84-88

Alaska Department of Fish and Game
Division of Wildlife Conservation
Federal Aid in Wildlife Restoration
Research Progress Report

STATUS, MOVEMENTS, RANGE USE PATTERNS, AND LIMITING FACTORS OF THE FORTYMILE CARIBOU HERD

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Project W-23-1
Study 3.32
December 1989

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FINAL REPORT (RESEARCH)

State: Alaska

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Project No.: W-23-1 Project Title: Wildlife Research and Management

Study No.: 3.32R Study Title: Status, Movements, Range Use Patterns, and Limiting Factors of the Fortymile Caribou Herd

Period Covered: 1 July 1984-30 June 1988
(Includes data through 30 September 1988)

SUMMARY

The Fortymile Caribou (Rangifer tarandus granti) Herd (FCH) grew from about 5,740-8,610 caribou in 1975 to about 10,192 in 1981 (λ = 1.10 to 1.03) and from 12,400 in 1983 to about 20,000 in 1988 (λ= 1.10). The mean annual natality rate of radio-collared female caribou (≥3 yrs old) between 1984 and 1988 was 90% (range = 82-100%), which was as high as those in the Delta and the rapidly growing Western Arctic Caribou Herds. The average peak of calving occurred from 22 to 24 May.

From 1981 through 1988 calf mortality during the first 4 months of life averaged 65%, representing the single greatest factor retarding herd growth. No quantitative data were obtained regarding the cause(s) of mortality. The fall ratio of calves:100 females older than calves averaged 31.6 (SD = 3.6, n = 7) during the period.

From 1983 through 1988, the x annual natural mortality rates for radio-collared female (n = 50) and male (n = 18) caribou ≥3 years old were 7-9% and 19-35%, respectively. Predation by wolves (Canis lupus) caused most deaths of females; the cause of death was unknown for most males.

Herd size increased about 3 times from the mid-1970's to 1988, but the herd's occupied range increased only slightly. Range expansion consisted of annual fall movements into the

Yukon Territory beginning in 1984 and year-round use of the area between Birch Creek and the Steese Highway since 1986.

Historically, the FCH has been unpredictable and/or inconsistent in its use of calving areas; however, calving behavior of radio-collared cows has been predictable: 54% have calved in open (as opposed to shrubby or wooded) habitat, they avoid snow-covered terrain for calving, and they move to higher elevations as snow melts. The mean elevation occupied during calving was 1,100 m (timberline averages 1,000 m).

In the fall of 1986, 265 wolves (38 packs and 24 singles) were estimated to reside within the range of the FCH (44,000 km^2). The 1986 wolf:caribou ratio was about 1:53 and the wolf:prey (including moose [Alces alces] and sheep [Ovis dalli]) ratio was about 1:103 caribou equivalents; in 1976, near the caribou population low, comparable ratios were 1:23 and 1:72, respectively.

In 1986 we estimated that about 2,200 FCH caribou (>3 mo old) were killed by wolves. We estimated that grizzly bears (Ursus arctos) may kill about 180 caribou (>3 mo old) annually.

Key Words: caribou, Fortymile Herd, mortality, predation, radio-collaring, Rangifer, wolf.

CONTENTS

BACKGROUND

The Fortymile Caribou (Rangifer tarandus granti) Herd (FCH), which numbered approximately 586,000 (Murie 1935) in the 1920's, was the largest caribou herd in Alaska and one of the largest in the world. The herd ranged from Rampart on the Yukon River to Whitehorse in the Yukon Territory, and it provided much of the food needed by miners, Athapaskans, and other early residents (Murie 1935). The FCH declined from its peak in the 1920's to 10,000-20,000 by the early 1940's (Skoog 1956). Although the cause(s) of the decline is unknown, possible contributing factors include emigration (Skoog 1956, 1968), large harvests by humans (LeResche 1975), a large increase in the wolf (Canis lupus) population (Davis et al. 1978), and reduction of the winter range by fire (Leopold and Darling 1953).

Skoog (1968) suggested that the FCH increased continuously during the 1940's; however, data are insufficient to determine if growth began (or accelerated) prior to or after initiation of wolf control by the Federal Bureau of Predator and Rodent Control in 1947 (Davis et al. 1978). The FCH numbered approximately 65,000 (including calves) from 1955 through 1960 (Davis et al. 1978). No censuses occurred between 1961 and 1973. By 1973 the population numbered approximately 6,500 caribou (Davis et al. 1978). Herd composition data suggest that the decline probably ended in 1975 when the herd numbered 4,000-6,000 (Davis et al. 1978).

The decline from 1960 to 1975 was attributed to high harvests in the late 1960's and early 1970's and increasing predation

by wolves (Davis et al. 1978). However, little biological information was collected during the 1960's and early 1970's, and additional and/or alternative causes for the decline, such as adverse weather or food limitation, cannot be unequivocably ruled out.

It is clear that overharvesting of caribou, especially during the late 1960's and early 1970's, contributed to the 1960-75 decline. Conventional wisdom in the 1960's and early 1970's (and there was little evidence to the contrary) was that predation did not control ungulate populations and that hunting-induced mortality was often compensatory (i.e., hunters killed many animals that would have otherwise died soon). In addition, the status of the FCH was inadequately monitored and its size was grossly overestimated.

Several other Alaskan caribou herds also declined during the 1970's, including the Nelchina, Western Arctic, Delta, Denali, and Fortymile (Gasaway et al. 1983). Subsequently, caribou populations recovered rapidly (i.e., 14-22% growth/year) in those areas where wolf populations were reduced through (1) control efforts by the Alaska Department of Fish and Game (ADF&G; i.e., Delta Herd), (2) high wolf harvests by the public (i.e., Nelchina and Western Arctic Herds), and (3) natural mortality resulting from disease in the wolf population (i.e., Western Arctic Herd). In contrast, where herds (i.e., Fortymile and Denali) were preyed upon by wolf populations primarily responding to natural factors (and where disease was not prevalent), herd growth was negative, stable, or much slower (0-9% annually).

The FCH has the greatest potential for growth of any relatively accessible big game population in the state; the population level of 12,500 in 1983 was <20% of ADF&G's interim goal of 65,000 and only 2% of Murie's (1935) estimated historic size of 586,000. Apparently, the FCH grew about 3-10% annually; the associated moose population was stable (W. Gasaway, pers. commun.) during the mid- to late 1970's because of mild winters, low harvests by hunters, and a wolf population lowered by natural factors. From 1981 through 1987, ADF&G advocated and implemented actions to reduce grizzly bear (Ursus arctos) and wolf predation in the area. The Department also implemented a comprehensive management plan that included reducing legal and illegal harvest and promoting habitat protection and enhancement. This study was initiated to obtain the information necessary to assess the efficacy of the plan.

GOAL

To determine the population status and trend, movements, distribution, range-use patterns, and limiting factors of the FCH.

OBJECTIVES AND PROCEDURES

Objective 1

To ascertain the growth rate of the FCH.

Procedure:

The FCH was censused 4 times during this study (1983, 1984, 1986, and 1988), using an aerial photo-direct count technique (Davis et al. 1979). Using the census data (Table 1) and data from Davis et al. (1978), we calculated the growth rate of the FCH since its apparent nadir in 1975.

Objective 2

To measure natality of the FCH and compare it with that of other herds with known demography.

Procedure:

Each year from 1983 through 1988, the natality rate of FCH females was estimated in late May by observing the proportion of radio-collared females judged to be parturient based upon 1 or more of the following: distended udders, hard antlers, the presence of a calf (Bergerud 1964). A helicopter and ground observers were used to conduct herd composition and natality surveys in late May 1984 and 1985; in other years, natality surveys were from Super Cub or Bellanca Scout airplanes. Results were compared with natality data from the Delta and Western Arctic Caribou Herds.

Objective 3

To ascertain the mortality rates of calves and adults.

Procedure:

The calf mortality rate between spring (i.e.,birth) and fall was calculated by comparing the natality rate to the ratio of calves:100 cows in the fall. The annual mortality rates for adult females and males were estimated from the measured mortality rate of the radio-collared females and males present each year, respectively (Trent and Rongstad 1974). Confidence limits were not calculated for the mortality estimates.

Natural mortality rates from the radio-collared sample were compared with those derived from modeling the FCH's population dynamics with a spreadsheet computer model (Lotus 1-2-3, Lotus Development Corp., Cambridge, Mass.). For modeling, the fall 1983 population estimate (Table 1) was considered the beginning population and recruitment was defined as calves:100 cows in fall. Recruitment data were available for 1983-88 (except 1984). Harvest data were available for 1983-87; they were extrapolated for subsequent years. After the beginning

population, annual recruitment and harvest data were entered into the model and iterative runs were made while manipulating adult mortality rates of males and females until "best fit" scenarios were produced. Best fit scenarios produced a population size and sex composition for 1988 that were closest to our empirical estimates for 1988. The adult mortality rates from the "best fit" scenarios were then compared with mortality rates of radio-collared caribou.

Objective 4

To determine patterns of range use, habitat selection, and food habits of the FCH.

Procedure:

In August 1985, at the 4th International Reindeer/Caribou Symposium, Whitehorse, Yukon, we presented a paper entitled "Calving Distribution of Alaska's Steese-Fortymile Herd: A Case of Infidelity?" (Valkenburg and Davis 1986). We also prepared a detailed analysis of the movements and distribution of the herd between 1981 and 1987, including maps of calving and winter distribution (Valkenburg and Davis 1988).

To initially assess the food habits of the FCH, we collected a fecal pellet from each of 25 pellet groups at 6 locations within the FCH's winter range (Sparks and Malechek 1968, Boertje et al. 1985). Delays at the analysis lab (up to 24 mo for sample processing) resulted in only 1 sample being analyzed for this report.

Objective 5

To determine predator:caribou ratios in the range of the FCH.

Procedure:

During winter 1986-87 we estimated the distribution and size of the wolf population present within the entire range of the FCH. Aerial surveys were primarily conducted by D. Grangaard in March and April 1987 (methodology followed Boertje et al. 1987). Additional and corroborating data on wolves were obtained from sealing certificates, trapper interviews, and incidental observations of wolves compiled by D. Haggstrom, ADF&G biologist (ADF&G Big Game Data Index File).

During the winter of 1987-88, we conducted aerial wolf surveys in areas not intensively surveyed in 1986-87, including the lower Fortymile (Yukon Territory), upper Sixtymile, North Fork Ladue, Goodpaster, and upper Salcha Rivers, and the entire Birch Creek drainage. We estimated the winter diet of wolves from the following: (1) general observations; (2) the juxtaposition of wolves, moose (Alces alces), Dall sheep (Ovis dalli), and caribou; and (3) the concentration of radio-cesium

(C-137) (Holleman and Stephenson 1981) in muscle tissue samples from 31 wolves sampled in Boertje et al.'s (1987) study.

RESULTS AND DISCUSSION

Growth Rate of the Fortymile Caribou Herd

Accurately determining how wolf control efforts from 1981 to 1983 (Boertje et al. 1987) influenced the growth rate of the FCH was the stimulus for reviewing and analyzing the FCH's post-1975 population dynamics; Davis et al. (1978) reviewed them through 1975. Unfortunately, available data proved insufficient to clearly determine the influence of wolf control on the FCH's population growth rate; however, the null hypothesis (i.e., precontrol growth rate equaled postcontrol growth rate) cannot be rejected because of circumstantial evidence.

Calculating the growth rate of the FCH before wolf control is complicated by not knowing the year that herd growth began or the population size when it began and because the 1981 population size estimate is known to be a biased underestimation (Table 1). Fall calf:cow and bull:cow ratios as indices of recruitment and/or mortality (Table 2) suggest that population growth began between 1973 and 1976; the exact year remains undetermined. The FCH population was estimated at 5,312 in fall 1973 and 4,000-6,000 in fall 1974 and 1975 (Davis et al. 1978), but precision and accuracy among these censuses were inadequate for establishing a population trend.

We suggest readers consider our calculated growth rates with the following caveats. Accurately calculating the mean rate of growth between any 2 censuses (Table 1) is problematic, because all of the census estimates are biased, some more than others. Determining the relative "goodness" of any given census is subjective, because the census techniques do not incorporate precise estimates. The calculated rate of growth between any 2 censuses is inconsistent with the growth rates our spreadsheet computer model, which used empirically determined recruitment and mortality inputs and assumed zero net emigration/immigration that were consistent with empirical evidence. Therefore, at least one empirically determined parameter (including population estimates) was biased.

A range of population growth rates prior to wolf control can be calculated, assuming different herd sizes in 1981 and an initial population of 5,740-8,610 wolves in 1975 (Davis et al. 1978). We compared summer populations rather than fall populations because recent census methodology produces summer population estimates that require no extrapolations, in contrast to extrapolated fall estimates that can be subject to compounding biases (Davis et al. 1979). We converted the 1975

fall estimates to summer estimates, using the conversion factor in footnote "a" in Table 1.

Because the 1981 population size estimate (Table 1) was insubstantial, we subjectively revised it upward by extrapolating from the 1983 estimate. We calculated the mean annual finite increase rate from 1983 to 1988 (λ = 1.10) and assumed the same rate had occurred from 1981 to 1983. The resulting 1981 population estimate was 10,192 wolves. By alternatively using the 1975 starting populations of 5,740 and 8,610, respective low and high finite rates of growth to 1981 were λ = 1.03 and λ = 1.10.

Inspection of the "calf percentage in herd" column in Table 2 (as an index of recruitment) shows that the 1976-81 (i.e., before wolf control) mean of 18.8% (SD = 3.2, n = 5) is as large as the 1982-88 (i.e., after wolf control) mean of 17.9% (SD = 2.0, n = 6). Therefore, the only way that the FCH could have increased more rapidly after wolf control (discounting dispersal) than before it was if the adult mortalty differed. No data are available regarding adult mortality before wolf control. The interim population size goal for the FCH (i.e., 50,000 precalving or 65,000 postcalving) should be reached by the year 2000. The interim population goal is based primarily on Davis et al.'s (1978) conclusions that the current FCH range could support at least 50,000 caribou without deterioration and the currently used range was a fraction of the historic range.

What the optimum herd size should be or whether the herd should be managed at a prescribed level is not clear. Murie (1935) estimated that the herd numbered 586,000 in the 1920's. In contrast, the herd declined during the 1960's after numbering only 60,000. As the herd grows, competition for resources will predictably cause caribou to occupy range that has been unused for many years. How this will affect body condition is unknown. How adverse weather and higher wolf predation will affect the herd are also conjectural.

Natality

From 1984 through 1988, mean annual natality was 90% for radio-collared females >3 years old (range 82-100%). Adult females in the FCH were at least as fecund as those in the increasing Delta and Western Arctic herds (Table 3). The FCH's apparent decline in natality from 1987 to 1988 (Table 3) may have been capture induced. Carfentanil (Wildnil, Wildlife Lab., Fort Collins, CO) was used to immobilize 13 cows on 29 September 1987 (the manufacturer cautions against use during the "breeding period"). Of females radio-collared before 1987, 13 of 14 calved in 1988; whereas only 7 of 13 females radio-collared on 29 September 1987 calved in 1988. However, these 2 ratios were only marginally different ($0.2 < P < 0.1$, $\chi^2 = 2.45$, df = 1).

The literature suggests that the timing of calving can indicate nutritional status of herds (Bergerud 1975, Espmark 1980, Reimers et al. 1983, Skogland 1985). The peak of calving, defined as when 50% of it is over (Lent 1964, Skoog 1968), was estimated only for 1985 (i.e., 23-24 May) and 1988 (i.e., 22 May).

Mortality

Calf Mortality:

From 1981 through 1988, calf mortality in the 1st 4 months of life averaged 65%; it was the single greatest factor restraining herd growth. The fall calf:adult female ratio averaged 31.6:100 (SD = 3.6, n = 7) during this period (Table 2).

Adult Mortality for Radio-collared Caribou:

Excluding 3 females with unknown fates, the mean annual total mortality rate (Trent and Rongstad 1974) was 7% for 47 radio-collared adult females between 1 October 1983 and 30 September 1988 (Table 4). Hunting of female caribou was prohibited during this study. The mean annual natural mortality rate of females was 6%, or it was 9% if we assume that the 3 caribou whose fates were unknown were mortalities. There was no apparent trend in adult mortality over the 5-year period. At least 6 radio-collared females were killed and eaten by wolves, 1 female was killed by a grizzly bear, one was mistaken for a male and shot, and one died of an unknown cause.

Excluding 3 radio-collared male caribou whose fates were unknown, the mean annual total mortality rate of 18 adult males was 26% between 1 October 1984 and 30 September 1988 (Table 5). The mean annual natural mortality rate of males was 19%. If the 3 males whose fates were unknown actually died, the mean annual total mortality rate would increase to 35%.

Assuming a mean adult sex ratio of 67 females:33 males from 1983 through 1988 (Table 2), the weighted mean annual adult natural mortality (verified deaths only) was 10.6% for the FCH. If all caribou whose fates were unknown died, then the weighted mean annual adult mortality rate would about 18%.

Adult Mortality from Modeling:

One combination of "best fit" natural mortality rates derived from modeling was 3.7% for females and 16% for males (Table 7). The model mortality rate for males was close to the 19% calculated for radio-collared males. The model female

mortality rate was considerably lower than that for radio-collared females (i.e., 3.7% vs. 7%).

Range Use, Habitat Selection, and Food Habits

Valkenburg and Davis (1988) summarized the seasonal distribution of the FCH from 1981 through 1987. The current range of the FCH encompasses about 44,000 km^2. During the winter of 1987-88 the herd ranged from the Salcha River east to the Canadian border. About two-thirds of the radio-collared caribou wintered in the Goodpaster River drainage as far west as Indian Creek. The remaining one-third wintered throughout the Fortymile, Charley, Salcha, Sixtymile, and Ladue River drainages and Birch Creek drainage.

In 1988 calving occurred in the upper Goodpaster, Charley, and Salcha River drainages and in the Joseph Creek drainage. As in past years (Valkenburg and Davis 1986), calving occurred in a variety of habitats (Table 8).

Valkenburg and Davis (1986) summarized data gathered through 1985 on the habitats selected by parturient FCH females. Since 1985, 54% of the parturient radio-collared females selected open (vs. shrubby or wooded) habitats for calving (Table 8). Mean elevation occupied by parturient radio-collared females was approximately 1,100 meters (Table 9). The elevation of calving sites is dependent upon snowmelt. In 1985 (i.e., year with late snowmelt) parturient females generally avoided calving in snow, moving to higher elevations as the snow receded. In other years, cows moved to entirely bare areas for calving. A fecal sample collected in mid-October 1985 near Prindle Volcano on the Dennison Fork Fortymile River contained primarily Cladonia spp. (including Cladina spp.), lichens, and Labrador tea (Ledum groenlandicus) (Table 10).

Predator:Caribou Ratios

We estimated that 38 packs of wolves (totaling 241 individuals) and 24 single wolves occupied the expanded range of the FCH in the fall of 1986 (Table 11, Fig. 1). Calculating a meaningful wolf:caribou ratio was confounded for 1986-87, because few caribou were available to wolves, particularly those on the periphery of the caribou range, and additional packs occurred in areas used primarily by bull caribou.

If 14,000-16,000 caribou were present after the fall hunting season in 1986 (Valkenburg and Davis 1987), the wolf:caribou ratio would have been from 1:53 to 1:60. All packs also had moose available as prey, and eight of the 38 packs had a few Dall sheep (i.e., about 400) available as prey. Moose density within the range of the FCH was estimated to be 100 moose/1,000 km^2 (Boertje et al. 1987; W. Gasaway, pers.

commun.). Based on a range size of 44,000 km^2 for the FCH in 1986-87, there were about 4,400 moose within the range of the herd. Assuming 1 moose = 3 caribou and 1 sheep = 0.5 caribou (Van Ballenberghe 1985), there were about 265 wolves:27,400 to 29,400 caribou equivalents present, or 1 wolf:103 to 111 caribou equivalents.

It is instructive to compare wolf:ungulate ratios in 1986, when the caribou population was increasing at approximately 10% per year, with the probable ratio present 10 years earlier, when the increase in caribou numbers apparently began. The caribou population in the fall of 1976 numbered about 4,000-6,000 (Davis et al. 1978). Moose and sheep numbers had declined dramatically prior to the early 1970's, and by 1976 they numbered about the same as in 1986: 4,400 and 400, respectively (Boertje et al. 1987; Gasaway et al. 1988; W. Gasaway and W. Heimer, pers. commun.). From 1973 to 1976 the wolf population declined dramatically from natural causes and increased vulnerability to trapping (Gasaway et al. 1988); by 1976 it numbered about the same as in 1986.

Assuming the above conditions occurred in 1976, the wolf:prey ratios were 1:23 caribou and 1:72 caribou equivalents. These low prey biomass levels are in the range where wolves are considered likely to control ungulate numbers (Pimlott 1967, Mech 1970, Parker 1972, Bergerud 1983). There are several possible explanations for the growth of the FCH under the unfavorable wolf:prey ratios of the mid- and late 1970's. Possibly, biased estimates of wolves and prey confounded the interpretation; the spacing of wolves and caribou were also of critical importance. For caribou herds that calve in high densities, the juxtaposition of wolves and caribou at calving time may be the single greatest variable influencing the effect of wolves on caribou population dynamics. Miller et al. (1985) documented surplus killing and high vulnerability of calves on a traditional calving ground.

As our understanding of predator-prey systems increases, we are recognizing that simple ratios alone do not explain the response of prey populations to their predators. Perhaps greater emphasis should be placed on spatial, functional, and behavioral aspects of predator-prey relationships.

As Pimlott (1967:273) suggested over 20 years ago:

> The nature of the universal variables of predation, predator and prey density, and the nature of the subsidiary variables are very different in the various environments. The studies that have been conducted or are being conducted suggest that we are likely to find that the interaction of the variables of predation produce such complexities that few generalizations are possible on the influence of predation by wolves on populations of prey.

Caribou Consumption by Wolves

We estimated the number of adult caribou (>3 mo old) consumed by the wolf population within the FCH range from 1 September 1986 through 31 August 1987. Observations and analyses by Burkholder (1959), Skoog (1968), and Kuyt (1972) suggested that each wolf kills the equivalent of about 24 caribou/year. In addition, Kelleyhouse et al. (ADF&G files) estimated that 3 wolf packs just south of the FCH range killed at a rate of 0.71 moose equivalents/wolf/month during the winter of 1986-87. Assuming that 1 moose = 3 caribou, the resulting 25.5 caribou/wolf/year estimate is very similar to the others.

The winter diet assumptions for the 38 wolf packs in the FCH's range were as follows: (1) 8 packs (38 wolves) consumed 75% caribou (513 caribou) (Table 12), (2) 12 packs (87 wolves) consumed 66% caribou (1,034 caribou), (3) 8 packs (56 wolves) consumed 33% caribou (333 caribou), and (4) the remaining 10 packs (60 wolves) consumed 10% caribou (108 caribou). Thus the average wolf would have consumed about 8.2 caribou/year. Assuming a similar diet for the 24 lone wolves, they would have killed about 197 caribou. Therefore, we estimated that all of the wolves within the range of the FCH would have killed 2,185 caribou, providing no wolves had died over winter. However, since we knew that at least 42 wolves had been removed from the population during thewinter, we assumed they consumed only half as many caribou as those surviving throughout the winter. Thus we estimated that wolves consumed 2,001 caribou within the range of the FCH from September through May 1986-87 (i.e., 9 mo). Assuming the summer predation rate of caribou older than calves to be half the winter rate, an additional 227 caribou were consumed. The total number of FCH caribou (>3 mo old) estimated to have been eaten by wolves in 1986-87 was 2,228.

The estimated 2,228 caribou killed by wolves equals 16% of the population (14,000 caribou $\geq$3 mo); this annual mortality rate is similar to the mortality of radio-collared adults (i.e., 13%. From 1985 through 1987 the mean calf:female ratio in fall was 34:100. Based on an assumed mean recruitment of 34 calves:100 females and a male:female ratio of 42:100, the maximum rate of increase for the population (assuming no adult mortality) was 24.3% per year. With 16% adult mortality estimated for wolf predation, the observed rate of population growth should have been about 8.3%, which compares with an estimated 10% rate of annual growth from 1984 to 1986 (Table 1).

Caribou Consumption by Grizzly Bears

Boertje et al. (1988) estimated that female grizzlies without cubs killed about 1 caribou (>3 mo old) per year and males and females with cubs killed none. There is little basis for

extrapolating from Boertje et al.'s study area to the range of the FCH, because only 3 caribou were killed during their study. Furthermore, their study area did not have a high caribou density in the summer. To allow for grizzly bear predation on adult caribou, we assumed that each adult bear in the FCH's range killed 1 caribou per year. The grizzly bear density for Boertje et al.'s (1988) study area was 1 adult per 100 km^2. Assuming this was the same density as that for the summer range of the FCH (i.e., 18,000 km^2), then about 180 adult caribou would have been killed by grizzly bears. As with wolves, predation in the calving areas may be the most important factor influencing their effect on caribou population dynamics.

IMPLICATIONS

Population size of the FCH, like other herds throughout North America, has fluctuated dramatically. These fluctuations display no predictable period or amplitude and therefore should not be called "cycles", which have a very specific meaning in the study of population dynamics. Causes and mechanisms of the long-term dynamics of caribou populations in general and the FCH in particular are poorly understood and speculative. It is clear, however, that mortality from hunting and wolf predation exceeded recruitment during the late 1960's and early 1970's. Data are inadequate to assess the rate of other potential causes, such as adverse weather and lowered productivity and/or survival from nutri-tional limitation.

Clearly, predation was the primary factor limiting or greatly retarding population growth in several Alaskan caribou herds, following the declines in the early 1970's (Davis et al. 1983, Singer 1985). However, contrary to moose (Crete and Messier 1984, Van Ballenberghe 1987), caribou may not become trapped in a "predator pit", even when they are at historic low levels (i.e., when wolf:caribou ratios are proportional to "predator pit" wolf:moose ratios) (Singer 1985).

Although simple wolf:moose (or wolf:moose equivalents) ratios appear to be reasonable predictors of the influence predation has on moose population growth (Gasaway et al. 1983), wolf:caribou (or wolf:caribou equivalents) ratios appear to be poor predictors of the caribou population trend. This contrast may imply that functional, spatial, and behavioral relationships may be more important than numerical relationships in determining the effects of wolves on caribou.

The speed at which caribou populations recover from declines depends on how low the caribou population falls and the degree and timing of predation during the latter stages of the decline and recovery. In times of population decline, wildlife managers can dampen caribou fluctuations by closing hunting or severely restricting or eliminating hunting of

females. Additionally, management programs can reduce wolf numbers more rapidly than the reductions occurring because of a lowered prey base.

The FCH has increased continuously for over a decade; it is currently increasing at ≥10% per year. Unless major adverse environmental changes occur, the current numerical and functional relationships between wolves and the FCH should not severely limit recovery of the FCH. However, the relationships between wolves and caribou are no less dynamic than those when levels of caribou were historically high; so change should be anticipated. Assuming continued herd growth, ADF&G should continue to monitor herd size, productivity, and composition; it should also intensify investigating and monitoring of population welfare as reflected by indicators of body condition.

ACKNOWLEDGMENTS

Funding for this study within ADF&G (primarily from P-R Federal Aid) was inadequate to accomplish the goals and objectives. Considerable funding was supplied by the National Park Service (NPS); special thanks are due to NPS and NPS personnel as follows: Layne Adams and Al Lovaas (State Office) and Don Chase and Steve Ulvi (Yukon-Charley Rivers National Preserve).

We are grateful to Rod Boertje and Steve Ulvi for helping with field work and to Chuck Gewin for his voluntary (i.e., non-paid) assistance with field work and creation of a computerized data storage file. We feel particularly fortunate to have had Ron Warbelow's assistance as a pilot for both Super Cub and helicopter flying. He was unusually competent and exhibited extraordinary interest in the work.

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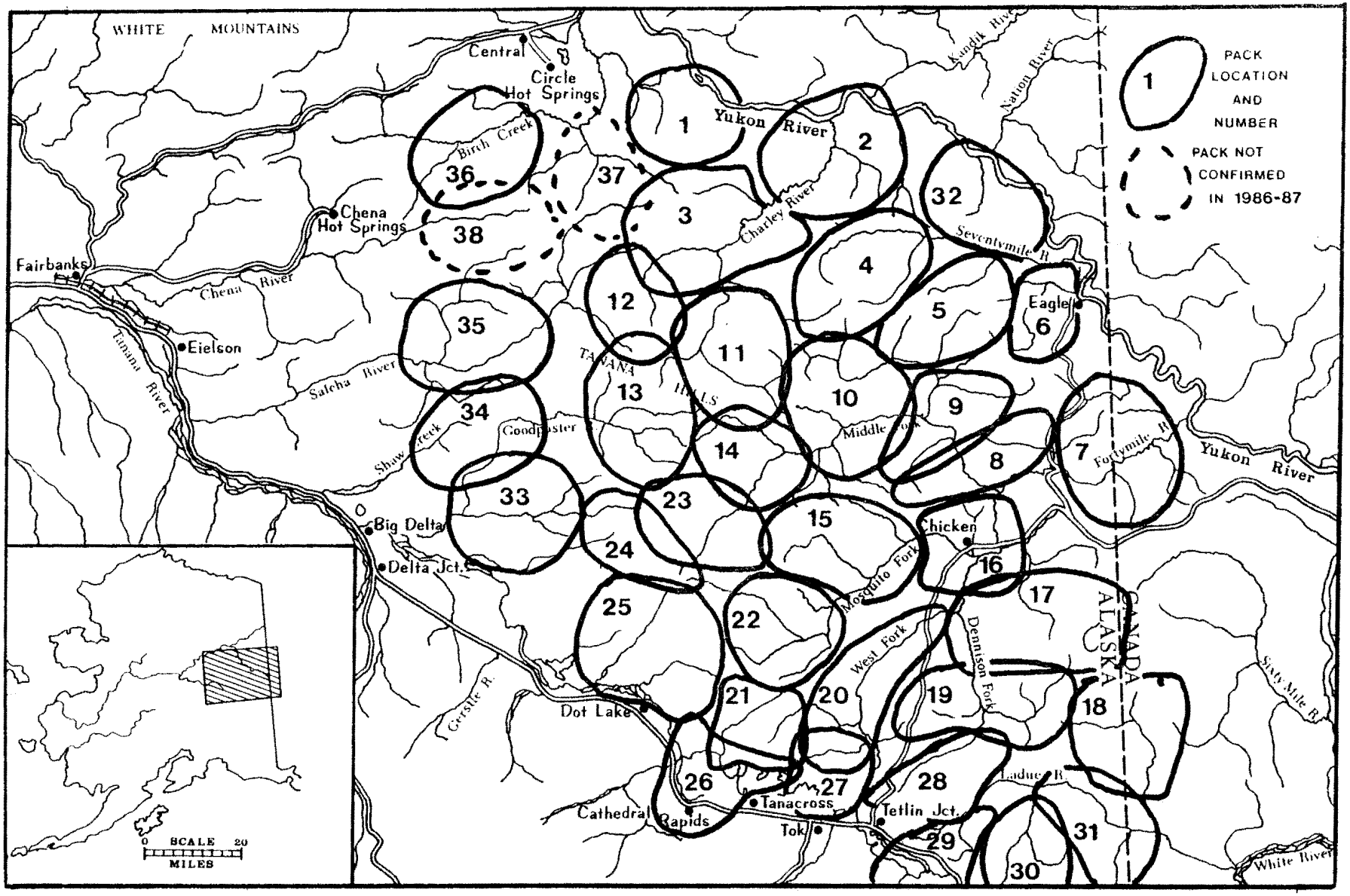

Fig. 1. Location and pack number of wolf packs within the range of the Fortymile Caribou Herd. Note: pack number corresponds to numbers in Table 11.

Table 1. Population estimates for the Fortymile Caribou Herd, 1973-88.

Date of census	Summer population (including calves)	Annual finite rate of growth since previous census (λ)	Remarks
6/6/73	6,624[a]	n.a.	Extrapolated from "cow base" and fall composition counts
6/10/81	7,914[b]	1.023	Photo and visual counts of postcalving aggregations
6/18/83	12,350	1.250	Photo and visual counts of postcalving aggregations
6/18/84	13,073-13,731	1.100	Photo and visual counts of postcalving aggregations
7/2/86	15,303	1.069	Photo and visual counts of postcalving aggregations located largely through radio tracking
6/22/88	19,975	1.143	

[a] The fall (September) population estimate of 5,312 has been widely used in previous reports. For comparison here, we converted it to a "summer" population estimate. See remarks.

[b] Due to problems with the census, this figure is probably a gross underestimate. A revised population estimate of 10,093 was calculated as described in the text.

Table 2. Sex and age composition of the Fortymile Caribou Herd, 1953-88.

Date	Bulls: 100 cows	Yrlgs: 100 cows	Calves: 100 cows	Yrlg % in herd	No. yrlg	Calf % in herd	No. calves	Cow % in herd	No. cows	Small bull % of bulls	Small bulls	Med. bull % of bulls	Med. bulls	Large bull % of bulls	Large bulls	Total bulls % in herd	Total bulls	Sample size
11/53	0	0	0	0	0	29	66	0	0	0	0	0	0	0	0	0	0	228
10/54	78	0	64	0	0	26	50	41	78	0	0	0	0	0	0	32	61	189
10/55	0	0	0	0	0	16	268	0	0	0	0	0	0	0	0	0	0	1,659
10/56	0	0	0	0	0	5	34	0	0	0	0	0	0	0	0	0	0	737
10/57	0	0	0	0	0	5	26	0	0	0	0	0	0	0	0	0	0	576
8/58	0	0	0	0	0	31	40	0	0	0	0	0	0	0	0	0	0	127
10/59	0	0	0	0	0	36	45	0	0	0	0	0	0	0	0	0	0	124
10/61	75	30	45	12	133	18	200	40	444	0	0	0	0	0	0	30	333	1,110
10-11/62	0	0	0	0	0	11	85	0	0	0	0	0	0	0	0	0	0	743
10/72	30	16	21	10	66	12	84	60	400	0	0	0	0	0	0	18	122	672
6/6/73	0	0	57	0	0	36	638	64	1,120	0	0	0	0	0	0	0	0	1,758
6/4/74	0	1	50	0	6	33	502	67	1,011	0	0	0	0	0	0	0	0	1,519
6/5/74	25	0	25	0	0	17	1	67	4	0	0	0	0	0	0	17	1	6
6/6/74	0	0	55	0	0	36	183	64	330	0	0	0	0	0	0	0	0	513
6/4-6/74	0	0	53	0	6	34	686	65	1,304	0	0	0	0	0	0	0	1	1,997
6/28/74	18	3	24	2	37	17	276	69	1,148	0	0	0	0	0	0	13	211	1,672
9/20/74	32	6	20	4	35	12	108	63	553	0	0	0	0	0	0	20	176	872
9/21/74	35	9	21	5	46	13	110	61	525	0	0	0	0	0	0	21	185	866
9/74	33	8	20	5	81	13	218	62	1,078	0	0	0	0	0	0	21	361	1,738
9/23/76	42	11	34	6	54	18	164	53	476	0	0	0	0	0	0	23	202	896
6/13/77	0	0	39	0	0	28	631	72	1,621	0	0	0	0	0	0	0	0	2,252
9/27/77	53	14	45	7	75	21	245	47	543	0	0	0	0	0	0	25	287	1,150
6/4/78	1	0	9	0	0	8	42	92	485	0	0	0	0	0	0	1	3	530
6/14/78	0	0	35	0	0	26	123	74	356	0	0	0	0	0	0	0	0	479
10/19/78	39	14	26	8	59	15	109	56	417	0	0	0	0	0	0	22	163	748
6/11/80	25	10	41	6	132	23	559	57	1,371	0	0	0	0	0	0	14	338	2,400

Table 2. Continued.

Date	Bulls: 100 cows	Yrlgs: 100 cows	Calves: 100 cows	Yrlg % in herd	No. yrlg	Calf % in herd	No. calves	Cow % in herd	No. cows	Small bull % of bulls	Small bulls	Med. bull % of bulls	Med. bulls	Large bull % of bulls	Large bulls	Total bulls % in herd	Total bulls	Sample size
10/15/80	109	0	61	0	0	23	222	37	364	24	96	51	200	25	100	40	396	982
6/10/81	22	0	31	0	0	20	600	65	1,928	0	0	0	0	0	0	14	427	2,955
9/26/81	52	0	31	0	0	17	171	54	547	0	0	0	0	0	0	28	286	1,004
9/29/82	54	0	27	0	0	15	241	55	901	38	185	30	143	32	155	30	483	1,625
4/19/83	35	0	29	0	0	18	68	61	236	0	0	0	0	0	0	21	83	387
6/8/83	6	7	35	5	142	24	743	67	2,097	0	0	0	0	0	0	4	136	3,118
6/19/83	22	9	38	6	70	22	279	59	741	0	0	0	0	0	0	13	162	1,252
9/20/83	44	0	30	0	0	17	166	58	560	46	113	0	0	54	134	25	247	973
10/7/83	61	0	36	0	0	18	180	51	498	27	81	34	104	39	117	31	302	980
3/22/84	18	0	27	0	0	19	206	69	754	0	0	0	0	0	0	12	132	1,092
5/31/84	1	2	73	1	29	41	1,072	57	1,478	0	0	0	0	0	0	0	10	2,589
6/20/84	42	0	45	0	0	24	954	53	2,098	0	0	0	0	0	0	23	888	3,940
4/27/85	16	0	32	0	0	22	190	68	593	0	0	0	0	0	0	11	93	876
5/24/85	8	70	39	32	135	18	75	46	193	0	0	0	0	0	0	4	15	418
6/19/85	18	0	48	0	0	29	1,103	60	2,285	0	0	0	0	0	0	11	415	3,803
10/16/85	50	0	36	0	0	19	208	54	574	39	111	23	65	38	109	27	285	1,067
4/29/86	14	0	40	0	0	26	153	65	380	0	0	0	0	0	0	9	53	586
10/13/86	36	0	28	0	0	17	235	61	842	35	106	24	73	41	125	22	304	1,381
6/26/87	46	0	47	0	0	25	883	52	1,860	0	0	0	0	0	0	24	853	3,596
9/28/87	40	0	37	0	0	21	475	57	1,274	13	67	43	215	44	222	22	504	2,253
6/30/88	54	0	36	0	0	19	339	53	946	0	0	0	0	0	0	29	514	1,799
10/2-3/88	38	0	30	0	0	18	229	59	770	29	86	41	121	30	89	23	296	1,295

Table 3. Natality rates of Delta, Western Arctic, and Fortymile Caribou Herds based on calf:cow ratios and proportions among radio-collared females ≥3 years old, 1981-87.

Herd and year	Calf counts (late May or early June)			Radio-collared caribou ≥36 mos.		
	No. calves counted	No. cows counted	Calves: 100 cows	No. pregnant	Total	Natality rate (%)
Delta 1981	--	--	--	10	13	77
Delta 1982	108	151	72	7	10	70
Delta 1983	1,629	2,052	79	17	22	77
Delta 1984	395	482[a]	82	28	31	90
Delta 1985	--	--	--	38	41	93
Delta 1986	--	--	--	33[b]	40	83
Delta 1987	649	1,080	60	25	28	89
Delta 1988	--	--	--	28	32	88
Western Arctic 1981	885	1,079	82	31	37	84
Western Arctic 1982	1,380	1,764	78	24	29	83
Fortymile 1984	1,072	1,478	73	20	23	87
Fortymile 1985	--	--	--	19	19	100
Fortymile 1986	--	--	--	20[c]	21	95
Fortymile 1987	--	--	--	18	19	95
Fortymile 1988	--	--	--	27	33	82[d]

[a] Includes some yearlings.

[b] Twenty-six had distended udders, 7 had hard antlers (indicating pregnancy but udder was not seen), 5 had no distended udder, and 2 were antlerless (udder was not seen, but neither one was a naturally polled animal).

[c] Sixteen had distended udders, 3 had hard antlers during calving, and 1 was seen in August and September with a calf following her.

[d] Thirteen of these were immobilized during the rut in 1987, and 5 of the 13 failed to produce calves in 1988.

Table 4. Mortality of radio-collared adult females in the Fortymile Caribou Herd, 1983-88.

Year	No. of collared caribou present	Collar months of operation	Killed by wolf	Killed by bear	Shot	Unknown	Total	% annual mortality
10/1/83-9/30/84	20	244	--	--	--	1	1	5
10/1/84-9/30/85	20	245	2	--	--	--	2	9
10/1/85-9/30/86	24	264	2	1	--	--	3[a]	13
10/1/86-9/30/87	21	229	--	--	--	--	0[b]	0
10/1/87-9/30/88	39	433	2	--	1	1	4	11
Total		1,529	6	1	1	1	9	7

[a] One additional caribou either died, shed its collar, or had a radio malfunction.

[b] Two caribou either died, shed their collars, or had radio malfunctions.

Table 5. Mortality of radio-collared adult males in the Fortymile Caribou Herd, 1984-88.

Year	No. of collared caribou present	Collar months of operation	Killed by wolf	Killed by bear	Shot	Unknown	Total	% annual mortality
10/1/84-9/30/85	9	62	1	--	1	--	2[a]	33
10/1/85-9/30/86	8	82	--	--	--	1	1	14
10/1/86-9/30/87	10	81	--	--	1	1	2[b]	26
10/1/87-9/30/88	8	57	2	--	--	--	2[a,c]	35
Total/mean		285	3	--	2	2	7	26

[a] Two additional caribou shed their collars.

[b] Three additional caribou either died, shed their collars, or had radio malfunctions.

[c] One caribou died, possibly from drug-related causes, within a month of being immobilized.

Table 6. Hunting seasons and harvest, Fortymile Caribou Herd, 1976-86.

Year	Season and limit	Males killed	Females killed	Reported total	Estimated total
1976	Aug 10-Sep 20 (1 caribou)	26	5	33	
1977	Sep 1-Sep 15 (1 caribou)	12	5	60	
1978	Sep 1-Sep 15 (1 caribou)	10	6	16	30
1979	Sep 1-Sep 15 (1 bull)	9	0	9	30
1980	Sep 1-Sep 15 (1 bull)	10	0	10	50
1981	Aug 10-Sep 20 Dec 1-Feb 28[a] (1 bull)	37 8	0 0	58	100
1982	Aug 10-Sep 20 Dec 1-Feb 28[a] (2 bulls)	65 45	0 0	115	200
1983	Aug 10-Sep 20 Nov 20-Feb 28 (2 bulls)	101 99	0 0	219	269-319
1984	Aug 10-Sep 20 Nov 20-Feb 28[b,c] (2 bulls)	245 0	0 0	245	450d
1985	Aug 10-Sep 20 Nov 20-Feb 28[b,e,f] (1 bull)	226 34	0 0	261	400d
1986	Aug 10-Sep 30[g] Dec 1-Feb 28[a,e] (1 bull)	221 2	0 0	223	370d

Table 6. Continued.

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[a] Only antlerless bulls could be taken from December 1 through February 28.

[b] Only antlerless bulls could be taken from December 10 through February 28.

[c] Through field contacts, Area Biologist D. Kelleyhouse determined that only 63% of harvested caribou were being reported, and 40-60 females were illegally shot as the herd crossed the highway in late August and early September.

[d] Total extrapolated with correction factor derived in 1984 (see footnote [c]).

[e] Subsistence hunters (i.e., local residents) only.

[f] Subsistence hunters could take an additional bull in the late season.

[g] Only subsistence hunters could hunt from September 21 through September 30.

Table 7. Modeled population dynamics for the Fortymile Caribou Herd, 1983-91.

Year	Cows	Calves	Bulls	Total population	Predicted Survival rate of cows	Predicted Survival rate of bulls	Harvest	Recruitment (calves: 100 cows in fall)	Bull: cow ratio[a]	Annual population growth (λ)
1983	6,469	2,156	3,355	11,980[b]	0.963	0.84	300[c]	0.296	51.9	
1984	7,268	2,398	3,274	12,940	0.963	0.84	450	0.330	45.0	1.080
1985	8,154	2,952	3,357	14,463	0.963	0.84	400	0.362	41.2	1.118
1986	9,273	2,587	3,690	15,550	0.963	0.84	370	0.279	39.8	1.075
1987	10,176	3,796	3,886	17,857	0.963	0.84	300	0.373	38.2	1.148
1988	11,627	3,453	4,358	19,438[b]	0.963	0.84	500	0.297	37.5	1.089
1989	12,709	4,080	4,611	21,401	0.963	0.84	650[d]	0.321[e]	36.3	1.101
1990	14,054	4,511	5,087	23,652	0.963	0.84	650[d]	0.321	36.2	1.105
1991	15,556	4,993	5,668	26,217	0.963	0.84	650[d]	0.321	36.4	1.108

[a] Smoothed data from Table 2 (recalcualted by model).

[b] Data from the 1983 and 1988 censuses (Table 1).

[c] Bulls only.

[d] Harvest assumed to be 500 bulls and 150 cows for these years.

[e] After 1988, average of previous 5 year's data was continued forward.

Table 8. Habitat selected by parturient radio-collared Fortymile Herd Caribou during the peak of calving, 1986-88.

	Open habitats				Shrub habitats				Forested habitats		
Year	Wet sedge	Dryas/ felfield	Eriophorum tussock	Muskeg	Shrub/ Eriophorum	Birch/ willow shrub	Riparian willow	Sparse spruce/ shrub	Open spruce forest	Closed spruce forest	Total
1986		4	2	1	2	1		2		5	17
1987		3	1			5		5	1	1	16
1988		1	9	5	6	4	1	1	4		30

Table 9. Mean elevation of habitat selected by parturient radio-collared Fortymile Herd Caribou during the peak of calving, 1985-88.

Year	Mean elevation of habitat selected Meters (SD, range)	n
1985	1,064 (209, 700-1,200)	12
1986	1,082 (143, 850-1,100)	18
1987	1,088 (204, 750-1,200)	16
1988	1,209 (257, 700-1,150	30
Mean 1985-88	1,111	

Table 10. Discerned plant fragments found in caribou fecal samples collected near Prindle Volcano, 15 October 1985.

Genus identified	Mean % occurrence[a]	SD
Unknown grass		
Bromus	0.54	1.20
Carex		
Eriophorum		
Luzula		
Poa		
Festuca		
Astragalus-Oxytropis	1.64	1.52
Cetraria (type)	1.45	2.09
Cladonia (type)	68.94	13.67
Equisetum		
Ledum	15.36	13.00
Loiseleuria	0.54	1.20
Lupinus		
Moss	8.54	4.18
Peltigera	1.05	1.44
Picea		
Pinus	0.49	1.10
Salix	1.45	2.09
Saxifraga		
Unknown forb		

[a] Based upon 5 slides of 20 fields (Sparks and Malechek 1968).

Table 11. Estimated size, harvest, and suspected diet of wolf packs within the range of the Fortymile Caribou Herd, 1986-87. (Data in part from Gasaway et al. 1988.)

Pack No.[a]	Pack name	Size in fall 1986[b]	Harvest in 1986-87[c]	Size and composition spring 1987[d]	Estimated diet	Radiocesium concentration (pCi/kg) in wolf muscle tissue $\bar{x}$, SD (n)
1	Webber	4	0	4	Mostly moose	--
2	Bonanza	5	1 Black	4	Mostly moose	--
3	Twin Mountain	9	0	8 All black	Caribou, moose, sheep	--
4	Seventymile	8	0	8	Caribou, moose, sheep	--
5	Copper/Slate	3	0	3	Mostly caribou, sheep	--
6	Mission	4	0	4	Moose, caribou, sheep	--
7	Steele	5	0	5	Bull caribou, moose	--
8	Alder	2	0	2	Mostly caribou	--
9	Portage	13	3 All black	10 Mostly black	Caribou, moose	1568,13 (3)
10	Slate	13	1 Black	12 Mostly black	Mostly caribou	8131,n.a.(1)
11	Copper Mountain	7	0	7	Mostly caribou	--
12	Paldo/Crescent	3	0	3	Caribou, moose, sheep	--
13	Eisenmenger	7	1 Gray	6	Caribou, moose, sheep	--
14	Joseph	5	0	5 All black	Caribou, sheep	--
15	Gold Creek	9	3 All black	6 All black	Caribou, moose	1451,264(3)
16	Chicken	7	4 3 black, 1 gray	3 2 gray/1 black	Caribou, moose	4803,198(4)
17	Liberty	6	0	6 All gray	Caribou, moose	--
18	McCord	9	0	9	Bull caribou, moose	--
19	Fairplay	2	2 Both gray	0	Mostly caribou	813,356(2)
20	West Fork	2	0	2	Mostly caribou	--
21	Mansfield	12	4 3 gray, 1 black	8 Mostly gray	Mostly moose	2053,1523(3)
22	Mitchels Ranch	8	3 All gray	5 All gray	Moose, caribou	4624,730(2)
23	Middle Fork	5	1 Gray	4 Mostly gray	Caribou, moose, sheep	3077,n.a.(1)
24	Divide	2	0	2	Caribou, moose	--
25	Billy	10	7 All gray	3 All gray	Mostly moose	513,47(8)
26	Cathedral	2	0	1 1 black/1 gray	Mostly moose	--

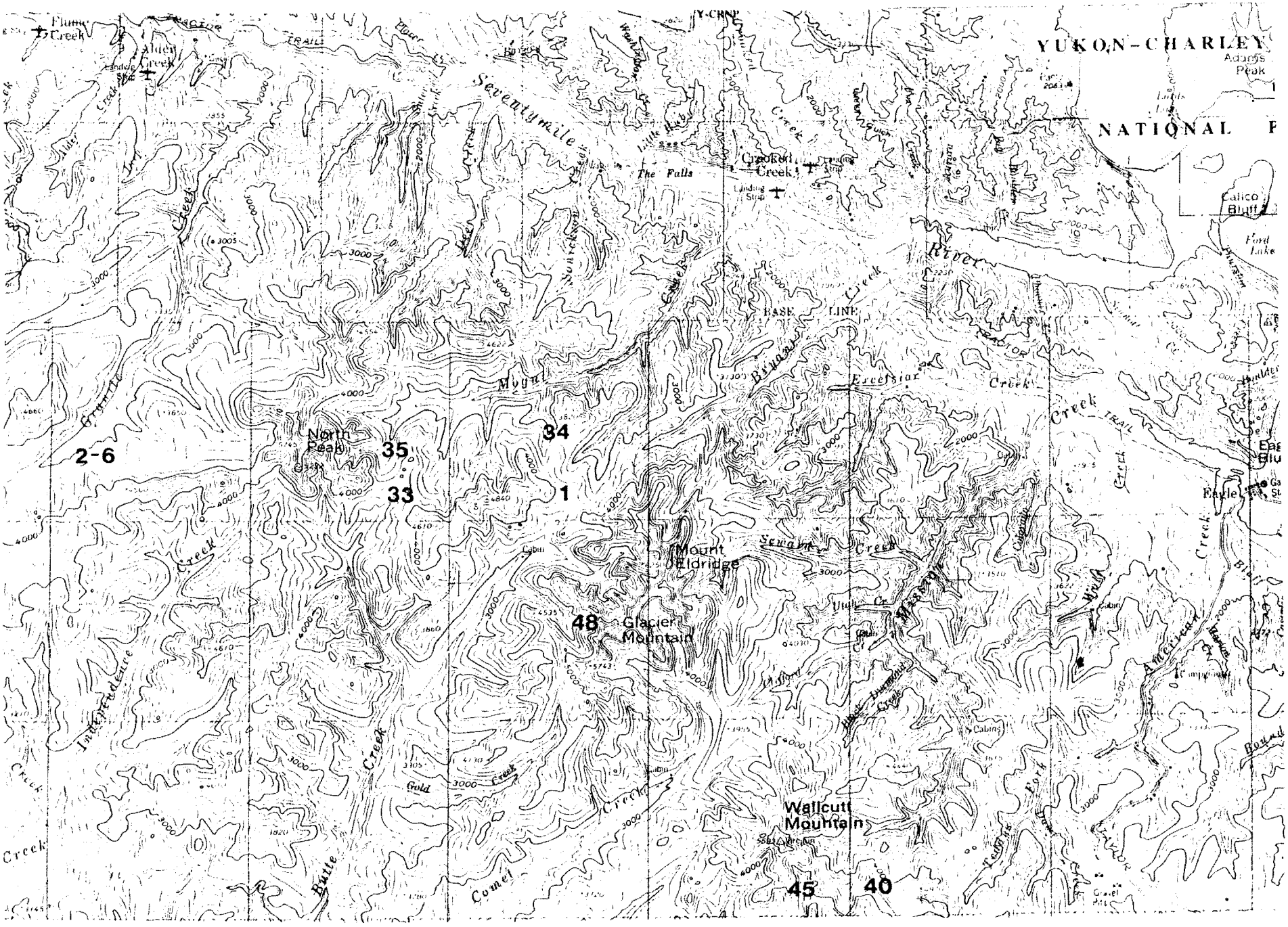
Table 11. Continued.

Pack No.[a]	Pack name	Size in fall 1986[b]	Harvest in 1986-87[c]	Size and composition spring 1987[d]	Estimated diet	Radiocesium concentration (pCi/kg) in wolf muscle tissue $\bar{x}$, SD (n)
27	Mosquito Flats	5	3 All black	2 Mostly black	Moose, caribou	5229,2762(3)
28	Dennison	3	0	3 Mostly gray	Mostly bull caribou	--
29	Big John	6	0	6	Moose, caribou	--
30	Black	7	2 Both black	5 All black	Moose, caribou	--
31	Ladue	7	1 Black	6	Mostly bull caribou	514,n.a.(1)
32	Michigan	5	0	5 All gray	Mostly moose	--
33	S Fk Goodpaster	10	0	10	Moose, caribou	--
34	Shaw	6	3 All gray	3 Mostly gray	Mostly moose	--
35	Caribou	9	3 All gray	6 Mostly gray	Mostly moose	--
36	Upper Birch	7	0	7 All gray	Mostly moose	--
37	South Birch	8	0	8	Moose, caribou	--
38	E Fk Chena	7	0	7	Mostly moose	--
Totals		241	42	199		
Plus 10% for lone wolves		24		20		
Grand total		265		219		

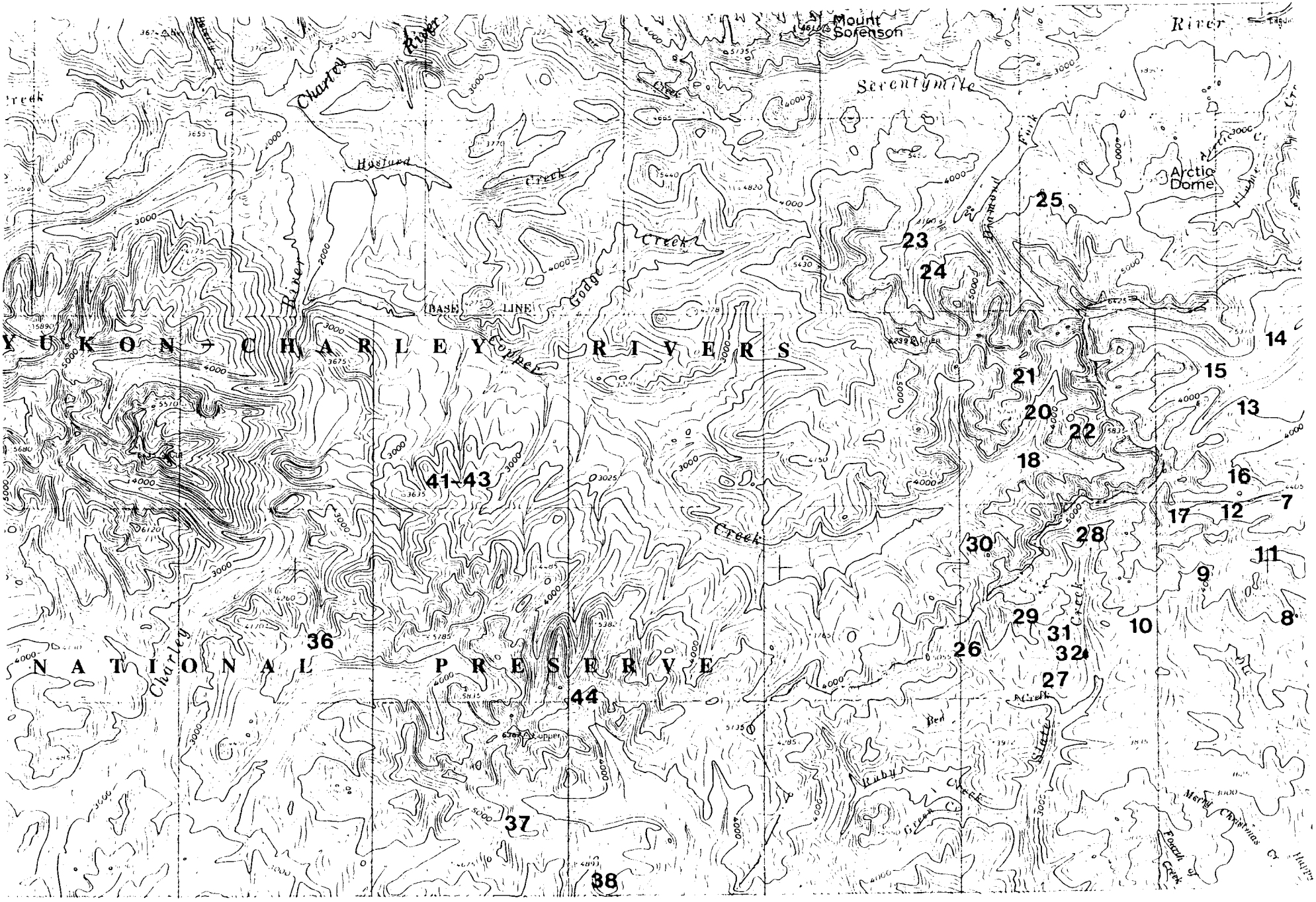
[a] Corresponds to numbers in Fig. 1.
[b] Size at start of trapping season. Estimated from results of spring wolf survey and harvest.
[c] Includes only reported harvest and wolves collected by ADF&G.
[d] Size after trapping (wolf surveys were conducted after the trapping season).

Appendix A. Distribution and size of groups of caribou found during the 22 June 1988 census.

Group no.	Estimated size	Caribou counted	No. of radiocollars in group	Remarks
1	225	424	0	Mostly bulls, no photos
2	NA	78	0	No photos
4	NA	33	0	
5	150	173	0	
6	30	57	0	
8	2,500	3,909	12	
9	300	307	0	
10	1,000	1,156	0	
11	NA	106	2	
12	30	90	0	
13	500	315	4	
14	300	499	1	
15	150	63	0	
16	450	631	0	
17	500	1,125	3	
18	200	348	0	
20	1,000	1,315	1	
21	300	599	1	
22	150	207	0	
23	300	651	0	
24	NA	174	0	
25	450	1,042	4	
26	200	254	0	
27	NA	1,187	0	
28	300	349	0	
29	300	555	0	
30	250	382	0	
31	100	119	0	
32	50	58	0	
33	NA	56	0	No photos
34	150	70	0	
35	350	470	0	
3, 7, 19, 36, 37, 38	NA	30	0	No photos, bulls
40	650	910	5	D. Kelleyhouse's group 11
41	NA	422	3	D. Kelleyhouse's group 5
42	NA	238	0	J. Davis' group 23A
43	NA	148	0	J. Davis' group 23B
44	NA	633	1	J. Davis' group 24
45	NA	529	0	D. Kelleyhouse visuals
46-47	NA	69	0	Beaver aircraft visuals
48	NA	194	0	K. Ogden visuals
Totals		19,975	37	



Appendix A. Continued. Distribution of groups (by group numbers) of caribou censused on 22 June 1988.



Appendix A. Continued.

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