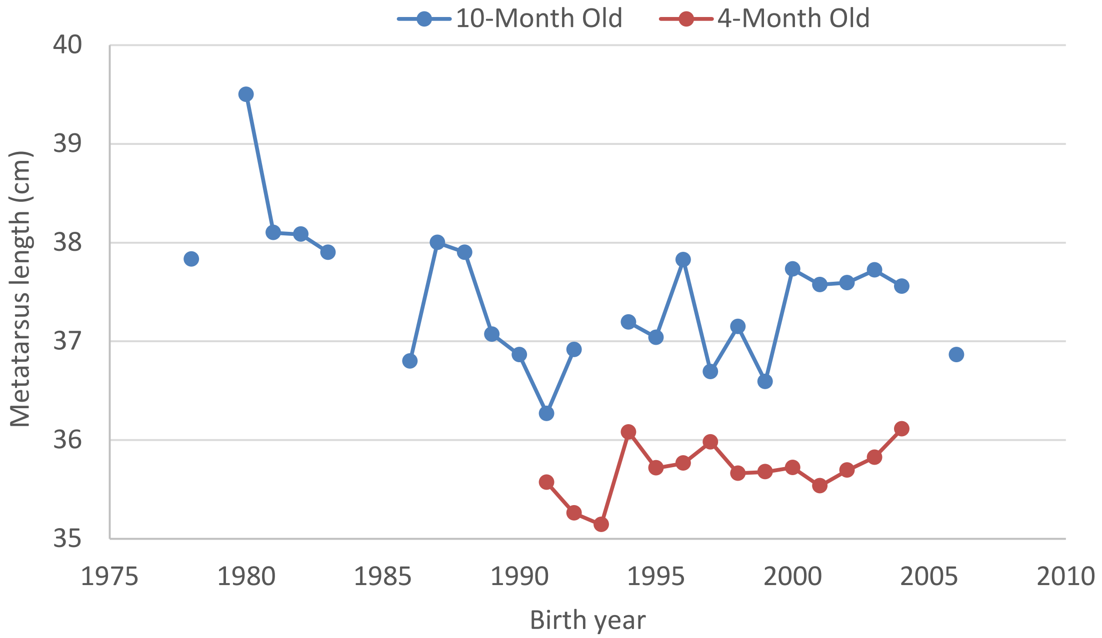


Figure 44. Mean metatarsus length for cohorts of 4- and 10-month-old female calves in the Delta herd, Alaska, 1978–2006.

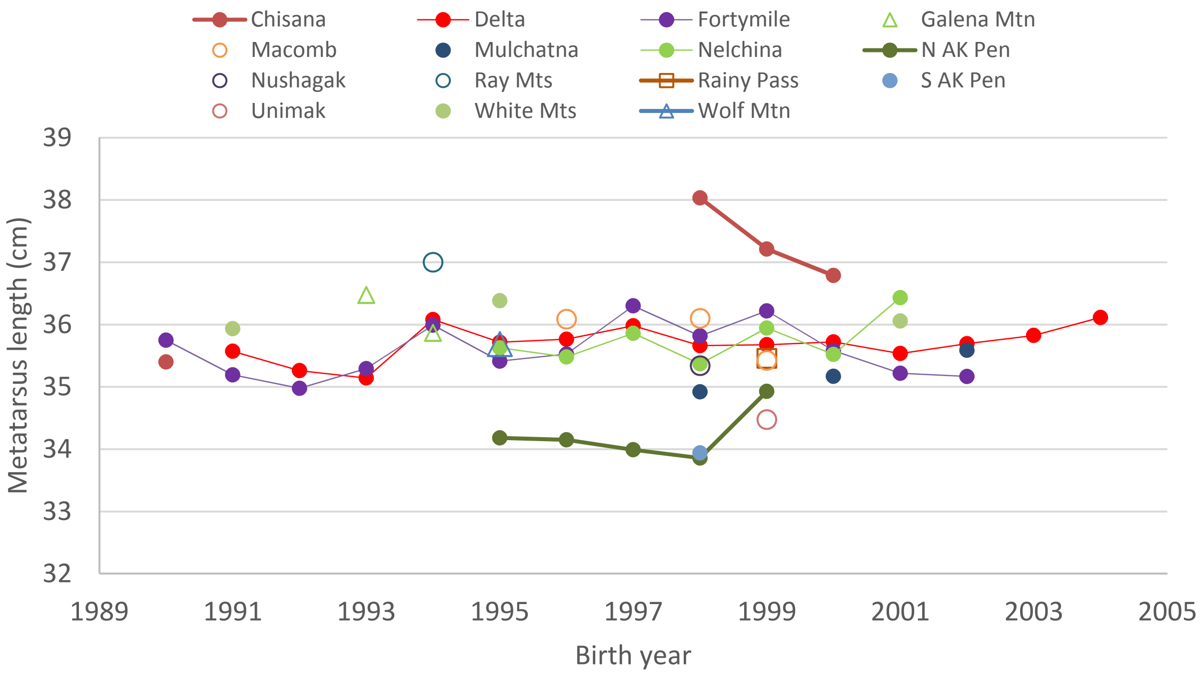


Figure 45. Mean metatarsus length of cohorts of 4-month-old female calves from 15 Alaska caribou herds, 1990–2004.

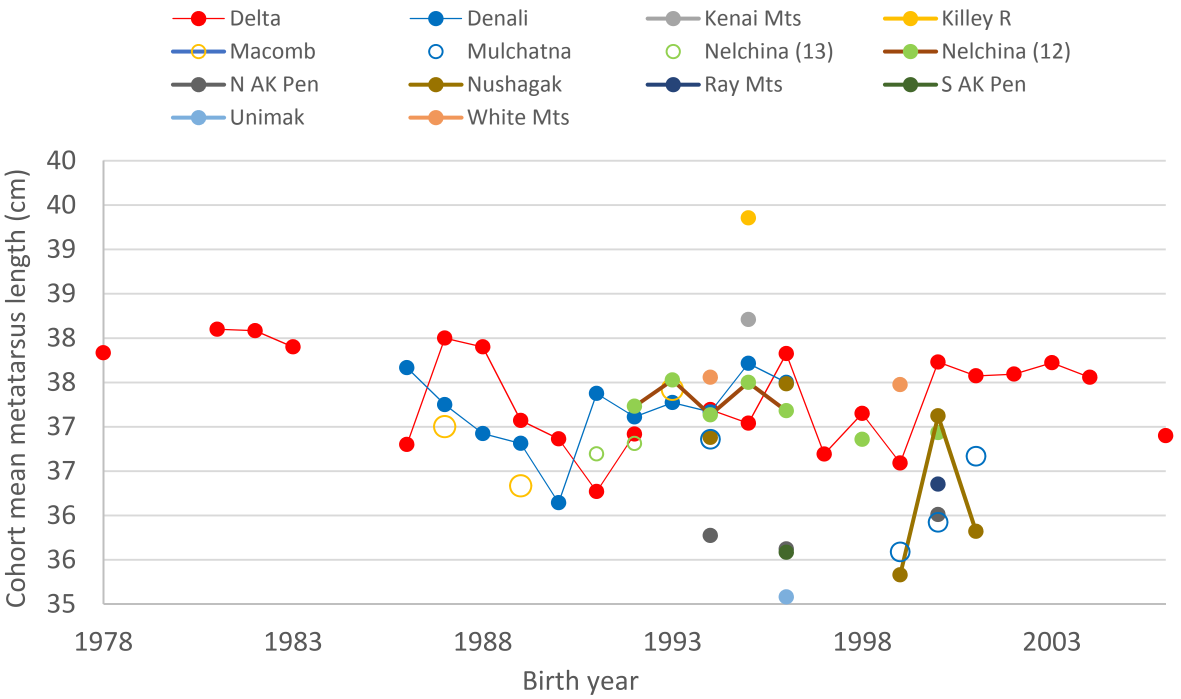


Figure 46. Mean metatarsus length of cohorts of 10-month-old female calves from 14 Alaska caribou herds, 1978–2006. In some year the Nelchina herd had 2 wintering areas, one in GMU 12 and one in GMU 13.

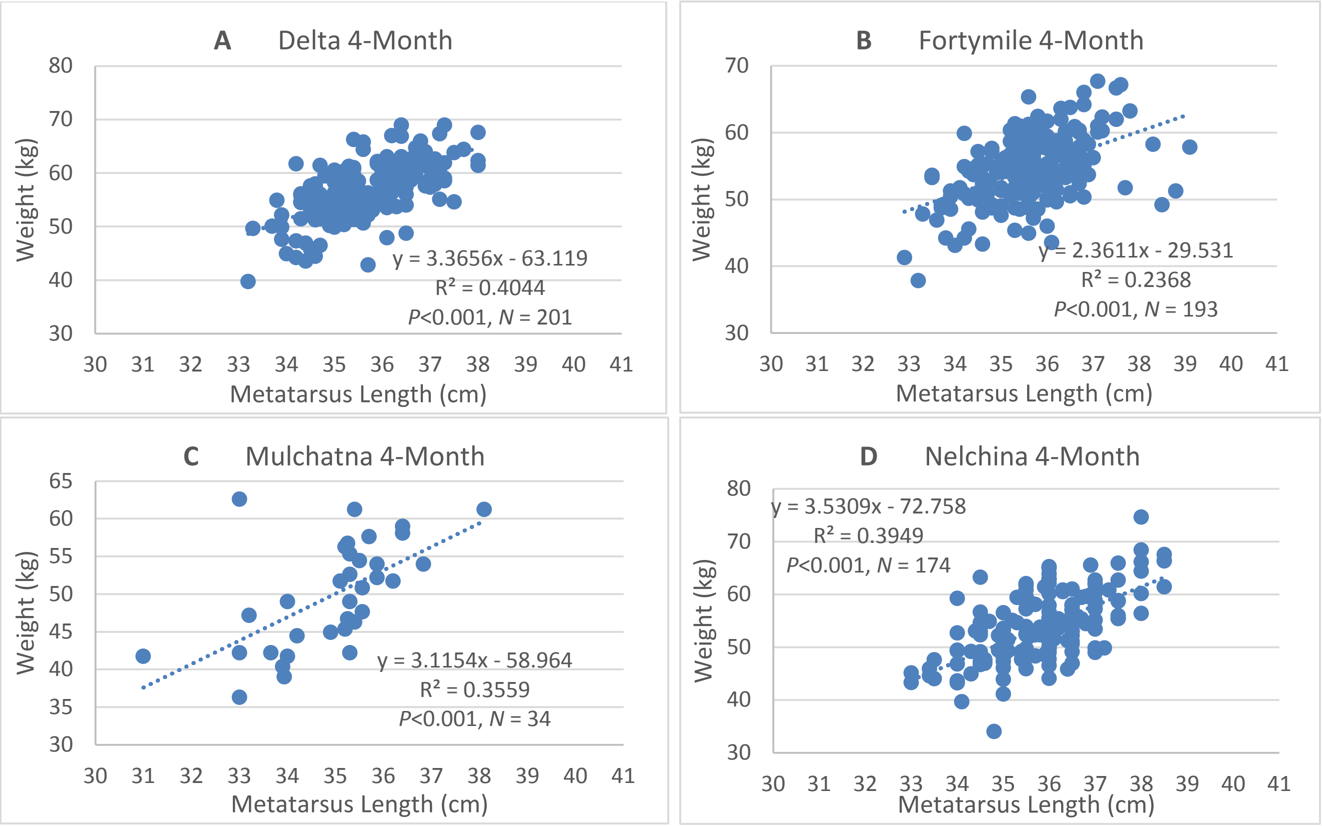


Figure 47. Metatarsus length as a predictor of weight in 4-month-old female calves from 4 Alaska caribou herds.

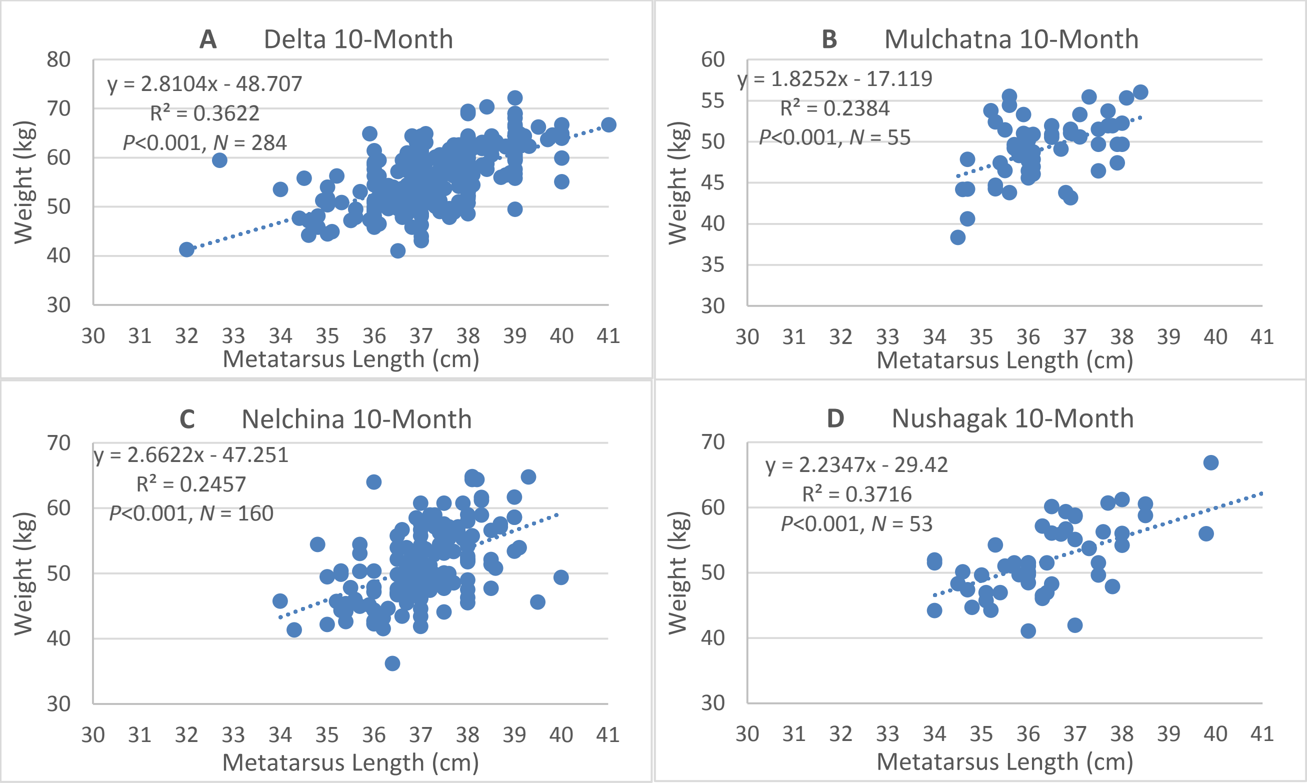


Figure 48. Metatarsus length as a predictor of weight in 10-month-old female calves from 4 Alaska caribou herds.

Although it was difficult to compare metatarsus length across all herds because caribou calves were handled more in the spring than in the fall in some herds and vice versa, there appeared to be considerable variation in mean metatarsus length across herds and across years (Figs. 45 and 46). The longest mean metatarsus lengths we observed were in the Chisana herd (4-month-old calves) and in the Killey River herd (10-month-old calves). Unfortunately, we did not have data on metatarsus length for the Western Arctic herd, which appears to have, by far, the smallest caribou in the state.

Weight:Metatarsus Ratio in the Delta Herd and Other Alaska Caribou Herds

Within cohorts of caribou calves from all herds, mean cohort weight:metatarsus ratio was usually higher in 4-month-old calves than in 10-month-old calves (Figs. 49–51). Mean cohort weight:metatarsus ratio in the Nelchina herd was similar in both seasons (1.48 in fall vs. 1.41 in spring) (t = 1.70, P = 0.11, df = 14), whereas it declined significantly from fall to spring in the Delta herd (1.60 in fall vs. 1.51 in spring) (t = 4.30, P<0.001, df = 36).

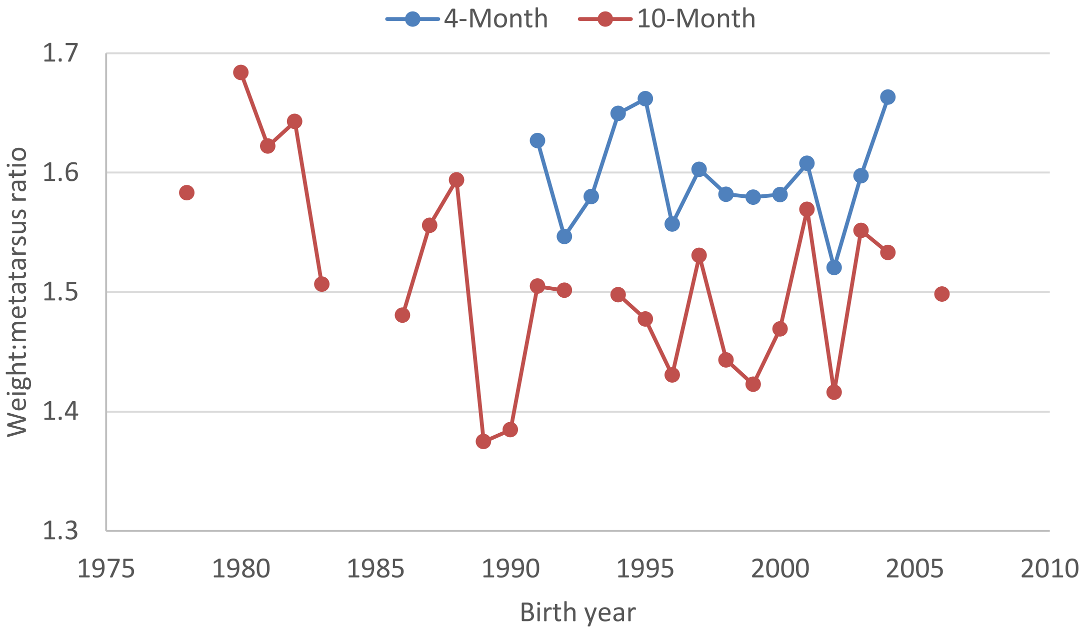


Figure 49. Mean cohort weight:metatarsus ratio of female calves in the Delta caribou herd, Alaska, 1978–2006.

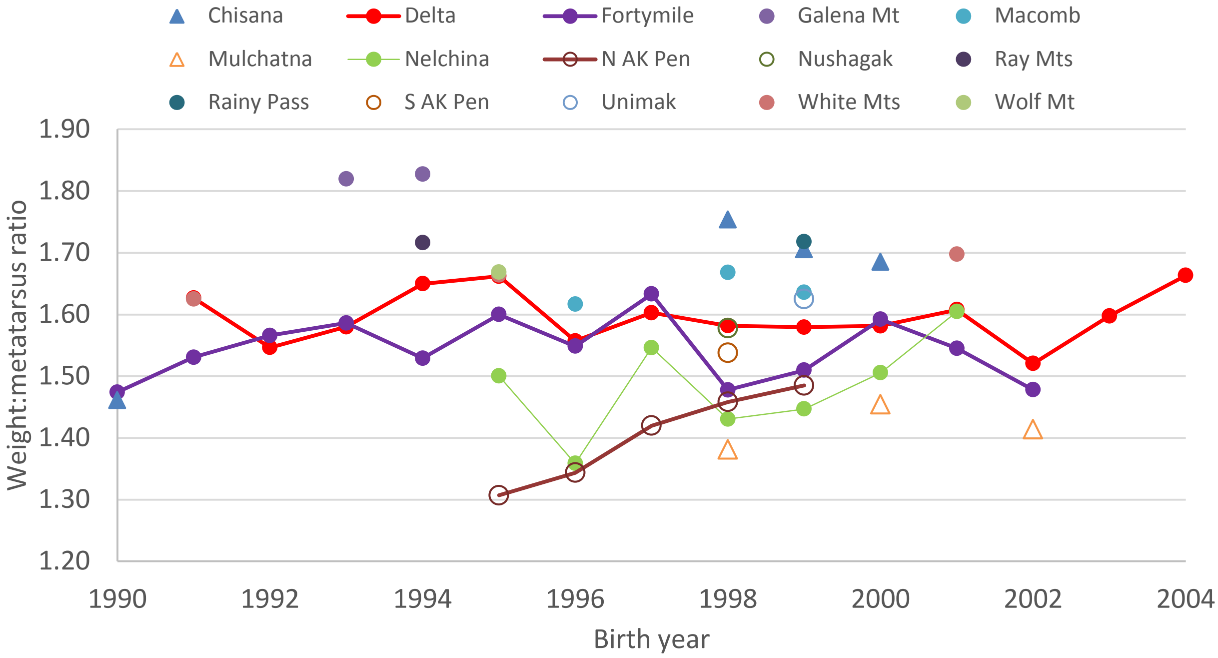


Figure 50. Mean weight:metatarsus ratio of cohorts of 4-month-old female calves in 15 Alaska caribou herds, 1990–2004.

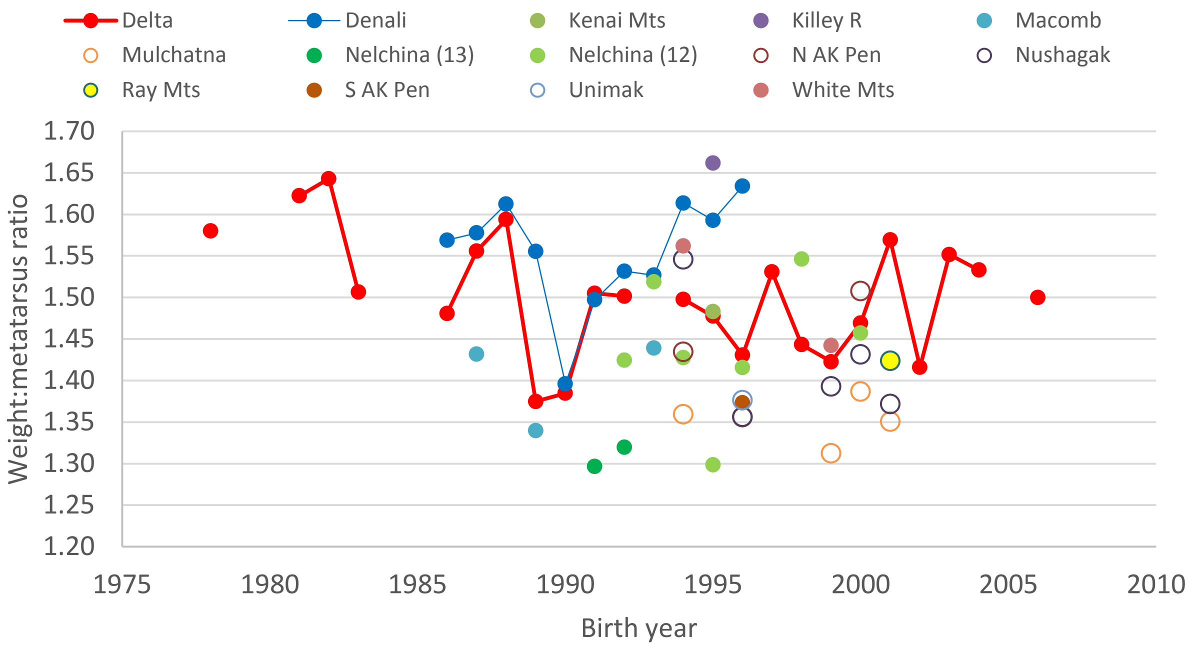


Figure 51. Mean weight:metatarsus ratio of cohorts of 10-month-old female calves from 14 Alaska caribou herds, 1978–2006.

Weight-Girth Relationships in the Delta Herd and Other Alaska Caribou Herds

Girth was highly correlated with weight and explained about 45–65% of the variation in weight of 4-month-old caribou calves in herds where sample sizes were adequate for comparison (Fig. 52A–D). Slightly poorer correlations were obtained with data for 10-month-old calves (Fig. 53A–D).

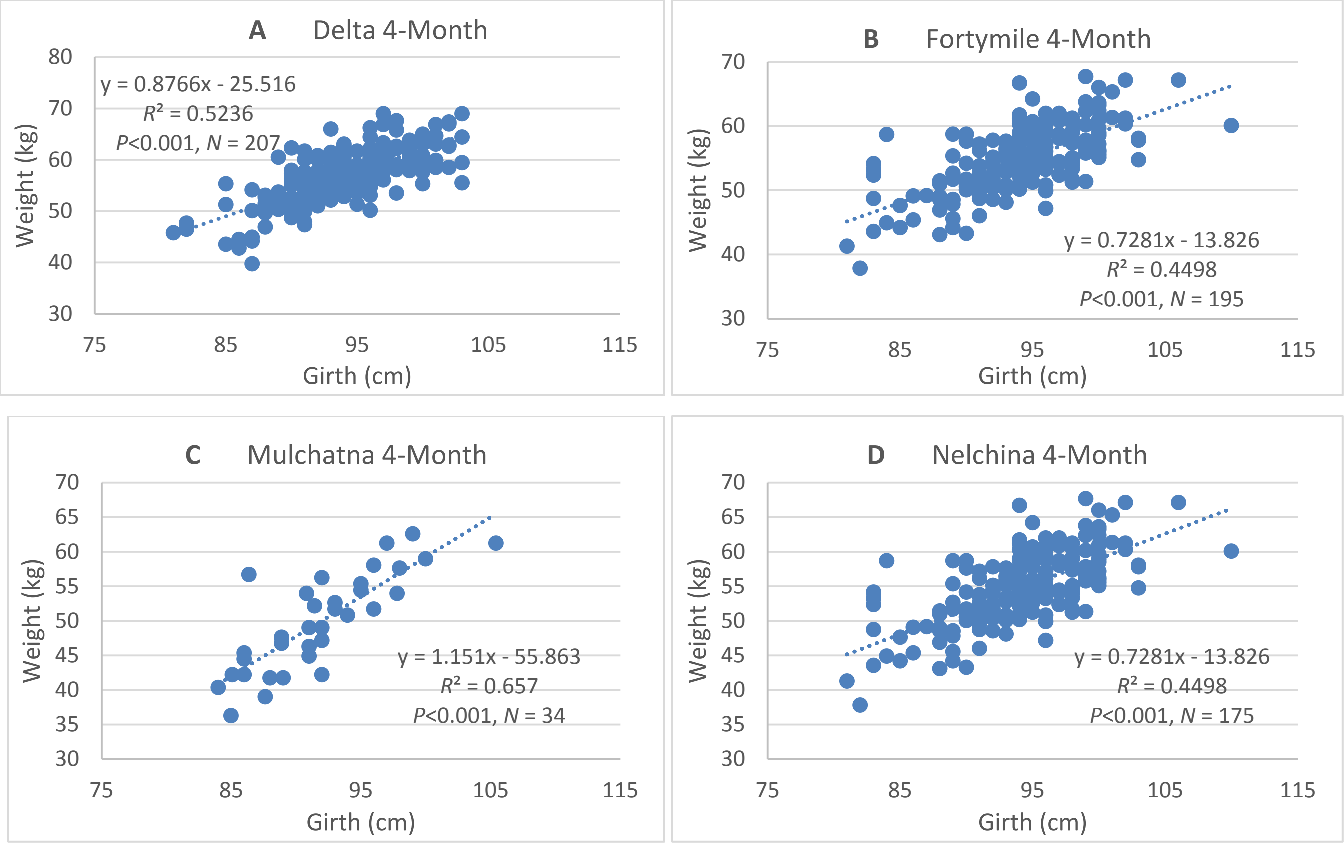


Figure 52. Girth as a predictor of weight in 4-month-old female calves from the Delta, Fortymile, Mulchatna, and Nelchina caricou herds, Alaska.

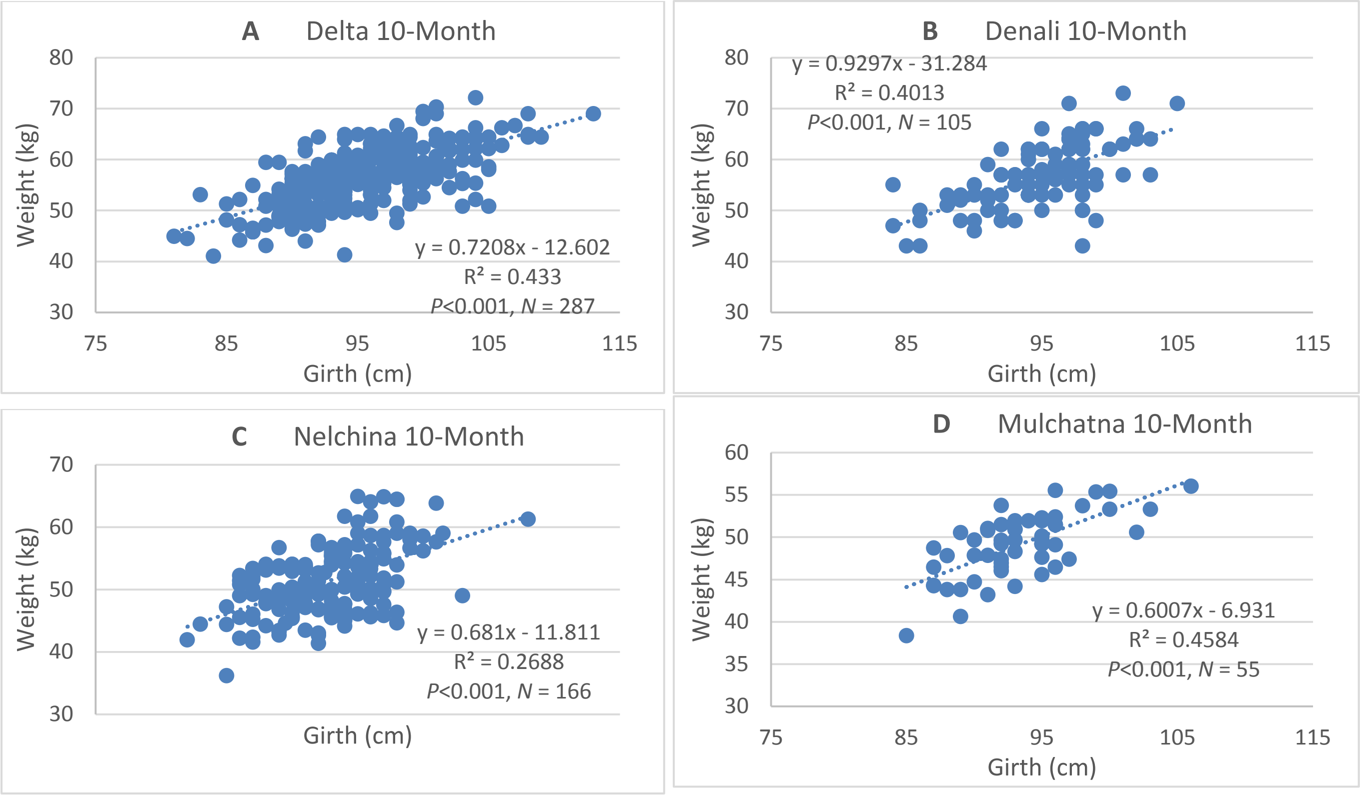


Figure 53. Girth as a predictor of weight in 10-month-old female calves from Delta, Denali, Nelchina, and Mulchatna caribou herds, Alaska.

Weights of Newborn Calves in the Delta Herd and Other Alaska Caribou Herds

Weights of cohorts of newborn calves ranged from ~5.5 kg to ~9.0 kg for females, and from ~7.7 kg to ~9.5 kg for males (Figs. 54 and 55; Table 9). Weights of newborn calves were generally lower in the Arctic herds and herds in Southwest Alaska than in the Interior herds. Newborn calves in the Northern Alaska Peninsula herd (1998 and 1999) appeared to be similar in weight to calves in the Interior herds but lack of continuous or comparable data made comparison problematic. Mean weights of male Interior calves seldom were <8 kg and mean weights of females were never recorded <7 kg (Figs. 54 and 55; Table 9). The low weights of newborn calves in the Southern Alaska Peninsula herd were from 1989, when calf mortality was high, the herd was doing poorly, and many calves were abandoned by their mothers during a calf mortality study (Pitcher et al. 1990). In the Northern Alaska Peninsula herd, male calves were heavier in 1998–1999 than male calves in the adjacent Southern Alaska Peninsula herd in 1999 ($P = 0.03$, $t = 2.25$). However, there was no difference between cohorts of female calves ($P = 0.57$, $t = 0.58$).

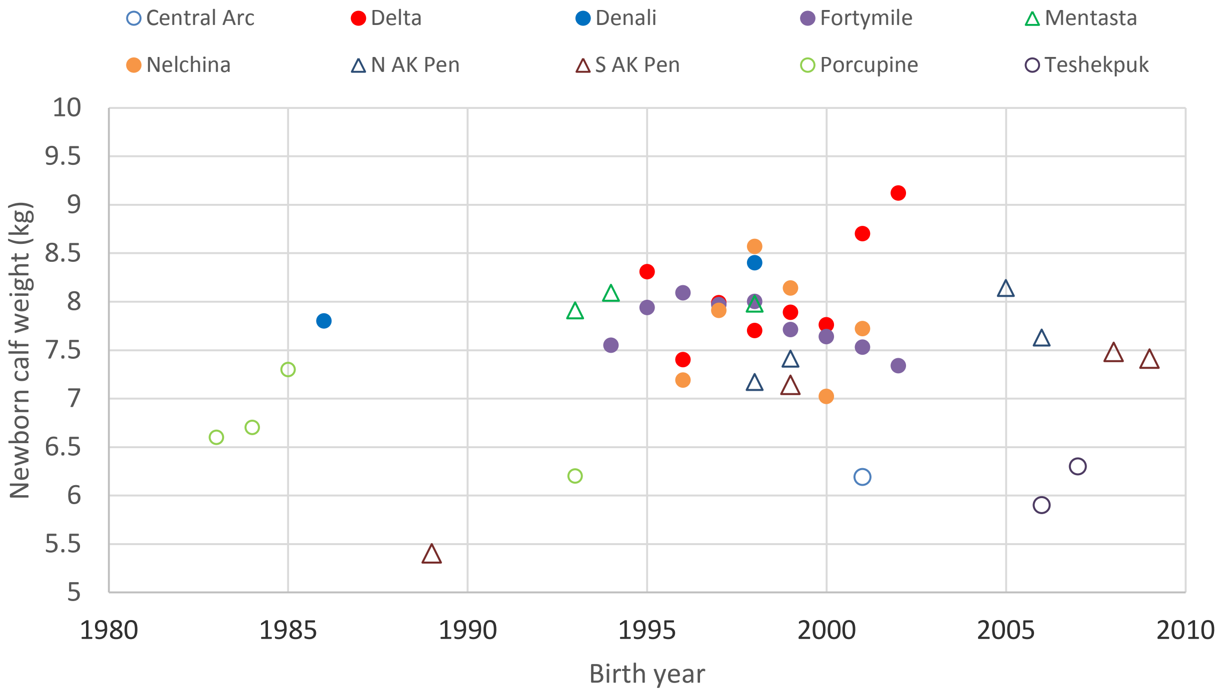


Figure 54. Mean weights of cohorts of newborn female (1983–2009) caribou calves from 10 Alaska caribou herds. See Table 9 for detailed data and summary statistics.

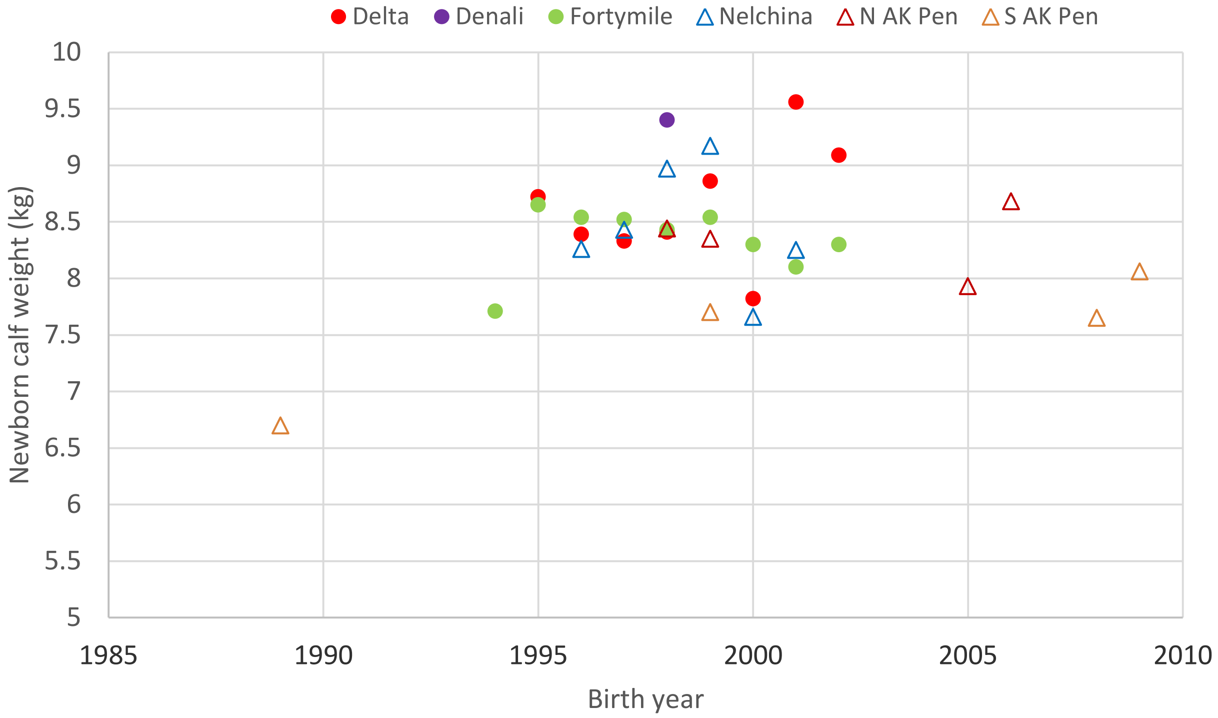


Figure 55. Mean weights of cohorts of newborn male (1989–2009) caribou calves from 6 Alaska caribou herds. See Table 9 for detailed data and summary statistics.

Table 9. Mean weights and standard errors of samples of cohorts of newborn caribou calves from 11 Alaska herds, 1965–2009.

	Caribou calves					
	Males			Females		
Herd and Year	Weight (kg)	$s_{\bar{x}}$[a]	*n*	Weight (kg)	$s_{\bar{x}}$[a]	*n*
Central Arctic 2001				6.19	0.37	65
Delta 1995	8.72	0.29	26	8.31	0.24	19
Delta 1996	8.39	0.23	22	7.40	0.19	28
Delta 1997	8.33	0.21	40	7.99	0.20	35
Delta 1998	8.41	0.22	15	7.70	0.29	15
Delta 1999	8.86	0.32	26	7.89	0.19	35
Delta 2000	7.82	0.28	25	7.76	0.32	16
Delta 2001	9.56	0.61	8	8.70	0.32	10
Delta 2002	9.09	0.30	22	9.12	0.22	18
Denali 1986–1987[b]	9.00	0.11	67	7.80	0.11	60
Denali 1998[c]	9.40	0.30	15	8.40	0.32	14
Fortymile 1994	7.71	0.20	22	7.55	0.27	22
Fortymile 1995	8.65	0.16	24	7.94	0.19	25
Fortymile 1996	8.54	0.24	26	8.09	0.17	32
Fortymile 1997	8.52	0.25	24	7.97	0.21	32
Fortymile 1998	8.43	0.14	30	8.00	0.15	39
Fortymile 1999	8.54	0.18	35	7.71	0.17	40
Fortymile 2000	8.30	0.17	27	7.64	0.18	39
Fortymile 2001	8.10	0.14	34	7.53	0.17	26
Fortymile 2002	8.30	0.17	41	7.34	0.18	23
Mentasta 1993[d]	8.90	0.23	15	7.91	0.20	23
Mentasta 1994[d]	8.83	0.21	18	8.09	0.19	23
Mentasta 1998[c]	8.66	0.27	15	7.98	0.32	12
Nelchina 1996	8.26	0.24	23	7.19	0.19	17
Nelchina 1997	8.43	0.18	30	7.91	0.21	30
Nelchina 1998	8.97	0.20	30	8.57	0.18	30
Nelchina 1999	9.17	0.23	26	8.14	0.21	27
Nelchina 2000	7.66	0.19	25	7.02	0.15	31
Nelchina 2001	8.25	0.21	25	7.72	0.19	25
N AK Peninsula 1998	8.44	0.24	19	7.17	0.30	20
N AK Peninsula 1999	8.35	0.25	22	7.41	0.24	22
N AK Peninsula 2005	8.14	0.35	15	7.93	0.24	26
N AK Peninsula 2006	8.7	0.37	19	7.6	0.16	30
N AK Peninsula 2007	9.2	0.24	28	8.4	0.13	22
S AK Peninsula 1989	6.70	0.67	9	5.40	0.57	9
S AK Peninsula 1999	7.70	0.28	25	7.14	0.16	29
S AK Peninsula 2008	7.65	0.17	32	7.48	0.16	31
S AK Peninsula 2009	8.06	0.17	39	7.41	0.18	26
Porcupine 1983[e]	7.40	0.19	24	6.60	0.16	28
Porcupine 1984[e]	7.30	0.22	33	6.70	0.18	23
Porcupine 1985[e]	7.70	0.23	27	7.30	0.20	26
Porcupine 1993[f]				6.20	0.70	68
Teshekpuk 2006[g]				5.9	0.22	20
Teshekpuk 2007[g]				6.3	0.20	34
Western Arctic 1965[h]				5.4		

[a] With standard errors of about 0.2 kg, a difference in means of 0.6 kg would be significant at the 0.05 level.

[b] Denali data is corrected for calf age; uncorrected weights would be 0.3–0.5 kg higher (Adams et al. 1995b).

[c] Unpublished data from L. G. Adams, U.S. Geological Survey, Anchorage.

[d] Unpublished data from K. Jenkins (1996).

[e] Data from Whitten et al. (1992).

[f] Data from Whitten et al. (1992).

[g] L. Parrett, ADF&G, unpublished data, 2015, Fairbanks.

[h] McGowan (1966). Weight given is for males and females combined.

Other Indicators of Nutrition in Individual Caribou Calves: Condition Scores, Gutted Weight, Femur Marrow Fat, Numbers of Warble Fly Larvae, and Mandible Length

Condition Scores

During the early years of the study, it quickly became apparent that condition scores (Gerhart et al. 1996) were subjective, even when biologists and technicians were trained and experienced. Most caribou were rated as “good--condition 4” in all herds and in all years despite large differences in body weight and size. The thick pelage of caribou makes condition scoring challenging and increases subjectivity. Although we continued to assign condition scores to caribou, we did not believe that condition scores provided additional information once body weight and size measurements were obtained. We had so little confidence in body condition scores that we did not analyze condition score data. These data are available on capture cards and were entered into electronic capture records in most cases.

Gutted (Carcass) Weight vs. Live Weight

We obtained carcass (i.e., gutted) weight data from approximately 180 female calves and there were sufficient data to evaluate the utility of using carcass weight as an indicator of nutrition in 3 herds (Nelchina, Mulchatna, and Northern Alaska Peninsula). In these 3 herds, live weight predicted 90–94% of the variation in carcass weight for both 4-month-old and 10-month-old calves (Fig. 56A–D).

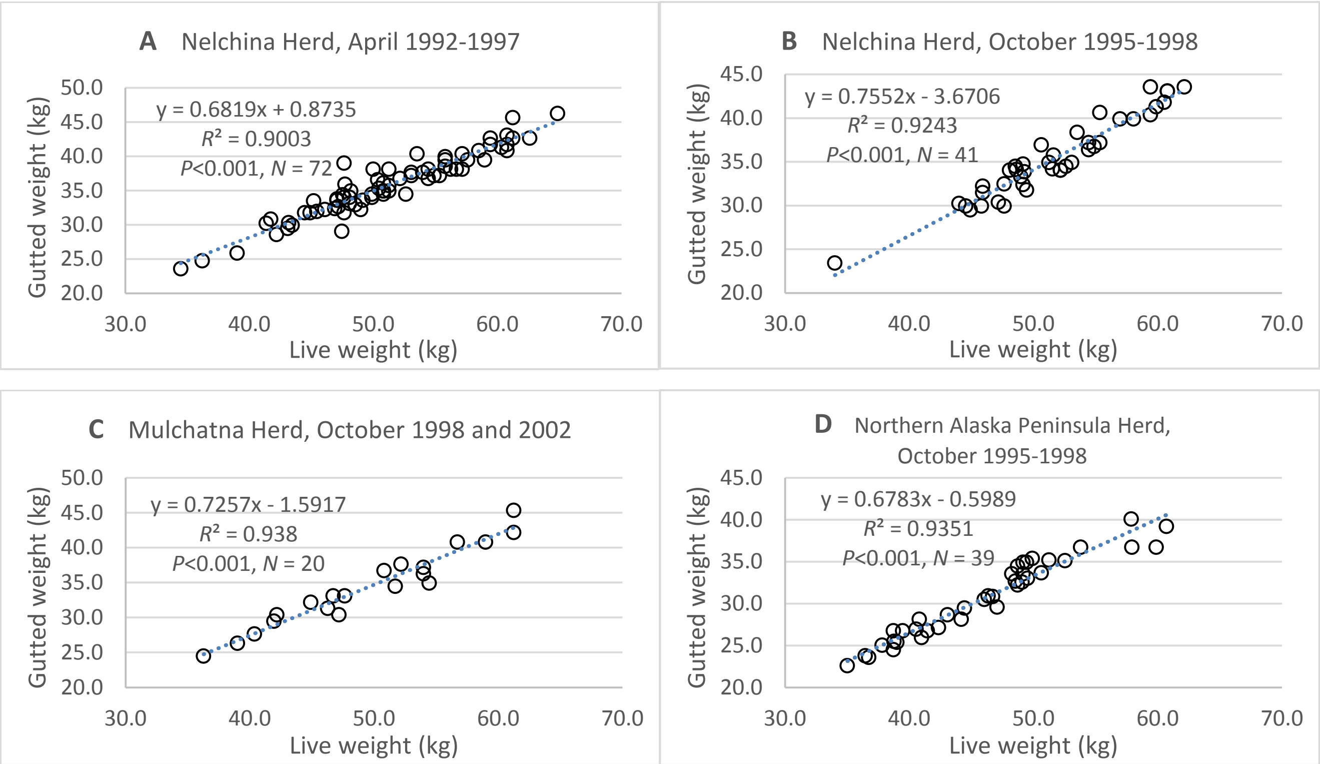


Figure 56. Regressions of live weight versus gutted weight in 3 Alaska caribou herds in which female calves were collected to evaluate health and condition during 1993–2002. Gutted weight was measured with heart, lungs, liver, and gastrointestinal tract removed.

Femur Marrow Fat

In April collections in the Nelchina herd, although calves with higher femur marrow fat content also tended to be heavier, and correlations were significant, marrow fat explained only ~15% of the variation in live weight (Fig. 57A). In October collections from the Nelchina, Mulchatna, and Northern Alaska Peninsula herds, percent femur marrow fat predicted ~24–34% of the variation in live weight and the slopes of regression lines were steeper (Fig. 57B–D). Lowest mean percent fat was observed in April (range 37–56%, Appendix C) and highest mean percent fat was in October (range 52–68%, Appendix C). However, significant differences in live weight of calves within herds between years did not necessarily indicate that marrow fat differences would also be significant. For example, in the collections in the Nelchina herd for spring 1993 versus spring 1995, there was a significant difference in weight of calves ($t = 3.65$, $P = 0.001$, df = 23) but marrow fat content was not different ($t = 1.35$, $P = 0.19$, df = 23). Conversely, in the 1996 versus 1998 fall collections in the Northern Alaska Peninsula herd, marrow fat content was significantly different ($t = 3.28$, $P = 0.004$, df = 18) while weight was not different ($t = 0.16$, $P = 0.87$, df = 18). In the Mulchatna herd, the highest mean percent femur fat (73%) was observed in the April 1995 collection (a time when the herd was still increasing), and the lowest mean percent femur fat (48%) was observed in October 1998 (after the population decline had begun).

We also considered mandible marrow fat content but determined that the relatively high nonfat residue (sinew and nerve tissue) of material in mandibles, especially those of calves, and the relatively small amount of material available in calf mandibles made mandibles less useful than femurs as a marrow fat index. Also, Davis et al. (1987) found that percent femur marrow fat and percent mandible marrow were highly correlated in adult caribou ($R = 0.93$), so we focused our efforts on femur marrow fat instead.

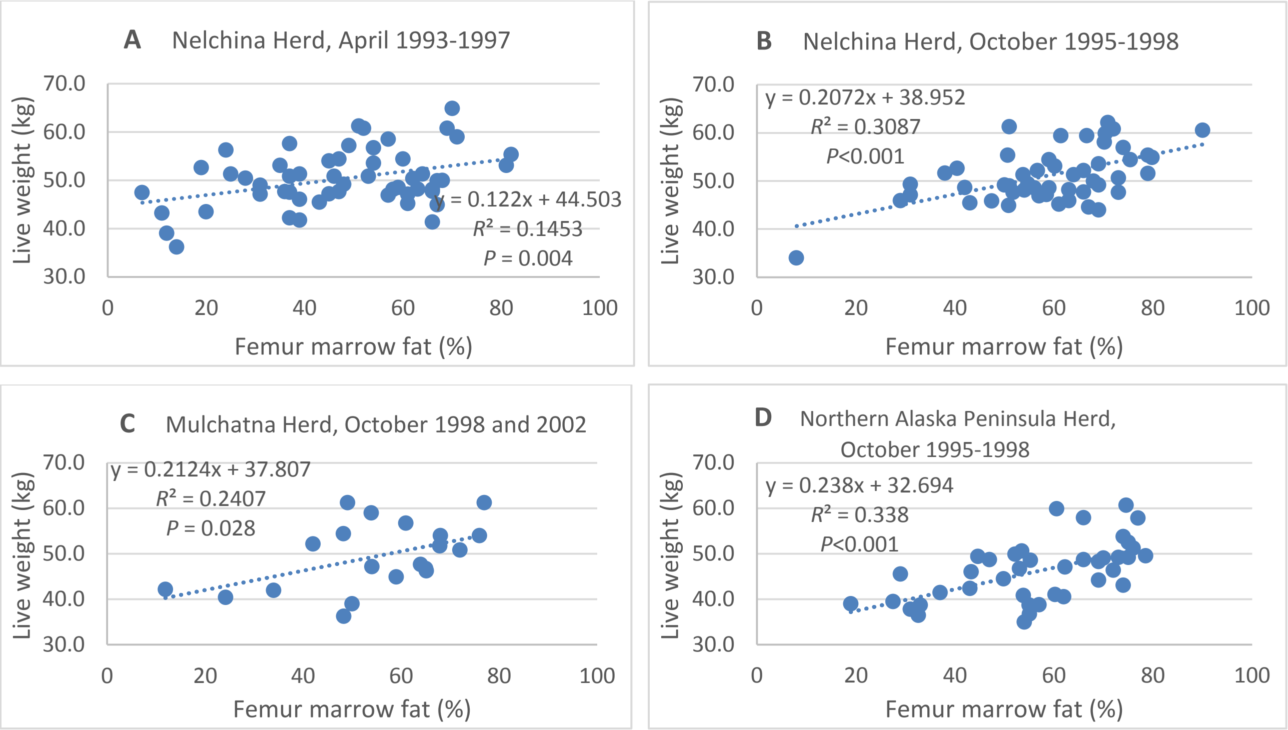


Figure 57. Regressions of femur marrow fat versus live weight for 3 caribou herds in which female calves were collected to evaluate health and condition during 1993–2002.

Number of Warble Fly Larvae

We counted numbers of warble fly larvae in April in 15 female calves that were collected in the Mulchatna herd and 53 female calves that were collected in the Nelchina herd (Appendix C). All calves had some larvae and the number of larvae in individual calves ranged from 7 to 410. The highest numbers of larvae were found in the April 1995 collection of 5 individuals in the Nushagak herd (average = 295, range 146–368). In 5 collections of calves from the Nelchina herd, average number of warble larvae ranged from 47 to 120. For the 53 female calves collected in the Nelchina herd, we found no relationship (R^2 = 0.002) between the number of warble fly larvae and femur marrow fat content (Fig. 58).

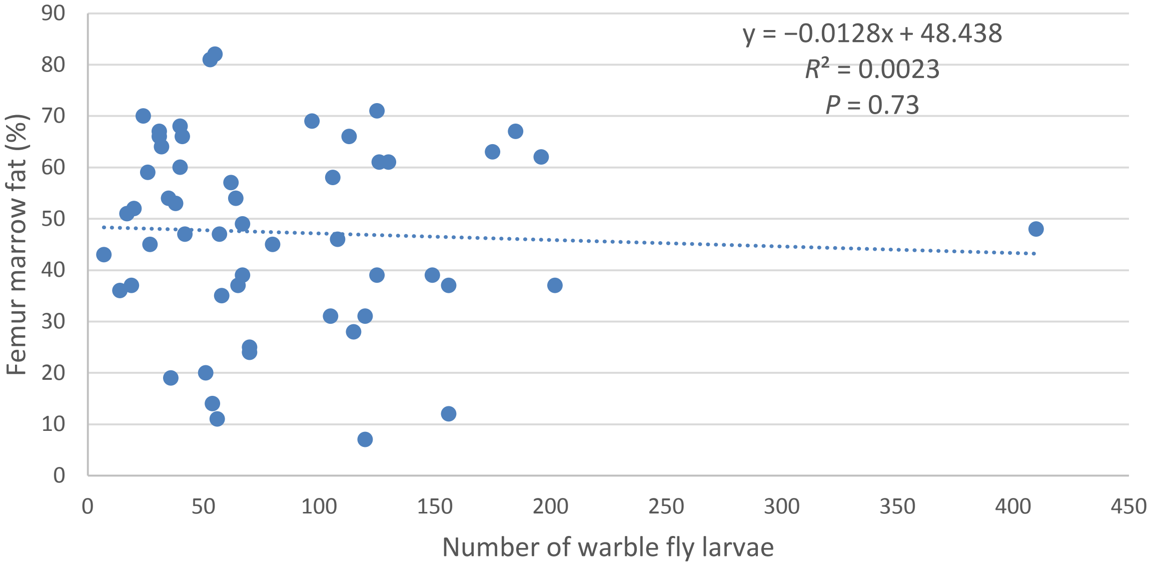


Figure 58. Relationship between number of warble fly larvae and femur marrow fat content for 53 female calves collected in the Nelchina caribou herd, Alaska, April 1993–1997.

Mandible Length of Female Calves

We obtained data from both live calves and collected (dead) calves. Mandible lengths of calves varied considerably between herds and regions (Appendix C). Mandible lengths of female calves were consistently greater in the Nelchina herd than in the Mulchatna and Northern Alaska Peninsula herds, and smallest in the Western Arctic herd (Table 10, Appendix C). For calves we collected in the Nelchina herd (the only herd where we collected an adequate number of calves for analysis in both fall and spring), mean mandible length of 10-month-old calves was greater than mean mandible length of 4-month-old calves indicating growth of mandibles over winter (221 cm ±1.33 mm SE vs. 203 mm ±2.0 mm SE, $t = -7.47$, $P < 0.0001$, df = 30). We also found that mandibles were consistently about 1–2 cm larger in 10-month-old calves than in 4-month-old calves in all 13 cohorts of collected calves in which we obtained samples in both fall and spring (Table 10). In fact, the longest mandibles of calves in fall were typically shorter than the shortest mandibles of calves in spring.

In the one cohort of Nelchina calves in which we were able to measure mandible length in live calves and then subsequently measure the individuals’ cleaned mandible, we found that measurements on the live animals tended to be ~1 cm longer (difference in means = 9.4 mm, t = 2.20, P = 0.19, df = 22). Despite the additional measurement error involved with measurements of mandibles in live calves compared with clean, dried mandibles from collected calves, live 10-month-old calves from the Delta herd had consistently longer mandibles than 4-month-old calves (Table 11).

In 4-month-old calves collected in the Nelchina, Mulchatna, Northern Alaska Peninsula, Nushagak, and Western Arctic herds, length of cleaned and dried mandibles predicted ~80% of the variation in live weight (Fig. 59). In 10-month-old calves collected in the Nelchina, Mulchatna, Northern Alaska Peninsula, Nushagak, and Western Arctic herds, length of cleaned and dried mandibles predicted ~70% of the variation in live weight (Fig. 60). Similar comparisons for measurements from live calves in the Delta herd yielded worse fits—mandible length predicted ~40% of the variation in 4-month-old calves and ~30% of the variation in 10-month-old calves (Figs. 61 and 62).

Table 10. Comparison of mandible lengths (mm) of 4- and 10-month-old female calves collected for condition-disease assessment in the Mulchatna, Nelchina, Northern Alaska Peninsula, and Western Arctic herds, Alaska, 1992–1996. All measurements are from cleaned, dried jaws, except for Nelchina 1993 4-month-old calves.

Age	Comparison (*n*)	Mean length±SE	Student's *t*-value	*P*-value	df
4 months	Nelchina (16) vs. Western Arctic (37)	203.3±1.9 vs. 183.8±1.7	7.50	<0.0001	36
4 months	Nelchina (16) vs. Northern Alaska Peninsula (20)	203.3±1.9 vs. 195.2±1.9	2.93	0.003	33
4 months	Western Arctic (37) vs. Northern Alaska Peninsula (20)	183.8±1.7 vs. 195.2±1.9	4.42	<0.0001	45
4 months	Western Arctic 1992 and 1995 cohorts (22) vs. 1994 (15)	189.7±1.6 vs. 174.5±1.8	6.07	<0.0001	32
10 months	Nelchina (60) vs. Western Arctic (45)	221.1±1.3 vs. 206.5±1.1	8.39	<0.0001	103
10 months	Nelchina (60) vs. Mulchatna (9)	221.1±1.3 vs. 215.2±2.3	2.24	0.02	14
10 months	Western Arctic (45) vs. Mulchatna (9)	206.5±1.4 vs. 215.2±2.3	3.48	0.002	12
4 months vs. 10 months	Nelchina fall (16) vs. Nelchina spring (60)	203.3±1.9 vs. 221.1±1.3	7.47	<0.0001	30
Nelchina 1993 4-month olds	Live calves (18) vs. cleaned mandibles (18)	230.6±4.0 vs. 221.2±1.6	2.20	0.019	22

Table 11. Comparisons of mandible lengths (cm) in live 4- and 10-month-old female calves in the Delta caribou herd, Alaska, 1991–2004. (Only caliper measurements are presented).

Cohort year	Mean for 4-month calves	Mean for 10-month calves	Difference	Student's *t*-value	*P*-value	df
1991	21.85	22.50	0.65	2.45	0.0214	28
1992	21.45	23.14	1.69	4.23	0.0003	23
1994	22.25	23.28	1.03	4.07	0.0005	22
1995	22.19	23.49	1.30	5.80	<0.0001	24
1996	22.10	23.33	1.23	3.22	0.0060	14
1997	22.41	23.12	0.72	2.26	0.0160	21
1998	21.88	23.08	1.20	3.36	0.0015	20
1999	22.06	22.93	0.86	2.86	0.0085	24
2000	22.16	23.72	1.56	5.81	<0.0001	20
2001	22.03	23.85	1.82	8.89	<0.0001	26
2002	21.75	23.77	2.01	6.07	<0.0001	25
2003	22.20	23.86	1.66	4.21	0.0006	16
2004	22.29	23.62	1.33	3.81	0.0008	25

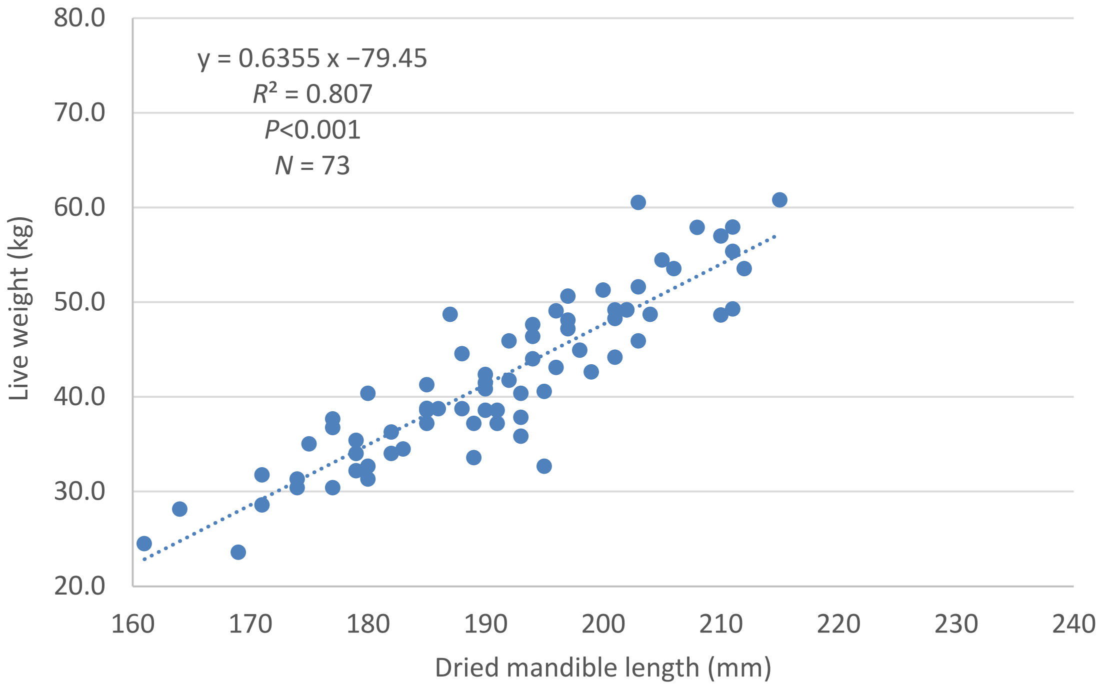


Figure 59. Mandible length (cleaned and dried) as a predictor of live weight in 4-month-old female calves in the Nelchina, Mulchatna, Northern Alaska Peninsula, Nushagak, and Western Arctic caribou herds, Alaska, 1992–1997.

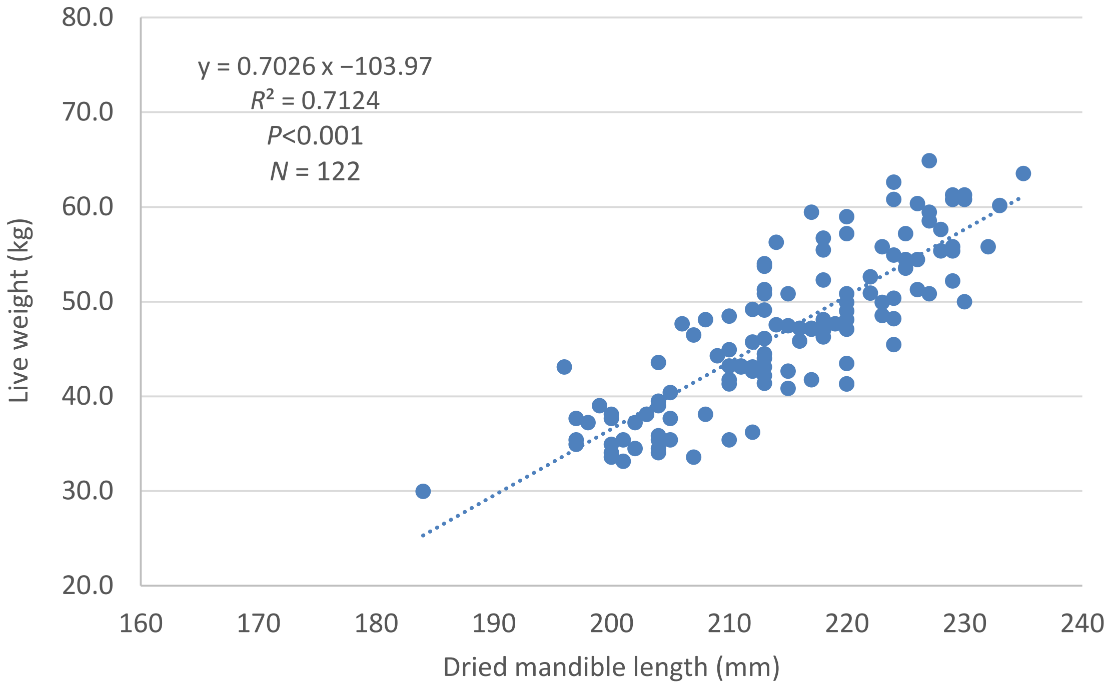


Figure 60. Mandible length (cleaned and dried) as a predictor of live weight in 10-month-old female calves in the Nelchina, Mulchatna, Northern Alaska Peninsula, Nushagak, and Western Arctic caribou herds, Alaska, 1992–1997.

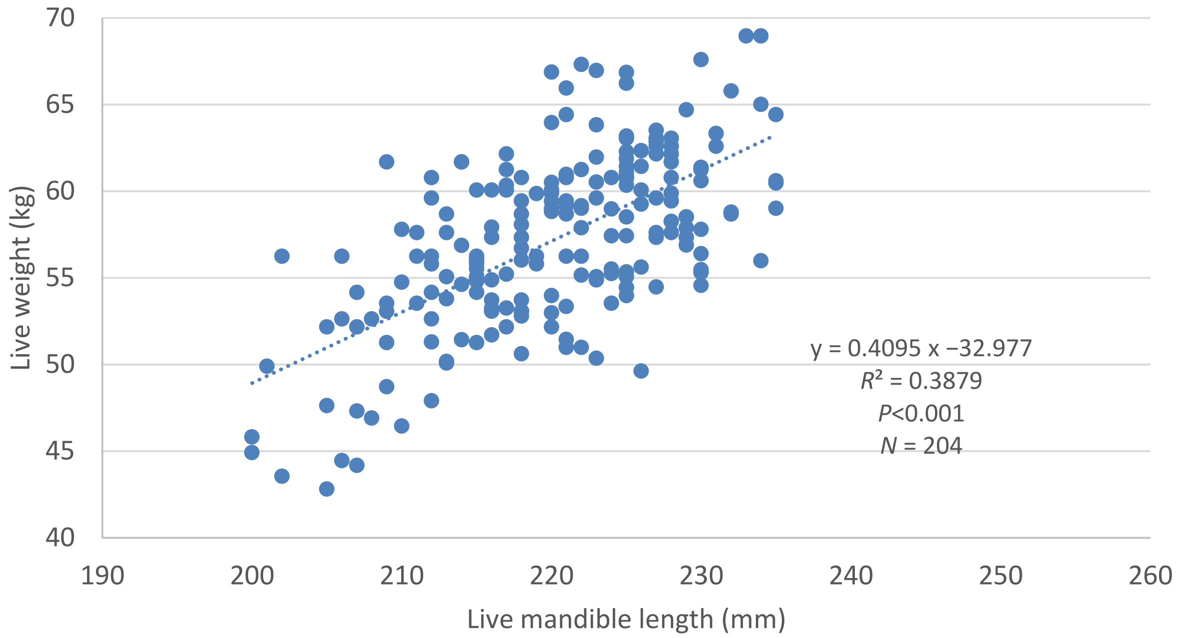


Figure 61. Mandible length (measured on live calves) as a predictor of live weight in 4-month-old female calves in the Delta caribou herd, Alaska, 1991–2004.

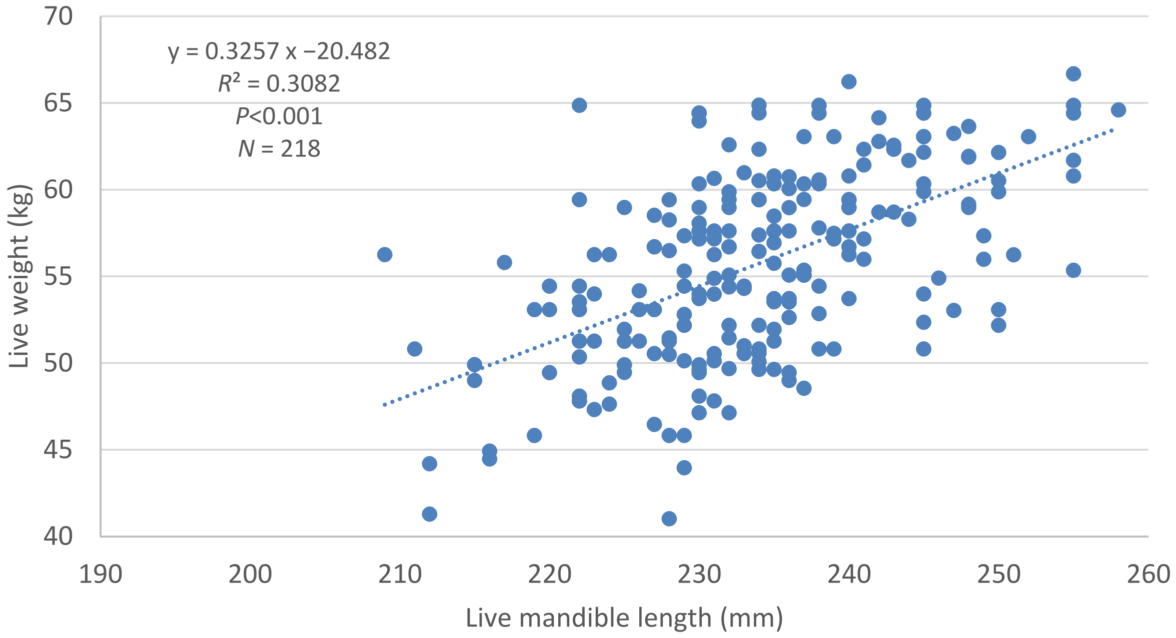


Figure 62. Mandible length (measured on live calves) as a predictor of live weight in 10-month-old female calves in the Delta caribou herd, Alaska, 1987–2007.

In the 160 caribou mandibles from hunter-killed males collected from the Delta herd during 1996–2002, we found no evidence of mandibular necrosis. For 3 years after hunting resumed in the Delta herd in 1996 (i.e., 1996, 1997, 1998), bull caribou ≥eruption-wear class 10 were well represented (17 mandibles) in mandible collections (Table 12). During hunts in 2000–2002 however, no bull caribou ≥eruption-wear class 10 were represented in mandible collections and only 7 caribou mandibles were from bulls ≥eruption-wear class 8 (Table 12).

Annual increases in mandible length were significant through eruption-wear class 4 (generally 52 months of age), after which P-values of annual differences were >0.1 (P-values: classes 1 to 2 = 0.002, 2 to 3 = 0.005, 3 to 4 = 0.05, 4 to 5 = 0.83, 5 to 6 = 0.32, 6 to 7 = 0.69, 7 to 8 = 0.68, 8 to 9 = 0.79, 9 to 10 = 0.91, 10 to >10 = 0.86). Growth from eruption-wear classes 4 to 6 was marginally significant (P = 0.13), but mandible length of the class 7 males was significantly greater than the class 4 males (P = 0.02). After class 7 there were no differences in mandible length through class 15 (for class 7 vs. classes 8–15, P = 0.32). We did not find differences in mandible length of caribou bulls that completed their first 3 years of growth before the period of bad winters began in 1989 compared with caribou bulls that completed their first 3 years of growth during the 5 bad winters from 1989 to 1993 (t = 1.06, P = 0.30, df = 36). Also there was no difference in mandible length of bulls that completed their first 3 years of growth during the period of bad winters and those that completed their first 3 years of growth after the bad winters (t = 0.48, P = 0.63, df = 49).

Table 12. Frequency distribution by eruption-wear class and 3 mandible measurements (mm) for 160 bull caribou taken by hunters in the Delta caribou herd, Alaska, 1996–2002.

	Eruption-wear class and mandible measurements (mm)											
Years	1	2	3	4	5	6	7	8	9	10	>10	Total
1996–1999	6	7	5	14	8	8	8	12	7	6	11	92
2000–2002	1	6	7	11	8	11	18	5	1			68
Total *N*:	7	13	12	25	16	19	26	17	8	6	11	160
Mean mandible length	262.4	286.0	301.3	306.8	307.6	311.8	313.1	314.4	315.5	316.2	317.0	
SE	4.61	2.81	1.94	1.91	3.28	2.52	1.92	3.28	4.08	3.86	2.84	
Mean diastema length	99.1	110.4	119.4	122.0	122.8	128.2	130.7	130.5	131.8	128.5	132.2	
SE	1.42	1.98	1.98	1.66	2.08	1.46	1.58	1.46	2.16	2.45	1.74	
Mean tooth row length	92.1	104.5	103.3	102.7	100.5	101.8	98.9	99.2	99.5	100.5	96.7	
SE	4.06	1.08	1.19	1.28	1.96	1.06	0.90	1.26	1.61	1.52	0.90	

Because there were no differences in mandible length between periods of good and bad winters, we lumped all mandibles together and fit polynomial and asymptotic (nonlinear) regression curves to mandible and diastema lengths (Figs. 63 and 64). The advantage of asymptotic regression is that the curve is forced to an asymptote and the oldest age classes cannot cause a wobble in the graph as happened with the polynomial regression. Because the 4 bulls with the greatest wear caused the polynomial growth curves to curve slightly upward for class 13 and 14 males, we eliminated these data points from consideration in the polynomial regressions and used 156 of the 160 available mandibles for curve construction. Another reason for excluding data points for wear classes >13 is that assignment to the oldest wear classes becomes increasingly subjective and is more likely that these extremely worn teeth result from factors other than age. All data were used in the asymptotic regression curves. We observed very little difference in shapes of the curves plotted with polynomial or asymptotic regressions of both mandible length and diastema length. In the polynomial regression, about 57–58% of the variation in mandible and diastema length was explained by wear class. The design of the asymptotic regression procedures in program R did not allow calculation of correlation coefficients (R^2) for the asymptotic regression.

Growth curves for mandible and diastema length appeared very similar so we did not analyze data on diastema length in detail but present them here for comparison. Tooth row length reached its maximum size when the caribou’s permanent teeth were fully erupted and then no further growth occurred. We did not analyze tooth row data but present them for comparison with data for mandible length and diastema length.

Boone and Crockett Records

Caribou bulls from the Northern Alaska Peninsula, Mulchatna, and Nelchina caribou herds comprised 71.6% of all caribou in recent Boone and Crockett records (Fig. 65, Table 13) (Boone and Crockett 2011). Despite the fact that herds with a higher proportion of nonresident hunters are more likely to have caribou entered into record books, we believe that, for its relative size, the Northern Alaska Peninsula herd was overrepresented (25.3% of all records). The Arctic herds (2.4% of all records for all Arctic herds) and Fortymile herd (1.9% of all records) were underrepresented.

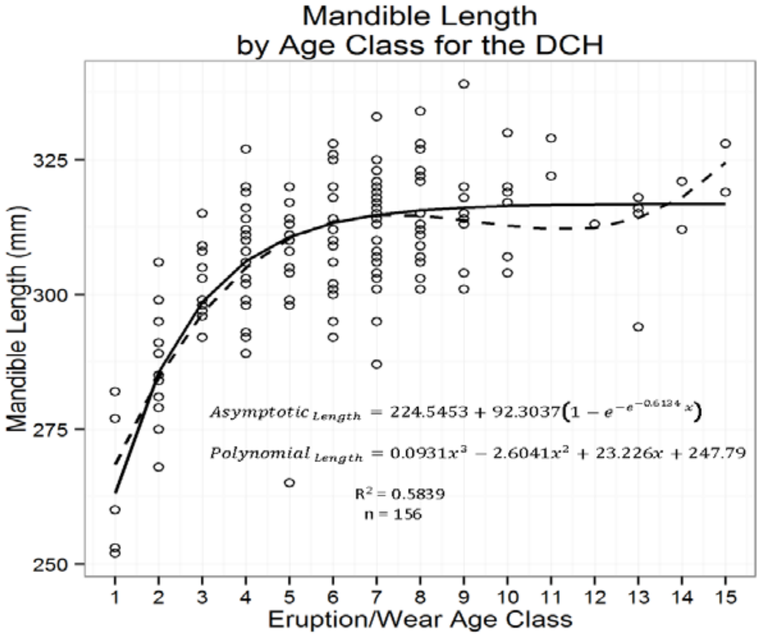


Figure 63. Mandible length by eruption-wear class for male Delta herd caribou killed by hunters, Alaska, 1996–2002. Correlation coefficient (R^2) is for the polynomial regression only.

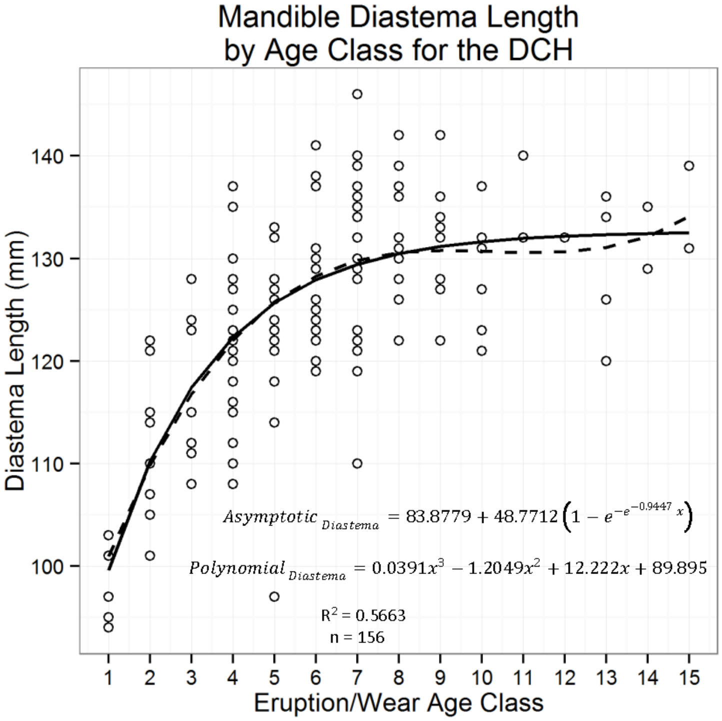


Figure 64. Diastema length by eruption-wear class for male Delta herd caribou killed by hunters, Alaska, 1996–2002. Correlation coefficient (R^2) is for the polynomial regression only.

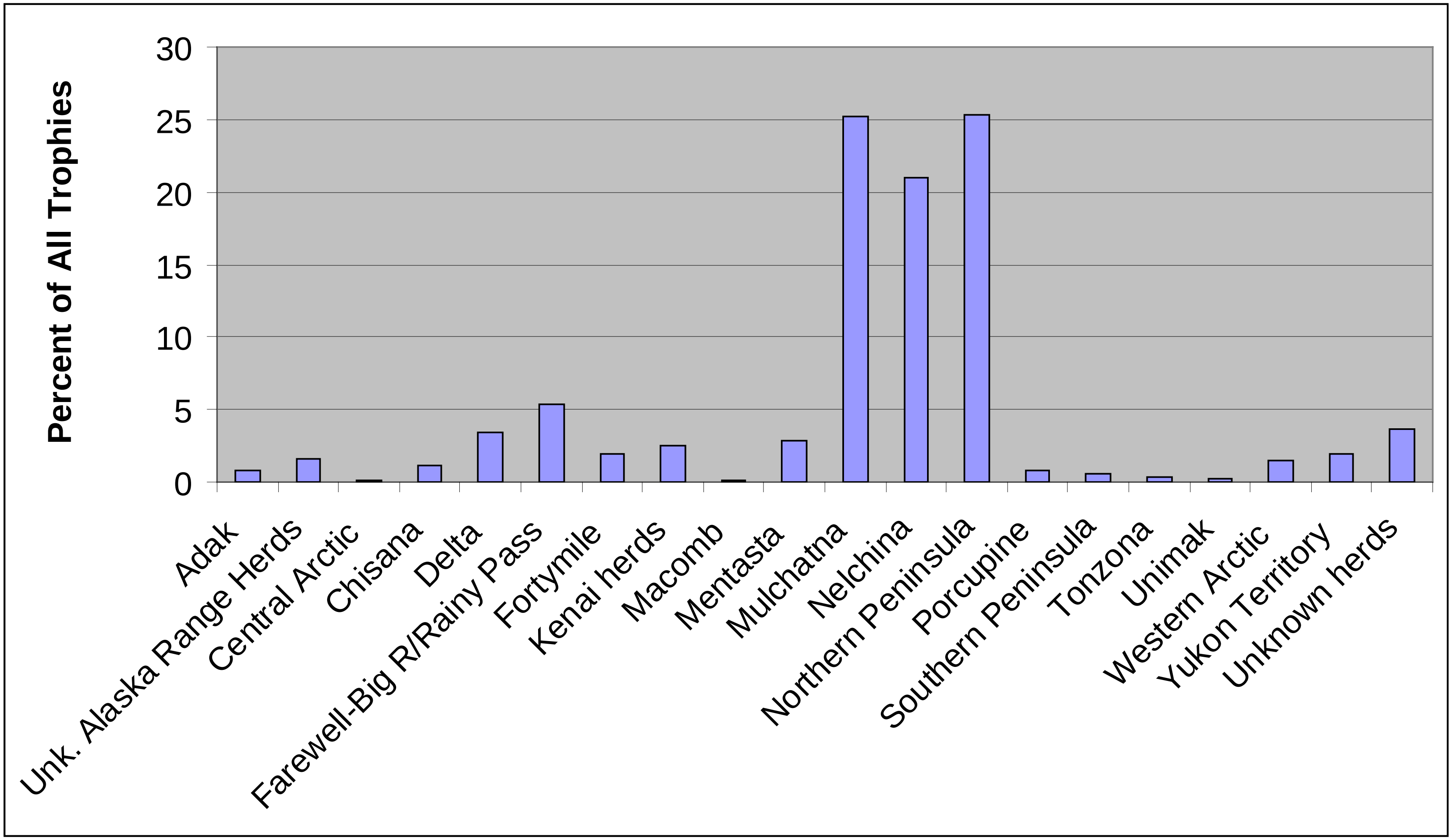


Figure 65. Proportion of caribou bulls by herd in Boone and Crockett (2011) records for barren-ground caribou, Alaska and Yukon, Canada. All bulls ≥400 points (*n* = 890).

Table 13. Number and proportion of barren-ground caribou ≥400 points in Boone and Crockett (2011) records by herd, Alaska and Yukon, Canada.

Herd	Number of trophies	Percent of trophies
Adak	7	0.8
Unknown Alaska Range herds	14	1.6
Central Arctic	1	0.1
Chisana	10	1.1
Delta	30	3.4
Farewell-Big River/Rainy Pass	48	5.4
Fortymile	17	1.9
Kenai herds	22	2.5
Macomb	1	0.1
Mentasta	25	2.8
Mulchatna	224	25.2
Nelchina	187	21.0
Northern Alaska Peninsula	225	25.3
Porcupine	7	0.8
Southern Alaska Peninsula	5	0.6
Tonzona	3	0.3
Unimak	2	0.2
Western Arctic	13	1.5
Yukon Territory	17	1.9
Unknown herds	32	3.6
Total trophies	890	100.0

Winter Diet of the Delta Herd and Other Alaska Caribou Herds

Proportion of lichens in winter fecal pellet samples from Delta herd caribou appeared to decline from 80–90% in the 1980s to 60–70% in the early 1990s and then to about 40% by the late 1990s (Fig. 66). Proportion of mosses and shrubs appeared to increase as proportion of lichens declined. Proportion of lichens in winter fecal pellet samples from 11 winter ranges of 9 other Alaska caribou herds varied from about 40% in Southwest Alaska to 90% on the Kenai Peninsula (Fig. 67). Proportion of sedges was relatively high on several caribou winter ranges including Pah River Flats (Western Arctic herd), Koktuli River (Mulchatna herd), and Northway area (Nelchina herd) (Fig. 67). Because we obtained samples opportunistically and we made no concerted effort to sample herd winter ranges in a representative manner, statistical analysis of fecal samples was not warranted. The information on fecal samples is intended to be qualitative in nature. Dates of collection and area of collection for individual samples were presented previously (Valkenburg et al. 2002).

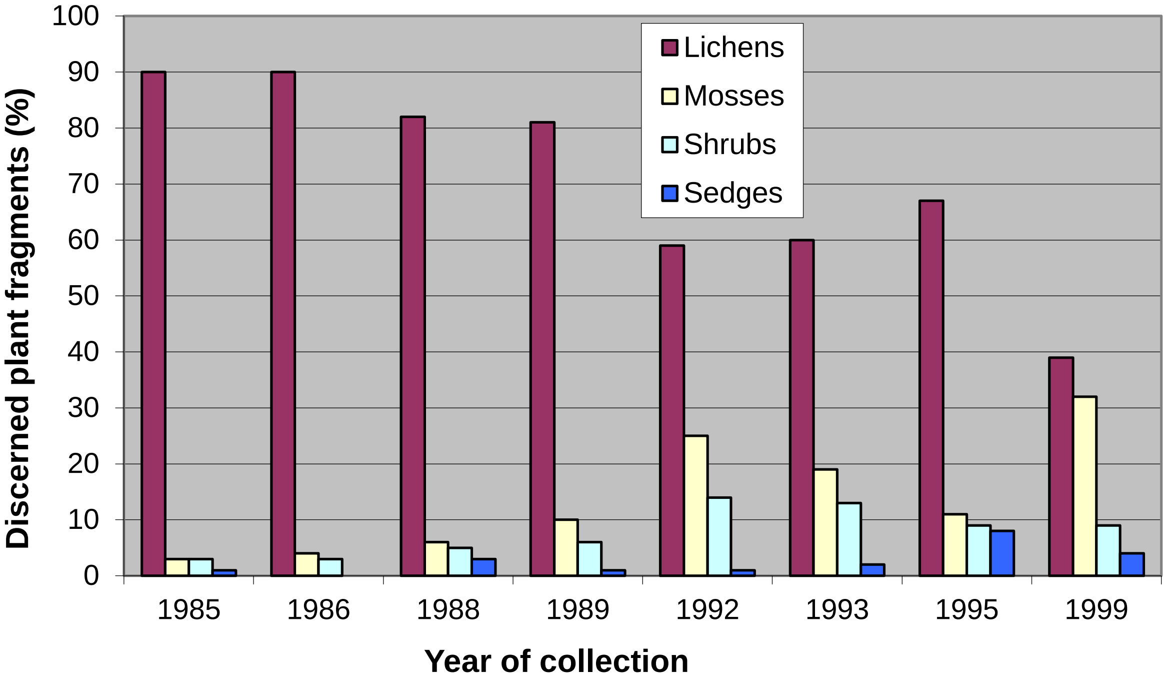


Figure 66. Proportion of lichens, mosses, shrubs, and sedges in discerned plant fragments in 34 samples (20 pellets each) of fecal pellets from the range of the Delta caribou herd, Alaska, 1985–1999.

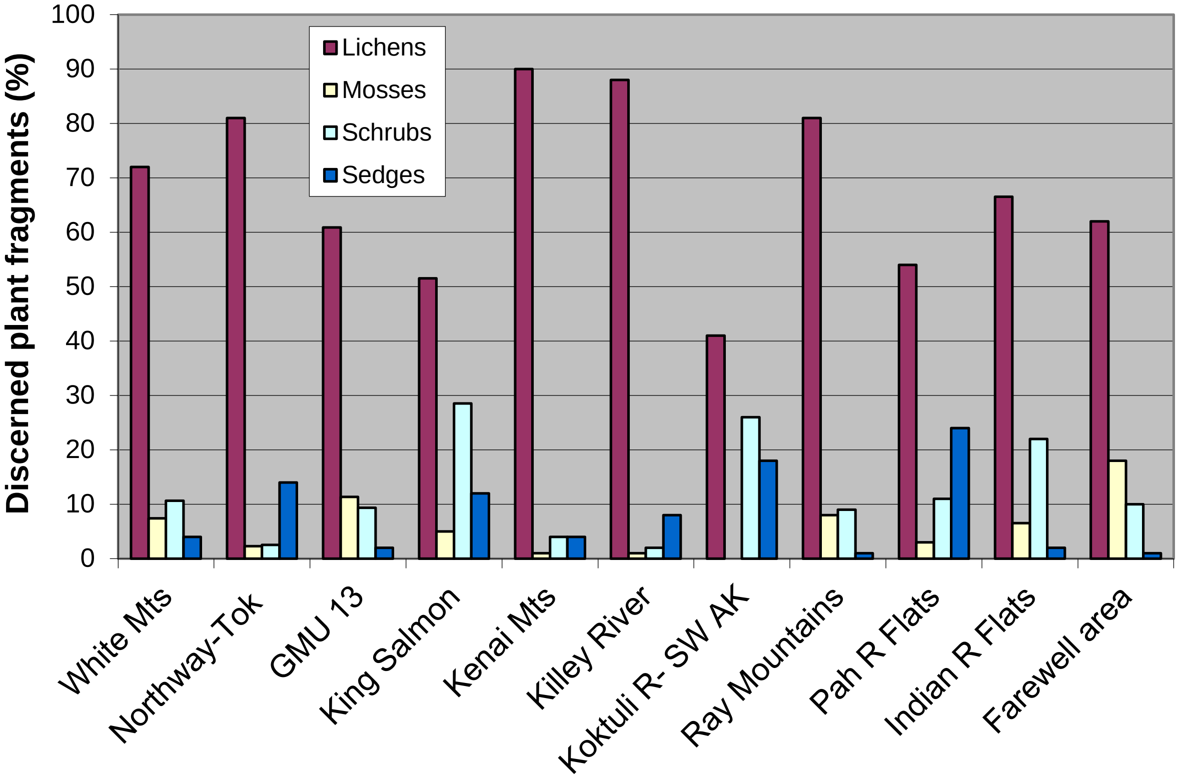


Figure 67. Proportion of lichens, mosses, shrubs, and sedges in discerned plant fragments in 27 samples (20 pellets each) of fecal pellets from 11 different caribou winter ranges in Alaska, 1992–1996.

MORTALITY AND SURVIVAL OF RADIOCOLLARED CARIBOU IN THE DELTA HERD

Causes and Timing of Mortality of Females

Calves

Of 320 calves (4- to 16-months old) that were on the air during 1979–2007, 76 (24%) died (Tables 14 and 15). Predation was the leading cause of death for most calves (74%) and wolves were responsible for a majority of all calf deaths (at least 55%). In 25% of all deaths, a cause could not be clearly determined, sometimes because the death occurred during the snow-free period when it was more difficult to find evidence, or because too much time elapsed before we were able to investigate the cause of death. In the unusual year of 1992–1993, lynx (*Lynx canadensis*) killed 3 of 20 (15%) radiocollared calves when most of the Delta herd moved north, out of its usual winter range. Illegal harvest was responsible for only 1 calf death (<1%). No calf deaths were attributed to disease or malnutrition. Deaths from predation were likely underestimated in this study, especially those by grizzly bears (*Ursus arctos*) because most would have occurred during the snow-free season when monitoring was less frequent and when it was often not possible to see evidence of hemorrhaging or definitive evidence of predator type.

Table 14. Proportion[a] dying and cause of death of radiocollared known-aged female Delta herd caribou, Alaska, 1978–1979 through 2006–2007.

Year[b]	Proportion dying (%) (cause of death) by age class Calves (4–16 mo old)	Yearlings (16–28 mo old)	Older than yearlings (>28 mo old)
1978–1979	0/11		
1979–1980	No collared calves	0/11 (0)	
1980–1981	0/7	0/2 (0)	0/19 (0)
1981–1982	0/10	0/7 (0)	0/19 (0)
1982–1983	1/12 (8) (1 unk)	2/10 (20) (2 unk)	0/26 (0)
1983–1984	0/10	0/11 (0)	2/34 (6) (1 unk, 1 hunting)
1984–1985	No collared calves	0/10 (0)	2/43 (5) (1 grizzly, 1 unk)
1985–1986	No collared calves	No collared yearlings	11/48 (23) (7 wolf, 2 hunting, 1 snared, 1 unk)
1986–1987	0/8	0/2	4/37 (11) (2 unk, 2 hunting)
1987–1988	0/12	2/10 (17) (1 hunting, 1 unk pred)	2/33 (6) (1 wolf, 1 wolf/wolverine)
1988–1989	1/10 (10) (1 unk)	0/12 (9)	6/36 (17) (6 unk)
1989–1990	No calves collared	2/9 (22) (1 wolf, 1 unk)	5/41 (12) (4 unk, 1 wolf)
1990–1991	0/4	No collared yearlings	9/41 (22) (5 unk, 2 wolf, 2 unk pred)
1991–1992	8/19 (42) (4 wolf, 2 unk pred, 2 unk)	0/8	5/32 (16) (3 wolf, 1 unk pred, 1 unk)
1992–1993	8/20 (40) (3 lynx, 2 unk pred, 2 unk, 1 bear,)	1/8 (9) (1 unk)	5/33 (15) (4 wolf, 1 coyote)
1993–1994	7/15 (47) (5 wolf, 1 unk, 1 poached)	0/12	3/33 (9) (2 unk, 1 wolf)
1994–1995	5/17 (29) (3 wolf, 2 unk pred)	2/7 (29) (1 grizzly, 1 hunting)	6/41 (15) (3 wolf, 1 unk pred, 1 breached birth, 1 unk)
1995–1996	5/20 (25) (3 wolf, 2 unk)	1/11 (9) (1 wolf)	4/39 (10) (3 wolf, 1 unk pred)
1996–1997	6/14 (43) (2 wolf, 3 unk pred, 1 unk)	2/14 (14) (2 wolf)	3/42 (7) (2 wolf, 1 unk)
1997–1998	3/19 (16) (2 wolf, 1 unk)	1/8 (13) (1 wolf)	9/48 (19) (4 wolf, 2 hunting, 2 unk, 1 avalanche)
1998–1999	7/20 (35) (6 wolf, 1 unk)	0/17	6/46 (13) (4 wolf, 2 unk)
1999–2000	8/16 (50) (6 wolf, 2 unk)	3/13 (23) (2 unk, 1 wolf/wolverine)	8/54 (15) (3 wolf, 4 unk, 1 unk pred)

	Proportion dying (%) (cause of death) by age class		
Year[b]	Calves (4–16 mo old)	Yearlings (16–28 mo old)	Older than yearlings (>28 mo old)
2000–2001	3/16 (19) (2 wolf, 1 grizzly)	0/8	9/55 (16) (5 wolf, 4 unk)
2001–2002	7/15 (47) (6 wolf, 1 unk)	3/13 (23) (2 wolf, 1 unk)	3/52 (6) (2 unk, 1 wolf)
2002–2003[c]	3/19 (16) (3 wolf)	0/8 (0)	7/54 (13) (6 wolf, 1 unk)
2003–2004[c]	2/8 (25) (2 unk)	1/16 (6) (1 unk)	5/53 (9) (4 unk, 1 wolf)
2004–2005[c]	1/8 (13) (1 unk)	1/6 (17) (1 wolf)	7/60 (12) (6 unk, 1 unk pred)
2005–2006[c]	No collared calves	0/6 (0)	6/51 (12) (5 unk, 1 wolf)
2006–2007[d]	1/10 (10) (1 unk)	No collared yearlings	
Totals	76/322 (24) (42 wolf, 19 unk, 9 unk pred, 3 lynx, 1 grizzly, 1 bear, 1 poached)	21/239 (9) (8 unk, 8 wolf, 2 hunting, 1 grizzly, 1 unk pred, 1 wolf/wolverine)	124/1,070 (12) (54 unk, 50 wolf, 7 hunting, 7 unk pred, 1 avalanche, 1 breached birth, 1 coyote, 1 grizzly, 1 snared, 1 wolf/wolverine)

[a] This is a crude proportion of radiocollared caribou that died and is not comparable to calculated or modeled annual mortality or survival rates.

[b] Mortality rate was calculated from 1 Oct to 30 Sep each year. Calves were first collared in April (10-months old) until 1991 when they were collared in early October (4-months old).

[c] After 2002 few mortalities were investigated.

[d] Mortality and survival rates not documented in adults after 2005–2006.

Table 15. Summary of causes of death by age category of radiocollared female caribou in the Delta caribou herd, Alaska, 1 January 1979–30 September 2008.

	Calves[a]			Yearlings[b]			Adults[c]		
Cause of death	Number dying	Percent of predation	Percent of total deaths	Number dying	Percent of predation	Percent of total deaths	Number dying	Percent of predation	Percent of total deaths
Predation									
Wolf	42	75.0	55.3	8	72.7	38.1	50	83.3	39.4
Grizzly bear	2	3.6	2.6	1	9.0	4.8	1	1.7	0.8
Lynx	3	5.4	3.8	0	0	0	0	0	0
Coyote	0	0	0	0	0	0	1	1.7	0.8
Unknown predation	9	16.1	11.8	2	18.1	9.5	8	13.3	6.3
Total predation	56	100.1	73.7	11	100.0	52.4	60	100.1	47.2
Other natural									
Breached birth	0		0	0		0	1		0.8
Avalanche	0		0	0		0	1		0.8
Human caused									
Legal	1		1.3	2		9.5	4		3.2
Illegal	0		0	0		0	4		3.2
Capture-related	n/a			0		0	3		3.2
Total	1		1.3	2		9.5	11		8.7
Unknown	19		25.0	8		38.1	54		42.5
Total mortality	76		100	21		100	127		100

[a] Individual calves collared = 321.

[b] Individual yearlings collared = 238.

[c] Individual adults collared = 218.

Deaths of calves appeared to be relatively evenly distributed throughout the year, although there was some evidence for increased mortality during April–May and during December–January (Table 16). There likely was bias in determining the month of death because of the timing of radiotracking flights. Deaths of calves from unknown causes were also relatively evenly distributed throughout the year (8 during the snow-free period, 15 May–30 September; 11 during the period of annual snow cover, 1 October–14 May).

In addition to the 76 calves that died from causes listed above, 4 additional calves died from predation (3 killed by wolves and 1 by a grizzly bear) within 2 weeks after they were initially radiocollared. Because their deaths were so close to the time they had been drugged, we could not discount predisposition to predation and did not count them as predation mortality.

Yearlings

Of the 239 radiocollared female yearlings we monitored during 1979–2006, 21 (9%) died (Table 14). Wolves were responsible for 8 deaths (38% of those that died, or 62% of the deaths where a cause could be determined) (Table 15). We were unable to determine cause of death in 8 cases (38% of all deaths). Deaths of yearlings occurred throughout the year, but small sample sizes precluded determining if seasonal patterns existed (Table 16).

Adults

During 1981–2006 we monitored 209 individual adult female radiocollared caribou as they aged from 2 years (actually 28 months) to as much as 14 years (a total of 1,070 collar years). We monitored 124 of these until they died. We lost contact with the remaining 85 individuals before we could document their deaths. Batteries on the vast majority of those 85 collars expired and many of these caribou were seen carrying nonfunctioning collars. A few collars (probably <10) were spotted lying on the ground, usually from the low-flying helicopter during capture operations or composition counts. We were only able to document a few cases of dispersal (see section *Emigration-Immigration*). We were able to determine the likely cause of death of 70 (56%) of the 124 deaths of radiocollared adult females. Predators killed 60 of these females (86%). Wolves were responsible for 50 (83%) of these predation-related deaths (Tables 14 and 15). Five (7%) of the 70 females that died of a known cause were shot during the legal hunting season (1 of these was either abandoned or escaped and was not recovered by the hunter) and 2 others (3%) were mistaken for males and shot during the hunting season for males only. Deaths of radiocollared adult females occurred throughout the year, but a majority (60%) died in the 6-month period from December through May (midwinter through spring) (Table 16). Nine adults died during or within 2 weeks of capture operations when we were changing their collars. Two of these were killed by wolves within 5 days of capture and were not included as predation mortalities.

Table 16. Deaths of radiocollared female caribou by age class and month of death in the Delta caribou herd, Alaska, 1978–1979 through 2006–2007.

	Number dying by month											
Age class	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
4–16 months	9	4	4	9	6	5	5	8	0	8	8	10
16–28 months	1	1		1	2		1	3		2	6	4
>28 months	14	12	13	10	12	5	12	8	12	5	8	13

Causes and Timing of Mortality of Males

Calves

In 1979 we radiocollared 11 males in early January and 2 additional males in late March. Of these, 5 went missing and 1 shed its collar within 6 months of collaring. One was killed by a wolf 1 month after it was collared, and another died of unknown causes within 2 months of being collared. Despite extensive searching throughout the range of the Delta herd and surrounding areas, we were never able to determine what happened to the 5 missing calves. However, after we gained more experience with radiocollaring male and female caribou, it became apparent that there were many more collar failures with males than with females, especially with early models of collars. In addition, the early expandable collars were not very successful and young caribou frequently shed them. Five of the original collared males survived with collars intact to enter the yearling age class.

Of the 10 male calves that were radiocollared with breakaway collars in late September 1993, 2 were killed by wolves (1 in late January and 1 in September 1994). The remaining 8 entered the yearling age class on 1 October 1994.

Yearlings

Of the 5 yearling male caribou with radio collars during the 1979–1980 mortality year, 1 was killed by a grizzly bear in August 1980. Of the 8 male calves surviving to become yearlings in 1994, none were killed as yearlings. However, 5 of the 8 collars broke away (2 at 76 days, and 1 each at 154, 288, and 350 days after the entering the yearling age class). The remaining 3 survived to enter the adult (>40 month) age class. One subsequently had its collar breakaway at 76 days and the other 2 survived the full period but their collar batteries expired during the next year.

Adults

Three of the original cohort of males collared in 1979 as calves survived to enter the adult age class. One of these was legally shot as a 2-year-old in September 1980. The other 2 survived their first year in the adult age class but were not seen or heard after late September 1981.

During 1984–1988, 20 radiocollared adult males were represented in a total of 33 collar-years. Twelve of these males died during this 4-year period. Seven (35%) of these were legally shot during the hunting season, 3 (15%) were killed by wolves, 1 was killed by a wolf or wolverine (*Gulo gulo*), and 1 died of unknown cause. In addition, 6 (30%) shed their collars at some time during the 4 years.

Survival Rates of Radiocollared Female Caribou

Calves and Yearlings

Modeled estimates of mean annual survival rate for calves (4- to 16-months old) ranged from 46% to 66% during 1979–2007, but confidence intervals of estimates overlapped in almost all years (Figs. 68 and 69, Table 17). During the years with only spring (10-month-old) captures, much less information (e.g., overwinter survival) was available to estimate year effects, leading to larger confidence intervals and more stable estimates for survival from 1980–1992 and 2004–2007. We did pick up some evidence for lower survival of radiocollared calves in 1992. Compared with the 1992–1997 period of fall captures, we observed slightly more variation in survival during 1997–2004 (Fig. 68). Annual survival rates for yearlings ranged from 82% to 91% during 1980–2006 and survival was relatively high during 1982–1990, relatively lower during most of the 1990s, with some evidence for slight recovery after 2000. In most years however, 95% confidence intervals overlapped likely due to relatively small sample sizes (Figs. 68 and 69, Table 17).

Adults

Modeled mean survival rates of all adults (ignoring age effects) were high (range 87–89%) and stable over the period (1981–2006) (Fig. 68, Table 17). However, the modeled survival estimates for radiocollared adult females were likely biased high because in the early years of the Delta herd study there were no older radiocollared caribou and in later years many radio collars expired before females died. Despite the relative lack of older females in the radiocollared sample, the data showed strong support for continuously declining survival with age ($B = -0.22 \pm 0.03$, $z = -6.41$, $P<0.0001$; Fig. 69). Once age was incorporated into survival estimates, there was no evidence for differences among years in adult survival ($\hat{\sigma}^2_{\mathrm{yr}} = 0$). Survival was highest (90–95%) in the 2-year-old age class (28- to 40-months old) and declined steadily to about 50–55% in 14-year olds.

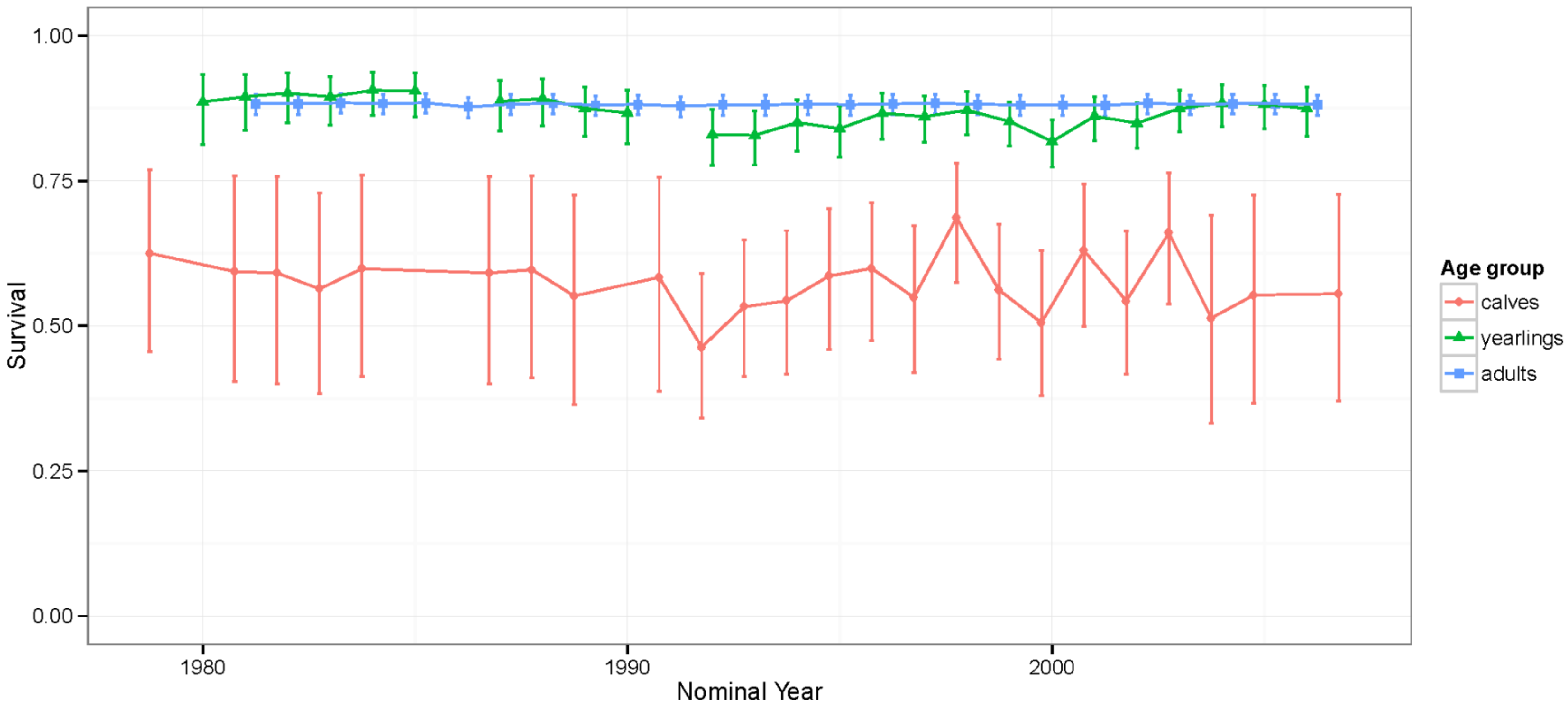


Figure 68. Estimated annual survival rates of radiocollared female Delta herd caribou by year and by age class, Alaska, 1979–2007.

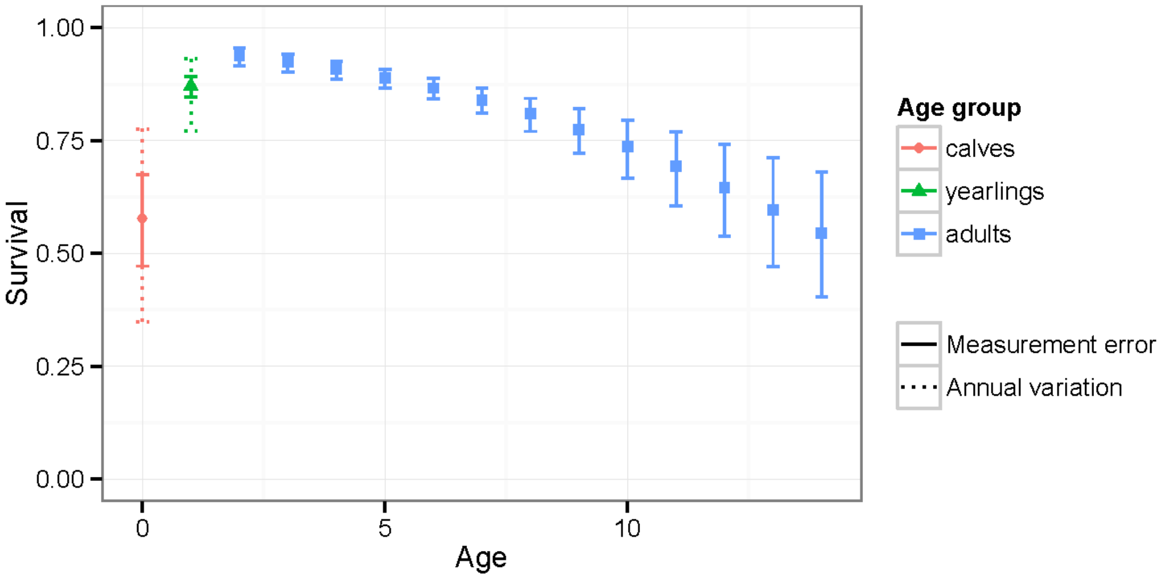


Figure 69. Estimated annual survival by age group for radiocollared female Delta herd caribou, Alaska, 1979–2007. Calf age group is 0–16 months, yearling 16–28 months, adult >28 months.

Table 17. Modeled annual survival estimates by age class for radiocollared female caribou in the Delta herd, Alaska, 1979–2007. Calves 4–16 months of age, yearlings 16–28 months of age, adults >28 months of age.

Nominal	Calves				Yearlings				Adults[a]			
year	*n*	$\hat{S}$	95% CI		*n*	$\hat{S}$	95% CI		*n*	$\hat{S}$	95% CI	
1979	11	0.625	0.455	0.769								
1980					11	0.886	0.813	0.933				
1981	7	0.593	0.404	0.759	2	0.895	0.837	0.933	20	0.883	0.864	0.899
1982	10	0.591	0.400	0.758	7	0.901	0.849	0.936	20	0.883	0.864	0.899
1983	12	0.564	0.383	0.729	10	0.895	0.846	0.929	26	0.884	0.866	0.900
1984	10	0.598	0.413	0.760	11	0.906	0.862	0.937	34	0.883	0.865	0.899
1985					10	0.905	0.860	0.936	43	0.884	0.866	0.900
1986									49	0.877	0.858	0.893
1987	8	0.591	0.400	0.758	2	0.887	0.836	0.923	37	0.882	0.864	0.898
1988	12	0.597	0.410	0.759	8	0.891	0.844	0.926	33	0.883	0.865	0.899
1989	10	0.552	0.364	0.725	12	0.874	0.826	0.911	36	0.880	0.862	0.896
1990					9	0.867	0.814	0.906	41	0.881	0.863	0.897
1991	4	0.584	0.388	0.756					41	0.878	0.860	0.895
1992	19	0.463	0.341	0.590	8	0.829	0.776	0.872	32	0.881	0.862	0.897
1993	20	0.533	0.413	0.648	11	0.828	0.777	0.870	33	0.881	0.862	0.897
1994	15	0.543	0.417	0.664	12	0.850	0.801	0.889	36	0.882	0.864	0.898
1995	17	0.586	0.459	0.702	7	0.840	0.791	0.879	43	0.881	0.863	0.897
1996	20	0.599	0.474	0.712	11	0.866	0.822	0.901	41	0.882	0.864	0.898
1997	15	0.549	0.419	0.673	14	0.860	0.816	0.896	44	0.883	0.865	0.899
1998	19	0.686	0.575	0.780	9	0.871	0.829	0.904	50	0.882	0.864	0.897
1999	20	0.562	0.442	0.675	17	0.852	0.810	0.886	48	0.881	0.862	0.897
2000	16	0.505	0.380	0.630	13	0.818	0.773	0.855	55	0.880	0.862	0.896
2001	16	0.630	0.499	0.744	9	0.861	0.819	0.895	56	0.880	0.862	0.896
2002	15	0.543	0.417	0.664	13	0.849	0.806	0.884	54	0.883	0.866	0.899
2003	19	0.660	0.538	0.764	8	0.875	0.834	0.906	55	0.881	0.863	0.897
2004	8	0.513	0.332	0.691	16	0.884	0.843	0.915	54	0.883	0.865	0.898
2005	8	0.553	0.366	0.726	6	0.882	0.840	0.913	61	0.882	0.865	0.898
2006	10				6	0.874	0.826	0.911	52	0.881	0.863	0.897
2007	10	0.555	0.370	0.726								

[a] Annual survival estimates for adults include data from all marked animals, ignoring the effect of age on survival. When age is taken into account (as shown here), there is no evidence for a difference in adult survival among years.

Modeling Effects of Covariates on Survival of Radiocollared Delta Caribou Herd Females

Calves

The scope of the models tested (survival data from Nominal Years 1992–2007) included the smallest model (intercept only) and the following covariates in the most comprehensive (global) model: *days.exposed, summer.rain, summer.mean.temp, aug.min.temp, length.green, cohort.mean.wt1, cohort.mean.wt2, cohort.mean.wt3, n.caribou, initial.weight*Denali.snow, wolf.index*n.caribou, n.caribou*Denali.snow, and wolf.index*Denali.snow*. The stepwise AIC algorithm flagged 203 models for testing. Of these, 50 models had a ΔAICc$\leq$7 (i.e., some support) and 3 models had a ΔAICc$\leq$2 (strong support) (Table 18). Only *summer.rain*, *initial.weight*, and *Denali.snow* appeared in the 3 models and only 13% of the relative weight was in the top model. In addition, R^2_L (Table 18) were low, indicating that only a small proportion of the variation in survival rates was explained by covariate information[1]. Although there was some evidence supporting the top model, none of the models fit the data very well and many of the covariates were equally inadequate at explaining the annual variation. However, according to the top model and other variant models in the top set of models, *initial.weight* and *Denali.snow* influenced calf survival--*initial.weight* had a positive influence and *Denali.snow* had a negative influence. Figure 70 graphically depicts the influence of *initial.weight* on the probability of survival for radiocollared calves captured at 4 months of age. In deep snow years, calf survival was generally lower and *initial.weight* had less influence. Conversely, when snow was shallow *initial.weight* had more influence on calf survival. Although *summer.rain* appeared with less consistency in the top set of models, it had a generally positive effect on calf survival.

Yearlings

The scope of the models tested (survival data Nominal Years 1992–2006) included the smallest model (intercept only) and the following covariates in the most comprehensive (global) model: *summer.rain, summer.mean.temp, length.green, cohort.mean.wt1, cohort.mean.wt2, cohort.mean.wt3, n.caribou, initial.weight*Denali.snow, wolf.index*n.caribou, n.caribou*Denali.snow, and wolf.index*Denali.snow*. We tested 389 models. The stepwise algorithm identified 23 models with a ΔAICc$\leq$2 (strong support) (Table 19) and 273 models with ΔAICc$\leq$7 (some support). There was little separation among models ($\sum$AICwt = 0.3 for models with ΔAIC$\leq$2 and only 0.02 for the top model). It was therefore not possible to identify a single best model. The top models generally described ~10–20% of the variation in yearling survival. The following variables were identified as having the most potential influence on yearling survival in the top 22 models: *initial.weight, summer.rain.yr1, cohort.mean.wt2, cohort.mean.wt3, cohort.mean.wt1, summer.mean.temp.yr2, wolf.index, Denali.snow, n.caribou, and length.green*. The influence of *wolf.index, cohort.mean.wt2,* and *cohort.mean.wt3* were negative. Influence of all other variables was positive.

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[1] A note about R^2_L values. Deviance based goodness-of-fit measures (e.g., R^2_L) tend to be low valued in general for binary response data. A general guideline is that R^2_L around 0.20–0.40 indicates an association in the data. This measures the amount of variation explained by the model compared to an intercept-only/constant model.

Table 18. Survival models with ΔAICc≤2 for radiocollared female calves (4–16 months) in the Delta herd, Alaska, 1979–2007.

Deviance	df.resid	*k*	AICc	ΔAICc	AICwt	ΣAICwt	R_L^2	Formula[a]
215.93	169	3	224.93	0.000	0.129	0.129	0.061	summer.rain.yr1 + initial.weight
212.34	168	4	226.06	1.124	0.073	0.202	0.077	Denali.snow*initial.weight
221.05	170	2	226.38	1.450	0.062	0.264	0.039	summer.rain.yr1

[a] Coefficients (in terms of log of the odds ratio for survival) for the top 2 models are as follow: top model-intercept 0.63, summer.rain.yr1 0.55, initial weight 0.38; second model-intercept 0.67, Denali.snow −0.69, initial weight 0.38, Denali.snow*initial weight −0.40.

Table 19. Survival models with ΔAICc<2 for radiocollared females yearlings (16–28 months) in the Delta herd, Alaska, 1979–2007. Notation "…" indicates that covariates in the top model are included. The covariate wolf.index was used as a numeric variable in these models.

Deviance	df.resid	*k*	AICc	ΔAICc	AICwt	ΣAICwt	R_L^2	Formula[a]
52.46	93	5	62.62	0.000	0.023	0.023	0.238	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + cohort.mean.wt3
50.40	92	6	62.62	0.003	0.023	0.047	0.268	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + cohort.mean.wt3
52.58	93	5	62.74	0.120	0.022	0.068	0.236	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index
53.55	93	5	63.71	1.088	0.014	0.082	0.222	initial.weight + cohort.mean.wt3 + summer.mean.temp.yr2 + Denali.snow
53.68	93	5	63.84	1.222	0.013	0.108	0.220	initial.weight + summer.rain.yr1 + cohort.mean.wt3 + summer.mean.temp.yr2
55.74	94	4	63.84	1.225	0.013	0.121	0.190	initial.weight + summer.mean.temp.yr1 + n.caribou
49.64	91	7	63.94	1.318	0.012	0.133	0.279	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + summer.mean.temp.yr1 +
51.72	92	6	63.94	1.324	0.012	0.145	0.249	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + cohort.mean.wt1
51.75	92	6	63.97	1.351	0.012	0.157	0.248	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + days.exposed
51.94	92	6	64.16	1.544	0.011	0.167	0.245	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + summer.rain.yr2
52.00	92	6	64.22	1.602	0.010	0.178	0.245	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + aug.min.temp
54.11	93	5	64.27	1.648	0.010	0.188	0.214	initial.weight + summer.mean.temp.yr1 + n.caribou + aug.min.temp
52.06	92	6	64.28	1.662	0.010	0.198	0.244	... + summer.mean.temp.yr2
50.01	91	7	64.31	1.688	0.010	0.208	0.273	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + summer.mean.temp.yr1 +
50.02	91	7	64.31	1.695	0.010	0.218	0.273	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + summer.mean.temp.yr1 +
50.04	91	7	64.34	1.721	0.010	0.228	0.273	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + summer.mean.temp.yr1 +
54.26	93	5	64.42	1.801	0.009	0.238	0.212	initial.weight + wolf.index + summer.mean.temp.yr1 + n.caribou
52.31	92	6	64.53	1.917	0.009	0.246	0.240	... + summer.rain.yr2
52.36	92	6	64.58	1.960	0.009	0.255	0.239	... + n.caribou
52.38	92	6	64.60	1.978	0.009	0.264	0.239	... + Denali.snow
52.39	92	6	64.61	1.991	0.009	0.272	0.239	initial.weight + summer.rain.yr1 + cohort.mean.wt2 + wolf.index + length.green
52.39	92	6	64.61	1.994	0.009	0.281	0.239	initial.weight + summer.rain.yr1 + cohort.mean.wt3 + summer.mean.temp.yr2 + length.green

[a] Coefficients for the top 3 models are as follow: **top model**-intercept 3.22, cohort.mean.wt3 −2.13, initial.weight 0.9, summer.rain.yr1 4.15, cohort.mean.wt2 −142; **second model**-intercept 5.7, cohort.mean.wt2 −3.1, cohort.mean.wt3 −1.4, initial.weight1.1, summer.rain.yr1 5.7, wolf.index −3.6; third model-intercept 5.7, cohort.mean.wt2 −2.8, initial.weight 1.2, summer.rain.yr1 4.0, wolf.index −4.3.

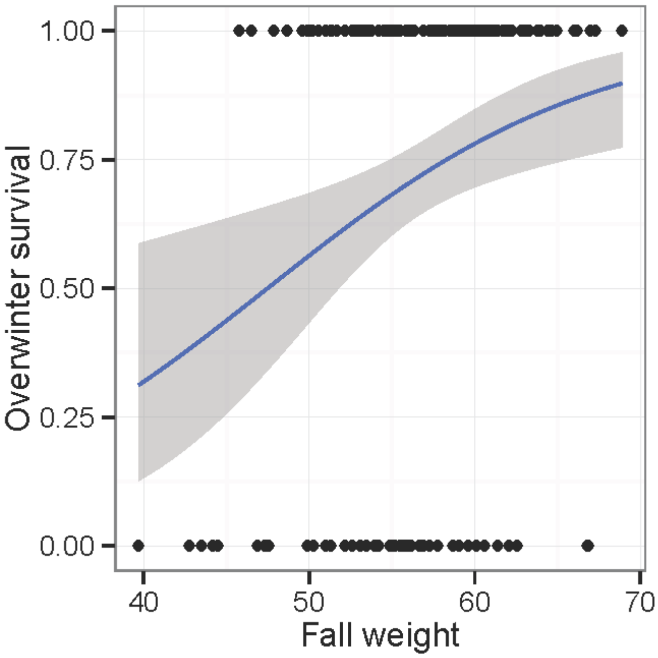


Figure 70. Probability of surviving a year from 1 October–30 September based on initial capture weight (fall captures only).

Adults

Preliminary analysis indicated that effects of *initial.weight* (i.e., an individual's weight at 4 months of age) continued beyond age 2 and affected survival of the 28- to 40-month-old age class. Thus, for consistency, our survival analysis had to be limited to the years when *initial.weight* represents fall capture weights only (Nominal Years 1992–2004). The simplest model included the intercept only, and the comprehensive model (the global model) included the following covariates: *summer.rain, summer.mean.temp, aug.min.temp, length.green, cohort.mean.wt1, cohort.mean.wt2, cohort.mean.wt3, wolf.index*n.caribou, n.caribou*Denali.snow, wolf.index*Denali.snow, initial.weight*Denali.snow*. We tested 351 models. Twenty-two models had ΔAICc$\leq$2 (strong support) (Table 20) and 151 models had ΔAICc$\leq$7 (some support). Across all models, the highest R^2_L was 0.17 (Table 20). The only variable that caused an appreciable jump in either AIC or goodness of fit was Age.at.MortYr (which was included as a fixed effect in all models in the top set). Other covariates that appeared frequently in the set of top models included *initial.weight, summer.mean.temp.yr2, cohort.mean.wt3, cohort.mean.wt1, n.caribou, aug.min.temp, length.green, summer.rain.yr1*, and *summer.rain.yr2*; although all of these covariates produced a negligible improvement in the generally poor model fit (Table 20).

NATALITY OF RADIOCOLLARED FEMALES IN THE DELTA CARIBOU HERD

Effects of Age and Year on Natality Rates

Observed and modeled natality rates of radiocollared females showed substantial variation by individual, age, and year (Figs. 71–73, Tables 21 and 22). None of 210 females produced calves at 1 year of age from 1980 to 2002, and we stopped looking at yearlings to determine pregnancy status after 2002 (Table 21). In most years, few females produced calves at age 2 (Table 21). The only year in which >50% of radiocollared 2-year olds produced calves was 1980 (*n* = 11). In all other years, observed natality rates ranged from 0% to 25% and modeled natality rates were around 10% or less (Figs. 71 and 72, Table 21). There was no observed natality in 2-year-old females during 1987–1995 (*n* = 56, Fig. 71, Table 21).

There was an abrupt increase in natality from age 2 to age 3, by which time usually at least 50% of females produced calves (Figs. 71 and 72). The one exceptional year was 1993, when none of the 3-year olds produced calves (Table 21). Natality in the 3-year-old age group was also the most variable, and modeled natality rates ranged from ~25% to >80% (Fig. 72). Over the duration of the study, modeled annual natality rates of 3-year olds were relatively high compared with modeled mean values during the early to mid-1980s, relatively low in the early 1990s, and then varied considerably around the mean during the last 10 years of the study. However, the variable nature of natality in 3-year olds and the generally small sample sizes constrained our ability to provide meaningful annual estimates of natality for this age class.

At age 4, observed and modeled natality rates generally were >75% and were less variable than at age 3 (Figs. 72 and 73, Tables 21 and 22). However, there was only 1 radiocollared 4-year-old in 1993, so we were unable to determine how this very unusual year affected the 4-year-old age class.

Table 20. Survival models with ΔAICc<2 for radiocollared adult females (>28 months) in the Delta herd, Alaska, 1979–2007. Notation "…" indicates that covariates in the top model. The covariate wolf.index was used as a numeric variable in these models.

Deviance	df.resid	*k*	AICc	ΔAICc	ΣAICwt	AICwt	R_L^2	Formula[a]
629.94	1024	4	638.06	0.000	0.026	0.026	0.168	Age.at.MortYr + initial.weight + summer.mean.temp.yr2
632.19	1025	3	638.26	0.204	0.023	0.049	0.165	Age.at.MortYr + initial.weight
630.16	1024	4	638.27	0.217	0.023	0.072	0.167	Age.at.MortYr + initial.weight + cohort.mean.wt3
628.29	1023	5	638.47	0.413	0.021	0.093	0.170	... + cohort.mean.wt3
628.79	1023	5	638.96	0.908	0.016	0.109	0.169	... + cohort.mean.wt1
631.10	1024	4	639.22	1.161	0.014	0.124	0.166	Age.at.MortYr + initial.weight + n.caribou
629.30	1023	5	639.47	1.418	0.013	0.136	0.169	Age.at.MortYr + initial.weight + cohort.mean.wt3 + aug.min.temp
629.40	1023	5	639.57	1.515	0.012	0.148	0.169	Age.at.MortYr + initial.weight + cohort.mean.wt3 + n.caribou
631.48	1024	4	639.60	1.544	0.012	0.160	0.166	Age.at.MortYr + initial.weight + cohort.mean.wt1
629.43	1023	5	639.60	1.548	0.012	0.172	0.168	... + days.exposed
629.56	1023	5	639.73	1.675	0.011	0.183	0.168	... + summer.mean.temp.yr1
629.58	1023	5	639.76	1.701	0.011	0.194	0.168	... + length.green
627.51	1022	6	639.76	1.702	0.011	0.205	0.171	... + cohort.mean.wt3 + cohort.mean.wt1
629.59	1023	5	639.76	1.707	0.011	0.216	0.168	... + cohort.mean.wt2
629.60	1023	5	639.78	1.722	0.011	0.227	0.168	... + summer.rain.yr1
629.60	1023	5	639.78	1.722	0.011	0.238	0.168	... + wolf.index
627.56	1022	6	639.81	1.752	0.011	0.249	0.171	... + cohort.mean.wt1 + days.exposed
629.65	1023	5	639.82	1.769	0.011	0.259	0.168	Age.at.MortYr + initial.weight + cohort.mean.wt3 + cohort.mean.wt1
631.74	1024	4	639.86	1.805	0.010	0.270	0.165	Age.at.MortYr + initial.weight + days.exposed
629.70	1023	5	639.87	1.814	0.010	0.280	0.168	... + n.caribou
631.92	1024	4	640.03	1.978	0.010	0.290	0.165	Age.at.MortYr + initial.weight + summer.rain.yr1
631.93	1024	4	640.05	1.990	0.010	0.299	0.165	Age.at.MortYr + initial.weight + summer.rain.yr2

[a] Coefficients for models 1, 4, and 5 are as follow: **model 1**-intercept 3.17, Age.at.MortYr −0.22, initial.weight 0.12, summer.mean.temp.yr2 0.14; **model 4**-intercept 3.21, Age.at.MortYr −0.21, initial.weight 0.10, summer.mean.temp.yr2 0.13, cohort.mean.wt3 0.16; **model 5**-intercept 3.18, Age.at.MortYr −0.21, initial.weight 0.10, summer.mean.temp.yr2 0.13, cohort.mean.wt3 0.14.

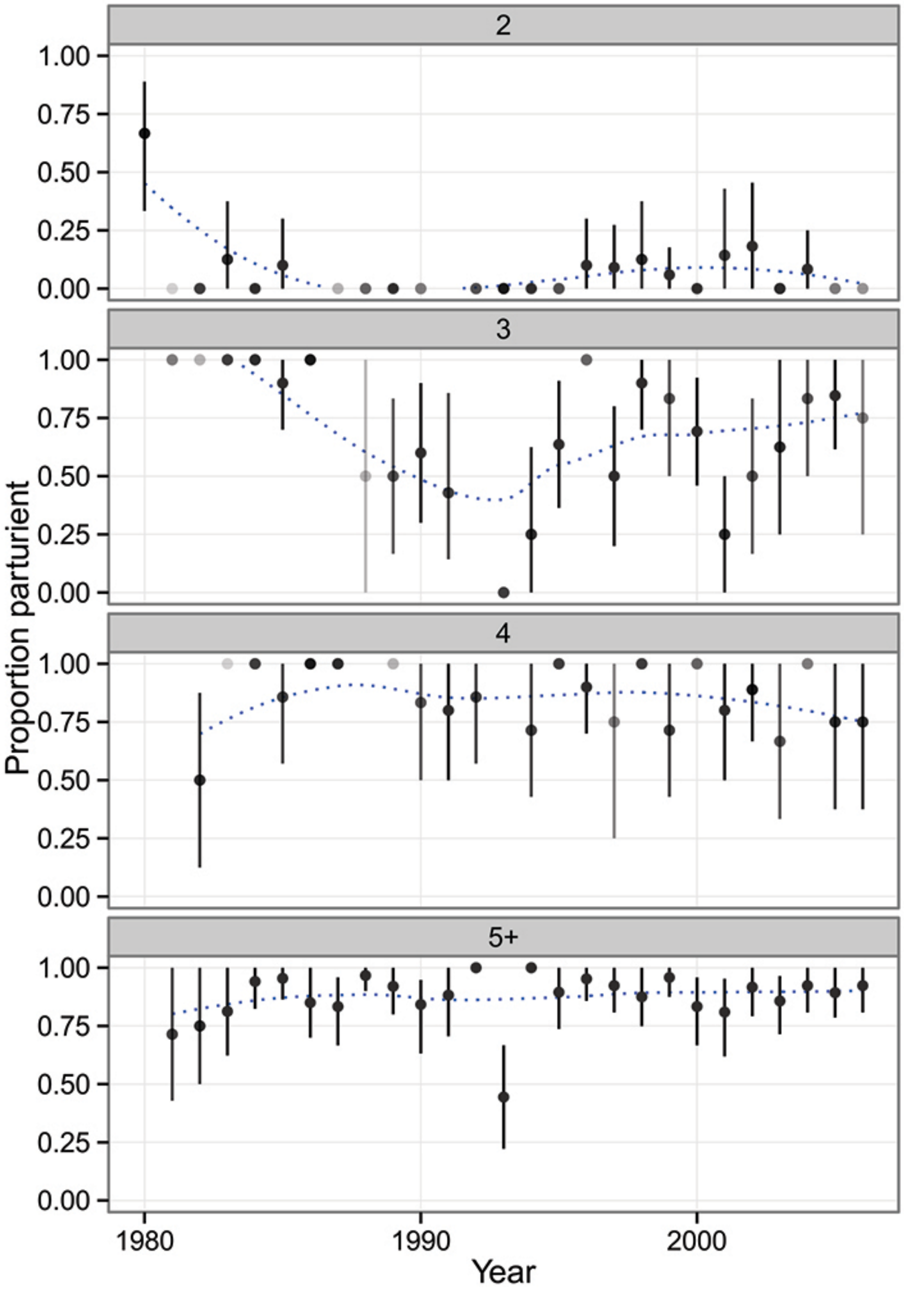


Figure 71. Observed (black dots with binomial confidence intervals) and modeled (dotted lines) natality rates by age class by year for radiocollared Delta caribou herd females, Alaska. Shading of dots shows comparative sample size.

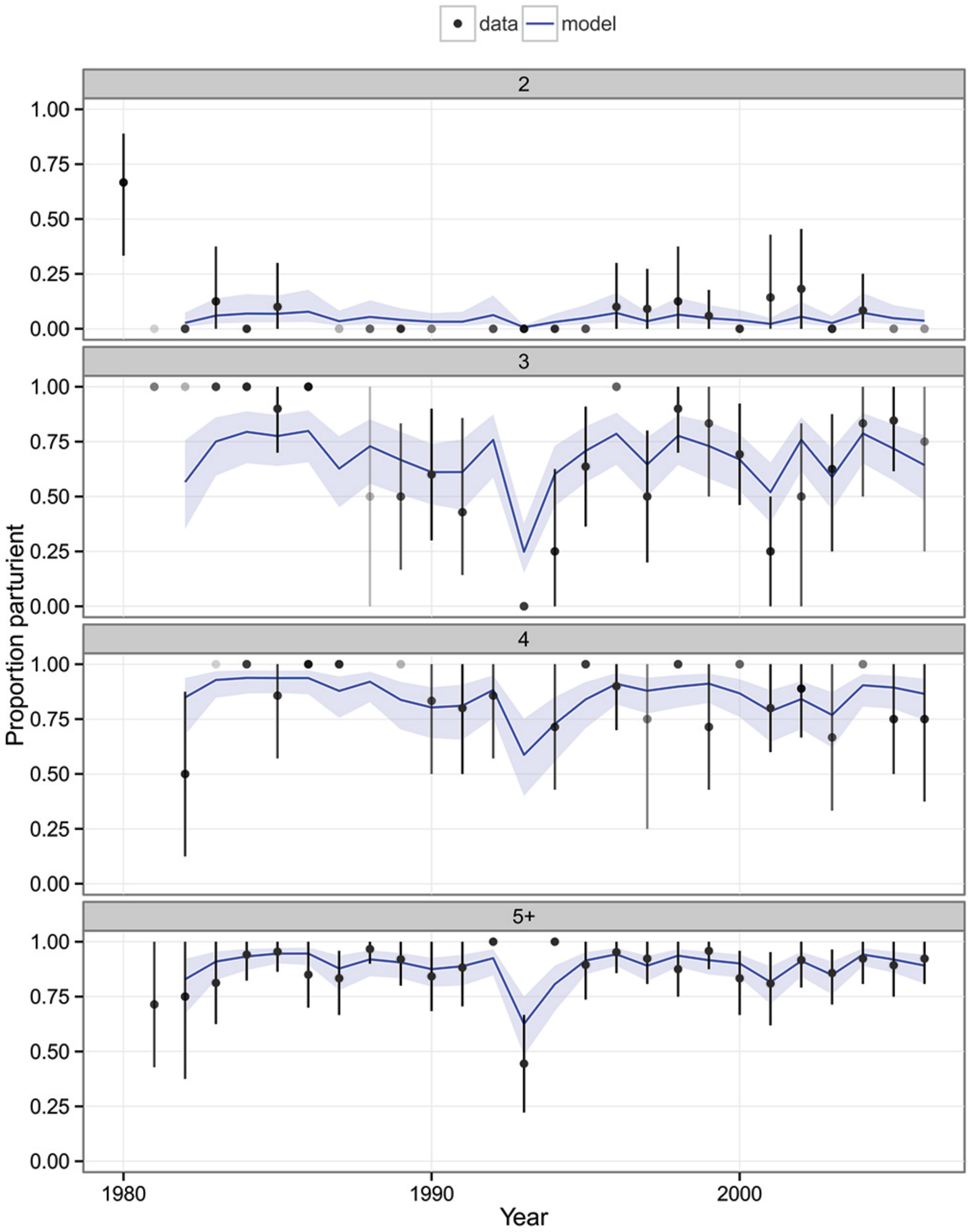


Figure 72. Observed natality rates of radiocollared Delta caribou, Alaska, by age with binomial confidence intervals (black dots with error bars), compared with model predictions with error bands based on uncertainty parameters for fixed effects (age and previous pregnancy) and prediction error for BLUPs (Best Linear Unbiased Predictors) for year effects. Shading of dots indicates sample size. Eight radiocollared caribou captured as adults (not of known age) in the Yanert herd are included in the 5+ age category.

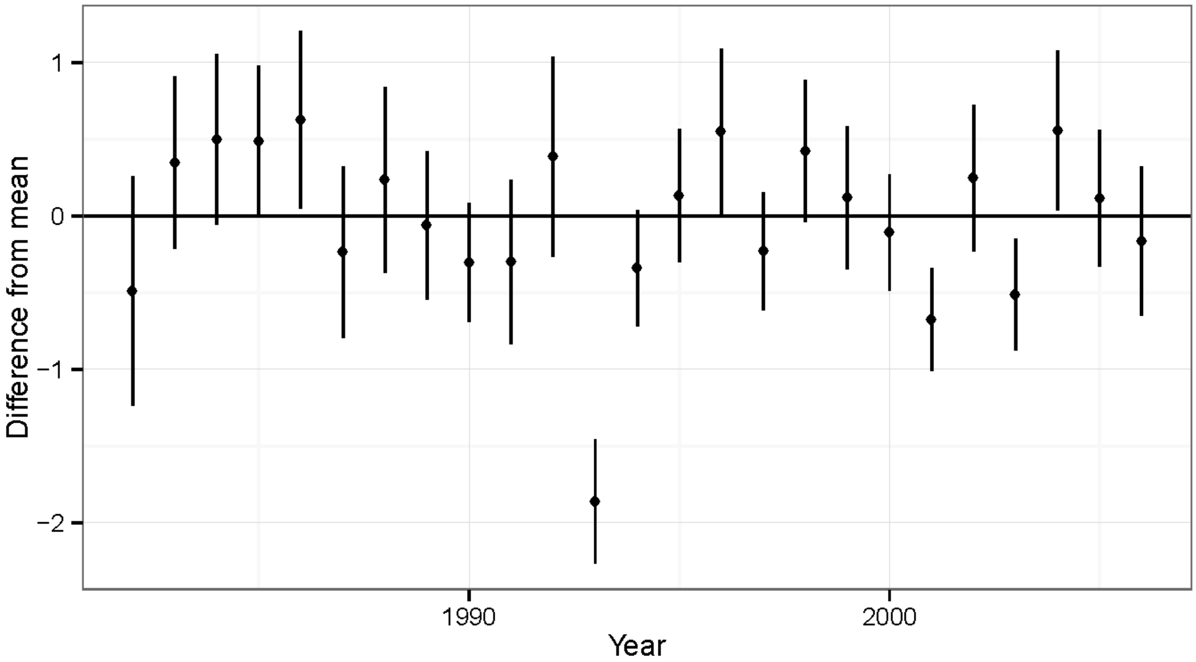


Figure 73. Year effects, represented as a difference from mean natality rates on a logit scale. Estimates are based on the best linear unbiased predictors and associated error (95% prediction intervals) for a mixed logistic regression model with age and previous pregnancy effects. The year effect was applied to the intercept of the model, thus affecting individuals equally across ages and prior pregnancy status on a logit scale. Actual results (on a probability scale) will vary based on the individual's baseline natality rate for their age and previous pregnancy.

Table 21. Natality (parturition) rates of radiocollared known-aged female caribou observed in late May in the Delta herd, Alaska, 1980–2007. Radiocollared "adult" caribou from the Yanert herd are not included here, but are included in Figure 70.

	Proportion parturient (%) by age (years) in late May						
Year	1[a]	2	3	4	5	≥6	All cows ≥3
1980		7/11 (64)					
1981	0/7 (0)	0/1 (0)	10/13 (77)				10/13 (77)
1982	0/10 (0)	0/7 (0)	2/2 (100)	5/8 (63)			7/10 (70)
1983	0/12 (0)	1/8 (13)	7/7 (100)		6/8 (75)		13/15 (87)
1984	0/12 (0)	0/11 (0)	8/9 (89)	6/6 (100)	1/1 (100)	6/7 (86)	21/23 (91)
1985		1/9 (11)	9/10 (90)	6/7 (86)	6/6 (100)	7/8 (88)	28/31 (90)
1986			8/9 (89)	9/9 (100)	3/4 (75)	8/9 (89)	28/31 (90)
1987	0/6 (0)	0/2 (0)		8/8 (100)	8/9 (89)	9/11 (82)	25/28 (89)
1988	0/11 (0)	0/5 (0)	1/1 (100)		8/8 (100)	15/16 (94)	24/25 (96)
1989	0/10 (0)	0/11 (0)	3/5 (60)	2/2 (100)		21/23 (91)	26/30 (87)
1990		0/4 (0)	6/10 (60)	5/6 (83)	0/1 (0)	17/17 (100)	28/34 (82)
1991	0/4 (0)		2/7 (29)	8/10 (80)	3/3 (100)	11/14 (79)	24/34 (71)
1992	0/16 (0)	0/5 (0)	0/1 (0)	6/7 (86)	8/8 (100)	12/12 (100)	26/28 (93)
1993	0/11 (0)	0/10 (0)	0/5 (0)	0/1 (0)	1/3 (33)	6/15 (40)	7/24 (29)
1994	0/10 (0)	0/12 (0)	2/9 (22)	4/5 (80)	1/1 (100)	13/15 (87)	20/30 (67)
1995	0/13 (0)	0/7 (0)	7/11 (64)	8/8 (100)	4/5 (80)	13/13 (100)	32/37 (86)
1996	0/16 (0)	1/11 (9)	5/5 (100)	9/10 (90)	6/6 (100)	15/16 (94)	35/37 (95)
1997	0/12 (0)	0/11 (0)	5/10 (50)	3/4 (75)	8/9 (89)	16/17 (94)	32/40 (80)
1998	0/17 (0)	1/8 (13)	9/10 (90)	7/7 (100)	3/3 (100)	18/22 (80)	37/42 (88)
1999	0/10 (0)	1/13 (8)	6/7 (86)	5/7 (71)	7/7 (100)	16/17 (94)	34/38 (89)
2000	0/9 (0)	0/10 (0)	8/12 (67)	5/5 (100)	6/6 (100)	14/18 (78)	33/41 (80)
2001	0/15 (0)	1/7 (14)	2/8 (25)	8/10 (80)	4/6 (67)	15/17 (88)	29/41 (71)
2002	0/9 (0)	2/11 (18)	3/6 (50)	8/9 (89)	11/11 (100)	11/13 (85)	33/39 (85)
2003	16	0/8 (0)	5/8 (63)	4/6 (67)	8/9 (89)	17/20 (85)	34/43 (79)
2004	6	1/12 (8)	5/6 (83)	5/5 (100)	5/6 (80)	19/20 (95)	34/37 (94)
2005	8	0/5 (0)	11/13 (85)	6/8 (75)	6/6 (100)	19/21 (90)	42/48 (88)
2006		1/5 (20)	3/4 (75)	5/7 (71)	5/5 (100)	20/21 (95)	33/37 (89)
2007	9		3/6 (50)	3/3 (100)	4/6 (75)	19/23 (83)	29/38 (76)
1980–2007	0/210 (0)	17/204 (9)	130/193 (67)	135/158 (85)	122/137 (89)	337/385 (88)	724/873 (83)

[a] After 2002, yearlings were not checked for the presence of distended udders, hard antlers, or calves-at-heel.

Table 22. Modeled annual natality rate estimates for known-aged female radiocollared caribou by age (years) and previous pregnancy status, Delta herd, Alaska, 1982–2006.

	2	3		4		≥5	
Year	−	−	+	−	+	−	+
1982	0.03	0.57	0.76	0.7	0.85	0.73	0.87
	(0.01–0.07)	(0.35–0.76)	(0.53–0.9)	(0.46–0.86)	(0.68–0.94)	(0.51–0.88)	(0.74–0.94)
1983	0.06	0.75	0.88	0.84	0.93	0.86	0.94
	(0.02–0.14)	(0.6–0.86)	(0.75–0.95)	(0.69–0.93)	(0.85–0.97)	(0.73–0.93)	(0.88–0.97)
1984	0.07	0.78	0.89	0.86	0.94	0.88	0.95
	(0.03–0.16)	(0.63–0.88)	(0.77–0.95)	(0.72–0.94)	(0.87–0.97)	(0.76–0.94)	(0.9–0.97)
1985	0.07	0.78	0.89	0.86	0.94	0.88	0.95
	(0.03–0.15)	(0.64–0.87)	(0.78–0.95)	(0.73–0.93)	(0.87–0.97)	(0.76–0.94)	(0.9–0.97)
1986	0.08	0.8	0.91	0.88	0.94	0.89	0.95
	(0.03–0.18)	(0.66–0.89)	(0.79–0.96)	(0.75–0.94)	(0.88–0.98)	(0.78–0.95)	(0.91–0.98)
1987	0.03	0.63	0.8	0.75	0.88	0.78	0.89
	(0.01–0.08)	(0.45–0.77)	(0.62–0.91)	(0.56–0.88)	(0.76–0.94)	(0.6–0.89)	(0.81–0.94)
1988	0.05	0.73	0.87	0.83	0.92	0.85	0.93
	(0.02–0.13)	(0.56–0.85)	(0.72–0.94)	(0.66–0.92)	(0.83–0.97)	(0.7–0.93)	(0.87–0.97)
1989	0.04	0.67	0.83	0.78	0.9	0.81	0.91
	(0.02–0.09)	(0.51–0.79)	(0.67–0.92)	(0.61–0.89)	(0.79–0.95)	(0.66–0.9)	(0.84–0.95)
1990	0.03	0.61	0.79	0.74	0.87	0.77	0.89
	(0.01–0.07)	(0.46–0.74)	(0.63–0.9)	(0.56–0.86)	(0.76–0.93)	(0.61–0.87)	(0.82–0.93)
1991	0.03	0.61	0.79	0.74	0.87	0.77	0.89
	(0.01–0.08)	(0.44–0.76)	(0.61–0.9)	(0.54–0.87)	(0.75–0.94)	(0.59–0.88)	(0.8–0.94)
1992	0.06	0.76	0.88	0.85	0.93	0.87	0.94
	(0.02–0.15)	(0.59–0.87)	(0.74–0.95)	(0.69–0.93)	(0.84–0.97)	(0.73–0.94)	(0.88–0.97)
1993	0.01	0.25	0.45	0.37	0.59	0.41	0.63
	(0–0.02)	(0.15–0.38)	(0.26–0.65)	(0.21–0.56)	(0.4–0.75)	(0.25–0.59)	(0.48–0.75)
1994	0.03	0.6	0.79	0.73	0.87	0.76	0.88
	(0.01–0.07)	(0.46–0.73)	(0.62–0.89)	(0.56–0.85)	(0.76–0.93)	(0.6–0.87)	(0.81–0.93)
1995	0.05	0.71	0.85	0.81	0.91	0.83	0.92
	(0.02–0.11)	(0.56–0.82)	(0.72–0.93)	(0.66–0.9)	(0.83–0.96)	(0.7–0.91)	(0.87–0.96)
1996	0.07	0.79	0.9	0.87	0.94	0.88	0.95
	(0.03–0.16)	(0.64–0.88)	(0.78–0.96)	(0.74–0.94)	(0.87–0.97)	(0.77–0.95)	(0.9–0.97)
1997	0.03	0.63	0.8	0.75	0.88	0.78	0.9
	(0.02–0.08)	(0.48–0.75)	(0.64–0.9)	(0.58–0.86)	(0.78–0.94)	(0.63–0.88)	(0.83–0.94)

	2	3		4		≥5	
Year	−	−	+	−	+	−	+
1998	0.06	0.76	0.89	0.85	0.93	0.87	0.94
	(0.03–0.14)	(0.63–0.86)	(0.77–0.95)	(0.72–0.93)	(0.86–0.97)	(0.76–0.94)	(0.9–0.97)
1999	0.05	0.71	0.85	0.81	0.91	0.83	0.92
	(0.02–0.11)	(0.56–0.82)	(0.71–0.93)	(0.65–0.9)	(0.82–0.96)	(0.7–0.91)	(0.87–0.96)
2000	0.04	0.66	0.82	0.77	0.89	0.8	0.91
	(0.02–0.08)	(0.52–0.77)	(0.67–0.91)	(0.61–0.88)	(0.8–0.94)	(0.66–0.89)	(0.85–0.94)
2001	0.02	0.52	0.72	0.66	0.82	0.69	0.85
	(0.01–0.05)	(0.38–0.65)	(0.54–0.85)	(0.48–0.8)	(0.69–0.91)	(0.53–0.82)	(0.76–0.9)
2002	0.05	0.73	0.87	0.83	0.92	0.85	0.93
	(0.02–0.12)	(0.59–0.84)	(0.74–0.94)	(0.68–0.92)	(0.84–0.96)	(0.72–0.92)	(0.88–0.96)
2003	0.03	0.56	0.76	0.69	0.85	0.73	0.87
	(0.01–0.06)	(0.42–0.69)	(0.58–0.87)	(0.52–0.83)	(0.72–0.92)	(0.56–0.84)	(0.79–0.92)
2004	0.07	0.79	0.9	0.87	0.94	0.88	0.95
	(0.03–0.16)	(0.65–0.88)	(0.79–0.96)	(0.74–0.94)	(0.88–0.97)	(0.77–0.95)	(0.91–0.97)
2005	0.05	0.7	0.85	0.81	0.91	0.83	0.92
	(0.02–0.11)	(0.56–0.82)	(0.71–0.93)	(0.66–0.9)	(0.82–0.96)	(0.7–0.91)	(0.87–0.96)
2006	0.04	0.64	0.81	0.76	0.89	0.79	0.9
	(0.02–0.08)	(0.48–0.78)	(0.65–0.91)	(0.59–0.88)	(0.78–0.95)	(0.63–0.89)	(0.83–0.95)

For females aged 5 and older, modeled natality rates were generally high (>85%), and variability was low, except for the odd year of 1993, when only 33% of these females produced calves (Figs. 71–73, Table 21). There were a few anomalous females that did not fit this pattern. One female never produced a calf during the 6 years she was observed (ages 1–6). Another produced calves at ages 3–7, and then apparently stopped reproducing after that (no calves at ages 8–10, and 12). However, there were too few of these individuals to determine if patterns in reproductive intervals existed.

We were able to observe 15 females aged 12–14 (8 aged 12, 5 aged 13, and 2 aged 14). All but 1 of these individuals (14/15) produced calves. We were unable to detect a decline in reproduction in older-aged females. Many older females had their transmitter batteries fail before they died, so we were unable to follow enough females to the end of their life to determine if reproduction declined in old aged females. It appeared that older females in the Delta herd generally died (usually from wolf predation) before they stopped having calves and the contribution of females >14 was likely low in most years.

Although modeled annual estimates of natality rates for all radiocollared females were variable from year to year, in many years the sample of radiocollared caribou was biased by age, and in some years sample sizes were rather small. In all years, except for 1993, confidence intervals overlapped each other and overlapped the overall mean across years (Fig. 71).

Effects of Previous Pregnancy on Natality of Radiocollared Females

Although occasional breeding pauses were observed (Fig. 6), modeled natality rates (including age and previous pregnancy as fixed effect terms) indicated that females that were pregnant in any one year had a higher probability of being pregnant the next year (Beta = 0.89, SE = 0.29, $z = 3.03$, $P = 0.0025$) (Fig. 74, Table 22). Of the 18 females that produced calves at 2 years of age, only one failed to produce a calf at age 3.

Logistic Regression Modeling of Natality Rates

Effects of Initial Weight, and Weight:Metatarsus Ratios on Modeled Natality Rates

In preliminary analyses, we included *initial.weight* as a covariate. To avoid problems involved in comparing *initial.weight* between spring (10-month-old) and fall (4-month-old) captures, we limited models to the period from 1993 to 2006 (fall captures only). Even when running model selection for each age group separately, *initial.weight* rarely appeared within ∆AIC <2 and never had AIC model weight >0.05, indicating lack of evidence for including weight as an explanatory variable. In subsequent analyses and model selection runs *initial.weight* was not included as a covariate.

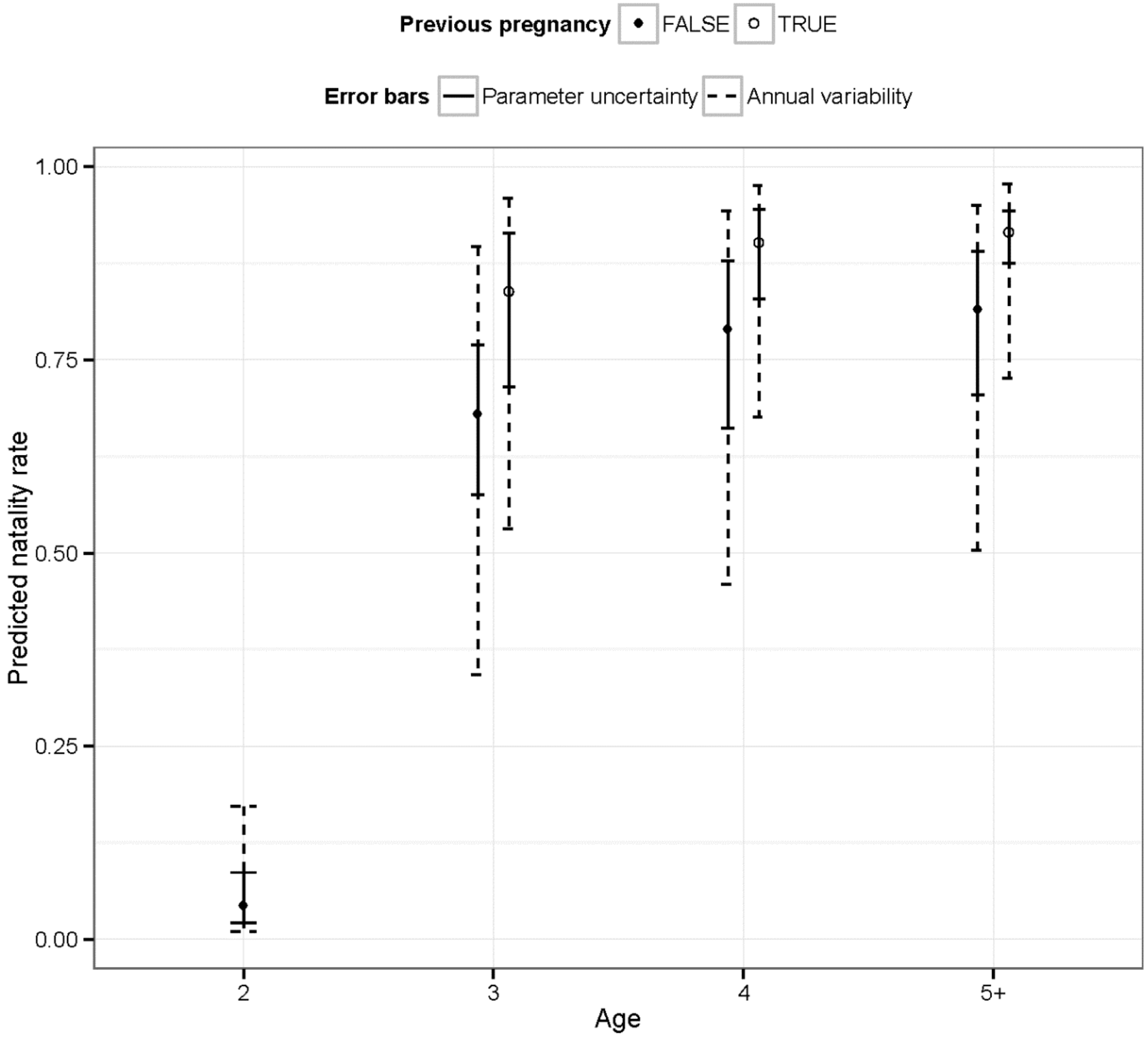
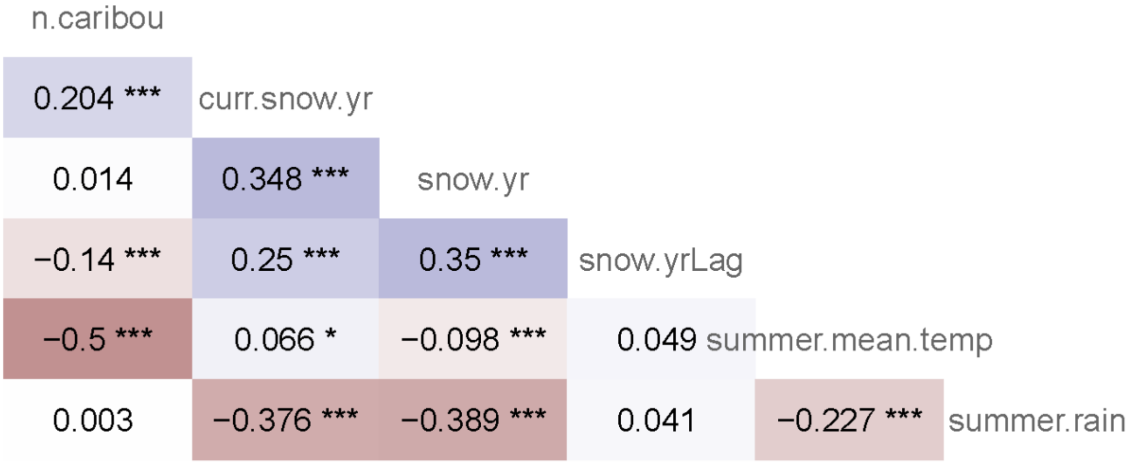


Figure 74. Predicted natality rate based on age group (years) and previous pregnancy status for radiocollared Delta caribou herd females, Alaska, 1980–2007.

We tried using weight:metatarsus (*weight.ratio*) ratio as a substitute for *initial.weight*, hoping that it might be a better indicator of environmental conditions because including a skeletal size indicator could help focus variation on nutrition derived immediately from the environment. However, when we re-ran all the preliminary analyses using *weight.ratio* instead of *initial.weight* and the cohort mean weight:metatarsus length ratio variables instead of cohort mean weight variables, there was no effect on the models selected. Goodness of fit was actually slightly higher using cohort mean weights instead of mean weight:metatarsus ratios, but the difference was negligible ($\Delta R^2 < 0.01$). Therefore, in subsequent analyses and model selection runs, we did not consider *weight.ratio* or the cohort mean weight:metatarsus ratio variables.

Effects of Covariates on Modeled Natality Rates

A key limiting factor in the covariate analysis was the substantial correlation among the environmental variables (including *n.caribou*) (Figs. 75 and 76). These correlations made it difficult to determine which environmental factors may have influenced caribou natality rates. Of the 112 models initially tested (with age and previous pregnancy status, and the environmental variables, with *n.caribou* included, but with *initial.weight* and *weight.ratio* excluded), 1 model had delta AIC<2 and 15 had ΔAIC<7 (Table 23). The top model contained a total of 32% of the AIC weight. Goodness of fit (R^2) did not change among models with ‘some’ support, suggesting that many of the models performed similarly and that the environmental variables (*snow*, *rain*, *temperature*, and *cohort10mnth*) all do a roughly equivalent job of explaining annual variation in natality rates.



	n.caribou	curr.snow.yr	snow.yr	snow.yrLag	summer.mean.temp
curr.snow.yr	0.204 ***				
snow.yr	0.014	0.348 ***			
snow.yrLag	−0.14 ***	0.25 ***	0.35 ***		
summer.mean.temp	−0.5 ***	0.066 *	−0.098 ***	0.049	
summer.rain	0.003	−0.376 ***	−0.389 ***	0.041	−0.227 ***

Figure 75. Correlation (R) matrix for environmental variables. Color indicates direction and strength of relationship (blue = positive correlation, red = negative correlation), stars indicate strength of evidence (significance level, * = 0.05, ** = 0.01, * = 0.001).**

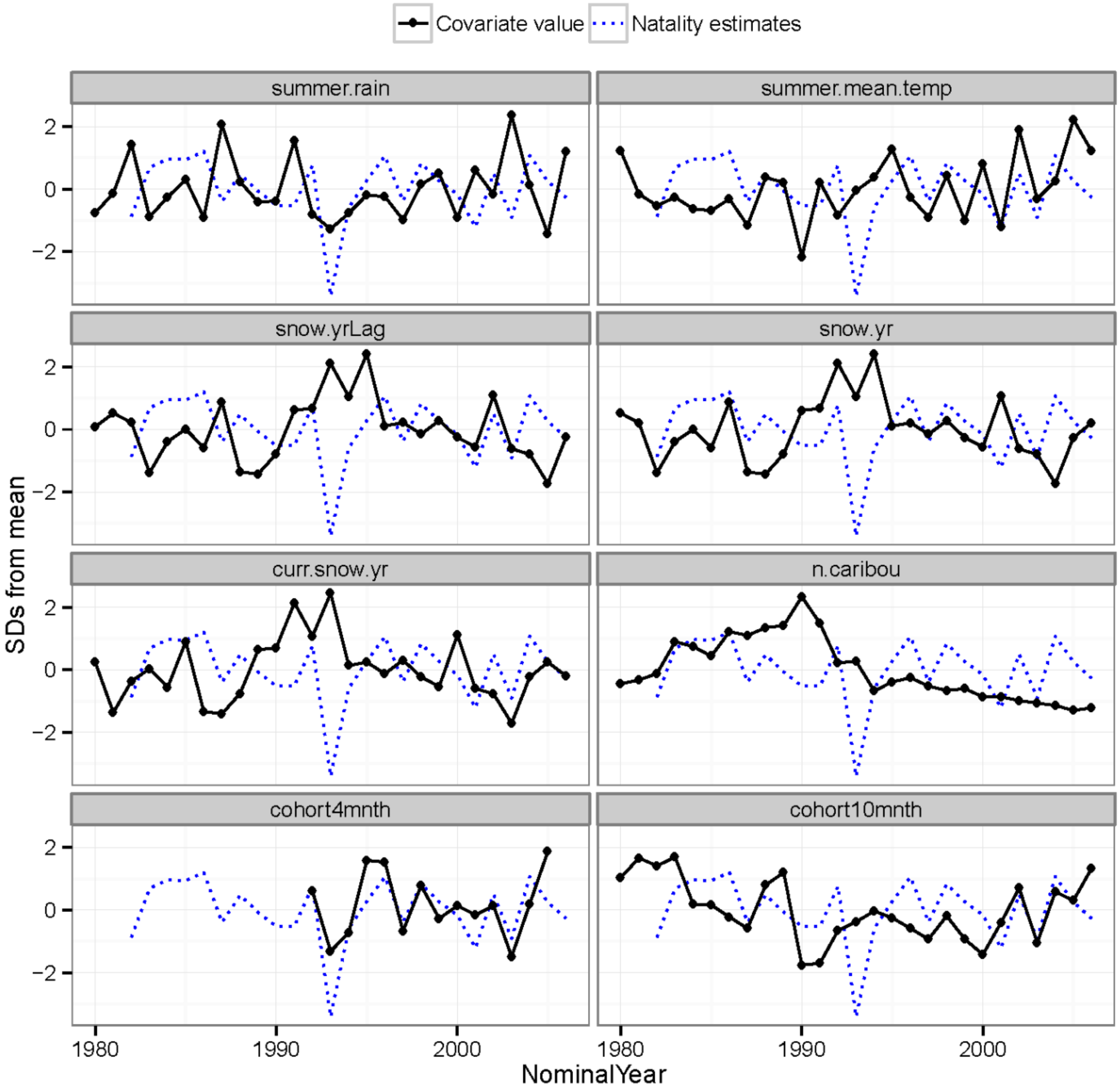


Figure 76. Variation in environmental covariates compared with modeled natality rates of radiocollared Delta caribou herd females, Alaska, 1981–2007. Variables are standardized by their mean and standard deviation to be comparable on an equal scale.

Table 23. Natality models with ΔAICc <7 for radiocollared caribou in the Delta herd, Alaska, 1980–2007. All age groups were included in one model with no interactions. Notation "…" indicates that both age and previous pregnancy were included as factors in the model.

Deviance	*k*	AICc	ΔAICc	AICwt	ΣAICwt	R_L^2	R_G^2	Formula
756.13	5	770	0.00	0.32	0.32	0.40	0.51	... + curr.snow.yr + summer.rain
758.46	5	772	2.33	0.10	0.41	0.40	0.51	... + curr.snow.yr + cohort10mnth
758.74	5	773	2.61	0.09	0.50	0.40	0.51	... + curr.snow.yr + summer.mean.temp
758.74	5	773	2.61	0.09	0.58	0.40	0.51	... + snow.yrLag + curr.snow.yr
759.36	5	773	3.24	0.06	0.65	0.39	0.51	... + snow.yrLag + summer.mean.temp
759.47	5	773	3.34	0.06	0.71	0.39	0.51	... + snow.yrLag + cohort10mnth
757.59	6	774	3.46	0.06	0.76	0.40	0.51	... + curr.snow.yr + cohort10mnth + n.caribou
762.53	4	775	4.40	0.03	0.80	0.39	0.51	... + curr.snow.yr
761.51	5	776	5.38	0.02	0.82	0.39	0.51	... + curr.snow.yr + snow.yr
761.87	5	776	5.74	0.02	0.84	0.39	0.51	... + curr.snow.yr + n.caribou
762.13	5	776	6.00	0.02	0.85	0.39	0.51	Age + curr.snow.yr + summer.rain + snow.yr
764.25	4	776	6.12	0.01	0.87	0.39	0.50	... + cohort10mnth
762.43	5	776	6.30	0.01	0.88	0.39	0.51	Age + snow.yrLag + curr.snow.yr + summer.rain
764.45	4	776	6.32	0.01	0.89	0.39	0.50	... + snow.yrLag
762.88	5	777	6.75	0.01	0.90	0.39	0.51	... + cohort10mnth + snow.yr

We were concerned about possible effects of the unusual year of 1993 on model selection. To get around the potentially undue influence of 1993, we re-ran the models excluding 1993 (Table 24). When 1993 was excluded, *cohort10mnth* appeared in the top model and the top model was stronger. However, this result depends on the time period considered. For example, if the analysis is limited to 1992–2005, when *cohort4mnth* is available, the strongest variables are *snow.year* and *cohort4mnth* with some support for *summer.mean.temp*. Overall, the environmental covariates (including *cohort10mnth* and *cohort4mnth*) explained ~50% of the annual variation in natality rates (Tables 22 and 24). Cohort mean weights did contribute additional information (over weather variables) and substituted for some weather variables, but they did not exclude the weather variables altogether. The choice of exactly which weather variables to use appeared somewhat arbitrary and was influenced by the years selected for the study period.

In model selection processes that included all years of the data, and those that excluded 1993, caribou population size (*n.caribou*) was included in some of the top 30 models, but it contributed very little to explaining variation in natality rate (Tables 23 and 24).

MODELING THE EFFECTS OF COVARIATES ON COHORT MEAN WEIGHT AND CALF:COW RATIO IN THE DELTA CARIBOU HERD

Cohort Mean Weight Models

We tested 94 models with 10-month cohort mean weight (*cohort.mean.wt3*) as the response variable and covariates used in the modeling of survival and natality above. Five models had a delta ΔAIC<2 (Table 25) and 15 models had a delta ΔAIC<7. Models showed more separation than the survival models and had a cumulative delta ΔAIC weight of ~0.7 for the models with delta ΔAICc ≤2. Coefficients for models with delta ΔAICc ≤2 and beyond were reasonably consistent in showing that cohort mean weight at 10 months of age increased with increasing previous summer mean temperatures (*summer.temp.yr1*) and decreased with snow depth (*Denali.snow*) and previous August minimum temperatures (*aug.min.temp*) (Table 25). August minimum temperature was included in all top models. Other variables included in top models were *summer.rain.yr1, n.caribou,* and *cohort.mean.wtPREV* (Table 25). Goodness of fit (R^2) indicated that 67–75% of the variation in *cohort.mean.wt3* was potentially explained by covariates used in the top models.

We also tested 88 models with weight of 4-month-old calves (*cohort.mean.wt2*) as the response variable; 6 models had ΔAICc weight ≤2 (Table 26), and 73 had ΔAICc weight ≤7. In modeling mean weight of 4-month-old calves as the response variable (*cohort.mean.wt2*), there was again less separation among models, with little evidence for a “best” model (Table 26). Covariates that ended up near the top included *summer.mean.temp*, *summer rain*, and *length.green*. Goodness of fit for these models was lower, with 20–30% of variation in *cohort.mean.wt2* potentially explained by covariates.

Table 24. Natality models with ΔAICc <7, excluding 1993 (year following effects of Mount Pinatubo eruption) for radiocollared caribou in the Delta caribou herd, Alaska, 1980–2007. All age groups were included in one model with no interactions. Notation "…" means that both age and previous pregnancy were included as factors in the model.

Deviance	*k*	AICc	ΔAICc	AICwt	ΣAICwt	R_L^2	R_G^2	Formula
698.69	5	713	0.00	0.41	0.41	0.41	0.52	... + summer.rain + cohort10mnth
703.50	4	716	2.81	0.10	0.51	0.41	0.51	... + summer.rain
701.57	5	716	2.88	0.10	0.61	0.41	0.52	... + summer.rain + snow.yr
701.66	5	716	2.97	0.09	0.70	0.41	0.52	... + summer.rain + summer.mean.temp
702.40	5	716	3.71	0.06	0.76	0.41	0.52	... + summer.rain + curr.snow.yr
704.82	4	717	4.13	0.05	0.82	0.41	0.51	... + cohort10mnth
703.39	5	717	4.70	0.04	0.86	0.41	0.51	... + summer.rain + n.caribou
703.46	5	717	4.77	0.04	0.89	0.41	0.51	... + summer.rain + snow.yrLag
704.28	5	718	5.59	0.02	0.92	0.41	0.51	... + cohort10mnth + n.caribou
704.34	5	718	5.65	0.02	0.94	0.41	0.51	... + cohort10mnth + curr.snow.yr
707.54	4	720	6.84	0.01	0.96	0.41	0.51	... + summer.mean.temp

Table 25. Models of 10-month cohort mean weight (cohort.mean.wt3) with ΔAICc <2 in the Delta caribou herd, Alaska, 1979–2007. Notation "…" means that covariates from the top model are included.

log(L)	df.resid	*k*	AICc	ΔAICc	AICwt	ΣAICwt	R^2	Formula[a]
−20.12	20	4	50.35	0.000	0.207	0.207	0.673	aug.min.temp + summer.mean.temp.yr1 + Denali.snow
−16.94	18	6	50.82	0.473	0.164	0.371	0.749	aug.min.temp + summer.mean.temp.yr1 + cohort.mean.wtPREV*Denali.snow
−18.82	19	5	50.97	0.619	0.152	0.523	0.707	... + summer.rain.yr1
−19.27	19	5	51.87	1.516	0.097	0.621	0.685	... + n.caribou
−19.49	19	5	52.31	1.955	0.078	0.699	0.690	... + cohort.mean.wtPREV

a Coefficients for models 1, 2, and 5 are as follow: model 1-intercept 0.0097, aug.min.temp −0.65, summer.mean.temp.yr1 0.41, Denali.snow −0.35; model 2-intercept 0.11, aug.min.temp −0.84, summer.mean.temp.yr1 0.42, cohort.mean.wtPREV*Denali.snow 0.25; model 5-intercept 0.011, aug.min.temp −0.78, Denali.snow −0.42, summer.mean.temp.yr1 0.42, cohort.mean.wtPREV −0.19.

Table 26. Models of 4-month cohort mean weight (*cohort.mean.wt2*) with ΔAICc <2 in the Delta caribou herd, Alaska, 1991–2007. Notation "…" means that covariate from the top model is included.

log(L)	df.resid	*k*	AICc	ΔAICc	AICwt	ΣAICwt	R^2	Formula
−17.45	12	2	39.99	0.000	0.085	0.085	0.237	length.green[a]
−17.52	12	2	40.13	0.140	0.079	0.163	0.230	summer.mean.temp
−16.29	11	3	40.98	0.988	0.052	0.215	0.354	... + summer.rain
−19.35	13	1	41.03	1.033	0.050	0.266	0.000	1
−16.41	11	3	41.22	1.228	0.046	0.311	0.343	summer.mean.temp + wolf.index
−16.42	11	3	41.24	1.244	0.045	0.357	0.342	... + wolf.index

[a] Coefficients for this model: intercept −0.06, length.green 0.62.

Calf:Cow Ratio Models

We tested 259 models using fall calf:cow ratio as the response variable and the suite of environmental variables and parturition rate as potential explanatory variables. One model had a delta ΔAIC<2 and 13 models had a deltaΔ AIC<7 (Table 27). The top model contained 37% of the ΔAIC weight, but goodness-of-fit measures (R^2) were low in all models, indicating a large amount of unexplained variation in fall calf:cow. Variables that were included in the top model and in all models with delta ΔAIC<7 were *cohort.mean.wt1* (previous spring cohort mean weight), *part* (predicted year effect for parturition rate), *Denali.snow*, *n.caribou*, and indicators of season length (*length.green*, *end.green, and greenup*). Increased snow depth (*Denali.snow*) was associated with reduced fall calf:cow ratios while all other covariates had a positive effect on fall calf:cow ratios. Figure 77 below depicts variation in environmental covariates, previous spring cohort mean weight, and predicted year effect for parturition rate in relation to observed fall calf:cow ratios.

SEASONAL DISTRIBUTION OF THE DELTA CARIBOU HERD, 1979‑2007

Calving Areas

During 1979–1983 almost all radiocollared female Delta herd caribou calved in the northern foothills and mountains of the Alaska Range in the Little Delta and Delta Creek drainages in GMU 20A (Fig. 78). During those years we recognized the “Yanert herd” as a separate calving group that remained largely in the Yanert and upper Wood River area, including during calving. During 1984–1987 the Delta herd began using the Yanert drainage and more of the western foothills of GMU 20A, so it was no longer possible to distinguish between Delta and “Yanert” caribou. In 1988, most calving abruptly shifted from the Little Delta-Delta Creek drainages to the upper Wood River (Fig. 78). The southwesterly shift in calving continued over the next several years and, in 1990, Delta herd caribou crossed the crest of the Alaska Range and began calving in northern GMU 13E in the Wells Creek drainage. During the mid-1990s, calving was concentrated in the Wells Creek drainage and the upper Yanert drainage with <15% of radiocollared caribou remaining in the old Delta Creek-Little Delta calving areas. During 1999–2003, most calving continued to be in the Wells Creek and Yanert drainages although the calving area continued to expand south to the Denali Highway and east into the upper Nenana and West Fork Susitna river drainages. During 2004–2007 there was a continued shift to the east and more use of the upper Susitna drainage, including the East Fork drainage and its eastern tributaries, including Valdez Creek, particularly during 2005–2007. Use of the old Little Delta-Delta Creek calving areas remained relatively stable, except during 1994–1998 when fewer animals used the area. In 2004 some radiocollared individuals calved further south around Black Rapids and at the head of 100-Mile Creek.

Table 27. Models of calf:cow ratio with ΔAICc <7in the Delta caribou herd, Alaska, 1979–2007.

R^2mar	R^2con	R^2G	AICc	ΔAICc	AICwt	Σ AICwt	Formula
0.05	0.054	0.116	20739.846	0.00	0.37	0.37	cohort.mean.wtSPR + Denali.snow + length.green + n.caribou + part
0.04	0.054	0.116	20743.400	3.55	0.06	0.43	cohort.mean.wtSPR + Denali.snow + end.green + n.caribou + part
0.04	0.054	0.120	20743.433	3.59	0.06	0.49	cohort.mean.wtSPR + Denali.snow + n.caribou + part
0.04	0.054	0.118	20744.136	4.29	0.04	0.53	cohort.mean.wtSPR + Denali.snow + n.caribou + part + summer.mean.tem
0.04	0.054	0.117	20744.487	4.64	0.04	0.57	cohort.mean.wtSPR + Denali.snow + part
0.04	0.054	0.115	20745.330	5.48	0.02	0.59	cohort.mean.wtSPR + Denali.snow + end.green + n.caribou
0.04	0.054	0.108	20745.481	5.63	0.02	0.62	cohort.mean.wtSPR + length.green + n.caribou + part
0.04	0.054	0.120	20745.615	5.77	0.02	0.64	cohort.mean.wtSPR + Denali.snow + greenup + n.caribou + part
0.04	0.054	0.119	20745.751	5.90	0.02	0.66	cohort.mean.wtSPR + Denali.snow + n.caribou
0.04	0.054	0.120	20745.763	5.92	0.02	0.67	cohort.mean.wtSPR + Denali.snow + july.rain + n.caribou + part
0.04	0.054	0.116	20745.968	6.12	0.02	0.69	cohort.mean.wtSPR + Denali.snow + length.green + n.caribou
0.04	0.054	0.117	20745.969	6.12	0.02	0.71	cohort.mean.wtSPR + Denali.snow + july.mean.temp + n.caribou + part
0.04	0.054	0.120	20746.070	6.22	0.02	0.73	cohort.mean.wtSPR + Denali.snow + july.rain + n.caribou

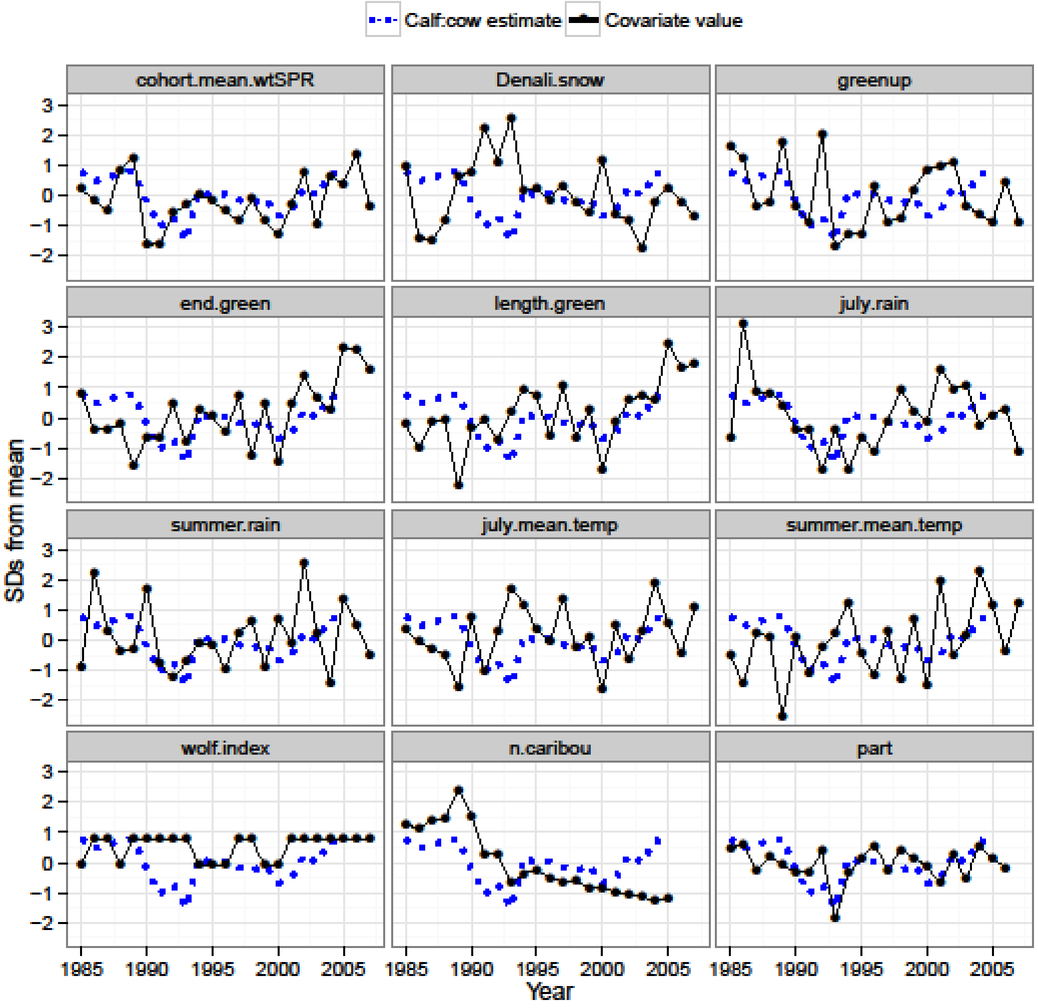


Figure 77. Annual variation in covariates compared with annual estimates of fall calf:cow. Covariates were standardized by the mean and standard deviation to be comparable on an equal scale.

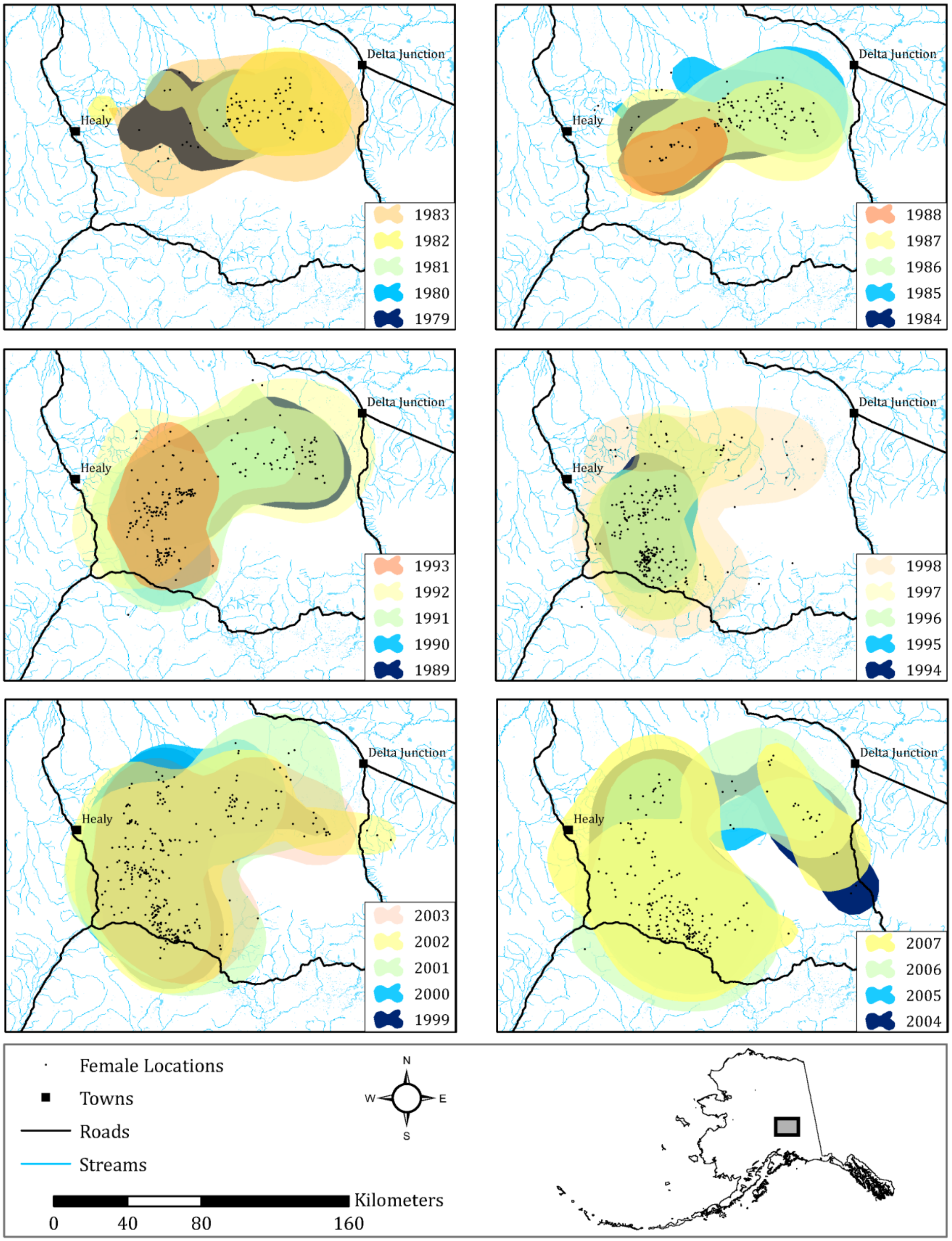


Figure 78. Distribution of radiocollared Delta herd caribou during calving, Alaska, 1979–2007. Distribution based on one annual location for each caribou that was thought to be closest to a birth site or to the date of peak calving.

Summer Ranges

Summer ranges of the Delta herd caribou were the least variable of the herd’s ranges during 1979–2007 (Fig. 79). During later years the herd included more areas along the crest of the Alaska Range and also used the extreme eastern portion of GMU 20A more than in the early years. In addition, there was some use of mountainous areas of the south side of the Alaska Range, including areas as far east as the Clearwater Mountain about 15 miles east of the East Fork Susitna River.

Rutting Areas

During 1979–2007, most Delta herd caribou used 3 main areas during the late September–early October rutting season. The most concentrated and regularly used rutting area throughout the study was in the drainages of Dry Creek, Little Delta, and Iowa Ridge (Fig. 80). The 2 other regularly used areas included the Gold King benches west to the Tatlanika, and Totatlanika drainages, and the Yanert drainage, particularly the tributary drainages of Dean Creek, Dick Creek, and Moose Creek. Starting in 2001 there was considerably more use of areas south of the crest of the Alaska Range, including the Wells Creek, upper Nenana, and Susitna drainages, with a few individuals south of the Denali Highway and east of the East Fork Susitna. In some of these years, Delta caribou were in groups mixed with Nelchina caribou.

Winter Ranges

As with most other Alaska caribou herds, winter range of the Delta herd was the most extensive of all seasonal ranges (Fig. 81). During the 1970s, the Gold King benches were used almost exclusively by the small, but growing herd. During the early to mid-1980s, winter range expanded steadily westward from the Gold King benches into the Tatlanika and Totatlanika drainages. In the late 1980s, instead of continuing west across the Parks Highway, most caribou expanded their winter range north onto the Tanana Flats. During 1986–1991 a few caribou did cross the Parks Highway and use winter ranges up to about 15 miles west of Healy. However, these areas were lightly used for just a couple of years. The first caribou to use the western Tanana Flats were primarily mature bulls (Fleischman 1990, Davis et al. 1991). Just before and during the population peak in 1989, Delta herd caribou made extensive use of the Tanana Flats west of the Wood River to a latitude just north of the Wood River Buttes. Once the population declined, after 1991 the Delta herd stopped using the Tanana Flats west of the Wood River. However, the winter ranges continued to change and to expand throughout the 1990s. The lower Yanert drainage became a major wintering area during the 1990s and continued to be the most heavily used of the herd's winter ranges. Periodically Delta herd caribou appeared to discover small areas of concentrated lichen range. The area along the Wood River between Sheep Creek and Snow Mountain Gulch was heavily used for a few years in the 1990s, as was a small area off the Wood River around the mouth of Coady Creek. During 2001–2007, the Delta caribou herd also expanded its winter range to the south into areas of the Nenana, Wells Creek, and Susitna drainages that had been used only as calving and summer range for many years.

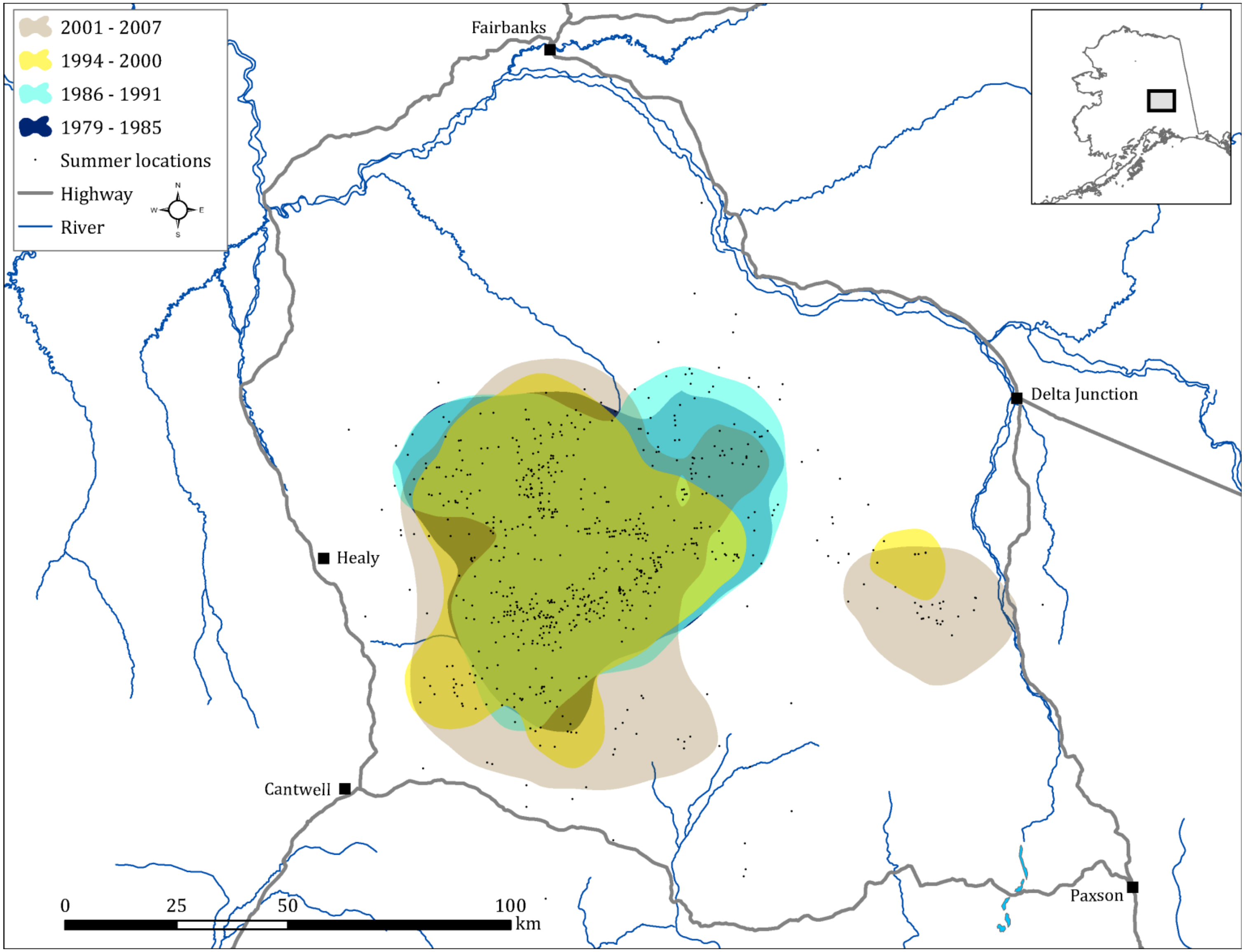


Figure 79. Distribution of radiocollared Delta herd caribou during summer (1 June–15 August), Alaska, 1979–2007.

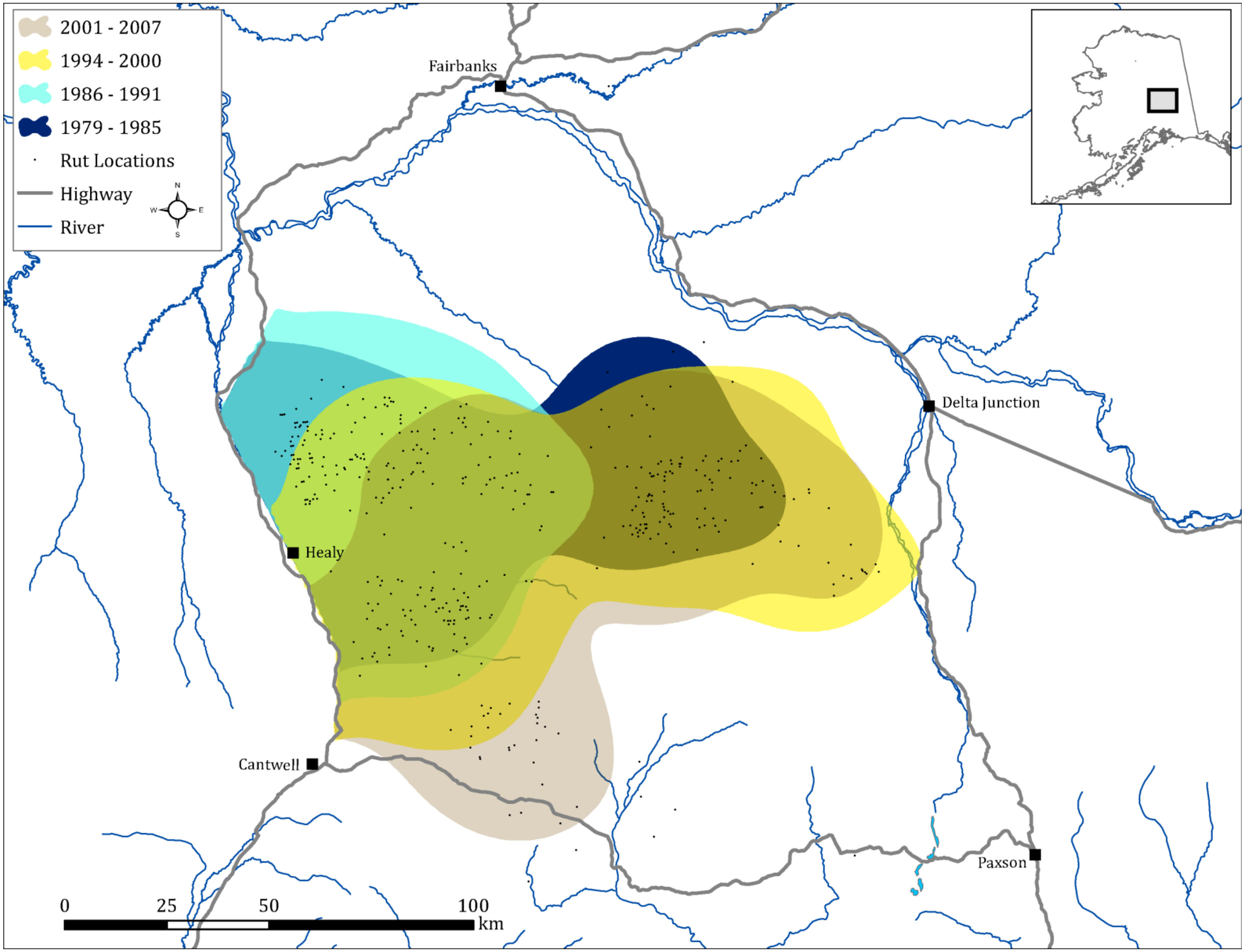


Figure 80. Distribution of radiocollared Delta herd caribou during the rut (15 September–15 October), Alaska, 1979–2007.

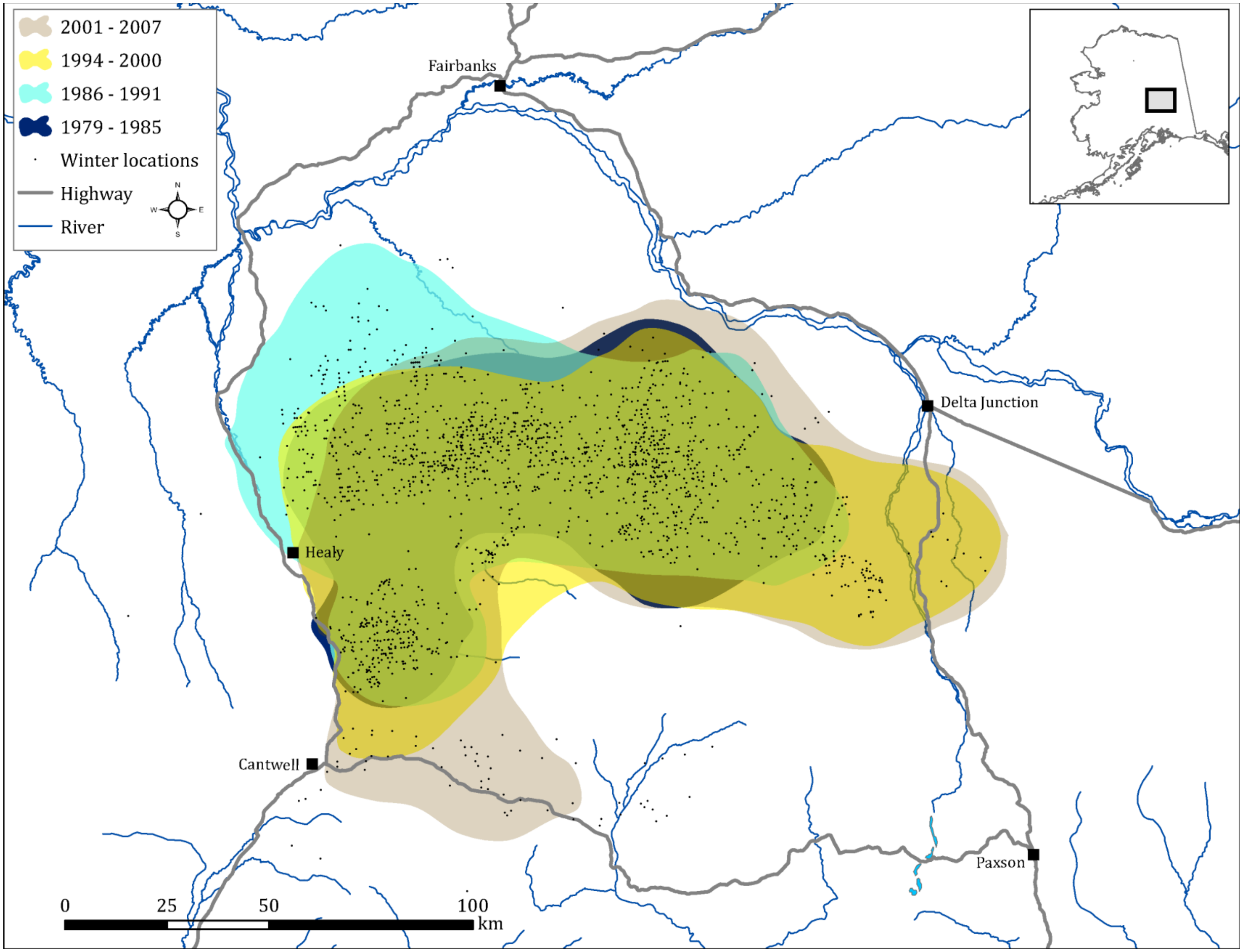


Figure 81. Distribution of radiocollared Delta herd caribou during winter (15 November–30 March), Alaska, 1979–2007. Mount Pinatubo year (1992–1993) excluded.

HERD IDENTITY, EMIGRATION-IMMIGRATION, AND UNUSUAL MOVEMENTS OF CARIBOU

Relationship Between the “Yanert” and “Upper Susitna” Herds and the Delta Herd

Based on movements and distribution of the first cohorts of caribou we radiocollared in the central Alaska Range during 1979 and 1980, and also based on reports from hunters and trappers, it appeared that a separate calving group (i.e., by definition a “herd”) of caribou lived year-round in the Yanert River drainage and that radiocollared caribou from the Delta herd did not use this area either for calving or during any other season (Davis et al. 1991). After we radiocollared 8 adult females in Dean Creek in April 1981 we were able to monitor their movements and calving locations through 1990. For the first 2 years (1981 and 1982) 7 of them (1 collar failed immediately after collaring) calved in the Yanert drainage. In 1983 however, 1 of the 7 females went to the main calving area of the Delta herd and calved there through 1987 (except perhaps in 1984 when she could not be found) and then died the following winter. The Delta herd continued to use its “traditional” calving area (West Fork Little Delta east to 100-Mile Creek, Fig. 78) through 1986, after which the calving area began to shift to the west and south (Fig. 78). Six of the 7 radiocollared “Yanert” females continued to calve between the upper Wood River and lower Yanert River until their collar batteries had all expired or until they died (1987). From 1987 on, because of continued mixing of “Yanert” and Delta herd caribou on all seasonal ranges, the fidelity of most “Yanert” caribou to the Yanert-upper Wood River drainages apparently broke down and we were no longer able to distinguish between these “herds.” Small numbers of caribou (including some with radio collars) continued to use the Yanert drainage and the upper Wood River for calving. One female that was radiocollared in the early 1990s in the Yanert drainage was never located outside of that drainage during her lifetime, so there was some evidence of continued fidelity to the Yanert drainage by at least a few individuals. Based on the 1985 and 1986 censuses, we estimated that approximately 600 caribou showed fidelity to the Yanert-upper Wood River drainages during the early to mid-1980s.

Beginning in 1990, it also became apparent that a group of 2,000–2,500 caribou were behaving like a “herd” with a calving area east of the upper Susitna River centered in Valdez Creek and a winter range in the Chulitna Mountains from Cantwell southeast. At the time, we referred to these caribou as “upper Susitna” caribou. We were able to observe the short seasonal movements of these caribou during winter and spring (including calving) for several years during the early 1990s and there was no apparent mixing with the Nelchina herd. However, none of these caribou were ever radiocollared. By the time the Delta herd began to use the adjacent area (i.e., the upper Susitna drainage) as a calving area in the mid-1990s, the “upper Susitna” caribou were gone. We were never sure what happened to them, but we were never able to document overlap in distribution between these caribou and the Delta herd. Based on the unexpected population spike that occurred in the Delta herd in 1989, it is tempting to conclude that the upper Susitna caribou could have been included in this census. This appeared unlikely, however, because all of the caribou in the census were counted north of the crest of the Alaska Range and there was no indication of a northerly movement of caribou from the upper Susitna to the range of the Delta herd.

Emigration-Immigration of Radiocollared Caribou from the Range of the Delta Herd

During the 30 years of the study, we documented what could be "dispersal" (see definition in Methods) by 3 of the 320 female caribou that were radiocollared as calves within the range of the Delta herd. However, we did not document any dispersals of the 46 males that were collared. Two of these females were confirmed to have died outside the range of the Delta herd. One (#106249, collar O (Orange) 35/1.810) was radiocollared at 4 months of age in the Jarvis Creek drainage (GMU 20D) on 18 October 2000. The radio collar was subsequently found in the upper Chistochina drainage of GMU 13 in spring 2002. It appeared that the animal had died, but the cause of death was unknown. It was too young to have calved outside the range of the Delta herd. Some caribou from the Delta herd had been using the Jarvis Creek drainage as winter range since 1994 and were occasionally mixed with Macomb caribou there. Although we did not locate any radiocollared Macomb animals in the area when we were radiocollaring in 2000, some doubt remains about where this caribou was born. Also, because it died, we were unsure if it would have calved on the calving area of the Delta or Macomb herds.

The second radiocollared female (#105184, O66/1.580 HHz) that died outside the normal range of the Delta caribou herd was radiocollared as a calf (4-months old) on 27 September 1997 in Dick Creek (Yanert River). She spent her first 2 years within the range of the Delta herd and then dispersed westward across the Nenana River and had her first calf on the upper Sushana River (in Denali Park) near the Denali Park road around 20 May 2000. She calved in the upper Sushana River drainage in 2001 and 2002 as well. We changed her radio collar on 27 October 2002 (NV/1.645), near the East Fork Toklat River, when she was 5-years old. She never returned to the range of the Delta herd and was likely killed by a wolf in February or March 2003 in the range of hills north of the Stampede Trail, west of the Teklanika River. During this period, Denali caribou were not documented east of the Nenana River, so it appeared unlikely that mixing between the 2 herds occurred.

The third disperser was caribou 104850 (O31/1.850). She was radiocollared as a calf (4-months old) in the range of the Delta herd on 3 October 1996, in the Slide Creek (Dry Creek) drainage. She was located within the normal range of the Delta herd over the next 2+ years, including on the Wells Creek calving area when she was 2-years old (not pregnant), and 3-years old (pregnant). On 18 May 2000, she was located alone at Last Tangle Lake at least 30 miles east of any other Delta herd radio collars. She had hard antlers and appeared to be pregnant. On 19 May 2001, she was documented as being pregnant and was located on the upper Susitna River with other radiocollared Delta herd caribou. The following year (19 May 2002) she was located in the Oshetna River drainage with large groups of calving Nelchina herd females. Her radio collar was not replaced and its batteries apparently expired shortly after the 19 May 2002 location.

Movements and Evidence for Dispersal of Radiocollared Caribou in the Delta, Denali, and White Mountains Herds After "The Perfect Storm"

The unusual movements of caribou throughout Interior Alaska that occurred during and after the 11–27 September 1992 "Perfect Storm" (Valkenburg et al. 2002, Adams et al. 2005; Fig. 82) could have resulted in some exchange of caribou, especially young animals among the Delta, Denali, and White Mountains herds, as well as between Fortymile, Macomb, and Nelchina herds. Despite active collaring and monitoring programs in all of the Interior herds, it would have been

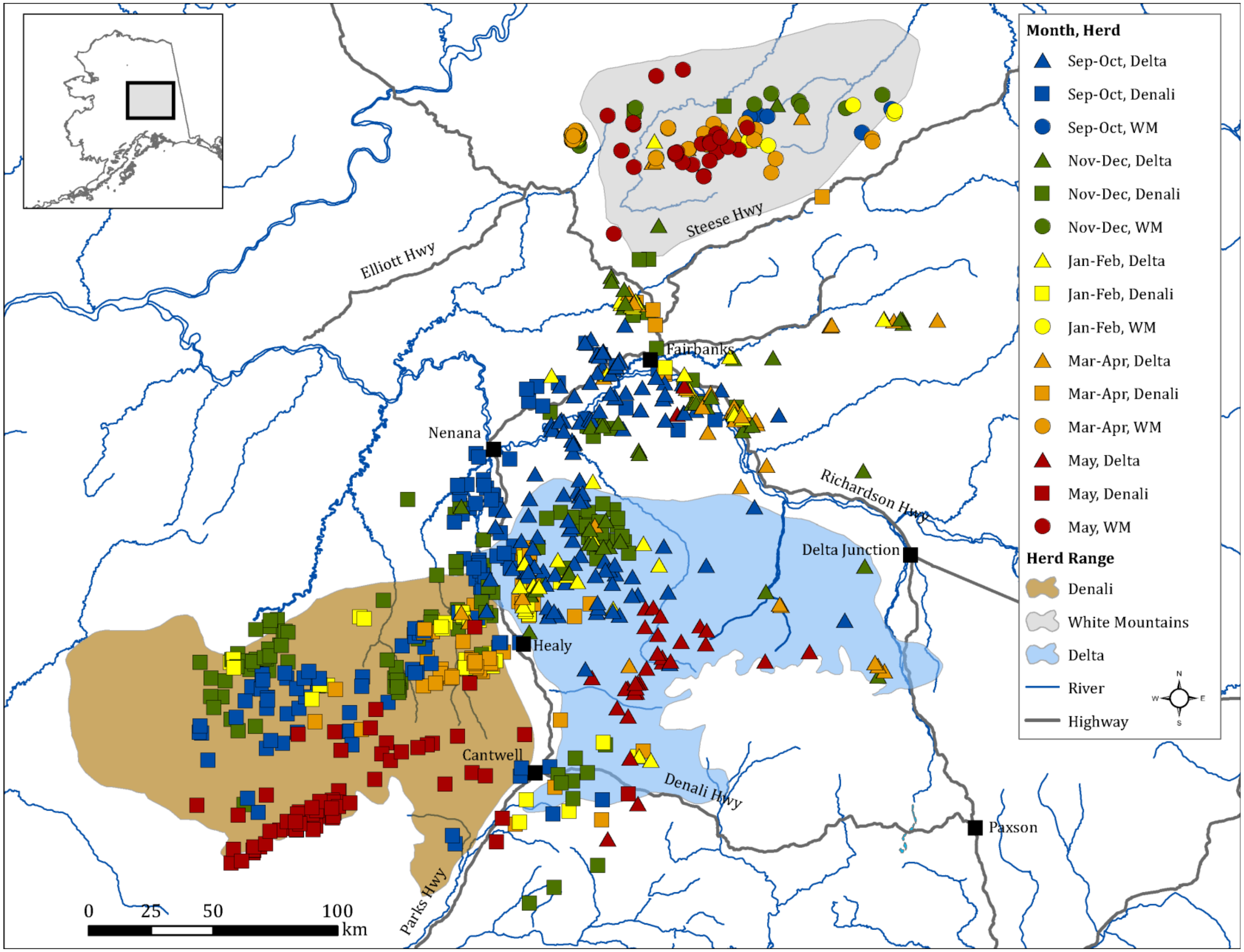


Figure 82. Distribution of radiocollared Delta, Denali, and White Mountains caribou during and after "the perfect storm," Alaska, 15 September 1992–31 May 1993.

difficult to document the exchange of small numbers of caribou that might have occurred. During the “Perfect Storm,” caribou from the Delta and Denali herds were extensively mixed as the 2 herds moved north together across the Tanana Flats and Tanana River during the last week of September and early October (Fig. 82). Many of these caribou also mixed with White Mountains herd in the vicinity of Beaver Creek by early November. Additional details about the unusual movements of caribou that occurred in fall 1992 were previously reported (Valkenburg et al. 2002, Adams et al. 2005).

L. Adams and B. Dale (NPS biologists at the time) radiocollared a sample of calves in mid-March 1993 between Savage River (along the Stampede Trail) and the Liberty Bell Mine (Rex Trail) as caribou (mixed Delta and Denali) were returning from their unusual wintering areas around Fairbanks and the White Mountains. Three of these caribou were subsequently recollared with ADF&G collars because they began associating more with Delta caribou than Denali caribou. One was collared within the range of Delta herd and remained within the range of Delta herd for the remainder of its life. However, one of them (NPS collar 5.640) was recollared (O90/0.040, accession #104214) at 16 months of age on 29 September 1993 in Moose Creek (Yanert drainage). She remained within the normal Delta herd range through October 1994. The radio collar was subsequently found on 25 February 1995 by G. Haber (biologist working independently in Denali Park and surrounding area) in the upper Sushana River in Denali Park. After dispersing from the Delta herd during winter 1994–1995, the caribou had apparently died of unknown causes. No other radiocollared Delta herd caribou were known to have made similar movements during that winter.

Another female calf (7.340) was collared by L. Adams and B. Dale on 14 March 1993 in the Savage River drainage (within the range of the Denali herd) about 10 miles west of Healy. She moved to the Delta caribou herd sometime during the summer and was recollared with an ADF&G collar (#104215, NV/0.200). While having her first calf at age 3, she died from a breached birth on the Wells Creek calving area of Delta herd on 23 May 1995.

All of the radiocollared adult females in the Delta and Denali herds that left their traditional ranges after the “Perfect Storm” either died or returned to their respective calving areas by late May 1993, except for 1 Denali female that did not return until late August or early September (Valkenburg et al. 2002, Adams et al. 2005). None of the radiocollared White Mountains caribou left the White Mountains (Fig. 82). A June 1993 census of the Denali herds indicated a marked decline but the decline was comparable to declines in previous years and fit with survival and recruitment estimates. No census of the White Mountains herd was conducted between 1992 and 1998 (Appendix A-2). Late June counts indicated that the Delta herd declined by over 2,000 caribou from 1992 to 1993 (Fig. 8; Table 1), and could only be explained by either a large increase in the mortality rate of females (from about 10–15% to about 40%), an undercount of caribou in 1993, or a loss of caribou from the herd. Although we were unable to document any loss of caribou from the Delta herd from emigration or exchange of radiocollared adults among herds, there was some evidence that the unusual movements caused some confusion among young animals and it is possible that some exchange of calves could have occurred.

Possible Cases of Dispersal of Caribou in Herds Other Than the Delta Herd

During our extensive work with other caribou herds and in the course of conducting collaring and composition counts for routine management activities, we had occasion to find possible cases of dispersal of radiocollared caribou among adjacent herds. We discuss these cases below:

Case 1

On 23 May 1988, we radiocollared a 1-year-old female caribou (#103303, Yellow 12/1.830) on the calving range of the Chisana herd. The animal was relocated on every radiotracking flight until 1993 when it was listed as "missing" on tracking forms. We (Glennallen Assistant Area Biologist B. Scotton and helicopter pilot J. Larrivee) subsequently found a Yellow 12 visual collar on 26 May 1997 with a newborn calf on the calving area of the Nelchina herd while capturing caribou calves. No other Yellow 12 collars were missing from other herds and yellow collars had not been used at all on the Nelchina herd. During the late 1980s and early 1990s, some Nelchina caribou had been wintering in the vicinity of Beaver Creek and the White River from the Alaska Range to as far north as Wellesley Lake.

Case 2

A Fortymile 4-month-old female (#104312); born 1994, radiocollared in the Fortymile range in early October 1994. Apparently emigrated to the Nelchina herd where it was found during the Nelchina summer composition counts in early July 1995. It was found again during fall composition counts in the Nelchina herd in late September 1998.

Case 3

A Fortymile 4-month-old (#104824); born 1996, radiocollared in the Fortymile range in early October 1996. Apparently traveled to the Nelchina herd where it was found in late May 1997 on the Oshetna calving area. It returned to the range of the Fortymile herd in November 1997 (apparently with other Nelchina caribou), but was subsequently found during the late June–early July census of the Nelchina herd in 1998.

Case 4

A Fortymile 4-month-old (#106214); born 2000, radiocollared in the Fortymile range in early October 2000. Apparently traveled to the Nelchina range where it was found dead in the Chistochina drainage on 1 May 2001.

Case 5

A Fortymile newborn male calf was collared by C. Gardner on 19 May 1996 about 3 miles east of Gelvin's airstrip (~64.91°N, 143.48°W) in the Copper Creek drainage. The calf's mother was not collared. Although the calf was <24-hours old it was large (19.5 lb). The calf spent the summer in the Yukon-Tanana uplands and most of the winter near Sixtymile Butte and it was heard in March in Mansfield Creek. It was last heard and seen alive on 22 April 1997, 22 miles south of Tok moving south with the Nelchina herd. Biologists from Glennallen did not detect the signal during summer 1997. The caribou was subsequently shot as a yearling in the upper Slana

River south of Gillette Pass. On 19 August 1997 the collar was returned to C. Gardner (Tok Area Biologist).

Case 6

A female 10-month-old caribou (#103609, O78/150.320) was radiocollared on 9 April 1990 on the Gerstle River (range of the Macomb herd). It was subsequently found south of Paxson Lake on 3 September 1992 and at Tangle Lakes on 18 March 1993 with ~5,000 Nelchina caribou.

Case 7

A female 11-month-old caribou (#103653, O48/150.290) was radiocollared on 25 April 1990 on the Macomb Plateau (range of the Macomb herd). It was subsequently found in the summer range of the Nelchina in 1992, 8–10 miles west of Fielding Lake on 3 September 1992, the West Fork Dennison River (Fortymile-Nelchina wintering area) in March 1993, and the calving area of the Fortymile herd in May 1993, where it produced its first calf at 3 years of age.

Case 8

During calf mortality studies in the Fortymile herd (Boertje et al., *In press*), 8 calf caribou (out of ca. 278 that remained collared during late winter 1995–2003) followed Nelchina caribou back to the range of the Nelchina herd at 9–11 months of age. The 8 calves were all heard the following September or October within the range of the Nelchina herd, but their radio collars were only designed to last a little more than a year and none were heard subsequently. The eventual calving area of the surviving females of this group (if there were any) was not determined.

Case 9

In fall 2004, 14 of 45 Teshekpuk caribou migrated east to winter in the Arctic National Wildlife Refuge. Although all headed back towards Teshekpuk Lake in spring 2005, only 7 arrived on the Teshekpuk calving area. Four remained between the Sagavanirktok River and the Colville River (calving area of the Central Arctic herd) and had their calves there and 1 remained there all summer. Three calved east of the Sagavanirktok River (calving area of the Central Arctic herd) and remained there all summer.

DETERMINISTIC POPULATION MODEL OF THE DELTA CARIBOU HERD

We were generally able to make the deterministic, spreadsheet model track population estimates (from the annual census) and fall bull:cow ratio by using fall calf:cow as the input for recruitment and then manipulating adult female and male survival rates by trial and error during 1969–1988 and during 1995–2005 (Table 28). From 1989 to 1994, after the population peaked and winters were generally severe, it was clear that fall calf:cow ratios overestimated recruitment and could not be used as recruitment inputs in the spreadsheet model (Table 28). This was not surprising because during the 1980s Davis et al. (1991) found that calf mortality over winter was low, but between 1991 and 1997, mortality of calves ranged from 25% to 47% (Fig. 68, Table 14) so fall calf:cow ratios clearly overestimated recruitment in most of those years.

In many years survival rates needed for inputs in the spreadsheet model were comparable to crude survival rates calculated for all radiocollared females >4-months old (Fig. 83). However, during 1989–1994 when the Delta herd experienced a rapid decline and population instability, the required input values for female survival and those calculated from radiocollared females differed widely (Fig. 83).

Discussion

PATTERNS IN POPULATION GROWTH AND DECLINE, CAUSES OF POPULATION CHANGE, AND OPTIMUM HERD SIZE

Patterns and Causes of Population Change in the Delta Caribou Herd

Pattern of Growth and Decline

The Delta herd has historically been one of a relatively small number of Alaska caribou herds whose population size has been influenced by hunting. During 1971–1973 the Delta herd declined because of unexpectedly high harvests that also affected the adjacent Nelchina and Fortymile herds (Figs. 7, 9, and 32; Doerr 1980, Van Ballenberghe 1985, Valkenburg et al. 1994). The herd grew rapidly from 1976 to 1982 ($\lambda = \sim 1.20$) while wolf numbers were controlled, weather (particularly snowfall) was favorable, and mean weight of 10-month-old calves was relatively high (Figs. 7, 13, and 34; Gasaway et al. 1992, Boertje et al. 1996). From 1983 to 1986, the herd grew more slowly ($\lambda = \sim 1.04$) as harvest was deliberately increased to try to limit population size to ≤4,000 in accordance with the Delta caribou herd management plan (Gasaway et al. 1983a). In 1986 the Delta herd management plan was unilaterally rescinded by order of the division director who believed that ADF&G should allow the herd to continue to grow. The herd then grew to a population peak of 10,690 in 1989 ($\lambda = \sim 1.10$). From 1989 to 1993 the Delta herd declined rapidly ($\lambda = \sim 0.76$) coincident with low fall calf:cow ratios (Figs. 7 and 13; Table 1), low mean 10-month-old calf weights in the Delta herd and adjacent herds (Figs. 34 and 35), deep snow winters during 1989–1993, a freak severe storm in early winter in September 1992 (Adams et al. 2005), higher wolf numbers (Fig. 13, Appendix F), and declines in other Interior caribou herds (e.g., Chisana, Macomb, Denali) (Figs. 8–10; Mech et al. 1998). Judging from declines in other Interior caribou herds that were not at record high levels in 1989, it is likely that the Delta herd would have declined anyway even if the herd had not been allowed to continue growing after 1986.

To try to arrest the decline of the Delta herd and to reestablish the widely popular caribou hunt, the Alaska Board of Game directed ADF&G to implement a wolf control program in 1993 using trapping and ground shooting of wolves instead of aerial shooting, as had been done in the late 1970s (Boertje et al. 1996, Valkenburg et al. 2002). Unlike the previous program from 1975 to 1982, which was primarily directed at improving moose numbers and harvest, the 1993–1994 wolf control program was directed only at improving caribou numbers and harvest. However, there were major flaws in the design of the 1993–1994 wolf control program. The most effective and efficient method of wolf control (i.e., aerial shooting) was ruled out by Alaska's Governor for political considerations, and the Board of Game refused to expand the program (also for

Table 28. Deterministic spreadsheet[a] model of Delta caribou herd, Alaska, 1969–2008. Bold figures are inputs; columns labeled in bold italics contain actual data.

Year	Cows	Calves	Bulls	Post hunt total	***Cow harv***	***Bull harv***	Cow survl	Bull survl	CA:100 cows	B:100 cows	Lambda	***Census***	***Fall calf:cow***	***Fall bull:cow***	***Fem Mort(n)[b]***
1969[c]	**3,000**	840	1,200	5,040	**86**	**271**	**0.88**	**0.95**	**28**	**40**			28	40	
1970	2,932	997	1,178	5,106	**115**	**321**	**0.88**	**0.95**	**34**	40	1.01		34	77	
1971	2,696	404	921	4,022	**366**	**624**	**0.88**	**0.95**	**15**	34	0.79		15	29	
1972	2,349	258	447	3,055	**219**	**601**	**0.88**	**0.95**	**11**	19	0.76		11	33	
1973	2,089	209	269	2,567	**104**	**266**	**0.85**	**0.95**	**10**	13	0.84	2,804	10	29	
1974	1,873	37	345	2,255	**0**	**0**	**0.85**	**0.95**	**2**	18	0.88		2	28	
1975	1,609	193	344	2,146	**0**	**0**	**0.95**	**0.95**	**12**	21	0.95				
1976	1,630	733	409	2,773	**0**	**0**	**0.95**	**0.95**	**45**	25	1.29		45	38	
1977	1,932	811	702	3,445	**0**	**0**	**0.95**	**0.95**	**42**	36	1.24		42	33	
1978	2,259	881	1,014	4,154	**0**	**0**	**0.93**	**0.95**	**39**	45	1.21		39	75	
1979	2,551	1,021	1,340	4,912	**0**	**0**	**0.92**	**0.95**	**40**	53	1.18	4,191	65	39	
1980	2,864	1,403	1,605	5,872	**0**	**104**	**0.92**	**0.95**	**49**	56	1.20	4,478	49	85	
1981	3,272	1,341	1,857	6,470	**73**	**268**	**0.92**	**0.95**	**41**	57	1.10	4,962	41	46	0(28)
1982	3,612	1,120	2,063	6,795	**77**	**274**	**0.91**	**0.97**	**31**	57	1.05	7,335	31	42	0(36)
1983	3,613	1,662	1,188	6,463	**234**	**1,302**	**0.91**	**0.97**	**46**	33	0.95	6,969	46	35	6(48)
1984	3,929	1,414	1,371	6,714	**191**	**507**	**0.91**	**0.98**	**36**	35	1.04	6,260	36	42	4(55)
1985	4,166	1,500	1,353	7,019	**117**	**614**	**0.95**	**0.98**	**36**	32	1.05	8,083	36	49	
1986	4,558	1,322	1,147	7,027	**183**	**841**	**0.97**	**0.98**	**29**	25	1.00	7,804	29	41	
1987	5,089	1,578	1,063	7,729	**38**	**644**	**0.97**	**0.98**	**31**	21	1.10	8,300	31	32	9(47)
1988	5,756	2,015	1,182	8,953	**22**	**555**	**0.97**	**0.98**	**35**	21	1.16	8,338	35	33	6(62)
1989	6,640	1,062	1,366	9,068	**18**	**681**	**0.80**	**0.98**	**16**	21	1.01	10,690	36	27	12(58)
1990	5,654	509	1,307	7,470	**83**	**552**	**0.80**	**0.98**	**9**	23	0.82	7,886	17	38	
1991	4,705	235	1,074	6,014	**22**	**456**	**0.90**	**0.90**	**5**	23	0.81	5,755	8	29	
1992	4,340	217	1,073	5,630	**0**	**0**	**0.60**	**0.75**	**5**	25	0.94	5,870	11	25	22(59)
1993	2,664	133	881	3,678	**5**	**5**	**0.97**	**0.78**	**5**	33	0.65	3,661	5	36	23(61)
1994	2,642	793	744	4,179	**0**	**0**	**0.98**	**0.80**	**30**	28	1.14	4,341	23	25	17(58)
1995	2,934	587	939	4,460	**5**	**5**	**0.80**	**0.85**	**20**	32	1.07	4,646	20	24	20(65)
1996	2,558	537	1,051	4,146	**0**	**22**	**0.80**	**0.85**	**21**	41	0.93	4,100	21	30	14(70)
1997	2,262	407	1,077	3,746	**0**	**44**	**0.90**	**0.85**	**18**	48	0.90	3,699	18	27	16(70)
1998	2,219	355	1,039	3,613	**0**	**50**	**0.83**	**0.85**	**16**	47	0.96	3,829	16	44	16(80)
1999	1,989	378	996	3,363	**0**	**38**	**0.88**	**0.80**	**19**	50	0.93	3,227	19	44	16(83)
2000	1,916	211	924	3,051	**0**	**24**	**0.87**	**0.80**	**11**	48	0.91	3,227	11	46	23(83)
2001	1,759	229	790	2,778	**0**	**33**	**0.87**	**0.80**	**13**	45	0.91	2,950	13	39	15(79)
2002	1,630	407	687	2,724	**0**	**37**	**0.85**	**0.80**	**25**	42	0.98	2,800	25	50	16(80)
2003	1,559	312	680	2,551	**0**	**32**	**0.80**	**0.80**	**20**	44	0.94	2,581	20	37	12(81)

Year	Cows	Calves	Bulls	Post hunt total	***Cow harv***	***Bull harv***	Cow survl	Bull survl	CA:100 cows	B:100 cows	Lambda	***Census***	***Fall calf:cow***	***Fall bull:cow***	***Fem Mort(n)***[b]
2004	1,372	480	624	2,476	**0**	**45**	**0.90**	**0.80**	**35**	45	0.97	2,211	35	49	10(77)
2005	1,450	479	656	2,585	**0**	**35**	**0.90**	**0.80**	**33**	45	1.04	2,400	33	50	12(74)
2006	1,521	411	691	2,623	**0**	**25**	**0.97**	**0.80**	**27**	45	1.01	2,400	27	40	
2007	1,674	402	687	2,763	**0**	**30**	**0.90**	**0.80**	**24**	41	1.05	2,985	24	35	
2008	1,688	422	681	2,790	**0**	**30**	**0.90**	**0.80**	**25**	40	1.01				

[a] Microsoft®Excel (Redmond, Washington).

[b] Percent annual crude mortality rate of all radiocollared females (>4 months of age) from Table 17 with sample size in parentheses. Years in which there were no radiocollared calves or yearlings are not included.

[c] Starting population in 1969 was estimated based on 6,250 counted in summer 1964 and fall composition counts in 1969.

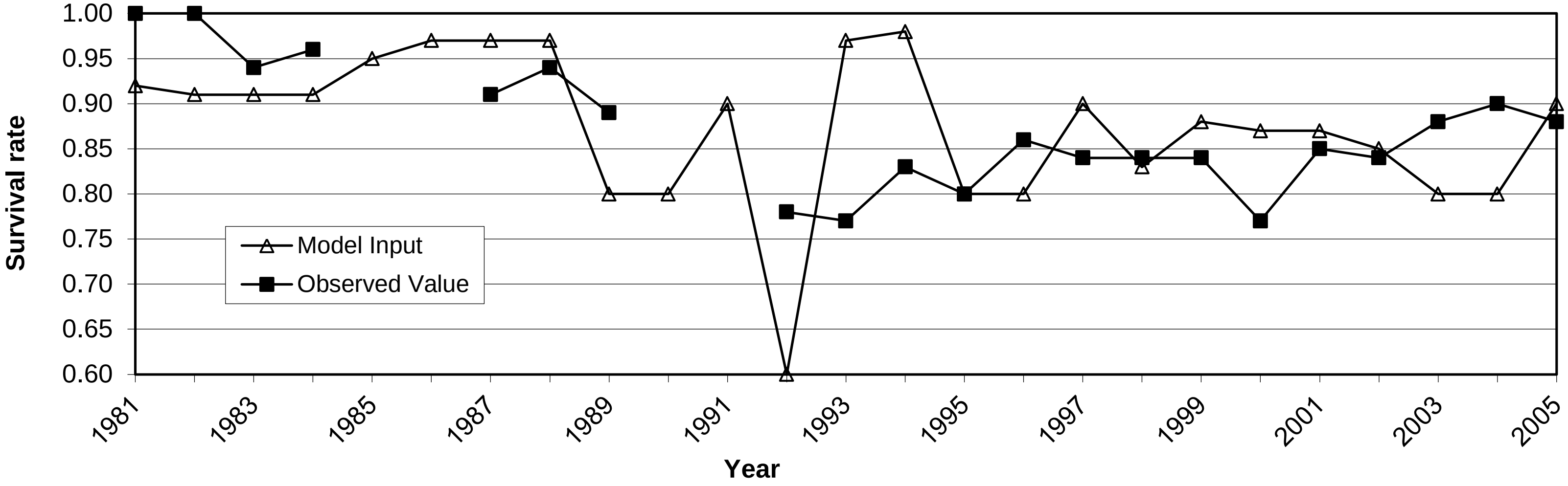


Figure 83. Comparison of survival rates for Delta caribou females derived from deterministic spreadsheet modeling (*Cow survl* column from Table 28) and crude estimates of observed survival rates of all radiocollared female caribou >4-months old, Alaska, 1981–2005.

political considerations) to include a major portion of the caribou calving area that had expanded from GMU 20A into northern GMU 13E. The poorly designed program was also short-lived, because it was terminated (also for political reasons after video clips of a snared wolf made national news). All predator control programs were then put on hold, pending review by the National Research Council of the National Academy of Sciences (National Research Council 1997).

Although the short wolf control program of winter 1993–1994 and October–November 1994 appeared to temporarily stop the decline of the Delta herd because recruitment improved, recruitment also improved to some degree in surrounding herds where wolf control did not occur (Valkenburg et al. 2004). The population increase in the Delta herd was not sustained, and after 2 years of growth the herd declined slowly for the next 9 years ($\lambda = \sim 0.92$), reaching a new population low of just over 2,000 caribou in 2004 (Fig. 7). After 2001 there was some increase in fall calf:cow ratios in the Delta herd (Fig. 14) and probably also in weights of 10-month-old calves (Fig. 35), but the slightly improving recruitment was only reflected in measurable population growth until 2004 (Fig. 7). Several other Interior caribou herds were also stable or slowly increasing during the early 2000s (e.g., Denali, Macomb, Ray Mountains) (Figs. 7–10), but many of smallest caribou herds remained at record low levels or continued to decline toward extirpation (e.g., Beaver Mountains, Mentasta, Sunshine Mountain, Wolf Mountain; Fig. 8). Despite the record low population size of the Delta caribou herd in 2004, weights of the 3 cohorts of 10-month-old calves (birth years 2003, 2004, and 2006) remained lower than weights of the first 4 cohorts of 10-month-old calves from the late 1970s and early 1980s when population size was also low (birth years 1978, 1980, 1981, and 1982) ($P = 0.003$, $t = 3.10$, df = 77) (Table 8). Conditions for population growth in the Delta herd were not as suitable during 2001–2007 as they were during 1976–1982 despite the low herd size in both periods. We believe it is likely that lingering effects of overgrazing during 1985–1990 retarded the recovery of body condition in Delta caribou after the 5 bad winters were over.

Major Causes of Population Decline in the Delta Herd

In the Delta herd, we identified recruitment of calves to 4 months of age as the most variable factor in the dynamics of the herd and also likely the factor that contributed most to population changes over the 30 years of the study, including the decline in population size in the early 1990s (Fig. 15; Table 1). However, in relatively long-lived species like caribou, small changes in adult female survival that are difficult to detect without very large numbers of radio collars can have a large affect on herd growth, and for several reasons, we believe that adult female mortality also played a significant role in the decline of the Delta herd from 1989 to 1994. We did detect reduced adult survival of radiocollared adult females after 1985 (Fig. 68; Table 14) and we found strong evidence for steadily declining annual survival rates as females aged (Fig. 69). Once females reached 10 years of age, mean estimated survival of radiocollared Delta caribou herd females fell below 75%, and by age 14 survival was down to slightly over 50% (Fig. 69). No radiocollared females >11-years old survived the period of bad winters in the early 1990s. We also believe the radiocollared sample overestimated adult survival in the Delta herd because the age structure of the collared sample of females was biased low and sample sizes were relatively low (~30–40 adult females >28 months old). We therefore believe that the Delta herd was predisposed to a major decline in herd size as the decade of the 1980s came to a close because there were so many older females in the population from the strong cohorts of calves that were recruited after the wolf control program began in 1975. At its population peak in 1989, the first strong cohort of females (birth year 1976) was already 13 years old. Over the next 4 years of above average snowfall, most of the females from the strong, post-wolf control cohorts, likely died. Almost all of the radiocollared females >10-years old died during this period and the radiocollared sample underrepresented older females because the collaring program started too late to include most of them, and our decision not to recollar older females in the late 1980s caused the radio collar batteries to fail before we could record the deaths of many.

Delta and Denali Herd Comparison

The Delta and Denali herds have an interesting history of population fluctuations and both herds occupy similar habitat on the north side of the Alaska Range. Information on the Denali herd dates from the 1920s, and the herd once reached a peak of 20,000–30,000 caribou during the 1930s (Singer 1987). Since the 1960s, the Denali herd has been relatively small (<3,500) and has had little hunting pressure (except possibly during the early 1970s). The persistently small size of the herd was a subject of concern for NPS during the late 1970s and early 1980s (Singer 1984). It is likely that the winter of 1970–1971 caused population declines in both the Delta and Denali herds but data were too sparse for meaningful comparison of population size and trajectory on a fine scale prior to the late 1970s. Beginning in the mid-1980s, similar and detailed population data were available for both herds.

Once the decision was made in the mid-1980s to allow the Delta caribou herd to continue growing instead of managing it at a prescribed population size, we anticipated having an opportunity to determine how high population size (i.e., density-dependent factors) might affect future herd trajectory, especially if bad winters occurred. Because of ongoing cooperation with researchers working with wolves and caribou in the adjacent Denali herd (c.f. Adams and Dale 1998a,b; Mech et al. 1998) we also hoped that comparisons between the unmanaged and unhunted Denali herd and the Delta herd would add strength to any conclusion we might draw from just the performance of the Delta herd alone. We did not have long to wait. The relatively mild weather conditions that prevailed through much of the 1980s (except 1985) ended in 1989 with the onset of 5 winters in a row with greater than average snowfall, including the unusual storm event of September 1992 ("Perfect Storm") (Fig. 13; Adams et al. 2005). Annual herd estimates of the Delta herd declined steeply from 10,690 in 1989 to 3,661 in 1993 ($\lambda = 0.75$) (Fig. 7; Table 1). The smaller Denali herd also peaked in 1989, but the subsequent decline was not nearly as steep—the herd declined from 3,210 in 1989 to 1,970 in 1993 ($\lambda = 0.89$) (Fig. 7). The magnitude and timing of declines in calf weight in both herds appeared similar (Fig. 40). The population decline ended in both herds in 1993 and the Delta herd numbered about twice as many caribou as the Denali herd (Fig. 7). Although the difference in number of caribou at the end of the bad weather of the early 1990s seemed to put the Delta herd in a position to recover to its previous size faster, mean calf weights in the Delta herd did not recover as quickly as they did in the Denali herd, perhaps indicating lingering density-dependent effects of the previously high or continued higher population size (Fig. 40). Both herds recovered slowly starting in 1994, and the Delta herd may have received a small boost from the brief wolf control program during 1993–1994 because calf:cow ratios may have improved more in the Delta herd (from a mean of 10:100 to 21:100 during 1990–1993 vs. 1994–1997; $P = 0.03$, $t = 2.80$, df = 6) than in the Denali herd (11:100 to 17:100; $P = 0.15$, $t = 1.93$, df = 6) (Fig. 14). After this brief period of slow recovery, the Delta herd entered a long, slow decline while the Denali herd remained stable. By 2004 the size of both herds was similar (Fig. 7).

Wolf predation may have hastened the decline of the Delta herd at the onset of the deep snow winters in 1989. Wolf numbers were elevated in GMU 20A (Delta herd range) compared with Denali Park (Denali herd range) because of higher moose and caribou numbers (Fig. 13; Appendix F; Boertje et al. 1996, Mech et al. 1998, Young 2000). We conducted a kill rate study of wolves in the northern foothills of GMU 20A from 6 March to 4 April 1989, when the Delta herd was at its population peak. Four packs of wolves (pack size 14, 7, 4, 2) killed the following, respectively: 6 caribou, 6 moose, 1 Dall sheep (*Ovis dalli*), 1 wolf; 2 caribou, 8 moose; 3 caribou, 2 moose; 7 caribou, 1 Dall sheep) (Valkenburg 1992). In a second kill rate study conducted in the same area 10 years later (during winters 1998–1999 and 2000–2001) with a 40% higher moose population and about one-third of the caribou, biologists determined that wolves were killing relatively fewer caribou and relatively more moose (McNay and Ver Hoef 2003; M. E. McNay, Wildlife Biologist, ADF&G, personal communication). After the onset of bad winters in 1989, if the relatively abundant caribou in the Delta herd had been more affected by the deep snow than moose, wolves could have switched to eating more caribou. After the bad winters were over, based on the later kill rate study, it appears that the impact of wolves on Delta herd caribou during the early 2000s was relatively low. However, given the relatively small number of caribou involved, their smaller area of occupancy in GMU 20A, and the fact that a high proportion of the herd used parts of GMU 13 during calving and early summer, the effect of the relatively high wolf numbers on the Delta herd caribou during 2001–2007 was difficult to determine. Numerical and functional response of wolves to prey movements, abundance, and vulnerability are complex and difficult to measure where multiple prey and predator species are involved (c.f. Dale et al. 1994). The presence of alternate prey may either result in increased predation on caribou (Seip 1992) or reduced predation on caribou (Hayes et al. 2003, Farnell 2009). After the Delta herd declined in the early 1990s and moose continued to increase, the predator-prey system in GMU 20A was largely dominated by the high biomass of moose. The difference in wolf numbers could perhaps explain the lower growth of the Delta herd during 2001–2007 compared with 1976–1982 (periods when the Delta herd was low), but the continued comparatively lower weights of 10-month-old calves during the latter period also indicated that nutrition (perhaps lingering density-dependent effects) could have been a factor during 2001–2007.

Patterns and Causes of Population Change in Other Herds

Although there was no clear regional pattern of herd growth in Interior caribou herds, many herds did decline in size during the severe winters between 1989 and 1993. Some herds (e.g. Fortymile, Nelchina, and Chisana) followed growth patterns similar to the Delta herd while others did not (Figs. 7–10). The Fortymile and Nelchina did not decline as strongly during the early 1990s and a few (e.g., White Mountains and probably Ray Mountains) did not appear to decline at all. The Fortymile and Nelchina herds were the largest Interior herds during the 30 years of this study and it is likely they were not as strongly influenced by wolf predation or the combination of wolf predation and weather during the early and mid-1990s (Boertje et al., *In press*). The relatively accessible calving and summer ranges of the Nelchina herd and the ability of trappers to use “land-and-shoot” methods during the early 1990s facilitated continuing high harvests of wolves that reduced wolf numbers in GMU 13 during 1990–1995 (Tobey 2000).

The calving and summer ranges of the Fortymile herd were not nearly as accessible as those in the Nelchina herd and wolf harvests in those areas were comparatively low, but there was a privately sponsored wolf harvest incentive program ("Caribou Calf Protection Program") implemented within the range of the Fortymile herd to attempt to reduce wolf numbers during 1995–1996 (Boertje and Gardner 2000a,b; Boertje et al., *In press*; J. Mattie, Fairbanks fur buyer, personal communication). Although the program did increase wolf harvest and may have resulted in some increase in calf:cow ratio, the effect on calf numbers could not be conclusively determined because calf:cow ratio started to increase in 1993, 2 years before the program was implemented. In addition, there were also moderate increases in calf:cow ratios in nearby herds without wolf control (e.g., Denali and White Mountains; Figs. 13–17), suggesting a regional improvement in caribou calf survival generally. Beginning in winter 1997–1998 the private "Caribou Calf Protection Program" was replaced by an experimental and localized ADF&G "nonlethal" wolf control program where adult males and females were sterilized and subordinate wolves were translocated away from the area. Boertje et al. (*In press*) concluded that there was no clearly detectable effect of the nonlethal wolf control program in the Fortymile herd and mortality of caribou from wolf predation remained unchanged before versus after the program was initiated, presumably because nonlethal wolf control efforts were too localized to decrease total wolf numbers, e.g., adjacent untreated wolf packs reached maximum mean numbers. It is possible that both the private "Caribou Calf Protection Program" and the ADF&G "nonlethal" wolf control program increased calf survival but the effects of the programs were too small to be detected using calf mortality studies (n = 52–78 radiocollared newborns per year and tracked year-round for cause of death) and/or the effects were insignificant for the population.

When we began collecting weights of 4-month-old or 10-month-old calves in the Fortymile and Nelchina herds in the early 1990s, it appeared that weights of these calves were low compared with the Delta and Denali herd calves from the late 1970s and early 1980s (Figs. 38 and 40). It is likely that both the Fortymile and Nelchina herds were affected by lower nutrition during the early 1990s (Fig. 40; Appendix C; Valkenburg et al. 2002, Dale et al. 2008). There also is reason to believe that the Fortymile herd's summer range may be inherently relatively poor compared with other Interior herds because of its relatively low elevation that could affect plant nutrition and insect relief. Besides relatively low 4-month-old calf weights and natality rates, the herd also produces very few trophy caribou (Figs. 38 and 65).

Population growth in the Fortymile and Nelchina herds, which had been ongoing in the 1980s, faltered during the early 1990s, thus providing additional anecdotal evidence for the regionwide influence of weather on caribou herd growth (Fig. 9). After 1995, population growth in the Nelchina herd was deliberately restrained by harvest to keep the herd around 40,000 (35,000 adults) because relatively low calf weights and natality rates (compared with the Delta herd) signaled that high herd size was resulting in overuse of summer range (Tobey 2000, Valkenburg et al. 2003b). The steady increase in mean weight of cohorts of 4-month-old calves after 1996 provided circumstantial evidence that the deliberate reduction in herd size in the Nelchina herd resulted in improved summer range (Fig. 38).

The 6 caribou herds in Southwest Alaska did not appear to show the same pattern of herd growth demonstrated by most Interior herds (Fig. 10; Appendix A). Rather, based partly on historic data from the early to mid-20th century and data collected during our study, we found evidence of a cyclic or eruptive pattern of population growth and decline (Murie and Scheffer 1959, Skoog

1968, Irvine 1976, Pitcher 1991, Post and Klein 1999, Valkenburg et al. 2003a, Hinkes et al. 2005). When we began to collect data from these herds in 1995, the Unimak and Southern Alaska Peninsula herds were at low relative population sizes, the Northern Alaska Peninsula was several years into a population decline (after reaching a peak during the mid-1980s), and the Mulchatna was approaching a population high (Valkenburg 1998, Appendix A-2). We also suspected that a population decline was imminent in the Mulchatna herd. Our recent information and historic data appeared to show that the southernmost herds (i.e., Unimak and Southern Alaska Peninsula) have peaked first, and the northernmost herd (Mulchatna) peaked last. However, this idea is based only on the observation of 2 cycles (or eruptions) over approximately 100 years, so it remains to be adequately tested. Nevertheless, the weather events that were coincident with declines in most Interior herds in the early 1990s did not accompany declines in herds in Southwest Alaska. Southern Alaska Peninsula and Northern Alaska Peninsula herds were already declining, and Nushagak and Mulchatna herds continued increasing.

Besides overgrazing, there are several other possible mechanisms that may facilitate cycles or eruptions in caribou herds in Southwest Alaska, including die offs of wolves, disease, and age structure of the female segment of the herd. Wolf predation pressure during caribou population lows could be relieved by zoonoses of rabies or other diseases, some of which are known to be enzootic in foxes and can be fatal to wolves (Chapman 1978, Davis et al. 1980, Carbyn 1982, Stephenson et al. 1982, Weiler et al. 1995, Ballard and Krausman 1997, Ballard et al. 1997). Caribou numbers can also decline to such a low level (Skoog 1968) that wolves might no longer be supported, especially on Unimak Island and the Southern Alaska Peninsula where alternate food sources for wolves are limited and unpredictable (Murie and Scheffer 1959; Skoog 1968; Riley 2011a,b). Another likely mechanism is that the insular nature of the ranges of the Unimak, Southern Alaska Peninsula, and Northern Alaska Peninsula herds may exacerbate overgrazing because of the limited ability of caribou to shift ranges, especially after stochastic events like icing or volcanic ash falls (c.f. Klein 1968, Skoog 1968, Leader-Williams 1980, Valkenburg et al. 2003a, Miller et al. 2005). We also found evidence that disease, and possibly parasites, may play a periodic role in hastening declines from high population density in Southwest Alaska. The prevalence of 3 respiratory viral diseases was high in the Mulchatna and Northern Alaska Peninsula herds (Zarnke 2000). We found bacterial pneumonia in >50% of calves in some collections. However, we do not have data that allowed us to estimate the numerical effects on caribou herds. We also observed limping caribou (estimated to be about 5% of all caribou observed) during fall composition counts in 1998 and hunters also reported limping caribou. We collected 4 limping caribou in early October and submitted samples to the Washington State University, Department of Veterinary Microbiology and Pathology Laboratory (Pullman, Washington). The lab was able to culture *Fusobacterium necrophorum*—the causative agent of hoofrot (necrobacillosis) (Woolington 1999). No similar outbreak was recorded the following year (Sellers 2001, Woolington 2001). Although many diseases are enzootic in caribou (Neiland et al. 1968, Neiland and Dukeminier 1972), there has been no evidence that disease has been a major cause of population change in Alaska caribou herds with the possible exception of the herds in southwestern Alaska.

The 4 Arctic herds (Central Arctic, Porcupine, Teshekpuk, and Western Arctic) did not follow the population growth patterns of the Southwest Alaska herds or most Interior herds, but the Arctic herds did appear to be influenced to some degree by the poor conditions that affected the Interior caribou herds during the early 1990s (Figs. 11 and 12). The steady growth of the Central

Arctic and Teshekpuk herds during 1975–1993 faltered for several years before resuming in the late 1990s (Fig. 11). This brief pause in growth may also have occurred in the Western Arctic herd, but evidence is weaker and based largely on a single census in 1999 (Fig. 12). A stronger decline was documented in the Porcupine herd, and it started in 1989 or 1990 (exactly the same timing as in the Interior herds) and continued at least until 2001 (Fig. 12). However, unlike Alaska's other major herds, historic population changes in the Porcupine herd have been relatively gradual with herd size ranging only between about 100,000 to 180,000, at least over the last 50 years since 1964 when the herd size was first estimated by biologists (Fig. 12) (Lentfer 1965, Skoog 1968, Hemming 1971). There is some historic evidence for range shifts in the Porcupine herd prior to the 1920s and these range shifts could also indicate larger changes in population size than have been documented in the last half century (Scott et al. 1950, Skoog 1968, Hemming 1971, Burch 2012).

Trying to characterize patterns of population change in Alaska's very small caribou herds (often numbering <1,000) is particularly tricky. Once herds reach very low levels, it is apparent that stochastic factors, including stochastic predation (because of the location of wolf dens in relation to calving concentrations), extreme weather events, volcanic eruptions, lightning strikes, avalanches, predation from unusual predators (e.g., lynx and black bears [*Ursus americanus*]), unexpectedly high local harvests, etc., can play a major role in determining whether the herd increases, decreases, or even becomes effectively extirpated. See further discussion below in section *Effects of Stochastic Factors on Population Growth in Alaska Caribou Herds*.

Because age had a strong influence on survival in the Delta caribou herd and likely in other herds as well, large cohorts that are overrepresented during a growth phase will have a great influence on herd trajectory when these cohorts reach about 10 years of age. This is particularly true after several years of declining recruitment if adverse weather conditions occur. This phenomenon can help explain why herds that have had a history of rapid increase also tend to have a history of rapid decline. The Mulchatna and Porcupine herds represent the 2 extremes of this continuum in Alaska.

Unreported, Unexpected, Wasteful, or Illegal Harvest as Causes of Population Change in Alaska Caribou, 1970–2008

In Interior Alaska, unexpectedly high, poorly regulated, and wasteful harvests during the early 1970s caused accelerating declines and significantly reduced herd size in the Nelchina and Fortymile herds (Van Ballenberghe 1985, Eberhardt and Pitcher 1992, Valkenburg et al. 1994). During the same time period, other, smaller herds were also being affected by poorly regulated high harvest (e.g., Delta, Denali, and Macomb). The more frequent censuses, composition counts, and the more conservative approach to harvest implemented after 1973 largely solved the problem of overharvest of caribou in Interior Alaska. However, the possibility of overharvest, high wounding loss, and wasteful harvest practices remains for some Interior herds, particularly Fortymile and Nelchina where high caribou abundance along roads can occur unexpectedly. ADF&G has successfully avoided heavy harvest and wounding loss along roads by using emergency regulatory authority to terminate hunts whenever caribou have become abundant along roads. An exception to this occurred in the mid-1990s in the Nelchina herd when ADF&G deliberately allowed large hunts along the Denali Highway to help reduce the herd down to the population objective.

After the unexpectedly high and wasteful harvests that occurred in the Western Arctic herd, particularly during the winter of 1975–1976, restricting harvest to control the rapidly accelerating decline in herd size was difficult and controversial (Davis 1976a; Klein 1976; Davis et al. 1980, 1985a; see section *Fieldwork Photos*:photograph 1). But after appeals to Alaska Governor Jay Hammond (c.f. Klein 1976) and Native leaders, excessive and wasteful harvest practices were reduced. After winter 1975–1976 we found no evidence that unreported or unexpected legal or illegal harvest of caribou was a significant factor in the dynamics of the Western Arctic herd, although unreported illegal and wasteful harvest practices continued to some degree (Davis and Valkenburg 1985a, Davis et al. 1985a; see section *Fieldwork Photos*:photograph 2). After the late 1990s, the Alaska Board of Game and the Federal Subsistence Board essentially legalized the practice of running down caribou with snowmobiles in northwestern Alaska by allowing hunters to "position caribou for harvest" with motorized vehicles. This continuing harvest method, along with the increasing popularity of small caliber (i.e., .223) semi-automatic rifles likely leads to high wounding rate and subsequent loss of many caribou.

When caribou herds are harvested under general hunts (using harvest report cards for reporting) we did find evidence that legal but unreported harvest was substantial. In the Delta herd (and therefore also likely in other herds with "general hunts") we found that reported harvest figures needed to be multiplied by a factor of ~1.33 (or divided by 0.63) to be reasonable estimates of total harvest when reminder letters were not sent in general hunts but where hunters were simply reminded to report through media advertising. With no advertising, the nonreporting correction was 0.56 and 0.57 in 2 years with no reminder letters (McNay 1990). During the late 1990s, reminder letters were again being sent to hunters, so reporting may have become more accurate.

In addition to the underreporting we discovered in "general hunts" during hunter interviews in the Delta herd during 1986–1989, we estimated that 10–20% of hunters reported wounding but not recovering caribou (McNay 1990). We also found evidence that some radiocollared (about 3% of all deaths) caribou were deliberately killed or inadvertently killed by people and not reported (Tables 14 and 15). There were undoubtedly some other radiocollared caribou that were killed that may not have come to our attention. However, given that there are such a small number of residents in GMU 20A, we believed that illegal (as opposed to unreported) harvest of Delta herd caribou was a negligible factor in population growth or decline of the herd.

In herds other than the Delta herd, we did find some evidence that either-sex harvest during winter was likely a significant factor in declines or extirpation of one or more small caribou herds (<5,000), particularly the Andreafsky and Kilbuck herds, and also possibly a separate calving group of caribou ("upper Susitna" herd) in GMU 13E. We discuss these cases in the paragraphs below.

Andreafsky Herd (Fig. 1)

The origin and historical persistence of the Andreafsky herd is somewhat obscure. In his very thorough review of the historical reports of caribou in northwestern Alaska, Burch (2012:78–81) believed there was enough evidence to conclude that the Andreafsky River drainages had historically been a major calving area for caribou. Also, based on various reports conveyed to ADF&G biologists during the early 1970s, Davis (1978) believed there may have been from

1,500–5,000 *Rangifer* in the area but whether the herd originated from feral reindeer or previous infusions of Western Arctic caribou is unknown. ADF&G and cooperating USFWS biologists began investigating reports of *Rangifer* (either reindeer or caribou) in the Andreafsky River drainage during the early 1980s as the statewide effort to improve data collection on caribou continued to expand. Dinneford (1983) found approximately 130 caribou in the Andreafsky and Golsovia watersheds (particularly around Needle Mountain) during reconnaissance flights in November 1981 and February and April 1982. Machida (1984) expressed concern that these animals were overharvested in spring 1983 because of good traveling conditions. However, actual harvest was unknown because compliance with harvest reporting requirements was poor. These observations occurred before Western Arctic caribou were known to cross the Unalakleet River but whether these animals were caribou or feral reindeer was never determined. During winter 1984–1985, reports of 2 harvested *Rangifer* with red ear tags (like those used on Seward Peninsula reindeer) and reports of thousands of caribou in northern GMU 18 indicated that some reindeer had come south with an influx of Western Arctic caribou to the south of the Unalakleet River (Patten 1986). On 19 May 1987, Hinkes (1989) found 86 caribou with a minimum of 8 neonate calves near Needle Mountain, confirming the presence of calving caribou (not reindeer). USFWS biologists surveyed the area again in 1988, 1991, and 1993 and found 39 cows with 8 newborn calves in May 1988 but only 3 adult caribou in August 1991 (Miller 1994). There were no reported movements of Western Arctic caribou into the area between 1986 and 1992. However, in December 1993 there was a major influx on Western Arctic caribou into the area around Needle Mountain when 5,762 caribou were counted and 1 Western Arctic satellite radio collar was also present (Miller 1994). In various reports, ADF&G and USFWS biologists concluded that there were up to 400 resident caribou in the area (although the basis for this estimate remains unclear), and that the animals were being overhunted by residents of lower Yukon villages (Machida 1984; Patten 1985, 1987, 1988, 1989, 1990; Hinkes 1989). In March 1984, ADF&G submitted a proposal to the Board of Game to close the hunting season in northern GMU 18 (Andreafsky Mountains) to try to protect the small number of calving caribou residing in the area. However, ADF&G Subsistence Division staff concluded that there was very little caribou hunting going on in the Andreasky Mountains and found that there was a divergence of opinion among area residents about whether the animals in the area were caribou or reindeer (Wolfe and Pete 1984). The proposal failed primarily because 1) the opinions expressed by local residents that *Rangifer* in the Andreafsky drainage were feral reindeer not caribou, 2) continued southward expansion of Western Arctic caribou into the Nulato Hills south of the Unalakleet River was likely, and 3) ADF&G wished to avoid complicating hunting regulations for the Western Arctic herd. Moreover, ADF&G did not strongly advocate to the Board of Game that the Andreafsky herd should be protected from winter hunting (Patten 1988, 1990; Kacyon 1992; observations by senior author). One survey was conducted in the Andreafsky Mountains after the large influx of Western Arctic caribou occurred in December 1993 (Miller 1994). The Andreafsky herd was no longer mentioned in management reports after 1992 (Kacyon 1992, 1993). However, in 1995 a resident of Russian Mission expressed disappointment to the senior author that ADF&G had not protected this small herd from hunting and had allowed it to be extirpated by including the area under the liberal hunting regulations for the Western Arctic herd. Review of the available evidence suggests that summer range in the Andreafsky Mountains is fairly limited and unlikely to support a herd of more than a few thousand caribou, but also that the small number of caribou present during the early 1980s likely was eliminated by winter hunting during the mid to late 1980s before many Western Arctic caribou began using the area. Whether it would have been possible to manage the Andreafsky herd separately from the Western Arctic herd or whether there was enough inundation from the Western Arctic to eventually have assimilated the Andreafsky herd is unknown.

Kilbuck Herd (Fig. 1)

Caribou were first noticed by biologists in the Kilbuck Mountains and recognized as a separate group of calving caribou (i.e., a “herd”) during the 1970s (Davis 1978, Jonrowe 1979). They were probably first surveyed from the air in May 1982 (Dinneford 1983). Surveys conducted in May 1983 and 1984 confirmed the presence of a distinct group of caribou that calved in late May (confirming they were not reindeer) and these animals were subsequently referred to as the Kilbuck herd (Patten 1987). In October 1987, 685 caribou were counted in the Kisaralik drainage (Patten 1989). People from Togiak also had discovered these caribou and had been traveling by snowmobile to hunt them. The season was closed in 1985 but some winter hunting apparently continued and at least 10 caribou were killed in 1986 (ADF&G memorandum,13 March 1990, R. Kacyon to J. Coady, ADF&G files, Fairbanks). Through a combination of education and increased enforcement presence, hunting was eventually greatly reduced or eliminated (S. Gibbons, Alaska Division of Fish and Wildlife Protection, personal communication). In 1986, ADF&G and USFWS began to collaborate on a project to monitor the herd (Patten 1989), and management planning with local residents occurred between 1990 and 1994 (Kacyon 1995). Rapidly growing numbers of calving caribou were observed in the Kisaralik drainage for 12 consecutive years (1982–1993) and many females were radiocollared (Seavoy 1999). A limited hunting season was reopened in 1992 and estimates of herd size eventually reached 4,220 in 1995 (Hinkes 1989; Ernst 1993, 1996; Patten 1997; Seavoy 1999). However, beginning in late winter 1994, the rapidly growing Mulchatna herd began using the Kilbuck Mountains and two-thirds of the radiocollared Kilbuck females departed with Mulchatna animals and probably calved east of Nishlik Lake in May 1994. The radiocollared Kilbuck caribou remained with the Mulchatna herd well to the east of their traditional range for the remainder of 1994 and in 1995 and 1996 as well. After the major mixing event of 1994, it was no longer possible to radiocollar Kilbuck caribou with certainty (Kacyon 1995, Hinkes et al. 2005). The Kilbuck herd was largely assimilated by the Mulchatna herd by 2000 when only about 150 caribou continued to calve in the Kilbuck Mountains and fidelity of most calving females to the Kilbuck calving areas was lost (Seavoy 2001; P. Valkenburg, Wildlife Biologist, ADF&G, personal observations). In contrast to the Andreafsky herd described above, the Kilbuck herd was successfully protected from overharvest for a period of over 10 years, but the herd essentially disappeared instead as a result of assimilation with its larger neighbor. Assimilation of the Kilbuck caribou herd by the Mulchatna herd was closely monitored with radiocollared caribou and provides the best documentation in Alaska of the assimilation process (Hinkes et al. 2005).

Upper Susitna Caribou

This group of up to 2,500 caribou was never formally recognized by ADF&G as a “herd” (and it is not depicted in Fig. 1), although it met the criteria for designation (i.e., a group of caribou that habitually used a distinct calving area that was separated from other calving areas). Between 1980 and 1995, biologists periodically counted up to 2,000 caribou with calves in late May or early June between the East Fork Susitna and the Maclaren River north of the Denali Highway (observations primarily by Valkenburg). Most of these caribou wintered in the Chulitna

Mountains southeast of Cantwell where they were subjected to relatively heavy hunting pressure during the early to mid-1990s under regulations designed for the much larger Nelchina herd. Although there was no known contact or range overlap with the Delta herd prior to the mid-1990s, the lack of radio collars on the upper Susitna caribou made it difficult to say for certain that no intermingling occurred. At least a thousand caribou were still exhibiting the characteristic movement pattern of the upper Susitna herd in the late 1990s, and between 1999 and 2001 a few of these caribou were radiocollared. Beginning in 2000, the Delta herd expanded its calving area to include Valdez Creek and East Fork Susitna and the Nelchina herd began using adjacent areas in summer as well. Over the next few years it was increasingly difficult to distinguish upper Susitna, Delta, and Nelchina caribou or place new collars on caribou with a known calving history, calving area, or birth place. With the benefit of hindsight, there was even doubt whether the animals radiocollared between 1999 and 2001 were really from the upper Susitna calving group, Nelchina, or Delta. By the end of our study in 2008, few caribou used the area between the East Fork Susitna and Maclaren River and movements to the previously used winter range in the Chulitna Mountains southeast of Cantwell were no longer detected. Herd size of Delta caribou after the mid-1990s did not change enough to account for a sudden merging of the upper Susitna caribou with the Delta herd. We therefore surmised that a combination of heavy hunting during the early to mid-1990s, followed by gradual assimilation of caribou with a tradition of calving in the upper Susitna with the Nelchina and/or the Delta herds, resulted in the disappearance of the upper Susitna calving tradition over the decade from 1995 to about 2005.

Emigration-Immigration as Causes of Population Change in Caribou Herds

Delta Caribou Herd

During the 30 years of the Delta caribou herd study reported here, we found no evidence that emigration or immigration affected numbers of Delta herd caribou. For the first 10+ years of the Delta herd study and the expanded monitoring program on caribou statewide, we were unaware of examples of emigration or immigration of individual caribou between calving areas of herds, except for the Yanert-Delta example. However, as the study progressed, herd sizes increased, and the number of radiocollared caribou in the Delta and other herds increased, we identified cases of possible or confirmed dispersals. By the time the Delta caribou herd study ended in 2008, we were aware of 9 cases of known and possible individual dispersals in the Delta herd and other herds (see *Emigration-Immigration of Radiocollared Caribou from the Range of the Delta Herd* in Results section). The fact that we did find evidence that a few radiocollared females dispersed from the Delta herd is significant, especially in view of the number of radiocollared females compared with uncollared females and the challenges inherent in detecting dispersal of radiocollared caribou. We likely would have detected most cases of emigration and immigration of individual radiocollared caribou, large groups of females, and large groups of males (from changes in bull:cow ratio or census numbers). However, we could easily have missed a few cases of immigration or emigration for many reasons. On the frequency lists for the Delta herd and surrounding herds there were almost always a few (generally <3%) radio collars that were noted as “missing,” and occasionally those missing radio collars were never accounted for. Judging from the “missing” collars that were eventually explained, most unexplained “missing” collars were likely collar failures or collars in which the batteries expired prematurely. Some were likely errors on frequency lists that were never caught. An important consideration, however, was that most radio collars in the Delta herd and surrounding herds were on females, so considerable actual dispersal of uncollared individual males or small groups of males could have gone undetected. In most years there were between 50 and 150 uncollared caribou in the Delta herd for each radiocollared caribou. It is therefore possible, though unlikely, that relatively large groups (i.e., several hundred) of Delta herd caribou could have left the herd without having a radiocollared individual in the group.

The only way we would have been able to detect immigration and emigration of males would have been if large changes occurred in the bull:100 cow ratios determined in fall composition counts. Therefore, the possibility exists that there were movements of bulls into and out of the Delta caribou herd during the approximately 30 years of intensive study.

Herds Other Than the Delta Caribou Herd

The 9 cases of dispersal or possible emigration-immigration we were able to document during 1979–2008, the Delta-Yanert calving area changes, the ephemeral nature of the “upper Susitna herd,” and the observation of Hinkes et al. (2005) suggest that dispersal of individual caribou and assimilation of small peripheral herds by their large neighbors is a relatively rare phenomenon and also one that is difficult to document. The extensive mixing between the Fortymile, Nelchina, and Macomb herds (and to some extent Chisana) that occurred starting in the late 1980s, and the later mixing of the Nelchina and Delta, could have resulted in the exchange of hundreds of caribou over the years. We did not detect permanent mass movements of caribou, and we found no evidence that exchanges of caribou between herds resulted in significant changes in herd size (see section *Caribou Herds as Populations or Metapopulations* below). However, the quality of censuses varied from year to year, and in some small herds (e.g., Kilbuck, Nushagak, and Chisana) we were unable to adequately explain apparent changes in herd size by modeling recruitment and mortality in some cases. In the case of the Chisana herd, our spreadsheet population model tracked herd size and bull:cow ratio reasonably well from 1991 until 2001, but then the herd was unexpectedly low in 2002 and unexpectedly high in 2003. Beginning in 2003, the Chisana herd became the focus of a major research effort and an experimental program to keep cows with new calves in temporary confinement to try to improve calf survival. The greater number of radio collars and more thorough searching to the east of the Generc River in the Yukon probably explained the unexpected increase in caribou numbers from 2002 to 2003 (L. G. Adams, USGS biologist, personal communication).

Nutrition and Weather as a Cause of Caribou Population Growth and Decline in Alaska

Both summer and winter nutrition have been widely shown to affect population performance in northern ungulates by influencing mortality and natality (c.f. Skogland 1984, 1985, 1990; Crête and Huot 1993; Crête et al. 1996; Reimers 1997; Keech et al. 2000; Cook et al. 2013). Nutrition can result from factors inherent to summer and winter ranges (e.g., elevation, soil fertility, vegetation type, etc.), population size (i.e., density dependent factors), weather, and combinations of these factors (c.f. Skogland 1990, Caughley and Gunn 1993, Crête and Huot 1993, Reimers 1997, Boertje et al. 2012, Cook et al. 2013). In caribou, as with other ungulates, there is considerable support for the hypothesis that summer nutrition primarily influences natality rate of females while winter nutrition has a greater influence on overwinter survival of calves (4–11 months of age), birth weight, and subsequent neonatal calf survival (Skogland

1984, 1985; Mech et al. 1987; Allaye-Chan 1991; Adams et al. 1995b; Gerhart 1995; Gerhart et al. 1996; Reimers 1997; Valkenburg et al. 2002; Dale et al. 2008; Boertje et al. 2012).

During our years of intensive study of the Delta caribou herd and extensive monitoring of other Alaska herds, we found considerable evidence of the importance of both density-dependent nutritional effects on body weight and herd growth rates, and of the importance of stochastic weather events that had a major short-term effect on nutrition and/or on herd growth. Morphological evidence for the importance of density-dependent factors came primarily from comparisons of weights of calves in the Delta, Denali, and Nelchina herds, and transplants to the Kenai Peninsula (Fig. 40; Appendix C) (Valkenburg et al. 2000, 2003a; Dale et al. 2008), and the comparisons between the Northern Alaska Peninsula herd and the transplanted Nushagak herd (Fig. 39; Appendix C) (Hinkes and Van Daele 1996, Valkenburg et al. 2000). We also found that declining nutritional condition was associated with reduced natality rates of 3-year-old females in the Delta herd and in other caribou herds (Fig. 71 and 72; Appendix I; Valkenburg et al. 2003a, Boertje et al. 2012). Boertje et al. (2012:34) found an association between average 36-month-old parturition (i.e., natality) rate and herd growth rates in 8 Alaska caribou herds (excluding Nelchina). In 3 cases where 36-month-old parturition rates were below 0.4, herds were declining; whereas, in 9 cases where 36-month-old parturition rates were above 0.65, most herds were stable or increasing slowly. Despite the associations with declining herd size and the indices of nutrition (36-month-old parturition rate and weight of calves at 4 or 10 months of age), it is important to recognize that “association is not causation.” The relatively small changes in 36-month-old parturition rate have an even smaller direct effect on recruitment (measured with fall calf:cow estimates) because 36-month olds are only one age class and most are first time mothers whose calves are probably less likely to survive (Ozoga and Verme 1986, Mech and McRoberts 1990). Also, smaller bodied 4- and 10-month-old calves may breed a year later than larger calves but this does not explain lowered herd growth rates either. In the section above (see section *Patterns and Causes of Population Change in Other Herds*), we identified recruitment of calves to 4 months of age as a likely major cause of changes in herd growth rate in the Delta herd. So lowered nutrition, however it is manifested in various indices, operates primarily on calf survival. Not only were we interested in exploring the mechanisms by which poor nutrition influences recruitment, we were also interested in finding indices of nutrition that were associated directly with calf survival (i.e., fall calf:cow ratio) rather than indirectly with 36-month-old parturition rates. Also, although parturition rate of 36-month-old females appeared to be a useful indicator of nutrition, it is a difficult thing to measure and will likely not be affordable in any except the largest, most economically important herds. To successfully use a running average of 36-month parturition rates, large enough samples of 4- or 10-month-old females must be radiocollared so that at least 14 will survive to be 36-months old (Boertje et al. 2012). There are also occasional false negatives or false positives found when determining parturition status of 3-year-old caribou unless they are observed many times during the entire calving period, so accurately determining natality rate in a sample of 36-month-old caribou every year is time-consuming and expensive. Effectively, it requires a major radiocollaring program every year and in periods when calf survival is high, the result will be accumulation of higher numbers of radiocollared caribou than might otherwise be needed for routine management purposes.

As an alternative to using natality rates of 3-year-old females or as an additional indicator of nutrition in the Delta herd and potentially in others herds, we explored using 10-month calf weight. Because of the reasonably strong correlation between 10-month calf weight in the Delta herd and fall calf:cow ratio (Fig. 37), we were initially encouraged that 10-month weight might be useful to managers interested in predicting recruitment several months ahead of the normal fall composition counts. Further support for the potentially predictive value of 10-month weight was that logistic regression models of calf:cow ratio in the Delta herd identified 10-month calf weight as a covariate of potential explanatory value along with snow depth, natality rate, and length of the growing season (Table 27). Boertje et al. (2012) also found that calf weight (in the Fortymile it was 4-month weight rather than 10-month weight) was included in all top models used to predict 36-month-old parturition rate in the Fortymile herd. However, in regression models of fall calf:cow ratios in the Delta herd, there remained a great deal of unexplained variation in fall calf:cow ratios and 10-month calf weight was not a strong predictor of fall calf:cow ratios in the Denali herd (Fig. 37). It appears that although calf weight is certainly a useful measure of nutrition, its value in directly predicting population parameters is probably limited in most herds.

It appears that in the Delta herd nutrition was an important factor that likely influenced fall calf:cow ratio, usually because of a combination of factors that include natality rate but act primarily to decrease calf survival, especially during periods of poor weather. Overgrazing appeared to exacerbate the effects of adverse weather in the Delta herd, but comparison with the Denali herd (where herd size and density remained low) indicated that overgrazing is not a necessary factor for Interior herds like the Delta and Denali to decline. Adams and Dale (1998b:1193) concluded that “reproductive performance and predation” are “inextricably linked” in the Denali herd because declines in nutrition affect calf weights and vulnerability to predation. In turn, when prey vulnerability increases, wolf numbers also tend to increase (Mech et al. 1998). Our results from the Delta herd confirm these conclusions.

The effects of nutrition on mortality rate of adult female caribou are less clear than effects on calves. We could not demonstrate increased mortality of adult radiocollared females either as the population reached its peak around 1989 or subsequently during the 5 years of deep-snow winters, except that the older age classes of females probably died at a higher rate. Stochastic population modeling did indicate that mortality of adult females was probably higher for several years after 1989. In Norway, Skogland (1990) found no population density effect on adult female survival rate in the Hardangervidda herd although survival of calves was strongly affected.

Effects of Stochastic Factors on Population Growth in Alaska Caribou Herds

The effects of stochastic factors (including short-term weather) on caribou nutrition and population performance can strongly influence herd growth. The June 1991 eruption of Mount Pinatubo had a relatively large and measureable effect on worldwide climate (and perhaps also on the Delta caribou herd) for about 2 years (Self et al. 1996). The first noticeable effect in Alaska may have been the very late spring of 1992 (Appendix D). The late spring was followed by 1 of the 5 shortest growing seasons of the 30-year period, and then extreme September snowfall (Adams et al. 2005). Mean weight of 4-month-old female calves in the Delta herd in 1992 was relatively low (Fig. 33), and the natality rate of the herd was by far the lowest on record (29%) the following spring (1993), and continued to be low during 1994 (Tables 21 and 22). The fall calf:cow ratio (5:100) measured in late September 1993 was the second lowest recorded in the Delta herd (Table 1). However, it is unclear if the extreme September snow of

1992 (i.e., “Perfect Storm”), deep snow in 1992–1993, the short summer of 1992, or the cumulative effect of all these events were most disruptive to the Delta and Denali herds, and why the effect lasted so long. The poor performance of the Delta herd (indicated by low fall calf:cow ratio) during 1993–1995 could not be linked to spring greenup. The record late spring greenup (25 May) of 1992 was followed by the 3 earliest greenups on record (29 April–1 May) during 1993–1995.

The poor performance of the Delta herd during 1993–1995 was not all attributable to the weather events that followed the Pinatubo eruption, however. Population size in the Delta herd had peaked in 1989 and the herd had been declining for several years before the 1991 Mount Pinatubo eruption and the extreme weather events that appeared to have been associated with it. The fall calf:cow ratio had declined significantly by 1990 in the Delta herd, before the eruption, and it was already very low in 1991, 3 months after the eruption but before the volcanic ash had time to reduce solar radiation around the globe, particularly in the northern hemisphere (Fig. 14; Table 1) (Self et al. 1996). It is therefore likely that an already occurring decline in the Delta caribou herd was exacerbated by the stochastic weather events associated with the eruption of Mount Pinatubo.

Unusual, unexpected, and largely stochastic events have been documented in several small caribou and reindeer herds in Alaska and other areas of the world, and some of these likely had population-level effects. Unexpectedly high predation on caribou calves in Newfoundland following the introduction and subsequent crash of snowshoe hares (*Lepus americanus*) during the late 1950s and early 1960s is a famous example (Bergerud 1971). In Alaska, lynx predation on Interior caribou calves has also been documented to change from near zero to measureable when snowshoe hares decline and hungry lynx are searching for alternate prey (Valkenburg et al. 2002; Boertje et al., *In press*). The deaths of 143 caribou in a single avalanche in the Killey River herd in 2001–2002 provide another good example of a major stochastic mortality event that has affected a small caribou herd in Alaska (Selinger 2003). On South Georgia Island, an avalanche killed all 20 reindeer that had been introduced on one part of the island in the 1920s (Bevanger and Jordhøy 2004:29). Similarly, Shaw and Neiland (1973) documented the deaths of 53 caribou from a lightning strike in the range of the Delta herd. In addition, when caribou herds number <1,000 animals or so, factors that would not normally be considered stochastic, such as wolf predation, tend to become much more stochastic in nature. For example, when 14 adult wolves associated with 2 dens were removed from the calving area of the Southern Alaska Peninsula herd in 2007, calf:cow ratio increased from near zero to >40:100 in 2008 (Fig. 18; Appendix B; Butler 2009b). Thus, it is difficult to generalize about mechanisms of population regulation or change in caribou once herd sizes fall to very low levels.

On the Alaska Peninsula, where volcanic eruptions are more frequent than in other areas of Alaska, their occasional influence could have direct and catastrophic effects on caribou. Skoog (1968) mentioned the possible effects of the 1912 Katmai eruption which deposited ash 1–2 feet deep in some areas. During the last 30 years, ash falls from many volcanic eruptions have occurred in Southwest Alaska, including from Mount Saint Augustine, Mount Spurr, Mount Chiginagak, the Pavlof Sisters, and several others. Even though these ash falls were minor compared the Katmai eruption, in the mid-1990s we found 10-month-old caribou calves in the Southern Alaska Peninsula herd with their deciduous incisors worn to the gum line from eating vegetation covered with volcanic ash (see section *Fieldwork Photos*:photograph 5). We were never able to detect direct population level effects of volcanic eruptions on Alaska caribou, but ashfalls probably reduced life expectancy and therefore mean population survival rates during some periods on the Alaska Peninsula.

Biologists have made attempts to develop models that incorporate stochastic factors and these models can be useful in demonstrating how stochastic factors can influence caribou population size and harvest management (c.f. McNay and DeLong 1998).

Predation

Between 1979 and 2007 we identified predation (by wolves) as the most common proximate cause of death of caribou calves and adults in the Delta herd (Tables 14 and 15). Grizzly bear predation on calves during summer is often as important as wolf predation (Adams et al. 1995a; Mech et al. 1998; Valkenburg et al. 2004; Boertje et al., *In press*). In some herds in Southwest Alaska, however, predation appeared to vary from being overwhelming (Southern Alaska Peninsula herd in 2006 and 2007) to rather insignificant (Mulchatna herd during the 1990s), judging from fall calf:cow ratios (Woolington 2007, Riley 2011a). The influence of wolf predation and the circumstances under which it influences caribou declines is complex. Mech et al. (1998) found strong evidence that deep snow facilitated wolf predation, particularly in adults older than 10, and Adams et al. (1995a,b) concluded that lingering snow was associated with increased predation on calves the following summer. In the Delta herd we found that once age was controlled for in regression modeling, annual survival rates of radiocollared caribou did not vary significantly, even during periods of deep snow. However, our sample of radiocollared caribou was biased towards younger females and most older females (>10 years old) did die during the deep snow winters in the early 1990s.

Except in the very small herds (e.g., Southern Alaska Peninsula) where predation has a stochastic element, we found no evidence that wolf predation (at the scale we were able to measure it), by itself, caused declines in caribou herds. Therefore, at least in the Interior caribou herds, several factors are usually required for herds to decline. These include 1) significant numbers of older females in the population; 2) adverse weather (including, but perhaps not solely, deep snow); and 3) sufficient numbers of wolves and grizzly bears to exert predation pressure on calves, and wolves to exert predation pressure on older aged cows. Overgrazing, either from natural increases in caribou herds (e.g., Mulchatna and Southern Alaska Peninsula), or from caribou increases as a result of predator control (e.g., Delta), could be an important compounding factor causing caribou herds to decline. In some Interior Alaska herds, but especially in the large circumpolar Arctic herds, natural overgrazing is probably a usual factor in herd dynamics (e.g., Western Arctic, Mulchatna, and George River).

Once major herds decline to relatively small sizes, wolf predation (in concert with other factors) likely can keep caribou declining, keep them from increasing, or eliminate potential harvest. Davis and Valkenburg (1978) estimated that wolves were likely taking over 20,000 caribou from the Western Arctic herd in the mid-1970s at a time when the caribou herd was likely around 100,000. However, based on our results from the Delta herd and the adjacent, similar-sized Denali herd, once a caribou decline is over and most of the older females have died, herds that occupy a large amount of suitable range should start to recover on their own as long as harvest is closely managed and restricted to bulls.

Wolf control has been successfully used to increase harvestable surpluses of caribou in some herds (e.g., Nelchina and Delta), but wolf control has been difficult to achieve in other herds (e.g., Fortymile). One of the problems with managing wolves over large areas in Alaska today is that many areas are off limits for any wolf control (e.g., NPS and most USFWS lands, and some Native-owned lands) (Boertje et al., *In press*). Having parts of the range that are excluded from wolf management increases the chance that wolf control programs will fail. In the Delta herd during 1994 and 1995, a wolf control program probably failed because not enough of the herd's range was included in the program but there may have been other factors as well (Valkenburg et al. 2004). In the Fortymile herd, much of the calving area is in the Yukon-Charley River National Preserve where predator control is prohibited. As a result, the effectiveness of the wolf control program to increase herd numbers under the Fortymile management plan was compromised (Boertje et al., *In press*). Wolf control certainly can be a successful management option for small caribou herds because the number of wolf packs involved are few and manageable (Hayes et al. 2003, Riley 2011a). Effects of wolf control can be short-lived because wolves can recover quickly and caribou numbers may not increase to the point where predator swamping occurs (Hayes and Harestad 2000, Hayes et al. 2003).

Disease

Davis and Valkenburg (1985a:15) reviewed evidence for disease in Alaska caribou through the early 1980s and concluded that disease had played a minor role in the dynamics of wild caribou. During the 1960s and 1970s, brucellosis was found in the Western Arctic herd—the only caribou herd in Alaska where prevalence of the disease has been significant (Neiland 1972; Zarnke 1996, 1997, 2000). Because the Western Arctic herd has been the only herd with significant evidence of brucellosis, current speculation is that the disease was introduced with reindeer in the 1890s. Despite relatively high prevalence of brucellosis in the herd and observations of up to 1.2% of females with retained placentas (9 June 1976 survey by J. L. Davis), we found no direct evidence that disease had a population-level effect in the herd (Davis and Valkenburg 1985a). The possibility remains that during the peak of brucellosis prevalence in the 1960s the disease may have influenced herd size. In the late 1970s in the Western Arctic herd and in the late 1990s in the Mulchatna herd, necrobacillosis (aka hoofrot) outbreaks were suspected based on caribou found dead in summer and limping caribou in fall (P. Valkenburg, personal observations). During the 1980s and 1990s several viral diseases were found to be enzootic in caribou. Except for the pneumonia detected in caribou calves in the Mulchatna and Northern Alaska Peninsula herds, strong evidence for potentially serious direct mortality from disease in Alaska caribou is lacking.

Is There an Optimum Population Size for Caribou Herds?

There was much discussion during the 1970s, 1980s, and 1990s among biologists about whether the best management option for some herds was to maintain them at stable levels and whether traditional and theoretical concepts of "carrying capacity" applied to caribou herds (Leopold 1948; Caughley 1976, 1979, 1981; Davis et al. 1986; Caughley and Gunn 1993; Valkenburg et al. 2002). Whether or not "carrying capacity" is a useful term for caribou herds (and very likely it is not), there are potential advantages of finding an optimum sustainable population size for a caribou herd. Advantages of trying to manage a caribou herd around an "optimum" size include 1) greater long-term sustainable harvest levels, 2) avoiding overgrazing on summer or winter ranges, 3) avoiding outbreaks of disease that could cause short- or long-term declines in herd size and harvest, and 4) greater predictability in range use. Conversely, potential advantages of allowing a caribou herd to continue to increase include 1) increasing population size would lead to expansion of range size and periodic but temporary opportunities for subsistence and other harvest on the periphery of the range, 2) processes of dispersal and gene flow among herds would be promoted, and 3) possible ecosystem changes such as increased nutrient flow and temporarily increased numbers of predators and scavengers.

In 1987, during the North American Caribou Workshop at Chena Hot Springs, biologists discussed the concept of managing caribou herds for an "optimum" size at which harvest might be sustainably maximized over the long term. At that time, only the Adak herd in Alaska had been deliberately controlled by hunting. ADF&G area management biologists were asked to review the status of caribou herds and the current management goals in their areas and make recommendations for future management. ADF&G staff decided to continue with plans to experimentally maintain the Nelchina herd at a predetermined population size through harvest. Biologists also recognized that there were few herds in the state where managers had the ability to restrain or increase herd size and that management programs could be altered for political reasons. In the Delta herd, a previous political decision to allow the herd to continue growing was made independently and in disregard of opinions of management biologists. Consequently, as researchers, we were able to study population processes in the Delta herd from shortly after a population low through a population high and subsequent decline. By the end of the study in 2008, besides observing the stable Nelchina herd and fluctuations in the Delta herd and Denali herds, we also had been able to make some comparative observations about events that transpired in other herds where herd size grew large and declined largely because of natural factors (e.g., Mulchatna, Northern Alaska Peninsula). Other herds had remained stable at relatively small sizes because of natural factors (e.g., White Mountains, Ray Mountains, Macomb, and Denali), and one small herd had declined from predation (Southern Alaska Peninsula). All of these observations have allowed Alaska caribou biologists and managers to make educated guesses about optimum herd sizes that might maximize long-term sustainable harvests (if that was the desired management direction). In the Conclusions section of this document we suggest optimum herd sizes for some caribou herds.

TRENDS IN FALL CALF:COW RATIO AND SEX RATIO IN THE DELTA HERD AND OTHER ALASKA CARIBOU HERDS

Fall Calf:Cow Ratio in the Delta Caribou Herd

Fall calf:cow ratio varied considerably in the Delta caribou herd during 1970–2008 (Fig. 13), and was a major factor affecting patterns of population growth (Fig. 7). It was apparent that wolf predation was a primary proximate cause of low fall calf:cow ratios in the Delta herd after the population had declined in the early 1970s (Boertje et al. 1996). Causes of other periods of low fall calf:cow ratios during 1990–2007 were less clear but there was evidence that both predation and weather-related nutritional factors were important (Valkenburg et al. 2002, 2004). Logistic regression modeling indicated that snow depth in late winter (*Denali.snow*), growing season length (*length.green*), herd size (*n.caribou*), and annual variation in natality (*part*) had possible explanatory value over the entire period of the study (Table 27). However, there was a large amount of unexplained variation suggesting that we were unable to adequately measure many variables and/or several important variables were not measured. In addition, it is likely that sampling error also played a role in the observed variation in fall calf:cow ratios in the Delta herd.

Of the 3 environmental variables that had strong support in logistic regression modeling of calf:cow ratios, 1 (snow depth) has been previously shown to involve mechanisms that can have a significant indirect influence on survival of calves in many northern cervids (c.f. Ozoga and Verme 1982; Skogland 1984; Verme and Ullrey 1984; Whitten et al. 1992; Singer et al. 1997; Mech et al. 1998:149; Keech et al. 2000). Previous studies on northern ungulates have also demonstrated that population density (*n.caribou*) has the potential to influence recruitment of caribou calves positively or negatively (c.f. Gasaway et al. 1983b, Messier et al. 1988, Bergerud et al. 2008). Through density-dependent nutritional factors, low caribou population density can result in higher natality rates in 2-year-old and 3-year-old females, and in higher survival rates of calves and vice versa (Skogland 1985; Valkenburg et al. 2002, 2004; Boertje et al. 2012). Conversely, high caribou population density can result in predator swamping so that predation has less influence on calf survival and caribou density can correlate positively with fall calf:cow ratio. Our experience with the Delta herd (including the regression modeling), and our observations during the same period from the many other small to moderately sized (<10,000) caribou herds in Alaska, suggest that higher relative population sizes of small to moderately sized caribou herds (<10,000) generally had a positive effect on fall calf:cow ratios. This is not surprising because all of Alaska's caribou herds (except Adak) had predator populations (wolves, bears, and eagles) that occurred at natural densities, except for brief periods in the ranges of the Delta, Nelchina, Fortymile, and Southern Alaska Peninsula herds where wolf numbers were reduced through control (Valkenburg et al. 2004; Butler 2009b; Tobey and Schwanke 2009; Boertje et al., *In press*). In very large caribou herds (e.g., George River and Mulchatna) and in some smaller herds as well (e.g., Northern Alaska Peninsula and Southern Alaska Peninsula, many herds in Norway), there is now ample evidence that high caribou numbers (i.e., density) can result in reduced natality, higher mortality, and population declines from overgrazing that resulted in nutritional stress (this study; Skogland 1985, Post and Klein 1999, Sellers 2001, Valkenburg et al. 2003b, Bergerud et al. 2008).

Fall Calf:Cow Ratio in the Delta Herd and Other Caribou Herds

Considerable variation in fall calf:cow ratios (or percent calves in the Arctic herds) was evident in herds other than the Delta herd (Figs. 14–19; Appendix B). In the worst years, fall calf:cow ratio even approached zero, indicating total recruitment failures in some of Alaska's smallest herds (i.e., those with <3,000 caribou) (e.g., Chisana, Southern Alaska Peninsula, Unimak). In the case of the Southern Alaska Peninsula herd, the extremely low calf:cow ratios were reversed simply by the removal of 14 adult wolves associated with 2 dens on the herd's main calving area in 2007 (Fig. 18) (Butler 2009b). The similarly low calf:cow ratios during 2005–2008 on Unimak Island were also thought to be primarily due to predation by <30 wolves on the island (Appendix B) (Riley 2011b).

In medium- (10,000–30,000) and larger-sized (>30,000) caribou herds, fall calf:cow ratio also fluctuated considerably over the period of the study but never reached the extreme low levels seen in small herds (Figs. 15–19). For example, in the Mulchatna herd, despite the dramatic decline (the highest sustained rate of decline of any Alaska caribou herd we monitored) that occurred during the late 1990s, the lowest fall calf:cow ratios recorded remained around 15:100 whereas in several of the smallest herds fall calf:cow ratios were commonly below 10:100 in bad years and approached zero during the worst years in some herds (e.g., Delta, Chisana, Southern Alaska Peninsula, Unimak). In the largest caribou herds, fall calf:cow ratios (or percent calves) were typically relatively high compared with the moderately sized and small caribou herds, even during periods when the large herds were at relatively high levels and stable or slightly declining.

BULL:COW RATIOS IN THE DELTA HERD AND OTHER ALASKA CARIBOU HERDS

Trends in Fall Bull:Cow Ratio in the Delta Caribou Herd and Delta-Denali Comparison

Despite the possibility of some bias in composition counts in the Delta herd, especially prior to 1981, the strong effect of recruitment and hunting on fall bull:cow ratio is apparent (Figs. 14, 20, and 32). The Delta herd was subject to moderate, either-sex hunting during the 1960s through 1971 (Fig. 32; Appendices G and H). During this period (1969 and 1970), recruitment was also moderate (calf:cow ratios in the 30s) and the bull:cow ratio remained relatively high (~40) (Fig. 20). After the onset of severe winters (starting with 1970–1971), recruitment (fall calf:cow) declined but harvest (particularly of females) remained high. Fall bull:cow declined to around 30 during this period (Fig. 20). Elimination of all harvest in 1975, and the substantial increase in calf:cow ratio to around 40–50:100 that was coincident with wolf control that began in 1975, resulted in an immediate and rapid increase the fall bull:cow ratio. During the period of high recruitment and no harvest (late 1970s) the bull:cow ratio then stabilized in the mid-50s (Fig. 20).

After 1980, when study of the Delta and Denali herds intensified and fall composition counts were more closely timed to the rut, we gained additional insight into the influence of recruitment and hunting on fall bull:cow ratio. Limited harvests (primarily of bulls) resumed in the Delta herd in 1980 and hunting resulted in a decline of about 10–15 bulls:100 cows in fall despite continued high recruitment. A further decline of about 10 bulls:100 cows occurred during the mid-1980s as harvests were greatly expanded to try to stabilize the Delta herd. The bull:cow ratio then remained relatively stable through 1989 as the herd was allowed to continue increasing. Coincident with the declines in recruitment that occurred after 1989, the bull:cow ratio in the Delta herd declined below 30 (the lowest level recorded during the study period) even though hunting was suspended in 1992 (Figs. 20 and 32). After the mid-1990s, herd size, recruitment, harvest, recruitment, and bull:cow ratio all remained relatively stable in the Delta herd (Figs. 7, 14, 20, and 32).

In the adjacent, unhunted Denali herd, fall composition counts were conducted regularly after 1984. During most of this period, the bull:cow ratio generally remained higher than in the Delta herd but also declined markedly after 1989 with the onset of bad weather and declining recruitment (Figs. 13 and 20). From 1997 to 2005 the bull:cow ratio in the Delta herd was consistently higher than in the Denali herd despite the harvest of 30–50 bulls per year in the Delta herd (Figs. 20 and 32). However, recruitment in the Denali herd was also slightly lower than in the Delta herd during the late 1990s and early 2000s (Fig. 14). The significance of this comparison is primarily that the bull:cow ratio in caribou herds declines almost immediately during periods of declining recruitment, even in herds that are not hunted. The mechanism here is that survival and life span of bulls is lower than cows and bull numbers decrease more quickly than cow numbers as fewer calves are recruited. Also, during severe winters when recruitment declines, mortality of bulls also increases because bulls, especially large bulls, enter the winter with little fat.

In unhunted herds, where bull:cow ratios are high after periods of average recruitment, the high proportion of older bulls also likely results in more intense fighting during the rut and higher mortality from fighting during and after the rut as wounded bulls die from predation and other causes. The dramatic effects of intense rutting battles and mortality associated with them was apparent during fall composition counts of the Mulchatna herd until the late 1990s when the bull:cow ratio declined (Fig. 23). We frequently saw dead and wounded large bulls and areas of bloody snow around rutting groups. Once the bull:cow ratio in the Mulchatna herd declined below ~40 bulls:100 cows in 1998 we seldom saw intense rutting battles or rut-wounded bulls. In other herds where the bull:cow ratio was<40:100, dead and wounded bulls were infrequently seen.

Because there were few radiocollared bulls in the Delta herd, we had no independent method of estimating natural mortality (i.e., non human-caused) of bulls. We therefore used the deterministic spreadsheet model to estimate survival rates of bulls using observed bull:cow ratios (Table 28). With trial and error we manipulated input survival rates of bulls to make model output track observed bull:cow ratios from fall composition counts. It became apparent that during periods when there was relatively heavy hunting pressure directed primarily at bulls in the Delta herd and the observed bull:cow ratio was relatively low (1983–1991), we were forced to increase survival inputs for bulls in the model to nearly 1.00 (0.98 or only 2% natural mortality) (Table 28). From this exercise we concluded that because hunting for bull caribou in the Delta herd is relatively selective for older bulls (most hunters tend to shoot the largest bull in any group in fall), and because age is also a likely major factor determining natural survival rates in bulls, hunters removed many of the older bulls that would have died from natural causes. In contrast, during periods when hunting pressure on males was light, or was directed to females, or occurred in winter (when hunters were less selective), natural mortality of males was higher (e.g., 1992–2008). We believe that the modeling exercise, corroborating evidence from the Delta-Denali comparison, and observations on the effects of rut battles on bulls in herds with high bull:cow ratios provides good evidence that hunting for mature male caribou can have a large compensatory component and helps explain why it is possible to have relatively high harvests of bulls (>5% of herd size) without greatly depressing bull:cow ratios even on very small caribou herds (e.g., Chisana, Kenai Mountains, White Mountains, Killey River, etc.) where recruitment was relatively low (often <20 calves:100 cows) (Figs. 15 and 16). In Alaska's national parks and preserves, where federal managers are interested in maintaining "natural" conditions, the compensatory nature of hunting on bull caribou provides a mechanism that allows hunting on small herds while still maintaining high bull:cow ratios in small, relatively sedentary herds.

Trends in Fall Bull:Cow Ratio in Herds Other than the Delta Caribou Herd

Bull:cow ratios in Alaska's caribou herds during the period of this study varied considerably, from a low of about 10:100 in the Southern Alaska Peninsula and Unimak herds in 2008 to a high of 132:100 in the Central Arctic herd in 1980 (Figs. 20–24). Lack of radio collars on bull caribou in most herds in most years and various sampling errors undoubtedly contributed to difficulties in accurately measuring bull:cow ratios in many herds. In addition, biologists continue to have a rather limited understanding of movements of bulls, especially in adjacent large herds where overlap of herd ranges and intermingling of herds may have occurred during late summer and fall (e.g., Central Arctic, Teshekpuk, and Western Arctic). The very high bull:cow ratios observed in the Central Arctic herd during the 1970s (Fig. 24) could have resulted from the inclusion of bulls from the Western Arctic, Teshekpuk, or Porcupine herds in the Central Arctic herd counts. Uneven distribution of males and females could also have contributed because there were few or no radio collars on bulls. We did not find bull:cow ratios over 100 in any other herds during this study, and in view of caribou breeding ecology and observed survival rates of bulls versus cows, there is no biological explanation other than mixing of adjacent herds. Bull:cow ratios of about 70:100 appear to be the approximate normal maximum value for caribou herds that are growing, have good calf survival, and relatively low or nonselective hunting pressure (e.g., Denali 1980s, Mulchatna 1980s) (Figs. 20 and 23). Bergerud (1971, 1974) reported that adult sex ratios in large herds that were not selectively hunted in Newfoundland and the Northwest Territories of Canada ranged from 26% to 40% (approximately 35–67 bulls:100 cows). Some smaller, stable but unhunted Interior Alaska herds have consistently had bull:cow ratios in the mid-30s with fall calf:cow ratios in the low or mid-20s (e.g., Denali, Ray Mountains) (Figs. 20 and 21).

With the exception of the Western Arctic herd, few fall composition counts were conducted in the Arctic herds (Central Arctic, Porcupine, Teshekpuk, and Western Arctic) during 1970–2008, primarily because of logistical and financial considerations and typically poor weather during the rut or pre-rut period in early October. The few fall composition counts that have been done on Arctic herds have generally shown that bull:cow ratios are relatively high (35–75) compared with Interior and Southwest Alaska herds (Figs. 22–24). Conversely, fall bull:cow ratios have reached their lowest levels in Alaska's smallest herds particularly during or following periods of very low recruitment of calves (e.g., Chisana, Southern Alaska Peninsula, Unimak) (Figs. 18, 21, and 23). An exception to this occurred in the Mulchatna herd during 2003–2006, when fall bull:cow ratios fell below ~20 bulls:100 cows overall (Fig. 23), and below 10 bulls:100 cows in GMU 17 (Woolington 2007). The herd was decreasing rapidly (but still numbered about 45,000) while recruitment was low–moderate and considerable selective hunting of males may have been occurring, especially in GMU 17 (Woolington 2007). However, we did not detect a major decline in bull:cow ratios in the Western Arctic herd during the period of very high and unsustainable harvest that occurred during 1974–1976. The main differences between the decline of the Mulchatna herd during 1998–2005 and the Western Arctic herd during the mid-1970s was that recruitment of calves in the Western Arctic herd was still relatively high (Davis 1976b, Davis et al. 1980, Woolington 2007). Both herds were mostly hunted in winter when hunters generally were not selecting caribou based on sex.

When caribou bull:cow ratios declined to about 10:100 in the Mulchatna, Southern Alaska Peninsula, and Unimak herds, biologists naturally began to question whether there were sufficient bulls in the herd for breeding. We found no evidence from the literature or this study that low bull:cow ratios were associated with low natality rates the following year. The lowest observed natality rate observed in the Delta herd during this study (29%) occurred in 1993 when bull:cow ratio in the herd was moderate (around 25–30:100) (Fig. 20; Tables 21 and 22; Appendix B). We attributed this unusually low natality rate to a severe weather event that occurred in September 1992 just before the rut (i.e., "perfect storm"; Adams et al. 2005).

Although we observed very low calf:cow ratios in the Southern Alaska Peninsula and Unimak herds when bull:cow ratios were among the lowest we recorded (about 10:100), natality rate of radiocollared females (judged from distended udders) was not low in the Southern Alaska Peninsula, and the low fall calf:cow ratio increased immediately following the removal of 14 adult wolves from the calving areas (Butler 2009b). In the Unimak herd, Riley (2011b) documented a small decline in natality rate (from 85% to 67%) in 2009 following a major decline in bull:cow ratio from 31:100 to 10:100 between 2007 and 2008 (Fig. 23), but the decline in natality rate may not have been statistically significant and the decline in bull:cow ratio may not have been biologically significant. It is also possible that the timing of the udder counts was not optimal.

Harvest-related declines in the bull:cow ratio in caribou herds tend to be largely self-limiting as long as calf:100 cow ratios remain >20:100. When harvest of bulls is high, age structure of the bull segment usually declines quickly and most of the remaining bulls have antlers that resemble those of cows. This typically occurs once the bull:cow ratio declines below about 25:100. In the field, at the distance that hunters typically shoot caribou, it is difficult for most hunters to distinguish between males and females using characteristics other than antlers. Once it becomes difficult for hunters to find animals that are obviously bulls by their antlers alone, and harvest of cows is not allowed, many hunters tend to be dissatisfied and advocate for more restrictive hunting, or they forgo harvesting caribou altogether (e.g., in the Delta herd in the mid-1980s). As a result, caribou bull:cow ratios in Alaska caribou herds seldom fall to the very low levels often seen in many heavily hunted moose populations.

Small Bull:Cow Ratios

Analyses of the influence of previous calf:cow ratios on small bull:cow ratios in the Delta, Fortymile, and Denali herds indicate that the “small bull” (i.e., bull caribou whose antlers appear similar in size and conformation to those of cows) category used in composition counts includes most yearling and 2-year-old bulls, and probably some 3-year olds as well (Figs. 26–31). The large amount of unexplained variation in regressions (Figs. 28–31) likely comes from sampling error, imperfect knowledge of distribution of bulls during the rut, and subjectivity in classification. It is also possible that antler growth varies from year to year, although we are unaware of any data on variation in antler growth from year to year. As a caribou herd declines in condition, there may also be more age classes of bulls that end up in the “small” category because antler size and mass is probably lower.

The experience of many of the authors of this technical bulletin is that there is a high degree of subjectivity involved in classifying bulls into the 3 categories; especially differentiating between “medium” and “large” bulls. Although there may continue to be some utility in collecting data on small bull (and large bull) numbers in some caribou herds, even with good training and an effort to ensure that classification is consistent, it will be difficult to greatly reduce the subjectivity involved in classification of bulls.

Once biologists have experience conducting fall composition counts, the qualitative information they collect on how the rutting groups appear may be more valuable than trying to rigorously segregate bulls by size class. For example, as an observer is flying along over groups of caribou while classifying them, the number and size of large bulls, the condition of bulls and cows in the herd (fat, rounded bodies, sleek coats, etc.), mass and shape of antlers of bulls and cows, and other qualitative information stands out but is difficult to encapsulate in any objective metrics. A good example of this was when we increased efforts to obtain more detailed data on fall composition in the Mulchatna herd in the mid-1990s. For the first several years the rutting groups in this herd were spectacular. Every major rutting group seemed to contain a trophy bull (massive antlers likely to be over 400 Boone and Crockett points) and all caribou appeared to be sleek, fat, healthy, and energetic. By the late 1990s as the herd began to decline, we observed substantially fewer bulls, trophy bulls were rare, and body condition had noticeably declined. In some years, many animals were also limping, indicating disease (likely hoofrot). Large bull and small bull numbers did decline (Appendix B) but the largely unrecorded qualitative (and admittedly somewhat subjective) data were far more dramatic than is reflected in those objective measures. Rather than (or in addition to) trying to classify bulls, it may be better to characterize qualitative aspects of the appearance of rutting groups to get an idea of herd health and to continue to rely on objective and quantitative sampling of calf:cow ratio to estimate recruitment.

HARVEST IN THE DELTA HERD

After 1991, harvest was not a factor that influenced population trajectory in the Delta herd and it likely had little influence on bull:cow ratios, partly because harvest was tightly controlled under a drawing permit, and partly because harvest of bull caribou is at least partially compensatory (i.e., it substitutes for some natural mortality). Interest in hunting Delta caribou is high and the herd has been included in the state's intensive management planning. Because the area is also occupied by a high density moose population, it is likely that moose management will take priority in management decisions. Managing the Delta herd for a high level of harvest is therefore complicated because the relatively dense wolf population is needed to help control the size of the moose population and incidental predation on caribou by wolves likely reduces the potential harvestable surplus of caribou.

WEIGHT, SIZE, AND NUTRITIONAL CONDITION OF CALVES

Trends in Mean Weight of Cohorts of 4- and 10-Month-Old Calves in the Delta Caribou Herd

In hindsight, we would have collected weights of cohorts of 4-month-old calves for the entire period of the Delta herd study, especially because the herd was small and rapidly growing in the early years and caribou were in excellent nutritional condition. Initially we radiocollared 10-month-old calves instead of 4-month-old calves because we were not sure if 4-month-old calves could carry an adult-sized collar during their first winter and because we were interested in measuring condition of calves after their first winter. By the time we started capturing and weighing calves in October (1991) the Delta herd was already declining from a combination of poor nutrition caused by high population size (i.e., density-dependent factors) and the onset of deep snow winters (and perhaps other adverse weather factors). For the remainder of the study, the Delta herd was recovering from the bad weather of the early 1990s but probably still being affected by the previous population high and lingering density-dependent effects. We believe that it was largely for this reason we were unable to detect a trend in weights of 4-month-old calves (Fig. 33). Calf weights (at 10 months) in the adjacent Denali herd had recovered to the 60 kg range by cohort year 1994 (i.e., as soon as snow levels returned to normal) (Fig. 40). Also, the missing 4-month calf weights in the Delta herd (1978–1990) probably reduced our ability to discriminate the effects of summer versus winter nutrition, and limited our ability to detect the effects of *initial.weight* on survival, natality, and fall calf:cow in the herd. Within herds, the size of a calf at birth plus growth of calves during their first and second summer are the most important factors that determine their eventual body size (Reimers 1972, Skogland 1983), subsequent survival over winter (this study), and their likelihood of producing their first calf at 2 or 3 years of age (Skogland 1983, 1985). Summer conditions are particularly important and good summers can at least partially compensate for small birth weights of calves (Dale et al. 2008).

We did detect a slight declining trend in mean weights of 10-month-old calves during the Delta herd study (Fig. 33). However, rather than a continuous trend over time, there were 3 rather distinct periodic trends in cohort mean weight. First, from cohort birth year 1978 to birth year 1988 there was a period with no statistically significant (but possibly declining) trend in cohort mean weights (slope = −0.30, R^2 = 0.18, P = 0.30). These cohorts were followed by 2 cohorts with particularly low calf weights (1989 and 1990). Finally, there was a third period of variable but relatively low calf weights with no statistically significant trend during 1991–2007 (slope = +0.13, R^2 = 0.09, P = 0.29) (Figs. 34 and 35). Because of the influence of initial weight (4-month-old weight) on survival, some of the smallest calves are likely to be selected out of the population over winter, thus reducing the likelihood of finding a difference in cohort weight between 4-month olds and 10-month olds. Nevertheless, differences in weight of cohorts from fall to spring can be significant and may provide an indicator of overwinter nutrition and quality of winter ranges (Valkenburg et al. 2003a).

Mean cohort weights of both 4-month-old and 10-month-old calves were not greatly lower after the “Perfect Storm” year (birth year 1992) (Figs. 33 and 35; Table 8). We suggest that the late greenup and relatively short summer of 1992 had less of an effect on the Delta herd caribou (particularly on natality rate) than the September snow storm itself. In fact, the 2 lowest mean weights of cohorts of 10-month-old calves occurred immediately before the effects of the Mount Pinatubo eruption were noticed in Alaska. In other words, although the late spring and short summer probably affected calf weights in October 1992, the effect was not as large as in some other years. The problem for Delta caribou was that the herd had just come out of a period of record population size (1985–1991) into a period of deep-snow winters (1991–1993). Further, the 1991–1992 deep snow winter was followed by a short summer which was, in turn, followed by the catastrophic September snowstorm that immediately preceded the rut. It is not surprising that natality in the Delta herd (and some other Interior herds) reached an all-time low during those years. The following year (1993), the fall calf:cow ratio was so low in the Delta herd (5:100) and the overwinter (1993–1994) calf mortality so high that we were unable to find even a minimum number of calves to obtain a sample of 10-month-old calf weights in April 1994 (i.e., for the 1993 birth year cohort). The chances of a similar sequence of events is remote but illustrates the interesting potential interactions of density-dependent factors, weather trends, and stochastic factors on herd growth.

Weight of Cohorts of 4- and 10-Month-Old Calves in Herds Other than the Delta Herd and the Delta-Denali Comparison

We had adequate samples of 4- and 10-month-old calf weights from the Denali, Fortymile, and Nelchina herds to examine trends in calf weight in herds other than the Delta herd. The

Delta-Denali comparison is particularly interesting because these 2 herds have historically been relatively similar in size, both occupy similar habitat on the north side of the central Alaska Range, and one was intensively managed (Delta), while the other was unhunted and unmanaged. Prior to the 1989 population high in the Delta herd and the onset of severe winters, 10-month-old calf weights in both herds were relatively high for Interior herds and similar (~60 kg). With the onset of deep snow winters in 1989, calf weights in both herds declined but subsequently recovered almost immediately in the Denali herd (Fig. 40). Recovery of calf weights in the Delta herd was slower and mean weight of cohorts of 10-month-old calves did not return to the high levels seen in the early 1980s. After the early 2000s, calf weights in both herds were more similar but likely more variable (Fig. 40). Sample sizes for these comparisons were small in some years and judging from the standard error of individual samples, the confidence interval of individual annual estimates of calf weight likely overlapped (Appendix C). However, we believe the evidence from trends in calf weight in both herds and similar evidence from natality rate data support the idea that the Delta herd reached an unsustainably high population size in the late 1980s and that there were long-term (>10 year) consequences for calf weight, and calf recruitment.

In the Nelchina herd there was perhaps a slightly increasing (but not statistically significant) trend in weights of 4-month-old calves between 1995 and 2001 (slope = 0.79, $R^2 = 0.26$, $P = 0.24$) (Fig. 38). These were the years during which the Nelchina herd was being deliberately reduced from a peak of about 50,000 adults to the management objective of about 35,000 adults (Appendix A) (Tobey 1999, 2001). The possibility of an increasing trend in 4-month calf weight (although not statistically significant) in the Nelchina herd somewhat increased our confidence that the management program to stop herd growth was also working to prevent overgrazing (Tobey 1999, 2001).

Between 1991 and 2002 there was no apparent trend in 4-month-old calf weights in the Fortymile herd, (slope = −0.009, $R^2 = 0.003$, $P>0.30$) (Fig. 38). At that time (early 2000s) the management goal for the Fortymile herd was to continue to promote herd growth while watching for signs of deteriorating nutrition (Boertje and Gardner 2000b, Gronquist et al. 2005). The first 12 years of calf weight data suggested that the herd could continue increasing without overgrazing its summer range. Data for the Fortymile herd have now been thoroughly reviewed and published elsewhere (Boertje et al. 2012; Boertje et al., *In press*).

Across all herds and all birth years, mean weights of cohorts of 4-month-old calves averaged slightly heavier than mean weights of cohorts of 10-month-old calves (55.4 kg for 68 cohorts vs. 53.5 kg for 69 cohorts from 1989 to 2006), suggesting that in most herds and most years calves can be expected to lose some weight over the winter (Fig. 42). Comparative analyses of overwinter weight change in the Delta and Nelchina herds were reported previously (Valkenburg et al. 2003b, Dale et al. 2008). Because initial weight (i.e., weight at 4 months of age) affects survival probability, estimates of overwinter weight loss are likely to be conservative. Therefore, any detected weight loss over winter is likely to be biologically meaningful and cohort weight differences between 4- and 10-month olds are likely to be an indicator of winter nutrition.

When population density is low and weather conditions are favorable in caribou herds in Interior and Southcentral Alaska (including those transplanted to the Kenai Peninsula), female calves (both at 4 months and 10 months of age) can achieve mean cohort weights in excess of 65 kg, with some individuals reaching 70 kg (Figs. 38–41, Appendix C). Caribou calves from all of these Interior herds appear capable of achieving these relatively large body weights, except possibly in the Fortymile herd, where calf weights remained relatively low for Interior herds even when the herd was small (Fig. 38). It is possible that the summer range of the Fortymile herd is inherently lacking some qualities that prevent caribou calves from reaching their maximum body weight potential during their first summer of life. Very likely, it is because the herd's summer range is comparatively low in elevation and it does not have the high quality alpine ranges that supply an abundance of protein from fast growing, early growth-stage forbs (Boertje 1990). Other indices of body condition that we analyzed also suggest inherent summer nutritional restrictions in the Fortymile herd (see *Results* section on *Boone and Crockett Records*). Cook et al. (2004, 2013) found that some elk (*Cervus elaphus*) herds also have inherently poor summer ranges that affect body size, population performance, and management goals. The likelihood that the Fortymile summer range is relatively poor compared with summer ranges of other Interior herds may mean that nutritional limitation becomes manifest at relatively lower population density compared with other herds.

In contrast to the Interior herds, caribou from the Southwest Alaska herds and the Central Arctic and Western Arctic herds (and probably the Teshekpuk herd, judging from weights of newborn calves) appear to be inherently smaller (Figs. 39–41). Female calves in the Southwest Alaska and Arctic herds did not reach the very large body sizes seen in the Interior and Kenai herds even when conditions were favorable and population density was relatively low or when transplanted to new, ungrazed range (e.g., Northern Alaska Peninsula to Nushagak Peninsula). There is a possibility that the small size of Western Arctic caribou calves is at least partially genetically determined, perhaps in part from the introgression of reindeer genes (Cronin et al. 2006). The Western Arctic herd has had the greatest opportunity of any herd for mixing with reindeer. Reindeer are considerably smaller in size than Alaska caribou—the Western Arctic herd animals being the exception. Generally, the largest Norwegian wild reindeer on the best ranges are about the same size as Western Arctic caribou (Skogland 1983). However, reindeer tend to calve about a month earlier than caribou and the Western Arctic herd is still one of the latest calving herds in the state—with the peak of calving ~8–10 June (similar to the Teshekpuk and Unimak herds) (Dau 2011). The possibility of introgression of reindeer genes in caribou herds and potential effects on leg length, body size, and antler conformation exists in several caribou herds in addition to the Western Arctic herd, and these herds include the Northern Alaska Peninsula, Southern Alaska Peninsula, Unimak, and Beaver Mountains.

The Nushagak herd was created by a transplant from the Northern Alaska Peninsula herd. The transplanted caribou were released on ungrazed range on the Nushagak Peninsula in 1988, but at a time when the Northern Alaska Peninsula herd was at a relatively high population for the size of its range (Fig. 10). When first assessed for body condition in 1995, females in the new Nushagak herd appeared to be in very good condition as evidenced by 0.5–1.0 cm of subcutaneous back fat on 10-month-old female calves. Also, all radiocollared females were producing calves at age 2 (Hinkes and Van Daele 1996). However, the maximum mean cohort weight we measured in the herd was 57.1 kg in the 1994 cohort (Appendix C).

Unfortunately, weight data for 4- or 10-month-old caribou calves are not available for the Porcupine herd. There may be a clinal trend in weight from Western Arctic to Porcupine because

Central Arctic calves are larger than Western Arctic calves. This is a hypothesis that still needs to be tested.

Relationship Between Weight and Metatarsus Length and Trends in Weight:Metatarsus Ratio for Caribou in the Delta Herd and Other Alaska Caribou Herds

The information we collected on metatarsus length over the course of the Delta herd study and monitoring programs in other herds indicated that long bones continue to grow over the winter in all caribou calves, even in herds where calf size is small during periods of nutritional limitation. Nutrients required for growth of bones are not likely to be limiting caribou during winter (Klein 1964). Therefore, continuing growth of the metatarsus over winter, regardless of body condition of caribou calves must be considered when using weight:metatarsus ratio as a potential indicator of condition. Weight:metatarsus ratios will be consistently lower in 10-month-old caribou than in 4-month olds (Figs. 43–51) because of either weight loss and bone growth, or bone growth alone.

Metatarsus did appear to be a reasonable predictor of weight in caribou calves; the steepest slopes of regression equations were in the herds that were likely in the best body condition (based on calf weight, natality rate of young females, and appearance of calves) (Figs. 47 and 48). We also thought that differences in leg length of caribou that could reflect ecotypical adaptation to environmental conditions in different regions of the state and genetic differences might manifest themselves in leg length (Klein 1964). However, we did not find differences between herds where caribou calves had unexpectedly short or long mean cohort metatarsus lengths that were independent of their body weight (i.e., unexpectedly high or low weight:metatarsus ratios (Figs. 43 and 51).

In logistic regression analyses (with survival, natality, calf weight, and calf:cow ratio as response variables) where we used *weight.ratio* as a substitute for weight variables, there was no change in models selected or in correlation coefficients indicating little utility in continuing to collect information on metatarsus length in most Alaska caribou herds. However, metatarsus length should continue to be measured in the Arctic herds, especially the Western Arctic herd (in which body size is very small) where we continue to have limited data with which to assess the relationship between metatarsus length and survival and natality. Also, the introgression of reindeer genes into Western Arctic caribou may have caused them to take on reindeer characteristics (such as short legs) and this question should be further addressed.

Relationships of Weight and Girth of Caribou in the Delta Herd and Other Alaska Herds

Although we found that girth and weight are closely related variables and that girth explained most of the variation in weight of 4- and 10-month-old calves (Figs. 52 and 53), we did not find that girth provides any additional information over weight in logistic regression models (with survival, natality, calf weight, and calf:cow ratio as response variables). In most cases, if biologists are in a position to collect girth measurements of caribou calves, they can get weight measurements as well. Weight is both a more meaningful and a potentially more accurately measured variable, so there is little value in continuing to collect girth measurements in Alaska caribou calves.

Body Weight of Newborn Caribou Calves in the Delta Herd and Other Herds

We found that weights of newborn female calves in Interior and Southcentral herds averaged over 8.5 kg in years when they are in good condition (Fig. 54). Newborn males averaged over 9 kg (Fig. 55). In years when weights of male calves averaged less than 8 kg and female calves averaged less than 7 kg, higher than normal neonatal and predation mortality occurred (Mech et al. 1998). In the Arctic herds, where lighter weight calves are the norm (Figs. 54 and 55; Table 9) and where predation on young calves is much less of factor than in the Interior, survival of lightweight calves may not be compromised unless calf weights fall below 7 kg for males and 6 kg for females. Unfortunately, there are few data for weights of neonates from the Western Arctic herd (the Alaska herd with the lowest 4- and 10-month-old calf weights, and introgression of reindeer genes). The only record of weights for Western Arctic neonates is 5.4 kg (12 lb) from 1965 for both males and females combined, but no estimate of variance or sample size is available (McGowan 1966). If correct, this estimate of newborn calf weights was likely the lowest of any herd in Alaska through 2007. The early to mid-1960s was also a time when mandible lengths were also low so nutrition may have been compromised in those years in the Western Arctic herd (Ver Hoef et al. 2001).

Weights of female newborn calves were 5.4 kg (11.9 lb) in the Southern Alaska Peninsula herd in 1989 and many calves were abandoned by their mothers during an attempted calf mortality study (Pitcher 1991; K. Pitcher, Wildlife Biologist, ADF&G, personal communication). It is likely that these very low newborn weights were indicative of severely compromised nutritional condition where calves were below a birth weight critical for calf survival.

Compared with Alaska caribou, Norwegian wild reindeer have newborn calf weights that are very low. This is true even in Norwegian herds that are at low density and on a high plane of nutrition (Skogland 1984). Skogland (1984) estimated that a critical birth weight for neonatal survival in Norwegian wild reindeer was about 3.5 kg. Based on our sampling of birth weights from Alaska caribou herds, we believe a critical value for caribou herds in Southwest Alaska is about 5.5–6.0 kg. Critical birth weights are likely higher for Interior caribou herds and lower for the Arctic herds. For many Alaska herds, where predation is a major factor in neonatal survival, the critical birth weight is less important than the fact than any reduction in birth weight predisposes calves to predation mortality (Adams et al. 1995b, Mech et al. 1998). Historically, Interior Alaska herds have rarely experienced situations where nutritional conditions were so poor that calves are born at weights below a critical birth weight.

Other Indicators of Nutrition

Condition Scores

We abandoned the idea of using condition scores of female calves as a useful index of nutrition. The method was subjective and most calves received similar scores regardless of their weight and size.

Gutted Weight vs. Live Weight of Female Calves

Other researchers have found that variation in the weight of rumen contents can make carcass weight a better indicator of nutritional condition than live weight (Langvatn 1977, Gerhart et al. 1996), and reindeer managers in Norway commonly use “carcass weight” collected during the hunting season as a primary index on condition (Bevanger and Jordhøy 2004). We found a very close correlation between gutted weight and live weight (Fig. 56), however, and for practical reasons (logistics, time, ease of handling, and politics), biologists will continue to routinely handle live calves rather than collect calves because collaring can be done at the same time. We suggest that any differences between gutted weight and live weight as indices of nutrition are minor enough that unless there are other compelling reasons for collecting calves (perhaps disease, etc.), live weight of calves at 4 and 10 months of age will continue to be the more widely used nutrition index for caribou. However, we did discover some very useful and unexpected information from our collections of caribou calves. For example, in the process of collecting calves in the Northern Alaska Peninsula and Mulchatna herds, we discovered that disease (pneumonia) was prevalent in those herds. This was the first evidence that disease likely played a role in the declines of those herds.

Femur Marrow Fat Content of Female Calves

Depletion of marrow fat in long bones, particularly the femur, has been widely used as an indicator of when animals are in poor condition (c.f. Cheatum 1949, Dauphiné 1976, Brooks et al. 1977, Kie 1978, Mech and DelGiudice 1985). Young of northern ungulates are especially prone to losing marrow fat when winters are severe (Franzman and Arneson 1976). For this reason, we expected to see a reasonably good correlation between live weight of female calves (our primary index of condition in caribou) and percent femur marrow fat, especially in April. However, in the Nelchina herd (the only herd with sufficient April data), the relationship, although positive, was relatively weak (R^2 = 0.15, Fig. 57). Although mean percent femur marrow fat tended to be higher in October collections than in April collections across all herds (R^2 = 0.24–0.34, Fig. 57), the number of collections was too low for definitive comparison (Appendix C). We did find that some of the lowest mean percent femur marrow fat values were found in October. For example, after the Mulchatna herd began declining (1996), we found that mean percent femur marrow fat was 48% in October compared with 73% in spring 1995 when the herd was still increasing. It appears that in some years, summer conditions are so poor or summer range is so overgrazed that calves either do not accumulate marrow fat by October or they are already mobilizing it by then. This result tended to support findings that summer nutrition can be nutritionally limiting in caribou (Valkenburg et al. 2003a).

Mean percent femur marrow fat in caribou calves appears to be a valuable index to condition and contains information that is additional to the information from live body weight. Marrow fat of calves may be more useful over a wider range of condition than marrow fat in adults, which is generally thought of only as an indicator of starvation or near starvation (Dauphiné 1976, Mech and DelGiudice 1985). However, the problems involved in obtaining robust samples of percent femur marrow fat from calves are the same as with the other indices of condition that must be obtained only from dead animals. Collections from hunters are inconsistent, hunters do not generally shoot calves, and biologists are constrained by the number of calves found killed by predators and other causes and by the number of animals it is practical and politically acceptable to collect.

Numbers of Warble Fly Larvae in Female Calves

Mosquitoes and oestrid flies (i.e., nose bots and warbles) influence caribou behavior in mid to late summer and biologists have studied and modeled potential effects of insects on caribou nutrition and behavior (Curatolo 1975; Kelsall 1975; Boertje 1981; Dau 1986; Downes et al. 1986; Fancy 1986; Mörschel 1996, 1999; Mörschel and Klein 1997). There is general consensus that the main effect of insect harassment is that it reduces energy intake in summer, and it is likely that mosquito harassment is more serious in this regard than disturbance by oestrid flies because oestrid flies are inactive at night (Bergerud et al. 2008). There is less information on the effects of developing warble larvae on nutrition and condition, but some studies have shown debilitating effects in semi-domestic reindeer (Dieterich 1980, Washburn et al. 1980, Helle and Tarvainen 1984). Huot and Beaulieu (1985) found a significant negative correlation between body fat reserves and number of warble fly larvae in a small sample of 8 yearling caribou in the George River herd in April. However, Huot and Beaulieu (1985) found no significant relationship in calves or pregnant adult females ($r = -0.32$, $n = 9$; $r = -0.24$, $n = 13$). Many authors have commented about numbers of warble larvae in caribou and there is general agreement that calves tend to have higher numbers of larvae than adults (Kelsall 1975, Dieterich 1980, Huot and Beaulieu 1985), and that Arctic or tundra herds have higher numbers. For example, Kelsall (1975) found as many as 2,000 larval breathing holes in some caribou hides in the central Canadian Arctic. In the Western Arctic herd, Davis and Valkenburg (1979; 1985a:14) found 1,500–2,000 warble fly larvae in some 10-month-old calves that were near death. Huot and Beaulieu (1985) found 40–900 larvae in calves but only 57–109 in yearlings and adults. Although it is not possible to count warble larvae numbers in live caribou with any degree of accuracy, it is possible to determine if infestations are heavy (>500) or extreme (>1,500). We did not notice extreme infestations of warble larvae in herds other than the Western Arctic and found a maximum of just over 400 larvae in Interior and Southwest Alaska herds in which we collected 10-month-old calves (Fig. 58, Appendix C). The poor correlation (Fig. 58) between femur marrow fat and number of warble larvae that we found in the best data set we had available (Nelchina), seems to indicate that normal numbers of warble larvae don’t affect caribou nutrition to the point that femur marrow fat is depleted over winter. There may also be a threshold below which the effects of warble larvae are minor. It may also be that extreme warble infestations, like the ones we observed in the Western Arctic herd, are another uncommon stochastic event that could occasionally have serious consequences for cohorts of caribou calves. All caribou herds in Alaska are infected by oestrid flies, except the Adak herd because it originated with bottle-raised neonates (from the Nelchina herd) that had no opportunity to become infected. It is interesting that the heaviest recorded body weight of a caribou (a 4-year-old male shot in 1965 weighed 706 lb; McGowan 1966) is also from Adak and there could be a connection with lack of warble flies and nose bots (Burris and McKnight 1973). However, Adak was ungrazed until the caribou were placed there in the late 1950s, so the pristine range probably influenced nutrition as well. Furthermore, the heaviest recorded weight of a caribou from the mainland (695 lb in the Nelchina herd) was not much lower than the record Adak weight (Skoog 1968). There are so few weights of whole, large male caribou in Alaska that meaningful comparison between herds is difficult, however.

As more information accrues from significant declines of large caribou herds from high density, it is becoming clear that overgrazing on summer range can play a major role (Bergerud et al. 2008). In Alaska, much will be learned from the decline of the Mulchatna herd and the Western Arctic herd as well. Insect harassment is likely to become much more serious for caribou on overgrazed summer ranges.

Mandible Length of Female Calves

Length of cleaned and dried mandibles is often used as an indicator of body size or potential body size (in calves) of cervids. Some researchers have suggested that length of long bones can be preferable to body weight because bones have a higher priority for growth than muscle, fat, and some other tissues, and bones do not decrease in size during periods of undernutrition (Hammon 1944, Klein 1964, Aarak and Lenvik 1980). Furthermore, the skull (including the mandible) has a higher priority for growth than other parts of the skeleton (Hammon 1944, Pálsson and Vergés 1952). We found that body weights of 4- and 10-month-old Alaska caribou calves varied considerably by herd, region, and year, and variation in weight was also weakly associated with some weather variables. We found similar variation in size of mandibles of 4- and 10-month-old calves and regional differences (Interior-Southwest-Western Arctic) were in the range of 1–2 cm and were all highly significant (Tables 10 and 11). Mandibles of calves of Western Arctic caribou were particularly small.

We found that mandible length when measured from the cleaned and dried jaws of collected calves was a reasonably good predictor of live weight, especially in 4-month-old calves (Figs. 59 and 60), so if weight or girth cannot be measured conveniently, mandible length is a reasonably good substitute. However, in live calves, fits of the regression lines were considerably worse in both 4-month-old calves and 10-month-old calves (Fig. 61), casting doubt on whether mandible length can be measured accurately (even with calipers) enough in live calves to make this measurement useful as an index of condition. Because mandibles continued to grow over the winter, regardless of winter conditions (Tables 10 and 11), weight of 10-month-old calves is likely a considerably better indicator of condition than mandible length. In the fall, however, mandibles of 4-month-old calves seem to reflect the condition at which calves will be entering the winter. For example, mandibles of the 1994 cohort of Western Arctic calves were particularly small and were coincident with reduced weights and lower femur marrow fat content (Table 10, Appendix C). Because only clean, dried mandibles appear to be useful as an index of condition, and because collecting caribou has constraints mentioned previously, the usefulness of mandibles is limited to herds where collecting (shooting) calves can routinely be done.

Skogland (1983) found that variation in mandible length (clean, dried mandibles) of wild reindeer calves was significant across herds, was related to both population density and lichen biomass on winter ranges, and increased significantly in herds when population size was reduced. Whether it is summer or winter nutrition that has a larger effect on size of calves (and length of mandibles) at 4 months of age is not clear (this study, Skogland 1983). Nutrition during late gestation (i.e., late winter) has a strong effect on newborn calf weight and size (Reimers 1972, Skogland 1983) and low newborn weights were thought to persist over the summer (Skogland 1983). However, Dale et al. (2008) demonstrated that summer nutrition can compensate for low birth weights and they found that the 2 smallest cohorts of newborn calves were the 2 largest cohorts by 4 months of age. Therefore, it is likely that the size of calves (and mandibles) at 4 months of age (the end of their first season of rapid growth) is influenced by 1) nutrition during late gestation (i.e., late winter nutrition); 2) milk production by their mother in early summer; and 3) quality and quantity of food in mid to late summer. In turn, nutrition during late gestation can be influenced by competition for food, depleted winter range, and adverse snow conditions. Nutrition during summer can be influenced by depleted summer ranges and length of the growing season, level of insect harassment, and other still poorly understood variables. For all these reasons, size (weight and skeletal size) of calves at 4 months of age is a useful integrator of a host of important variables that eventually influence survival of calves over winter and natality rate of adult females the following spring. Mandible length of calves collected at 4 months of age could therefore be a useful metric that can be added to other indicators of nutrition (like body weight) if biologists are planning to collect caribou calves to assess condition and prevalence of disease. In some cases where sample sizes are small, it may be that mandible length is a better index of condition than either live weight or gutted weight. In comparisons of the 3 indices (comparing Western Arctic 4-month-old calves from the 1992 and 1995 cohorts with the small 1994 cohort), differences in mandible length were somewhat more pronounced than differences in live weight or gutted weight (mandible length, $t = 6.07$, $P = 0.0001$; live weight, $t = 3.70$, $P = 0.0004$; gutted weight, $t = 2.60$, $P = 0.07$). Rather than collecting calves to obtain the most accurate possible measurement of mandible length, it is often more feasible to simply weigh a few more calves to boost sample size.

It may also be possible to use mandible length of live calves as an index to nutrition, but it is more difficult to measure live mandible length. To measure mandible length on live calves most accurately a caliper (we used a tree-measuring Haglöf, Inc. caliper) should be used, but measuring mandible length of a live, moving calf under field conditions will always be less accurate than measuring lengths of cleaned mandibles. Also, we found that mandible measurements of live calves average about 1 cm (9.4 mm) longer than measurements taken on cleaned jaws (Table 10).

Mandible Length of Bull Caribou Harvested in the Delta Herd

Although we found that most radiocollared female caribou >10 years of age died during the 5-year period of bad weather from 1989 to 1993, bull caribou that were in eruption-wear class >10 during the bad weather period were still represented in mandibles collected from hunters during 1996 to 2002 (Table 12). Ages from known-aged females and eruption-wear classes from older males are not comparable but the data suggest that some older males were still present after the bad winters of the early 1990s. However, hunters are quite selective for large bull caribou and will usually shoot the largest bulls in a group and these bulls are likely to also be the oldest. Even a few remaining old bulls would be easily noticed in the open habitats of the Alaska Range and selected by hunters. During the last 3 years of mandible collections, we found no caribou > eruption-wear class 9 represented. It is likely that even the modest harvest (albeit from a much smaller herd) that began in 1996 was effective in selecting the oldest bulls from the herd.

Although we found no differences in mandible growth of bull caribou through their first 3 seasons of growth during the 1980s (good weather period) and the early 1990s (bad weather period), the fact that the Delta herd was approaching a record high population size and density may have meant that density-dependent factors could already have been affecting mandible growth.

The pattern of growth we saw in mandibles collected from hunters in the Delta herd during 1996–2002 was similar to the patterns observed in the Western Arctic herd during 1965–1968 and 1977–1989 (Figs. 63 and 64) (Ver Hoef et al. 2001). That is, mandible length increased rapidly during the first 52 months of life then slowed. Growth continued to be statistically significant from 52 months of age to 88 months of age, but then no significant growth occurred. Skogland (1983) also found that mandibles of wild Norwegian reindeer males grew through 5 years of age (actually 64 months) at which point growth was no longer statistically significant, but maximum size of mandibles was strongly influenced by population density in different herds.

During 1977–1989, herd size in the Western Arctic herd was relatively low and the herd was growing rapidly during a period of favorable weather. Maximum mean mandible length approached an asymptote of about 300 mm during this period. In the Delta herd (as the herd was approaching high population size), mandible length approached an asymptote of about 315 mm (about 5% larger than mandible length of Western Arctic caribou bulls). During the period of relatively high population size in the Western Arctic herd (1965–1968), mandible length approached an asymptote of just over 280 mm (Ver Hoef et al. 2001). Therefore during likely comparable periods of suboptimal nutrition, Delta herd bulls had a maximum mandible size that was about 12% larger than Western Arctic caribou. In a large sample of jaws collected from Western Arctic and Nelchina caribou during the late 1950s and early 1960s, Skoog (1968:30) found that mandible (ramus) length of adult male caribou ≥6 years averaged 300 mm ($n = 92$), and 316 mm ($n = 180$), respectively.

Boone and Crockett Records

Although there is bias in the records of trophy animals because animals are most likely to be included if they are taken by guided hunters or hunters with a primary interest in taking large males for trophies, antler size as represented in Boone and Crocket records has proven useful for biological assessments (c.f. Foley et al. 2012, Monteith et al. 2012, Hewitt et al. 2014). With caribou in Alaska, we believed there was utility in examining the records to determine if some herds were over- or under-represented considering herd size, and history of guided and nonresident hunting. All medium- to large-sized (>15,000) herds in Alaska (e.g., Central Arctic, Fortymile, Mulchatna, Nelchina, Northern Alaska Peninsula, Porcupine, and Western Arctic), and many minor (<15,000) herds (e.g., Chisana, Delta, Macomb, Mentasta, Rainy Pass, Southern Alaska Peninsula, and Unimak) have a long history of trophy hunting, including guided and nonresident hunting. Most herds from Interior and Southwest Alaska are well represented in Boone and Crockett records for barren-ground caribou (Fig. 65) (Boone and Crockett 2011). However, the Fortymile herd, despite its long history of guided and nonresident hunting, appears to be an exception. The Fortymile and Nelchina herds have been similar in size for much of their history (Van Ballenberghe 1980, Valkenburg et al. 1994), are closely related genetically (Mager et al. 2014), and both herds have been accessible by road and aircraft to large numbers of hunters, including trophy hunters for at least 50 years. The Nelchina herd has contributed 21% of the trophy bulls to the Boone and Crockett records whereas the Fortymile herd contributed only 1.9%. The small (herd size <2,500) western Alaska Range herds (Rainy Pass, Farewell-Big River, and Tonzona) contributed 5.7% (in aggregate) despite their sizes. Even the Delta herd contributed 3.4% despite the fact that it was generally <10% as large as the Fortymile herd since the early 1960s.

The Southwest Alaska herds (particularly the Northern Alaska Peninsula and Mulchatna herds) appear overrepresented, and together have contributed 50.5% of trophies to the records (Fig. 65). Data for the Northern Alaska Peninsula herd may be more biased than data for many other herds because the area has a long history of primarily guided trophy hunting for brown bears (referred to as “grizly bears” elsewhere in this document), moose, and caribou and relatively few subsistence hunters. Nevertheless, for a caribou herd that has usually numbered around 10,000–20,000 it is remarkable that the herd has contributed so many trophy caribou to the record books. Considering the relatively short history of caribou hunting in the Mulchatna herd, this herd’s contribution to the record books is also impressive. Observed differences in body weight potential of Interior versus Southwest Alaska caribou herds (Skoog 1968, this study) lead us to hypothesize that trophy potential of herds in Southwest Alaska is independent of body size. Body size of caribou calves in Southwest Alaska should have reached its maximum potential by October 1998 when we collected 10 female calves on the Nushagak Peninsula. These caribou were transplanted from the Northern Alaska Peninsula herd 10 years earlier (1988) to previously ungrazed range on the Nushagak Peninsula and winters were mild (Hinkes and Van Daele 1996). Therefore, these caribou had several generations on ungrazed range and should have been able to reach their maximum potential size. However, mean weight of the 1988 cohort of female calves in the Nushagak herd was only 55.8 kg compared with mean weights of Interior caribou calves that have commonly reached 60–65 kg (Appendix C). After 2 generations with good nutrition, transplanted red deer have been shown to reach their maximum body size potential (Beninde 1937). Also, all 2-year-old females in the Nushagak herd were producing calves, an indication that the new range was excellent (Valkenburg et al. 2000, Boertje et al. 2012). There is some evidence of genetic differentiation between caribou herds on the Alaska Peninsula-Unimak Island and other Alaska herds (Mager et al. 2014). Trophy potential is obviously high in both groups despite the smaller body size of caribou in Southwest Alaska.

Lack of representation of trophy caribou from the Western Arctic and other Arctic caribou herds is also interesting. The great majority of all caribou in Alaska are in these herds. Although most caribou in the large Arctic herds are taken by local residents for meat, the Western Arctic and Porcupine herds also have a long history of guided trophy hunting. Whether the low trophy potential of these herds has a genetic origin or is an ecotypical adaptation to shorter growing seasons remains to be determined. The Porcupine herd has been shown to be only slightly genetically differentiated from Interior caribou (Mager et al. 2014).

Winter Diet of the Delta Herd and Other Alaska Caribou Herds

Observed declines in proportion of lichens in fecal pellets, declines in body weights of calves, and changing winter ranges used by the Delta herd added evidence to our suspicion that the Delta caribou were searching for better winter ranges (Figs. 34, 66, and 81) during the late 1980s and 1990s. Although caribou may not require lichens during winter (Skoog 1968, Boertje et al. 1985, Bergerud 1996), if lichens are available they seem to be highly preferred and caribou will search for winter ranges where lichens are abundant. Sufficient data are lacking to determine if free-ranging caribou will consistently lose weight over winter if lichens are not available, but that is a likely outcome because lichens are a good source of readily digestible energy (Boertje 1984, 1990). We have shown previously that Nelchina caribou calves were able to maintain their weight over winter on good lichen ranges in northern GMU 12 (Northway-Tok) area where lichens composed 80% of discerned plant fragments in pellet samples (Fig. 67) (Valkenburg et al. 2003a, Dale et al. 2008). As discussed previously, because body weight at 10 months of age is positively correlated with recruitment (i.e., fall calf:cow), at least in the Delta herd, it is likely that good winter ranges that have abundant lichens will contribute to herd growth in some herds. Caribou herds in Alaska have certainly been shown to increase on ranges where lichen abundance and consumption is low (e.g., Central Arctic, Teshekpuk, and Southwest Alaska herds) but those areas also have compensating factors like low wolf numbers on calving and summer ranges, or a longer growing season (Fig. 67; Boertje et al. 1985; Valkenburg et al. 2003a).

The high proportion of lichens in the winter diet of caribou on the Kenai was not surprising because caribou have only relatively recently reoccupied the Kenai (Burris and McKnight 1973; Spraker 1992, 1995) and the relatively moist climate of the Kenai may be more conducive to lichen growth than Interior caribou ranges.

Lichen biomass and proportion of lichens in the winter diet can decline after just a few winters if caribou do not shift winter ranges or if selection of winter ranges is restricted by geography (c.f. Moser et al. 1979). The low proportion of lichens in the winter diet of caribou from Southwest Alaska was also noteworthy and data from the Mulchatna herd confirmed our visual estimates that lichen biomass on winter ranges of the Mulchatna herd west of Iliamna Lake had declined during the 1990s. In some areas of Southwest Alaska and some Nelchina winter ranges in some years (e.g., Koktuli River-Mulchatna herd range and Suslota Lake-Northway flats-Nelchina herd range), sedges made up a relatively high proportion of the winter diet of caribou (Fig. 67). Sedges were also an important diet component on some ranges of the Western Arctic herd (e.g., Pah River flats) where sedges were 25% of discerned plant fragments (Fig. 67). We had noticed that caribou on some of the Western Arctic herd's southern winter ranges were using lakes for resting and ruminating, and also were feeding around the edges of lakes. In feeding craters on these lakes we found that the basal portions of sedges were still somewhat green and therefore likely high in protein. The combination of protein from partially green sedges and carbohydrate from lichens in the adjacent uplands would be an unexpectedly good diet for caribou in winter because caribou generally experience a shortage of winter protein and are adapted to recycle urea nitrogen as a result (Klein 1970, 1990; Boertje 1981, 1984).

MORTALITY AND SURVIVAL OF RADIOCOLLARED CARIBOU IN THE DELTA HERD

Causes and Timing of Mortality of Radiocollared Females

Calves 4–16 Months of Age

Our initial information on calf mortality was from radiocollared calves that were first collared in April (10 months of age; 1979–1990), and later from radiocollared calves that were first collared in early October (4 months of age; 1991–2006). We realize that survival rates for these calves are biased high because most calf mortality in caribou occurs prior to 4 months of age (Adams et al. 1995b; Boertje et al., *In press*). More comprehensive calf mortality data were collected during the 3 years from 1995 to 1997 when we radiocollared neonates 0–2 days old. From all available evidence (radio collars, population modeling, fall and spring composition counts, and general observations), we believe that overwinter survival of Delta herd calves was relatively high (>75%) from 1975 to 1982 (during the wolf control program) and moderate to high (60–75%)

during 1982–1989 (before the onset of severe winters). Most calf deaths were from predation during these years and most predation was by wolves (Tables 14 and 15). Caribou numbers also increased through the period and peaked in 1989. Wolf numbers were low during 1978–1980, and then increased to generally high levels after 1985 (Fig. 13; Appendix F). During the "Perfect Storm" winter (1992–1993), when many Delta herd caribou moved north to winter mostly in boreal forest of the Tanana Valley, White Mountains, and Tanana hills, we also documented lynx predation on caribou calves and yearlings—the only documented lynx predation during the entire study (Fig. 82, Tables 14 and 15). Snowshoe hare populations had declined and many adult lynx were present in the winter ranges used that year. Lynx predation on caribou calves in Alaska has been reported previously in the Fortymile herd but it appears to be an uncommon phenomenon and is rather stochastic in nature (Boertje and Gardner 2001). For lynx predation to be significant in caribou requires an overlap of caribou and lynx distribution (which is uncommon), and likely also that snowshoe hare abundance has recently declined. Lynx (and coyotes [*Canis latrans*]) can occasionally become common in the Alaska Range foothills and mountains when hares decline but these situations don't seem to result in measurably increased caribou mortality, whereas mortality of Dall sheep lambs may increase (Arthur and Prugh 2010).

We found no evidence that disease or parasitism played a role in direct deaths of calves in the Delta herd or that calves were predisposed to mortality from those causes. We found no evidence of bone deformities that have been reported in the Western Arctic herd (Doerr and Dieterich 1979), or low marrow fat in bones (Davis et al. 1987). We did not collect calves from the Delta herd as we did from some other caribou herds, but in all the spring radiocollaring and handling efforts we did not see warble fly infestations that rivaled those seen in the Nushagak herd in 1995, or in the single calf with over 400 warbles in the Nelchina herd, or in the Western Arctic herd in 1978 when 6 calves were found dead or near death with 1,500–2,000 warble larvae each (Davis and Valkenburg 1979, 1985a:14) (see section *Fieldwork Photos*:photograph 6).

Based on data during 1991–2007 (when calves were radiocollared at 4 months of age), it appeared that calf deaths were relatively evenly spaced throughout the year although there may have been some tendency for more deaths during October–January and in April (Table 16). Social disruption during the rut, the onset of cold weather, and increased mobility and food requirements of wolf packs are likely reasons to expect that calf mortality would be higher in early winter. In April, snow depth is typically at its maximum and wolves likely have a relatively easy time catching calves.

Yearlings 16–28 Months of Age

Mortality of yearlings was relatively low compared with calves but sample sizes were often low and many causes of death were undetermined (Tables 14 and 15). Part of the reason for the relatively large number of undetermined causes of death was that yearlings tended to wander more widely than adult females, especially during calving (Valkenburg et al. 1988) and mortalities were often not detected in a timely manner. More yearlings probably died during early winter than other times of the year, but small sample sizes limited our ability to detect seasonal patterns in timing of deaths.

Adults >28 Months of Age

As with calves and yearlings, wolf predation was the leading cause of death of adult female radiocollared caribou in the Delta herd (Tables 14 and 15). Grizzly bears likely caused 2 deaths of radiocollared caribou but because most predation by bears occurs during the snow-free period, we could have underestimated bear predation. During the “Perfect Storm” winter 1992–1993, 1 radiocollared female was killed by a coyote. However, when the collar was retrieved it had an ice ball about 20 cm in diameter packed onto the radio transmitter, so the caribou likely was encumbered.

One radiocollared caribou was killed in a snare set for wolves. Although a seemingly minor cause of caribou mortality, nontarget catch of moose and caribou by wolf trappers has occasionally been a controversial issue in Alaska. We therefore attempted to estimate the number of caribou that might be killed in the Delta herd annually by trappers. Estimating unintentional catches is difficult because it is likely that many would not be reported. However, during the 1993–1994 and 1994–1995 wolf control program that was designed to take wolves by trapping and snaring, we were able to document the numbers on nontarget species that were taken and the number of snares and traps set. In 1993–1994 there were 1,050 snares and 24 traps set in 82 locations from 1 October to 30 April, and 82 wolves were snared and 3 were trapped (ADF&G, Fairbanks files). Other nontarget big game animals caught included 29 moose, 8 caribou, 2 grizzly bears and 2 wolverines, of which 17 moose, 5 caribou, and 2 grizzly bears were released alive (some unknown number of these could have died after release). The following year (1 October to about 1 December), 685 snares and no traps were set in 36 locations and 27 wolves were taken. Nontarget catches included 6 moose, 7 caribou, and 1 wolverine, of which 5 moose and 2 caribou were released alive. In this program, 1 caribou was captured for every 100–130 snares that were set. The number of trappers and trapping effort varies each year in the range of the Delta herd and there is no direct way to estimate numbers of snares set. However it is likely that the trapping-based wolf control program administered by ADF&G during 1993–1995 represented a maximum effort within the caribou range in GMU 20A, and it is not likely not to be duplicated by all other trappers combined. We therefore estimate that the number of caribou captured inadvertently by trappers would not be a significant cause of mortality for the Delta herd. Non-target catch and mortality of caribou from wolf snares could be locally high in Interior Alaska if trappers happen to have a large number of snares out in areas that are heavily used by wintering caribou. From a practical standpoint, trappers are likely to discontinue snaring when caribou are abundant both to avoid catching caribou and because wolf snaring becomes less effective when caribou disrupt wolf snares.

Causes and Timing of Mortality of Radiocollared Males

We had limited data on type and timing of adult male mortality because there were relatively few radiocollared male caribou and males experienced many more collar failures, shed collars (6 out of 20), and other problems. We saw no major differences between causes of death of males than females, except that legal hunting was important in males (most legal hunting was for males only). Over a 4-year period, 7 of 20 (35%) radiocollared males were shot by hunters. Radiocollaring males was more difficult and expensive than radiocollaring females because we had to design special collars that could expand as male necks increased in size during the rut.

These designs were moderately successful but still resulted in many more shed collars and missing collars.

Survival Rates of Radiocollared Female Caribou

Quality of the modeled estimates for 4– to 16-month-old calf survival was severely constrained by lack of data for overwinter survival during 1979–1991 (calves were captured at 10-months of age), by low sample sizes (below 10) in some years, and by missing data in years no calves were collared (Fig. 68; Tables 14 and 15). However, there was evidence that calf survival was generally lower than survival of yearlings (16–28 months) and adults (>28 months), and that calf survival was particularly low in 1992–1993 when the estimate for calf survival was below 0.5 ("Perfect Storm" year) (Figs. 68 and 69). Quality of modeled survival estimates for yearlings also suffered from low sample sizes, but survival estimates for yearlings were high and confidence intervals consistently overlapped those of adults, except in the early 1990s and in 2000 (Figs. 68 and 69; Table 17). Yearlings can be considered as recruited into the adult population at 16 months of age and perhaps earlier in normal years.

Disregarding the effects of age on survival, modeled survival estimates for adults (>28 months of age) were high (~88%) and stable throughout the period of the study (Fig. 68; Table 17). Most of the variation in annual survival rates was caused by deaths of older aged females when deep snow winters occurred.

The apparent decline in survival with age (Fig. 69) and the lack of evidence for a year effect on survival once age is controlled for (despite changes in weather) has major implications for the dynamics of the Delta herd and other caribou herds. The major decline of the Delta herd that occurred after 1989 with the onset of deep snow winters was exacerbated by the previous years of high recruitment (1976–1983) because there were many older females in the herd. The implication is that the timing and magnitude of population growth for caribou is heavily dependent on the age structure of adult females, and that populations are subject to population "inertia." For example, herds with a young age structure from recent periods of high recruitment are likely to continue increasing, even in the face of adverse conditions. Conversely, those with a preponderance of old-aged females because of recent periods of chronically low recruitment are apt to decline rapidly, especially when weather deteriorates. Recent examples of herd declines because of an old age structure include the Mulchatna herd and the Unimak herd (Riley 2011b, Woolington 2011). Population "inertia" from age structure could be one mechanism that contributes to an eruptive or a cyclic pattern of population growth (c.f. Koons et al. 2007).

Modeling Effects of Covariates on Survival of Radiocollared Delta Caribou Herd Females

Calves

Of the 3 top models that had strong support (Table 18), *initial.weight* and *Denali.snow* were the most likely to influence calf survival during the period modeled (nominal years 1992–2007). In addition, we found that the effects of *initial.weight* on calf survival decreased with increasing snow depth. When snow was deepest, calves were more likely to die regardless of how heavy they were at the start of winter. These findings make intuitive sense in view of the abundant literature showing that heavy calves have higher survival than light calves and that all calves are prone to higher survival when snow is not deep. Because none of the regression models fit the data very well and there was a great deal of unexplained variation, there were obviously factors we did not measure that had a strong influence on calf survival. Inadequate sample size during some years probably influenced quality of data for *initial.weight*, and survival estimates were likely part of the problem. There were probably other factors as well, such as distribution of wolves in relation to caribou, specific snow conditions in wintering areas that occur at a finer scale than we can measure, and weather variables during the second summer of a calf's life that were unknown or difficult to measure. There was some indication that *summer.rain.yr1* positively influenced calf survival and it was retained as a variable in 4 of the 10 top models and 2 out of 3 models with ΔAIC weight <2 (Table 18). Many environmental covariates are autocorrelated (Figs. 4 and 75) but some of the correlations make intuitive sense and may help explain associations of covariates with survival. For example, *aug.min.temp* is negatively correlated with calf weights. August is a critical time for weight gain (Boertje 1981) because there is a variety and abundance of food, but caribou, especially calves, can be harassed by warbles if temperatures are high.

Yearlings

As in the calf models, *initial.weight* was included in all top models and it appears that weight of calves at 4 months of age continues to influence survival of female caribou through at least their second winter and possibly their third summer of life (Table 19). The fact that calves can achieve high 4-month-old weights with good summer growing conditions during their first 2 summers (Dale et al. 2008) adds additional weight to the argument that summer nutrition is an important component of subsequent survival of young caribou and is consistent with the findings of Cook et al. (2004) for elk.

The effects of snowfall on survival of yearlings may not be as pronounced as the effects of snowfall on calf survival. Unlike the calf survival models, *Denali.snow* was seldom included in the yearling survival models, but none of the models fit very well and they explained only 10–20% of the relatively small variation in annual yearling survival. However, as with calves, sample sizes of yearlings were low.

Adults

Other than age (which was included as a fixed effect), variables that appeared in the top 22 models (with ΔAIC weight <2) and likely affected survival were *n.caribou* and *wolf.index* (Table 20). Another covariate that appeared frequently in the set of top models was *cohort.mean.wt3* (spring cohort weight), although these covariates produced a negligible improvement in the generally very poor model fit. The take home message is that adult female caribou survive quite well until they get old and environmental conditions can vary greatly without affecting them much until they are older. Although wolf abundance may have some influence on survival of adult caribou, prime-aged females (ages 2–10) are relatively invulnerable. These data also support many previous findings about wolf predation on moose (c.f. Mech 1966, Peterson 1977, Fuller and Keith 1980, Ballard et al. 1987, Gasaway et al. 1992) and some other findings for wolf predation on caribou (Parker and Luttich 1986, Mech et al. 1998).

NATALITY OF RADIOCOLLARED FEMALES IN THE DELTA CARIBOU HERD

Effects of Age and Year on Natality Rates

Lack of reproduction in radiocollared Delta herd females at 12 months of age was not surprising because we are not aware of any observations that free-ranging caribou in North America have produced their first calves as yearlings, although some well-nourished reindeer have been reported to do so (Palmer 1934, Nowosad 1975). In Alaska caribou, reproduction at 2 years of age has been reported in the Adak, Delta, Denali, Fortymile, Nelchina, and Nushagak herds (Skoog 1968, Davis and Valkenburg 1985b, Hinkes and Van Daele 1996, Adams and Dale 1998b, Boertje et al. 2012). Mean rate of population growth for the transplanted Kenai Mountains herd during 1965–1975 ($\lambda = 1.37$) also indicates that most 2-year-old females were producing calves and that the rate of growth was not only an artifact of the skewed sex ratio of the initial transplant (Spraker 1995). Although parturition in 2-year-old females is not common in many Alaska caribou herds, it certainly is an indicator that caribou are on a high plane of nutrition. In Interior herds, once weights of cohorts of female calves approached 60 kg in fall or spring, we expected to begin seeing 2-year-old females with calves. In Southwest Alaska, although data were insufficient to make a strong comparison with Interior herds, it appears that 2-year-old females will calve at lower 4- and 10-month-old calf weights (probably around 55 kg) than in Interior herds (Hinkes and Van Daele 1996) (Figs. 39 and 41).

Most caribou females in North America produce their first calf when they are 3-years old and the Delta herd was no exception (Figs. 71 and 72; Tables 21 and 22) (Dauphiné 1976, Bergerud 1978, Adams and Dale 1998b, Boertje et al. 2012). The 3-year-old age class has also been shown to have the most variable parturition rate of any age class and the reproductive rate of a 3-year-old provides a good relative index to nutrition (Adams and Dale 1998b, Boertje et al. 2012). Although 2- and 3-year olds are often the largest age classes in the population and their more variable reproduction contributes to the variation in natality rate, the total contribution of natality in these age classes to recruitment may be smaller than expected in many years. Females in these age classes are inexperienced mothers and survival of their calves may not be as high as the survival of calves of older females (Ozoga and Verme 1986, Mech and McRoberts 1990). After age 3, natality rate of female caribou in Interior herds was relatively high and stable and usually remains above 70% (Figs. 71 and 72) (Adams and Dale 1998b, Boertje et al. 2012).

Although there was some variability in natality rate of Delta herd caribou from year to year, driven primarily by the 3-year-old age class, and to some extent by the 4-year-old age class, the odd year of 1993 (following the “Perfect Storm”) in both the Delta and Denali herds indicates there can occasionally be years when natality is substantially lower than average (Fig. 71; Table 21) (Adams and Dale 1998b). The 1973 cohort in the Western Arctic herd was also unexpectedly weak and may have contributed in a major way to the caribou decline in the early 1970s (Doerr 1979, Davis and Valkenburg 1985a). Bergerud (1978) reviewed reproductive rates of caribou from many herds in North America and concluded that natality is relatively constant, except perhaps on the Arctic islands, and that variable natality rates have a relatively small effect on recruitment. Our finding supports that conclusion, with the caveat that reduced natality in 3-year olds can have a noticeable (although small) affect on fall calf:cow ratios in some years and in herds with chronically poor nutrition. The effects of variable natality rates are likely much greater in the large Arctic herds and in some herds in Southwest Alaska. As Adams and Dale

(1998b) have pointed out previously, the effects of nutrition on natality are reduced where predation on neonates is high, partly because fewer females lactate over the summer and nonlactating females are in better condition during the rut as a result. Also, the effect of variable natality on recruitment is often obscured by predation because so many calves die before they are recruited (Adams and Dale 1998b, Mech et al. 1998, Valkenburg et al. 2004). In the Arctic herds in Alaska, where most adult females lactate each year, natality in adult caribou appears to be lower and more variable than in the Interior herds (Cameron et al. 1993).

Effects of Previous Pregnancy on Natality of Radiocollared Females

Biologists have debated whether early parturition (i.e., in 2-year olds) could lead to reproductive failure the following year or to reproductive pauses in subsequent years, and whether reproductive pauses are a part of the reproductive ecology of caribou (Cameron 1994, Cameron and Ver Hoef 1994, Adams and Dale 1998b). In the Delta herd, females that produced calves at 2 year of age also produced calves at 3 years of age (17 of 18 times). Also, although reproductive pauses were estimated to occur in 11% of cases from 1982 to 1990 in the Delta herd (Davis et al. 1991), over the entire dataset from 1982 to 2007 reproduction in any given year had no effect on the chance that a female would produce a calf the following year (Figs. 6 and 74; Table 22). Reproductive pauses are likely to be least common in Interior herds where nutrition is generally good and/or where predation on neonates is high, and more common in very large herds, especially the Arctic herds where nutrition will likely be limiting at higher population sizes and where predation on neonates is low (Reimers 1983, Cameron 1994, Cameron and Ver Hoef 1994, Adams and Dale 1998b).

Effects of Initial Weight on Modeled Natality Rates

In contrast to the survival models (see section *Discussion* on *Modeling Effects of Covariates on Survival of Radiocollared Delta Caribou Herd Females*), where *initial.weight* continued to have an effect on survival of adults beyond age 2, *initial.weight* had no discernable effect on natality rate of radiocollared female caribou in the Delta herd. However, the change in initial capture date (from spring to fall) before 1991, prevented us from using data from the earlier time period when calf weights were consistently highest. We suggest that *initial.weight* has less effect on natality in the Delta herd than it has on survival.

Effects of Environmental Covariates on Modeled Natality Rates

Logistic regression models indicated that age, previous pregnancy, several environmental covariates, and weight of cohorts at 10 months of age explained about half of the annual variation in natality rates of radiocollared Delta herd caribou (Table 23). These results suggest some environmental influence on the small variations in annual natality rates. The top model (the only one with ΔAIC weight<2) included *snow.yr* and *summer.rain* as explanatory variables. All of the models in the top model set did a similar job in explaining variation in natality indicating that *snow.yr, summer.rain, summer.mean.temp, and cohort10mnth* are roughly equivalent. An important consideration however, was that the unusually low natality year and deep snow winter of 1993 appeared to be contributing a great deal of significance to the correlation with snow. When that year was removed, *cohort10mnth* was the only variable that appeared in the top model, and the top model was stronger (Table 24). Adams and Dale (1998b:1186) viewed late winter snow as an index of nutrition in caribou because they found that snow explained about 30% of the variation in autumn weight of cows >1-year old. They also found significant correlations between snow and probability of parturition (i.e., natality) in 6 age classes of caribou. Their regressions (Adams and Dale 1998b:1189) also suggest that the odd low natality year of 1993 contributed much of the significance to the regressions (except in the 2-year-old age class where many years contributed). Although there seems to be significant environmental influence on annual natality rates in caribou and much of the influence is reflected in weights of calves at 10 months age, we are less sure about exactly which environmental influences are most important, especially because many environmental covariates are correlated (Figs. 4 and 75). Also, winter 1992 (i.e., 1991–1992) was only 1 of 5 deep snow winters that began in 1989 (Table 3) and that summer (1992) was only one of several short summers between 1977 and 2007 (Appendix D). For these reasons, we believe it is more likely the significant weather event of September 1992 (i.e., “the perfect storm”) had more influence on the natality rate of the Delta and Denali herds in 1993 than snow depth or the length of the summer in 1992. There were no indices or measurements that adequately reflected effects of the storm. This view differs somewhat from the view of Adams and Dale (1998b) who believed it was the short summer of 1992 that resulted in the reduced natality in 1993 in the Denali herd.

Although Fortymile females also experienced their lowest natality in 1993, the Fortymile herd was not affected as much as the Denali and Delta herds (Boertje et al. 2012), suggesting a relatively local influence where the storm was worst, rather than a regional influence from widespread deep snow or a short summer growing season. In the Yukon, where all caribou herds were strongly predator limited, Hegel et al. (2010) did find a regional influence of deep snow associated with the Pacific Decadal Oscillation but found more support for the effects of snow on recruitment (i.e., through mortality of calves) than on natality.

The fact that weight of calves explains additional variation beyond that explained by the environmental variables in regression models may mean that there were density-dependent effects on natality rate in the Delta herd as well as environmental effects, but it is also possible that weight of calves just integrates environmental influences on natality better than direct measures of environmental variable. Some support for the idea of density-dependent effects on natality also comes from the finding that calf weights in the Delta herd were lower during periods when the herd was high and also generally lower than in the neighboring Denali herd (Fig. 40). Also see section below, *Cohort Mean Weight Models*.

MODELING THE EFFECTS OF COVARIATES ON COHORT MEAN WEIGHT AND CALF:COW RATIO IN THE DELTA CARIBOU HERD

Cohort Mean Weight Models

Associations between environmental covariates and 10-month cohort mean weight were rather weak but showed better separation and fit than survival models (Fig. 25). *Denali.snow* was included in some top models (ΔAICc <2) but not all, whereas all models “some” support (ΔAICc <7) included *aug.min.temp* and most included *summer.mean.temp*. The weak associations with most covariates and seemingly contradictory associations with some (e.g., the negative association with previous 10-month cohort weight), made it difficult to interpret which environmental variables are most likely to affect 10-month cohort weights.

Models using fall calf weights (4-month cohort weight) as the response variable showed better separation among models and more evidence for a top model that included *cohort.mean.wt1, summer.mean.temp,* and *length.green* (Fig. 26). However, the top model carried relatively little weight. Similar to previous models using 10-month weight as the response variable, the association with the previous cohort weight (*cohort.mean.wt1*) and 4-month-old calf weight was negative, indicating that low cohort weight of the previous cohort of calves would result in higher weights of the following cohort. We can think of no biological mechanism for this association and suggest that the association is likely spurious.

A likely problem with associating weather variables and any response variable relating to caribou in the Delta herd is that the weather covariates may not be good representations of the actual conditions experienced by caribou. Caribou range all over the mountains in summer in response to insects (which are not measured), changing plant phenology (not measured), harassment by predators (not measured), wind (not measured), etc. Most of the weather variables we included in our models were measured only at Denali Park (at the dog kennels at the park headquarters). Therefore, *Denali.snow,* which is likely one of the best weather variables, is not necessarily representative of actual snow conditions experienced by wintering Delta or Denali caribou. We tried to improve the *Denali.snow* index for the Delta herd by establishing 4 other snow stakes within the winter ranges of the Delta herd caribou. The snow index developed from these snow stakes (*NRCS.snow*) was only available from 1994 on (essentially after the deep snow winters were over). Further, *NRCS.snow* did not contain any additional value in models over *Denali.snow*. From 1994 to 2008 the linear correlation between *Denali.snow* and *NRCS.snow* was not as good as might be expected ($R^2 = 0.59$), with about 40% of the variation unexplained. Local snowfall patterns within the central Alaska Range are the likely cause of most of this unexplained variation and these local patterns are likely of importance to caribou.

Calf:Cow Ratio Models

Although we did identify a top model that contained 37% of the AIC weight, goodness-of-fit measures (R^2) were low in all models (Table 27). Covariates included in top models were *cohort.mean.SPR, Denali.snow, n.caribou,* and *part*. Included in other models with less support were indicators of season length (*length.green, end.green,* and *greenup*). The modeling exercise suggests that natality rate (*part*) has an effect on calf:100 cow ratio that is independent of calf survival, and that calf survival could be associated to a degree by previous winter snow and various summer weather variables. Also, there is a suggestion that weight of 10-month-old calves (i.e., the previous cohort) contains information that is independent of snow. Problems with measuring environmental variables as they relate to caribou were discussed in the section above, *Cohort Mean Weight Models*.

Although the potential explanatory value of weights of 10-month-old calves on fall calf:cow ratio was supported by a relatively strong univariate relationship as well as the regression models in the Delta herd, we did not find support for the univariate relationship in the Denali herd (Fig. 37). We found no support for the relationship in other herds as well.

MOVEMENTS AND DISTRIBUTION OF THE DELTA CARIBOU HERD, 1978–2007

Calving

Changes in calving distribution of the Delta herd that began in 1988 were sudden and unexpected, especially when most radiocollared caribou crossed the crest of the Alaska Range and traveled in long lines through the Louis Creek-Wells Creek pass into a new and completely unfamiliar area (to most caribou) in 1990 (Fig. 78). Before 1990, we were not aware of any radiocollared Delta herd caribou that had crossed the Alaska Range. A similar abrupt change in calving areas had occurred in the Fortymile herd in 1978 (when the herd suddenly abandoned its main calving area in Clums Fork of Birch Creek and began calving in the upper Salcha drainage). However, this eastward movement was to familiar areas that the Fortymile herd had used previously as summer and winter range (Valkenburg and Davis 1986). We did not observe any weather conditions, including late or early snowmelt, or unusually warm or cold temperatures that could have explained the sudden shift in calving ranges of the Delta herd.

The shift in Delta herd calving areas is even more difficult to understand because caribou generally favored snow-free areas as calving sites, but the new calving areas in Wells Creek were higher in elevation; generally had deeper, more continuous snow cover; and snowmelt generally occurred 7–10 days later than on the Little Delta-Delta Creek calving areas (P. Valkenburg, personal observations). On the Little Delta-Delta Creek calving areas, we had observed the first *Eriophorum* flowers emerging as early as 20 April (often under thin snow cover). On the Wells Creek calving areas we did not record emergence of *Eriophorum* flowers before 1 May.

Some members of the public and even some biologists have suggested that increased use of the Delta Creek bombing ranges during the 1980s could have caused the caribou to abandon the old Little Delta-Delta Creek calving areas. It was difficult to objectively evaluate whether increased practice bombing by the U.S. Air Force during the military build-up of the 1980s could have resulted in the 80–90% reduction in use of the Little Delta-Delta Creek calving areas. However, we believe it was unlikely that increased bombing or jet overflights caused the shift. Only in the few years, when snowmelt was particularly late, did many Delta caribou actually use the lower elevation impact area for calving. In these years, the caribou we were able to observe seemed oblivious to low-flying jets. In most years, even during active bombing periods (always involving dummy bombs), most caribou were in areas removed from the impact area but in areas where jet noise was audible and sometimes loud but jets were generally over 500 feet above ground level. Several studies have evaluated the impacts of overflights on calving Delta caribou females. Davis et al. (1985b) and Valkenburg and Davis (1985) found that Delta caribou were insensitive to aircraft disturbance compared with Western Arctic and Teshekpuk caribou. However, Murphy et al. (1993) and Maier et al. (1998) concluded that although initial responses to jet overflights in the Delta herd were mild, overflights did change caribou behavior and caused more movement. In a later study in the adjacent Fortymile caribou herd, even when F-16 and A-10 jets were deliberately vectored in to fly low (<500 ft above ground level) over calving groups of caribou, in a majority of cases, reaction of caribou was mild (Magoun et al. 2003, Lawler et al. 2005). In many cases, very loud, low flying jets with afterburners engaged elicited “no visible response” from caribou cows (Magoun et al. 2003, Lawler et al. 2005). If anything, our experience with Delta caribou indicated that they were less reactive to aircraft than Fortymile caribou, or caribou from other herds (Valkenburg and Davis 1985; P. Valkenburg, personal observations).

The major shift in Delta herd calving areas occurred coincident with peak herd numbers in 1989 (Fig. 7), perhaps suggesting that increasing grazing pressure and declining body condition (as indicated by 4- and 10-month-old calf weight and size) caused the range shift. However, in other rapidly increasing caribou herds (e.g., Central Arctic, Mulchatna, and Western Arctic) calving areas increased in size, but continued to overlap traditional calving areas (Cameron et al. 1986, Hinkes et al. 2005, Dau 2009, Lenart 2009). Use of the Little Delta-Delta Creek calving area by a small number of radiocollared Delta herd females continued after the major calving range shift but by many fewer caribou, especially during 1994–1997 when the area was almost totally abandoned (Fig. 78). During the last 4 years of the study (2004–2007), the Delta herd caribou continued to use the Little Delta-Delta Creek calving area in slightly increasing numbers and calving areas seemed to be dividing into 2 nodes, 1 in western portion of the herd's range and 1 in historically used Little Delta-Delta Creek calving area (Fig. 78).

Summer Range

We did not relocate radiocollared Delta herd caribou frequently enough to gain a detailed understanding of summer range use. However, summer range changes appeared to be relatively minor compared with changes in calving, rutting, and winter ranges (Fig. 79). After the shift in the calving area after 1988, most of the herd continued to return to GMU 20A after calving. However, a few individuals used mountainous areas between the Yanert and Wells Creek drainages and eventually all the way east to include Clearwater Mountains between the East Fork Susitna and Clearwater Creek.

Rutting Areas

The most noteworthy change in rutting areas of the Delta herd was that after 2001 many caribou used areas in the Wells Creek, upper Nenana, and Susitna drainages (Fig. 80). These areas were also being used by some radiocollared Nelchina caribou, so it is likely that genetic exchange was occurring. Periodic overlap of rutting areas of adjacent herds or movements of bulls to rutting ranges of adjacent herds are likely mechanisms explaining the close genetic relationship of most Interior caribou herds (Roffler et al. 2012). Whether these range overlaps resulted in exchange of bulls is unknown because so few bulls were radiocollared.

Winter Range

We believe Delta herd caribou changed their winter ranges at least partially because winter nutrition was deteriorating (Fig. 81) and that caribou were searching for better feeding areas (Fleischman 1990; Valkenburg et al. 1991, 2003b). During the late 1980s as the population was reaching its peak size, Fleischman (1990) found that fecal pellet samples collected in the foothills of GMU 20A had decreasing lichen content and increasing moss and shrub content on a gradient from west to east. When caribou (most mature bulls) first began using the western Tanana Flats, lichen content of fecal pellets was high (about 70%) and moss was low (7%). Once the herd declined rapidly after 1989, caribou stopped using the western Tanana Flats but we were not sure if lichens were depleted there or if caribou preferred to use more open terrain in the foothills where they may have been less vulnerable to wolf predation.

Movements and Distribution of Caribou During "The Perfect Storm"

A reasonable hypothesis for the cause of the unusual movements of 1992–1993 (Fig. 82) is that a combination of global cooling of temperatures from the eruption of Mount Pinatubo on 15 June 1991 and local weather conditions caused an unusual storm that swept down on the Alaska Range from the northwest around 10 September 1992. The result was a very heavy early snowfall and continued below normal temperatures during September and October (Self et al. 1996, Cole et al. 1999, Adams et al. 2005). The storm appeared to have had a major influence of short-term caribou movements and distribution in several Interior caribou herds, primarily Delta, Denali, Macomb, and Fortymile.

One of the benefits of conducting the long-term study of the Delta herd was that we were in a good position to observe and document the movements of caribou in the Delta herd and surrounding herds during an unusual stochastic event (i.e., "the perfect storm") (Fig. 82). We believe these kinds of movements have major implications for understanding unusual historic movements of caribou (c.f. Skoog 1968) and also for helping to understand possible mechanisms for genetic interchange between adjacent herds (Cronin et al. 1995, 2003, 2005, 2006; Zittlau et al. 2000; Colson et al. 2014; Mager et al. 2014). Events like the "perfect storm" are rare enough that individual biologists may never have an opportunity to observe them during the course of a 20- to 30-year career. For example, movements of the Delta herd caribou, such as those that occurred in the Delta and Denali herds during the "perfect storm" of 1992, have probably not occurred since the early 1940s (W. Waugaman, hunting guide, personal communication), and have never been previously reported by biologists. Evidence of other extreme movements was reported by Skoog (1968). He found records of movements of caribou north through Nenana toward the Wiseman area in the 1920s, and also south through Isabel Pass in the fall in the 1920s. The extent of these movements was never clear and it was not possible to people to know the herd of origin in most cases.

We found no evidence that a significant number of caribou either left the Delta, Denali, or other herd or were added to them, but there may have been increased low-level dispersal of individuals. The storm probably had a major effect on the Delta herd in other ways (see section *Nutrition and Weather as a Cause of Caribou Population Growth and Decline in Alaska*).

Range Expansion of the Delta Herd

Range expansion occurred frequently in the Delta herd, even during periods when population size was not increasing. The first major range expansion we observed was an increase in the herd's winter range and a change in location to the west and north during the 1980s while the herd grew rapidly (Fig. 81). Major range expansion also occurred during the early 1990s when the Delta herd shifted the major part of its calving area to the Wells Creek drainage south of the crest of the Alaska Range, outside its previously known range. This expansion of the calving range continued through the 1990s and early 2000s (while the Delta herd was declining) until the herd calved in a large area bounded on the south by the Denali Highway and on the east by the crest of the Clearwater Mountains (upper Valdez Creek). Range expansion eastward across Delta

Creek also occurred in fall and winter in the late 1990s (also while the Delta herd was declining) to the area around Donnelly Dome and Jarvis Creek. As far as we could tell (from radio collars and herd censuses), essentially all of the caribou that participated in the range expansions returned to the Delta herd in summer and the new areas became regularly used seasonal ranges for the Delta herd in future years, except the winter range on the western Tanana Flats of GMU 20A.

Changes in seasonal ranges of the Delta herd are not surprising in view of the many other documented changes in range use of caribou herds in Canada and Alaska (c.f. Harper 1955, Kelsall 1968, Skoog 1968, Parker 1972, Adams and Connery 1983, Valkenburg et al. 1983b, Valkenburg and Davis 1986, Healy 2001, Hinkes et al. 2005, Harper 2009, Boertje et al. 2012). Expansions or shifts in calving ranges have also been well documented, especially the larger herds in Alaska (e.g., Fortymile, Mulchatna, Western Arctic, Central Arctic, Northern Alaska Peninsula, Denali) but calving ranges have remained relatively stable in many other herds, especially the smaller herds (e.g., Galena Mountain, Macomb, Nelchina, Ray Mountains, Wolf Mountain) (Skoog 1956, Valkenburg and Davis 1986, Hinkes et al. 2005, Harper 2009, Boertje et al. 2012). What is unusual about range changes in the Delta herd is that the calving shifted to an area completely outside the herd’s formerly used range. We are not aware of another case where a calving area shifted to an area not formerly used during any other season of the year.

Unoccupied Caribou Habitat in Interior Alaska

If caribou are excellent dispersers, one would think that all suitable caribou habitat in Alaska would be occupied. Almost all of it is occupied, even if not by recognized herds. For example, it is possible to find a few individual caribou in any part of the Brooks Range at any time of year (P. Valkenburg, personal observations). There are also small groups throughout the Kuskokwim Mountains from Wien Lake to just north of Sleetmute, but only 2 are large enough to be named (Beaver Mountains and Sunshine Mountains herds). There are, however, a few areas where caribou are absent despite apparently excellent range. One of those areas is the Sawtooth Mountains south of the village of Rampart. Local residents used to see caribou there until the 1940s, but presently there are no caribou trails evident, and caribou have not been reported in the area since the 1940s.

GENETIC INTERCHANGE, CARIBOU HERDS AS POPULATIONS OR METAPOPULATIONS, AND “CARIBOU REGIONS”

Genetic Relationships of Caribou Herds

Although genetic research on caribou herds has been ongoing for many years (c.f. Braend 1964, Røed and Whitten 1986), it is only recently that genetic relationships between herds are becoming clearer (Zittlau et al. 2000; Cronin et al. 2003, 2005, 2006; Zittlau 2004; Colson et al. 2014; Mager et al. 2014). The most recent genetic work seems to confirm that many Interior caribou herds are closely related, although there appears to be little recent genetic exchange between some small herds and their neighbors. There are some surprising conclusions that are interesting but likely need further work for clarification. For example, caribou herds south of the Kvichak River (i.e., Alaska Peninsula-Unimak herds) are differentiated from each other and from caribou herds to the north. Mixing between Northern Alaska Peninsula and Mulchatna caribou has been documented on winter range between King Salmon and Iliamna Lake but there apparently have been limited opportunities for gene flow (Sellers 2001, Mager et al. 2014).

Where gene flow does occur between adjacent caribou herds, there are several likely mechanisms involved. The cases of immigration and emigration (described below in section *Caribou Herds as Populations or Metapopulations*) provide one potential explanation. The largely unknown and undocumented, but possible, movements of bulls between herds is perhaps another. A third, and perhaps more significant, is overlap of animals from adjacent herds during the rut (Roffler et al. 2012) even if the overlap includes mostly peripheral groups of young bulls because breeding success of young bulls is likely to be substantial (Lent 1965, Clutton-Brock et al. 1982, Butler 1986, Røed et al. 2005). In the Delta herd we documented overlap between the Delta and the Nelchina herds during the rut in the early 2000s (Seaton 2009). In addition, during the “perfect storm” movements of September–October 1992, caribou from the Delta, Denali, and White Mountains herds mixed extensively during the rut and interbreeding could easily have occurred (see section *Movements and Distribution of Caribou During “The Perfect Storm”*) (Fig. 83; Adams et al. 2005). More recently, mixing of Teshekpuk, Central Arctic, and in some years Western Arctic has been documented to occur to some extent during the rut (Harper 2009, 2011).

Whether there are morphological differences that result from genetic differentiation in Alaskan caribou is still an open question. Unfortunately there are very few weights and measurements of adult caribou from the Alaska Peninsula and sample sizes reported by Skoog (1968:26) are too small for comparison with weights and measurements of adult caribou from other areas of Alaska. However, based on the comparison of adult and calf weights of Western Arctic caribou (Skoog 1968:25) and the relatively small 4- and 10-month-old calves that we found in the Western Arctic herd, it appears that much of the size difference in calves is maintained in adults as well. Adult female caribou >3-years old in the Western Arctic herd average 75 kg versus 104.5 kg for adult females >3-years old in the Nelchina herd (Skoog 1968).

Trophy potential might be another morphological metric that could confirm whether observed genetic differentiation in Interior and Alaska Peninsula caribou is accompanied by morphological differentiation. Some Interior herds (e.g., Nelchina and Delta) have a very high trophy potential while others have a low potential (e.g., Fortymile) suggesting that, at least in Interior caribou, antler size differences are nutritionally rather than genetically based. The unusually high trophy potential of Alaska Peninsula caribou despite their relatively small body size may indicate morphological and/or physiological differences with Interior caribou.

In the Western Arctic herd, bull caribou have comparatively small antlers as well, but the possibility exists that mixing with reindeer may also be a factor in that herd. Early genetic work (Røed and Whitten 1986) appeared to show no genetic mixing of caribou and reindeer in Alaska, even in the Western Arctic herd where hundreds of thousands of semi-domestic reindeer were known to have wandered off with caribou (Lantis 1950, Skoog 1968, Stern et al. 1980, Adams and Connery 1983, Burch 2012). However, more recent work has confirmed that female mediated gene flow from reindeer to caribou has occurred in the Western Arctic herd (Cronin et al. 2006). As mentioned elsewhere in this document, introgression of reindeer genes into Alaska caribou herds remains a possibility for several herds.

Caribou Herds as Populations or Metapopulations

The question of what constitutes a "population" of caribou has been the subject of considerable debate among biologists for decades (c.f. Skoog 1968; Hemming 1971; Haber 1977; Bergerud 1978:89; Carruthers 1985; Davis et al. 1986; Hinkes et al. 2005). The question was identified as 1 of the 2 major areas of disagreement among biologists during the 1970s when long-term caribou research was planned, and addressing the question was 1 of the 4 main goals of the recommended long-term research program (see section *Introduction*). Over the approximately 30-year period covered in this technical bulletin the debate over "caribou populations" changed and evolved as new information accrued, but the question is by no means completely settled. Semantic differences, and time frame, still confuse the debate to some degree. For example, Skoog (1968:200–201) considered all caribou west of the McKenzie River to be from the same "population" while the recognized herds in Alaska, such as Nelchina and Western Arctic, were "parts" of the population or "subpopulations." Skoog's (1968) reference to "population" clearly involves a geological or long-term biological (millennial) time frame, rather than the short-term time frame that managers must use to prevent overharvests from occurring. Indeed, confusion over whether caribou move "en masse" between regions or "herds" contributed to the overharvests that occurred in Alaska in the early 1970s because caribou were considered difficult to manage because of their unpredictable movements (Valkenburg 2001). Over the last 40+ years since Skoog (1968:201) and Hemming (1971:3) discussed their ideas of "population" and described poorly documented mass movements during population peaks from one herd to another, we have found no evidence that these kinds of permanent mass interchanges between herd ranges (i.e., calving areas) or regions have occurred. Assimilation of the Kilbuck herd by the much larger, surrounding Mulchatna herd during the 1990s (Hinkes et al. 2005), the Delta and Yanert herd interactions, and the disappearance of the "upper Susitna" herd certainly indicates that fidelity of females to calving areas can break down but we view these cases as being different from a mass emigration to an area outside a herd's regularly used range. Recent movements and extensive mixing of the Central Arctic, Teshekpuk, and Porcupine caribou herds, and of the Porcupine and Fortymile herds may provide evidence to the contrary (Harper 2013). During the last 30 years, there have been several major mixing events, similar to those described by Skoog (1968), that could potentially have resulted in mass movements, but permanent exchange or egress of detectable numbers of caribou was not documented. We discuss several of these cases in detail below:

Case 1

In late November 1981, 5,000–15,000 Porcupine caribou crossed the Yukon River downstream from Eagle and wintered in the Birch Creek and Charley River drainages (Kelleyhouse 1983). They became mixed with the Fortymile herd (estimated to be about 7,500 in 1981). There remained some segregation as most of the caribou that remained near Circle Hot Springs, the most western portion of the caribou distribution, were most likely Porcupine caribou. At that time there were only 4 radiocollared caribou in the Fortymile herd and only 1 radiocollared among the Porcupine caribou that crossed the Yukon. We (P. Valkenburg, R. D. Boertje, and K. R. Whitten, Wildlife Biologists, ADF&G, Fairbanks) worked out of Circle Hot Springs for several days in an attempt to put more collars on caribou before the 2 herds mixed. However, we were too late and we were not sure which herd the caribou we collared were from. In the spring, the one known Porcupine radio collar and all the recently collared caribou traveled north in a direct line, across the Yukon Flats, toward the coastal plain calving area of the Porcupine herd. The 4 known Fortymile radio collars remained behind and we did not detect a change in numbers of the Fortymile herd between the 1981 and the 1983 censuses that could not be explained by recruitment and mortality within the herd.

Case 2

Nelchina herd began expanding its range north across the Mentasta Mountains and frequently mixed with Mentasta herd and to some extent with the Fortymile, Macomb, and Chisana herd caribou beginning in the late 1980s (Lieb and Tobey 1990; Gardner 1993a,b; Tobey 1993). Although mixing on winter range with the Chisana herd occurred for just a few years in the late 1980s, mixing between Fortymile, Macomb, and Nelchina caribou has occurred to varying degrees since the late 1980s. No changes in size of the Chisana, Macomb, Nelchina, or Fortymile herds were documented that could not be explained by recruitment and mortality. Influence of the extensive mixing with Mentasta caribou is less clear, but the Mentasta herd was quite small to begin with and certainly has not greatly increased in size. The genetic relationship between the Mentasta and Nelchina caribou is very close and it is likely that male-mediated interbreeding occurs virtually every year (Roffler et al. 2012).

Case 3

During the mid-1990s, tens of thousands of Western Arctic herd caribou used the Indian River flats in the Koyukuk drainage, where they mixed with both the Galena Mountain and Wolf Mountain herds. No change in size of these small herds following that winter was noted. It is interesting to consider that there are major differences in body size of caribou in these herds. Caribou calves of the Galena Mountain and Wolf Mountain herds are among the largest in Alaska, and are about 50% larger than calves of Western Arctic caribou (Appendix C).

Case 4

During the "perfect storm" event (see section *Movements and Distribution of Caribou During "The Perfect Storm"* above), caribou from the Delta, Denali, and White Mountains herds mixed during the rut and remained extensively mixed during the winter (Fig. 82), but separated in spring and all adult radiocollared females returned to their respective calving areas.

Case 5

In November 1996, as the Mulchatna herd reached its peak population size (around 200,000), about 25,000 Mulchatna caribou moved north, well outside their previously used range, to the McGrath area (Woolington 1999). Some groups traveled as far northeast as the South Fork Kuskokwim River. These large numbers of Mulchatna caribou completely inundated the winter range of the Farewell-Big River herd but did not appear to reach the ranges of the Tonzona or Denali herds. Even though there were no active radiocollared caribou left in the Farewell-Big River herd (9 adult females were collared in the Farewell area on 26 April 1982), and the herd was not censused in 1997, there did not appear to be any gross change in winter distribution or wintering numbers of the herd in subsequent years. Thus, there was no indication that substantial numbers of Mulchatna caribou (or radio collars) remained with the Farewell-Big River herd. All radiocollared Mulchatna caribou appeared to have returned to calving ranges in GMU 17 and southern GMU 19. Although the Mulchatna herd continued to expand its winter range as the herd declined, the expansions were southeast to the King Salmon area and west into GMU 18 rather than north into the McGrath area (Woolington 2001, 2003). Some movements of small numbers of Mulchatna caribou continued into the McGrath area for a few years as the herd was declining, but these movements ceased by the early 2000s (Woolington 1999, 2001, 2003; Boudreau 2001). Despite the very large peak size of the Mulchatna herd in 1996, no extra-regional (*sensu* Skoog 1968, Hemming 1971) movements or exchanges of animals were documented.

Evidence that has accrued over the last 30+ years of radiotracking thousands of collared caribou, and the greatly increased monitoring of groups of uncollared caribou, continues to indicate that female caribou have a strong homing instinct and strong fidelity to traditional calving ranges. However, there is also increasing evidence that calving ranges can move and fidelity to calving areas can erode if enough mixing occurs with adjacent herds (Valkenburg and Davis 1986; Hinkes et al. 2005; this study, see section above, *Movements and Distribution of the Delta Caribou Herd, 1978–2007*). Nevertheless, the herd-based management model that ADF&G has been using for management purposes for many decades has been strongly supported by movement data. There may be times and cases where unusual herd movements or assimilation or amalgamation of adjacent herds requires adjustment in management and harvest planning, but those cases continue to be rare.

The term "metapopulation" has been used to describe subpopulations or "parts" of populations that are generally distinct, but where genetic exchange occurs and might even be required for subpopulation persistence (Levins 1969). A metapopulation was originally defined as a "population of populations" (Levins 1969), and many caribou herds may conform to that definition, especially those that are typically of small size and subject to risk of extinction through the stochastic factors described in the section above (see *Patterns and Causes of Population Change in Other Herds*). Whether a herd or herds, or a region functions as a metapopulation depends to a great degree on the time frame considered, herd size, and the mechanisms for genetic exchange. For example, the relative genetic isolation of Southwest herds from Interior herds and the Western Arctic herd documented over the last 30–35 years indicates that little exchange occurs (Mager et al. 2014), and we were unable to document any exchange of caribou between these regions over the last 30–35 years. The Southwest region may therefore comprise a metapopulation. The very low genetic differentiation and the documented cases of dispersal among the Fortymile, Macomb, Nelchina, and Mentasta herds indicate that genetic exchange is frequent and that caribou in the eastern Interior could be considered a metapopulation.

An important part of the "metapopulation" concept is the idea of genetic "sources and syncs" (Levins 1969). With caribou, small herds that arise from a very small number of founders (either naturally or through transplants) and are isolated for relatively long periods (perhaps decades or longer) can become sources of new genetic material through the process of mutation (i.e., genetic drift). When major herds increase and expand their ranges, the unique genetic signatures that have developed over time in the small isolated herds can be captured by the invading larger herd. Thus, the small herds could become sources and the larger herds become syncs for new alleles, even if (as it appears in most cases) the small caribou herds persist despite swamping by the larger herd. The Kenai herds and the Adak herd that arose from transplants are not likely to be swamped by any other caribou herds but are likely to become increasingly differentiated genetically. These herds will make interesting genetic laboratories that can help determine how fast genetic differentiation occurs in caribou.

DETERMINISTIC POPULATION MODEL OF THE DELTA CARIBOU HERD

Deterministic computer modeling of changes in population size in the Delta herd indicated that much greater variability in average annual mortality rates of females was occurring during 1989–1994 than we estimated from radiocollared caribou. For the deterministic population model to accurately track observed changes in population size and bull:cow ratios, recruitment (fall calf:cow ratio) inputs needed to be reduced and adult female survival rates needed to be greatly manipulated following the onset of bad winters in 1989 (Table 28, Fig. 83). Besides the greatly reduced calf survival observed during the late 1980s and early 1990s and the likely greatly reduced survival of older females during this period, a portion of the discrepancy between observed and modeled values likely came from the fact that age distribution of radiocollared females in the Delta caribou herd did not often mirror age distribution of females in the herd and estimates of herd size may have been better in some years than in others. Our decision not to change radio collars on adult females >10 years of age also contributed to the biased age distribution of the collared sample. In years when older females are relatively numerous and winter weather is bad, the average survival rate of all females can be expected to be lower. However, even if radio collars are evenly distributed across age classes, it is clear that very large numbers of radio collars are needed and follow-up radiotracking must be rigorous to obtain reasonable estimates of survival with acceptable confidence intervals.

The spreadsheet population model indicated that annual changes in bull:100 cows ratio could not be completely explained by harvest or reasonable adjustments to annual survival rates of males in the model, suggesting that either there was movement of bulls into the Delta herd, that sampling error during annual surveys was substantial, or that there was a high degree of compensatory mortality associated with harvest of bulls (Table 28). Particularly during periods of high harvest of bulls (i.e., 1983–1991), we were unable to force the model to track observed bull:100 cows (including the 3-year running averages) without increasing annual survival rates of males to 0.98 during 1984–1990 (i.e., natural mortality had to be reduced to nearly zero) (Table 28). We believe the most likely explanation for this is that hunters are generally selective with groups of caribou bulls in the fall, and will almost invariably shoot the largest (and likely the oldest) bulls in a group. The largest and oldest bulls are also likely to be most prone to natural mortality (particularly predation after the rut). We did not have sufficient numbers of bull caribou collared during the Delta herd study to characterize mortality of males, but we observed many dead or dying bulls during and after the rut in herds with high bull:cow ratios (principally Mulchatna during the mid-1990s and Western Arctic during the late 1970s and early 1980s) (see section *Fieldwork Photos*:photograph 7). From the early 1980s through about 2003 when the Delta herd was regularly hunted (or during periods of poor recruitment) and bull:cow ratios were usually below 45:100, we observed few wounded and no dead caribou bulls during and after the rut. It is possible there are other explanations beside compensatory mortality, including those mentioned above (e.g., sampling error or movements of bulls between herds). However, our findings that natural mortality of bulls was low during periods with heavy hunting pressure may help explain why it is possible to maintain hunting seasons for bulls even in very small herds without having bull:cow ratios decline to unacceptably low levels (e.g., Kenai Peninsula herds, Macomb herd) as long as calf survival is not unusually poor (i.e., below 20:100 cows in fall).

There are reasons to try to construct a more complicated spreadsheet population model with more age classes because during bad winters calf survival can be relatively poor through 16 months of age (i.e., through the first 2 summers and intervening winter of life). Also, once females reach 10 years of age, survival declines significantly, especially if deep snow winters prevail (as during 1989–1993). Separate age classes in the model for calves (4–16 months of age), adult females (16–124 months of age), and older females (>124 months of age) may be useful in a caribou population model, especially in cases where there are large numbers of older-aged females either because of periods of high recruitment in past years and good adult survival, or following long periods of low recruitment (e.g., Unimak, Southern Alaska Peninsula, Northern Alaska Peninsula, and Mulchatna herds during the early 2000s). However, for most herds, additional complexity in population models introduces additional untested assumptions and a need for additional inputs for which there may not be data of sufficient quality.

Despite its limitations, our simple deterministic spreadsheet model proved useful for tracking population performance, helping determine the likely quality of censuses, and calculating allowable annual harvests in the Delta caribou herd. Caribou managers used the model routinely in many other caribou herds, and with modifications, we also adapted it for the Delta bison herd. Despite obvious shortcomings in the deterministic model, especially during periods of population instability, the model has proven useful as a tool for caribou managers to use in determining potential harvestable surplus of caribou males and females, projecting population estimates for a year or 2 after a good census has been conducted, and helping determine whether results of a particular census are believable.

Conclusions

FOUR ORIGINAL QUESTIONS ANSWERED BY LONG-TERM RESEARCH

1. Can caribou "herds" be considered as "populations" for management purposes, or do mass shifts of caribou from one herd's range to another influence herd size and management, especially when herds reach high densities?

During the 30+ years of long-term research on the Delta herd and the enhanced monitoring program for caribou statewide, we found no evidence that permanent mass shifts occur from one herd's range, or from one region, to another. Several herds reached historic or near historic high population sizes during the period, including Central Arctic, Delta, Mulchatna, Nelchina, Porcupine, and Western Arctic herds. For management purposes, caribou herds in Alaska can be considered populations and the current management model based on this framework continues to be an appropriate model. However, even 30 years is a relatively short time and the question should still be considered open.

2. Are periodically observed low calf numbers (i.e., poor recruitment) in caribou herds most likely the result of low natality rates in females (i.e., resulting from nutritional, or density dependent factors, including disease), or is mortality of calves the main reason for low calf numbers and recruitment?

Evidence gathered from the Delta herd and other Interior herds in Alaska strongly supports a conclusion that low natality rates in Interior caribou are rare and that low calf numbers in fall result primarily from mortality of calves. In only one case in Alaska (Delta herd in 1993) was a herd natality rate observed to be below 50% (Boertje et al. 2012, this study). Low natality rates are probably also rare in the Arctic herds but less information is available and no Alaska herds have reached the extremely high densities seen in the George River herd (Bergerud et al. 2008, Dau 2011, Boertje et al. 2012).

Evidence from Alaska herds, the recent decline of the George River herd, and older information from Norwegian wild reindeer provide good evidence that there are a variety of factors that influence low calf numbers in fall and these factors act either singly or in various combinations with or without density-dependent factors (this study, Skogland 1985, 1990; Adams and Dale 1998b; Dale et al. 2008; Boertje et al. 2012). If late winter conditions are severe (either from weather conditions like snow or icing and/or overgrazed winter ranges), calves tend to be born later, their birth weights are light, and neonatal survival is relatively poor (primarily because of predation in Interior Alaska herds), resulting in lower fall calf:cow ratios. Similarly, if summer conditions are poor (either from climate, weather, and/or overgrazing combined with the demands of lactation), females will have lower body weight in fall and lower probability of becoming pregnant (Skogland 1985, 1990; Cameron 1994; Cameron and White 1996; Adams and Dale 1998b). Lower body weights in fall then reduce the likelihood of reproduction. At extremely high summer densities ($>10/\text{km}^2$), even natality of adults can be severely reduced (Bergerud et al. 2008). It also appears that either summer or winter ranges (or both) can be overgrazed and once overgrazing becomes severe, both natality and calf survival (with or without predation) are affected (Skogland 1985, 1990; Valkenburg et al. 2003b; Bergerud et al. 2008).

Mortality of calves (primarily from predation in Interior herds) was the leading cause of low fall calf:cow ratios, but there is strong evidence that environmental factors (either working alone or in concert with weather) predisposed caribou calves to mortality from predation (Adams and Dale 1998b, Mech et al. 1998, this study). However, predation on calves can also limit herd growth in some small herds with good nutrition, good environmental conditions, and where herds are well below thresholds where density-dependent effects are observable. In Southwest Alaska, and in the Western Arctic herd, historical and recent evidence indicates that disease could also have been a major cause of low fall calf:cow ratios or mortality of adults, but documentation has been insufficient to be conclusive. Davis and Valkenburg (1985a:15) reviewed evidence for disease in Alaska caribou through the early 1980s and concluded that disease has played a minor role in the dynamics of wild caribou. In the late 1970s in the Western Arctic herd and in the late 1990s in the Mulchatna herd, necrobacillosis (i.e., hoofrot) outbreaks were suspected based on caribou found dead in summer and limping caribou in fall (P. Valkenburg, personal observations). During the 1980s and 1990s several viral diseases were found to be enzootic in caribou but, except for the pneumonia detected in caribou calves in the Mulchatna and Northern Alaska Peninsula herds, strong evidence for potentially serious direct mortality from disease is lacking (Neiland 1972; Zarnke 1996, 2000).

To fully understand the causes of low fall calf:cow ratios and manage appropriately, managers must consider population density on summer and winter ranges, weather conditions, herd size in relation to predator numbers (i.e., predator:prey ratios), and the prevalence and possibility of disease.

3. What are the major causes of mortality in adult and calf caribou?

In Interior caribou herds, predation by wolves was the leading cause of death of adults and predation (by wolves, grizzly bears, and golden eagles [*Aquila chrysaetos*]) was the leading cause of death of calves <1 month old. However, there is strong evidence from detailed studies of the Delta and Denali herds that weather-related and density-related nutritional factors can predispose calves to high predation rates (this study; Adams et al. 1995a,b; Mech et al. 1998). In Southwest Alaska we found evidence that disease may contribute to mortality of caribou but we were not able to quantify the effects of disease. In separate studies of the Porcupine herd, predation by golden eagles was the most important mortality factor for neonates, but nonpredation mortality was also important (Whitten et al. 1992). In the Fortymile herd, predation was found to be the primary limiting factor in Fortymile caribou (Boertje et al., *In press*)

In the Delta herd, regression models identified age of adult female caribou as the most important factor associated with the probability of survival for an individual in any year. Once age was considered, no other factors were significant in regression models. Although the deterministic spreadsheet model suggested that survival declined markedly during the early 1990s, coincident with deep snow, that was also a time when many radiocollared females were entering the 10+ age classes. If mortality in caribou is closely tied to age, even when weather is bad, this finding has major implications for management, including the fact that managers must be more cognizant of "population inertia," and that herds can be preconditioned to decline about 10 or more years after periods of rapid population growth.

4. Is predation a major limiting factor that can be managed to increase harvest of caribou?

The answer to this question is a qualified "yes." In Interior herds, predation was certainly found to be a major limiting factor, and predation was successfully reduced in the Delta herd to increase herd size and harvest (Boertje et al. 1996, National Research Council 1997). In Yukon, caribou numbers and harvest also increased after wolf control in 2 cases but the effects of wolf control did not last for longer than 5 years (National Research Council 1997, Hayes and Harestad 2000, Hayes et al. 2003). However, not all wolf management programs in Alaska have been successful because of political and biological reasons (National Research Council 1997; Valkenburg et al. 2004; Boertje et al., *In press*). It is likely that caribou have been successfully reallocated from predators to hunters in the Nelchina herd at a reasonable cost (because predator control has been done by the public), but the program is still being evaluated. In the Fortymile herd, caribou growth rates have been largely unaffected by wolf control of several kinds over many years largely because much of the calving area was not included in the wolf control area (Boertje et al., *In press*). Potential for harvest may be higher with wolf control than without it.

In Southwest Alaska, one small wolf control program involving just 2 wolf packs was successful in preventing the decline of the Southern Alaska Peninsula herd to a historic low level, improving recruitment, and reestablishing a hunting program (Riley 2011a). The circumstances under which predator management programs can be successful for caribou are still under investigation and most programs should still be considered experimental.

Our understanding of caribou ecology and management options is now sufficiently advanced that informed decisions can be made about management programs that are intended to restore depleted caribou herds or improve caribou harvests. In many cases the information needed to make management decisions or recommend courses of action to policymakers is affordable and can be gathered in a timely manner (2–3 years) if the information is not already available from ongoing studies. For example, if a large herd has declined and there is public pressure for managers to restore the herd or improve harvest, there are a few basic questions that need to be addressed before a course of action can be recommended. Presumably, some very basic population parameters will have been collected on an ongoing basis (like fall calf:cow and bull:cow ratios and a periodic census). If fall calf:cow ratios are low, cohorts of about 30 male and 30 female newborn calves should be weighed to compare with baseline data on newborn calf weights (if they exist). Baseline data need to be herd-specific, or at least specific to the region. If calf weights are low (suggesting that winter weather conditions are bad or winter range is overgrazed), it is unlikely that predator control on the calving area and summer range will improve fall calf:cow ratios much. In addition to weights of newborns, weights of cohorts of 4-month-old calves should also be obtained. If these are relatively low, indicating that summer nutrition is reduced, calf mortality over winter will be relatively high, recruitment will be low, and wolf control on winter ranges may be ineffective, especially if snow is deep. Sometimes after major caribou declines, managers will need to wait until nutrition improves before predator control actions have a likelihood of improving recruitment. In growing caribou herds (as opposed to declining herds), where managers are faced with deciding when to restrain herd growth, data on natality rates of 2- and 3-year-old females can be helpful (Boertje et al. 2012). If any 2-year-old females are producing calves then nutrition is good and herd growth should be allowed to continue. If natality of 3-year-old females is beginning to decline (to <55%), managers could consider restraining herd growth (Boertje et al. 2012). Other information, in addition to newborn and 4-month-old calf weights, are 10-month-old calf weights, and relative date of the peak of calving. When caribou are in good condition, the peak of calving tends to be relatively early and abrupt (versus late and drawn out). The range of variation in peak calving dates can be as much as 10 days (Skogland 1990; Adams and Dale 1998a; P. Valkenburg, personal observations). A few years of this kind of data will suggest to managers whether it is winter or summer range or predation that is limiting (Valkenburg et al. 2003a).

OTHER CONCLUSIONS

Major Factors Affecting Growth of Alaska Caribou Herds-Small vs. Large Herds

Mortality

Causes of mortality of adults and survival rates have been difficult to document in Alaska caribou, even with the use of VHF and GPS radio collars because of the intensity of monitoring required. Often, sample sizes have been small and there is uncertainty about cause of death or even whether a caribou has died or collars were simply shed. This was especially true for wide-ranging large herds, even when large numbers of collars are deployed, because winter weather is severe, logistics are expensive, and many collars are not retrieved.

In the Delta caribou herd (and by inference, in other Interior herds), where wolf predation on adults is a major mortality factor, age is a primary factor associated with the probability that a female will survive to the next year. For this reason, age structure of the adult female component of the population is important information for management because it can cause “population inertia,” where rapidly growing herds tend to continue growing and declining herds will tend to continue declining until a majority of older females have died. For example, if herds are started from transplants of yearling females, mortality can be expected to be low for many years and herds will grow for many years if recruitment of calves is adequate. Conversely, after periods of low calf recruitment, as mean age of females increases, mortality of older females, either alone or in concert with low natality and/or calf survival, will tend to drive caribou herds down. The interaction of weather factors (primarily operating on calf survival), age structure of females, and predation can be complex and difficult to predict and can influence outcomes of management programs.

Patterns of mortality in small- to medium-sized Interior herds appear to be quite different than mortality patterns in herds in Southwest Alaska and the large Arctic herds. In general, Interior herds experience very high neonatal calf mortality from predation and have relatively low fall calf:cow ratios when herds are stable (15–35 calves:100). In contrast, during periods of relative stability, herds in Southwest Alaska (Northern Alaska Peninsula and Southern Alaska Peninsula herds particularly) tend to have low neonatal calf mortality but calf mortality continues at moderate levels throughout the summer and fall calf:cow ratios are moderate (30–40:100). In the Arctic herds, except during major population declines, early calf survival is almost always high and fall calf:cow ratios are high compared with Interior herds. In contrast to Interior herds, calf mortality after fall composition counts are conducted, and/or adult mortality, must compensate for the higher fall calf:cow ratios seen in the Arctic herds.

Although we had few radio collars on bull caribou in the Delta herd, casual observation by many biologists in Alaska suggest that age is at least as important in influencing survival of males as it is in females. Stress, declining body reserves, and mortal combat among older bulls during the rut result in many wounded and dying bulls being observed during composition counts when bull:cow ratios are high.

Natality

Intensive radiotracking (particularly in the Delta, Denali, Fortymile, and Nelchina herds during the calving period) has allowed biologists to draw firm conclusions about some aspects of natality in caribou that were previously subject to considerable debate. For example, at least for Interior caribou, there appears to be no reproductive cost to early reproduction. If caribou produce calves at 24 months of age, they are more likely to keep producing calves in subsequent years than encounter a breeding pause at 36 months of age (Adams and Dale 1998b, this study). Also, for all adults, females that produce calves in one year are more likely, not less likely, to produce a calf the following year. These findings for Interior herds are contrary to findings for the Central Arctic herd (Cameron 1994) and possibly for other large Arctic herds where predation on calves is light. Part of the explanation for the difference is likely that most females in Interior herds lose their calves quickly to predators, do not lactate over the summer, and therefore enter the rut in excellent condition (Adams and Dale 1998b). Also, because they are strongly limited by predation, the Interior herds are not likely to encounter density-dependent nutritional limitation. In contrast, in the large Arctic herds in North America, where caribou can reach very high densities (>10/km^2) on summer range, there is now ample evidence that declines in natality can have a major effect on recruitment (Bergerud et al. 2008). Similarly, Skogland (1985, 1990) found strong evidence for density-dependent effects on natality in Norwegian wild reindeer (largely predator free) where he had opportunities to study many herds at varying (relatively high) densities and also to study a herd (Hardangervidda herd) that was deliberately reduced by hunting from a high population density where predation was negligible. However, even in the declining Western Arctic herd (where summer densities are more moderate) calf recruitment has not been related to lower natality (Dau 2011).

Regional Patterns in Population Change

By monitoring changes in population size of the Delta and many other Alaska caribou herds during 1978–2007, in relation to weather, recruitment, sex ratio, body weight and other measures of nutrition, we improved our general understanding of major factors that likely caused population changes in many Alaska caribou herds during this period. We found evidence for synchrony in population growth and decline in Alaska caribou herds that is apparently caused by regional weather patterns. However, influence of grazing pressure on winter and summer ranges, and predation, especially in smaller-sized herds, seemed to act independently or synergistically with weather to modify population growth. We also found great variation in the relative severity of weather patterns associated with climate cycles, but that characteristics of weather are difficult to measure at a scale meaningful to caribou. Over the 30 years of this study, we documented changes in caribou growth that appeared to result from all of the causes mentioned above. Synchrony in population growth and decline in Alaska and Yukon caribou is a growing area of research (Hegel et al. 2010, Joly et al. 2011) and should continue to be a major area of caribou research.

All Caribou Herd Ranges are Different in Important Ways

During the intensive study and monitoring of the Delta herd and the extensive monitoring of the many other Alaska caribou herds, we were constantly impressed at ecological differences among caribou herds. This was true across regions and within regions. These herd specific and regional differences make it difficult to generalize about limiting and/or regulating factors that might apply to all caribou in general, or to all caribou in Alaska. We found evidence that in some herds winter range appears to be most limiting (Delta and probably Northern Alaska Peninsula), while in other herds summer range appears most limiting (Nelchina and Fortymile) (Valkenburg et al. 2000, 2002, 2003b; Boertje et al. 2012). It is likely that winter range is more limiting than summer range in the Delta herd and should be the major consideration in determining optimum herd size.

Other differences we observed include the lack of lichens, absence of golden eagles, and volcanic ash falls (that increase tooth wear) on the Alaska Peninsula. The possibility that rabies can reduce wolf numbers in coastal areas also has the potential to influence survival of caribou in these areas.

In the Western Arctic herd we were impressed by the quality of the southern winter ranges, particularly in the Nulato Hills and Koyukuk drainage where lichens are abundant on upland areas and where there are small lakes (including “grass lakes”) with partially green sedges. These areas provide juxtaposition of predator escape areas (i.e., caribou can ruminate in the open where they can see), and foods high in protein (sedges with green bases) and carbohydrate (lichens). The southern winter ranges of the Western Arctic herd have provided the primary winter range for very high numbers of caribou for a surprisingly long time (>30 years) (Dau 2011).

The range of the Sunshine Mountains herd is also rather unique. It is 1 of only 2 herds (the other being Kenai Lowlands) in Alaska where caribou calve primarily in lowland muskeg habitat.

The summer range of the Fortymile herd is relatively low in elevation and includes areas of spruce forest and spruce woodland that caribou with young calves must pass through. This opens up the possibility that black bear and lynx can prey on neonates. The herd lacks high quality alpine summer range and could be protein limited as well as being subjected to more insect harassment. The lack of trophy caribou from the Fortymile caribou also suggests that the herd's range is inherently inferior compared with ranges of other Interior herds (notably the Nelchina and Delta).

In parts of the Alaska Range (parts of the Delta range, Chisana range, and Macomb Plateau), snow is commonly shallow in winter from wind scouring. On these winter ranges, frequent winds cause fine sediments to coat forage plants and tooth wear in caribou is likely increased (P. Valkenburg, personal observations). Also, these areas tend to periodically have more coyotes than other caribou ranges so that caribou in these herds can experience predation from this additional predator (Arthur and Prugh 2010).

Because of these differences in caribou ranges, it is important for management and research biologists to spend considerable time on the ground and in the air observing caribou and their habitats. There can be no substitute for years of familiarity that management and research biologists develop with the caribou herds in their areas. Qualitative data are important and help biologists formulate new hypotheses for testing.

Indices of Nutrition in Caribou

The search for nutritional indices in caribou has been long and has involved many dead ends in Alaska. For many years biologists tried to emulate work done in Norway and measured biomass of lichens on caribou winter range, lichen consumption rates (using exclosures), and proportion of lichens in rumen contents and fecal samples (c.f. Pegau 1972, 1974; Pegau and Hemming 1972; Pegau et al. 1973; Dearden et al. 1975; Reiswig 1981; Adams and Connery 1983; Boertje 1984; Lieb et al. 1985). However, sampling problems, changing caribou movements and winter distribution, logistics, cost, and other factors gradually led biologists away from this approach during the late 1970s and 1980s. Similarly, attempts to gather meaningful biological information from samples from hunter-killed caribou were fraught with insurmountable problems (many are discussed above in *Methods*). Collections of mandibles taken by hunters in the Western Arctic, Nelchina, and Delta herds since the 1950s did provide valuable information but the information was most useful for retrospective analyses. Checkstations have provided a good way for managers and researchers to communicate with hunters in the field but the amount of useful biological information collected about caribou has been minimal.

Information from samples from caribou collected (i.e., shot) by biologists proved more useful than samples from hunters and will continue to be useful in special cases, particularly in large herds and where disease may be an important management issue. Cleaned and dried mandibles of collected calves, especially those collected in October, are a reasonably good substitute for live weight as an index on condition. However, for routine monitoring of nutritional condition, collecting presents political and logistical problems and will likely never be routinely used. In the long-term study of the Delta herd and related studies (particularly on the Fortymile and Denali herds), we believe that biologists have finally found indices of nutritional condition that can be used by managers to determine optimal herd sizes, provide information about reasons for caribou declines, and help guide predator management programs.

To date, the most useful indices appear to be 1) measuring natality rates of known-aged young female caribou with radio collars (2-, 3-, and 4-year olds); 2) measuring live weights of caribou calves at 4 and 10 months of age; 3) measuring live weights of newborn calves; and 4) documenting shifts in peak calving dates, although documenting peak calving dates requires intensive flying. All of these indices have been found useful and will continue to be used in combination with data on calf recruitment (preferably fall calf:cow ratios). The combination of nutritional indices selected will depend on the economic importance of the herd, logistical considerations, cost, and whether the herd is likely to be most limited by winter or summer range. In the Fortymile herd, that is economically very important, logistically easy to work on, and likely limited primarily by summer range, Boertje et al. (2012) recommended using a running 5-year mean natality rate of 3-year-old females as the primary index of nutrition. Four-month-old calves (15–20 per year) would continue to be captured and radiocollared so both calf weight data and known-aged female natality data would be available. The expenses involved with this protocol are high but likely justifiable because of the economic importance of the herd. However, in herds that are less economically important, it will be impractical to monitor nutritional status by using 5-year running averages of 36-month-old natality rates. In the less economically important or remote herds, weighing 4-month-old and 10-month-old calves, weighing newborn calves, and monitoring fall calf:cow and bull:cow ratios should be adequate. Some information will be available on natality as well, either from radiocollared caribou or from surveys of distended udders. To be most useful for managers, techniques for monitoring condition need to be repeatable and affordable so that data gaps are avoided and data sets are as continuous as possible. ADF&G has already gradually incorporated much of this information into caribou management programs (Valkenburg et al. 2002, 2003a; Healy 2003; Brown 2005; Harper 2007, 2009, 2011; Boertje et al. 2012), and the idea of using weights of 4- and 10-month-old caribou calves as indices of nutrition that was originally developed as part of the long-term study of the Delta herd has been adopted, tested, and used as a condition index for moose as well (Boertje et al. 2007, Harper 2010).

In addition to the indices of nutrition suggested above, there are some other clues that managers can use to help determine if high herd sizes are resulting in overgrazing. These include observations that caribou are frequently searching for new winter or summer ranges, increasing prevalence of disease, changing numbers of trophy caribou harvested by hunters, decreasing body size of caribou (indicated by decreased mandible lengths), and changing proportions of lichens in the winter diet. Assessing proportion of lichens in the winter diet has been a bit frustrating, however. There is only one lab currently performing these analyses (Washington State University), there may be differences in processing procedures that influence interpretation of the data, and processing times have been long (i.e., years) so data have not been available on a timely basis.

In many small, stable, or less economically valuable caribou herds, monitoring fall calf:cow ratios, periodic estimates of population size, and general observations by management biologists will continue to be the only information needed for management. Assessing nutritional condition of caribou in these herds is usually unnecessary.

Measuring Weather Variables

Adequately measuring weather variables and determining which variables are most biologically meaningful proved to be difficult. Primary weather stations that have maintained weather records for long enough periods (e.g., Fairbanks, Anchorage) are located far from most caribou herds. With secondary weather stations (e.g., Denali Park airstrip, Dawson, Gulkana), there are often data gaps and the location of the stations still may not be representative of caribou ranges. Even snow measurements had problems. For example, a considerable amount of variation in our *NRCS.snow* index was not explained by the *Denali.snow* index ($R^2 = 0.59$) and snow at Dawson was poorly related to snow at nearby Eagle ($R^2 = 0.32$). Some satellite-based range information, such as the normalized difference vegetation index (NDVI), may have potential for caribou (Griffith et al. 2000, Pettorelli 2013).

Need to Maintain Radio Collars on Caribou

In general, the value of maintaining radio collars on wildlife is diminishing, especially with carnivores. This is not true with caribou. Perhaps more than any other species in Alaska, caribou managers need to maintain adequate numbers of radio collars on caribou for management purposes in economically important herds. It is important for biologists be able to track caribou to distinguish between herds on adjacent ranges, find caribou groups for population censuses and composition counts, and ensure that overharvests do not occur. In large part, it was the inability to monitor movements of individual caribou in the late 1960s and early 1970s that led to major management errors and overharvests.

Optimum Population Size

The combined experience of caribou researchers and managers in the circumpolar north over the last 40 years has been that population stability is rare in caribou herds, especially large Arctic herds. But population fluctuations in economically important herds have caused considerable strife and caribou managers have considered for decades whether it is possible to manage herd size to reduce population fluctuations, provide for more predictability of caribou harvests, and optimize harvest over the long term. There are many potential advantages in managing caribou herds around a long-term sustainable herd size. Perhaps the greatest advantage is that harvests can be made sustainable. Additionally, in Alaska, ADF&G and the Board of Game have a constitutional mandate to manage game species on a “sustained yield” basis, perhaps implying managing for long-term sustainable harvests. In Alaska, only the Nelchina herd has been successfully managed in this way, although some other herds, like the Porcupine herd, have remained relatively stable naturally.

While it is not unusual for caribou herds to reach unsustainably high population sizes and overgraze their winter and/or summer ranges naturally, if herds are deliberately managed, it seems desirable for managers to avoid allowing herds to overgraze. It can take overgrazed ranges at least a decade to recover and overgrazing has consequences for reduced short-term harvest.

With regard to managing herds for sustainable herd sizes and optimum long-term harvests, our experience is that there are essentially 3 categories of caribou herds in Alaska. First, there are herds that can feasibly be managed to control herd size and where there is sufficient experience with past population fluctuations and enough data to make an educated guess about what an optimum herd size might be. Second, there are herds where biologists have enough historical and current information to suggest an optimum herd size, but for logistical, political, or policy reasons, managing for an optimum herd size is unfeasible or undesirable. Third, there are herds for which biologists lack a sufficient understanding of historical fluctuations and for which there is relatively little data on trends in body condition or overgrazing of ranges so that guesses about optimum herd size are not yet warranted.

In the first category, we include the Nelchina, Northern Alaska Peninsula, and Southern Alaska Peninsula herds, and perhaps the Delta herd. We discuss our conclusions about these herds below:

Nelchina Herd

The Nelchina herd is the only caribou herd in Alaska that was maintained at a stable "optimum" population size (1989–2007) for almost 30 years (Tobey 1993, 1999, 2001, 2003; Tobey and Schwanke 2009). The current population management goal (35,000 adults) was suggested by Lieb et al. (1988). This estimate was based on historical population fluctuations (Skoog 1968, Van Ballenberghe 1985, Eberhardt and Pitcher 1992), assessments of lichen ranges (Pegau 1972, Lieb et al. 1985), and comparative information from other herds (e.g., Northern Alaska Peninsula) where herd size was maintained at unsustainably high levels. It is noteworthy that previous suggestions (Lieb et al. 1988, Lieb 1989) for optimum herd size for the Nelchina were made before direct information of nutritional status (i.e., calf weights and natality rates) became available during the mid-1990s. Information on nutritional status of Nelchina caribou (i.e., natality rates, 4- and 10-month-old calf weights and newborn calf weights) has confirmed the original ideas about the likely optimum size for the herd (Valkenburg et al. 2003a, Dale et al. 2008, Boertje et al. 2012).

Northern Alaska Peninsula Herd

Because the Northern Alaska Peninsula herd had been relatively stable (15,000–20,000, Table 10) at a high density (>1 caribou/km^2), a panel of biologists at the Third North American Caribou Workshop in November 1987 (Cameron and Davis 1988) selected the herd as 1 of 2 Alaska herds (the other being the Nelchina herd) to experimentally maintain at a stable population size (Sellers 2001). However, within about 7 years of that decision the herd began a sustained decline and managers were concerned that the herd had been maintained at an unsustainably high level (Fig. 10) (Sellers 1995, 1997). During the mid-1990s, as we began collecting information on nutritional condition of the herd, it was clear that condition was severely compromised. Calf weights were relatively low, caribou were searching for new winter ranges (near Iliamna Lake), and disease was prevalent (Sellers 1997, Valkenburg et al. 2000, Zarnke 2000, Valkenburg et al. 2003b, Butler et al. 2006). Despite efforts to prevent further declines in herd size by eliminating harvest of females during the late 1990s, the herd continued to decline and eventually reached 2,000 caribou by 2008. In hindsight, it is clear that 15,000–20,000 caribou was far in excess of a sustainable herd size, particularly after the Mulchatna herd also began using the northern lichen ranges of the Northern Alaska Peninsula between the Naknek River and Lake Iliamna during the mid-1990s. Previously this area had been exclusively used by the Northern Alaska Peninsula herd. It has taken many years for winter ranges and herd health to recover (Butler 2007). Based on the herd's history and information from this study, we believe that optimal herd size and a reasonable experimental management goal for the Northern Alaska Peninsula herd would be about 6,000. Although the herd is reasonably accessible in years when snowcover is suitable for use of snowmobiles from Port Heiden to King Salmon, whether or not harvest can be used to adequately restrain herd size during periods of rapid herd growth is uncertain. The trend towards milder winters and less snow cover on the Alaska Peninsula from climate change will reduce accessibility of the Northern Alaska Peninsula herd for hunters.

Southern Alaska Peninsula Herd

This herd has had a history of marked population fluctuations with a maximum size of about 10,000 (although this estimate is questionable) and minimum size of about 300 (Fig. 10) (Valkenburg et al. 2003b). At high population sizes, the herd has been nutritionally limited by winter range (i.e., indicated primarily by underweight neonates) (Figs. 55 and 56) (Riley 2011a). As the herd increased in size, it expanded its range south into the Cold Bay area where there is a small road system and boat access to a large portion of its winter range. However, whether herd size can be deliberately restrained through harvest is still unknown, but access is generally poor except around Cold Bay and snow cover is seldom suitable for travel in most winters. We believe that a reasonable experimental optimum population size and interim herd management goal would be about 2,500.

Delta Herd

The Delta herd is 1 of the 4 most studied herds in Alaska (the others being the Denali, Nelchina, and Fortymile). There is good evidence from trends and calf weight and natality rates of young females that the herd reached an unsustainably high population size in the late 1980s, at least partly as a result of the wolf control program from 1975 to 1982, but also because herd size was not restrained by harvest as had been originally intended. It seems clear in hindsight that the original population management goal for the Delta herd (4,000 caribou) was prudent and that the population should have been maintained well below its peak size of 10,690. This population goal was a guess based simply on the size of the herd's range, previous history of fluctuations between the late 1950s and the early 1980s, and an intuitive idea about how many caribou the range was likely to support over the long term (O. E. Burris, personal communication). Given the information available at the time, the original estimate of optimum sustainable herd size (4,000) suggested in the early 1980s is remarkably close to the current estimate we provide here based on 25 more years of study. We believe the Delta herd should be managed so that it does not exceed 3,500–5,000. The herd has apparently mostly recovered from the effects of the overgrazing of the late 1980s and early 1990s and the range could likely support a herd size of this level indefinitely.

Unfortunately, despite our extensive knowledge of this herd, it is also one of the more complex to manage. The herd has shifted its range and now mixes with the Nelchina herd during fall and winter. It also ranges an area with a relatively high moose population and density (for Alaska), so wolf numbers are high. Any management of predation in the range of the Delta herd must also consider moose management goals (Young 2010) because the GMU 20A moose population is one of Alaska’s most economically valuable wildlife populations and it is also one of the most intensively studied moose populations in the world. Whether it is desirable to try to increase caribou herd size or allowable harvest through active predator management in GMU 20A remains uncertain because of the complications associated with managing the unit’s large moose population.

In addition to the group of herds discussed above, we also discuss another group of herds that fall into the second and third categories (i.e., herds that are economically important, but where it is unlikely that herd size can be controlled or where there is inadequate information to determine an optimum herd size):

Fortymile Caribou Herd

The Fortymile herd is 1 of 4 international herds that frequently or occasionally range between Alaska and Yukon (Porcupine, Chisana, and Nelchina are the others), and there are management agreements in place between Alaska and Yukon for managing the herd. The primary thrust of management of the herd is to promote herd growth, reinvasion of former winter ranges in the western Yukon, and expansion into former calving ranges west of the Steese Highway in Alaska. There are compelling reasons to believe that historic high estimates of herd size are incorrect but also that the often cited previous population spike in the 1920s was an anomaly (Valkenburg et al. 1994, Boertje et al. 2012). Based on the size and quality of the summer range (including the White Mountains) and historic and recent information about herd size, natality rates, and calf weights, we expect that the optimum size for the Fortymile herd is likely much lower than the historic population high of the 1920s. Our understanding of the history of herd fluctuations is currently insufficient to suggest an optimum herd size. The current management strategy of continuing to promote herd growth while monitoring natality rates of 3-year-old females and body condition of calves as the herd grows is probably the most appropriate one in view of the importance of the herd to people in both Alaska and Yukon. Boertje et al. (2012) provide a complete discussion of considerations about size and nutritional status of the herd and revisions of previous estimates of herd size.

Western Arctic Herd

Perhaps more than any other herd, the Western Arctic and its users would benefit most if the herd could be reliably managed for an optimum size. In recent times (about the last 150 years), the Western Arctic herd has had 3 population highs. The first probably occurred during the 1870s but duration and amplitude of the high was poorly documented (Skoog 1968). The second population high occurred during the 1960s when the herd was likely ~300,000 or more (Lent 1966). The first accurate census of the herd was in 1970, when the minimum population estimate was 242,000 but the herd was probably already declining (Fig. 13) (Pegau and Hemming 1972). During the early 1970s, some ADF&G biologists were concerned that the herd was too high because there was evidence of disease (Neiland 1972) and that overgrazing was a concern, although there was no direct evidence (C. Grauvogel, Wildlife Biologist, ADF&G, personal communication with P. Valkenburg). Population decline was suspected in 1974 and documented in 1976 (Grauvogel and Pegau 1976, Davis 1976b, Davis et al. 1976, Davis and Valkenburg 1978). Swift action by the Alaska Board of Game prevented further decline in 1976 and then the herd grew at 13% per year to a new population high of about 463,000 in 2003 (Fig. 12) (Dau 1999, 2003).

The Western Arctic herd occupies the largest contiguous area of good caribou habitat in Alaska (about 140,000–170,000 mi^2), including a large summer range and exceptionally good southern winter range on the eastern Seward Peninsula and in the Nulato Hills (O’Connor 1979, Adams and Connery 1983, Dau 2011). However, the history of population fluctuations, high and unpredictable harvests, introgression of reindeer genes, prevalence of disease during the 1960s population high, and lack of a long and continuous data set on condition of caribou calves and natality rates of young females make it difficult to estimate a herd size that might be considered “optimum.” Regardless of whether there is a good enough understanding of the herd’s historical changes in numbers or adequate information on body condition, managing the herd around an “optimum” population size may not be feasible because it could be logistically and politically difficult to harvest enough females during rapid growth phases.

Mulchatna Herd

The Mulchatna herd grew at the highest sustained rate of increase (about 17% annually during 1981–1996) of any herd in Alaska during the last 50+ years. The herd numbered about 190,000 caribou at its peak (Fig. 12, Appendix A). Its subsequent decline was equally impressive, and it was down to 20,000 by 2008. The limited data on nutritional condition that we collected during the 1990s indicated that its 1990s peak herd size was unsustainable. The herd had access to extensive winter ranges with abundant lichens, but in many of these areas casual observations indicate that lichens were noticeably depleted by the late 1990s. Further, there is evidence that the summer range was probably also overgrazed. Once range recovers from the natural overgrazing that occurred during the 1990s and early 2000s and the herd grows once again, biologists will be in a position to monitor the weight and size of calves and natality rates on young females to begin to determine what might be an optimum size for the herd. However, the remote nature of the herd’s range will likely make it difficult to manage around an optimum size because it will be difficult to restrain herd growth and it is unlikely that future declines can be prevented.

There are many other herds we have not discussed in this section because their economic importance is low, our knowledge of them is too incomplete, they are so restrained by predation that they are unlikely to ever increase to the point where overgrazing will occur, or they are so remote that managing herd size is currently not possible.

Future Research and Management Needs

During the last 30+ years of caribou research in Alaska, many interesting questions and ideas surfaced that we did not have the knowledge, money, time, or ability to address. We identify some of these ideas below. Some suggestions involve broad areas where ecological knowledge needs to be improved. Others are specific hypotheses that might be tested or questions that might be answered.

ECOLOGY OF BULL CARIBOU

Ecology of bull caribou is a major area that requires further research. Although some radio collars have been placed on bulls over the last 30+ years in Alaska, priorities associated with understanding age-specific birth and death rates of females, problems and expense encountered in maintaining samples of collared males, and devising indices to nutrition in females have taken precedence in designing research programs. Recently, increased mixing between adjacent caribou herds (Delta-Nelchina, Nelchina-Fortymile-White Mountains-Macomb, Northern Alaska Peninsula-Mulchatna, and Teshekpuk-Central Arctic-Porcupine) and results of recent genetic analyses (Cronin et al. 2003, 2005; Roffler et al. 2012; Colson et al. 2014; Mager et al. 2014) show both differentiation in some comparisons and lack of differentiation in others. A large proportion of gene flow between caribou herds may be male mediated so studies of movements and dispersal of bull caribou would be valuable. Some fall migratory movements of caribou herds and resulting mixing with adjacent herds have occurred at the end of September and early October, raising the possibility that there is interbreeding among animals from adjacent herds. Considerable data from radiocollared cows exist but would require careful analysis to determine whether cows from adjacent herds really did overlap during the rut.

Peak calving dates of Alaska caribou herds have varied considerably (from ~15 May to 10 June), and peak calving dates within herds can vary by about 10 days (Davis and Valkenburg 1978). Peak calving date depends on the timing of breeding and length of the gestation period. A reevaluation of the timing of the peak of rut is probably needed. Most researchers have relied on Bergerud’s (1978:84) estimate of 227–229 days for the gestation period of caribou and much of the information on rutting behavior of caribou in Alaska is from the Western Arctic herd and dates back to the early 1960s (Lent 1964, 1965). How the peak of the rut may vary in wild Alaska caribou on different planes of nutrition has never been determined and will certainly be challenging to determine in the future.

Radiocollaring more bulls with GPS collars, determining when the peak of rut occurs, and more detailed genetic analyses using larger samples from adjacent herds could all be worthwhile efforts to advance our knowledge of the ecology of males. Some biologists are already aware of the lack of information on the movements and ecology of bull caribou and have begun collaring more bulls in the Denali and Mulchatna herds.

COMPENSATORY NATURE OF HUNTING MORTALITY ON BULL CARIBOU

The Delta herd research and comparisons with the adjacent, unhunted Denali herd led us to suspect that much of the hunting of bull caribou in the Delta herd was compensatory. This hypothesis needs to be explored further, perhaps by radiocollaring a large number of bulls in a lightly hunted herd with a high bull:cow ratio and a similar number of bulls in a herd that is heavily hunted herd with a low bull:cow ratio. Survival rates and causes of mortality can then be compared. Population modeling will also continue to contribute toward an understanding of compensatory mortality. It is important for managers to understand how significant compensatory hunting mortality is and under what circumstances hunting is likely to be compensatory or additive, especially when designing hunting programs for the very small herds.

REGIONAL PATTERN IN POPULATION CHANGE IN CARIBOU HERDS

We identified regional patterns of population change in Alaska caribou over the last 30 years, and there is increasing evidence linking population performance of ungulates to indices of climatic variability in the North Pacific although population performance is difficult to associate with climate and weather (Hebblewhite 2005, Hegel et al. 2010, Joly et al. 2011). The effects of climatic oscillations (Mantua et al. 1997, Biondi et al. 2001, Mantua and Hare 2002), climate shifts (Hartmann and Wendler 2005), and climate change (Klein and Shulski 2009) should continue to be an important area of caribou research. Unfortunately, the problems we encountered in trying to determine herd-level effects of weather will likely also hinder studies of regional or global climatic patterns and climate change and their affects on caribou. It is tempting and popular to invoke climate change related causes to caribou declines (c.f. Post et al. 2009, Vors and Boyce 2009), when in fact, declines are more likely to have been caused by overgrazing as large herds approach natural population highs. While there likely will be both positive and negative population effects of climate change on caribou, biologists must guard against "bandwagon biology" in the search for climate-related causes for population change.

GENETICS OF ALASKA CARIBOU HERDS AND INTROGRESSION OF REINDEER GENES

Although much progress has been made in the study of caribou genetics in North America and in Alaska, there are still as many questions as answers. More research on the effects of introgression of reindeer genes, particularly into the 4 Arctic herds, the Alaska Peninsula herds, and the Beaver Mountains herd in Alaska, is needed. Is the small body size of Western Arctic caribou and Central Arctic caribou a phenotypic (i.e., ecotypical) adaptation to the arctic climate, or have there been morphological changes to caribou as a result of introgression of reindeer genes?

The small size of Western Arctic caribou calves (4- and 10-month olds), slightly greater size of Central Arctic herd calves and Porcupine herd calves, and the relative lack of genetic differentiation of the Porcupine herd from Interior caribou herds raises the possibility that there is a clinal change in phenotype (and perhaps genotype) of caribou across the arctic slope from west to east.

Are differences in trophy potential of Alaska caribou herds genetic or nutritional in origin?

THE EFFECTS OF AGE STRUCTURE ON CARIBOU POPULATION CHANGES

Age appeared to be the primary variable that predisposed caribou to predation and reduced survival of adult female caribou in the Delta herd. If this is true for the large caribou herds as well, "population inertia" is something that caribou managers must take into consideration in management programs. An understanding of age structure of a caribou herd will help biologists determine the likelihood of success of predator management programs. Understanding "population inertia" will also be an important consideration when designing harvest management programs.

MONITORING HERD MIXING, DISPERSAL, AND SEARCHING FOR EXAMPLES OF MASS DISPERSAL

As several caribou herds have increased in size, mixing on adjacent ranges has become more common and we documented cases of dispersal in this study. Although we found no cases of mass dispersal from one herd's range to another, based on historical anecdotal evidence, biologists should still consider the possibility that caribou could emigrate en masse.

EFFECTS AND MAGNITUDE OF WOUNDING LOSS ON CARIBOU HERDS

Wounding loss is a potentially important and largely unmeasured parameter that could be of significant management importance. The collective experience of many of the authors of this technical bulletin suggests that wounding loss is particularly high in hunts where large numbers of caribou are available to large numbers of hunters. During the road system hunts on the Fortymile and Nelchina herds, many wounded caribou escaped from the proximity of roads and eventually died away from the roads, particularly where crossings occurred in wooded areas (P. Valkenburg, personal observations). High wounding losses were also documented in the range of the Western Arctic herd during winter hunting with snowmobiles. In the late 1990s, the Board of Game essentially legalized chasing caribou with snowmobiles by allowing caribou to be "positioned for harvest" with motor vehicles. The popularity of small caliber semi-automatic rifles has likely increased wounding loss in this kind of hunting. Although it may be difficult to do and politically controversial, wounding loss should be studied.

Acknowledgments

This project was a testament to how well biologists from state and federal agencies and universities can work together to achieve common goals. Many biologists, technicians, supervisors, pilots, veterinarians, university professors, and graduate students participated in this study or contributed ideas and/or their unpublished data over the years and we are indebted to all of them for all of their years of cooperation, dedication, and perseverance, even if we have forgotten to mention them. Layne G. Adams (biologist with BLM, NPS, and USGS), although not a coauthor on this technical bulletin, provided valuable data on the Denali herd for comparison with the Delta herd throughout the study. Layne also provided an independent review of an early draft of the manuscript. We would also like to acknowledge the following people: biologists Torsten Bentzen (ADF&G), Toby Boudreau (ADF&G), Ray Cameron (ADF&G), Gail Collins (USFWS), Danny Caudill (ADF&G), Jim Dau (ADF&G), Dominic Demma (ADF&G), Steve DuBois (ADF&G), Bill Gasaway (ADF&G), Jim Herriges (Bureau of Land Management [BLM]), Michael Hinkes (USFWS), Larry Jennings (ADF&G), David Kelleyhouse (ADF&G), Tim Osborne (ADF&G), Harry Reynolds III (ADF&G), Michael Roy (USFWS), Jeff Selinger (ADF&G), Jeff Schrier (BLM), Kalin Seaton (ADF&G), Ron Squibb (USFWS), Kenneth Whitten (ADF&G), and John Wright (ADF&G); technicians Scott Brainerd (ADF&G), Ed Crain (ADF&G), Patty Del Vecchio (ADF&G), Ross Dorendorf (ADF&G), Danny Grangaard (ADF&G), Herman Griese (U.S. Army, Fort Greely and ADF&G), Ruth Gronquist (ADF&G and BLM), Ed Kutuk (ADF&G), Tina Laird (Swift Fork Air), Elizabeth Lenart (ADF&G), Ned Manning (Naval Arctic Research Laboratory), Ken Neiland (ADF&G), Carol Nielsen (ADF&G and University of Alaska, Institute of Arctic Biology [IAB]), Diane

Preston (ADF&G), Brad Schults (NPS), Marilyn Sigman (ADF&G), and V. Leigh Tutterrow (ADF&G); veterinarians John Blake (IAB), Kimberlee Beckmen (ADF&G), Bob Dieterich (IAB), and Don Ritter (University of Alaska, Rabies Virology Unit); graduate students Joe Doerr (Cooperative Wildlife Research Unit [CWRU], University of Alaska), Steve Fleischman (CWRU), and Frank Mörschel (CWRU); volunteers Barney Booysen, Michael Potter; and university professors David R. Klein (CWRU), and Robert G. White (IAB). Long-term projects such as this are necessarily dependent on the support of supervisors and we would like to thank, Dick Bishop, Scott Brainerd, John Burns, Bud Burris, John Coady, Bob Hinman, David James, Steve Peterson, Ron Somerville, Dan Reed, Wayne Regelin, Matt Robus, John Schoen, Chris Smith, and Ken Whitten for their continued support over the years often in the face of competing priorities.

During the course of the study (not including studies on the Fortymile and Western Arctic herds), we flew over 10,000 hours in state-owned and chartered aircraft and we thank the ADF&G pilot-biologists, private contract pilots, and federal agency pilot-biologists involved for the 30 years of injury-free flying done on behalf of the project. Most of the agency pilot-biologists are also coauthors of this technical bulletin. We are particularly indebted to the following private charter pilots: helicopter pilots Jim Ackles, Ken Butters, Troy Cambier, Fred Fredericks, John Kennebec, Larry Larrivee, Jonathan Larrivee, Rick Swisher, and Ron Warbelow; and fixed-wing pilots Tony Burnhardt, Bill Lentsch, Dennis Miller, Lee Peet, Steve Reynolds, Nelson Walker, Marty Webb, and Paul Zackowski. The development and use of economical, piston-powered Robinson (models R-22 and R-44) helicopters played a major role in improving data collection, reducing costs, and increasing safety. In addition to being more economical for ADF&G, these helicopters were less disturbing to wildlife and they made it possible for small operators to begin to specialize in animal capture techniques. From the mid-1990s on, we used Robinson helicopters exclusively for all survey and capture work. Having pilots who specialized in animal capture work was a major breakthrough in cost, efficiency, convenience, and safety. We are particularly indebted to the owner-operators of Chena River Aviation (Troy Cambier), Pollux Aviation Ltd. (Larry and Jonathan Larrivee), and Quicksilver Air, Inc. (Rick Swisher) who had the courage to acquire their own helicopters and develop their skills to become specialists in animal capture and survey work.

Almost all of the money for this research project was provided through the Federal Aid in Wildlife Restoration program with matching money from the State of Alaska’s Fish and Game Fund derived from hunting license and big game tag fee sales. The USFWS (Alaska Peninsula/Becharof, Togiak, Yukon Delta, and Nowitna National Wildlife Refuges) provided logistical support and some financial support for work on caribou herds in Southwest and western Interior Alaska. The National Park Service, Bureau of Land Management, North Slope Borough, and Department of Defense (Army and Air Force) also provided small amounts of funding and occasional logistical support.

We would also like to thank the hunters and trappers (particularly Bob Ahgook, Gary Bamford, Seth Kantner, and Steve O’Brien), and big game guides in Interior and Southwest Alaska (particularly, Lynn Castle, Dick Gunlogsen, Bill Lambert, Rod Schuh, and Bill Waugaman) who have consistently and willingly cooperated with ADF&G in contributing specimens, returning radio collars from study animals, providing us with much useful information on wolves and caribou, and allowing us access to their private lands, cabins, and airstrips.

ADF&G Publications Technicians Laura McCarthy and Laura McManus assisted in preparing the many reports and technical papers that were published during the course of the project. Publications Specialist Laura McCarthy assisted with the preparation of this manuscript for publishing. Her technical expertise and consistent attention to detail in preparing manuscripts over the last 25 years has been a critical part of the success of this project and the success of the ADF&G wildlife research program in Interior Alaska.

References Cited

Aarak, E., and D. Lenvik. 1980. Weight development in young reindeer. Pages 355–359 [*In*] E. Reimers, E. Gaare, and S. Skjenneberg, editors. Reindeer/Caribou Symposium II Norway 1979. Direktoratet for Vilt og Ferskvannsfisk, Trondheim, Norway.

Adams, L. G., and B. A. Connery. 1983. Buckland River reindeer/caribou conflict study final report. Bureau of Land Management, BLM-Alaska Open File Report 8, BLM/AK/OF-83/08, Anchorage.

Adams, L. G., and B. W. Dale. 1998a. Timing and synchrony of parturition in Alaskan caribou. Journal of Mammalogy 79(1):287–294. doi:10.2307/1382865

Adams, L. G., and B. W. Dale. 1998b. Reproductive performance of female Alaskan caribou. Journal of Wildlife Management 62(4):1184–1195. doi:10.2307/3801982

Adams, L. G., B. W. Dale, and L. D. Mech. 1995a. Wolf predation on caribou calves in Denali National Park, Alaska. Pages 245–260 [*In*] L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta, Canada.

Adams, L. G., B. W. Dale, and G. H. Roffler. 2005. Extraordinary movements of the Denali caribou herd following the perfect storm. Pages 19–25 [*In*] R. E. Haugerud, editor. Proceedings of 10th North American Caribou Workshop, 4–6 May 2004, Girdwood, Alaska. Rangifer, Special Issue 16.

Adams, L. G., B. W. Dale, and B. Schults. 1989. Population status and calf mortality of the Denali caribou herd, Denali National Park and Preserve, Alaska, 1984–1988. U.S. National Park Service-Alaska Region, Natural Resources Progress Report AR-89/13, Anchorage.

Adams, L. G., F. J. Singer, and B. W. Dale. 1995b. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59(3):584–594.

Adams, L. G., P. Valkenburg, and J. L. Davis. 1988. Efficacy of carfentanil citrate and naloxone for field immobilization of Alaskan caribou. Pages 167–168 [*In*] R. D. Cameron and J. L. Davis, editors. Reproduction and calf survival. Proceedings of 3rd North American Caribou Workshop, Chena Hot Springs, 4–6 November 1987. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 8, Fairbanks.

Aderman, A. R., and J. D. Woolington. 2001. Population monitoring and status of the reintroduced Nushagak Peninsula caribou herd. U.S. Fish and Wildlife Service, Togiak National Wildlife Refuge and Alaska Department of Fish and Game, Progress Report, Dillingham.

Allaye–Chan, A. C. 1991. Physiological and ecological determinants of nutrient partitioning in caribou and reindeer. Dissertation, University of Alaska Fairbanks.

Arthur, S. M., and L. R. Prugh. 2010. Predator-mediated indirect effects of snowshoe hares on Dall's sheep in Alaska. Journal of Wildlife Management 74(8):1709–1721.

Ballard, W. B., L. A. Ayres, P. R. 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.

Ballard, W. B., and P. R. Krausman. 1997. Occurrence of rabies in wolves of Alaska. Journal of Wildlife Diseases 33(2):242–245. doi:10.7589/0090-3558-33.2.242

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in Southcentral Alaska. Wildlife Monographs 98.

Banfield, A. W. F. 1954. Preliminary investigation of the barren ground caribou. Part 1. Former and present distribution, migrations and status. Part 2. Life history, ecology, and utilization. Canadian Department of Northern Affairs and Natural Resources, National Parks Branch, Canadian Wildlife Service, Wildlife Management Bulletin, Series 1, 10A and 10B, Ottawa, Ontario.

Barten, N. L., R. T. Bowyer, and K. J. Jenkins. 2001. Habitat use by female caribou: Tradeoffs associated with parturition. Journal of Wildlife Management 65(1):77–92. doi:10.2307/3803279

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. https://cran.r-project.org/web/packages/lme4/index.html (Accessed 12 October 2016).

Beckmen, K. B. 2014. Wildlife health and disease surveillance in Alaska. Alaska Department of Fish and Game, Division of Wildlife Conservation, Annual Research Performance Report 1 July 2013–30 June 2014, Federal Aid in Wildlife Restoration Project 18.74, Juneau.

Benhamou, S., and D. Cornelis. 2010. Incorporating movement behavior and barriers to improve kernel home range space use estimates. Journal of Wildlife Management 74(6):1353–1360.

Beninde, J. 1937. Zur naturgeschichte des rothirsches (Natural history of red deer). Paul Parey (1988 reprint), Hamburg and Berlin, Germany. (translated from German)

Bergerud, A. T. 1964. A field method to determine annual parturition rates for Newfoundland caribou. Journal of Wildlife Management 28(3):477–480.

Bergerud, A. T. 1967. Management of Labrador caribou. Journal of Wildlife Management 31(4):621–642.

Bergerud, A. T. 1971. The population dynamics of Newfoundland caribou. Wildlife Monographs 25.

Bergerud, A. T. 1974. Rutting behavior of Newfoundland caribou. Pages 395–435 [*In*] V. Geist, and F. Walter, editors. The behavior of ungulates and its relationship to management. Volume 1, ICUN New Series Publication 24, Morges, Switzerland.

Bergerud, A. T. 1978. Caribou. Pages 83–101 [*In*] J. L. Schmidt, and D. L. Gilbert, editors. Big game of North America. Stackpole Books, Harrisburg, Pennsylvania.

Bergerud, A. T. 1996. Evolving perspectives on caribou population dynamics, have we got it right yet? Pages 95–115 [*In*] R. E. Haugerud, editor. Proceedings of 6th North American Caribou Workshop, 1–4 March 1994, Prince George, British Columbia, Canada and George River Caribou Workshop, 27–29 January 1994, Labrador City, Labrador, Canada. Rangifer, Special Issue 9.

Bergerud, A. T., S. N. Luttich, and L. Camps. 2008. The return of caribou to Ungava. McGill-Queen’s University Press, Montreal, Canada.

Bevanger, K., and P. Jordhøy. 2004. Reindeer – the mountain nomad. Naturforlaget, Oslo, Norway.

Biondi, F., A. Gershunov, and D. R. Cayan. 2001. North Pacific decadal climate variability since 1661. Journal of Climate 14(1):5–10.

Bo, S., and O. Hjeljord. 1991. Do continental moose ranges improve during cloudy summers? Canadian Journal of Zoology 69:1875–1879.

Boertje, R. D. 1981. Nutritional ecology of the Denali caribou herd. Thesis, University of Alaska Fairbanks.

Boertje, R. D. 1984. Seasonal diets of the Denali caribou herd. Arctic 37(2):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 2nd North American Caribou Workshop, Val Morin, Quebec, 17–20 October 1984. McGill Subarctic Research Paper No. 40, McGill Subarctic Research Station, Schefferville, Quebec, Canada.

Boertje, R. D., and C. L. Gardner. 1999. Reducing mortality on the Fortymile caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Performance Report 1 July 1998–30 June 1999, Federal Aid in Wildlife Restoration Study 3.43, Juneau.

Boertje, R. D., and C. L. Gardner. 2000a. Reducing mortality on the Fortymile caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Performance Report 1 July 1999–30 June 2000, Federal Aid in Wildlife Restoration Study 3.43, Juneau.

Boertje, R. D., and C. L. Gardner. 2000b. The Fortymile caribou herd: Novel proposed management and relevant biology, 1992–1997. Pages 17–37 [*In*] R. E. Haugerud, editor. Proceedings of 8th North American Caribou Workshop, Whitehorse, Yukon, Canada, 20–24 April 1998. Rangifer, Special Issue 12.

Boertje, R. D., and C. L. Gardner. 2001. Reducing mortality on the Fortymile caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Performance Report 1 July 2000–30 June 2001, Federal Aid in Wildlife Restoration Study 3.43, Juneau.

Boertje, R. D., C. L. Gardner, M. M. Ellis, T. W. Bentzen, and J. A. Gross. *In press*. Demography of an increasing caribou herd with restricted wolf control. Journal of Wildlife Management.

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.

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(3):314–327.

Boertje, R. D., K. A. Kellie, C. T. Seaton, M. A. Keech, D. D. Young, B. W. Dale, L. G. Adams, and A. R. Aderman. 2007. Ranking Alaska moose nutrition: Signals to begin liberal antlerless harvests. Journal of Wildlife Management 71(5):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(3):474–489.

Boone and Crockett Club. 2011. Records of North American Big Game, 13th Edition. Missoula, Montana.

Bos, G. N. 1975. A partial analysis of the current population status of the Nelchina caribou herd. Pages 170–180 [*In*] J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, editors. Proceedings of 1st International Reindeer/Caribou Symposium, 9–11 August 1972. Biological Papers of the University of Alaska, Special Report No. 1, Fairbanks.

Boudreau, T. A. 2001. Units 19A,B,C,D and 21A,E caribou. Pages 114–126 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Braend, M. 1964. Genetic studies on serum transferrins in reindeer. Hereditas 52(2):181–188.

Brewer, M. C. 1976. The western arctic caribou mystery. Unpublished manuscript, Naval Arctic Research Lab, Barrow, Alaska. (Available from Alaska Department of Fish and Game, Fairbanks).

Brooks, P. M., J. Hanks, and J. V. Ludbrook. 1977. Bone marrow as an index of condition in African ungulates. South African Journal of Wildlife Research 7:61–66.

Brown, C., editor. 2005. Caribou management report of survey-inventory activities, 1 July 2002–30 June 2004. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Buchholtz, M. 1974. Unit 20 caribou. Pages 205–211 [*In*] D. E. McKnight, editor. Caribou annual report of survey-inventory activities 1 July 1972–30 June 1973. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration, Job 3.0, Juneau.

Burch Jr., E. S. 2012. Caribou herds of northwest Alaska, 1850–2000. University of Alaska Press, Fairbanks.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: A practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Burris, O. E., and D. E. McKnight. 1973. Game transplants in Alaska. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 4, Juneau.

Butler, H. E. 1986. Mating strategies of woodland caribou (*Rangifer tarandus caribou*). Dissertation, University of Calgary, Ottawa.

Butler, L. 2007. Units 9C and 9E Northern Alaska Peninsula caribou herd. Pages 33–42 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2004–30 June 2006. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Butler, L. 2009a. Unit 10 Unimak herd caribou. Pages 52–57 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Butler, L. 2009b. Unit 9D Southern Alaska Peninsula herd caribou. Pages 43–51 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Butler, L., B. Dale, J. Gude, K. Beckmen, and R. Squibb. 2006. Production and early calf mortality in the Northern Alaska Peninsula Herd, 2005–2006. Final Report. Cooperative Agreement 06-069. Alaska Department of Fish and Game, Division of Wildlife Conservation, Juneau or U. S. Fish and Wildlife Service, Anchorage.

Calenge, C. 2011. Home range estimation in R: The adehabitatHR package. R Foundation for Statistical Computing, Vienna, Austria.

Cameron, R. D. 1994. Reproductive pauses by female caribou. Journal of Mammalogy 75(1):10–13.

Cameron, R. D., and J. L. Davis, editors. 1988. Reproduction and calf survival. Proceedings of 3rd North American Caribou Workshop, Chena Hot Springs, Alaska, 4–6 November 1987. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 8, Fairbanks.

Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Canadian Journal of Zoology 71:480–486.

Cameron, R. D., and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. Journal of Wildlife Management 58(4):674–679.

Cameron, R. D., and R. G. White. 1996. Importance of summer weight gain to the reproductive success of caribou in Arctic Alaska. Page 397 [*In*] R. E. Haugerud, editor. Proceedings of 6th North American Caribou Workshop, 1–4 March 1994, Prince George, British Columbia, Canada and George River Caribou Workshop, 27–29 January 1994, Labrador City, Labrador, Canada. Rangifer, Special Issue 9.

Cameron, R. D., and K. R. Whitten. 1976. First interim report of the effects of the trans-Alaska pipeline on caribou movements. Joint State-Federal Fish and Wildlife Advisory Team, Special Report No. 2, Anchorage.

Cameron, R. D., K. R. Whitten, and W. T. Smith. 1986. Summer range fidelity of radio-collared caribou in Alaska's Central Arctic herd. Pages 51–55 [*In*] A. Gunn, F. L. Miller, and S. Skjenneberg, editors. Proceedings of 4th International Reindeer/Caribou Symposium, 22–25 August 1985. Whitehorse, Yukon, Canada. Rangifer, Special Issue 1.

Carbyn, L. N. 1982. Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park Manitoba. Pages 106–116 [*In*] F. H. Harrington, and P. C. Paquet, editors. Wolves of the world: Perspectives of behavior, ecology and conservation. Noyes Publications, Park Ridge, New Jersey.

Carruthers, D. R. 1985. The myth of the Central Arctic herd [Abstract]. Page 61 [*In*] A. M. Martell, and D. E. Russell, editors. Caribou and human activity. Proceedings of 1st North American Caribou Workshop, 28–29 September 1983, Whitehorse, Yukon. Canadian Wildlife Service, Special Publication, Ottawa.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Pages 183–246 [*In*] T. H. Coaker, editor. Applied Biology, Volume I. Academic Press, London.

Caughley, G. 1979. What is this thing called carrying capacity? Pages 2–8 [*In*] M. S. Boyce and L. D. Hayden-Wing, editors. North American elk: Ecology, behavior, and management. University of Wyoming Press, Laramie.

Caughley, G. 1981. Comments on natural regulation of ungulates (what constitutes a real wilderness?). Wildlife Society Bulletin 9:232–234.

Caughley, G., and A. Gunn. 1993. Dynamics of large herbivores in deserts: Kangaroos and caribou. Oikos 67(1):47–55.

Chapin III, F. S., and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66(2):564–576. doi:10.2307/1940405

Chapman, R. C. 1978. Rabies: Decimation of a wolf pack in arctic Alaska. Science 201:365–367. doi:10.1126/science.566470

Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. New York State Conservationist 3:19–22.

Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. Red deer: Behaviour and ecology of two sexes. University of Chicago Press, Illinois.

Cole, H., V. Colonell, and D. Esch. 1999. The economic impacts and consequences of global climate change on Alaska's infrastructure. Pages 43–56 [*In*] G. Weller and P. A. Anderson, editors. Assessing the consequences of climate change for Alaska and the Bering Sea region. Proceedings of a workshop at the University of Alaska Fairbanks 29–30 October 1998. Center for Global Change and Arctic System Research.

Collins, G. H., M. T. Hinkes, A. R. Aderman, and J. D. Woolington. 2003. Population growth, movements, and status of the Nushagak Peninsula caribou herd following reintroduction, 1988–2000. Pages 143–151 [*In*] R. E. Haugerud, editor. Proceedings of 9th North American Caribou Workshop, 23–27 April 2001, Kuujjuaq, Quebec, Canada. Rangifer, Special Issue 14.

Colson, K. E., K. H. Mager, and K. J. Hundertmark. 2014. Reindeer introgression and the population genetics of caribou in southwestern Alaska. Journal of Heredity 105(5):585–596. doi:10.1093/jhered/esu030

Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant, and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155. doi:10.2193/0084-0173(2004)155[1:EOSNAP]2.0.CO;2

Cook, R. C., J. G. Cook, D. J. Vales, B. K. Johnson, S. M. McCorquodale, L. A. Shipley, R. A. Riggs, L. L. Irwin, S. L. Murphie, B. L. Murphie, K. A. Shoenecker, F. Geyer, P. Briggs Hall, R. D. Spencer, D. A. Immell, D. H. Jackson, B. L. Tiller, P. J, Miller, and L. Schmitz. 2013. Regional and seasonal patterns of nutritional condition and reproduction in elk. Wildlife Monographs 184. doi:10.1002/wmon.1008

Crête, 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. Pages 27–36 [*In*] R. E. Haugerud, editor. Proceedings of 6th North

American Caribou Workshop, 1–4 March 1994, Prince George, British Columbia, Canada and George River Caribou Workshop, 27–29 January 1994, Labrador City, Labrador, Canada. Rangifer, Special Issue 9.

Crête, M., and J. Huot. 1993. Regulation of a large herd of migratory caribou: Summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 71(11):2291–2296. doi:10.1139/z93-321

Cronin, M. A., M. D. MacNeil, and J. C. Patton. 2005. Variation in mitochondrial DNA and microsatellite DNA in caribou (*Rangifer tarandus*) in North America. Journal of Mammalogy 86(3):495–505.

Cronin, M. A., M. D. MacNeil, and J. C. Patton. 2006. Mitochondrial DNA and microsatellite DNA variation in domestic reindeer (*Rangifer tarandus tarandus*) and relationships with wild caribou (*Rangifer tarandus groenlandicus* and *Rangifer tarandus caribou*). Journal of Heredity 97(5):525–530. doi:10.1093/jhered/esl012

Cronin, M. A., J. C. Patton, N. Balmysheva, and M. D. MacNeil. 2003. Genetic variation in caribou and reindeer (*Rangifer tarandus*). Animal Genetics 34(1):33–41. doi:10.1046/j.1365-2052.2003.00927.x

Cronin, M. A., L. Renecker, B. J. Pierson, and J. C. Patton. 1995. Genetic variation in domestic reindeer and wild caribou in Alaska. Animal Genetics 26(6):427–434. doi:10.1111/j.1365-2052.1995.tb02695.x

Curatolo, J. A. 1975. Factors influencing local movements and behavior of barren-ground caribou (*Rangifer tarandus granti*). Thesis, University of Alaska Fairbanks.

Dale, B. W., L. G. Adams, and R. T. Bowyer. 1994. Function response of wolves preying on barren-ground caribou in a multi-prey ecosystem. Journal of Animal Ecology 63:644–652.

Dale, B. W., L. G. Adams, W. B. Collins, K. Joly, P. Valkenburg, and R. Tobey. 2008. Stochastic and compensatory effects limit persistence of variation in body mass of young caribou. Journal of Mammalogy 89(5):1130–1135.

Dau, J. 1986. Distribution and behavior of barren-ground caribou in relation to weather and parasitic insects. Thesis, University of Alaska Fairbanks.

Dau, J. 1999. Western Arctic caribou. Pages 160–185 [*In*] M. V. Hicks. Caribou management report of survey-inventory activities 1 July 1996–30 June 1998. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Dau, J. 2003. Western Arctic caribou. Pages 204–251 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Dau, J. 2009. Western Arctic caribou. Pages 176–239 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Dau, J. 2011. Western Arctic caribou. Pages 187–250 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2008–30 June 2010. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Dauphiné Jr., T. C. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4: Growth, reproduction, and energy reserves. Canadian Wildlife Service Report Series 38, Ottawa.

Davis, J., and D. Preston. 1980. Calf mortality in the Delta caribou herd. Alaska Department of Fish and Game, Division of Game, Research Project Progress Report 1 July 1978–30 June 1979, Federal Aid in Wildlife Restoration Job 3.26R, Juneau.

Davis, J. L. 1976a. Some aspects of human use of the Western Arctic caribou herd. Alaska Department of Fish and Game, Division of Game, Report presented to Alaska State Senate Resources Committee, 17 May 1976, Juneau.

Davis, J. L. 1976b. Partial results of caribou surveys in arctic Alaska. Alaska Department of Fish and Game, Division of Game, Unpublished Report, Fairbanks.

Davis, J. L. 1978. History and current status of Alaska's caribou herds. Pages 1–8 [*In*] D. R. Klein, and R. G. White, editors. Parameters of caribou population ecology in Alaska. Proceedings of a symposium and workshop, 17–19 November 1977. Biological Papers of the University of Alaska, Special Report No. 3, Fairbanks.

Davis, J. L., C. A. Grauvogel, and H. V. Reynolds. 1976. The Western Arctic caribou herd. Staff report to Alaska Board of Game. Alaska Department of Fish and Game, Division of Game, Unpublished Report, Juneau.

Davis, J. L., C. A. Grauvogel, and P. Valkenburg. 1985a. Changes in subsistence harvest of Alaska's Western Arctic caribou herd, 1940–1984. Pages 105–118 [*In*] T. C. Meredith, and A. M. Martell, editors. Proceedings of 2nd North American Caribou Workshop, Val Morin, Quebec, 17–20 October 1984. McGill Subarctic Research Station, McGill Subarctic Research Paper No. 40, Schefferville, Quebec, Canada.

Davis, J. L., R. Shideler, and R. E. LeResche. 1978. Fortymile caribou herd studies. Alaska Department of Fish and Game, Division of Game, Final Research Report 1 July 1973–30 June 1975, Federal Aid in Wildlife Restoration Jobs 3.13R, 3.15R, and 3.16R, Juneau.

Davis, J. L., and P. Valkenburg. 1978. Western Arctic caribou herd studies. Alaska Department of Fish and Game, Division of Game, Final Research Report 1 July 1975–30 June 1977, Federal Aid in Wildlife Restoration Jobs 3.19, 3.20, 3.21R, Juneau.

Davis, J. L., and P. Valkenburg. 1979. Caribou distribution, population characteristics, mortality, and responses to disturbance in Northwest Alaska. Chapter 2 [*In*] P. C. Lent, editor. National Petroleum Reserve in Alaska 105(c), Field Study 3. U.S. Department of Interior, Bureau of Land Management, Fairbanks.

Davis, J. L., and P. Valkenburg. 1981. Yearling mortality in the Delta caribou herd. Alaska Department of Fish and Game, Division of Game, Final Research Report 1 July 1979–30 June 1980, Federal Aid in Wildlife Restoration Job 3.26R, Juneau.

Davis, J. L., and P. Valkenburg. 1985a. Qualitative and quantitative aspects of natural mortality of the Western Arctic caribou herd. Alaska Department of Fish and Game, Division of Game, Final Research Report 1 July 1981–30 June 1984, Federal Aid in Wildlife Restoration Job 3.24R, Juneau.

Davis, J. L., and P. Valkenburg. 1985b. Demography of the Delta caribou herd under varying rates of natural mortality and harvest by humans. Alaska Department of Fish and Game, Division of Game, Final Research Report 1 July 1980–30 June 1984, Federal Aid in Wildlife Restoration Job 3.27R, Juneau.

Davis, J. L., P. Valkenburg, and R. D. Boertje. 1982. Home range use, social structure, and habitat selection of the Western Arctic caribou herd. Final Research Report to U.S. Department of Interior, National Park Service (Contract No. CX 9100-8-0032), Alaska Department of Fish and Game, Division of Game, Juneau.

Davis, J. L., P. Valkenburg, and R. D. Boertje. 1985b. Disturbance and the Delta caribou herd. Pages 2–6 [*In*] A. M. Martell, and D. E. Russell, editors. Caribou and human activity. Proceedings of 1st North American Caribou Workshop, 28–29 September 1983, Whitehorse, Yukon. Canadian Wildlife Service Special Publication, Ottawa, Ontario.

Davis, J. L., P. Valkenburg, and R. D. Boertje. 1986. Empirical and theoretical considerations toward a model for caribou socioecology. Pages 103–109 [*In*] A. Gunn, F. L. Miller, and S. Skjenneberg, editors. Proceedings of 4th International Reindeer/Caribou Symposium, 22–25 August 1985, Whitehorse, Yukon, Canada. Rangifer, Special Issue 1.

Davis, J. L., P. Valkenburg, and S. J. Harbo Jr. 1979. Refinement of the aerial photo-direct count-extrapolation caribou census technique. Alaska Department of Fish and Game, Division of Game, Research Final Report 1 July 1978–30 June 1979, Federal Aid in Wildlife Restoration Job 3.25R, Juneau.

Davis, J. L., P. Valkenburg, M. E. McNay, R. M. Beasley, and V. L. Tutterrow. 1991. Demography of the Delta caribou herd under varying rates of natural mortality and human harvest and assessment of field techniques for acquiring demographic data. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 July 1986–30 June 1990, Federal Aid in Wildlife Restoration Job 3.33, Juneau.

Davis, J. L., P. Valkenburg, and D. J. Reed. 1987. Correlations and depletion patterns of marrow fat in caribou bones. Journal of Wildlife Management 51(2):365–371.

Davis, J. L., P. Valkenburg, and D. J. Reed. 1988. Mortality of Delta herd caribou to 24 months of age. Pages 38–51 [*In*] R. D. Cameron, and J. L. Davis, editors. Reproduction and calf survival. Proceedings of 3rd North American Caribou Workshop, Chena Hot Springs, 4–6 November 1987. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 8, Fairbanks.

Davis, J. L., P. Valkenburg, and H. V. Reynolds. 1980. Population dynamics of Alaska's Western Arctic caribou herd. Pages 595–604 [*In*] E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of 2nd International Reindeer/Caribou Symposium, Røros, Norway, 1979. Direktoratet for vilt og Ferskvannsfisk, Trondheim.

Davitt, B. B. 1979. Elk summer diet composition and quality on the Colockum Multiple Use Research Unit, central Washington. Thesis, Washington State University, Pullman.

Dearden, B. L., R. E. Pegau, and R. M. Hansen. 1975. Precision of microhistological estimates of ruminant food habits. Journal of Wildlife Management 39(2):402–407.

Del Vecchio, P. A., B. Schultz, and L. G. Adams. 1995. Status and distribution of the Tonzona caribou herd, 1988–1991. U.S. Department of the Interior, National Park Service, Unpublished Final Report, Anchorage, Alaska.

Dieterich, R. A. 1980. Current status of reindeer/caribou diseases in Alaska. Pages 438–441 [*In*] E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings of 2nd International Reindeer/Caribou Symposium, Røros, Norway, 1979. Directoratet for vilt og ferskvannsfisk, Trondheim.

Dinneford, W. B. 1983. Unit 18 caribou. Pages 24–27 [*In*] J. A. Barnett, editor. Caribou management report of survey-inventory activities 1 July 1981–30 June 1982. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Doerr, J. G. 1979. Population analysis and modeling of the Western Arctic caribou herd with comparisons to other Alaskan *Rangifer* populations. Thesis, University of Alaska Fairbanks.

Doerr, J. G. 1980. Modeling the population decline of two Alaskan caribou herds. Pages 611–623 [*In*] E. Reimers, E. Gaare, and S. Skjenneberg, editors. Proceedings 2nd International Reindeer/Caribou Symposium, Røros, Norway, 1979. Direktoratet for vilt og ferskvannsfisk, Trondheim.

Doerr, J. G., and R. A. Dieterich. 1979. Mandibular lesions in the Western Arctic caribou herd of Alaska. Journal of Wildlife Diseases 15(2):309–318.

Doerr, J. G., and J. C. Shea. 1979. Observations of hunting waste of caribou in northwestern Alaska. Alaska Department of Fish and Game, Division of Game, Unpublished Manuscript, Fairbanks.

Downes, C. M., J. B. Theberge, and S. M. Smith. 1986. The influence of insects on the distribution, microhabitat choice, and behaviour of the Burwash caribou herd. Canadian Journal of Zoology 64(3):622–629. doi:10.1139/z86-092

Duquette, L. S. 1984. Patterns of activity and their implications to the energy budget of migrating caribou. Thesis, University of Alaska Fairbanks.

Durtsche, B. M., and W. Hobgood. 1990. Distribution, movements and seasonal use areas of caribou in the White Mountains National Recreation Area, Alaska, 1982–1988. U.S. Department of the Interior, Bureau of Land Management BLM-Alaska Open File Report 29, Anchorage.

Eagan, R. M. 1993. Unit 20A caribou. Pages 122–147 [*In*] S. M. Abbott, editor. Caribou management report of survey-inventory activities 1 July 1990–30 June 1992. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Eastland, W. G. 1991. Influence of weather on movements and migrations of caribou. Dissertation. University of Alaska Fairbanks.

Eberhardt, L. L., and K. W. Pitcher. 1992. A further analysis of the Nelchina caribou and wolf data. Wildlife Society Bulletin 20(4):385–395.

Ernst, R. D. 1993. Populations, movements, and seasonal distribution of the Kilbuck caribou herd, Southwest Alaska. Unpublished progress report, U.S. Fish and Wildlife Service, Bethel, Alaska.

Ernst, R. D. 1996. Populations, movements, and seasonal distribution of the Kilbuck caribou herd, Southwest Alaska. Unpublished Final Report. U.S. Fish and Wildlife Service, Bethel, Alaska.

Fancy, S. G. 1986. Daily energy budgets of caribou: A simulation approach. Dissertation, University of Alaska Fairbanks.

Fancy, S. G., and K. R. Whitten. 1991. Selection of calving sites by Porcupine herd caribou. Canadian Journal of Zoology 69:1736–1743.

Fancy, S. G., K. R. Whitten, and D. E. Russell. 1994. Demography of the Porcupine caribou herd, 1983–1992. Canadian Journal of Zoology 72:840–846.

Farnell, R. 2009. Three decades of caribou recovery programs in Yukon: A paradigm shift in wildlife management. Department of Environment, Fish and Wildlife Branch, Government of Yukon, Unpublished paper, Whitehorse, Canada.

Fleischman, S. J. 1990. Lichen availability on the range of an expanding caribou (*Rangifer tarandus*) population in Alaska. Thesis, University of Alaska Fairbanks.

Foley, A. M., R. W. DeYoung, S. D. Lukefahr, J. S. Lewis, D. G. Hewitt, M. W. Hellickson, D. A. Draeger, and C. A. DeYoung. 2012. Repeatability of antler characteristics in mature white-tailed deer in South Texas: Consequences of environmental effects. Journal of Mammalogy 183(2):1149–1157. doi:http: //dx.doi.org/10.1644/11-MAMM-A-183.2.

Franzman, A. W., and P. D. Arneson. 1976. Marrow fat in Alaskan moose femurs in relation to mortality factors. Journal of Wildlife Management 40:336–339.

Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in Northeastern Alberta. Journal of Wildlife Management 44:583–602.

Gardner, C. L. 1993a. Unit 12 Chisana caribou. Pages 62–73 [*In*] S. M. Abbott, editor. Caribou report of survey-inventory activities 1 July 1990–30 June 1992. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Gardner, C. L. 1993b. Units 20B, 20C, 20D, 20E, and 25C Fortymile caribou. Pages 148–164 [*In*] S. M. Abbott, editor. Caribou annual report of survey-inventory activities 1 July 1990–30 June 1992. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Gardner, C. L., and N. J. Pamperin. 2014. Intensive aerial wolf survey operations manual for Interior Alaska. Alaska Department of Fish and Game, Wildlife Special Publication ADF&G/DWC/WSP-2014-01, Fairbanks.

Gasaway, W. C., R. D. Boertje, D. V. Grangaard, D. G. Kelleyhouse, R. O. Stephenson, and D. G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. Wildlife Monographs 120.

Gasaway, W., R. Stephenson, and J. Davis. 1983a. Wolf-prey relationships in Interior Alaska. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin No. 6, Juneau.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983b. Interrelationships of wolves, prey, and man in Interior Alaska. Wildlife Monographs 84.

Gerhart, K. L. 1995. Nutritional and ecological determinants of growth and reproduction in caribou. Dissertation, University of Alaska Fairbanks.

Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. 1996. Body composition and nutrient reserves of arctic caribou. Canadian Journal of Zoology 74:136–146.

Grauvogel, C., and R. Pegau. 1976. Units 23, 24, and 26 caribou. Pages 36–37 [*In*] D. E. McKnight, editor. Annual caribou survey-inventory progress report 1 January 1974—31 December 1974. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Griffith, B., D. C. Douglas, D. E. Russell, R. G. White, T. R. McCabe, and K. R. Whitten. 2000. Effects of recent climate warming on caribou habitat and calf survival [Abstract]. Page 65 [*In*] R. E. Haugerud, editor. Proceedings of 8th North American Caribou Workshop, 20–24 April 1998, Whitehorse, Yukon, Canada. Rangifer, Special Issue 12.

Gronquist, R. M., T. L. Haynes, and C. L. Gardner. 2005. Rebuilding the Fortymile caribou herd: A model of cooperative management planning. Pages 163–175 [*In*] R. E. Haugerud, editor. Proceedings of 10th North American Caribou Workshop, 4–6 May 2004, Girdwood, Alaska. Rangifer, Special Issue 16.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Dissertation, University of British Columbia, Vancouver, Canada.

Hammon, J. 1944. Physiological factors affecting birth weight. Proceedings of the Nutrition Society 2:8–14.

Harbo, S. J., and F. C. Dean. 1983. Historical and current perspectives on wolf management in Alaska. Pages 51–64 [*In*] L. N. Carbyn, editor. Wolves in Canada and Alaska: Their status, biology, and management. Canadian Wildlife Service Report Series 45, Ottawa.

Harper, F. 1955. The barren ground caribou of Keewatin. University of Kansas, Museum of Natural History, Miscellaneous Publication No. 6, Lawrence.

Harper, P., editor. 2007. Caribou management report of survey-inventory activities, 1 July 2004–30 June 2006. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Harper, P., editor. 2009. Caribou management report of survey-inventory activities, 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Harper, P., editor. 2010. Moose management report of survey-inventory activities, 1 July 2007–30 June 2009. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 1.0, Juneau.

Harper, P., editor. 2011. Caribou management report of survey-inventory activities, 1 July 2008–30 June 2010. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Harper, P., editor. 2013. Caribou management report of survey-inventory activities, 1 July 2010–30 June 2012. Alaska Department of Fish and Game, Division of Wildlife Conservation, Species Management Report ADF&G/DWC/SMR-2013-3, Juneau.

Hartmann, B., and G. Wendler. 2005. The significance of the 1976 Pacific climate shift in the climatology of Alaska. Journal of Climate 18:4824–4839.

Hayes, R. D., R. Farnell, R. M. P. Ward, J. Carey, M. Dehn, G. W. Kuzyk, A. M. Baer, C. L. Gardner, and M. O'Donoghue. 2003. Experimental reduction of wolves in the Yukon: Ungulate responses and management implications. Wildlife Monographs 152.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Healy, C., editor. 2001. Caribou management report of survey-inventory activities, 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Healy, C., editor. 2003. Caribou management report of survey-inventory activities, 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. Journal of Animal Ecology 74(2):226–233. doi:10.1111/j.1365-2656.2004.00909.x

Hegel, T. M., A. Mysterud, F. Huettmann, and N. C. Stenseth. 2010. Interacting effect of wolves and climate on recruitment in a northern mountain caribou population. Oikos 19:1453–1461. doi:10.1111/j.1600-0706.2010.18358.x

Helle, T., and L. Tarvainen. 1984. Effects of insect harassment on weight gain and survival in reindeer calves. Rangifer 4(1):24–27.

Hemming, J. E. 1971. The distribution and movement patterns of caribou in Alaska. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin No. 1, Juneau.

Hemming, J. E., and L. P. Glenn. 1968. Caribou annual project segment report, 1 January 1967–31 December 1967. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Study W-15-R-2 and W-15-R-3, Juneau.

Hewitt, D. G., M. W. Hellickson, J. S. Lewis, D. B. Wester, and F. C. Bryant. 2014. Age-related patterns of antler development in free-ranging white-tailed deer. Journal of Wildlife Management 78(6):978–984. doi:10.1002/jwmg.741

Hinkes, M. T. 1989. Populations, movements, and seasonal distribution of the Kilbuck caribou herd, Southwest Alaska. Cooperative study between U.S. Fish and Wildlife Service-Yukon Delta National Wildlife Refuge and the Alaska Department of Fish and Game. Unpublished Report, U.S. Fish and Wildlife Service, Bethel.

Hinkes, M. T., G. H. Collins, L. J. Van Daele, S. D. Kovach, A. R. Aderman, J. D. Woolington, and R. J. Seavoy. 2005. Influence of population growth on caribou herd identity, calving ground fidelity, and behavior. Journal of Wildlife Management 69(3):1147–1162.

Hinkes, M. T., and L. J. Van Daele. 1996. Population growth and status of the Nushagak Peninsula caribou herd in Southwest Alaska following reintroduction, 1988–1993. Pages 301–309 [*In*] R. E. Haugerud, editor. Proceedings of 6th North American Caribou Workshop, 1–4 March 1994, Prince George, British Columbia, Canada and George River Caribou Workshop, 27–29 January 1994, Labrador City, Labrador, Canada. Rangifer, Special Issue 9.

Holleman, D. F., and J. R. Luick. 1977. Lichen species preference by reindeer. Canadian Journal of Zoology 55(8):1368–1369.

Holleman, D. F., J. R. Luick, and R. G. White. 1979. Lichen intake estimates for reindeer and caribou during winter. Journal of Wildlife Management 43(1):193–201.

Huot, J., and M. Beaulieu. 1985. Relationship between parasite infection levels and body fat reserves in George River caribou in spring and fall. Pages 317–327 [*In*] T. C. Meredith and A. M. Martell, editors. Proceedings of 2nd North American Caribou Workshop, Val Morin, Quebec, Canada, 17–20 October 1984. McGill Subarctic Research Paper 40.

Irvine, C. 1976. Population size of the Alaska Peninsula caribou herd. Alaska Department of Fish and Game, Division of Game, Research Final Report 15 January 1974–1 February 1976, Federal Aid in Wildlife Restoration Job 3.17R, Juneau.

Jenkins, K. J. 1996. Population dynamics of the Mentasta caribou herd, Wrangell–St Elias National Park and Preserve: Progress report and preliminary assessment. U.S. National Park Service, WRST Research and Management Report 95-1, Anchorage, Alaska.

Jenkins, K. J., and N. L. Barten. 2005. Demography and decline of the Mentasta caribou herd. Canadian Journal of Zoology 83:1174–1178.

Joly, K., D. R. Klein, D. L. Verbyla, T. S. Rupp, and F. S. Chapin III. 2011. Linkages between large-scale climate patterns and the dynamics of Arctic caribou populations. Ecography 34(2):345–352. doi:10.1111/j.1600-0587.2010.06377.x

Jonrowe, D. A. S. 1979. Unit 18 caribou. Pages 161–162 [*In*] R. A. Hinman, editor. Caribou annual report of survey-inventory activities 1 July 1977–30 June 1978. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Josse, J., J. Pagès, and F. Husson. 2011. Multiple imputation in principal component analysis. Advances in Data Analysis and Classification 5(3):231–246. doi:10.1007/s11634-011-0086-7

Kacyon, R. H. 1992. Unit 18 caribou. Pages 75–80 [*In*] S. M. Abbott, editor. Caribou management report of survey-inventory activities 1 July 1989–30 June 1991. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Kacyon, R. H. 1993. Unit 18 caribou. Pages 101–110 [*In*] S. M. Abbott, editor. Caribou management report of survey-inventory activities 1 July 1990–30 June 1992. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Kacyon, R. H. 1995. Unit 18 Kilbuck caribou. Pages 92–101 [*In*] M. V. Hicks, editor. Caribou management report of survey-inventory activities 1 July 1992–30 June 1994. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64(2):450–462.

Keech, M. A., and P. Valkenburg. 2007. Population dynamics of Interior and Southwest Alaska caribou herds. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Performance Report 1 July 2001–30 June 2007, Federal Aid in Wildlife Restoration Project 3.45, Juneau.

Kelleyhouse, D. G. 1983. Unit 20E Fortymile caribou. Pages 37–40 [*In*] J. A. Barnett, editor. Caribou annual report of survey-inventory activities 1 July 1981–30 June 1982. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Kelleyhouse, R. A. 2001. Calving ground habitat selection: Teshekpuk Lake and Western Arctic caribou herds. Thesis, University of Alaska Fairbanks.

Kelsall, J. P. 1960. Cooperative studies of barren-ground caribou 1957–58. Canadian Wildlife Service, Wildlife Management Bulletin, Series 1, No. 15.

Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Canadian Wildlife Service, Monograph Series No. 3, Ottawa.

Kelsall, J. P. 1975. Warble fly distribution among some Canadian caribou. Pages 509–517 [*In*] J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, editors. Proceedings of 1st International Reindeer and Caribou Symposium, 9–11 August 1972. Institute of Arctic Biology and Alaska Cooperative Wildlife Research Unit, Occasional Paper No. 1, University of Alaska Fairbanks.

Kie, J. G. 1978. Femur marrow fat in white-tailed deer carcasses. Journal of Wildlife Management 42:661–663.

Kistner, T. P., C. E. Trainer, and N. A. Hartmann. 1980. A field technique for evaluating physical condition in deer. Wildlife Society Bulletin 8:11–17.

Klein, D. R. 1964. Range-related growth of deer reflected in skeletal ratios. Journal of Mammalogy 45(2):226–235.

Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. Journal of Wildlife Management 32:351–367.

Klein, D. R. 1970. Tundra ranges north of the boreal forest. Journal of Range Management 23:8–14.

Klein, D. R. 1976. Letter to Governor Jay Hammond, March 25, 1976. Appendix XII [*In*] J. L. Davis, report presented to Alaska State Senate Resources Committee. Alaska Department of Fish and Game, Division of Game, Fairbanks.

Klein, D. R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. Pages 123–130 [*In*] C. Rehbinder, O. Eriksson, and S. Skjenneberg, editors. Proceedings of 5th International Reindeer/Caribou Symposium, Arvidsjaur, Sweden, 18–22 August 1988. Rangifer, Special Issue 3.

Klein, D. R., and M. Shulski. 2009. Lichen recovery following heavy grazing by reindeer delayed by climate warming. Ambio 38:11–16.

Klein, D. R., and R. G. White. 1978. Parameters of caribou population ecology in Alaska. Proceedings of a symposium and workshop, 17–19 November 1977. Special Report No. 3, Biological Papers of the University of Alaska Fairbanks.

Koons, D. N., R. R. Holmes, and J. B. Grand. 2007. Population inertia and its sensitivity to changes in vital rates and population structure. Ecology 88:2857–2867.

Langvatn, R. 1977. Criteria of physical condition, growth and development in Cervidae–suitable for routine studies. Nordic Council for Wildlife Research, Stockholm.

Lantis, M. 1950. The reindeer industry in Alaska. Arctic 3:27–44.

Lawler, J. P., A. J. Magoun, C. T. Seaton, C. L. Gardner, R. D. Boertje, J. M. Ver Hoef, and P. A. Del Vecchio. 2005. Short-term impacts of military overflights on caribou during calving season. Journal of Wildlife Management 69(3):1133–1146.

Leader-Williams, N. 1980. Population dynamics and mortality of reindeer introduced into South Georgia. Journal of Wildlife Management 44(3):640–657. doi:10.2307/3808011

Lenart, E. A. 1997. Effects of weather on caribou forage productivity and nutrition within the range of the Chisana herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 May 1994–30 June 1997, Federal Aid in Wildlife Restoration Study 3.41, Juneau.

Lenart, E. A. 2009. Central Arctic caribou. Pages 299–325 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Lenart, E. A., R. T. Bowyer, J. Ver Hoef, and R. W. Ruess. 2002. Climate change and caribou: Effects of summer weather on forage. Canadian Journal of Zoology 80:664–678. doi:10.1139/Z02-034

Lent, P. 1966. The caribou of northwestern Alaska. Pages 481–517 [*In*] N. J. Wilimovsky and J. N. Wolfe, editors. Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Commission, Washington, D.C.

Lent, P. C. 1964. Calving and related social behaviour in the barren-ground caribou. Dissertation, University of Alberta, Edmonton.

Lent, P. C. 1965. Rutting behaviour in a barren–ground caribou population. Animal Behaviour 13(2–3):259–264.

Lentfer, J. 1965. Caribou report. Alaska Department of Fish and Game, Division of Game, Annual Project Segment Report 1 January 1964–31 December 1964, Federal Aid in Wildlife Restoration Jobs 1–8, Juneau.

Leopold, A. 1948. Game management. Charles Scribner's Sons, New York.

LeResche, R. E. 1975. The international herds: Present knowledge of the Fortymile and Porcupine caribou herds. Pages 127–139 [*In*] J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, editors. Proceedings of 1st International Reindeer-Caribou Symposium, 9–11 August 1972. Biological Papers of the University of Alaska, Special Report No. 1, Fairbanks.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Lieb, J. W. 1989. Nelchina caribou herd. Pages 72–91 [*In*] S. O. Morgan, editor. Caribou management report of survey-inventory activities 1 July 1987–30 June 1988. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Lieb, J. W., W. B. Cella, and R. W. Tobey. 1994. Population dynamics of the Mentasta caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 October 1986–31 March 1990, Juneau.

Lieb, J. W., K. W. Pitcher, and R. W. Tobey. 1988. Optimum population size for the Nelchina caribou herd? Pages 135–145 [*In*] R. D. Cameron, and J. L. Davis, editors. Reproduction and calf survival. Proceedings of 3rd North American Caribou Workshop, Chena Hot Springs, 4–6 November 1987. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 8, Fairbanks.

Lieb, J. W., and B. Tobey. 1990. Units 13 and 14B Nelchina caribou. Pages 66–83 [*In*] S. O. Morgan, editor. Caribou annual report of survey-inventory activities 1 July 1988–30 June 1989. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Lieb, J. W., R. W. Tobey, and S. H. Eide. 1985. Analysis of Nelchina caribou range. Alaska Department of Fish and Game, Division of Game, Unpublished Report, Anchorage.

Machida, S. 1984. Unit 18 Andreafsky and Kilbuck Mountain caribou. Pages 24–25 [*In*] J. A. Barnett, editor. Caribou annual report of survey-inventory activities 1 July 1982–30 June 1983. Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Mager, K. H., K. E. Colson, P. Groves, and K. J. Hundertmark. 2014. Population structure over a broad spatial scale driven by nonanthropogenic factors in a wide-ranging migratory mammal, Alaskan caribou. Molecular Ecology 23(24):6045–6057. doi:10.1111/mec.12999

Magoun, A. J., J. P. Lawler, C. L. Gardner, R. D. Boertje, and J. M. Ver Hoef. 2003. Short-term impacts of military jet overflights on the Fortymile caribou herd during the calving season. Cooperative study between Alaska Department of Fish and Game, National Park Service, and the 11th U.S. Air Force. Alaska Department of Fish and Game, Division of Wildlife Conservation, Fairbanks.

Maier, J. A. K., S. M. Murphy, R. G. White, and M. D. Smith. 1998. Responses of caribou to overflights by low-altitude jet aircraft. Journal of Wildlife Management 62(2):752–766.

Mantua, N. J., and S. R. Hare. 2002. The Pacific Decadal Oscillation. Journal of Oceanography 58(1):35–44. doi:10.1023/A:1015820616384

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

McGowan, T. A. 1966. Arctic, Nelchina, Fortymile, and Adak caribou. Alaska Department of Fish and Game, Division of Game, Work Plan Segment Report 1 January 1965–31 December 1965, Federal Aid in Wildlife Restoration Projects W-6-R-6 and W-15-R-1, Juneau.

McNay, M. E. 1990. Unit 20 Delta and Yanert caribou. Pages 106–119 [*In*] S. O. Morgan, editor. Caribou management report of survey and inventory activities 1 July 1988–30 June 1989. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

McNay, M. E. 1993. Evaluation and standardization of techniques for estimating wolf numbers in Interior and Arctic Alaska. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 July 1992–30 June 1993, Federal Aid in Wildlife Restoration Study 14.15, Juneau.

McNay, M. E. 1998. Investigation of wolf population response to intensive trapping in the presence of high ungulate biomass. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Annual Performance Report 1 July 1997–30 June 1998, Federal Aid in Wildlife Restoration Study 14.17, Juneau.

McNay, M. E. 2000. Unit 20A, 20B, 20C, 20F, and 25C wolf. Pages 151–167 [*In*] M. V. Hicks, editor. Wolf management report of survey and inventory activities 1 July 1996–30 June, 1999. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 14.0, Juneau.

McNay, M. E., and R. A. DeLong. 1998. Development and testing of a general predator-prey computer model for use in making management decisions. Research Final Report, Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 1.46, Juneau.

McNay, M. E., and J. M. Ver Hoef. 2003. Predation by moose and caribou by a regulated wolf population. Alaska Department of Fish and Game, Division of Wildlife Conservation, Final Research Performance Report 1 July 2000–30 June 2003, Federal Aid in Wildlife Restoration Study 14.19, Juneau.

Mech, L. D. 1966. The wolves of Isle Royale. National Park Service, Fauna of the National Parks Series No. 7, Washington, D.C.

Mech, L. D. 1973. Wolf numbers in the Superior National Forest of Minnesota. U.S. Department of Agriculture, Forest Service Research Paper NC-97, North Central Forest Experiment Station, St. Paul, Minnesota.

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.

Mech, L. D., and G. D. DelGiudice. 1985. Limitations of the marrow-fat technique as an indicator of body condition. Wildlife Society Bulletin 13(2):204–206.

Mech, L. D., and R. E. McRoberts. 1990. Survival of white-tailed deer fawns in relation to maternal age. Journal of Mammalogy 71(3):465–467. doi:10.2307/1381963

Mech, L. D., R. E. McRoberts, R. O. Peterson, and R. E. Page. 1987. Relationship of deer and moose populations to previous winters' snow. Journal of Animal Ecology 56(2):615–627.

Menard, S. 2000. Coefficients of determination for multiple logistic regression analysis. The American Statistician 54(1):17–24. doi:10.1080/00031305.2000.10474502

Messier, F., J. Huot, D. Le Henaff, and S. Luttich. 1988. Demography of the George River caribou herd: Evidence of population regulation by forage exploitation and range expansion. Arctic 41(4):279–287.Miller, D. R. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 3: Taiga winter range relationships and diet. Canadian Wildlife Service Report Series 36, Ottawa.

Miller, F. L. 1974. Biology of the Kaminuriak population of barren-ground caribou. Part 2: Dentition as an indicator of age and sex composition and socialization of the population. Canadian Wildlife Service Report Series 31, Ottawa.

Miller, F. L. 1978. Numbers and distribution of Peary caribou on the arctic islands of Canada. Pages 16–19 [*In*] D. R. Klein and R. G. White, editors. Parameters of caribou population ecology in Alaska. Proceedings of a symposium and workshop, 17–19 November 1977. Biological Papers of the University of Alaska, Special Report No. 3, Fairbanks.

Miller, F. L., S. J. Barry, and W. A. Calvert. 2005. St. Matthew Island reindeer crash revisited: Their demise was not nigh—but then, why did they die? Pages 185–197 [*In*] R. E. Haugerud, editor. Proceedings of 10th North American Caribou Workshop, 4–6 May 2004, Girdwood, Alaska. Rangifer, Special Issue 16.

Miller, G. 1994. Caribou survey Andreafsky Mountains, Alaska, December 1993. U.S. Fish and Wildlife Service, Yukon Delta National Wildlife Refuge, Unpublished Report, Bethel.

Montieth, K. L., R. A. Long, V. C. Bleich, J. R. Heffelfinger, P. R. Krauseman, and R. T. Bowyer. 2012. Effects of harvest, culture, and climate on trends in size of horn-like structures in trophy ungulates. Wildlife Monographs 183.

Mörschel, F. M. 1996. Effects of weather and parasitic insects on summer ecology of caribou of the Delta herd. Thesis, University of Alaska Fairbanks.

Mörschel, F. M. 1999. Use of climatic data to model the presence of oestrid flies in caribou herds. Journal of Wildlife Management 63(2):588–593.

Mörschel, F. M., and D. R. Klein. 1997. Effects of weather and parasitic insects on behavior and group dynamics of caribou of the Delta herd, Alaska. Canadian Journal of Zoology 75:1659–1670.

Moser, T. J., T. H. Nash III, and J. N. Thomson. 1979. Lichens of Anaktuvuk Pass, Alaska, with emphasis on the impact of caribou grazing. The Bryologist 82(3):393–408.

Murie, O. J., and V. B. Scheffer. 1959. Fauna of the Aleutian Islands and Alaska Peninsula: Invertebrates and fishes collected in the Aleutians, 1936–38. North American Fauna 61.

Murphy, S. M., M. D. Smith, R. G. White, J. A. Kitchens, B. A. Kugler, and D. S. Barber. 1993. Behavioral responses of caribou to low-altitude jet aircraft. Armstrong Laboratory, Air Force Material Command, Final Report April 1989–December 1993, Wright-Patterson Air Force Base, Ohio.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4(2):133–142. doi:10.1111/j.2041-210x.2012.00261.x

National Research Council. 1997. Wolves, bears, and their prey in Alaska: Biological and social challenges in wildlife management. National Academies Press, Washington, D.C.

National Weather Service. 2011. Climatological data. National Oceanic and Atmospheric Administration, National Climatic Data Center, Asheville, North Carolina.

National Weather Service. 2012. Fairbanks greenup data (a.k.a. “Anderson-Fathauer Index”). National Oceanic and Atmospheric Administration, Unpublished Data, Fairbanks.

Neiland, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. Journal of Wildlife Management 34(4):904–907. doi:10.2307/3799158

Neiland, K. A. 1972. Caribou disease studies. Alaska Department of Fish and Game, Division of Game, Research Final Report 1 January 1970–30 June 1971, Federal Aid in Wildlife Restoration Job 18.1R, Juneau.

Neiland, K. A., and C. Dukeminier. 1972. A bibliography of the parasites, diseases, and disorders of several important wild ruminants in the northern hemisphere. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 3, Juneau.

Neiland, K. A., J. A. King, B. E. Huntley, and R. O. Skoog. 1968. The diseases and parasites of Alaskan wildlife populations. Part 1: Some observations on brucellosis in caribou. Bulletin of the Wildlife Disease Association 4(2):27–36. doi:10.7589/0090-3558-4.2.27

Nowosad, R. F. 1975. Reindeer survival in the MacKenzie Delta herd, birth to four months. Pages 199–208 [*In*] J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, editors. Proceedings of 1st International Reindeer and Caribou Symposium, 9–11 August 1972. Institute of Arctic Biology and Alaska Cooperative Wildlife Research Unit, Occasional Paper No. 1, University of Alaska Fairbanks.

O’Connor, R. M. 1979. Buckland report: History of caribou use of the Buckland/Selawik winter range and other areas south of the Brooks Range. Alaska Department of Fish and Game, Division of Game, Unpublished Report, Fairbanks.

Olson, S. T. 1957. Management studies of Alaska caribou: Movements, distribution and numbers - Steese Fortymile herd. Pages 45–48 [*In*] R. F. Scott, editor. Caribou management studies. U.S. Fish and Wildlife Service, Alaska Game Commission, Job Completion Report 31 March 1956–30 April 1957, Federal Aid in Wildlife Restoration Job 2-b, Juneau.

Orth, D. J. 1967. Dictionary of Alaska place names. U.S. Department of the Interior, Geological Survey Professional Paper 567. U.S. Government Printing Office, Washington, D.C.

Ozoga, J. J., and L. J. Verme. 1982. Physical and reproductive characteristics of a supplementally-fed white-tailed deer herd. Journal of Wildlife Management 46(2):281–301. doi:10.2307/3808640

Ozoga, J. J., and L. J. Verme. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. Journal of Wildlife Management 50(3):480–486. doi:10.2307/3801110

Palmer, L. J. 1934. Raising reindeer in Alaska. U.S. Department of Agriculture, Miscellaneous Publication 207, Washington, D.C.

Pálsson, H., and J. B. Vergés. 1952. Effects of the plane of nutrition on growth and the development of carcass quality in lambs, Part I: The effects of high and low planes of nutrition at different ages. Journal of Agricultural Science 42(1–2):1–92.

Parker, G. R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part 1: Total numbers, mortality, recruitment, and seasonal distribution. Canadian Wildlife Service Report Series 20, Ottawa.

Parker, G. R., and S. Luttich. 1986. Characteristics of the wolf (*Canis lupus labradorius Goldman*) in Northern Quebec and Labrador. Arctic 39:145–149.

Patten Jr., S. 1985. Unit 18 caribou. Pages 23–28 [*In*] A. Seward, editor. Caribou annual report of survey-inventory activities 1 July 1983–30 June 1984, Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Patten Jr., S. 1990. Unit 18 caribou. Pages 96–100 [*In*] S. O. Morgan, editor. Caribou annual report of survey–inventory activities 1 July 1988–30 June 1989, Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Patten Jr., S. M. 1986. Unit 18 caribou. Pages 20–22 [*In*] B. Townsend, editor. Caribou annual report of survey-inventory activities 1 July 1984–30 June 1985, Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Patten Jr., S. M. 1987. Unit 18 caribou. Pages 24–29 [*In*] B. Townsend, editor. Caribou annual report of survey-inventory activities 1 July 1985–30 June 1986, Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Patten Jr., S. M. 1988. Unit 18 caribou. Pages 36–39 [*In*] S. O. Morgan, editor. Caribou annual report of survey-inventory activities 1 July 1986–30 June 1987, Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Job 3.0, Juneau.

Patten Jr., S. M. 1989. Unit 18 caribou. Pages 94–99 [*In*] S. O. Morgan, editor. Caribou annual report of survey–inventory activities 1 July 1987–30 June 1988, Alaska Department of Fish and Game, Division of Game, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Patten Jr., S. M. 1997. Unit 18 caribou. Pages 98–107 [*In*] M. V. Hicks, editor. Caribou management report of survey-inventory activities 1 July 1994–30 June 1996, Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Pegau, R. E. 1972. Analysis of the Nelchina caribou range. Alaska Department of Fish and Game, Division of Game, Unpublished report, Nome.

Pegau, R. E. 1974. Caribou report. Alaska Department of Fish and Game, Division of Game, Research Progress Report 1 January 1973–31 December 1973, Federal Aid in Wildlife Restoration Jobs 3.3R and 3.5R, Juneau.

Pegau, R. E., G. N. Bos, and K. A. Neiland. 1973. Caribou report. Alaska Department of Fish and Game, Division of Game, Research Progress Report 1 January 1972–31 December 1972, Federal Aid in Wildlife Restoration Jobs 3.3R, 3.5R, 3.8R, and 3.9R, Juneau.

Pegau, R. E., and J. E. Hemming. 1972. Caribou report. Alaska Department of Fish and Game, Division of Game, Research Progress Report 1 January 1970–31 December 1970, Federal Aid in Wildlife Restoration Jobs 3.1R, 3.3R, 3.4R, 3.5R, and 3.6R, Juneau.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Department of Interior, National Park Service, Scientific Monograph Series No. 11, Washington, D.C.

Pettorelli, N. 2013. The normalized difference vegetation index. Oxford University Press, New York.

Pitcher, K. W. 1987. Susitna Hydroelectric Project, Volume IV: Caribou. Alaska Department of Fish and Game, Division of Game, Final Report, Anchorage.

Pitcher, K. W. 1991. Nutritional status of the Southern Alaska Peninsula, Nelchina, and other Southcentral Alaska caribou herds. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Progress Report 1 July 1990–30 June 1991, Federal Aid in Wildlife Restoration Study 3.36, Juneau.

Pitcher, K. W., C. Dau, D. Johnson, D. Sellers, and R. West. 1990. Causes of low calf recruitment in the Southern Alaska Peninsula caribou herd and recent herd history. Research Progress Report on a cooperative project between Alaska Department of Fish and Game – Division of Wildlife Conservation and U.S. Fish and Wildlife Service – Izembeck National Wildlife Refuge. Alaska Department of Fish and Game, Juneau.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Høye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E. Schindler, I. Stirling, M. P. Tamstorf, N. J. C. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt, and P. Aastrup. 2009. Ecological dynamics across the arctic associated with recent climate change. Science 325:1355–1358. doi:10.1126/science.1173113

Post, E., and D. R. Klein. 1999. Caribou calf production and seasonal range quality during a population decline. Journal of Wildlife Management 63(1):335–345. doi:10.2307/3802517

Post, E. S. 1995. Comparative foraging ecology and social dynamics of caribou (*Rangifer tarandus*). Dissertation, University of Alaska Fairbanks.

R Development Core Team. 2007. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rearden, J. 1998. Alaska’s wolf man: The 1915–1955 wilderness adventures of Frank Glaser. Alaska Northwest Books.

Reimers, E. 1972. Growth in domestic and wild reindeer in Norway. Journal of Wildlife Management 36:612–619.

Reimers, E. 1983. Reproduction of wild reindeer in Norway. Canadian Journal of Zoology 61:211–217.

Reimers, E. 1997. *Rangifer* population ecology: A Scandinavian perspective. Rangifer 17(3):105–118. doi:10.7557/2.17.3.1359

Reimers, E., D. R. Klein, and R. Sørumgård. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. Arctic and Alpine Research 15(1):107–118. doi:10.2307/1550986

Reiswig, B. 1981. Caribou herd productivity and range investigation. U.S. Fish and Wildlife Service, Alaska Maritime National Wildlife Refuge, Unpublished Study Outline, Anchorage.

Riley, M. 2011a. Unit 9D Southern Alaska Peninsula caribou. Pages 44–52 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2008–30 June 2010. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Riley, M. 2011b. Unit 10 Unimak caribou. Pages 53–59 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2008–30 June 2010. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Riney, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. New Zealand Journal of Science and Technology 36:429–463.

Riney, T. 1960. A field technique for assessing physical condition of some ungulates. Journal of Wildlife Management 24(1):92–94. doi:10.2307/3797362

Robinson, S. R. 1985. Status of the Ray Mountains caribou herd. U.S. Department of the Interior, Bureau of Land Management, BLM-Alaska Open File Report 12, Fairbanks.

Røed, K. H., Ø. Holand, H. Gjøstein, and H. Hansen. 2005. Variation in male reproductive success in a wild population of reindeer. Journal of Wildlife Management 69(3):1163–1170.

Røed, K. H., and K. R. Whitten. 1986. Transferrin variation and evolution of Alaskan reindeer and caribou, *Rangifer tarandus* L. Pages 247–251 [*In*] A. Gunn, F. L. Miller, and S. Skjenneberg, editors. Proceedings of 4th International Reindeer-Caribou Symposium, Whitehorse, Yukon, Canada, 22–25 August 1985. Rangifer, Special Issue 1.

Roffler, G. H., L. G. Adams, S. L. Talbot, G. K. Sage, and B. W. Dale. 2012. Range overlap and individual movements during breeding season influence genetic relationships of caribou herds in south-central Alaska. Journal of Mammalogy 93(5):1318–1330. doi:10.1644/11-MAMM-A-275.1

Saperstein, L. B. 1997. Distribution, movements, and population status of the Galena Mountain caribou herd, Alaska, April 1992–November 1996. U.S. Fish and Wildlife Service, Progress Report, Galena.

Scott, R. F., E. F. Chatelain, and W. A. Elkins. 1950. The status of Dall sheep and caribou in Alaska. Transactions of the North American Wildlife Conference 15:612–626.

Seaton, C. T. 2009. Unit 20A caribou. Pages 122–135 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Seavoy, R. 1999. Unit 18 caribou. Pages 97–104 [*In*] M. V. Hicks, editor. Caribou management report of survey-inventory activities 1 July 1996–30 June 1998. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Seavoy, R. 2001. Unit 18 caribou. Pages 106–113 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70:1494–1503.

Self, S., J-X. Zhao, R. E. Holasek, R. C. Torres, and A. J. King. 1996. The atmospheric impact of the 1991 Mount Pinatubo eruption. [*In*] C. G. Newhall and R. S. Punongbayan, editors. Fire and mud: Eruptions and lahars of Mt Pinatubo, Philippines. Philippine Institute of Volcanology and Seismology, Quezon City. University of Washington Press, Seattle. http://pubs.usgs.gov/pinatubo/self/index.html (Accessed 12 October 2016).

Selinger, J. 2003. Units 7 and 15 caribou. Pages 1–33 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Sellers, R. A. 1995. Northern Alaska Peninsula herd caribou. Pages 38–46 [*In*] M. V. Hicks, editor. Caribou management report of survey–inventory activities 1 July 1992–30 June 1994. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Sellers, R. A. 1997. Northern Alaska Peninsula herd caribou. Pages 37–48 [*In*] M. V. Hicks, editor. Caribou management report of survey–inventory activities 1 July 1994–30 June 1996. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Sellers, R. A. 2001. Northern Alaska Peninsula herd caribou. Pages 39–49 [*In*] C. Healy, editor. Caribou management report of survey–inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Sellers, R. A., P. Valkenburg, B. W. Dale, R. C. Squibb, and M. Roy. 1999. Survival, natality, and calf weights of caribou on the Alaska Peninsula, 1998–99. Alaska Department of Fish and Game, Division of Wildlife Conservation and U.S. Fish and Wildlife Service, Anchorage. Final Report, 1 October 1998–30 September 1999, Cooperative Agreement 99-017, Juneau.

Sellers, R. A., P. Valkenburg, R. C. Squibb, B. W. Dale, and R. L. Zarnke. 2003. Natality and calf mortality of the Northern Alaska Peninsula and Southern Alaska Peninsula caribou herds. Pages 161–166 [*In*] R. E. Haugerud, editor. Proceedings of 9th North American Caribou Workshop, 23–27 April 2001, Kuujjuaq, Québec, Canada. Rangifer, Special Issue 14.

Sellers, R. A., P. Valkenburg, R. L. Zarnke, and R. C. Squibb. 1998a. Natality and early calf mortality of Northern Alaska Peninsula caribou, 1997–98. Alaska Department of Fish and Game, Division of Wildlife Conservation and U.S. Fish and Wildlife Service, Anchorage. Final Report, 1 October 1997–30 September 1998, Cooperative Agreement 98-079, Juneau.

Sellers, R. A., P. Valkenburg, R. L. Zarnke, R. C. Squibb, and M. Roy. 1998b. Fall sex/age composition, body condition, disease screening, and collaring of Northern and Southern Alaska Peninsula caribou herds, 1998. Alaska Department of Fish and Game, Division of Wildlife Conservation and U.S. Fish and Wildlife Service, Anchorage. Final Report, 1 October 1997–30 September 1998, Cooperative Agreement 99-014, Juneau.

Shaw, G. E., and K. A. Neiland. 1973. Electrocution of a caribou herd caused by lightning in central Alaska. Journal of Wildlife Diseases 9(4):311–313.

Shea, J. C. 1979. Social behaviour of wintering caribou in northwestern Alaska. Thesis, University of Alaska Fairbanks.

Singer, F. J. 1984. Problem analysis into the decline of the Denali caribou herd. Unpublished report of the Advisory Committee to the Superintendent of Denali National Park and Preserve. (Available from ADF&G, Fairbanks).

Singer, F. J. 1987. Dynamics of caribou and wolves in Denali National Park. Proceedings of the Toward the Year 2000 Conference on Science in the National Parks, Fort Collins, Colorado, 1986. Published by the George Wright Society and The National Park Service, Washington, D.C.

Singer, F. J., A. Harting, K. K. Symonds, and M. B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. Journal of Wildlife Management 61(1):12–25.

Siniff, D. B., and R. O. Skoog. 1964. Aerial censusing of caribou using stratified random sampling. Journal of Wildlife Management 28(2):391–401.

Skogland, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. Oecologia 60(2):156–168.

Skogland, T. 1984. The effects of food and maternal conditions on fetal growth and size in wild reindeer. Rangifer 4(2):39–46.

Skogland, T. 1985. The effects of density-dependent resource limitations on the demography of wild reindeer. Journal of Animal Ecology 54(2):359–374.

Skogland, T. 1990. Density dependence in a fluctuating wild reindeer herd: Maternal vs. offspring effects. Oecologia 84(4):442–450.

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

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

Spraker, T. H. 1992. Reintroduction of caribou to the central and southern Kenai Peninsula, 1985–86. Alaska Department of Fish and Game, Division of Wildlife Conservation Wildlife Technical Bulletin 9, Juneau.

Spraker, T. H. 1995. Units 7 and 15 caribou. Pages 1–21[*In*] M. V. Hicks, editor. Caribou management report of survey-inventory activities 1 July 1992—30 June 1994. Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Spraker, T. H. 2001. Units 7 and 15 caribou. Pages 1–22 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Stephenson, R. O., D. G. Ritter, and C. A. Nielsen. 1982. Serologic survey for canine distemper and infectious canine hepatitis in wolves in Alaska. Journal of Wildlife Diseases 18(4):419–424. doi:10.7589/0090-3558-18.4.419

Stern, R. O., E. L. Arobio, L. L. Naylor, and W. C. Thomas. 1980. Eskimos, reindeer and land. University of Alaska, Agricultural Experiment Station Bulletin 59, Fairbanks.

Thing, H. 1977. Behavior, mechanics, and energetics with winter cratering by caribou in northwestern Alaska. Biological Paper 18, University of Alaska Fairbanks.

Tobey, B. 1993. Units 13 and 14B Nelchina caribou. Pages 86–100 [*In*] S. M. Abbott, editor. Caribou management report of survey-inventory activities 1 July 1990–30 June 1992. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Tobey, B. 1999. Units 13 and 14B Nelchina caribou. Pages 80–96 [*In*] M. V. Hicks, editor. Caribou management report of survey-inventory activities 1 July 1996–30 June 1998. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Tobey, B. 2001. Units 13 and 14B Nelchina caribou. Pages 90–105 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Tobey, B. 2003. Units 13 and 14B Nelchina caribou. Pages 108–124 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 3.0, Juneau.

Tobey, B., and R. Schwanke. 2009. Units 13 and 14B Nelchina caribou. Pages 83–98 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2006–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Tobey, R. W. 2000. Unit 13 wolf. Pages 80–87 [*In*] M. V. Hicks, editor. Wolf management report of survey-inventory activities 1 July 1996–30 June 1999. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 14.0, Juneau.

Valkenburg, P. 1992. Central Arctic caribou. Pages 187–198 [*In*] S. M. Abbott, editor. Caribou management report of survey-inventory activities 1 July 1989–30 June 1991. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration, Study 3.0, Juneau.

Valkenburg, P. 1997. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 July 1991–30 June 1996, Federal Aid in Wildlife Restoration Study 3.37, Juneau.

Valkenburg, P. 1998. Herd size, distribution, harvest, management issues, and research priorities relevant to caribou herds in Alaska. Pages 125–129 [*In*] R. E. Haugerud, editor. Proceedings of 7th North American Caribou Conference, 19–21 August 1996, Thunder Bay, Ontario, Canada. Rangifer, Special Issue 10.

Valkenburg, P. 2001. Stumbling towards enlightenment: Understanding caribou dynamics. Alces 37(2):457–474.

Valkenburg, P., D. A. Anderson, J. L. Davis, and D. J. Reed. 1985. Evaluation of an aerial photocensus technique for caribou based on radio-telemetry. Pages 287–299 [*In*] T. C. Meredith, and A. M. Martell, editors. Proceedings of 2nd North American Caribou Workshop, Val Morin, Quebec, 17–20 October 1984. McGill Subarctic Research Station, Research Paper No. 40, Schefferville, Quebec, Canada.

Valkenburg, P., R. D. Boertje, and J. L. Davis. 1983a. Effects of darting and netting on caribou in Alaska. Journal of Wildlife Management 47(4):1233–1237.

Valkenburg, P., and J. L. Davis. 1985. The reaction of caribou to aircraft: A comparison of two herds. Pages 7–9 [*In*] A. M. Martell, and D. E. Russell, editors. Caribou and human activity. Proceedings of 1st North American caribou workshop, Whitehorse, Yukon, 28–29 September 1983, Canadian Wildlife Service, Special Publication, Ottawa, Ontario.

Valkenburg, P., and J. L. Davis. 1986. Calving distribution of Alaska's Steese-Fortymile caribou herd: A case of infidelity? Pages 315–323 [*In*] A. Gunn, F. L. Miller, and S. Skjenneberg, editors. Proceedings of 4th International Reindeer-Caribou Symposium, 22–25 August 1985, Whitehorse, Yukon, Canada. Rangifer, Special Issue 1.

Valkenburg, P., J. L. Davis, and P. F. Karczmarczyk. 1983b. Historical movements and distribution of the Western Arctic caribou herd—an overview, 1983. Alaska Department of Fish and Game, Division of Game, Unpublished Report, Fairbanks.

Valkenburg, P., J. L. Davis, and D. J. Reed. 1988. Distribution of radio-collared caribou from the Delta and Yanert herds during calving. Pages 14–25 [*In*] R. D. Cameron and J. L. Davis, editors. Reproduction and calf survival. Proceedings of 3rd North American Caribou Workshop, Chena Hot Springs, Alaska, 4–6 November 1987. Alaska Department of Fish and Game, Division of Game, Wildlife Technical Bulletin 8, Fairbanks.

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. 1996a. Population decline in the Delta caribou herd with reference to other Alaskan herds. Pages 53–62 [*In*] R. E. Haugerud, editor. Proceedings of 6th North American Caribou Workshop, Prince George, British Columbia, 1–4 March 1994 and Proceedings of George River Caribou Workshop, Labrador City, Labrador, 27–29 January 1994, Canada. Rangifer, Special Issue 9.

Valkenburg, P., M. A. Keech, R. A. Sellers, R. W. Tobey, and B. W. Dale. 2002. Investigation of regulating and limiting factors in the Delta caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 July 1996–30 June 2002, Federal Aid in Wildlife Restoration Project 3.42, Juneau.

Valkenburg, P., D. G. Kelleyhouse, J. L. Davis, and J. M. Ver Hoef. 1994. Case history of the Fortymile caribou herd, 1920–1990. Rangifer 14(1):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(3):746–756.

Valkenburg, P., K. W. Pitcher, D. J. Reed, E. F. Becker, J. R. Dau, D. N. Larsen, and J. L. Davis. 1991. Density dependent responses in mandible length, calving date, and recruitment in three Alaskan caribou herds. Pages 288–298 [*In*] C. Butler, and S. P. Mahoney, editors. Proceedings of 4th North American Caribou Workshop, 31 October–3 November 1989, St. John's, Newfoundland. Newfoundland and Labrador Wildlife Division, Canada.

Valkenburg, P., R. A. Sellers, R. C. Squibb, J. D. Woolington, A. R. Aderman, and B. W. Dale. 2003a. Population dynamics of caribou herds in southwestern Alaska. Pages 131–142 [*In*] R. E. Haugerud, editor. Proceedings of 9th North American Caribou Workshop, 23–27 April 2001, Kuujjuaq, Quebec, Canada. Rangifer, Special Issue 14.

Valkenburg, P., T. H. Spraker, M. T. Hinkes, L. H. Van Daele, R. W. Tobey, and R. A. Sellers. 2000. Increases in body weight and nutritional status of transplanted Alaskan caribou. Pages 133–138 [*In*] R. E. Haugerud, editor. Proceedings of 8th North American Caribou Workshop, 20–24 April 1998, Whitehorse, Yukon, Canada. Rangifer, Special Issue 12.

Valkenburg, P., R. W. Tobey, B. W. Dale, B. D. Scotton, and J. M. Ver Hoef. 2003b. Body size of female calves and natality rates of known-aged females in two adjacent Alaskan caribou herds, and implications for management. Pages 203–209 [*In*] R. E. Haugerud, editor. Proceedings of 9th North American Caribou Workshop, 23–27 April 2001, Kuujjuaq, Quebec, Canada. Rangifer, Special Issue 14.

Valkenburg, P., R. W. Tobey, and D. Kirk. 1999. Velocity of tranquilizer darts and capture mortality of caribou calves. Wildlife Society Bulletin 27(4):894–896.

Valkenburg, P., J. M. Ver Hoef, and R. L. Zarnke. 1996b. Investigation and improvement of techniques for monitoring recruitment, population trend, and nutritional status in the Western Arctic caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 July 1992–30 June 1996, Federal Aid in Wildlife Restoration Study 3.40, Juneau.

Van Ballenberghe, V. 1980. Utility of multiple equilibrium concepts applied to population dynamics of moose. Pages 571–586 [*In*] R. R. Stewart, editor. Proceedings of 16th North American Moose Conference and Workshop, 1–4 April 1980, Prince Albert, Saskatchewan, Canada. Alces.

Van Ballenberghe, V. 1985. Wolf predation on caribou: The Nelchina herd case history. Journal of Wildlife Management 49(3):711–720.

Ver Hoef, J. 2012. From Galton to generalized linear models: The rise and fall of R^2. Unpublished Manuscript. (Available from the author).

Ver Hoef, J. M., P. Valkenburg, and J. R. Dau. 2001. Modeling growth of mandibles in the Western Arctic caribou herd. Rangifer 21(1):29–34.

Verme, L. J., and D. E. Ullrey. 1984. Physiology and nutrition. Pages 91–118 [*In*] L. K. Halls, editors. White-tailed deer: Ecology and management. Stackpole Books, Harrisburg, Pennsylvania.

Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. Global Change Biology 15(11):2626–2633. doi:10.1111/j.1365-2486.2009.01974.x

Washburn, R. H., L. J. Klebesadel, J. S. Palmer, J. R. Luick, and D. P. Bleicher. 1980. The warble fly problem in Alaska reindeer. Agroborealis 12(1):23–28.

Watson, G. W., and R. F. Scott. 1956. Aerial censusing of the Nelchina caribou herd. Transactions of the North American Wildlife Conference 21:499–510.

Weiler, G. J., G. W. Garner, and D. G. Ritter. 1995. Occurrence of rabies in a wolf population in northeastern Alaska. Journal of Wildlife Diseases 31(1):79–82.

Whitten, K. R. 1995a. Influence of body condition on productivity of adult female caribou in the Porcupine caribou herd. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 1 July 1992–31 December 1994, Federal Aid in Wildlife Restoration Study 3.39, Juneau.

Whitten, K. R. 1995b. Antler loss and udder distention in relation to parturition in caribou. Journal of Wildlife Management 59(2):273–277.

Whitten, K. R., G. W. Garner, F. J. Mauer, and R. B. Harris. 1992. Productivity and early calf survival in the Porcupine caribou herd. Journal of Wildlife Management 56(2):201–212.

Wolfe, R. J., and M. Pete. 1984. Use of caribou and reindeer in the Andreafsky Mountains. Alaska Department of Fish and Game, Division of Subsistence, Technical Paper 98, Bethel.

Woolington, J. D. 1999. Units 9B, 17, 18(S), 19A, and 19B Mulchatna caribou. Pages 21–34 [*In*] M. V. Hicks, editor. Caribou management report of survey-inventory activities 1 July 1996–30 June 1998. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Woolington, J. D. 2001. Units 9B, 17, 18(S), 19A, and 19B Mulchatna caribou. Pages 23–38 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 1998–30 June 2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Woolington, J. D. 2003. Units 9B, 17, 18(S), 19A, and 19B Mulchatna caribou. Pages 34–52 [*In*] C. Healy, editor. Caribou management report of survey-inventory activities 1 July 2000–30 June 2002. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Woolington, J. D. 2007. Units 9B, 17, 18(S), 19A, and 19B Mulchatna caribou. Pages 14–32 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2004–30 June 2006. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Woolington, J. D. 2011. Units 9B, 17, 18 south, 19A, and 19B Mulchatna caribou. Pages 11–32 [*In*] P. Harper, editor. Caribou management report of survey-inventory activities 1 July 2008–30 June 2010. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 3.0, Juneau.

Young, D. D. 2000. Units 20A, 20B, 20C, 20F, and 25C wolf. Pages 151–167 [*In*] M. V. Hicks, editor. Wolf management report of survey-inventory activities 1 July 1996–30 June 1999. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Study 14.0, Juneau.

Young, D. D. 2006. Units 20A, 20B, 20C, and 20F wolf . Pages 154–165 [*In*] P. Harper, editor. Wolf management report of survey-inventory activities 1 July 2002–30 June 2005. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 14.0, Juneau.

Young, D. D. 2009. Units 20A, 20B, 20C, and 20F wolf. Pages 162–173 [*In*] P. Harper, editor. Wolf management report of survey-inventory activities 1 July 2005–30 June 2008. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 14.0, Juneau.

Young, D. D. 2010. Unit 20A moose. Pages 320–344 [*In*] P. Harper, editor. Moose management report of survey-inventory activities 1 July 2007–30 June 2009. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 1.0, Juneau.

Young, D. D., and R. D. Boertje. 2011. Prudent and imprudent use of antlerless moose harvests in Interior Alaska. Alces 47:91–100.

Yuan, Y. C. 2010. Multiple imputation for missing data: Concepts and new development (Version 9.0). SAS Institute Inc., Rockville, Maryland.

Zarnke, R. L. 1996. Serologic survey of Alaska wildlife for microbial pathogens. Alaska Department of Fish and Game, Division of Wildlife Conservation, Final Research Report 1 July 1991–20 April 1996, Federal Aid in Wildlife Restoration Study 18.70, Juneau.

Zarnke, R. L. 1997. Serologic survey of Alaska wildlife for microbial pathogens. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Progress Report 1 July 1996–30 June 1997, Federal Aid in Wildlife Restoration 18.71, Juneau.

Zarnke, R. L. 2000. Alaska wildlife serologic survey, 1975–2000. Alaska Department of Fish and Game, Division of Wildlife Conservation, Research Final Report 20 April 1996–20 April 2000, Federal Aid in Wildlife Restoration Study 18.71, Juneau.

Zittlau, K. 2004. Population genetic analyses of North American caribou. Dissertation, University of Alberta, Edmonton.

Zittlau, K., J. Coffin, R. Farnell, G. Kuzyk, and C. Strobeck. 2000. Genetic relationships of three Yukon caribou herds determined by DNA typing. Pages 59–62 [*In*] R. E. Haugerud, editor. Proceedings of 8th North American Caribou Workshop, 20–24 April 1998, Whitehorse, Yukon, Canada. Rangifer, Special Issue 12.

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Appendix A-1. Results of censuses or census-based estimates in Alaska Department of Fish and Game files for Alaska caribou herds, 1970–1985.

	Year															
Herd	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985
Adak	214	230	347	230			223	214	233	276	297	381	274	177	360	460
Andreafsky								1,500+					130		400	
Beaver Mtns	1,100													1,200		1,000
Central Arctic						5,000			6,000			8,537		12,905		
Chisana											1,000	1,000				
Delta				2,804						4,191	4,478	4,962	7,335	6,969	6,260	8,083
Denali[a]							1,050		1,350						2,200	
Farewell-Big R														700	750	
Fortymile				5,312	4,000	4,000						7,900		12,350	13,731	
Fox R																
Galena Mtn																
Kenai Lowlands		27								70	70		80	80		85
Kenai Mtns	119										250	256	266	276		400
Kilbuck Mtns											17	32		66		83
Killey R																
Macomb												700				
Mentasta							2,000	2,300	2,800		2,400	2,700	2,800		2,800	3,150
Mulchatna	14,250			6,030	13,079		9,097		6,340			18,599		25,416	33,214	42,945
Nelchina[b]			8,094	8,136	10,245		8,081	13,936	18,981		18,713	20,694	21,356	24,838	24,095	27,528
N AK Peninsula[c]						10,342						16,000	17,000	18,000	20,000	19,000
Nushagak																
Porcupine			99,959					105,000		105,683			125,174	135,284		
Rainy Pass				1,000										1,500		
Ray Mtns																
S AK Peninsula[c]						2,627						6,000	7,000	10,203[d]		4,044
Sunshine Mtns	700									500				600		550
Teshekpuk												3,009			11,822	13,406
Tonzona														1,100		
Twin Lakes																
Unimak Island[c]						3,334										
Western Arctic[e]	242,000						75,000	83,000	105,000	113,000	140,000		175,000			
White Mtns									125					350		
Wolf Mtn																
Yanert												550		930		

[a] Denali estimates from L. G. Adams (U.S. Geological Survey, Alaska Science Center) unpublished.

[b] Nelchina estimates from Pitcher (1987:Table 9a).

[c] For population estimates prior to 1970 see Hemming and Glenn 1968.

[d] The 1983 peak estimate of 10,203 was obtained over 2 days, likely includes duplicate counts, and cannot be explained by survival, recruitment, or immigration.

[e] First population estimate was 238,000 in 1950 (Davis et al. 1980).

Appendix A-2. Results of censuses or census-based estimates in Alaska Department of Fish and Game files for Alaska caribou herds, 1986–2001.

	Year															
Herd	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Adak				475	535	437		827								
Andreafsky		<100														
Beaver Mtns					1,050			550	600	400				129		136
Central Arctic						19,046	23,444			18,100		19,730			27,128	
Chisana		1,100	1,350	1,660	1,200	1,285	1,235	935	800	775		600		350	412	356
Delta	7,804	8,380	8,535	10,690	8,700	5,755	5,877	3,661	4,341	4,646	4,019	3,699	3,829	3,625	3,227	2,965
Denali	2,470	2,430	2,950	3,210	3,100	2,610	2,340	1,970	2,140	2,170	2,060	2,070	1,790	1,760	1,930	1,840
Farewell-Big R																
Fortymile	15,307		19,975		22,766		21,884		22,104	22,558	23,458	25,910	31,029	33,110	34,640	
Fox R				32		40		57	83	85		81	70		70	70
Galena Mtn						260	241	259		310			313			105
Kenai Lowlands		100	125	125	125	130	75	75	85	90		98	130	150		
Kenai Mtns					325	350	410	425				460	450			
Kilbuck Mtns[a]	188	685	1,587	1,384	1,220	2,584		3,682							150	
Killey R				91		197		281		290		376	530		640	650
Macomb			772		775	560	527	458	532		586			640		
Mentasta	3,100	3,160	2,480	2,600		1,940	1,430	970	880	850	780	610	540	430	470	390
Mulchatna		45,742	60,328			60,851	110,073		168,351		192,818			147,012		
Nelchina		30,300		36,000	36,900	45,000	45,500	40,400	44,100	50,300	44,300	35,000	38,600	33,000	33,125	35,106
N AK Peninsula	15,300	16,500			17,000				12,500	12,000	11,500	10,500	9,000	9,000	7,000	6,300
Nushagak[b]			146	268	383	561	734	1,007			1,304	1,429	1,381	1,159	1,037	1,000
Porcupine		165,000		178,000			160,000		152,000				129,000			123,000
Rainy Pass											1,093					
Ray Mtns		600								1,731			1,800		1,800	
S AK Peninsula	4,600	4,100	4,000	2,321	3,750	3,000	3,000		2,200	1,550		2,000		3,600	3,500	3,000
Sunshine Mtns					800			700	700	500				100		
Teshekpuk				16,649				27,686		25,076				28,627		
Tonzona	400		1,200		1,600	1,300										
Twin Lakes[c]										50		73			65	67
Unimak Island					200							650			983	
Western Arctic	229,500		343,000		416,000			450,000			463,000			430,000		
White Mtns				750		761	832						961		687	
Wolf Mtn							595		474		561					489
Yanert	600[d]															

[a] Considered to be assimilated by the Mulchatna herd after 1994. A survey of the Kilbuck Mtns calving area in 2000 found about 100 caribou still calving there.

[b] Data from Collins et al. 2003.

[c] Included with Killey River after 2001.

[d] Assimilated by the Delta herd after 1986.

Appendix A-3. Results of censuses or census-based estimates in Alaska Department of Fish and Game files for Alaska caribou herds, 2002–2008.

	Year						
Herd	2002	2003	2004	2005	2006	2007	2008
Adak							
Beaver Mtns						73	
Central Arctic	31,857						66,772
Chisana	258	603[a]	538	646	628	719	
Delta	2,803	2,581	2,211			2,985	
Denali	2,050	1,880	2,120	1,930	2,090	2,060	2,070
Farewell-Big River							
Fortymile		43,375				38,364	
Fox River			29				
Galena Mtn	102		95	78	95	61	
Hodzana Hills		306	242	1,115	389	361	395
Kenai Lowlands		88	83	100		98	
Kenai Mtns				295			
Kilbuck							
Killey River					216		
Macomb		563	625	640	857	1,305	
Mentasta							319[b]
Mulchatna	121,680		77,303		40,766		20,545
Nelchina	35,939	31,114	38,961	36,993		33,744	
Northern AK Peninsula	6,600		3,400				2,000
Nushagak							
Porcupine							
Rainy Pass							61
Ray Mtns			1,858				
Southern AK Peninsula	4,100		1,872	1,651	770	600	
Sunshine Mtns						59	
Teshekpuk	45,166						64,106
Tonzona							
Unimak Island	1,262		1,006	1,009	806		
Western Arctic		490,000				377,000	
White Mtns			642	514		590	
Wolf Mtn	516	271	146		95	268	

[a] The increase from 2002 to 2003 could not be adequately explained but was probably a result of increased numbers of radio collars in the herd and more thorough searching east of the Generc River in Yukon Territory.

[b] Estimated using census data and fall bull:cow ratio of 30:100. Bull caribou from the Nelchina herd also occur within the range of the Mentasta herd, especially during fall.

Appendix B. Fall composition counts of Alaskan caribou herds, 1952–2008.

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Central Arctic	Oct 1976	44	0.17			122	0.46	1,223	Lenart 2009
Central Arctic	Oct 1977	55	0.20			118	0.43	628	Lenart 2009
Central Arctic	Oct 1978	58	0.23			96	0.38	816	Lenart 2009
Central Arctic	Oct 1980	49	0.18			132	0.47	1,722	Lenart 2009
Central Arctic	Oct 1981	64	0.26	18	29	81	0.33	1,712	Lenart 2009
Central Arctic	1982–1992								No surveys
Central Arctic	10/16–18/1992	47	0.19	35	26	96	0.40	2,469	Lenart 2009
Central Arctic	10/22/1996	67	0.29	9	26	61	0.27	3,062	Lenart 2009
Central Arctic	10/12/2000	56	0.24	38	12	84	0.35	3,335	Lenart 2009
Central Arctic	10/13/2001	54	0.24	38	31	73	0.32	4,092	Lenart 2009
Central Arctic	10/24/2002	71	0.30	24	14	67	0.28	1,732	Lenart 2009
Chisana	10/20/1978	18	0.11			34	0.21	100	Sample size unknown
Chisana	10/5/1980		0.14				0.00	582	Fixed-wing survey
Chisana	10/13/1982	21	0.13	12	8	36	0.23	409	
Chisana	10/14/1986	33	0.19	8	14	43	0.25	507	
Chisana	10/9/1987	28	0.17	21	8	39	0.23	760	
Chisana	10/27/1988	31	0.19	10	9	36	0.21	979	
Chisana	10/16–17/1989		0.09				0.00	625	Fixed-wing survey
Chisana	10/4–5/1990	11	0.07	13	7	36	0.25	572	
Chisana	9/29/1991	1	0.01	18	5	40	0.28	855	
Chisana	9/27/1992	0	0.00	10	7	31	0.24	1,142	
Chisana	10/5/1993	2	0.02	7	6	24	0.19	732	
Chisana	9/29/1994	11	0.08	6	10	27	0.20	543	
Chisana	9/30/1995	4	0.03	6	10	21	0.17	528	
Chisana	9/30/1996	5	0.04	6	7	16	0.13	377	
Chisana	10/1/1997	14	0.10	1	7	24	0.18	520	
Chisana	9/28/1998	4	0.03	9	7	19	0.15	231	
Chisana	10/1/1999	7	0.06	10	5	17	0.14	318	
Chisana	9/30/2000	6	0.05	10	5	20	0.16	412	
Chisana	10/1/2001	4	0.03	10	8	23	0.18	356	Bentzen 2011
Chisana	9/30/2002	14	0.10	7	12	25	0.18	258	Bentzen 2011
Chisana	9/30/2003	23	0.14	7	18	37	0.23	603	Adams (unpublished)
Chisana	2004	17	0.11	15	12	38	0.25	538	Adams (unpublished)
Chisana	9/30/2005	16	0.10	16	15	46	0.28	646	Adams (unpublished)
Chisana	10/12/2006	18	0.11	16	16	48	0.29	628	Adams (unpublished)
Chisana	10/13–14/2007	13	0.08	15	17	50	0.31	719	Adams (unpublished)

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Chisana	10/9/2008	21	0.13			44	0.27	532	Bentzen 2011
Delta	10/13–15/1969	22	0.15			39	0.27	777	
Delta	10/21–23/1970	25	0.14			66	0.38	896	
Delta	10/29–31/1971	13	0.10			30	0.22	1,139	
Delta	10/27–31/1972	10	0.07			33	0.24	1,185	
Delta	10/23–24/1973	10	0.07			29	0.21	1,050	
Delta	10/23–25/1974	2	0.01			28	0.22	1,141	
Delta	1975								No survey
Delta	10/29–31/1976	45	0.24			38	0.21	1,055	
Delta	10/26–31/1977	39	0.23			33	0.20	1,365	
Delta	10/26/1978	34	0.17			69	0.36	725	
Delta	12/7/1979	65	0.32			39	0.19	361	
Delta	10/25/1980	49	0.21			85	0.36	1,369	
Delta	10/2/1981	41	0.22	21	23	46	0.25	1,451	
Delta	10/8/1982	29	0.17	14	24	39	0.23	1,241	
Delta	10/4/1983	46	0.25	21	13	35	0.20	1,208	
Delta	10/17/1984	36	0.20	12	17	42	0.24	1,093	
Delta	10/9–12/1985	36	0.20	28	9	49	0.26	1,164	
Delta	10/22/1986	29	0.17	20	9	41	0.24	1,934	
Delta	10/5/1987	31	0.19	17	8	32	0.20	1,682	
Delta	10/14/1988	35	0.21	17	4	33	0.20	3,003	
Delta	10/10/1989	36	0.22	17	2	27	0.16	1,965	
Delta	10/4/1990	17	0.11	17	6	37	0.24	2,411	
Delta	10/1/1991	8	0.06	15	5	29	0.21	1,705	
Delta	9/28/1992	11	0.08	12	3	25	0.19	1,240	
Delta	9/25/1993	4	0.03	15	7	33	0.24	1,525	
Delta	10/4/1994	24	0.16	7	9	24	0.16	1,205	
Delta	10/3/1995	20	0.14	10	10	24	0.17	1,567	
Delta	10/3/1996	21	0.14	15	9	30	0.20	1,532	
Delta	9/27/1997	18	0.13	13	9	27	0.18	1,598	
Delta	10/1/1998	16	0.10	13	9	44	0.27	1,519	
Delta	10/2/1999	19	0.11	16	10	44	0.27	674	
Delta	10/3–4/2000	11	0.07	19	10	47	0.30	1,010	
Delta	9/30/2001	12	0.08	18	9	39	0.26	1,378	
Delta	9/28/2002	25	0.14	22	17	51	0.29	924	
Delta	10/6–7/2003	20	0.13	11	10	36	0.23	1,023	Seaton 2009
Delta	9/29/2004	35	0.19	15	15	50	0.27	1,267	Seaton 2009

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Delta	9/26/2005	33	0.18	14	11	49	0.27	1,182	Seaton 2009
Delta	10/5+10/15/2006	27	0.16	18	8	40	0.24	1,022	Seaton 2009
Delta	10/8/2007	24	0.15	7	10	35	0.22	719	Seaton 2009
Delta	2008								No survey
Denali	9/21/1976	16	0.12			15	0.11	414	
Denali	10/21/1977	28	0.19			21	0.14	244	
Denali	11/1978	38	0.24			22	0.14	257	
Denali	9/25/1979	33	0.21			25	0.16	336	
Denali	1980								No survey
Denali	1981								No survey
Denali	1982								No survey
Denali	1983								No survey
Denali	09/27/1984	41	0.22			49	0.26	713	Adams (unpublished)
Denali	9/25–26/1985	28	0.15			56	0.31	1,205	Adams (unpublished)
Denali	09/27/1986	38	0.20			56	0.29	1,062	Adams (unpublished)
Denali	09/25/1987	37	0.19	16	19	56	0.29	1,221	Adams (unpublished)
Denali	9/27–28/1988	33	0.16	18	26	67	0.33	1,350	Adams (unpublished)
Denali	9/28/1989	30	0.16	18	17	52	0.28	1,504	Adams (unpublished)
Denali	9/26–27/1990	17	0.10	19	16	50	0.30	1,294	Adams (unpublished)
Denali	9/26/1991	6.7	0.05	12	11	38	0.26	1,548	Adams (unpublished)
Denali	9/25/1992	16	0.10	14	13	44	0.27	1,028	Adams (unpublished)
Denali	9/27/1993	6.4	0.04	10	11	40	0.27	1,239	Adams (unpublished)
Denali	9/27–28/1994	20	0.12	8	16	39	0.25	1,029	Adams (unpublished)
Denali	9/25/1995	19	0.13	9	13	30	0.20	1,020	Adams (unpublished)
Denali	9/29/1996	13	0.09	9	12	30	0.21	1,166	Adams (unpublished)
Denali	9/26/1997	16	0.11	11	10	29	0.20	1,129	Adams (unpublished)
Denali	9/26/1998	12	0.09	12	9	29	0.20	1,010	Adams (unpublished)
Denali	9/29/1999	14	0.09	12	14	39	0.26	1,020	Adams (unpublished)
Denali	9/24–26/2000	7.1	0.05	11	13	35	0.25	1,039	Adams (unpublished)
Denali	9/27/2001	12	0.08	7	13	32	0.22	1,116	Adams (unpublished)
Denali	9/29/2002	16	0.11	7	20	32	0.22	670	Adams (unpublished)
Denali	9/30/2003	7.8	0.05	8	19	36	0.25	1,065	Adams (unpublished)
Denali	9/27/2004	28	0.16	8	20	40	0.24	1,297	Adams (unpublished)
Denali	9/26/2005	19	0.13	11	13	33	0.22	1,290	Adams (unpublished)
Denali	9/28/2006	21	0.13	12	16	39	0.24	1,105	Adams (unpublished)
Denali	9/28/2007	23	0.14	11	12	36	0.23	997	Adams (unpublished)
Denali	9/29/2008	22	0.14	10	12	33	0.21	1,051	Adams (unpublished)

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Fortymile	Oct 1954	64	0.26			78	0.32	189	
Fortymile	Oct 1955		0.16				0.00	1,659	Fixed-wing survey
Fortymile	Oct 1956		0.05				0.00	737	Fixed-wing survey
Fortymile	Oct 1957		0.05				0.00	576	Fixed-wing survey
Fortymile	Oct 1959		0.36				0.00	450	Fixed-wing survey
Fortymile	Oct 1960		0.36				0.00	901	Fixed-wing survey
Fortymile	Oct 1961	39	0.18			78	0.36	1,110	
Fortymile	Oct–Nov 1962		0.11				0.00	743	Fixed-wing survey
Fortymile	1963–1971								No surveys
Fortymile	Oct 1972	19	0.13			36	0.23	672	
Fortymile	9/30/1973	15	0.10	4		45	0.28	3,307	
Fortymile	9/21–24/1974	19	0.13			36	0.23	1,738	
Fortymile	9/23/1976	33	0.18			46	0.26	896	
Fortymile	9/27/1977	42	0.21			56	0.28	1,150	
Fortymile	10/19/1978	24	0.15			43	0.26	748	
Fortymile	1979								No survey
Fortymile	10/15/1980	61	0.23	26	27	109	0.40	982	
Fortymile	9/26/1981	31	0.17			52	0.28	1,004	
Fortymile	9/29/1982	27	0.15	21	17	54	0.30	1,625	
Fortymile	9/20, 10/7/1983	33	0.18	18	24	52	0.28	1,953	
Fortymile	1984								No survey
Fortymile	10/16/1985	36	0.19	19	19	50	0.27	1,067	
Fortymile	10/13/1986	28	0.17	13	15	36	0.22	1,381	
Fortymile	9/28/1987	37	0.21	5	17	40	0.22	2,253	
Fortymile	10/2–3/1988	30	0.18	11	12	38	0.23	1,295	
Fortymile	10/13/1989	24	0.16	9	7	27	0.18	1,781	
Fortymile	9/27–28/1990	29	0.17	19	9	44	0.26	1,742	
Fortymile	10/10/1991	16	0.10	16	10	39	0.25	1,445	
Fortymile	1992								No survey
Fortymile	10/3/1993	29	0.16	22	8	46	0.26	3,659	
Fortymile	9/3/1994	33	0.19	19	9	42	0.24	2,989	Gardner 2001
Fortymile	9/28/1995	32	0.18	19	11	43	0.25	3,303	Gardner 2001
Fortymile	9/29/1996	36	0.20	19	9	41	0.23	4,598	Gardner 2001
Fortymile	9/30/1997	41	0.22	22	11	46	0.25	6,196	Gardner 2001
Fortymile	9/29/1998	38	0.21	20	10	40	0.23	4,322	Gardner 2001
Fortymile	9/29/1999	37	0.20	26	8	48	0.26	4,336	Gardner 2001
Fortymile	10/1/2000	27	0.16	22	11	45	0.26	6,513	Gardner 2001

Herd	Date	Calves: 100 cows	Proport ion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Fortymile	9/29/2001	38	0.20	22	12	51	0.27	6,878	Gardner 2001
Fortymile	9/28/2002	38	0.21	18	13	44	0.24	6,088	Gross 2009
Fortymile	9/27/2003	17	0.10	26	11	50	0.30	6,296	Gross 2009
Fortymile	9/28/2004	27	0.16	13	14	42	0.25	4,157	Gross 2009
Fortymile	10/5/2005	17	0.10	13	26	51	0.30	2,350	Gross 2009
Fortymile	10/5/2006	33	0.19	11	19	42	0.24	4,995	Gross 2009
Fortymile	10/4/2007	36	0.21	12	12	36	0.21	5,228	Gross 2009
Fortymile	10/7–8/2008	32	0.19	11	10	37	0.22	4,119	Gross 2011
Galena Mountain	Oct 1983	20	0.17				0.00	136	
Galena Mountain	Oct 1984	5	0.04			19	0.15	181	
Galena Mountain	Oct 1985	21	0.17				0.00	185	
Galena Mountain	Oct 1986	38	0.17			86	0.38	47	
Galena Mountain	Oct 1988	17	0.12			27	0.19	117	
Galena Mountain	10/12/1993	25	0.16			32	0.20	259	
Galena Mountain	10/21/1994	40	0.25	3	14	22	0.13	186	
Galena Mountain	10/13/1995	19	0.13	4	13	28	0.19	310	
Galena Mountain	10/11/1996	13	0.08	21	8	41	0.27	232	
Galena Mountain	Oct 2004	11	0.08			20	0.15	84	
Galena Mountain	Nov 2005	16	0.12			10	0.08	73	
Hodzana Hills	Oct 2003	25	0.14			52		306	
Hodzana Hills	Oct 2005	17	0.10			52		1,115	
Hodzana Hills	Oct 2006	8	0.05			49		389	
Hodzana Hills	Sept 2007	19	0.11			61		361	
Hodzana Hills	Sept 2008	28	0.16			43		395	
Kenai Lowlands	Oct 2003		0.28				0.00	88	Fixed-wing survey, Selinger 2009
Kenai Lowlands	Oct 2004		0.19				0.00	83	Fixed-wing survey, Selinger 2009
Kenai Lowlands	Oct 2005		0.23				0.00	100	Fixed-wing survey, Selinger 2009
Kenai Lowlands	Oct 2007		0.23				0.00	98	Fixed-wing survey, Selinger 2009
Kenai Mountains	10/31/1990	34	0.20			39	0.23	286	
Kilbuck	10/30/1989	22	0.12			65			
Kilbuck	11/11/1990						0.00	1,220	Fixed-wing survey
Kilbuck	Nov 1991	43	0.20			79	0.35	715	
Kilbuck	10/31/1992	27	0.11			115	0.48	1,007	
Killey River	11/14/2000	24	0.14			42	0.25	607	
Macomb	10/25/1974	14	0.09			45	0.28	445	
Macomb	1975								No survey
Macomb	10/16/1976	19	0.12			45	0.27	277	

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Macomb	10/21/1977	30	0.17			47	0.26	321	
Macomb	1979								No survey
Macomb	Oct 1980	12	0.08			46	0.29	306	
Macomb	11/31/1981	30	0.16			58	0.31	445	
Macomb	Oct 1982	26	0.18	13	2	21	0.14	218	
Macomb	Oct 1983	24	0.15	16		33	0.21	238	
Macomb	12/1/1984	40	0.24	12	6	28	0.17	351	
Macomb	10/30/1985	31	0.17	19	9	45	0.26	518	
Macomb	1986								No survey
Macomb	1987								No survey
Macomb	10/16/1988	32	0.18	19	13	46	0.26	671	
Macomb	10/26/1989	34	0.20	18	5	33	0.20	617	
Macomb	10/9/1990	17	0.11	15	14	44	0.27	600	
Macomb	9/25/1991	9	0.06	7	13	34	0.24	560	
Macomb	9/26/1992	14	0.10	8	9	25	0.18	455	
Macomb	10/2/1993	18	0.13	8	6	22	0.16	374	
Macomb	10/2/1994	13	0.10	11	7	21	0.16	345	
Macomb	10/1/1995	10	0.06	17	15	39	0.26	477	
Macomb	10/2/1996	30	0.17	12	17	43	0.25	586	
Macomb	10/28/1997	18	0.12	11	9	28	0.19	451	
Macomb	9/30/1998	25	0.14	16	11	50	0.28	472	
Macomb	10/15/1999	22	0.12	28	17	57	0.32	606	
Macomb	10/2/2000	11	0.07	19	13	45	0.29	605	
Macomb	10/9/2001	11	0.07	16	12	39	0.26	467	
Macomb	11/2/2002	21	0.12	20	10	52	0.30	234	
Macomb	10/4/2003	20	0.12	21	14	47	0.28	526	
Macomb	10/9/2004	40	0.20	11	27	60	0.30	546	
Macomb	10/4/2005	16	0.09	34	20	64	0.35	628	
Macomb	10/6/2006	30	0.17	7	20	48	0.27	857	
Macomb	10/9/2007	29	0.15	35	19	67	0.34	951	
Macomb	2008								No survey
Mentasta	10/18–19/1973	32	0.19			40	0.23	1,434	
Mentasta	Sep 1974								No survey
Mentasta	Sep 1975								No survey
Mentasta	Sep 1976								No survey
Mentasta	Sep 1977	27	0.16			42			No data on sample size
Mentasta	Sep 1978	25	0.15			42			No data on sample size

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Mentasta	Sep 1979								No survey
Mentasta	Sep 1980	42	0.22			46			No data on sample size
Mentasta	Sep 1981	40	0.22			43			No data on sample size
Mentasta	Sep 1982	39	0.22			36			No data on sample size
Mentasta	Sep 1983	28	0.16			44			No data on sample size
Mentasta	Sep 1984	29	0.18			36			No data on sample size
Mentasta	Sep 1985	46	0.25			41			1973–1985 data from Lieb et al. 1989
Mentasta	Sep 1986								No survey
Mentasta	Sep 1987	12	0.08			41	0.27	803	Tobey 1993
Mentasta	Sep 1988	18	0.11			43	0.27	675	Tobey 1993
Mentasta	Sep 1989	16	0.10			45	0.28	694	Tobey 1993
Mentasta	Sep 1990								No survey
Mentasta	10/14/1991	2	0.02			42	0.29	456	
Mentasta	Sep 1992	6				41			
Mentasta	9/24/1993	4	0.03	9	17	38	0.27	671	
Mentasta	9/1/1994	11	0.07	9	13	38	0.26	666	
Mentasta	9/22/1995	22	0.14			35	0.22	556	
Mentasta	9/8/1998	10	0.06	17	8	42	0.28	357	
Mulchatna	10/16–17/1974		0.35				0.00	1,311	Fixed-wing survey
Mulchatna	10/27/1978		0.65				0.00	533	Fixed-wing survey
Mulchatna	1979								No survey
Mulchatna	10/29/1980	57	0.30			34	0.18	2250	
Mulchatna	9/30/1981	45	0.23			53	0.27	1,235	
Mulchatna	1982								No survey
Mulchatna	1983								No survey
Mulchatna	1984								No survey
Mulchatna	1985								No survey
Mulchatna	10/19/1986	37	0.19			56	0.29	2,171	
Mulchatna	10/13/1987	60	0.26			68	0.30	1,858	
Mulchatna	10/6/1988	54	0.24			66	0.30	536	
Mulchatna	1989								No survey
Mulchatna	1990								No survey
Mulchatna	1991								No survey
Mulchatna	1992								No survey
Mulchatna	Oct 1993	44	0.24			42	0.23	5,907	
Mulchatna	1994								No survey

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Mulchatna	1995								No survey
Mulchatna	10/7/1996	34	0.19	21	9	42	0.24	1,727	
Mulchatna	1997								No survey
Mulchatna	10/2/1998	34	0.19	11	12	41	0.23	3,086	
Mulchatna	10/12+20/1999	14	0.10	18	4	30	0.21	4,731	
Mulchatna	10/2–9/2000	24	0.15	18	8	39	0.24	3,894	
Mulchatna	Oct 2001	20	0.14	8	5	26	0.18	5,728	
Mulchatna	Oct 2002	28	0.18	15	3	26	0.17	5,734	
Mulchatna	Oct 2003	26	0.18	6	3	17	0.12	7,821	
Mulchatna	Oct 2004	20	0.14	13	1	21	0.15	4,608	
Mulchatna	Oct 2005	18	0.14	8	2	14	0.11	5,211	
Mulchatna	Oct 2006	25	0.18	9	1	15	0.11	2,971	
Mulchatna	Oct 2007	16	0.11	12	3	23	0.17	3,943	
Mulchatna	Oct 2008	23	0.16	11	4	24	0.17	3,728	
Nelchina	Oct 1971	30	0.18			34	0.21	3,540	
Nelchina	10/7–8/1972	30	0.18			34	0.21	2,381	
Nelchina	1973								No survey
Nelchina	1974								No survey
Nelchina	1975								No survey
Nelchina	Sep–Oct 1976	29				33			No data on sample size
Nelchina	Sep–Oct 1977	47				38			No data on sample size
Nelchina	Sep–Oct 1978	48				45			No data on sample size
Nelchina	Sep–Oct 1979								No survey
Nelchina	Sep–Oct 1980	42	0.21			62	0.30	821	
Nelchina	Sep–Oct 1981	43	0.21			61	0.30	1,624	
Nelchina	10/6/1982	54	0.26			55	0.26	865	
Nelchina	10/4/1983	27	0.14			61	0.32	1,325	
Nelchina	Sep–Oct 1984	34	0.19			40	0.23	3,483	
Nelchina	Sep–Oct 1985	46	0.23			54	0.27	2,118	
Nelchina	Sep–Oct 1986	42				44			
Nelchina	Sep–Oct 1987	51	0.25			50	0.25	5,134	
Nelchina	Sep–Oct 1988	48	0.24			55	0.27	2,502	
Nelchina	Sep–Oct 1989	39	0.21			49	0.26	2,817	
Nelchina	10/5/1990	33	0.19			42	0.24	3,671	
Nelchina	10/15/1991	45	0.23			51	0.26	2,187	
Nelchina	9/25–26/1992	40	0.21			48	0.25	4,135	
Nelchina	10/3/1993	24	0.14	18	9	41	0.25	4,318	

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Nelchina	9/26–27/1994	41	0.22	21	9	46	0.25	3,564	
Nelchina	9/30/1995	38	0.21	18	14	43	0.24	5,354	
Nelchina	9/29/1996	38	0.22	20	6	34	0.20	3,086	
Nelchina	9/29/1997	26	0.17	13	6	26	0.17	3,553	
Nelchina	9/27/1998	38	0.24	12	3	21	0.13	2,394	
Nelchina	10/5/1999	23	0.15	19	3	30	0.20	3,000	
Nelchina	10/3/2000	20	0.14	16	3	25	0.17	3,017	
Nelchina	Sep–Oct 2001	39	0.22			37	0.21	3,949	Schwanke 2003
Nelchina	Sep–Oct 2002	48	0.27			30	0.17	1,710	Schwanke 2003
Nelchina	Sep–Oct 2003	35	0.21			32	0.19	3,140	Schwanke 2009
Nelchina	Sep–Oct 2004	46	0.26			30	0.17	1,640	Schwanke 2009
Nelchina	Sep–Oct 2005	40	0.23			35	0.20	3,263	Schwanke 2009
Nelchina	Sep–Oct 2006	41	0.25			23	0.14	3,380	Schwanke 2009
Nelchina	Sep–Oct 2007	36	0.21			34	0.20	3,027	Schwanke 2009
Nelchina	Sep–Oct 2008	39	0.22			39	0.22	3,378	Schwanke 2009
N AK Peninsula	Oct 1970	46				48			No data on sample size
N AK Peninsula	Oct 1975	45				33			No data on sample size
N AK Peninsula	Oct 1978	55				48			No data on sample size
N AK Peninsula	Oct 1980	56				53			No data on sample size
N AK Peninsula	Oct 1981	39				34			No data on sample size
N AK Peninsula	Oct 1982	52	0.26			43	0.22	1,392	
N AK Peninsula	Oct 1983	27	0.16	20	10	39	0.24	1,410	
N AK Peninsula	Oct 1984	39	0.22	26	7	39	0.22	1,087	
N AK Peninsula	Oct 1985								No survey
N AK Peninsula	Oct 1986	34	0.18			51	0.27	2,540	
N AK Peninsula	Oct 1987	51	0.25	27	9	54	0.26	1,536	
N AK Peninsula	Oct 1988	48	0.26	23	10	49	0.25	1,156	
N AK Peninsula	Oct 1989		0.20					2,934	Fixed-wing survey
N AK Peninsula	Oct 1990	29	0.17			41	0.24	1,484	
N AK Peninsula	Oct 1991	47	0.25	22	5	42	0.22	1,639	
N AK Peninsula	Oct 1992	44	0.24	18	8	40	0.22	2,766	
N AK Peninsula	Oct 1993	39	0.21	23	8	44	0.24	3,021	
N AK Peninsula	Oct 1994	34	0.20	20	5	34	0.20	1,857	
N AK Peninsula	Oct 1995	24	0.15	20	9	41	0.25	2,907	
N AK Peninsula	10/5–6/1996	38	0.19	34	5	48	0.26	2,572	
N AK Peninsula	10/3–4/1997	27	0.16	25	7	47	0.27	1,064	
N AK Peninsula	10/3–11/1998	30	0.19	17	5	31	0.19	1,342	

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
N AK Peninsula	10/22–23/1999	21	0.13	23	5	40	0.25	2,567	
N AK Peninsula	10/10–11/2000	18	0.12	22	7	38	0.24	1,083	
N AK Peninsula	Oct 2001	28	0.16	30	7	49	0.28	2,392	
N AK Peninsula	Oct 2002	24	0.14	26	11	46	0.27	1,007	
N AK Peninsula	Oct 2003	12	0.08	16	8	35	0.24	2,776	
N AK Peninsula	Oct 2004	7	0.05	14	8	34	0.24	1,355	
N AK Peninsula	Oct 2005	8	0.06	9	5	23	0.18	1,914	
N AK Peninsula	Oct 2006	14	0.10	7	8	25	0.18	1,725	
N AK Peninsula	Oct 2007	7	0.05	8	9	27	0.20	1,719	
N AK Peninsula	Oct 2008	10	0.08	6	8	19	0.15	1,841	
Nushagak	Feb 1988	10	0.08			12		146	Data from Aderman, USFWS
Nushagak	1989								No survey
Nushagak	1990								No survey
Nushagak	1991								No survey
Nushagak	10/29/1992	72	0.31			60		611	Data from Aderman, USFWS
Nushagak	1993								No survey
Nushagak	10/30/1994	65	0.27			71		986	Data from Aderman, USFWS
Nushagak	1995								No survey
Nushagak	1996								No survey
Nushagak	10/10/1997	62	0.28			64		641	Data from Aderman, USFWS
Nushagak	10/12/1998	63	0.28	17	19	57	0.26	429	Data from Aderman, USFWS
Nushagak	10/19/1999	53	0.26	14	12	48	0.24	672	Data from Aderman, USFWS
Nushagak	10/8/2000	38	0.20	23	12	52	0.27	707	Data from Aderman, USFWS
Nushagak	10/14/2001	35	0.19	21	12	46	0.25	602	Data from Aderman, USFWS
Nushagak	10/9/2002	36	0.20	15	16	43	0.24	342	Data from Aderman, USFWS
Nushagak	10/12/2003	44	0.23	19	18	47	0.25	425	Data from Aderman, USFWS
Nushagak	10/12/2004	34	0.19	23	9	43	0.24	365	Data from Aderman, USFWS
Nushagak	10/9/2005	32	0.19	21	9	38	0.22	558	Data from Aderman, USFWS
Nushagak	10/13/2006	36	0.21	15	7	31	0.19	389	Data from Aderman, USFWS
Nushagak	10/7/2007	40	0.21	24	12	49	0.26	454	Data from Aderman, USFWS
Nushagak	10/8/2008	60	0.29	21	11	44	0.22	423	Data from Aderman, USFWS
Porcupine	Oct 1972	28	0.15			59	0.31	2,998	
Porcupine	Oct 1973	31	0.17			54	0.29	200	Sample size unknown
Porcupine	Oct 1977	42	0.19			80	0.36	8,941	
Porcupine	Oct 1978	58	0.30			35	0.18	980	
Porcupine	Oct 1980	49	0.23		26	64	0.30	13,871	Chapman Lk-Yukon
Ray Mountains	10/25–26/1984						0.00	63	Fixed-wing survey

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Ray Mountains	11/17/1986						0.00	19	Fixed-wing survey
Ray Mountains	10/21/1987						0.00	54	Fixed-wing survey
Ray Mountains	Oct 1991						0.00	140	Fixed-wing survey
Ray Mountains	10/18/1994	19	0.12	7	17	37	0.24	629	
Ray Mountains	10/3/1995	12	0.08	5	16	34	0.23	994	
Ray Mountains	10/5/1996	15	0.10	4	12	28	0.20	1,387	
Ray Mountains	10/15/1997	13	0.09	7	17	33	0.23	1,114	
Ray Mountains	10/2/1998	32	0.20	9	12	26	0.16	1,756	
Ray Mountains	1999								No survey
Ray Mountains	10/11/2000	19	0.12	16	14	38	0.24	1,736	
Ray Mountains	9/1/2001	15	0.11	15	7	30	0.21	1,685	
Ray Mountains	9/2/2002	31	0.17	20	4	51	0.28	140	
Ray Mountains	10/3/2003	18	0.12	15	11	33	0.22	921	
Ray Mountains	Oct 2004						0.00	1,403	Fixed-wing survey
Ray Mountains	Oct 2005	10	0.07	14	12	35	0.24	795	
Ray Mountains	Oct 2006	10	0.07	11	8	27	0.20	815	
Ray Mountains	Oct 2007	26	0.17	3	15	26	0.17	785	
Ray Mountains	Sep 2008	28	0.16	6	3	47	0.27	780	
Rainy Pass	10/28/1999	8	0.06	16	2	29	0.21	441	
Rainy Pass	10/13/2000	12	0.05			115	0.51	152	Bad survey?
S AK Peninsula	Oct 1983		0.15				0.00	10,203	Fixed-wing survey
S AK Peninsula	Oct 1984		0.15				0.00	7,500	Fixed-wing survey
S AK Peninsula	Oct 1985		0.09				0.00	4,044	Fixed-wing survey
S AK Peninsula	Oct 1986	20	0.13	19	4	32	0.21	2,307	
S AK Peninsula	Oct 1987	26	0.16	19	8	36	0.22	3,407	
S AK Peninsula	Oct 1988	20	0.12	25	2	41	0.24	3,386	
S AK Peninsula	10/14/1989		0.03				0.00	1,654	Fixed-wing survey, Pitcher 1991
S AK Peninsula	Oct 1990	12	0.09			19	0.14	2,287	
S AK Peninsula	Oct 1991	19	0.13	15	4	28	0.19	2,380	
S AK Peninsula	Oct 1992	21	0.15	10	5	22	0.15	1,495	
S AK Peninsula	Oct 1993	25	0.16	18	5	30	0.20	2,137	
S AK Peninsula	Oct 1994	28	0.18	13	8	29	0.19	1,434	
S AK Peninsula	Oct 1995								No survey
S AK Peninsula	Oct 1996								No survey
S AK Peninsula	10/3–4/1997	19	0.12	15	18	42	0.42	546	
S AK Peninsula	10/5–10/1998	35	0.21	14	11	32	0.19	987	
S AK Peninsula	10/24–25/1999	25	0.14	25	11	51	0.29	1,049	

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
S AK Peninsula	10/11–12/2000	37	0.21	21	11	42	0.23	982	
S AK Peninsula	Oct 2001	37	0.19	34	10	59	0.30	1,313	
S AK Peninsula	Oct 2002	15	0.10	17	9	38	0.25	932	
S AK Peninsula	Oct 2003	7	0.05	16	13	40	0.27	1,257	
S AK Peninsula	Oct 2004	7	0.05	9	14	36	0.25	966	
S AK Peninsula	Oct 2005	7	0.05	8	8	30	0.22	1,040	
S AK Peninsula	Oct 2006	1	0.01	4	8	15	0.13	713	
S AK Peninsula	Oct 2007	1	0.01	3	5	14	0.12	431	
S AK Peninsula	Oct 2008	39	0.26	0	7	10	0.07	570	
Teshekpuk	Nov 1994		0.27				0.00	1,681	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 1995		0.27				0.00	1,931	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 1996		0.21				0.00	924	Fixed-wing survey, Carroll 2001
Teshekpuk	Nov 1997		0.14				0.00	1,040	Fixed-wing survey, Carroll 2001
Teshekpuk	Nov 1998		0.20				0.00	458	Fixed-wing survey, Parrett 2009
Teshekpuk	1999								No survey
Teshekpuk	2000								No survey
Teshekpuk	Nov 2001		0.11				0.00	1,458	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 2002		0.21				0.00	3,510	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 2004		0.05				0.00	658	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 2005		0.18				0.00	1,700	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 2006		0.25				0.00	3,371	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 2007		0.19				0.00	2,213	Fixed-wing survey, Parrett 2009
Teshekpuk	Nov 2008		0.16				0.00	1,895	Fixed-wing survey, Parrett 2011
Tonzona	Sep 1988	36	0.21	14	13	36	0.21	463	Del Vecchio et al. 1995
Tonzona	Sep 1989	24	0.14	13	8	50	0.29	667	Del Vecchio et al. 1995
Tonzona	9/27/1990	15	0.10	15	9	37	0.24	488	Del Vecchio et al. 1995
Tonzona	9/28/1991	8	0.06	14	10	35	0.25	526	Del Vecchio et al. 1995
Unimak	10/24–25/1999	46	0.20	40	21	81	0.36	129	Butler 2009
Unimak	10/12/2000	21	0.13	14	13	40	0.25	406	Butler 2009
Unimak	Oct 2002	31	0.17	27	16	54	0.29	392	Butler 2009
Unimak	Oct 2005	8	0.05	11	17	44	0.29	730	Butler 2009
Unimak	Oct 2007	5	0.04	9	12	32	0.23	433	Butler 2009
Unimak	Oct 2008	6	0.05	3	3	10	0.09	260	Butler 2009
Western Arctic	10/18/1952		0.26				0.00	320	Fixed-wing survey
Western Arctic	10/16–19/1953		0.24				0.00	164	Fixed-wing survey
Western Arctic	9/20–24/1954		0.28				0.00	393	Fixed-wing survey
Western Arctic	10/18–21/1961	36	0.19			57	0.30	1,006	

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
Western Arctic	10/26–28/1968	31	0.16			66	0.34	2,217	
Western Arctic	Oct 1970	40	0.19			67	0.32	6,219	
Western Arctic	10/18–19/1975	45	0.25			35	0.19	2,243	
Western Arctic	10/16–18/1976	42	0.21			63	0.31	7,140	
Western Arctic	10/19–21/1977	36	0.19			50	0.27	6,888	
Western Arctic	10/14–20/1978	45	0.22			56	0.28	5,097	
Western Arctic	1979								No fall surveys
Western Arctic	Nov 1980	46	0.22			59	0.29	3,187	
Western Arctic	Oct 1981		0.22				0.00	5,050	Fixed-wing survey
Western Arctic	Oct 1982	60	0.27			59	0.27	6,998	
Western Arctic	1983–1991								No fall surveys
Western Arctic	10/10–12/1992	52	0.24			64	0.30	5,397	
Western Arctic	10/15/1993	37	0.21			37	0.21	4,039	
Western Arctic	10/9–10/1994	36	0.19	11	25	49	0.26	5,756	
Western Arctic	Oct 1995	52	0.25			58	0.28	4,262	Dau 2001
Western Arctic	Oct 1996	49	0.25			51	0.26	10,265	Dau 2001
Western Arctic	Oct 1997	43	0.22			49	0.26	10,072	Dau 2001
Western Arctic	Oct 1998	45	0.23			54	0.27	8,438	Dau 2001
Western Arctic	Oct 1999	47	0.24			49	0.25	8,210	Dau 2001
Western Arctic	Oct 2001	38	0.22			37	0.21	5,155	Dau 2009
Western Arctic	Oct 2004	48	0.26			35	0.19	11,157	Dau 2009
Western Arctic	Oct 2006	40	0.22			42	0.23	8,212	Dau 2009
Western Arctic	Oct 2008	48	0.25			45	0.23	12,755	Dau 2009
Wolf Mountain	Oct 1982	33	0.18			50	0.27	77	
Wolf Mountain	Oct 1983	34	0.24			9	0.06	163	
Wolf Mountain	10/12/1995	27	0.15	4	28	54	0.30	346	
Wolf Mountain	10/11/1996	22	0.14	17	6	37	0.23	266	
White Mountains	9/29/1983	31	0.18	12	19	44	0.25	135	
White Mountains	Oct 1985	31	0.18			36	0.22	65	
White Mountains	9/29/1988	33	0.19	22	14	43	0.24	211	
White Mountains	10/6/1989	36	0.19	23	11	50	0.27	744	
White Mountains	10/11/1991	24	0.16	8	5	23	0.15	312	
White Mountains	10/13/1992	23	0.14	20	12	39	0.24	247	
White Mountains	9/27/1993	22	0.13	16	20	48	0.28	497	
White Mountains	10/4/1994	25	0.15	13	17	39	0.24	418	
White Mountains	10/16/1995	31	0.19	16	10	37	0.22	418	
White Mountains	10/2/1996	54	0.27	27	9	44	0.22	513	

Herd	Date	Calves: 100 cows	Proportion calves	Small bulls: 100 cows	Large bulls: 100 cows	Bulls: 100 cows	Percent bulls	Sample total	Remarks
White Mountains	10/2/1997	38	0.22	17	10	34	0.20	341	
White Mountains	10/2/1998	18	0.11	21	10	50	0.30	759	
White Mountains	10/30/1999	39	0.20	21	16	62	0.31	644	
White Mountains	9/29/2000	13	0.08	21	11	54	0.32	399	
White Mountains	9/25/2001	25	0.14	26	11	56	0.31	441	
White Mountains	9/24/2002	30	0.18	16	7	34	0.21	405	
White Mountains	9/5/2003	16	0.11	14	6	29	0.20	308	
White Mountains	10/5/2004	24	0.15	16	7	35	0.22	321	
White Mountains	10/6/2005	21	0.13	15	18	44	0.27	391	
White Mountains	10/16/2006	20	0.13	15	9	36	0.23	362	
White Mountains	10/10/2007	37	0.21	21	7	39	0.22	358	
Yanert	11/26/1982	36	0.18	39		59	0.30	304	
Yanert	10/12/1985	40	0.19	28	15	66	0.32	787	
Yanert	10/22/1986	38	0.18	31	16	70	0.34	570	
Yanert	10/5/1987	38	0.21	19	10	41	0.23	906	Some mixing with Delta

Appendix C. Means of weights (kg) and measurements (cm), standard errors (SE), and sample sizes of cohorts of female Alaska caribou calves handled during 1979–2008 (through 2007 for Delta caribou herd).

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Central Arctic	2002	Spring	45.9	35.3								
SE			1.03	0.25								
n			25	25								
Central Arctic	2003	Spring	45.8	35.2								
SE			0.8	0.16								
n			25	25								
Central Arctic	2004	Spring	45.3	35.2								
SE			0.8	0.16								
n			21	21								
Central Arctic	2005	Spring	44.4	35.0								
SE			0.7	0.18								
n			28	28								
Central Arctic	2006	Spring	45.2	35.2								
SE			0.8	0.19								
n			23	23								
Central Arctic	2007	Spring	46.2	34.7								
SE			1.0	0.33								
n			10	10								
Central Arctic	2008	Spring	44.0	35								
SE			1.1	0.2								
n			5	5								
Chisana	1990	Fall	51.7	35.4	89.1	154.1		1.46				
SE			1.8	0.3	1.3	2.4		0.05				
n			13	13	13	13		13				
Chisana	1998	Fall	66.7	38.0	99.8	171.3	23.0	1.75				
SE			1.2	0.6	2.2	3.7	0.2	0.01				
n			3	3	3	3	3	3				
Chisana	1999	Fall	63.5	37.2	99.3	164.1	22.0	1.71				
SE			1.5	0.7	0.3	0.1	0.1	0.03				
n			8	8	8	8	8	8				
Chisana	2000	Fall	62.0	36.8	101.0	165.5	22.5	1.68				
SE			1.4	0.3	1.2	1.9	0.3	0.03				
n			8	8	8	8	8	8				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Delta	1979	Spring	60.0	37.8	102.9	168.5		1.58				
SE			1.1	0.4	1.4	1.9		0.03				
n			11	12	12	12		11				
Delta	1981	Spring	62.1	39.5	105.0	174.5		1.68				
SE			3.4	0.5	2.9	2.7		0.08				
n			5	4	6	6		3				
Delta	1982	Spring	61.3	38.1	96.9	165.0		1.62				
SE			1.7	0.3	1.5	2.7		0.04				
n			11	10	9	7		10				
Delta	1983	Spring	62.2	38.1	97.8	168.3		1.64				
SE			1.5	0.4	1.6	2.0		0.03				
n			13	12	12	12		12				
Delta	1984	Spring	57.3	37.9	97.6	164.0		1.51				
SE			0.6	0.2	1.0	2.3		0.02				
n			12	10	10	10		10				
Delta	1987	Spring	54.8	36.8	94.4	163.1	23.6	1.48				
SE			1.3	0.4	1.1	2.3	0.4	0.03				
n			9	10	10	9	7	9				
Delta	1988	Spring	59.3	38.0	101.7	171.4	24.1	1.56				
SE			1.0	0.2	0.7	1.6	0.3	0.02				
n			16	16	17	17	16	15				
Delta	1989	Spring	60.6	37.9	98.2	171.6	24.3	1.59				
SE			1.2	0.5	1.5	1.9	0.3	0.02				
n			9	10	10	10	10	9				
Delta	1990	Spring	51.0	37.1	96.0	167.6		1.37				
SE			1.3	0.5	1.1	1.4		0.03				
n			14	14	14	14		14				
Delta	1991	Spring	51.2	36.9	92.1	164.6		1.38				
SE			1.1	0.3	1.0	2.3		0.03				
n			10	11	11	11		10				
Delta	1991	Fall	57.9	35.6	94.6	162.2	21.9	1.63				
SE			1.2	0.2	0.8	2.0	0.2	0.03				
n			14	14	14	14	14	14				
Delta	1992	Spring	54.6	36.3	91.5	163.8	22.5	1.50				
SE			1.3	0.3	0.7	2.0	0.2	0.04				
n			16	16	16	16	16	16				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Delta	1992	Fall	54.6	35.3	90.8	158.8	21.5	1.55				
SE			1.4	0.2	1.1	2.3	0.2	0.03				
n			14	15	14	14	15	14				
Delta	1993	Spring	55.5	36.9	92.8	165.6	23.1	1.50				
SE			1.3	0.3	0.8	1.7	0.3	0.03				
n			12	12	11	11	12	12				
Delta	1993	Fall	55.6	35.1	91.4	161.1	21.3	1.58				
SE			1.4	0.2	1.3	2.3	0.2	0.04				
n			14	14	14	14	13	14				
Delta	1994	Fall	59.6	36.1	96.5	167.9	22.2	1.65				
SE			1.3	0.2	1.0	1.7	0.2	0.03				
n			15	15	15	15	15	15				
Delta	1995	Spring	55.9	37.2	96.1	169.5	23.3	1.50				
SE			1.2	0.2	0.9	1.2	0.1	0.03				
n			15	14	15	15	14	14				
Delta	1995	Fall	59.5	35.7	93.8	169.4	22.2	1.66				
SE			1.3	0.3	0.6	1.8	0.1	0.03				
n			13	12	12	12	12	12				
Delta	1996	Spring	54.8	37.0	95.0	167.6	23.5	1.48				
SE			1.5	0.2	1.2	2.1	0.2	0.04				
n			15	15	15	15	15	15				
Delta	1996	Fall	55.7	35.8	94.1	161.1	22.1	1.56				
SE			1.4	0.2	1.1	1.7	0.2	0.03				
n			14	14	14	14	14	14				
Delta	1997	Spring	53.7	37.8	96.0	166.1	23.4	1.43				
SE			1.1	0.4	0.7	2.1	0.2	0.03				
n			14	8	14	14	13	8				
Delta	1997	Fall	58.2	36.0	95.0	159.4	22.4	1.60				
SE			1.0	0.3	0.9	2.0	0.2	0.03				
n			20	15	20	20	20	15				
Delta	1998	Spring	56.1	36.7	98.4	168.9	23.3	1.53				
SE			1.4	0.5	1.1	1.9	0.3	0.04				
n			12	12	12	12	11	12				
Delta	1998	Fall	56.4	35.7	95.2	159.1	21.6	1.58				
SE			1.2	0.2	1.2	2.3	0.3	0.03				
n			16	16	16	16	16	16				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Delta	1999	Spring	53.7	37.2	92.3	161.7	22.9	1.44				
SE			1.3	0.2	0.9	12.1	0.3	0.03				
n			14	14	14	13	14	14				
Delta	1999	Fall	57.1	35.7	91.9	160.6	22.1	1.58				
SE			1.3	2.7	1.2	2.1	0.2	0.12				
n			14	13	14	14	14	13				
Delta	2000	Spring	52.1	36.6	89.0	159.6	22.9	1.42				
SE			1.2	0.3	3.4	2.0	0.2	0.02				
n			12	12	12	12	12	12				
Delta	2000	Fall	56.6	35.7	95.6	162.4	22.2	1.58				
SE			1.8	0.3	1.1	2.6	0.2	0.0				
n			14	14	14	14	14	14				
Delta	2001	Spring	55.4	37.7	94.4	166.8	23.7	1.47				
SE			1.4	0.3	0.9	3.2	0.2					
n			11	11	11	11	11	11				
Delta	2001	Fall	57.1	35.5	93.6	163.6	22.0	1.61				
SE			1.1	0.3	0.9	2.0	0.2					
n			14	14	14	14	14	14				
Delta	2002	Spring	59.1									
SE			0.9									
n			15									
Delta	2002	Fall	54.4									
SE			1.5									
n			15									
Delta	2003	Spring	53.4									
SE			1.6									
n			15									
Delta	2003	Fall	57.4									
SE			0.9									
n			16									
Delta	2004	Spring	58.8									
SE			1.7									
n			14									
Delta	2004	Fall	60.2									
SE			1.3									
n			15									

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Delta	2005	Spring	57.8									
SE			1.7									
n			14									
Delta	2007	Spring	55.4									
SE			1.6									
n			11									
Denali[a]	1987	Spring	59.4	37.7	97.5	163.5	23.6	1.57				
SE			3.3	0.3	1.1	3.9	0.2	0.08				
n			5	6	6	6	7	5				
Denali	1988	Spring	59.2	37.3	97.3	167.0	23.4	1.58				
SE			2.4	0.3	2.0	2.3	0.5	0.06				
n			9	8	8	8	8	8				
Denali	1989	Spring	59.5	36.9	96.8	169.2	24.9	1.61				
SE			1.7	0.1	1.0	1.5	0.9	0.05				
n			13	13	13	13	14	13				
Denali	1990	Spring	57.3	36.8	95.2	165.4	24.1	1.56				
SE			1.2	0.3	1.0	2.0	0.3	0.03				
n			15	16	16	16	16	15				
Denali	1991	Spring	50.7	36.1	91.5	157.2	23.6	1.40				
SE			1.4	0.4	1.1	2.5	0.8	0.03				
n			15	14	14	14	14	14				
Denali	1992	Spring	56.0	37.4	94.2	165.7	24.3	1.50				
SE			1.2	0.2	0.8	1.3	0.4	0.03				
n			16	16	16	16	16	16				
Denali	1993	Spring	56.9	37.1	93.5	164.7	23.1	1.53				
SE			2.0	0.3	1.1	2.7	0.4	0.05				
n			9	9	8	9	9	9				
Denali	1994	Spring	56.9	37.3	95.7	167.5	23.8	1.53				
SE			1.5	0.3	0.9	1.7	0.3	0.04				
n			11	11	11	11	11	11				
Denali	1995	Spring	60.0	37.2	95.7	168.0	23.8	1.61				
SE			2.7	0.4	2.4	3.2	0.2	0.07				
n			6	6	6	6	6	6				
Denali	1996	Spring	60.1	37.7	94.9	165.4	23.6	1.59				
SE			2.1	0.5	1.6	3.9	0.3	0.04				
n			7	7	7	7	7	7				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Denali	1997	Spring	61.0	37.5	102.3	167.0	24.3	1.63				
SE			2.1	0.3	2.9	3.2	0.5	0.05				
n			3	4	3	4	4	3				
Denali	1998		62.9									
SE			2.5									
n			5									
Denali	1999		62.1									
SE			1.3									
n			11									
Denali	2000		58.9									
SE			1.6									
n			13									
Denali	2001		58.6									
SE			1.6									
n			13									
Denali	2002		66.9									
SE			2.2									
n			6									
Denali	2003		59.2									
SE			2.0									
n			5									
Denali	2004		56.8									
SE			2.0									
n			7									
Denali	2005		61.4									
SE			1.6									
n			11									
Denali	2006		55.7									
SE			2.0									
n			12									
Denali	2007		59.0									
SE			1.7									
n			12									
Denali	2008		60.2									
SE			1.5									
n			12									

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Fortymile	1990	Fall	52.7	35.8	93.0	157.9		1.47				
SE			1.2	0.2	1.2	1.5		0.03				
n			14	14	14	14		14				
Fortymile	1991	Fall	53.9	35.2	94.1	157.0	22.0	1.53				
SE			1.4	0.2	1.4	2.1	0.2	0.03				
n			14	14	13	14	14	14				
Fortymile	1992	Spring	50.2	36.8	89.7	158.5	22.2	1.31				
SE			2.3	0.5	2.1	4.4	0.3	0.03				
n			7	6	6	6	5	6				
Fortymile	1992	Fall	55.1	35.0	96.7	154.5	21.4	1.57				
SE			1.7	0.3	1.2	2.6	0.2	0.05				
n			14	13	13	13	13	13				
Fortymile	1993	Fall	56.1	35.3	93.9	158.5	21.3	1.59				
SE			0.9	0.2	1.1	1.7	0.1	0.02				
n			15	14	14	14	15	14				
Fortymile	1994	Fall	54.4	36.0	94.1	159.5	22.4	1.53				
SE			1.2	0.4	0.8	1.8	0.2	0.05				
n			14	11	13	13	13	11				
Fortymile	1995	Fall	56.7	35.4	94.1	163.6	22.1	1.60				
SE			1.2	0.3	0.9	2.2	0.2	0.03				
n			15	15	14	14	15	15				
Fortymile	1996	Fall	55.1	35.5	94.5	156.9	22.0	1.55				
SE			1.4	0.3	1.4	2.1	0.2	0.03				
n			15	15	15	15	15	15				
Fortymile	1997	Fall	59.3	36.3	96.5	158.7	22.2	1.63				
SE			1.3	0.2	0.8	2.2	0.2	0.03				
n			15	15	15	15	15	15				
Fortymile	1998	Fall	53.0	35.8	91.8	152.1	21.7	1.48				
SE			1.3	0.3	1.4	3.5	0.3	0.03				
n			17	17	17	17	17	17				
Fortymile	1999	Fall	54.7	36.2	95.9	158.5	21.9	1.51				
SE			1.0	0.3	1.2	1.6	1.5	0.02				
n			15	15	15	15	14	15				
Fortymile	2000	Fall	56.7	35.6	95.6	157.6	21.4	1.59				
SE			1.1	0.2	0.6	2.0	0.2	0.03				
n			15	15	15	15	15	15				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Fortymile	2001	Fall	54.1	35.2	92.5	160.8	21.6	1.55				
SE			1.1	0.2	1.6	1.5	0.2	0.03				
n			17	17	17	17	17	17				
Galena Mtn	1993	Fall	66.5	36.5	96.3	170.3	22.4	1.82				
SE			3.2	0.6	2.3	6.7	0.4	0.06				
n			4	4	4	3	4	4				
Galena Mtn	1994	Fall	65.6	35.9	99.2	177.3	23.5	1.83				
SE			1.3	0.1	1.4	2.1	0.2	0.03				
n			9	9	9	9	9	9				
Kenai Mtns	1996	Spring	57.6	38.2	97.6	166.6	23.4	1.48				
SE			1.5	0.3	0.9	2.5	0.1	0.03				
n			11	11	11	11	11	11				
Kenai Mtns	2000	Fall	60.3		101.0	164.4						
SE			1.0		1.1	1.7						
n			14		13	7						
Kenai Mtns	2001	Fall	59.5		100.2	161.0						
SE			1.9		1.3	3.3						
n			11		7	8						
Killey River	1996	Spring	65.7	39.4	102.4	174.4	24.6	1.66				
SE			0.6	0.3	1.4	2.0	0.2	0.02				
n			10	9	7	8	9	9				
Killey River	2001	Fall	61.0		102.0	166.8						
SE			1.9		1.3	2.7						
n			13		10	10						
Macomb	1988	Spring	53.0	37.0	99.3	164.8	23.1	1.43				
SE			0.6	0.4	0.6	2.6	0.3	0.02				
n			4	4	4	4	4	4				
Macomb	1990	Spring	48.7	36.3	94.3	166.0	23.0	1.34				
SE			1.2	0.5	1.0	2.4	0.4	0.03				
n			12	12	12	12	6	12				
Macomb	1994	Spring	53.9	37.4	97.0	162.5	23.1	1.44				
SE			1.4	0.3	1.6	2.2	0.2	0.03				
n			10	10	9	10	10	10				
Macomb	1996	Fall	58.4	36.1	96.8	165.4	21.9	1.62				
SE			2.6	0.4	2.0	2.1	0.3	0.06				
n			8	8	8	8	8	8				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Macomb	1998	Fall	60.2	36.1	96.4	165.7	22.7	1.67				
SE			1.4	0.2	1.4	2.2	0.2	0.04				
n			12	12	12	12	12	12				
Macomb	1999	Fall	58.1	35.4	94.8	158.3	23.0	1.64				
SE			4.4	0.7	2.1	4.6	0.5	0.09				
n			4	4	4	4	4	4				
Mulchatna	1995	Spring	50.1	36.9	93.9	156.0	22.4	1.36	34.4	73.3	38.8	108.3
SE			1.4	0.3	1.5	2.1	0.2	0.03	1.0	4.1	3.4	19.9
n			10	10	10	10	10	10	10	10	10	10
Mulchatna	1998	Fall	48.3	34.3	92.1	151.6	20.8	1.4	32.9	48.2		
SE			2.6	0.4	1.3	3.1	0.3	0.1	1.7	5.5		
n			10	14	14	14	13	10	10	10		
Mulchatna	2000	Spring	46.9	35.6	91.0	158.0	22.0	1.31				
SE			1.2	0.3	0.9	3.1	0.2	0.03				
n			11	10	11	10	10	10				
Mulchatna	2000	Fall	51.2	35.2	91.8	154.4	21.2	1.45				
SE			1.8	0.2	1.3	2.5	0.4	0.05				
n			10	10	10	10	9	10				
Mulchatna	2001	Spring	49.8	35.9	92.4	153.7	22.0	1.39				
SE			0.9	0.2	0.9	2.5	0.5	0.03				
n			13	13	12	12	11	13				
Mulchatna	2002	Fall	50.4	35.6	91.7	146	21.9	1.42	35.6	60.9		
SE			2.1	0.4	1.9	2.9	0.3	0.05	1.7	4.6		
n			10	10	10	10	10	10	10	10		
Nelchina GMU[b] 12	1992	Spring	56.4						39.5		34	
SE			1.2						0.9		3.7	
n			9						9		9	
Nelchina GMU[b] 12	1993	Spring	57.0	36.9	93.6	162.7	23.7	1.55	39.4	50.7	29.1	56.7
SE			1.8	0.3	1.3	3.4	0.9	0.04	1.4	6.4	4.6	10.4
n			7	7	7	7	7	7	7	7	7	7
Nelchina GMU[b] 13	1992	Spring	49.6						34.5		15.4	
SE			1.6						2.2		2.5	
n			8						8		8	
Nelchina GMU[b] 13	1993	Spring	53.8	36.9	93.6	156.7	22.6	1.46	37.5	49.9	23.3	46.7
SE			1.4	0.4	1.3	1.7	0.2	0.03	0.9	3.8	2.4	7.8
n			12	12	11	12	12	11	12	12	12	12

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Nelchina	1994	Spring	48.9						34.0	45.6	26.7	111.1
SE			1.9						1.4	6.4	4.6	18
n			11						11	11	11	11
Nelchina	1995	Spring	47.6	36.7	92.2	159.8	22.6	1.30	32.8	36.9	26.1	120.2
SE			0.8	0.2	0.8	1.3	0.1	0.02	0.8	2.9	5	24.9
n			29	29	29	29	29	29	14	14	14	14
Nelchina	1995	Fall	53.5	35.6	94.1	160.2	21.4	1.50	36.3	65.5		
SE			1.5	0.3	1.2	1.7	0.2	0.03	1.1	4.2		
n			15	15	15	15	15	15	11	11		
Nelchina	1996	Spring	53.1	37.2	94.0	167.4	22.7	1.42				
SE			1.2	0.3	1.0	2.1	0.2	0.02				
n			16	16	16	16	16	16				
Nelchina	1996	Fall	48.3	35.5	88.3	149.5	21.2	1.36	33.0	51.9	25	
SE			2.1	0.3	1.6	1.9	0.2	0.05	1.5	7.6	4.1	
n			10	10	10	10	9	10	10	10	8	
Nelchina	1997	Spring	49.1	36.8	93.9	159.9	23.0	1.32	35.5	56.3	34.9	63.1
SE			1.0	0.2	1.0	2.0	0.1	0.02	1.3	3.7	3.1	17.3
n			23	18	23	23	23	18	10	10	10	10
Nelchina	1997	Fall	55.5	35.9	92.1	156.6	21.8	1.55	38.0	67.7	33.4	
SE			1.8	0.3	1.5	2.0	0.5	0.05	1.5	2.7	3.6	
n			10	10	10	10	10	10	10	10	10	
Nelchina	1998	Spring	57.0	37.5	94.4	168.6	23.1	1.52				
SE			1.1	0.1	0.9	1.4	0.2	0.03				
n			15	15	15	15	15	15				
Nelchina	1998	Fall	50.6	35.4	93.0	153.8	20.9	1.43	34.2	53.6		
SE			0.9	0.2	0.7	1.6	0.2	0.02	1.0	1.9		
n			25	25	25	25	25	25	10	10		
Nelchina	1999	Spring	53.1	37.1	92.1	163.7	22.9	1.43				
SE			1.2	0.3	0.9	1.6	0.2	0.03				
n			15	15	15	15	15	15				
Nelchina	1999	Fall	52.0	35.9	91.3	154.6	21.7	1.45				
SE			0.8	0.2	0.6	1.0	0.1	0.02				
n			38	38	38	38	38	38				
Nelchina	2000	Spring	48.6	37.5	91.7	159.5	23.4	1.3				
SE			0.8	0.2	0.9	1.4	0.1	0.0				
n			27	28	27	28	27	27				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Nelchina	2000	Fall	53.5	35.5	92.4	154.9	21.6	1.51				
SE			1.1	0.2	0.9	1.4	0.2	0.03				
n			37	36	37	36	37	36				
Nelchina	2001	Spring	52.5	37.2	91.2	162.3	23.6	1.42				
SE			0.9	0.2	0.8	1.6	0.2	0.02				
n			26	25	25	25	25	25				
Nelchina	2001	Fall	58.5	36.4	96.1	160.3	22.5	1.60				
SE			0.9	0.2	0.8	1.1	0.1	0.02				
n			40	40	40	40	40	40				
Northern AK Peninsula	1995	Spring	51.4	35.8	92.6	161.1	22.5	1.43				
SE			1.3	0.3	1.1	2.1	0.2	0.03				
n			19	19	19	19	19	19				
Northern AK Peninsula	1995	Fall	44.7	34.2	88.6	145.1	20.2	1.31	30.0	55.5		
SE			1.6	0.3	0.9	1.6	0.2	0.04	1.3	5.5		
n			10	10	10	10	10	10	10	10		
Northern AK Peninsula	1996	Fall	46.0	34.2	89.1	143.5	20.3	1.34	30.6	65	33.3	
SE			2.4	0.3	2.3	2.6	0.4	0.06	1.7	3.5	3.8	
n			10	10	10	10	10	10	10	10	10	
Northern AK Peninsula	1997	Spring	48.4	35.6	91.8	157.4	22.2	1.36				
SE			1.4	0.2	0.9	1.5	0.2	0.03				
n			14	14	14	14	14	14				
Northern AK Peninsula	1997	Fall	48.3	34.0	92.9	152.8	20.3	1.42	31.9	58.3	33.2	
SE			2.1	0.2	1.4	3.2	0.3	0.06	1.6	5.5	3.7	
n			10	10	10	10	10	10	9	10	9	
Northern AK Peninsula	1998	Fall	49.4	33.9	90.9	151.4	20.6	1.46	30.4	47.1		
SE			1.3	0.2	0.9	1.6	0.2	0.03	1.4	4.2		
n			29	29	29	29	29	29	10	10		
Northern AK Peninsula	1999	Fall	51.9	34.9	93.6	154.0	21.4	1.48				
SE			1.3	0.3	1.5	2.3	0.3	0.04				
n			11	11	11	11	10	11				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Northern AK Peninsula	2001	Spring	54.3	36.0	96.7	158.4	22.4	1.51				
SE			0.9	0.3	1.1	2.2	0.2	0.02				
n			21	20	19	19	19	20				
Nushagak Peninsula	1995	Spring	57.1	36.9	98.3	167.5	23.4	1.55	40.1	78.8	49.4	295.2
SE			1.3	0.3	0.9	2.7	0.2	0.03	3.2	2.1	1.0	40.9
n			15	15	15	15	15	15	5	5	5	5
Nushagak Peninsula	1997	Spring	50.9	37.5	96.8	151.9	22.8	1.36				
SE			1.9	0.5	1.5	3.0	0.3	0.04				
n			10	13	13	13	13	10				
Nushagak Peninsula	1998	Fall	55.8	35.3	94.8	156.2	21.7	1.58	39.6			
SE			1.6	0.3	0.9	3.0	0.2	0.03	1.3			
n			5	5	5	5	5	5	5			
Nushagak Peninsula	2000	Spring	49.2	35.3	95.0	165.9	22.3	1.39				
SE			0.7	0.2	0.9	2.0	0.2	0.02				
n			10	10	10	10	10	10				
Nushagak Peninsula	2001	Spring	51.3	37.1	93.6	156.7	23.1	1.43				
SE			1.6	0.6	1.5	1.5	0.5	0.05				
n			10	9	11	11	9	9				
Rainy Pass	1999	Fall	63.6	37.0	102.8	170.8	22.8	1.72				
SE			2.5	0.5	2.0	1.7	0.4	0.05				
n			5	5	5	5	5	5				
Ray Mtns	1994	Fall	60.9	35.5	96.7	170.7	22.3	1.72				
SE			1.3	0.3	0.6	1.5	0.2	0.03				
n			20	20	20	20	17	20				
Unimak	1997	Spring	48.4	35.1	93.0	157.6	21.7	1.38				
SE			3.0	0.8	2.0	3.1	0.3	0.06				
n			5	5	5	5	5	5				
Unimak	1999	Fall	56.0	34.5	96.1	166.2	21.4	1.62				
SE			1.5	0.3	0.9	2.0	0.3	0.05				
n			12	12	12	12	12	12				
Southern AK Peninsula	1997	Spring	48.9	35.6	93.6	153.9	22.3	1.37				
SE			1.0	0.2	1.0	2.1	0.1	0.03				
n			13	13	13	13	13	13				

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
Southern AK Peninsula	1998	Fall	52.2	33.9	91.9	153.9	20.9	1.54				
SE			1.2	0.3	0.8	1.7	0.2	0.03				
n			13	13	13	13	13	13				
Western Arctic	1992	Spring	39.5				20.8		28.2		42	
SE			0.9				0.17		0.80		4.3	
n			16				16		16		10	
Western Arctic	1992	Fall	40.4				19.3		27.4		43.5	
SE			1.8				0.19		1.3		0.98	
n			13				13		13		2	
Western Arctic	1993	Spring	37.2				20.4		26.2	39.8	33.4	
SE			1.0				0.22		0.7	6.1	2.9	
n			14				14		14	10	10	
Western Arctic	1994	Spring	40.1				20.7		27.7	23.6	24.8	
SE			1.3				0.20		0.8	4.5	5.5	
n			15				15		15	15	11	
Western Arctic	1994	Fall	32.4				17.5		22.8	16.6	12.3	
SE			1.2				0.17		0.9	3.2	3.0	
n			17				17		17	17	13	
Western Arctic	1995	Fall	36.8				18.5		24.6	46.4		
SE			1.2				0.21		1.1	8.3		
n			9				9		9	9		
White Mtns	1988	Fall		36.0	103.9	166.5	22.4					
SE				0.5	1.5	2.5	0.4					
n				10	8	10	9					
White Mtns	1991	Fall	58.5	35.9	95.4	164.8	22.2	1.63				
SE			2.1	0.4	1.5	2.0	0.4	0.05				
n			9	9	9	9	9	9				
White Mtns	1995	Spring	59.0	37.6	98.5	172.5	24.4	1.56				
SE			1.4	0.4	1.3	1.7	0.2	0.03				
N			8	7	8	8	8	7				
White Mtns	1995	Fall	60.6	36.4	96.2	170.0	23.0	1.66				
SE			2.1	0.5	1.3	3.5	0.3	0.04				
n			6	6	6	6	6	6				
White Mtns	1997	Fall	61.6		98.3	164.8	22.7					
SE			1.1		1.0	3.2	0.4					
n			6		6	6	6					

Herd	Year	Season	Weight	Metatarsus	Girth	Total length	Mandible length	Weight: metatarsus ratio	Gutted weight	Femur fat (%)	Mandible fat (%)	Warble larvae
White Mtns	2000	Spring	53.9	37.5	94.3	167.5	23.1	1.44				
SE			1.9	0.6	2.3	1.8	0.1	0.1				
n			4	4	4	4	4	4				
White Mtns	2001	Fall	61.2	36.1	100.2	166.8	22.3	1.70				
SE			1.4	0.2	1.3	2.4	0.1	0.04				
n			3	3	3	3	3	3				
White Mtns	2002	Fall	54.7	35.8	95.0	159.3	22.2	1.52				
SE			4.9	0.9	4.6	4.7	0.2	0.10				
n			3	3	3	3	3	3				
White Mtns	2003	Fall	62.3	35.7	99.5	167.5	22.5	1.75				
SE			0.9	0.4	1.2	3.8	0.4	0.02				
n			6	6	6	6	6	6				
White Mtns	2007	Fall	65.9	35.3	102.2	173.2	22.9	1.86				
SE			2.2	0.7	1.5	1.4	0.3	0.03				
n			6	6	6	6	6	6				
Wolf Mtn	1995	Fall	59.6	35.7	97.0	166.1	22.7	1.67				
SE			2.1	0.3	1.1	2.2	0.3	0.05				
n			8	8	8	7	8	8				
Wolf Mtn	1995	Fall	59.6	35.7	97.0	166.1	22.7	1.67				
SE			2.1	0.3	1.1	2.2	0.3	0.05				
n			8	8	8	7	8	8				

[a] All Denali data provided by L. G. Adams (unpublished).

[b] GMU = game management unit.

Appendix D. Summer weather data used as covariates in modeling survival, natality, calf weight, and calf:cow ratio in the Delta caribou herd, Alaska, 1977–2007. Variable names are in italics.

Year	Greenup day	*greenup* (ordinal)	First fall day below –2°C End green	*end.green* (ordinal)	°C Temp	*length.green* (*end.green-greenup*)	*july.rain* Total rain Jul (mm)	*summer.rain* Total rain Jun–Aug (mm)	°C Mean Jul temp[a]	°C Mean Jun–Aug temp[a]	°C Mean Aug min[a]
1977	5/18/1977	138	9/3/77	246	–2.8	108					
1978	5/6/1978	126	8/25/1978	237	–2.8	111	531	1,756	12.6	11.9	4.2
1979	5/5/1979	125	9/1/1979	244	–3.3	119	806	1,731	12.3	12.6	6.1
1980	5/5/1980	126	8/24/1980	237	–2.2	111	590	2,093	12.6	10.0	4.2
1981	5/6/1981	126	8/17/1981	229	–6.1	103	1,063	2,987	10.7	9.3	3.2
1982	5/20/1982	140	8/27/1982	239	–2.8	99	715	1,658	12.1	9.8	2.8
1983	5/11/1983	131	9/2/1983	245	–6.1	114	651	2,021	13.0	9.1	4.1
1984	5/16/1984	137	8/28/1984	241	–6.7	104	1,090	2,344	12.2	9.0	4.5
1985	5/23/1985	143	9/13/1985	256	–2.6	113	569	1,644	13.5	9.7	4.5
1986	5/20/1986	140	8/16/1986	228	–2.8	88	1,950	3,347	13.1	8.1	2.2
1987	5/8/1987	128	8/30/1987	242	–5.0	114				11.0	4.4
1988	5/8/1988	129	8/31/1988	244	–2.2	115	1,123	1,928		10.7	4.5
1989	5/14/1989	134	9/15/1989	258	–2.8	124	963	1,951			
1990	5/8/1990	128	8/26/1990	238	–2.2	110	671	3,058	13.9	10.7	4.7
1991	5/4/1991	124	8/26/1991	238	–2.8	114	678	1,705	12.1	8.7	3.2
1992	5/25/1992	146	9/8/1992	252	–3.3	106	194	1,438	13.4	10.2	4.9
1993	4/29/1993	119	8/24/1993	236	–2.2	117	678	1,725	14.8	11.0	6.5
1994	5/1/1994	121	9/7/1994	250	–2.8	129	194	2,060	14.3	12.7	6.5
1995	5/1/1995	121	9/4/1995	247	–2.8	126	589	2,029	13.5	9.8	4.5
1996	5/12/1996	133	8/27/1996	240	–3.3	107	411	1,603	13.1	8.6	3.0
1997	5/4/1997	124	9/14/1997	257	–2.2	133	771	2,254	14.5	11.1	6.2
1998	5/5/1998	125	8/19/1998	231	–3.3	106	1,152	2,453	12.9	8.4	3.8
1999	5/12/1999	132	9/9/1999	252	–2.2	120	891	1,642	13.2	11.8	6.4
2000	5/16/2000	137	8/16/2000	229	–3.3	92	770	2,509	11.5	8.0	3.7
2001	5/18/2001	138	9/9/2001	252	–2.8	114	1,406	2,068	13.6	13.9	9.3
2002	5/19/2002	139	9/20/2002	263	–2.2	124	1,167	3,516	12.5	9.7	4.3
2003	5/8/2003	128	9/13/2003	254	–4.4	126	1,215	2,238	13.4	10.8	5.4
2004	5/5/2004	126	9/6/2004	250	–4.4	124	726	1,346	15.0	14.5	6.8
2005	5/4/2005	124	10/1/2005	274	–2.8	150	849		13.7	12.6	5.8
2006	5/14/2006	134	9/30/2006	273	–3.9	139	925	2,394	12.7	9.9	4.8
2007	5/4/2007	124	9/22/2007	265	–3.3	141	400	1,841	14.2	12.7	6.0

[a] Variable names for temperature variables: *july.mean.temp*, *summer.mean.temp*, *aug.min.temp*.

Appendix E. Winter weather variables used as covariates in modeling survival, natality, calf weight, and calf:cow ratios in Delta caribou herd females, Alaska, 1978–2008. Denali.snow is the sum of the 1 February, 1 March, and 1 April snow depth readings (cm) at the Denali Park climate station. NRCS.snow is the sum of the averaged snow depth readings (converted to cm) for 4 NRCS snow stakes that were read annually on 1 February, 1 March, and 1 April (or as closely as possible to those dates).

	Snow indices (cm)	
Year	*Denali.snow*	*NRCS.snow*
1978	158	
1979	191	
1980	168	
1981	46	
1982	122	
1983	152	
1984	107	
1985	218	
1986	48	
1987	43	
1988	92	
1989	198	
1990	203	
1991	312	
1992	231	
1993	335	
1994	160	165
1995	168	191
1996	140	132
1997	173	168
1998	132	150
1999	109	124
2000	234	212
2001	104	140
2002	91	126
2003	20	65
2004	132	161
2005	168	251
2006	135	88
2007	97	157
2008	99	128

Appendix F. Counts and estimates of wolf and moose numbers within Game Management Unit (GMU) 20A, and categorical values for wolf abundance used in modeling survival rates of radiocollared females in the Delta caribou herd, 1975–2008. Categories are as follow: 1 = <100, 2 = >100<150, 3 = >150<200, 4 = >200.

Year	Wolves (GMU 20A)	Wolves within the Delta range (abundance category)[a]	GMU 20A moose
1975	239[b]	220 (4)	2,500
1976	125[b]	110 (2)	2,800
1977	100[b]	100 (1)	3,300
1978	80[b]	65 (1)	3,600
1979	64–84[b]	50 (1)	4,200
1980	100–125[b]	80 (1)	4,900
1981	130–157[b]	110 (2)	5,600
1982		110 (2)	6,300
1983		110 (2)	7,000
1984		110 (2)	7,663
1985	195[c]	175 (3)	8,100
1986		220 (4)	8,500
1987		205 (4)	9,000
1988	183[c]	170 (3)	9,430
1989		180 (3)	10,000
1990		210 (4)	10,500
1991	267[c]	250 (4)	11,500
1992		240 (4)	11,600
1993	281[c]	250 (4)	12,300
1994	193[c]	170 (3)	13,800
1995	198[c]	180 (3)	12,650
1996	207[c]	190 (3)	11,500
1997	227[c]	205 (4)	13,000
1998	268[c]	245 (4)	12,100
1999		190 (3)	13,446
2000	210[d]	170 (3)	12,668
2001		175 (3)	13,813
2002		175 (3)	15,700
2003		190 (3)	17,621
2004		190 (3)	16,279
2005	216–226[e]	190 (3)	16,018
2006		190 (3)	15,328
2007		190 (3)	n.a.
2008		190 (3)	12,537

[a] Excludes estimate of wolf numbers on western Tanana Flats where caribou did not range.

[b] Gasaway et al. 1983b.

[c] Young 2000.

[d] Young 2006.

[e] Young 2009.

Appendix G. Hunting seasons and bag limits for Delta herd caribou, Alaska, regulatory years[a] 1968–2006.

Regulatory year	Area, season, and bag limit
1968–1969 through 1972–1973	Game Management Units (GMU) 11–14, 16, 17, 20, 10 Aug–31 March, 3 caribou
1972–1973	GMUs 12, 17, 20, 10 Aug–31 March, 3 caribou
1973–1974	GMUs 20A and 20D, 10 Aug–31 Dec, 1 caribou[b]
1974–1980	No open season
1980–1981	GMU 20A, 1 Sep–30 Sep, 1 male by drawing permit, 200 permits
1981–1982	GMU 20A, 10 Aug–30 Sep, 1 caribou by drawing permit (150 permits), 15 Nov–31 Dec, antlered caribou by registration permit, harvest quota of 400
1982–1983	GMU 20A, 10 Aug–30 Sep, 1 caribou by drawing permit (175 permits), 1 Dec–31 Mar, antlered caribou by registration permit, harvest quota of 500
1983–1984	GMU 20A, general open season 10 Aug–31 Mar, 1 caribou[c]
1984–1985	GMU 20A, 20 Aug–20 Sep, 1 caribou by registration permit, harvest quota of 600
1985–1986	Western portion of GMU 20A, 10 Aug–31 Dec, Tier II (i.e., subsistence) permits, 200 permits; remainder of GMU 20A, general open season 1 Sep–15 Sep, 1 caribou
1986–1987	Western portion of GMU 20A, 6 Sep–31 Dec, 1 caribou by drawing permit, 200 permits issued; remainder of GMU 20A, general open season 1 Sep–15 Sep, 1 caribou
1987–1988 through 1989–1990	Western portion of GMU 20A, 10 Aug–25 Aug and 21 Sep–31 Dec, 1 caribou by drawing permit, 200 permits; remainder of GMU 20A, general open season 1 Sep–15 Sep, 1 bull
1990–1991	Western portion of GMU 20A, 10 Aug–10 Sep, 1 caribou by drawing permit, 100 permits, and 1 Feb–28 Feb, antlered caribou by registration permit, 75 permits; remainder of GMU 20A , general open season, 1 Sep–10 Sep, 1 bull, and 1 Feb–31 Mar, antlered caribou by registration permit, 75 permits
1991–1992	Ferry Trail Management Area, 10 Aug–10 Sep, 1 caribou by drawing permit (up to 200 permits issued); or 1–15 Feb, 1 caribou by registration permit (up to 75 permits issued in Nenana); Yanert Controlled Use Area 1–15 Sep, 1 bull; or 1–15 Jan, 1 caribou; remainder of GMU 20A, 1–10 Sep, 1 bull; or 16 Feb–1 Mar, 1 antlered caribou by registration permit (up to 175 permits issued in Nenana)[d]
1992–1996	GMU 20A, no open season
1996–1997 through 2001–2002	GMU 20A, 1 bull by drawing permit, 100 permits
2002–2003 through 2006–2007	GMU 20A, 1 bull by drawing permit, 175 permits

[a] Regulatory year begins 1 July and ends 30 June (e.g., regulatory year 1968 = 1 July 1968–30 June 1969).
[b] Closed by emergency order in October 1973.
[c] Closed by emergency order on 20 September.
[d] All winter seasons were closed by emergency order (No. 3-11-91).

Appendix H. Harvest of Delta herd[a] caribou, regulatory years[b] 1968–2006.

Regulatory	Reported harvest			Estimated
year	Males	Females	Total[c]	total harvest
1968	119	25	147	205
1969	169	54	225	324
1970	198	68	275	428
1971	387	226	624	740
1972	372	132	517	700
1973	158	67	233	301
1974[c]				
1980	104	0	104	104
1981	191	73	268	268
1982	193	77	274	274
1983	616	110	748	1,187[d]
1984	335	175	534	848[d]
1985	304	74	381	605[d]
1986	404	110	520	841[d]
1987	391	38	430	522[d]
1988	415	22	441	555[d]
1989	459	18	480	686[d]
1990	275	83	361	549[d]
1991	277	22	302	456[d]
1992[c]				
1996	22	0	22	22
1997	44	0	44	44
1998	49	1	50	50
1999	38	0	38	38
2000	34	0	34	34
2001	32	0	32	32
2002	37	0	37	37
2003	32	0	32	32
2004	45	1	46	46
2005	35	0	35	35
2006	25	0	25	25

[a] Includes Yanert herd harvest during years the 2 herds could be separated.

[b] Regulatory year begins 1 July and ends 30 June (e.g., regulatory year 1968 = 1 July 1968–30 June 1969).

[c] Includes caribou of unknown sex.

[d] No open season.

[e] Estimated by dividing reported general harvest by 0.63 (estimated proportion of successful hunters that report with harvest tickets).

Appendix I. Natality rates of radiocollared known-aged female caribou in the Nelchina herd, Alaska, 1993–2007.

	Proportion parturient (%) in late May						
Year	Yearlings	2-year olds	3-year olds	4-year olds	5-year olds	≥6-year olds	All cows 3 years and older
1993							19/29 (66)
1994							n/a
1995							18/20 (90)
1996		0/7 (0)					10/15 (66)
1997		0/2 (0)	3/6 (50)	n/a	n/a	5/6 (83)	8/12 (66)
1998		0/2 (0)	5/11 (45)	6/8 (75)	n/a	6/7 (86)	17/26 (65)
1999		n/a	3/12 (25)	6/9 (66)	2/6 (33)	6/7 (86)	17/34 (50)
2000		n/a	0/8 (0)	6/10 (60)	4/10 (40)	5/5 (100)	15/33 (45)
2001		0/5	1/6 (10)	6/6 (100)	7/8 (75)	9/14 (64)	23/34 (68)
2002			7/11 (64)				
2003			3/10 (30)				
2004			6/11 (55)				
2005			3/8 (38)				
2006			2/2 (100)				
2007			2/4 (50)				
1993–2007		0/16 (0)	35/89 (35)	24/33 (73)	13/24 (54)	31/39 (79)	127/203 (65)

Fieldwork Photos

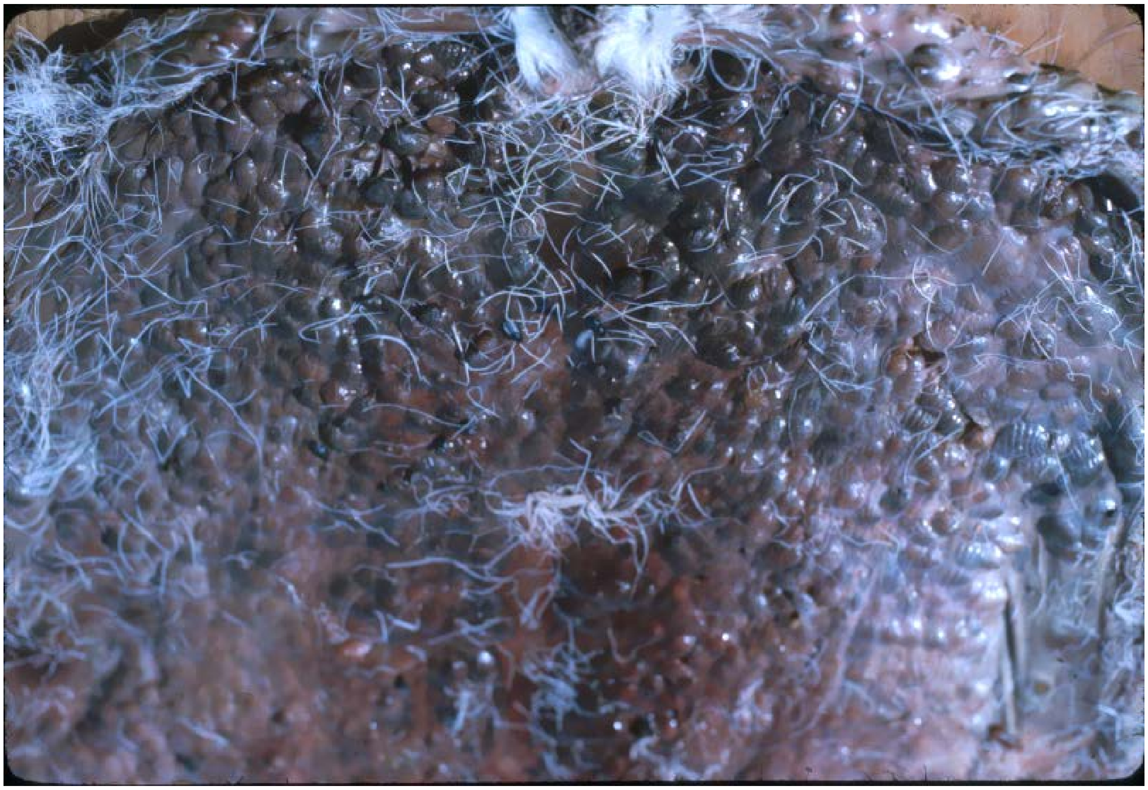
Photograph 1. Carcasses of caribou abandoned by hunters north of Kiana (Game Management Unit 23, Western Arctic herd) during winter 1975–1976. Most of the Western Arctic herd migrated south along the coast of Northwest Alaska in fall 1975 and many wintered in the Kobuk Valley and Selawik flats adjacent to many villages. Heavy harvest (including wasteful harvest) was a major factor in an accelerating caribou population decline. In one survey in May 1976, ADF&G biologists found 950–1,000 carcasses of caribou that had been largely wasted near the villages of Kobuk, Shungnak, Ambler, Kiana, Selawik, Kotzebue, Kivalina, and Point Hope (Davis 1976a). Photo by James L. Davis, May 1976.

Photograph 2. Carcasses of caribou abandoned by hunters in the Rabbit Mountain area (Game Management Unit 23, Western Arctic herd), Alaska, in winter 1979–1980. Photo by Patrick Valkenburg, April 1980.

Photograph 3. ADF&G Wildlife Technician Danny Grangaard preparing to weigh (using a weighing pole he developed in the late 1980s) a collected caribou calf from the Nelchina herd in April 1992. The weighing pole greatly simplified weighing caribou and other animals up to 135 kg (300 lb), even on steep slopes. The pole was 2.6 m (100 inches) long, with an eye-bolt 0.7 m (27 inches) from one end. Photo by Patrick Valkenburg.

Photograph 4. ADF&G Wildlife Biologist Randall L. Zarnke (Fairbanks) examines calf (Mulchatna herd, 4 months old) lung tissue for the presence of parasites and pneumonia. Although it was labor intensive, collecting samples of calves provided valuable and timely information on animal condition and presence of disease. Photo by Patrick Valkenburg, Dillingham vicinity, October 1998.

Photograph 5. Caribou calf (10 months old) in the Southern Alaska Peninsula herd, Alaska, with deciduous incisors worn to the gum-line in April 1997. Volcanic ash fell in a large part of the herd's range during winter 1996–1997. Photo by Patrick Valkenburg.



Photograph 6. Caribou calf (about 10-months old) skin from Western Arctic herd winter range near Point Lay, Alaska, with approximately 2,000 warble fly larvae (April 1980). Photo by James L. Davis.

Photograph 7. Large bull caribou participate in intense rutting battles that result in many wounded bulls in herds where bull:cow ratios are high. Photo by James L. Davis.

© Photo by James L. Davis. Cow and newborn calf on the Delta herd's Delta Creek calving area near Mount Hayes, Alaska.