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Patrick Valkenburg

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Mary Hicks
Publications Specialist
ADF&G, Wildlife Conservation
P.O. Box 25526
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(907) 465-4190

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COOPERATORS: Layne G Adams, Rodney D Boertje, Toby A Boudreau, Bruce W Dale, Craig L Gardner, David R Klein, Timothy O Osborne, Richard A Sellers, Jeff Selinger, Ted H Spraker, Robert W Tobey, Lawrence Van Daele, and Jay M Ver Hoef

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AUTHOR: Patrick Valkenburg

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SUMMARY

Continued research on the Delta Caribou (*Rangifer tarandus*) Herd (DCH) supports the hypothesis that fluctuations in caribou numbers and recruitment (i.e., fall calf:cow ratio) in this herd are largely determined by interactions of predation and weather. Unfavorable weather conditions in summer and winter predispose caribou to predation, resulting in increased wolf (*Canis lupus*) numbers, higher predation on calves and adults, and declines in caribou.

After declining rapidly from 10,700 in 1989 to less than 4000 in 1993, the Delta Caribou Herd (DCH) stabilized to just over 4000 in 1996. Radiocollared DCH females had variable annual natality rates during the 1990s. In contrast, during the 1980s radiocollared females had relatively constant natality rates. Most variation in natality was due to delayed production in 3-year-olds, except in 1993 when all adult females experienced decreased productivity. In 1996 natality in all females 3-years old and older was high, and 1 of 11 2-year-olds produced a calf.

Of 8 independent variables tested, wolf numbers, April calf weight, previous winter snow, and previous summer precipitation were the only significant predictors of fall calf:cow ratio. Natality rate was not significant as a predictor of fall calf:cow ratio, and its effects were overridden by other variables. There were no significant associations between natality rate and the 8 other variables tested.

Approximately 20% to 40% of radiocollared calf caribou were not found within 2 miles of radiocollared adult females in late winter in the DCH. Dissolution of calf:cow bonds,

movements, and clumped distributions of calves and adults can cause unacceptable biases in late winter composition counts.

In the DCH during the late 1970s and 1980s, weights of 10-month-old calves were generally high. In the early 1990s calf weights declined and then increased again but remained below previous high levels. In the DCH calves lost a significant amount of weight over winter in most years since fall weights were first measured in 1991. Newborn female calves were lighter in 1996 than in 1995.

Mean weight of female calves in April was a significant predictor of fall calf:cow ratios in the DCH from 1979 to 1996. Presumably, calf weight reflects condition of adult females and vulnerability of their calves to predation over the summer. In the Nelchina Herd calf weight in April was not correlated with fall calf:cow ratios from 1991 to 1996. The large size of the Nelchina Herd and low predator:caribou ratios on the summer range indicate that predation is of relatively minor importance now to that herd.

Weight and condition of female caribou calves in the Nelchina Herd is primarily being influenced by the high density of caribou on the summer range. Newborn calf weights were similar to those of adjacent herds in 1996, but by late September female Nelchina calves were over 20 lbs (9 kg) lighter than calves from adjacent herds. Calves that wintered in Unit 13 during the early 1990s were lighter and had lower femur and mandible marrow fat levels than those wintering in northern Unit 12. In April 1996 Nelchina caribou transplanted to the Kenai Peninsula in 1986 had calves that were 50% heavier than those found on the Nelchina range. Annual variation in weather has also influenced calf weight and condition. Summer 1996 was dry in the Talkeetna Mountains, the summer range was noticeably brown by early August, and mean October weight of female calves was significantly lower than in 1995.

Mortality rates of radiocollared caribou in the DCH were low during the early 1980s (0%-7%), increased during the late 1980s and early 1990s (5%-22%), and stabilized (10%-15%) at moderate levels from 1992 to 1996. Mortality of calves 4 to 16 months old was relatively high during the 1990s and higher than older females. However, small sample sizes and uncertainty about causes of death compromised quantification of mortality rates for all age classes.

A wolf control program conducted from October 1993 to December 1994 may have stopped the decline of the DCH, but the program did not result in expected increases in caribou calf survival to fall. Reduced wolf numbers may have resulted in lower adult mortality and may have increased the fall calf:cow ratio to about 20:100. However, calf:cow ratios in adjacent herds also increased, and the ratio in the DCH was less than half the level reached after the previous wolf control program in the 1970s. In the recent program, entire wolf packs were not removed from the summer range of the DCH due to the relative inefficiency of the trapping program, its premature termination, and because the most important wolf pack on the calving area was not included. In addition, reduced caribou nutrition could have caused caribou calves to be more vulnerable to predation than they were during the 1970s.

Wolves were the most important predator of radiocollared caribou calves in the DCH in 1995 despite the wolf control program. Wolves killed fewer collared calves in 1996, probably as a

result of an experimental diversionary feeding program, but total mortality by 30 September was similar in both years. Calves may have been relatively more vulnerable to predation of all kinds in 1996 because mean weight of newborn female calves was lower. Grizzly bears (*Ursus arctos*) and golden eagles (*Aquila chrysaetos*) were other major predators.

An experimental diversionary feeding program in the DCH successfully changed hunting behavior of a wolf pack and probably reduced caribou calf mortality from wolf predation. However, small sample sizes and confounding factors that change annually will make evaluation of diversionary feeding difficult. In the long-term, diversionary feeding could prove to be an effective way to mitigate heavy predation by key packs on high density calving areas, especially as the technique becomes more refined with increased knowledge.

Traditional winter ranges of the DCH, Nelchina, and Northern Alaska Peninsula caribou herds seem to be in relatively poor condition, but since the late 1980s Nelchina caribou have moved to new ranges in Unit 12 and the lightly used winter range of the Fortymile Herd in southern Unit 20E. At present, caribou density on summer range and summer weather conditions have been the most important factors affecting body condition in the Nelchina Herd. In this way the Nelchina Herd may be similar to the George River Herd in northern Quebec.

There is mounting evidence that density-dependent limitation occurs in Alaskan caribou herds. So far, however, the effects of food limitation on population dynamics have been minor relative to predation. There is undoubtedly a significant interaction between available food reserves (which are partly determined by caribou numbers) and weather. Herds with large food reserves (e.g., White Mountains, Ray Mountains, and Denali herds) are probably more resilient during and after periods of severe weather and may not be as easily reduced by predation because body condition can remain high, even during times of relative food scarcity. However, predation is usually so high in these small herds that harvest potential is limited. In herds where predator-prey ratios are high, declines in body condition are probably much more serious from a management perspective because population declines will more likely occur and harvest levels will have to be reduced.

Key words: body condition, calf mortality, caribou, distribution, diversionary feeding, natality, Nelchina, predation, range condition, weather, wolf.

CONTENTS

SUMMARY.....	i
BACKGROUND.....	2
STUDY OBJECTIVES.....	2
JOB OBJECTIVES.....	3
METHODS.....	3
RESULTS.....	6
POPULATION SIZE AND TREND.....	6
NATALITY RATE IN THE DCH.....	7
1995 AND 1996 FALL COMPOSITION COUNTS.....	7
WEIGHT AND SIZE OF CALVES.....	7
WEATHER.....	8
MORTALITY OF FEMALE RADIOCOLLARED CARIBOU OLDER THAN 4 MONTHS.....	8
REGRESSION MODELS.....	9
EFFECTS OF WOLF CONTROL ON THE DCH.....	9
CALF MORTALITY STUDIES.....	9
DIVERSIONARY FEEDING.....	10
<i>Effects of Diversionary Feeding on Numbers of Calves Killed by Wolves on the</i> <i>Wells Creek Calving Area.....</i>	10
<i>Effects of Diversionary Feeding on Pack Hunting Behavior.....</i>	10
GPS Collar.....	11
DISTRIBUTION OF MALE AND FEMALE CALVES IN LATE WINTER.....	11
MOVEMENTS, DISTRIBUTION, AND HARVEST.....	11
DISCUSSION.....	13
POPULATION SIZE AND TREND AND POPULATION MODELING.....	13
NATALITY RATE.....	14
WEIGHT AND SIZE OF CALVES.....	15
REGRESSION MODELS.....	15
EFFECTS OF WOLF CONTROL ON THE DCH.....	15
CALF MORTALITY STUDIES.....	16
DIVERSIONARY FEEDING.....	16
DISTRIBUTION OF MALE AND FEMALE CALVES IN LATE WINTER.....	17
MOVEMENTS AND DISTRIBUTION.....	18
WEATHER.....	18
CONDITION OF CARIBOU RANGES.....	18
EVIDENCE FOR DENSITY-DEPENDENT LIMITATION IN ALASKAN CARIBOU.....	20
CONCLUSIONS.....	20
RECOMMENDATIONS FOR MANAGEMENT AND RESEARCH.....	22
ACKNOWLEDGMENTS.....	23
LITERATURE CITED.....	23
Figure 1 Spreadsheet computer model of the DCH, 1969-2000.....	27
Figure 2 Temporal trends of 6 variables (5-year moving averages, scaled to vary in same range) as predictors of fall calf:100 cow ratios in the DCH.....	29
Tables.....	30

APPENDIX A Data used to construct a correlation matrix (Appendix E) of 9 variables from the DCH data set.....	40
APPENDIX B Delta Caribou Herd fall composition counts, 1969-1996.....	41
APPENDIX C Student's <i>t</i> -test of mean weights of samples of caribou calves from Interior Alaskan caribou herds (significant differences are bolded).....	42
APPENDIX D Whole weight, gutted weight, mandible length, diastema length, mandible fat, femur fat, warble numbers, and fat deposit index of female calves from the Nelchina and other selected caribou herds, 1992-1995.....	44
APPENDIX E Matrix of Spearman correlation coefficients (<i>r</i>), significance level, and number of observations in correlations of 9 variables from the DCH data set (significant correlations are shaded; <i>P</i> < 0.05).....	45

BACKGROUND

A continuing long-term population dynamics study of the Delta Caribou (*Rangifer tarandus*) Herd (DCH) began in 1979. Results of the first 11 years of research were presented in 8 progress reports, 2 final reports (each covering 5 years) (Davis and Valkenburg 1985, Davis et al. 1991), and numerous scientific papers (Davis et al. 1991). Predator-prey relationships and human harvest of moose (*Alces alces*), caribou, sheep (*Ovis dalli*), grizzly bears (*Ursus arctos*), and wolves (*Canis lupus*) within the range of the DCH were reviewed by Gasaway et al. (1983) and Boertje et al. (1996).

Since 1979 the DCH has gone through 4 growth phases. Herd size rapidly grew from 1979 to 1982 ($r = 0.18$), with high recruitment and low mortality from hunting and natural causes. The herd grew slowly ($r = 0.05$) from 1982 to 1985, with moderate to high recruitment, low to moderate natural mortality, and high hunting mortality. The herd also grew slowly ($r = 0.07$) from 1986 to 1988, with moderate recruitment, moderate to high natural mortality, and low hunting mortality. Then the herd rapidly declined ($r = -0.20$) from 1989 to 1992, with low recruitment, high natural mortality, and low hunting mortality.

In June 1993 the Board of Game approved a 3-year ground-based wolf predation control program for a portion of Unit 20A. One of the objectives of the program, which began in October 1993, was to reverse the decline of the Delta Caribou Herd and increase the midsummer population to 6000-8000 caribou, with a sustainable annual harvest of 300-500 caribou. To better evaluate the effectiveness of intensive management (i.e., control of wolf numbers) of the DCH, we extended the project with state funds to include annual calf mortality studies. Results of these studies will be reported in this and future Pittman-Robertson documents.

STUDY OBJECTIVES

- Evaluate the influence of weather, density, food limitation, hunting, and predation on the population dynamics of the DCH and other Interior herds.

JOB OBJECTIVES

- Census the DCH from 1991 to 1995 annually.
- Determine annual natality rate and timing of calving in the DCH.
- Determine recruitment from annual fall and spring composition counts.
- Monitor harvest annually.
- Radiocollar male and female calves in fall to assess accuracy of April composition counts and timing of mortalities.
- Determine weight and size of calves in April to determine influence of summer versus winter weather on body condition, and test a model that predicts recruitment (i.e., fall calf:cow ratio) from April calf weights in the Delta, Fortymile, and Nelchina herds.
- Radiocollar female calves in fall to maintain known-aged cohorts in the DCH.
- Determine if weather is a factor that limits growth of the DCH.
- Assess and analyze food habits of the DCH and other Interior herds.
- Monitor movements, dispersal, and mortality in the DCH.
- Recollar adult females to maintain cohorts of collared, known-aged females.

METHODS

The DCH was censused annually in late June from 1992 through 1996. From 1 to 2 weeks before the census, radiocollared caribou were located every few days to determine their distribution and degree of aggregation. Search areas were delineated the day before the census and 4 to 6 aircraft were assigned individual search areas based on our knowledge of caribou distribution. Two to 4 of these aircraft were equipped with radiotracking gear, and the entire range of the herd was flown to ensure that all caribou with active collars were found. Details of individual censuses and maps with locations of all aggregations were published in previous progress reports. All groups > 100 caribou were photographed with either 35-mm cameras, a 9-inch Fairchild T-11, or a Zeiss RMK-A camera. Small groups (< 100) were often counted visually. In some censuses 1 to 2 radiocollared caribou were not found, and their frequencies were given to biologists working in adjacent areas to determine if these individuals had dispersed from the range of the Delta Herd.

Annual natality rates of radiocollared females were estimated by inspecting them repeatedly during the calving period (12-31 May) for the presence of a distended udder, hard antlers, or a calf-at-heel (Bergerud 1964; Adams et al. 1995b; Whitten 1995). From 1992 through 1994 cows were observed 2 to 3 times from fixed-wing aircraft during the calving period. In 1995 and 1996 cows with distended udders or hard antlers were observed daily from a Robinson

(R-22) helicopter or fixed-wing aircraft until the birth of their calf or until their udder regressed, and those without distended udders or hard antlers were observed 3 times during the calving period.

We conducted annual fall composition counts to estimate recruitment of calves to 4 months and to monitor trends in the proportion of bulls in the herd. Counts were done during the last week of September or first week of October during or just before the rut. A day or 2 before the fall counts, all radiocollared caribou were located, and count effort was distributed accordingly. We used the Robinson helicopter and classified caribou as cows, calves, small bulls, medium bulls, or large bulls. Because we collared female calves in fall and could estimate their overwinter mortality, we did not do late winter composition counts from 1992 through 1996.

There was no open season on the DCH from 1992 through 1995. A permit drawing hunt was open in 1996 for bulls and 75 permits were issued. The 22 bulls taken during this hunt were reported with permit hunt report cards. In winter 1993-1994 caribou from the DCH were mixed with Nelchina and Denali caribou near Cantwell, and a few DCH caribou may have been taken during an open hunt for Nelchina caribou. We estimated the number of DCH caribou killed by calculating the number of caribou/radiocollared caribou in each herd and determining the number of radiocollared caribou in the area.

In early April and early October each year from 1992 through 1996 (except for Apr 1994), we immobilized, weighed, measured, and condition-scored 13 to 16 female calves in the DCH. Differences in mean weights between cohorts and seasons were tested with the 2-tailed Student's *t*-test. All calves caught in October were radiocollared with Telonics Model 605 collars (Telonics, Inc., Mesa, Ariz) with a numbered orange vinyl-over-canvas visual collar attached (total weight 2.2 lbs). Additional collars were placed on female calves the following April to bring the size of collared cohorts up to 15, so that 15 collared female 10-month-olds entered the population each year. All calves were immobilized with 1 cc Cap-Chur darts with 3/4" (2 cm) barbed needles filled with 1 mg carfentanil citrate (Wildnil®, Wildlife Pharmaceuticals, Fort Collins, Colo), 66 mg xylazine hydrochloride (Anased®, Lloyd Laboratories, Shenandoah, Ia) except in fall 1996. In early October 1996 weather was unusually cold (about -20°C), and the 1 cc darts were loaded with a solution composed of 39% carfentanil citrate (1.17 mg at 3mg/ml), 31% xylazine hydrochloride (31 mg at 100 mg/ml), and 29% propylene glycol (0.29 ml) to avoid problems with the drug freezing in the darts and needles. This mixture was tested and did not freeze at -15°C. Before October 1994 we used a Palmer Cap-Chur rifle with brown (extra low velocity) charges to propel the darts. However, in April 1994, after 5 caribou calves died (primarily from dart injuries) in a capture operation for Nelchina caribou, we began using a Palmer CO2 pistol with very good results. The CO2 pistol imparted a more consistent, much reduced velocity to the darts. One drawback is the CO2 pistol must be kept warm in temperatures below -10°C or power degrades significantly. In addition, greater vigilance is necessary to ensure safety when using the short-barreled pistol.

In October 1993 we collared 15 male caribou calves with expandable drop-off radiocollars to help determine persistence of the cow/calf bond during winter and distribution of male calves relative to adult females in April. We compared distribution of these caribou and female calves

collared during 1991 to 1996 to the distribution of adult cows during March-April of each year to determine the likelihood of including collared calves in composition counts based on distribution of radiocollared adult females. Collared calves found > 2 miles from a collared cow were considered likely to have been missed during composition counts. We also compared distribution of collared cows and their collared calves from the calf mortality study in October 1995 and March-April 1996.

We had hoped to construct multiple regression models with 9 variables, but missing data compromised utility of this approach. Instead, with regression we constructed a correlation matrix of all variables used, including April (10-month-old) calf weight, previous October (4-month-old) calf weight, wolf numbers, moose numbers, previous winter snow, previous summer temperature, previous summer precipitation, and natality rate of radiocollared females ≥ 2 years. Data used in these regressions are in Appendix A.

We analyzed summer temperature and snowfall from Fairbanks and rainfall for 15 June-15 August from Healy. The sum of mean monthly temperatures (May through Aug), total rainfall (15 Jun-15 Aug), and a snow index (Boertje et al. 1996) were used in regressions as predictors of fall calf:cow ratios and natality rates of collared females.

We continued to collect fecal pellets from caribou in the DCH, Fortymile, Nelchina, Northern Peninsula, and Mulchatna caribou herds. However, pellet analyses take 2 years and when this report was written results were still not available. Results from the early 1990s appear in a progress report (Valkenburg 1994). We did record subjective observations about the relative abundance of lichens on the winter ranges of the Nelchina, DCH, Northern Peninsula, Mulchatna, and Ray Mountains herds.

We tracked collared caribou monthly in the DCH to determine herd distribution, dispersal, and annual mortality rates. To monitor possible dispersal, radio frequencies of missing collars were provided to other biologists working in the ranges of adjacent herds. Dead radiocollared caribou were examined to determine cause and time of death, and determine if there were any obvious predisposing factors.

During 1992-1996 we recollared adult female caribou in October when their collars passed 5 years of use. A small number of these females were not recollared because their collars failed before 5 years.

In April 1992 we began collecting and/or collaring 10 to 15 female caribou calves in the Nelchina Herd to monitor body weight and fatness as the herd approached a relatively high density. We also worked with biologists throughout the state to standardize collaring and data collection in ways that would allow comparison of body weight, condition, and fatness among herds. Calves were collected in the Northern Alaska Peninsula Herd in October 1995 and 1996 and in the Mulchatna and Nushagak herds in April 1995. Results of all collections, data from statewide collaring of female caribou calves, and weights of newborn calves recorded in the Nelchina Herd and other herds are presented.

To evaluate effectiveness of a wolf control program that began in October 1994, we extended work in the DCH to include a calf mortality study. We established a field camp in the Alaska Range and lived there from 12 May to 10 June during 1995 and 1996. During 12-31 May 1995, 45 newborn calves were collared. Collaring methods were similar to those used by other workers in Alaska (Whitten et al. 1992; Adams et al. 1995a,b; Boertje and Gardner 1996). Twenty-five of the calves had collared mothers, and 20 were collared at random. In 1996, 25 calves had collared mothers and 25 were collared at random. Collared calves were monitored daily until 10 June. Thereafter they were monitored weekly through 31 July. During 1 August-30 September collared calves were monitored every 2 weeks and then monthly. Dead calves were picked up the same day they died, except when weather was bad. From 12 May to 10 June there were 2 days in 1995 and 1 day in 1996 when we were not able to monitor collared calves or pick up dead calves due to bad weather.

In addition to other work in the DCH in May 1996, we experimented with a diversionary feeding technique to determine if wolves from the Wells Creek Pack could be kept from hunting on the calving area. Eight wolves were in the pack at the end of the hunting/trapping season in 1996. In early April we radiocollared 1 adult female and 2 subadults and placed a visual (pink flag) collar on 1 female pup (11 months old). On 16 May we caught and collared 1 of the remaining uncollared wolves (a small yearling female) about 1 mile east of the den. On 22 May we caught a large dominant male (apparently the alpha male) and put a GPS collar (Telonics Inc.) on him. The collar was programmed to record a GPS location every half hour for up to 3 weeks, and it was removed from the wolf on 9 June. The GPS collar was then sent to the factory to have the data retrieved. The remaining uncollared wolf in the pack was collared on 1 June with a conventional collar. Beginning 15 May we provided carcasses of bull caribou to the wolves every other day except on 23 May when bad weather prevented access to the calving area. Caribou were either driven to the vicinity of the wolf den with the helicopter and then shot or were shot some distance away and moved to the den. Carcasses were not touched to minimize chances of rejection by the wolves (Magoun 1976). Observers watched the wolf den and carcasses from a vantage point about a half mile from the den from 18 May to 28 May. These observers recorded reactions of wolves to carcasses and also recorded their movements and activity pattern as much as possible, both visually and with telemetry gear.

RESULTS

POPULATION SIZE AND TREND

After rapid decline from 1989 to 1993, the DCH has remained relatively stable (Fig 1). During the census on 22 June 1996, 3819 caribou were counted. However, we added 200 additional caribou to that number because we believed it probable that a group of about 200 bulls that was seen on the Gold King Benches the day before had not been found during the census. The estimate was then rounded up to the nearest 100, making the 1996 postcalving population estimate 4100. The 1996 census may have been an undercount. We anticipate being able to confirm this with the 1997 count.

We constructed a simple, deterministic, spreadsheet population model of the DCH from 1969 to the present (Fig 1). The model was constructed using a starting population of about 5000 in 1969, harvest estimates, and estimates of recruitment and mortality. By manipulating mortality rates of cows and bulls, we were able to make the model approximately track census estimates and fall bull:cow ratios. The DCH is now stable, with relatively low-moderate natural adult mortality and low recruitment. Unless recruitment improves, the population has low potential for harvest.

NATALITY RATE IN THE DCH

In all years, except 1993, natality rates of females older than 3 were relatively high (Table 1). The low natality in 1991 and 1994 was due primarily to nonbreeding in 3-year-olds, but in 1993 most cows of all ages failed to produce calves. Age at puberty in females has varied considerably over time in the DCH. In 1980-1981, 8 of 12 2-year-olds produced calves. During 1982-1985 only 2 of 35 2-year-olds produced calves, and during 1986-1995 none of 56 produced calves. In 1996, 1 of 11 2-year-olds produced a calf. Prior to 1989, 88% of 3-year-olds produced calves (45 of 51). However, from 1989 to 1995 only 42% (20 of 48) of 3-year-olds produced calves. In 1996 all 5 3-year-olds produced calves.

1995 AND 1996 FALL COMPOSITION COUNTS

Recruitment of calves to fall has not changed for 3 years, and bull:cow ratios remain relatively low (Appendix B). Data on bull:cow ratios are variable from year to year, depending on timing of fall counts and behavior of bulls, which is affected by weather and timing of rutting activities. No bulls are collared in the DCH, and distribution of bulls cannot be determined objectively.

WEIGHT AND SIZE OF CALVES

Mean weight of newborn female calves was significantly lower ($P < 0.05$) in the DCH in 1996 than in 1995, although mean weight of newborn male calves was not different ($P > 0.1$) (Table 2). Similarly, mean weight of 4-month-old female calves was lower in 1996 than in either 1995 or 1994 ($P < 0.1$) (Table 3). In addition, the 1991, 1994, and 1995 cohorts of calves lost weight over winter ($P < 0.1$), indicating that feeding conditions and/or forage was limiting on winter range. Mean weight of 10-month-old female calves has been consistently low since 1989 when the population reached its peak of about 10,700 and has not fully recovered.

In 1996 newborn male Nelchina calves were also significantly heavier than females ($P < 0.01$) (Table 6). Newborn Nelchina male calf weights were similar to those in the nearby Delta and Fortymile herds (Table 4, Appendix C). Newborn female calves were similar in weight to calves in the Delta Herd, but significantly lighter than Fortymile calves (Table 4, Appendix C). Newborn female Nelchina calves in 1996 were also significantly lighter than female Mentasta calves sampled in 1993 and 1994, and Denali calves sampled from 1984 to 1987 (Table 4, Appendix C). Weights of 10-month-old female Nelchina calves declined since data collection began in 1991 (Table 5, Appendix D). Weights of 4-month-olds were also low in 1995 and 1996.

Since 1979 we obtained mean weights of 53 cohorts of 4- and 10-month-old caribou calves throughout Alaska (Table 5). Mean calf weight varied from 79 lbs (36 kg) to 145 lbs (66 kg). In general, the heaviest calves have come from low-density herds, and the smallest have come from high density herds, such as the Nelchina, Northern Alaska Peninsula and Western Arctic. Supplemental data from the Nelchina and other selected herds where collection of calves occurred are in Appendix D.

WEATHER

In the range of the DCH, snowfall was very light in fall 1995 and there were only a few inches of snow on the ground until early February. Thereafter snowfall was heavy, and snow depths were near normal by early April. May was cold and snowmelt was delayed somewhat. Leafout was nearly normal in 1996, occurring about 10 May in Fairbanks and about 25 May in willow stands in the northern foothills of the Alaska Range.

Summer temperatures continued to be relatively high during 1993 to 1995, rainfall continued to be relatively low, and snow depth was variable (Table 7). Data from 4 snow markers in the range of the DCH are accumulating and will allow comparisons with Fairbanks data in the future. Weather data were analyzed in relation to the decline of the DCH and published in the *Journal of Wildlife Management* (Boertje et al. 1996). A graduate student project to investigate the influence of weather and insect abundance on caribou behavior was completed in 1996 (Morschel 1996).

MORTALITY OF FEMALE RADIOCOLLARED CARIBOU OLDER THAN 4 MONTHS

Mortality rates of radiocollared female DCH caribou continued to be relatively high throughout the early 1990s, compared with rates observed in the early 1980s (Table 8). Mortality of radiocollared females aged 4 to 16 months was 44% (29 of 66 died) since collaring of 4-month-old calves began in 1991. Mortality of adult females (yearlings and older) was 14% (48 of 346 died, excluding those taken by legal hunting) from 1988 to 1996. From 1982 to 1987, 9% of collared females died (18 of 205 died, excluding those taken by legal hunting). Data on mortality is biased by age structure of collared females. In the early years of the study most females were young. However, deaths of young females also seemed to increase in later years.

Predation by wolves was the most significant known cause of death of radiocollared DCH females in all age groups (Table 8). Cause of death was not determined in 33 of 66 cases where collared females, yearlings and older, died. In 7 of these cases "unknown predator" was listed as the cause of death, and these were killed by grizzly bears or wolves, the only predators that are known to consistently kill adult caribou. In most cases where cause of death was listed as "unknown," deaths occurred in summer when evidence disappeared rapidly, and most were probably killed by wolves or grizzly bears. In the 33 cases where cause of death was known, wolves were responsible for 23 deaths. Predation on adults by grizzly bears is undoubtedly underestimated. In the DCH and other Interior caribou herds, documented deaths from causes other than predation by bears and wolves are uncommon (Table 8). However, during the winter of 1992-1993, when the DCH was widely dispersed in forested winter ranges and snowshoe hares were declining, lynx killed significant numbers of caribou calves

(Table 8). Poaching was responsible for 3 of 33 (9%) deaths of radiocollared females (yearlings and older) where cause of death was known. However, this figure probably overestimates poaching because few, if any, females that died of unknown causes were likely to have been poached. There are few people living within the range of the DCH and opportunities for poaching are limited.

REGRESSION MODELS

Of the 9 variables used in regression models for the DCH data set, only wolf numbers, April calf weight, winter snow, and previous summer precipitation were significantly related to fall calf:cow ratio (Fig 2, Appendix E). Natality rate of radiocollared females ≥ 3 years was not significantly correlated with any of the other 8 variables.

EFFECTS OF WOLF CONTROL ON THE DCH

The caribou decline stopped when wolf control was implemented, but we could not determine if these 2 events were related. Decline in the Denali Herd also stopped and wolf control was not conducted there. The program was suspended in early December 1994 before wolves could be reduced to the goal of 75 wolves remaining in Unit 20A prior to caribou calving. Although the caribou decline stopped, primarily from increased calf survival to fall and reduced adult mortality, fall calf:cow ratios did not increase to expected levels based on experience during the control program conducted from 1975 to 1982. In addition, the adjacent Denali and Macomb herds have similar fall calf:cow ratios, and wolves were not reduced by control in these areas.

CALF MORTALITY STUDIES

Wolves and grizzly bears were the most important predators of collared caribou calves from birth to 4 months of age (Table 9). Wolves killed more radiocollared calves than grizzly bears in 1995, but they killed fewer than bears in 1996 probably because of the diversionary feeding experiment. Golden eagles (*Aquila chrysaetos*) were also important predators, and, like grizzlies, they primarily killed calves less than 3 weeks old. However, 1 collared calf was killed by a golden eagle on 21 July 1995. Of 33 collared calves killed by grizzlies and golden eagles in 1995 and 1996, only 2 were killed by eagles and 4 killed by grizzlies after 10 June. In contrast, of 22 calves killed by wolves in both years, 8 were killed after 10 June. Due to small sample sizes, not one of the differences was significant ($P > 0.1$).

Patterns and timing of calf mortality seemed to differ in the DCH between years, but sample sizes were too small to provide conclusive results (Table 10). Although calving peaked (50% of calves born) about 17-18 May in both years, more radiocollared calves were killed early in the calving period in 1996 than in 1995. In addition, more collared calves died in August and September in 1996 than in 1995, and despite the apparent success of diversionary feeding in 1996, overall calf mortality was similar in both years. The significantly lower weight of newborn female calves in 1996 may have increased their vulnerability to predation, especially by bear and eagle. Four calves died from unknown causes in 1996. In 3 or 4 cases, only the blood-stained collar was found, characteristic of bear predation than either wolf or eagle predation.

DIVERSIONARY FEEDING

Effects of Diversionary Feeding on Numbers of Calves Killed by Wolves on the Wells Creek Calving Area.

Diversionary feeding may have been successful in reducing the number of caribou calves killed by wolves, but sample sizes of collared calves were too small to be conclusive and there was doubt about the cause of death of several calves in both years. During the 1995 calving season, wolves killed 5 collared caribou calves on the Wells Creek calving area. In addition, 3 calves that seemed to have been killed by eagles may actually have been killed by wolves and scavenged by eagles because wolves were known to have been in the vicinity near the time of death of the calves. In 1996, 3 calves were killed by wolves and not one was thought to have been killed by wolves and scavenged by eagles but several other calves died of unknown causes.

Effects of Diversionary Feeding on Pack Hunting Behavior

Diversionary feeding in 1996 kept wolves at the den site, and they probably spent less time hunting away from the den than in 1995 when they were not fed.

In 1995, 2 wolves from the Wells Creek Pack were collared, and many of the 11 members of this pack regularly hunted on the calving area which was about 4 miles from their den site. In 1996 there were 8 wolves in the Wells Creek Pack, and they occupied the same den as in 1995. The 10 caribou and 2 moose carcasses that were placed near the den successfully kept most pack members in the vicinity of the den from 18 May to 9 June when caribou left the area. One collared wolf was seldom with the pack and was usually alone in an area about 20 miles southeast of the den, well away from the Wells Creek calving area. The other 7 members of the pack were already centering their activities around the den when intensive tracking began on 12 May. Three collared caribou calves were killed by wolves on the Wells Creek calving area in 1996. One was killed on 17 May, 1 on 25 May, and 1 on 27 May. Although the first caribou was shot near the den on 15 May, the wolves did not find it for over 3 days. They probably continued to hunt on the calving area and did not become accustomed to feeding on carcasses near the den until the night of 17 May after the second carcass was placed nearer the den in a more open area. Carcasses were delivered to or shot within a mile of the den on 19 and 21 May, but weather was bad on 23 May and no carcass was delivered. Some of the wolves were already hunting away from the den on 24 May when the wolves were next located. A cow moose was shot about a mile from the den on 24 May, but the wolves did not discover the carcass until 28 May. On 28 May we realized the moose carcass was too far away from the den for the wolves to find easily, so we placed a bull caribou carcass near the den in the same area as carcasses 2 through 4. Some of the collared wolves were located on the calving area near nursery bands of caribou during 24-27 May, and 2 collared caribou calves were killed (1 on the night of 24-25 May and 1 on the night of 26-27 May). No other collared calves were killed by the Wells Creek wolves, and they did not visit the calving area again until after the caribou left the area about 9 June.

GPS Collar

A GPS collar was placed on the pack's alpha male on 22 May and initialized at 0915 h. The 600 mg dose of Telazol® kept the wolf immobilized for about 5 hours, and the wolf did not seem to fully recover until sometime on 24 May when it was seen at the mostly eaten carcass of the first moose about ¼ mile from the den. The male remained near the den on 25 May and did not find the carcass of the second moose that was shot about a mile east of the den. On 26 May the male moved to the calving area and was located there on 27 May when 1 of the collared calves was killed. From 28 May until 9 June, the GPS male (and other collared wolves) remained within 1 to 2 miles of the den, except for 1 foray that took the wolves about 7 miles away from the den in the opposite direction from the calving area in early June.

DISTRIBUTION OF MALE AND FEMALE CALVES IN LATE WINTER

From 1992 to 1996, approximately one-fifth of collared male calves and two-fifths of collared female calves were found > 2 miles from a collared female in late winter, although all calves wintered in roughly the same area as adults in the DCH (Table 11). Of 9 collared cow/calf pairs, 7 were still together in early October. In early March, 4 of 6 pairs were still together, but in early April only 2 of 6 were together.

MOVEMENTS, DISTRIBUTION, AND HARVEST

During 1992-1996 most radiocollared DCH caribou remained in Unit 20A. However, there was an unusual movement of caribou out of the area in September 1992 following an unusually severe snowstorm from 11 to 23 September (Valkenburg 1993:7; Valkenburg et al. 1996a). In addition, in May 1996 some collared DCH females crossed the Nenana River and Denali Highway and calved a few miles south of the highway in Unit 13. All collared caribou, except for 1 2-year-old female, returned to Unit 20A by mid June. In October 1994, 2 collared caribou cows crossed the Delta River and wintered east of the Richardson Highway southeast of Donnelly Dome and in the Granite Mountains. This movement also occurred in October 1996 when 8 collared cows wintered in the same area. The main calving area has been in the Wells Creek Drainage of Unit 13 since 1987, but varying numbers of cows have calved in the upper Wood River, Dick Creek and the upper Yanert drainages.

Since radiocollaring began in the DCH in 1979, no collared caribou have permanently dispersed from the DCH's range in Unit 20A, although the Delta and Yanert herds merged during the late 1980s. After the mixing of Delta and Denali caribou in 1992-1993, a 10-month-old female that was thought to be Denali caribou (based on collar distribution) was collared near Rex Dome in April 1993. It remained in the range of the DCH in fall 1993 and was recollared with a DCH collar frequency. This caribou spent at least the early part of the winter in the 100-Mile Creek drainage in eastern Unit 20A before its signal was lost. The following winter, it was found dead in the Toklat drainage in Denali Park.

Until 1987 most DCH cows used upper 100-Mile Creek, upper Delta Creek, and upper Buchanan Creek drainages during calving. Shortly after calving, most caribou traveled up the West Fork Little Delta into the Wood River and Dick Creek, and spent early June in this area before going back up the Wood River to its head and then into the West Fork Little Delta in

mid to late June. In July most caribou used the upper Gold King Benches, upper Moose Creek (Tatlanika drainage), upper Totatlanika, and upper Healy Creek areas. Alternatively, Iowa Ridge, upper Buchanan Creek, East Fork Little Delta, and Delta Creek were used. After 1987, calving and early summer movements changed. Most cows still used the 100-Mile/upper Delta Creek area in early May but moved up the West Fork into the Wood River, Dick Creek and Wells Creek as calving was beginning. From 1988 to the early 1990s, the upper Wood River was an important calving area, but since then, most cows have used upper Wells Creek. From 1992 to the present, movement into Wells Creek began about 5-10 May each year and continued until the end of May. Return movements began in early June, and by 15 June almost all cows had returned to Unit 20A. Late summer movements have not changed. During 10-15 June most cows and their new calves cross the divide from the head of the Wood River into the West Fork, and then turn west into the head of Dry Creek en route to Mystic and Moose creeks and the Gold King Benches. An alternate route that has been used each year for at least 2 decades is for caribou to head east from the West Fork into upper Buchanan and the upper East Fork, and sometimes as far east as upper Delta Creek. Iowa Ridge can also be used by aggregations in July, and caribou get there by either of the above postcalving movements, sometimes from the Gold King benches and Buchanan Creek. During the last few days of July and the first week of August, aggregations disperse and caribou spread throughout alpine areas north of the Yanert River, east to the Delta River and west to the Nenana River. They also have ventured north onto the southern edge of the Tanana Flats from 7-Mile Lake east to Delta Creek during August, where they can occasionally be seen feeding on vegetation around lake margins.

Since the mid-1970s, when detailed observations of DCH movements began, winter range use has changed considerably. During the late 1970s and early 1980s, most caribou used the Gold King Benches as primary winter range. As the herd increased in size, caribou extended their winter range to the west into the Tatlanika and Totatlanika drainages and also used the Tanana Flats north of Iowa Ridge. During the late 1980s as the population peaked, caribou used the western Tanana Flats and upper Totatlanika extensively, and wintering caribou were seen north almost to the Tanana River and east to the Wood River Buttes. The Tanana Flats north and east of Wood River Buttes was rarely used by wandering small groups of caribou and was never an important range even during the population peak. After the population decline in 1990-1993, caribou again used mountain and foothill winter ranges, including previously used areas like the Gold King Benches, Tatlanika, Totatlanika, and flats north of Iowa and Dinosaur ridges. However, they also moved into new winter ranges in the lower Yanert drainage, Wood River between Cody Creek and Snow Mountain Gulch, and 100-Mile Creek. In 1996-1997, 8 collared caribou even crossed the Delta River and used winter range in the Jarvis Creek drainage previously used by the Macomb Herd.

Hunting for DCH caribou was closed after fall 1991. A few DCH caribou (probably < 15) were taken in hunts for Nelchina caribou in 1992-1993 and 1994-1995. A limited drawing hunt (75 permits) for DCH caribou was reopened in fall 1996. The season was 10 August-20 September; 22 bull caribou were taken, 22 permittees were unsuccessful, and the remainder did not hunt.

DISCUSSION

POPULATION SIZE AND TREND AND POPULATION MODELING

The DCH has been relatively stable at about 4000 since 1993. It is unlikely to increase in the near future and has only a limited potential for providing a harvest due to continued low recruitment.

To track census data, given the starting population and observed recruitment (i.e., fall calf:cow ratio), a simple spreadsheet model required reasonable estimates for adult female mortality rates (Fig 1). Although we could have started the spreadsheet model with the 1964 population estimate of 6250, there were no consistent estimates of fall bull:cow and calf:cow ratios prior to 1969 and no harvest estimates before 1968 (Fig 1). In recent years, adult female natural mortality rates required by the model were similar to those observed in radiocollared cows. In 1985, however, over 20% of radiocollared cows died, but the model generated mortality rates of 5% to 10%. In addition, from 1979 through the early 1980s, the model required higher mortality rates than those observed in collared cows, probably because the observed rates were biased low by the age structure of collared cows. Discrepancies can be expected because of the small number of radiocollared caribou that die annually. The total population of collared cows in the DCH has generally been in the range of 50 to 75. It is probably unrealistic to expect much refinement in mortality estimates because agencies cannot afford to maintain age-justified samples of several hundred collared females which would be necessary to accurately estimate mortality. An alternative is to continue to obtain refined estimates of population size and recruitment from which adult mortality can be estimated by modeling.

In recent years (at least since 1991), calves could not be considered recruited into the adult population in fall because of their much higher mortality rate than adult females until they reached 16 months (Table 8). To refine recruitment estimates we need overwinter estimates of mortality of calves.

It was apparent from the model that observed fall bull:cow ratios are subject to considerable sampling error; observed year-to-year changes in the bull:cow ratio could not be simulated without unbelievably large adjustments in mortality of bulls. Survey data are often biased due to clumped distributions of bulls and inadequate knowledge of distribution of bulls prior to surveys. In addition, caribou movements, timing of surveys in relation to the rut, and weather all affect survey results.

The population model elucidated the relative importance of various factors involved in the population declines during the early 1970s and early 1990s. The population decline of the DCH from 1970 to 1974 was due primarily to high harvests in 1971 and 1972 and low recruitment during 1971-1974. Harvest was reduced in 1973 and eliminated in 1974, preventing further decline. The magnitude of the declines in the early 1970s and early 1990s was similar, but in the early 1990s harvest was lower and adult natural mortality (primarily from wolf predation) was probably higher. After the decline in the early 1970s ended, population recovery was rapid. Since the 1990s decline, the population has been stable.

Interestingly, the model required very low estimates of natural mortality for bulls, especially when harvest of bulls was high. This implies a high degree of compensatory mortality and indicates that when bull:cow ratios are kept relatively low by hunting, with a young age structure in bulls, natural mortality of bulls will also be low. In the DCH, access is good, and hunters have always been relatively selective in taking the largest bulls available. The large bulls that are selected by hunters in August and September are also the ones most likely to die after the stresses of rut and early winter. Within a few years after the hunting season closed in 1991, biologists began observing carcasses of large bulls killed by wolves during October and November. Although these observations were not quantified, it was previously uncommon to find large bulls killed in early winter in the DCH during the hunting season. Observations of large bulls killed by wolves are common in herds where bull:cow ratios are high (e.g., Ray Mountains, White Mountains, Denali, Mulchatna, and Fortymile herds). Large, decrepit bulls may be an important food source for wolves in fall.

NATALITY RATE

During the 1970s and 1980s many biologists working with caribou concluded that natality rates and age at puberty in females were relatively fixed (Bergerud 1980:557). Recent data from the DCH and other Interior herds indicate more variability than previously thought. However, in contrast to Reimers' (1983a) opinion that body weight was the only significant determinant of the age at first reproduction in caribou, the DCH data (and Reimers' own data reviewed by Davis et al. 1991) indicate that other variables such as age and perhaps population size/density are also important (Davis et al. 1991). Work with roe deer (Gaillard et al. 1993) also indicates that age is an important factor in determining puberty.

There is no doubt that body condition and fat reserves are important determinants of natality rate in caribou (Reimers 1983a; Skogland 1985; Allyn-Chan 1991; Cameron et al. 1993; Cameron 1994; Cameron and Ver Hoef 1994; Gerhardt et al. 1996). In the DCH there is evidence that weather (presumably as it affects body weight and condition) was important during 1990-1996 in determining natality rate and probably age at puberty. In the DCH in May 1993, following the severe September snow and a short growing season, natality was low in all Interior herds studied (except White Mountains) and ranged from 30% to 75% with the DCH being lowest (Valkenburg 1994; Boertje et al. 1996; Valkenburg et al. 1996a). In the DCH in 1992, fall body weight of female calves was the lowest ever recorded, and no collared females produced their first calves at 3 years of age in May 1993 (presumably puberty was delayed).

The combination of periodically lower natality (presumably from suboptimal nutrition prior to the rut) and high calf mortality of low birthweight calves can be major factors influencing the population dynamics of caribou herds. Effects of suboptimal nutrition on natality rate will be more pronounced in herds where predation on neonates is low, because more cows are subject to the additional demands of lactation during the summer in these herds (Cameron 1994). In most Interior Alaskan herds where predation on neonates is very high, cows have all summer to regain condition without the demands of lactation, and predation is a far more important factor in caribou dynamics than natality.

WEIGHT AND SIZE OF CALVES

Although genetics may account for some of the weight differences of cohorts of calves between herds, the primary source of variation is nutritional. Some of the lightest calves have come from the Nelchina Herd, but the heaviest have come from the Killey River Herd on the Kenai Peninsula. The Killey River caribou were transplanted from the Nelchina Herd in 1985 and 1986 (Spraker 1995) (Table 5). In addition, caribou transplanted from the high-density Northern Peninsula Herd increased in size on new range on the Nushagak Peninsula.

Low fall calf weights in the Nelchina Herd are indicative of poor summer foraging conditions. In 1996 newborn female calf weights in the Delta and Nelchina herds were similar ($P > 0.1$) (Table 4). By the end of September, however, Nelchina calves averaged almost 20 lbs (9 kg) lighter than Delta calves ($P < 0.05$) (Table 5). Repeated sampling in both herds will help determine if decreased weight gain in Nelchina calves is a response to high summer density in the Nelchina Herd or a short-term response to adverse weather.

In the DCH female calves have a tendency to lose weight in winter (Table 3). We suspect this tendency has become stronger over time and is related to a decline in quality of winter range and weather. Data on weight loss in calves over winter is scant, but on Coats Island in the Canadian arctic weight loss of calves over winter was not significant despite starvation conditions (Adamczewski et al. 1987). Huot (1989) also found that mean body weight of calves did not decline significantly over winter. However, in the Coats Island study, sample sizes were too small to be conclusive (< 10), and in the George River Herd, winter range was considered to be adequate. In the Western Arctic Herd, where winter range was considered good, calves did not lose weight over winter and body growth continued (Valkenburg et al. 1996b). In the Nelchina Herd calves did not lose weight over winter 1995-1996, the only year for which data is available.

REGRESSION MODELS

The DCH data set supports the hypothesis that fluctuations in caribou numbers in the DCH are caused largely by interactions of weather and wolf predation. Deep snow in winter *and* low precipitation in summer probably reduced weight and condition of caribou and made them more vulnerable to wolf predation. Numerical and functional responses in wolves result in increased winter and summer predation on calves and adults (Dale et al. 1994; Adams et al. 1995a,b; Mech et al. 1996). High moose numbers could also serve to support higher wolf numbers and thus increase predation by wolves on caribou calves. High caribou density during the late 1980s may have also played a role in reducing condition of caribou by reducing food supply, especially in winter. A longer data set, over a wider range of values will be needed to determine the relative importance of October calf weight versus winter snow in determining April calf weight.

EFFECTS OF WOLF CONTROL ON THE DCH

Despite significantly reduced wolf numbers due to control, the 1993-1994 program was not as successful as the 1970s program in reducing wolf numbers or improving survival of caribou in the DCH, and wolves remained the most significant predator of calves and adults (Boertje et

al. 1996). There were approximately 267 wolves in the precontrol fall population in 1993 and about 180 in fall 1994. After winter 1993-1994 there were about 100 wolves remaining, and after control ended in winter 1994-1995, there were about 114 wolves remaining (Boertje et al. 1996). Adult wolves were generally the last to be removed during the trapping program and few, if any, packs were completely removed. In the adjacent Denali Herd, where wolves were not controlled, fall calf:cow ratios continued to be similar to those in the DCH (20:100 vs 23:100). However, wolves also declined naturally in the Denali Herd's range, probably due to lack of food (Adams, pers commun). It is unlikely that wolves in the DCH range would have declined naturally to similar densities because of the large number of moose in the range of the DCH compared with few moose within the range of the Denali Herd (Mech et al. 1996; Stahlnecker 1997). In fall 1996 there were about 220 wolves in Unit 20A.

During the previous wolf control program (Boertje et al. 1996) weights of 10-month-old caribou calves were at all time high levels, and there was no indication of nutritional limitation in the DCH (Davis et al. 1991). In contrast, calf weights were relatively low in the DCH during the early 1990s, and newborn calves could have been more vulnerable to predation during summer than they were in the 1970s. In the Nelchina Herd, where summer wolf:caribou ratios are low (about 1:300; Tobey 1994), caribou have declined greatly in condition but calf survival to fall was high enough to allow for herd growth and a substantial harvest, except in 1993, when there were only 24 calves:100 cows. In the George River Herd, calf numbers in fall have also remained relatively high in most years despite reduced summer nutrition (Crete et al. 1996). This reinforces the argument that calf survival in the DCH would have been higher if wolves had been effectively removed.

CALF MORTALITY STUDIES

Wolves remained one of the most important predators of caribou calves in the DCH in 1995 after they had been reduced from 267 in fall 1993 to 114 in spring 1995. Sample sizes were too small to determine if wolves or bears were the most important predator of calves, or to determine if diversionary feeding reduced wolf predation on calves in 1996. In the adjacent Denali Herd, wolf predation was the single greatest cause of death of radiocollared newborn calves in 1996 and wolf predation was higher in 1996 than in 1995 (Adams, pers commun).

In the DCH the calf mortality study was initiated in 1995 to determine if wolves remained a significant cause of mortality after the wolf control program. With that question answered, there is no compelling reason to continue this work after the third year in 1997. Information on the relative vulnerability of cohorts of calves to mortality can still be obtained by randomly weighing a larger sample of calves during the calving period.

DIVERSIONARY FEEDING

In 1996 there were about as many calves available to wolves in the Wells Creek calving area as in 1995, and the number of cows was similar in both years. Although natality may have been slightly higher in 1996 than in 1995, neonatal mortality may also have been slightly higher (Tables 1 and 9). Distribution of parturient cows was also similar in both years. Although fewer cows were in the Yanert and upper Wood River in 1996 than in 1995 (out of the pack's range), more were south and east of the Wells Creek area. Assuming there were

about 2250 calves available on the calving area in both years, there were about 50 calves/radiocollared calf in 1995 and about 45 calves/radiocollared calf in 1996. Therefore, we estimated that Wells Creek wolves killed about 135 calves in 1996 versus 250-400 in 1995. If the 115 calves that were "saved" had all survived to fall, the fall calf:cow ratio should have increased by about 4 calves:100 cows. However, unlike 1995 when calf mortality ceased after early August, calves continued to die in August and September 1996. By the end of September, total mortality of calves was similar in both years, 67% in 1995 versus 64% in 1996.

The diversionary feeding experiment demonstrated that hunting behavior of wolves can be modified. All but 1 wolf remained near the den when carcasses were available, except for 1 foray, when most of the pack traveled at least 5 miles from the den in the opposite direction of the calving area. Many years of experiments will be needed to determine if survival of calves to fall can be measurably improved using this technique. It is difficult to find suitable comparisons for use in controlled experiments, and between-year comparisons may be invalid because of differing weather conditions, pack sizes, vulnerability of caribou calves, and caribou and wolf distribution. Effects of diversionary feeding may be subtle but significant over several years, although they may not be measurable within statistical bounds in any single year.

DISTRIBUTION OF MALE AND FEMALE CALVES IN LATE WINTER

To obtain estimates of recruitment in caribou herds, many biologists have advocated composition counts in late winter, after mortality rates of calves begin to approach that of adult females (Bergerud 1980). There is little information on distribution of calves in relation to cows in late winter. However, calves and cows separate during September to May, and in the larger migratory herds, it is not uncommon to see large numbers of short yearlings mixed with bulls on late winter ranges after most females have departed for calving areas. In some herds, calf:cow ratios in late winter surveys are sometimes higher than during fall. Consequently, some biologists have lost faith in late winter counts (Adams, pers commun). In addition, in years of herd growth and low mortality in general, mortality rates of calves > 4 months can be quite low and fall counts provide good estimates of recruitment (Davis and Valkenburg 1985; Adams et al. 1995b). However, with unfavorable winter weather or low body condition of calves in fall, September-October calf:cow ratios can grossly overestimate recruitment because of high overwinter mortality in calves (Doerr 1980; Valkenburg et al. 1996a). In the nonmigratory DCH, late winter counts may have provided reasonably accurate calf:cow ratios in most years when counts were done during 1983-1991 (Table 12). During 1991-1996 collared calves were generally within the distributions of collared cows, but some calves left their mothers in March and April.

During the decline of the DCH, female caribou continued to have high mortality rates through their second summer of life. Collaring calves in fall could help managers objectively determine distribution of calves in relation to cows, improve accuracy of late winter counts, and provide estimates of calf mortality to 16 months of age when mortality rates are equal to or lower than those of older cows even under the worst conditions.

MOVEMENTS AND DISTRIBUTION

After the DCH declined in the early 1990s, range size of the herd also declined slightly. The main area not used by the DCH after the herd declined was the Tanana Flats west of the Wood River. However, continued southward expansion of the calving area near the Denali Highway occurred in 1996. In addition, some caribou crossed the Delta River and are using winter range previously used by the Macomb Herd.

Since biologists began radiocollaring caribou in the mid 1970s there have been few documented cases of dispersal, and none from the Delta Herd. Dispersal means cases where a cow calved at least once with 1 herd and subsequently with a different herd. The DCH increased to the relatively high density of about 0.9/km² in 1989 and declined primarily from high natural mortality (Valkenburg et al. 1996a) and not from dispersal. In view of their migratory nature, extensive movements, and developed sense of direction, the very low level of dispersal documented in caribou so far is surprising. As a rule female caribou, especially pregnant females, seem to be faithful to their calving areas, although some shifting does occur (Valkenburg and Davis 1986).

WEATHER

Over the last 5 to 7 years, it has become clear that weather plays a major role in population dynamics and movements of caribou herds in Alaska (Valkenburg et al. 1996a,b; Whitten 1996). Natality rates have been shown to vary with condition of cows in fall (see Weight and Size of Calves above), and underweight calves have poorer survival rates than heavy calves (Skogland 1985; Adams et al. 1995a,b). Precisely how weather influences body condition is unclear, although snow depth, timing of snowmelt, summer temperature, and summer rainfall have all been found to correlate with survival of calves to fall, natality rates, or weight of newborn calves (Valkenburg et al. 1994, 1996a; Adams et al. 1995a,b; Boertje et al. 1996). In the present study, winter snow and summer rainfall were next in importance to wolf numbers in predicting fall calf:cow ratios (Appendix E). In Alaska shading in summer increases nitrogen levels in *Salix pulchra*, tundra forbs, and graminoids (Klein and Valkenburg 1995; Lenart, in press), and cloudy summers are thought to increase the quality of moose ranges in Norway (Bo and Hjeljord 1991). Data are lacking despite much speculation about the influence of weather on insect abundance and effects of insect abundance on body condition in caribou. One problem is that warble and bot flies may be more important than mosquitoes, but abundance of these insects has seldom been measured and related to body condition (for review, see Morschel 1996).

CONDITION OF CARIBOU RANGES

Judging from the relatively low proportion of preferred lichens in the diet, frequent loss of body weight of female calves over winter, and frequent shifts in winter range, we conclude that DCH caribou have suboptimal winter range within Unit 20A (Valkenburg 1994). DCH caribou were at high densities for many years, and there are indications that range condition and body condition of caribou have been affected. Despite similar weather and adjacent ranges, Denali caribou seem to be in generally better condition than DCH caribou, and 2-year-old females produce calves more frequently than those in the DCH. There is

undoubtedly an interaction between weather and caribou range that influences condition of caribou. During the 1989-1994 period, weather conditions were poor over a wide area.

Condition of the Nelchina Herd's traditional winter range also seems poor. Lichens have been severely depleted since 1983 when range stations were rated 1/3 good, 1/3 fair, and 1/3 poor (Lieb 1994). In 1989, based on percent cover of lichens at the same 39 range stations, the range was rated 21% good, 2% fair, and 77% poor (Lieb 1994). The good range was in the northwest, northeast, and southwest parts of Unit 13. Our incidental observations during a radiotracking flight in mid August 1996 led us to conclude that lichen cover is very poor in the Lake Louise Flats and adjacent areas and in the Talkeetna Mountains. During the early 1990s several thousand caribou wintered in the vicinity of the Tangle Lakes where lichen cover seemed fair. However, caribou calves collected from this area in April 1992 averaged 18 lbs lighter than those collected in the Unit 12 winter range, and their marrow fat levels were also significantly lower ($P < 0.05$) (Appendix D). Several thousand caribou have consistently wintered in the northwest corner (Cantwell area) of Unit 13 since before 1990, and in some years 1 or 2 collared Nelchina caribou were present in the area. Most of the caribou wintering here were from the small Upper Susitna "subherd" that numbered about 2000 in summer 1995. Some of these caribou have also wintered in the southern Yanert drainage of Unit 20A. Some lichen ranges in this area still seem to be fair, but how long the area can continue to support the several thousand caribou that winter there is unknown. Poor condition of lichen ranges in Unit 13 makes it unlikely that very many Nelchina caribou will winter there in the near future. Winter range is probably not limiting herd size, however, because caribou have the option of using alternate ranges in northern Unit 11, northern Unit 12, and the traditional winter range of the Fortymile Herd in southern Unit 20E and the Yukon. For several years in the early 1990s, the Nelchina Herd wintered in the Yukon as far northeast as Wellesley Lake. However, condition of lichen ranges in western Yukon is unknown, and more recently (winter 1996-1997) most Nelchina caribou have chosen to winter in the Ladue and upper Dennison drainages of Unit 20E, where they mixed with Mentasta and Fortymile caribou. Over the next few years, we hope to assess relative condition of caribou winter range in western Yukon, Unit 12, and Unit 20E through continued fall and spring collection of calves, fecal pellet analysis, and observations of lichen abundance.

The summer range of the Nelchina Herd may also be in relatively poor condition, based on size of caribou calves in fall (Table 5; Appendix B), and incidental observations of range condition. However, annual weather patterns also influence caribou summer nutrition, and it is difficult to separate effects of weather from those of population density and range depletion. Presumably, summer range can recover more quickly than winter range once herd size is reduced. The apparent condition of summer range and the small size of caribou calves are the primary reasons for recommending reduction in size of the Nelchina Herd from 50,000 to 35,000-40,000.

Condition of winter range of the Northern Peninsula Herd also seems to be poor (low lichen biomass) after many years of relatively high caribou numbers. Lichen cover and biomass remain high near King Salmon, where human disturbance provides a de facto enclosure. As in the Nelchina Herd, mean weight of female calves in the Northern Peninsula Herd is relatively low (Appendix B).

EVIDENCE FOR DENSITY-DEPENDENT LIMITATION IN ALASKAN CARIBOU

Evidence for density-dependent responses in body size of Alaskan caribou has been available for several years (Valkenburg et al. 1991; Eberhardt and Pitcher 1992), and responses in body size and population performance in wild Norwegian reindeer are well documented (Reimers 1983a,b; Skogland 1985). More recently, there is mounting evidence that density-dependent limitation to population growth occurs in Alaskan caribou herds. For many years in the 1970s and 1980s while herds were generally low, little evidence of density-dependent population limitation existed for mainland caribou. However, after the nutrition-related decline of the Southern Peninsula Herd and sustained high densities in the Northern Peninsula, Nelchina, Central Arctic, and Delta herds, more evidence accrued. So far, the effects of density on population dynamics have been minor relative to predation in Interior Alaskan herds. For example, in the Nelchina Herd, where predation is low and caribou have declined sharply in body size, the herd continues to be productive and provides a high harvest. Whereas in the Delta Herd, where predation is high and caribou have also declined in condition, the herd has declined and harvest has been curtailed. Even in herds where body condition remained good during the early 1990s (e.g., White Mountains Herd), herd size was stable and harvest was restricted to bulls. There is undoubtedly a significant interaction between available food reserves (which are partially determined by caribou numbers) and weather. Herds with large food reserves (e.g., Denali, White Mountains and Ray Mountains) are probably more resilient during and after periods of severe weather and may not be as easily reduced by predation because body condition can remain higher even during times of relative food scarcity. Where predator-prey ratios are high, declines in body condition are probably much more serious from a management perspective because population declines will be more likely to occur and harvest levels will be reduced. Whether predictable density-dependent regulation occurs in Alaskan caribou is still an open question. Weather and other unpredictable phenomena may effectively mask density-dependent responses, and it could be difficult to conclusively document these population responses. If predator management is not an option, it may be possible to provide higher harvests of larger-bodied caribou by reducing herd size where nutrition is affecting body size and condition. However, there is a risk that predation may periodically have a great effect on a smaller caribou herd when weather is unfavorable, and without predator control herd recovery could be prolonged.

CONCLUSIONS

- 1 Natality in caribou is not as stable as previously thought, although most females 3 years old and older can be expected to be pregnant every year in Interior herds where most cows do not lactate because of high neonatal predation. In the larger herds or herds where predation is low, natality will be more variable and could contribute significantly to population stabilization or decline.
- 2 Mean calf weight can be an objective predictor of population performance in herds where predation is high, presumably because light calves are more vulnerable to predation. In herds where summer predation of calves is low, 4- and 10-month-old caribou calves can decline markedly in weight and condition before natality and

mortality rates in adult females change sufficiently to stabilize the population or cause it to decline.

- 3 Severe weather can cause declines in nutritional condition of caribou and make them more vulnerable to predation, resulting in steep declines in small, Interior caribou herds even where range conditions are relatively good, and herds are not at high densities.
- 4 Fall calf:cow ratios can overestimate recruitment. Mortality rate of calves older than 4 months is variable depending on weather, fall body condition, food availability, and predation, and these fall calves cannot be considered as recruited into the adult population in some years. In intensively managed herds, radiocollars should be placed on female calves in fall to help estimate calf mortality to 16 months. April composition counts have been used to gain more realistic estimates of recruitment than fall surveys, but these counts are subject to considerable sampling error because of clumped distributions of adults and calves and because many male and female calves separate from their mothers beginning in September. Having a random sample of collared calves on the air in April (i.e., those collared the previous October) could help improve accuracy of late winter counts.
- 5 Wolf control in 1993-1994 was terminated before desired numbers of adult wolves were eliminated, and most packs remained intact because of the relative inefficiency of the ground-based wolf control program. The DCH stopped declining but summer and winter predation on calves remained high enough to prevent herd growth and preclude significant harvest.
- 6 Diversionary feeding was successful in modifying the hunting behavior of wolves. Possible confounding effects of weather, vulnerability of calves to predation, and small sample sizes made quantitative evaluation of increased calf survival tenuous. However, the technique may have the potential to increase allowable harvest of caribou; it is inexpensive and is likely to be less controversial than wolf control. Continued experimentation could also make it more effective.
- 7 Dispersal rates in Interior caribou herds are extremely low. Since radiocollaring began in the DCH in 1979, no radiocollared DCH caribou have been found to emigrate to other adjacent herds, and no other caribou were known to immigrate into the DCH. Except in winter 1992-1993 and during calving in late May and early June, DCH caribou have largely remained in Unit 20A.
- 8 Judging from body size and condition of caribou calves, age at first reproduction in the DCH compared with the Denali Herd, caribou movements, and relative abundance of preferred lichens in the winter diet, we conclude that winter range quality for caribou in Unit 20A is relatively poor and was affected in the late 1980s by the high density of caribou. However, the DCH remains relatively productive and could probably support a higher level of harvest if predation (particularly by wolves) could be reduced.

- 9 The Nelchina Caribou Herd has heavily used its winter and summer ranges in Unit 13. Lichens are severely depleted, and it is unlikely that caribou will winter in Unit 13 unless herd size declines markedly. Even though Nelchina caribou declined in body size and condition, the herd continues to have a high potential for growth and provides a high harvest. Winter range in Unit 11, 12, 20E and the adjacent Yukon Territory may be sufficient to maintain the herd for many years, but some of this range is also used by the Fortymile Herd. The Nelchina Herd and the George River Herd in northern Quebec may be at similar growth stages; both are significantly affected by high population densities on their summer ranges, and modeling indicates the George River Herd has decreased in some years from increased mortality and decreased fecundity in adult females (Crete et al. 1996). High harvest levels in the Nelchina Herd restrained growth rate and population size and may have prevented the herd from reaching high levels and declining.

RECOMMENDATIONS FOR MANAGEMENT AND RESEARCH

- 1 Long-term DCH research project (including collection of data from any other relevant Alaskan herd) should continue for at least 5 years, but calf mortality studies in the DCH should be terminated after 1997.
- 2 Diversionary feeding experiments should continue in the DCH and other herds for several more years to thoroughly explore feeding behavior of wolves on calving areas to determine potential of the technique to improve recruitment of caribou calves.
- 3 The Nelchina Herd should be reduced to 35,000 caribou in summer as soon as is practical. Reduced herd size should improve fall body condition, maintain productivity of cows, and prevent further degradation of summer ranges. Monitoring of body weight and femur marrow fat content of calves in October and April should continue, and a sample of neonates should be weighed each year. Cohorts of 10 to 15 calves should be collared each fall until there are at least 70 active collars in the herd that can be used for censusing, determining natality rates, age at first reproduction, distribution, and mortality rates.
- 4 Unit 13 range stations should be maintained and read again as soon as possible. The estimated periodic cost of about \$20,000 is economic because the Nelchina Herd can be expected to provide most of the new information in Alaska about caribou-range relationships in the near future.
- 5 The department should fund a molecular genetics study to determine the relatedness of caribou herds in Alaska. We now have over 1000 samples of whole blood and blood clots that have been collected over the last 10 years. Estimated cost of this project would be \$25,000 to \$40,000 and the project could be completed in less than 1 year.

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PREPARED BY:

Patrick Valkenburg
Wildlife Biologist III

APPROVED BY:


Wayne L Regelin, Director
Division of Wildlife Conservation

SUBMITTED BY:

Kenneth R Whitten
Research Coordinator

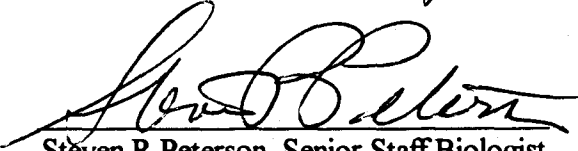

Steven R Peterson, Senior Staff Biologist
Division of Wildlife Conservation

Figure 1 Spreadsheet computer model^a of the DCH, 1969-2000

Year	Cows	Calves	Bulls	Posthunt total	Cow harvest	Bull harvest	Cow survival	Bull survival	Calves: 100 Cows	Bull: 100 Cows	λ	Census	Fall calf:cow	Fall bull:cow	Adult female mortality rate
1969	3000 ^b	840	1200	5040	86	271	0.88	0.95	28	40			28	40	
1970	2932	997	1178	5106	115	321	0.88	0.95	34	40	1.01		34	77	
1971	2696	404	921	4022	366	624	0.88	0.95	15	34	0.79		15	29	
1972	2349	258	447	3055	219	601	0.88	0.95	11	19	0.76		11	33	
1973	2089	209	269	2567	104	266	0.85	0.95	10	13	0.84	2804	10	29	
1974	1873	37	345	2255	0	0	0.85	0.95	2	18	0.88		2	28	
1975	1609	193	344	2146	0	0	0.95	0.95	12	21	0.95				
1976	1630	733	409	2773	0	0	0.95	0.95	45	25	1.29		45	38	
1977	1932	811	702	3445	0	0	0.95	0.95	42	36	1.24		42	33	
1978	2259	881	1014	4154	0	0	0.93	0.95	39	45	1.21		39	75	
1979	2551	1021	1340	4912	0	0	0.92	0.95	40	53	1.18	4191	65	39	0
1980	2864	1403	1605	5872	0	104	0.92	0.95	49	56	1.20	4478	49	85	0
1981	3272	1341	1857	6470	73	268	0.92	0.95	41	57	1.10	4962	41	46	0
1982	3612	1120	2063	6795	77	274	0.91	0.97	31	57	1.05	7335	31	42	7
1983	3613	1662	1188	6463	234	1302	0.91	0.97	46	33	0.95	6969	46	35	6
1984	3929	1414	1371	6714	191	507	0.91	0.98	36	35	1.04	6260	36	42	6
1985	4166	1500	1353	7019	117	614	0.95	0.98	36	32	1.05	8083	36	49	18
1986	4558	1322	1147	7027	183	841	0.97	0.98	29	25	1.00	7804	29	41	9
1987	5089	1578	1063	7729	38	644	0.97	0.98	31	21	1.10	8300	31	32	5
1988	5756	2015	1182	8953	22	555	0.97	0.98	35	21	1.16	8338	35	33	14
1989	6640	1062	1366	9068	18	681	0.80	0.98	16	21	1.01	10690	36	27	12
1990	5654	509	1307	7470	83	552	0.80	0.98	9	23	0.82	7886	17	38	22
1991	4705	235	1074	6014	22	456	0.75	0.90	5	23	0.81	5755	8	29	14
1992	3617	181	1073	4870	0	0	0.78	0.75	5	30	0.81	5870	11	25	15
1993	2887	144	867	3898	5	5	0.93	0.78	5	30	0.80	3661	5	36	10
1994	2745	467	739	3950	0	0	0.93	0.80	17	27	1.01	4341	23	25	15
1995	2743	411	791	3946	5	5	0.92	0.85	15	29	1.00	4646	20	24	10
1996	2694	404	835	3933	0	30	0.92	0.90	15	31	1.00	4100	21	30	
1997	2664	400	883	3947	0	50	0.92	0.90	15	33	1.00				
1998	2635	395	925	3955	0	50	0.92	0.90	15	35	1.00				
1999	2606	391	960	3957	0	50	0.92	0.90	15	37	1.00				

Year	Cows	Calves	Bulls	Posthunt total	Cow harvest	Bull harvest	Cow survival	Bull survival	Calves: 100 Cows	Bull: 100 Cows	λ	Census	Fall calf:cow	Fall bull:cow	Adult female mortality rate
2000	2577	387	990	3954	0	50	0.92	0.90	15	38	1.00				

^a Model developed by D Reed and P Valkenburg to simulate caribou populations using the recruitment, census, and harvest data that is routinely collected from most Alaskan caribou herds. The population is calculated in fall, after natural mortality and harvest is subtracted, and recruitment is added. Shaded figures are inputs; i.e., they are put into the model each year as values. The 2 harvest columns and the last 4 columns contain actual data. All other values except "year" are calculated by the model. Mortality figures were manipulated by trial and error to make the calculated population track census data.

^b Starting population based on the 1972 census.

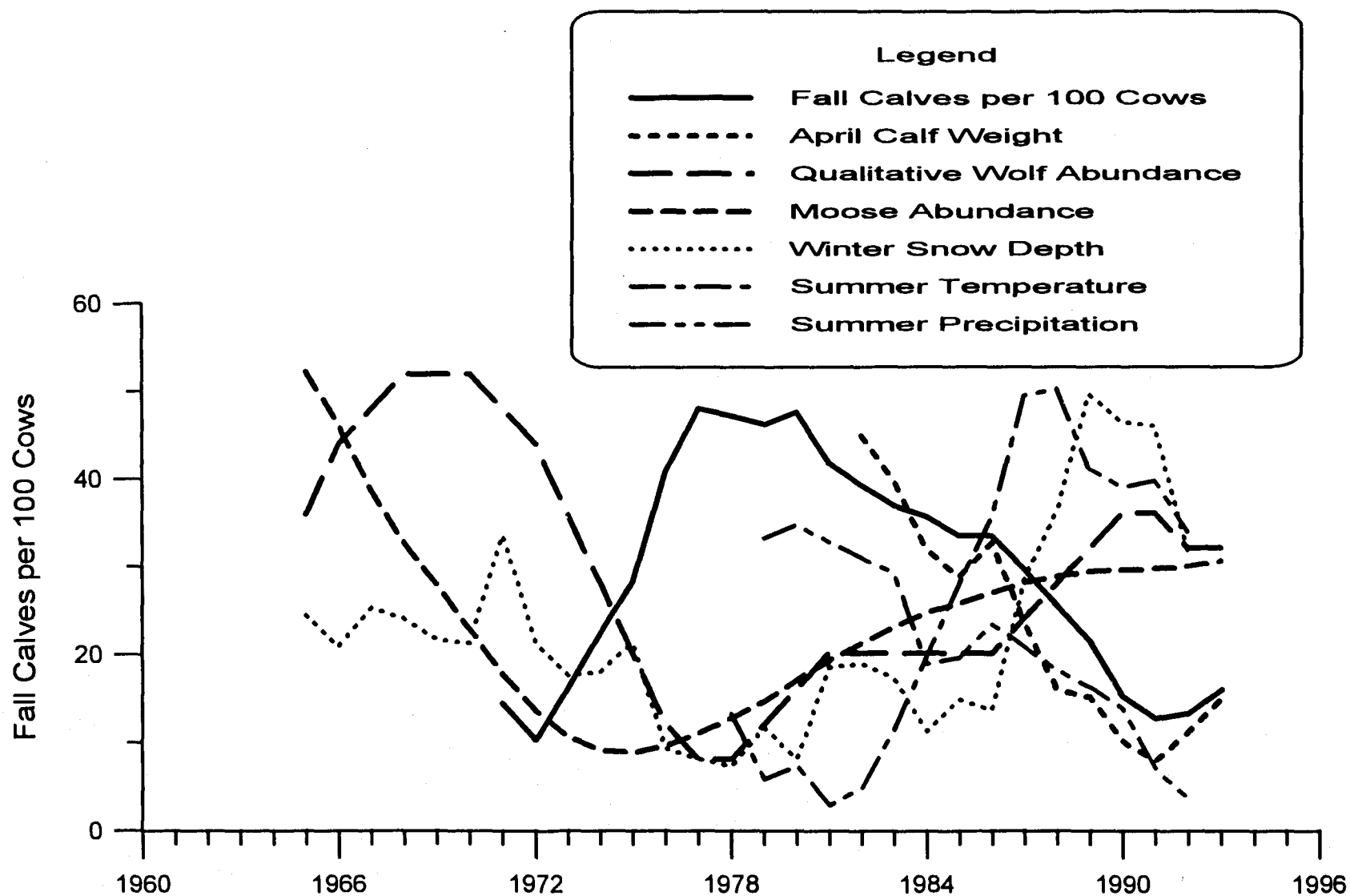


Figure 2 Temporal trends of 6 variables (5-year moving averages, scaled to vary in same range) as predictors of fall calf:100 cow ratios in the DCH

Table 1 Natality rates of radiocollared known-aged DCH^a females observed in late May, 1980-1996

Year	Proportion parturient (%) in late May						All cows 3 years and older
	Yearlings	2-year olds	3-year olds	4-year olds	5-year olds	6+ year olds	
1980		7/11 (64)					
1981	0/7 (0)	1/1 (100)	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)

^a Figures may differ slightly from previous reports because only DCH female were considered here (no Yanert females or those whose age was not known were used in this analysis).

Table 2 Weights of newborn Delta Herd caribou calves in 1995 and 1996

	1995				1996			
	Male	Corrected ^a	Female	Corrected	Male	Corrected	Female	Corrected
	11.50	11.50	14.75	14.75	14.50	14.50	11.00	11.00
	15.00	15.00	15.00	12.00	14.50	14.50	12.00	12.00
	16.00	16.00	15.00	15.00	15.00	15.00	12.50	12.50
	16.00	15.00	16.25	16.25	16.00	16.00	12.50	12.50
	17.00	17.00	16.50	16.50	16.00	14.50	15.25	15.25
	17.50	17.50	17.00	17.00	16.50	16.50	15.50	15.50
	17.50	17.50	17.50	17.50	17.00	17.00	16.00	16.00
	17.50	17.50	18.00	18.00	18.00	18.00	16.00	16.00
	17.75	17.75	18.00	16.50	18.00	18.00	16.00	16.00
	18.00	18.00	18.00	18.00	18.50	17.00	16.00	16.00
	18.50	18.50	18.75	18.75	19.00	18.00	16.00	16.00
	18.50	17.00	19.00	17.50	19.00	19.00	16.00	16.00
	18.75	18.75	19.50	18.00	19.00	18.00	16.00	16.00
	18.75	18.75	19.75	19.75	19.50	19.50	16.50	16.50
	18.75	18.75	19.75	18.25	19.50	19.50	16.50	16.50
	19.00	19.00	20.50	20.50	19.75	18.25	17.00	17.00
	20.00	18.50	20.50	19.00	20.00	20.00	17.00	17.00
	20.25	17.25	21.00	18.50	20.00	20.00	17.00	17.00
	20.50	20.50	23.15	23.15	21.00	21.00	17.00	15.50
	20.75	20.75			21.00	21.00	17.20	17.20
	21.83	18.83			21.00	18.50	17.25	17.25
	22.00	19.00			24.00	21.00	17.50	17.50
	23.00	20.00					17.50	17.50
	23.00	20.00					17.50	17.50
	24.50	23.00					18.00	16.50
	28.22	23.72					19.50	19.50
							20.00	18.50
							20.75	20.75
$\bar{x}$	19.23	18.27	18.31	17.63	18.49	17.94	16.32	16.16
$s\bar{x}$	0.65	0.48	0.52	0.54	0.51	0.45	0.42	0.40
N	26	26	19	19	22	22	28	28
Kgs	8.72	8.29	8.31	8.00	8.39	8.14	7.40	7.33
$s\bar{x}$	0.30	0.22	0.23	0.24	0.23	0.21	0.19	0.18
N	26	26	19	19	22	22	28	28
P value ^b	0.386	0.626	0.004	0.031				

^a Corrected for age by subtracting 1.5 lbs for each day of age older than 1.

^b Student's *t*-test probability of making a Type I error with an alpha level of 0.05 in comparing weights of male and female calves between years.

Table 3 Mean weight of samples of 4- and 10-month-old female calves from the DCH, 1979-1996

Year	10-month olds				4-month olds			
	$\bar{x}$ (lbs)	$\bar{x}$ (kgs)	$s\bar{x}$ (lbs)	N	$\bar{x}$ (lbs)	$\bar{x}$ (kgs)	$s\bar{x}$ (lbs)	N
1979	132.3	60.1	2.4	11				
1981	137.0	62.1	7.4	5				
1982	135.1	61.3	3.9	11				
1983	137.2	62.2	3.3	13				
1984	126.9	57.5	1.3	14				
1987	120.8	54.8	2.8	9				
1988	131.3	59.6	2.9	12				
1989	133.6	60.6	2.7	9				
1990	119.9	54.4	3.3	9				
1991	113.1	51.3	2.3	9	127.6	57.9	2.6	14
1992	119.1	54.0	2.6	17	119.1	54.0	2.6	17
1993	122.3	55.5	2.9	12	122.9	55.8	3.0	11
1994 ^a					131.4	59.6	3.0	15
1995	123.1	55.8	2.7	15	131.1	59.5	2.7	15
1996	120.8	54.8	3.3	15	123.0	55.8	3.0	14

^a There were too few calves to obtain a sample of 10-month olds in April 1994.

Table 4 Weights of newborn calves from selected Alaskan Herds

Herd and year	Males			Females		
	Weight (kgs)	SE ^a	N	Weight (kgs)	SE	N
Delta 1995	8.72	0.29	26	8.31	0.24	19
Delta 1996	8.39	0.23	22	7.40	0.19	28
Denali 1984-1987 ^b	9.00	0.11	67	7.80	0.11	60
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
Mentasta 1993 ^c	8.90	0.23	15	7.91	0.20	23
Mentasta 1994 ^c	8.83	0.21	18	8.09	0.19	23
Nelchina 1996	8.26	0.24	23	7.19	0.19	17
Porcupine 1983	7.40	0.19	24	6.60	0.16	28
Porcupine 1984	7.30	0.22	33	6.70	0.18	23
Porcupine 1985	7.70	0.23	27	7.30	0.20	26

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

^b Denali data is corrected for calf age; uncorrected weights would be 0.3-0.5 kgs higher (Adams et al. 1995a).

^c Data from Jenkins 1996.

Table 5 Ranked mean weight, standard error, and sample size of 43 cohorts of female caribou calves from 8 Alaskan herds, 1979-1996

Herd	Year of sample	Season	$\bar{x}$ weight (lbs)	$s \bar{x}$ (lbs)	n
Western Arctic	1994	Fall	71.5	2.8	15
Western Arctic	1995	Fall	81.1	2.6	9
Western Arctic	1993	Spring	82.1	2.2	14
Western Arctic	1992	Spring	87.0	2.0	16
Western Arctic	1994	Spring	88.3	2.8	15
Western Arctic	1992	Fall	89.2	4.1	13
N AK Peninsula	1995	Fall	98.6	3.6	10
N AK Peninsula	1996	Fall	101.5	5.3	10
Nelchina	1995	Spring	105.0	1.9	29
Nelchina	1996	Fall	106.5	4.7	10
Macomb	1990	Spring	107.3	2.6	12
Nelchina	1994	Spring	107.8	4.2	11
Nelchina (Unit 13)	1992	Spring	109.4	7.2	8
Mulchatna	1995	Spring	110.6	3.0	10
Chisana	1990	Fall	112.6	3.8	14
N AK Peninsula	1995	Spring	112.6	3.0	10
Delta	1991	Spring	113.1	2.9	18
Fortymile	1990	Fall	116.3	2.5	14
Nelchina	1996	Spring	117.1	2.7	16
Nelchina (Unit 13)	1993	Spring	118.0	3.3	11
Nelchina	1995	Fall	118.0	3.4	15
Macomb	1994	Fall	118.8	3.1	10
Fortymile	1991	Fall	118.9	3.0	14
Delta	1992	Spring	119.1	2.6	17
Delta	1990	Spring	119.9	3.3	12
Fortymile	1994	Fall	120.0	2.7	14
Delta	1992	Fall	120.4	3.0	14
Delta	1987	Spring	120.8	2.8	9
Delta	1996	Spring	120.8	3.3	15
Fortymile	1996	Fall	121.4	3.0	15
Fortymile	1992	Fall	121.5	3.7	14
Delta	1993	Spring	122.3	2.9	12
Delta	1993	Fall	122.9	3.0	11
Delta	1996	Fall	123.0	3.0	14
Delta	1995	Spring	123.1	2.7	15

Herd	Year of sample	Season	$\bar{x}$ weight (lbs)	$s \bar{x}$ (lbs)	n
Fortymile	1993	Fall	123.7	1.9	15
Nelchina (Unit 12)	1992	Spring	124.4	2.7	9
Fortymile	1995	Fall	125.0	2.6	15
Nelchina (Unit 12)	1993	Spring	125.7	4.0	7
Nushagak	1995	Spring	125.8	2.9	15
Kenai Mtns	1996	Spring	126.5	3.3	11
Delta	1984	Spring	126.9	1.9	14
Delta	1991	Fall	127.6	2.6	14
Macomb	1996	Fall	128.3	6.0	8
White Mtns	1995	Spring	130.1	3.0	8
White Mtns	1991	Fall	131.1	4.7	9
Delta	1995	Fall	131.1	2.7	13
Wolf Mtn	1995	Fall	131.1	4.7	8
Delta	1988	Spring	131.3	2.9	12
Delta	1994	Fall	131.4	3.0	15
Delta	1979	Spring	132.3	2.4	11
White Mtns	1995	Fall	133.3	4.7	6
Delta	1989	Spring	133.6	2.7	9
Ray Mtns	1994	Fall	134.4	3.8	20
Delta	1982	Spring	135.1	3.9	11
Delta	1981	Spring	137.0	7.4	5
Delta	1983	Spring	137.2	3.3	13
Galena Mtn	1994	Fall	143.4	3.2	9
Killey R	1996	Spring	144.8	1.4	10

Table 6 Weights^a of newborn Nelchina Herd calves captured on 25 May 1996

Males uncorrected	Males corrected	Males kgs	Females uncorrected	Females corrected	Females kgs
21.00	18.50	8.39	17.00	14.50	6.58
21.00	18.50	8.39	17.50	15.00	6.80
20.00	17.50	7.94	16.50	14.00	6.35
18.00	15.50	7.03	17.00	14.50	6.58
19.00	16.50	7.48	16.50	14.00	6.35
18.00	15.50	7.03	16.00	13.50	6.12
18.00	15.50	7.03	21.00	18.50	8.39
24.50	22.00	9.98	16.00	13.50	6.12
20.50	18.00	8.17	20.00	17.50	7.94
20.00	17.50	7.94	20.50	18.00	8.17
16.50	14.00	6.35	20.00	17.50	7.94
19.50	17.00	7.71	19.00	16.50	7.48
21.50	19.00	8.62	18.00	15.50	7.03
18.50	16.00	7.26	23.00	20.50	9.30
20.50	18.00	8.17	18.00	15.50	7.03
23.50	21.00	9.53	18.25	15.75	7.14
22.00	19.50	8.85	17.75	15.25	6.92
23.00	20.50	9.30			
23.00	20.50	9.30			
22.50	20.00	9.07			
27.50	25.00	11.34			
18.75	16.25	7.37			
19.50	17.00	7.71			
$\bar{x}$	18.21	8.26		15.85	7.19
$s\bar{x}$	0.54	0.24		0.42	0.19
N	23	23		17	17

^a Weights were corrected for scale error; the scale read 2.5 lbs high.

Table 7 Snow index, total rainfall, and May-Aug temperature for the range of the DCH, 1975-1995

Year	Snow index	Total rainfall	Sum of May-Aug temperature
1975	1.8		
1976	2.0		55.8
1977	2.0	6.5	58.8
1978	2.7		55.2
1979	1.1	15.2	56.2
1980	1.5	14.2	52.1
1981	1.8	13.9	51.4
1982	3.2	22.5	53.5
1983	1.9	13.9	56.3
1984	3.7		53.0
1985	1.6	12.4	53.5
1986	1.4	12.1	56.1
1987	1.7	12.2	59.4
1988	2.8	14.6	62.2
1989	3.4	17.0	58.5
1990	5.3	9.9	63.4
1991	3.4	9.4	56.7
1992	5.0	10.3	52.8
1993	2.0	12.2	60.7
1994	3.3	10.0	59.0
1995	1.7	6.7	59.3

Table 8 Annual total mortality^a of radiocollared known-aged female DCH^b caribou, 1979-1996

Year	Proportion dying (%) (Cause of death) by age class			
	Calves (4 to 16 months old)	Yearlings (16 to 30 months old)	Older than yearlings (> 30 months old)	Yearlings and older (> 16 months old)
1979-1980		0/11 (0)		0/11 (0)
1980-1981		0/2 (0)	0/11 (0)	0/13 (0)
1981-1982		0/7 (0)	0/11 (0)	0/18 (0)
1982-1983		2/10 (20) (2 unk)	0/18 (0)	2/28 (7)
1983-1984		0/12 (0)	2/24 (8) (1 unk, 1 hunting)	2/36 (6)
1984-1985		0/11 (0)	2/21 (10) (1 grizzly, 1 unk)	2/32 (6)
1985-1986			7/39 (18) (4 wolf, 1 hunting, 1 poached, 1 unk)	7/39 (18)
1986-1987			3/32 (9) (2 unk, 1 poached)	3/32 (9)
1987-1988		1/6 (17) (1 poached)	1/32 (3) (1 unk pred)	2/38 (5)
1988-1989		1/11 (9) (1 unk pred)	5/32 (16) (5 unk)	6/43 (14)
1989-1990		1/8 (13) (1 wolf)	5/41 (12) (4 unk, 1 wolf)	6/49 (12)
1990-1991			9/41 (22) (5 unk, 2 wolf, 2 unk pred)	9/41 (22)
1991-1992	5/12 (42) (2 wolf, 2 unk pred, 1 unk)	0/4 (0)	5/31 (16) (3 wolf, 1 unk pred, 1 unk)	5/35 (14)
1992-1993	8/15 (53) (3 lynx, 3 unk pred, 2 unk)	1/11 (9) (1 unk)	5/30 (17) (4 wolf, 1 coyote)	6/41 (15)
1993-1994	7/10 (70) (5 wolf, 1 unk., 1 poached)	0/7	4/32 (13) (3 unk, 1 wolf)	4/39 (10)
1994-1995	5/15 (33) (3 wolf, 2 unk pred)	2/7 (1 grizzly, 1 hunting)	5/41 (12) (3 wolf, 1 unk pred, 1 breached birth)	7/48 (15)
1995-1996	4/14 (29) (3 wolf, 1 unk)	1/11 (9) (1 wolf)	4/39 (10) (3 wolf, 1 unk pred)	5/50 (10)
Totals	29/66 (44)(13 wolf, 7 unk pred, 5 unk, 3 lynx, 1 poached)	9/118 (8)(3 unk, 2 wolf, 1 unk pred, 1 grizzly, 1 poached, 1 hunting)	57/475 (12)(23 unk, 21 wolf, 6 unk pred, 2 hunting, 2 poached, 1 grizzly, 1 coyote, 1 breached birth)	66/593 (11)

^a Mortality rate was calculated from 1 Oct to 30 Sep each year.^b Mortality rates differ slightly from previous reports because only DCH caribou are considered here (no Yanert caribou are included).

Table 9 Mortality of radiocollared calves and calves of radiocollared females by cause in the DCH from birth to 30 September, 1995-1996

	Year	Proportion dying (%)						Total	Capture induced
		Neonatal	Wolf	Grizzly bear	Golden eagle	Coyote	Unk		
All radiocollared calves	1995		13/43 (30)	9/43 (21)	7/43 (16)	0	0	29/43 (67)	2/45 (4)
	1996		9/50 (18)	11/50 (22)	6/50 (12)	1/50 (2)	4/50 (8)	31/50 (62)	0/50 (0)
All calves of known-aged radiocollared cows	1995	7/31 (23)*	5/31 (16)	5/31 (16)	3/31 (10)		1/31 (3)	21/31 (68)	1/32 (3)
	1996	4/33 (12)	5/33 (15)	8/33 (24)	3/33 (9)		1/33 (3)	21/33 (64)	0/33 (0)

* Includes 1 due to breached birth where both cow and calf died.

Table 10 Timing of mortality of radiocollared calves in the DCH from birth to 30 September, 1995-1996

Year	All radiocollared calves dying by period, proportion dying (%)						
	15-21 May	22-31 May	1-15 Jun	16-30 Jun	1-31 Jul	1-31 Aug	1-30 Sep
1995	1/43 (2)	12/43 (28)	8/43 (19)	2/43 (5)	5/43 (12)	1/43 (2)	0/43 (0)
1996	8/50 (16)	8/50 (16)	7/50 (14)	2/50 (4)	1/50 (2)	3/50 (6)	2/50 (4)

Table 11 Proportion of radiocollared male and female DCH calves found > 2 miles from radiocollared adult females during late winter

Month and year	Proportion of calves >2 mi from a collared female >1 year old	Total number of radiocollared cows located
March 1992	3/8 females	21
Late February 1993	3/9 females	25
March 1994	4/9 females, 3/9 males	40
April 1994	3/10 females, 2/7 males	40
March 1995	6/11 females	50
March 1996	5/10 females, 2/9 males	46
April 1996	4/11 females, 1/9 males	49
Totals	28/68 (41%) females, 8/34 (24%) males	271

Table 12 Late winter composition counts in the DCH, and comparison of fall and late winter calf:cow ratios

Survey date	Bulls:100 cows	Calves:100 cows; April (previous fall)	Calves (%)	Bulls (%)	Total caribou counted
4/20/83	23	29 (31)	19	15	1079
4/10/84	10	49 (46)	31	6	628
5/3/85	1	51 (36) ^a	34	1	759
4/20/86	21	44 (36) ^a	26	13	1141
4/6/88	22	29 (31)	19	14	1473
4/18/89	15	21 (35)	15	11	1053
4/18/90	16	16 (36)	10	11	835
4/18/91	22	9 (17)	7	16	1387

^a Late winter ratio higher than fall ratio.

APPENDIX A Data used to construct a correlation matrix (Appendix E) of 9 variables from the DCH data set

Year	Calves:100 Cows	Calves	Cows	April calf weight	October calf weight	Fall wolf numbers	Wolf index	Moose numbers	Moose index	Snow index	Summer temp	Summer precip	Natality rate of females	Number of pregnant females
1963							mod	22600	very high	1.4				
1964							mod		very high	1.9				
1965							high	23000	very high	3.8				
1966							high		very high	3.2				
1967							high	14500	high	2.6				
1968							high		high	2.1				
1969	28						very high	12000	high	1.0				
1970	34						very high		mod	4.9				
1971	15						very high	8000	mod	2.9				
1972	11					265	high		mod	2.0				
1973	10					260	high	4200	low	2.0				
1974	2					250	high	3100	very low	4.1				
1975	13					239	high	2500	very low	1.8				
1976	45					125	mod	2800	very low	2.0	55.8			
1977	42					100	low	3300	very low	2.1	58.8	6.5		
1978	39					80	low	3600	very low	2.8	55.2			
1979	65*			60.1		74	low	4400	low	1.1	56.2	15.2		
1980	49					110	mod	5100	low	1.5	52.1	14.2		
1981	41	319	776	62.3		145	mod	5800	low	1.8	51.4	13.9		
1982	37	318	860	61.4			mod	6600	low	3.2	53.5	22.5		
1983	46	305	665	62.3			mod	7900	low	1.9	56.3	13.9		
1984	36	222	613	57.4			mod	8100	mod	3.7	53.0		90	28
1985	36	232	629			195	mod	8500	mod	1.6	53.5	12.4	93	38
1986	29	329	1141				mod	9200	mod	1.4	56.1	12.1	83	33
1987	31	320	1026	54.8		191	mod	9400	mod	1.7	59.4	12.2	89	25
1988	35	631	1802	59.7		184	mod	9700	mod	2.8	62.2	14.6	88	28
1989	36	432	1218	60.7			mod	10300	high	3.4	58.5	17.0	83	25
1990	17	265	1567	53.0			high	10500	high	5.3	63.4	9.9	72	28
1991	8	102	1245	51.7	57.9	267	high	10500	high	3.4	56.7	9.4	71	25
1992	11	99	918	54.1	54.6		high	10300	high	5.0	52.8	10.3	96	27
1993	4	46	1113	55.5	55.8	262	high	10000	high	2.0	60.7	12.2	30	7
1994	23	276	1280		59.6	180	mod	10500	high	3.3	59.0	10.0	66	20
1995	20	219	1085	55.8	59.5	180	mod	11000	high	1.7	59.3	6.7	87	33
1996	21	209	1015	54.8	55.8	220	high	11500	high				95	35

* Counts in 1979 were probably biased.

APPENDIX B Delta Caribou Herd fall composition counts, 1969-1996

Approximate survey date	Bulls: 100 cows	Calves: 100 cows	Calves %	Cows %	Small bulls % of bulls	Medium bulls % of bulls	Large bulls % of bulls	Total bulls %	Composition sample size
10/13-15/69 ^a	40	28	15	53	0	0	0	21	777
10/21-23/70 ^a	77	34	14	43	0	0	0	33	896
10/29-31/71 ^a	29	15	10	65	0	0	0	19	1139
10/27-31/72 ^a	33	11	7	67	0	0	0	22	1185
10/23-24/73 ^a	29	10	7	70	0	0	0	20	1050
10/23-25/74 ^a	28	2	1	76	0	0	0	21	1141
10/29-31/76 ^a	38	45	24	54	0	0	0	21	1055
10/26-31/77 ^a	33	42	23	55	0	0	0	18	1365
10/26/78 ^a	75	39	17	45	0	0	0	33	725
12/7/79	39	65	32	49	0	0	0	19	361
10/25/80	85	49	21	43	0	0	0	36	1369
10/2/81	46	41	22	53	47	3	50	25	1451
10/8/82	42	31	18	58	48	4	48	24	1565
10/4/83	35	46	25	55	59	6	36	20	1208
10/17/84	42	36	20	56	28	32	40	24	1093
10/9-12/85	49	36	20	54	57	24	19	26	1164
10/22/86	41	29	17	59	49	30	21	24	1934
10/5/87	32	31	19	61	53	23	24	20	1682
10/14/88	33	35	21	60	50	38	12	20	3003
10/10/89	27	36	22	62	64	28	7	16	1965
10/4/90	38	17	11	65	45	39	16	24	2411
10/1/91	29	8	6	73	55	29	16	21	1705
9/28/92	25	11	8	74	46	43	11	19	1240
9/25/93 ^b	36	5	3	72	45	33	22	25	1525
10/3-4/94 ^b	25	23	16	68	33	29	39	17	2131
10/03/95	24	20	14	69	41	19	40	17	1567
10/3/96	30	21	14	66	51	20	29	20	1532

^a Ratios may not be comparable because yearlings were classified in this count.

^b Data was weighted by distribution of radiocollars.

APPENDIX C Student's *t*-test of mean weights of samples of caribou calves from Interior Alaskan caribou herds (significant differences are bolded).

Sex/Herd/Yr(s)	$\bar{x}$ (kgs)	<i>N</i>	<i>s</i> $\bar{x}$	Variance ^a	<i>t</i> -statistic ^a	Degrees of freedom ^a	<i>P</i>
Males							
Delta 1996	8.4	22	0.23	0.053	0.45	46	0.654
Fortymile 1996	8.5	26	0.24	0.058			
Denali 1984-1987 ^b	9.0	67	0.11	0.012	2.27	33	0.030
Delta 1995	8.4	24	0.24	0.058			
Fortymile 1996	8.5	26	0.24	0.058	0.82	47	0.414
Nelchina 1996	8.3	23	0.24	0.058			
Delta 1996	8.4	22	0.23	0.053	0.39	43	0.698
Nelchina 1996	8.3	23	0.24	0.058			
Delta 1995	8.4	24	0.24	0.058	0.03	44	0.976
Delta 1996	8.4	22	0.23	0.053			
Nelchina 1996	8.3	23	0.24	0.058	1.93	35	0.063
Mentasta 1993 ^c	8.9	15	0.23	0.053			
Nelchina 1996	8.3	23	0.24	0.058	1.79	39	0.082
Mentasta 1994 ^c	8.8	18	0.21	0.044			
Fortymile 1995	8.7	24	0.16	0.026	3.67	41	0.001
Fortymile 1994	7.7	22	0.20	0.040			
Fortymile 1994	7.7	22	0.20	0.040	2.66	46	0.011
Fortymile 1996	8.5	26	0.24	0.058			
Fortymile 1995	8.7	24	0.16	0.026	0.38	43	0.705
Fortymile 1996	8.5	26	0.24	0.058			
Females							
Delta 1996	7.4	28	0.19	0.036	2.71	56	0.009
Fortymile 1996	8.1	32	0.17	0.029			
Denali 1984-1987 ^b	7.8	60	0.11	0.012	1.14	26	0.266
Delta 1995	8.1	19	0.24	0.058			
Fortymile 1996	8.1	32	0.17	0.029	3.53	39	0.001
Nelchina 1996	7.2	17	0.19	0.036			
Delta 1996	7.4	28	0.19	0.036	0.78	40	0.439
Nelchina 1996	7.2	17	0.19	0.036			
Delta 1995	8.1	19	0.24	0.058	2.29	38	0.028
Delta 1996	7.4	28	0.19	0.036			
Nelchina 1996	7.2	17	0.19	0.036	2.61	38	0.013
Mentasta 1993 ^c	7.9	23	0.20	0.040			
Nelchina 1996	7.2	17	0.19	0.036	3.35	37	0.002
Mentasta 1994 ^c	8.1	23	0.19	0.036			
Fortymile 1995	7.9	25	0.19	0.036	1.18	39	0.245
Fortymile 1994	7.6	22	0.27	0.073			
Fortymile 1994	7.6	22	0.27	0.073	1.69	37	0.099
Fortymile 1996	8.1	32	0.17	0.029			

Sex/Herd/Yr(s)	$\bar{x}$ (kgs)	N	$s\bar{x}$	Variance ^a	t -statistic ^a	Degrees of freedom ^a	P
Fortymile 1995	7.9	25	0.19	0.036	0.59	52	0.559
Fortymile 1996	8.1	32	0.17	0.029			

^a Statistical tests from Gasaway et al. 1986.

^b From Adams et al. 1995a.

^c From Jenkins et al. 1996.

APPENDIX D Whole weight, gutted weight, mandible length, diastema length, mandible fat, femur fat, warble numbers, and fat deposit index of female calves from the Nelchina and other selected caribou herds, 1992-1995

Collection	Month	Whole weight (lbs)			Gutted weight (lbs)			Mandible length (cm)			Diastema length (cm)			% ^a Mandible fat			% ^a Femur fat			Warbles			Fat deposit index ^b (n)
		Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	Mean	SE	n	
Nelchina (Unit 13)	1992 Apr	109.4	7.2	8	76.0	4.9	8	216.7	4.9	7	83.1	2.2	8	15.5	2.8	8	--	--	--	--	--	--	3.0 (8)
Nelchina (Unit 12)	1992 Apr	124.4	2.7	9	87.1	2.0	9	224.8	1.5	9	86.9	1.0	9	34.4	3.6	9	--	--	--	--	--	--	4.0 (9)
Nelchina (Unit 13)	1993 Apr	118.0	3.3	11	82.5	2.2	11	221.3	1.9	12	84.6	0.9	12	23.7	2.4	12	50.0	4.0	11	46.7	7.8	12	3.5 (12)
Nelchina (Unit 12)	1993 Apr	125.7	4.0	7	86.9	3.1	7	221.2	3.0	7	83.4	1.1	7	29.4	4.9	7	50.7	6.4	7	56.7	11.3	7	3.9 (7)
Nelchina	1994 Apr	107.8	4.2	11	75.0	3.1	11	219.2	2.6	9	84.4	1.3	9	26.7	5.1	9	48.0	7.1	10	111.1	18.0	11	3.7 (11)
Nelchina	1995 Apr	105.0	1.9	29	71.7	1.9	15	214.7	1.3	13	80.6	0.8	14	27.3	3.0	15	39.9	5.6	15	116.0	24.0	15	3.5 (15)
Nelchina	1995 Oct	118.0	3.4	15	80.0	2.5	11	202.5	2.5	11	79.6	1.3	11	--	--	--	65.3	4.2	11	--	--	--	3.4 (11)
Nelchina	1996 Apr	117.1	2.7	16	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Nelchina	1996 Oct	106.5	4.7	10	72.8	3.4	10	204.6	2.4	8	80.4	1.4	9	25.0	4.1	8	51.9	7.6	10				3.2 (10)
Northern Peninsula	Alaska 1995 Apr	112.6	3.0	18	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Northern Peninsula	Alaska 1995 Oct	98.6	3.6	10	66.2	2.9	10	195.1	2.2	10	73.8	1.2	10	--	--	--	56.6	5.1	11	--	--	--	3.6 (9)
Northern Peninsula	Alaska 1996 Oct	101.5	5.3	10	67.5	3.8	10	195.2	3.3	10	72.7	1.4	10	33.3	3.8	10	65.0	3.5	10	--	--	--	3.5 (10)
Nushagak Peninsula	1995 Apr	125.8	2.9	15	88.3	7.0	5	225.4	6.2	5	85.0	2.8	5	49.4	1.0	5	78.8	2.1	5	--	--	--	4.0 (5)
Mulchatna	1995 Apr	110.6	3.0	10	75.8	2.3	10	215.3	2.3	9	80.8	0.8	10	53.5	4.4	10	76.3	3.3	10	108.0	21.0	10	3.8 (9)

^a After Neiland (1970). Percent marrow fat calculated from % dry weight as follows: % fat = (% dry weight*1.05)-6.95.

^b Fat deposit index was calculated by assigning a value of 1 point for the presence of fat in each of 4 sites on the carcass (i.e., rump, brisket, mesenteries, heart), summing the values for all animals, and dividing by the number of animals in each collection. For example, if each calf in a collection of 10 all had fat in each of the 4 fat deposit sites, the Fat Deposit Index would be 40/10 = 4.0.

APPENDIX E Matrix of Spearman correlation coefficients (r), significance level, and number of observations in correlations of 9 variables from the DCH data set (significant correlations are shaded; $P < 0.05$)

	CC	AW	POC	WF	MO	PWS	PST	PSP	NT
CC	1								
P	0								
N	27								
AW	0.87	1							
P	0.0001	0							
N	13	13							
POC	0.30	0.40	1						
P	0.62	0.60	0						
N	5	4	5						
WF	-0.88	-0.85	-0.63	1					
P	0.0001	0.02	0.37	0					
N	17	7	4	17					
MO	-0.32	-0.72	0.80	0.25	1				
P	0.11	0.006	0.10	0.34	0				
N	25	13	5	16	28				
PWS	-0.51	-0.48	-0.50	0.51	0.17	1			
P	0.008	0.10	0.39	0.04	0.38	0			
N	27	13	5	17	27	32			
PST	-0.37	-0.47	0.30	0.19	0.61	0.18	1		
P	0.12	0.10	0.62	0.55	0.006	0.45	0		
N	19	13	5	12	19	19	19		
PSP	0.52	0.59	-0.60	-0.30	-0.33	-0.22	-0.34	1	
P	0.03	0.03	0.28	0.40	0.19	0.40	0.18	0	
N	17	13	5	10	17	17	17	17	
NT	0.38	0.08	0.60	0.00	-0.21	-0.31	-0.19	-0.30	1
P	0.20	0.83	0.28	1.00	0.49	0.29	0.53	0.34	0
N	13	10	5	8	13	13	13	12	13

CC = Fall calf:cow ratio

AW = Apr (10-month-old calf weight)

POC = Previous Oct calf weight

WF = Wolf numbers

MO = Moose numbers

PWS = Previous winter snow (i.e., calf:cow ratio in 1995 vs snow index in 1994-1995)

PST = Previous summer temperature

PSP = Previous summer precipitation

NT = Natality in radiocollared females ≥ 3 year old

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