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Demography of the Delta Caribou Herd Under Varying Rates of Natural Mortality and Human Harvest and Assessment of Field Techniques for Acquiring Demographic Data

James L. Davis
Patrick Valkenburg
Mark E. McNay
Robin M. Beasley
V. Leigh Tutterrow

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SUMMARY

This report summarizes a 5-year (1986-90) demographic study of the Delta Caribou (*Rangifer tarandus granti*) Herd (DCH) and the Yanert Caribou Herd (YCH). It was preceded by another 5-year study focusing on the population dynamics of the DCH. The many administrative reports and publications emanating from this study over the years are listed in Appendix A.

The DCH grew continuously during the period in which the 2 studies were conducted: approximately 3,800 in 1979 to over 10,000 in 1989. The rate of growth progressively ranged from nearly 20% to less than 5% annually. The bull:cow ratios declined continuously in response to the selective harvest of males. The cow:calf ratios in the fall declined concurrently to increases in wolf (*Canis lupus*) abundance and population densities. Based on fall calf:cow ratios, yearling recruitment estimates showed a declining trend throughout the study, but they remained high enough to allow continued population growth, despite considerable mortalities from hunting and predation. To test the validity of recruitment estimates based on April calf:cow ratios, we calculated confidence intervals around the ratio estimates and concluded they were imprecise.

Annual natality has remained relatively high ($\bar{X} = 84 \pm 4\%$). Natality estimates from as few as 22 radio-collared cows were similar to estimates from samples of the herd, ranging from 482 to 2,052.

We found no apparent pattern to indicate "pregnancy resting" at 36 months of age for individuals that first reproduced at 24 months of age. We detected cohort-specific differences in pregnancy probabilities for 24-month-old caribou, but not for 36-month-old caribou. We also detected considerable variation in parturition frequencies among individuals. We concluded that although weight may reasonably predict pregnancy in some populations, one or more additional variables must be considered to create a universal predictor of pregnancy probability in all Rangifer populations.

Hunting seasons varied tremendously, ranging from a closed season, to limited bulls-only hunting by permit, to open general seasons for either sex. Reported harvests were as high as 694; however, there is good evidence that reported harvests in recent years may constitute only 56-57% of the total harvest. In addition, a wounding rate of 10-20% is not included in the harvest estimates.

Caribou:predator ratios changed during the study from about 1 wolf:101 caribou and 1 grizzly bear (Ursus arctos):31 caribou in 1979 to about 1 wolf:50 caribou and 1 grizzly bear:61 caribou in 1989. Throughout the history of the DCH, wolf abundance has correlated negatively with the caribou recruitment rate and positively with the natural mortality rate. Determining if this relationship is one of cause and effect is confounded because of unknown density-dependent relationships within the caribou population.

Concurrent to population growth of the DCH, total range use has expanded. Winter distribution has expanded to the west and north well into the Tanana Flats. Profound changes in calving distribution and social organization were documented. During the study, the DCH expanded into the range of the previously discrete YCH. The range expansion included a shift in calving from the traditional DCH calving area to the YCH's traditional calving area; in 1990 the DCH even expanded its calving distribution into the range of the Nelchina Caribou Herd (NCH). No dispersal was documented in the sense of mass emigration or immigration; however, individuals dispersed from the YCH to the DCH and NCH.

Fleischman (1990) concluded that mean lichen abundance in the DCH range was relatively low at 10-85 g/m^2, but that even on relatively heavily used range caribou ate only 7% of lichen standing crop annually.

Key Words: caribou, census, Delta herd, demography, dispersal, grizzly bear, mortality, natality, population dynamics, Rangifer, recruitment, wolf, Yanert herd.

CONTENTS

BACKGROUND

Some objectives of this study were more intensively addressed than others, and two were not addressed at all because the study proposal called for more personnel time and operating funds than were subsequently allocated to the project. In addition, the due date for this final report was made 1 year earlier than scheduled because of early retirement of J. Davis, the principal investigator.

This 5-year study was immediately preceded by another 5-year study of the demography of the Delta Caribou (*Rangifer tarandus granti*) Herd (DCH) (Davis and Valkenburg 1985*a*). Hence, we have synthesized and discussed all accrued data for many of the objectives; for other objectives, the discussion has been limited to the 5 most recent years of study.

When this study was initiated, the Alaska Department of Fish and Game's (ADF&G) goal for some caribou herds was to stabilize them at specific levels. For other herds, the goal was to ensure that they did not decline below set minimum populations. However, caribou herds in Alaska have rarely remained stable for more than a few years, and it has been particularly rare for a heavily harvested herd to remain stable. If the above goals were to be accomplished and the management programs successful, understanding the mechanisms involved in the population dynamics of caribou was essential. Although the factors determining population dynamics for all wildlife species are the same (i.e., births, deaths, emigration, and immigration), the specific variables affecting these factors can differ greatly.

Prior to this study, a quantitative assessment of the demography of an Alaska caribou herd had never been conducted over a period when rates of natural mortality and human harvests varied greatly. During a past workshop Klein and White (1978) identified the need for an intensive demographic study of one or more caribou herds in Alaska.

Proximity of the DCH to Fairbanks, considerable background information on the herd, and options for intensively managing (i.e., manipulating) the herd made it ideal for a long-term demographic study. Hypotheses regarding many aspects of general caribou ecology could be more feasibly tested on the DCH than on larger herds; e.g., the Western Arctic and Porcupine herds. Intensified study of the DCH (Davis and Preston 1980) revealed that herd demography had been misunderstood from 1975 through 1979. The DCH will continue to be intensively managed, so a thorough understanding of its demography is essential for sound management.

Davis and Neiland (1975) reviewed and compiled available data for the DCH in 1974. Additional background information has been presented by Davis and Preston (1980), Davis and Valkenburg (1981, 1983, 1985a), and Davis et al. (1982, 1983, 1987, 1988). During the past 16 years, the DCH has fluctuated dramatically, declining from 5,000 in 1969 to about 1,500-2,000 in 1975 and then increasing to 7,000 in 1982. Since 1982 herd growth has been slowed by hunting. During the past 16 years, high and low levels of both natural mortality and harvest have occurred, and much has been learned about population dynamics (Davis et al. 1983). More importantly, much has been learned about the interrelationships among large predators, prey, and humans in Subunit 20A (Gasaway et al. 1983).

Growing pressures on caribou and their habitat require additional understanding of caribou ecology. This understanding can be enhanced through continued study of the DCH's demography and by simultaneous study of the herd's behavior, nutrition, energetics, and interaction with its environment, including predators.

As populations increase, caribou travel more widely and may increase their use of adjacent and/or marginal ranges (Skoog 1968:202, 655; Bergerud 1974a). Use of marginal ranges could result in lower natality and increased mortality because of greater energy expenditures, poorer quality forage, and greater vulnerability to predation.

We possess only rudimentary understanding of the relationship between movements and distribution and the demography of caribou herds; however, because we know there is a relationship, collation and analysis of existing movement and distribution data are certainly warranted. Because study of the DCH was intensified in 1979, considerable data on herd movements and distribution have been collected, but it is essential to continue documenting the changes. If the DCH continues to increase, any changes in movements and distribution will be better interpreted if earlier patterns have been well documented.

Opposing views are emerging among caribou biologists regarding the basic social organization of caribou, including herd identity, definition, and fidelity to calving areas and seasonal ranges (Bergerud et al. 1984, Carruthers 1985, Martell and Russell 1985). The known histories of radio-collared caribou in the DCH and the Yanert Caribou Herd (YCH) could prove invaluable in contributing empirical evidence about the social organization of caribou (Davis et al. 1986).

Aerial-photography techniques are being increasingly used for estimating population size of caribou herds; however, the assumption that all of the caribou (including calves) photographed can be counted from photos has not been validated. Many other caribou management-research techniques that are presently employed require validation. For example, the reliability of conducting herd composition counts in April as an indication of "yearling recruitment" has not been critically examined. Also, using a small cohort of radio-collared cows to estimate herd natality has not been critically evaluated.

Availability of radio-collared caribou with known histories is requisite for several objectives of this study. Fortunately, caribou collared during a previous study (Davis and Valkenburg 1985a) still had functioning radio collars and were available for study when this project began.

GOAL

To estimate population parameters (i.e., birth, death, and dispersal rates) of the DCH and YCH and to evaluate field procedures for estimating those parameters.

OBJECTIVES

The objectives that follow are labeled by a letter (a. through r.). The letter identifying each objective is carried throughout the other sections of the report; e.g., so the various headings in the Methods, Results, Discussion, and Conclusions sections labeled a. all correspond to objective a., etc.

a. To census the DCH and the YCH in 1986, 1987, 1988, 1989, and 1990.

b. To determine if all caribou photographed during censuses appear as discrete images and are enumerated during photo interpretation.

c. To annually determine herd sex and age composition.

d. To determine yearling recruitment in the DCH and the YCH annually.

e. To determine if yearling recruitment is precisely and accurately estimated by conducting herd composition surveys in April.

f. To determine the annual natality rate and calving chronology.

g. To evaluate the validity of using a small sample of radio-collared cows to estimate herd natality and recruitment.

h. To determine if bearing a calf when a cow is 24-36 months old, or for several successive years, influences the probability of calving in subsequent years.

i. To determine if there are any differing cohort-specific pregnancy probabilities for cows 24 or 36 months old.

j. To determine if the natality rate of 24- and 36-month-old cows is determined by their weight at the time of the rut.

k. To measure harvest by hunters annually.

l. To determine when major mortality occurs to both calves and adults and to characterize caribou mortality from natural causes.

m. To determine caribou:predator ratios in the range of the DCH and YCH.

n. To determine the correlation between wolf abundance and the number of caribou killed by wolves.

o. To determine if caribou killed by predators are taken in proportion to their representation in the population in terms of sex and age.

p. To determine the seasonal movements, distribution, and fidelity to respective calving grounds of radio-collared caribou.

q. To determine if dispersal is important to the population dynamics of the DCH and YCH.

r. To compare food habits of the Delta, Yanert, Denali, and Fortymile herds.

HERD IDENTITIES AND STUDY AREA

Study Herds

The DCH and YCH were the focus of this study. Davis and Valkenburg (1985a) previously discussed identity and history of the DCH. Although caribou have resided on the northern slopes of the Alaska Mountain Range between the Canadian border and the Nenana River since at least 1918 (Murie 1935), their subpopulation (i.e., herd as defined by Skoog [1968]) identity has been poorly understood. Skoog (1968) and Hemming (1971) considered these caribou to be members of the Mentasta, Chisana, or Delta Caribou Herds. They agreed on the distribution and identity of the Chisana Herd, but defined the ranges of the other 2 herds differently.

Skoog (1968) described the range of the DCH as, ". . .the north slopes of the Alaska Range from the upper Wood River on the west to the Robertson River on the east." Hemming (1971) described the DCH as ranging the northern slopes of the Alaska Range between the Alaska Railroad on the west and the Richardson Highway on the east. Skoog included the caribou inhabiting the area between the Delta and Robertson Rivers as part of the DCH; however, Hemming included these as part of the Mentasta Herd.

On the basis of more recent information, Davis and Neiland (1975) and Davis (1978, 1980) redefined the identities of caribou occupying the area between the Nenana River and the Glenn Highway to include the Delta and Macomb herds. Since 1969 (or earlier) caribou inhabiting the northern slopes of the Alaska Range west of Alaska Highway #1 (Tok Cutoff) and east of the Alaska Railroad have existed as 2 discrete groups. One group, the DCH, has consistently ranged west of the Delta River and east of the Alaska Railroad and calved near Trident and McGinnis Glaciers. This is consistent with Hemming's (1971) description of the DCH. The 2nd group, the Macomb herd, has occupied the area east of the Delta River and west of Alaska Highway #1. The Macomb herd has calved annually on the Macomb Plateau since at least the mid-1950's, according to the late Marvin Warbelow, a long-time pilot from Tanacross (L. Jennings, ADF&G, pers. commun.). ADF&G biologists have observed calving on the Macomb Plateau annually since 1969.

Skoog (1968) included the Macomb subpopulation as part of the DCH. Hemming (1971) considered the Macomb subpopulation as part of the Mentasta herd, although he reported that ". . . local bush pilots have observed some calving activity on the Macomb Plateau east of the Johnson River."

Davis and Neiland (1975) concluded that Macomb Plateau caribou composed a herd distinct from either the DCH or Mentasta herd. The designation of Macomb caribou as a herd was consistent with Skoog's (1968) herd definition: ". . . a herd becomes an entity (subpopulation) when it establishes a calving area distinct from that of any other herd and uses this area repeatedly over a period of years." The Macomb herd has calved in an area distinct from that of any other herd since at least the mid-1950's. The Mentasta herd has continued to calve in the Wrangell Mountains and has not recently (perhaps never) occupied the range of the Macomb herd, even during winter and summer (Bos 1974). Sex and age structure and recruitment in the Macomb herd differ from those of the Delta and Mentasta herds. For management purposes, the Macomb herd has been considered distinct from the Mentasta and Delta herds. Between October 1966 and March 1968, 205 Delta Herd caribou were marked with metal ear tags and plastic ear streamers by the University of Oklahoma (Department of the Army Project No. 1577), and none of these marked animals has been seen east of the Delta River (Hemming 1971).

Existence of a herd of several hundred caribou, residing year-round primarily in the Yanert River drainage (i.e., the YCH), was suggested in the 1970's by observations by ADF&G staff (ADF&G files, Fairbanks) as well as by people familiar with the area (L. Castle, Upper Wood River resident and big game guide, pers. commun.). Radio-collaring of 8 adult females in the Yanert River drainage during April 1981 and subsequent monitoring of them confirmed the existence of the YCH as a herd separate and distinct from the DCH. The radio-collared cows remained in the Yanert River drainage or the adjacent headwaters of the Wood River. Of the 8 radio-collared cows, one was not located during the 1st year because a transcribing error caused us to monitor an erroneous frequency. However, the 7 others were all distributed during calving time within the headwaters of Dean and Dick Creeks or adjoining areas; six of them calved. All calved at locations above 1,500 m, which was usually higher than the nearby Dall sheep (Ovis dalli). Unlike the DCH, they were widely dispersed during calving, perhaps to avoid predation. No mixing between Delta and Yanert radio-collared caribou was observed during 1981 and 1982. Delta caribou rarely ranged south of the crest of the Alaska Range, and although Yanert caribou ranged into the upper Wood River, this usually occurred when most Delta caribou were farther north.

During the June 1981 photocensusing of the DCH, 431 caribou were observed in the Yanert drainage and believed to be the bulk of the YCH. In November 1981, P. Valkenburg and R. Boertje observed about 500 Yanert caribou during a monitoring flight for radio-collared caribou. Because this was an incomplete survey, the YCH probably contained a minimum of 500-600 caribou.

Study Area

Skoog (1968) originally described the range of the DCH. Based on a subsequent study, Hemming (1971) modified Skoog's description of the physical environment, and little has changed since that revision. When this study was initiated in 1985, the DCH ranged over about 10,000 km^2 on the northern slopes of the Alaska Range between the Nenana River on the west and the Delta River on the east. The area lies approximately 110 km south of Fairbanks (Fig. 1). The Alaska Range rises abruptly from its foothills and consists of rugged, glaciated ridges at elevations of 1,830-2,740 m interspersed with glacier-capped mountains exceeding 3,660 m. The northern foothills of the Alaska Range are flat-topped ridges at elevations of 610-1,370 m separated by rolling tussock tundra, muskegs, and spruce- (*Picea* spp.) covered lowlands. North of the foothills lies the predominantly spruce-covered Tanana Flats. The entire area is drained by the Tanana River. The transition is abrupt from the foothills to the Tanana Flats. The Flats have little relief, and elevations range from 130 to 300 m. The Flats are underlain by permafrost, and drainage is poor, resulting in numerous shallow ponds and extensive bogs.

Fire has greatly influenced the lowland vegetation, resulting in the creation of a mosaic of shrub and young forest-dominated seres, climax bogs, and mature black spruce (*P. mariana*) forest (LeResche et al. 1974). Fires have also occurred on the calving area and adjacent tundra and uplands (Davis et al. 1985). Vegetation in the hills, foothills, and mountains grades from taiga of white spruce (*P. glauca*), black spruce, paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*) into shrub communities of willow (*Salix* spp.) and dwarf birch (*B. glandulosa* and *B. nana*) at low elevations, with alpine tundra at high elevations (LeResche et al. 1974).

The study area is largely snow-free from May until October. Annual temperatures range from approximately 29 C to -51 C. Annual precipitation averages about 30 cm; snow accumulation averages 50 cm and rarely exceeds 80 cm. Ground vegetation in the foothills and mountains is frequently exposed during winter because of strong winds. Although the DCH is widely distributed from the mountains to the flats during winter, foothills appear most used. However, with increasing herd size there has been increased use of the Flats, and for the first time ever during the winter of 1988-89 more radio-collared caribou were on the Flats than in the foothills.

As calving time approaches, cows and many short yearlings move into the upper portion of the Little Delta River and Delta Creek, which has been used as the traditional core calving area since before the 1950's and into the mid-1980's and has been called the

Major Calving Area (MCA) in past publications (Valkenburg et al. 1988). The MCA was identified as the DCH's traditional calving area by extensive aerial surveys conducted from the late 1950's through the mid-1970's; it consists of 2 adjacent areas separated by a timbered river valley about 2 km wide (Skoog 1968; Hemming 1971; M. Buchholtz and L. Jennings, retired ADF&G employees, pers. commun.). Most calves are born in tussock tundra, but many others are born in the low-shrub and sparse spruce-dominated areas. Most bulls and some yearlings remain widely scattered throughout the herd's entire range during calving.

METHODS

Radio-collaring

Because monitoring radio-collared caribou was central to accomplishing many of our study objectives, we present a general description of radio-collaring procedures. This will eliminate describing the procedure repeatedly for the various relevant objectives.

A helicopter (Bell 206B or Hughes 500C or D) and darting or netting equipment were used for capturing caribou. Immobilizing drugs and doses used from 1979 through 1982 were reported by Valkenburg et al. (1983). Davis and Valkenburg (1985a) reported doses of M99 (etorphine hydrochloride, Lemmon Co., Sellersville, PA) and its antagonist, M50-50 (diprenorphine hydrochloride, Lemmon Co., Sellersville, PA) used from 1983 through spring 1985. In the fall of 1985 we began using carfentanil (Wildnil, Wildlife Lab., Fort Collins, CO) and Naloxone (naloxone hydrochloride, Wildlife Lab., Fort Collins, CO) as immobilizing drug and antagonist, respectively; results were summarized by Adams et al. (1988b). Caribou captured with a shoulder-held net gun (Valkenburg et al. 1983) or a net gun mounted on the skids of a helicopter were handled without chemical immobilization or sedation. Age of radio-collared caribou was based on the presence of deciduous incisiform teeth for calves; older caribou were aged by cementum annuli (Miller 1974).

In each of 9 years between 1979 and 1990, 7 to 19 DCH caribou were captured for the first time (Table 1). One hundred forty-six individual caribou were captured; most were 8- to 12-month-old females. Radio collars were put on 120 of these, many of which were recollared at 3- to 4-year intervals prior to battery exhaustion in the radiotransmitters. Eight YCH females were radio-collared as adults during April 1981, and 4 adult males were radio-collared during the fall of 1984.

All radio collars (Telonics, Inc., Mesa, Ariz.) were in the 150-151 Mhz frequency range and contained movement-sensitive mortality switches. On 8- to 12-month-old female calves, collars could be put on tight enough so they would not slip over the head when antlers had been shed, while allowing growth of the neck to adult size. On males this was not possible because of their greater neck development as adults. We improvised an expandable collar for males in 1979, but it worked poorly; thereafter, we avoided collaring male calves.

Radio-collared caribou were relocated periodically from fixed-wing aircraft; details are in reports summarized in Davis et al. (1987). When a mortality signal was heard, the collar site was visually located and evidence of mortality was noted. For confirmed mortalities, a helicopter was flown to the vicinity at a later date, the collar was relocated, and the site closely inspected. The caribou remains and adjacent areas were investigated to ascertain the cause of death. Samples were obtained from the carcasses, and nearby tracks, scats, and hair were noted and photographed.

a. Census of the DCH and YCH

We used the modified aerial photo-direct count-extrapolation (APDCE) (Davis et al. 1979) and/or radio-search techniques (Valkenburg et al. 1985) to annually census the 2 herds. All census results from the DCH and YCH through 1984 were reported in a previous Pittman-Robertson (P-R) final report (Davis and Valkenburg 1985a).

The 1985 census was conducted on 16 July, the latest census date on record. Late snowmelt in the spring of 1985 retarded postcalving aggregation for the DCH and YCH. We monitored the 2 herds from late May until 16 July before they were aggregated suitably for censusing. D. Miller and K. Whitten used a Super Cub to locate 8 and 47 YCH and DCH caribou with radio collars, respectively; P. Valkenburg used a U.S. Army 206 helicopter to photograph all aggregations with 35-mm color print film (Kodak VRG, ASA 100).

In 1986 we used a Bellanca Scout (P. Valkenburg and E. Crain) and a Piper Super Cub (M. McNay and J. Davis) to census the DCH and YCH on 26 and 27 June, respectively. All groups containing more than 50 caribou were photographed with 35-mm SLR cameras using color print film (Kodak VRG, 100 ASA). Both aircraft combined radio-tracking and visual searches to cover the entire Yanert River watershed and the adjacent Wood River drainage. The Bellanca Scout was used on 27 June to search areas peripheral to where caribou had been located on 26 June.

On 2 July 1987 J. Davis and E. Crain used a Bellanca Scout to census the combined DCH and YCH. All groups containing more than 50 caribou were photographed with 35-mm SLR cameras using color print film (Kodak VRG, 100 ASA). The aircraft combined radio-tracking and visual searches of the area adjacent to the locations of radio-collared caribou in the Yanert River watershed and the adjoining portion of the Wood River drainage. The Bellanca Scout was used on 3 July to search areas peripheral to where caribou had been located on 2 July and to locate 2 radio-collared caribou not found on 2 July.

In 1988 the DCH and YCH census was initiated on 15 July; 3 aircraft were employed. J. Davis and J. Wright crewed a Bellanca Scout, M. McNay and R. Boertje crewed a Piper Super Cub, and P. Valkenburg, R. Beasley, V. Crichton, and J. Winters crewed a DeHavilland Beaver. The Scout and Super Cub combined radio-tracking and visual searches of the area adjacent to the locations of radio-collared caribou in the upper Wood River watershed and adjoining areas.

Groups of caribou located by the Scout and Super Cub were photographed or visually enumerated. Photographs were taken with 35-mm SLR cameras using color print film (Kodak VRG, 100 ASA). The crew in the Beaver aircraft searched for and enumerated caribou on the north side of the Yanert River drainage.

A huge storm prematurely terminated the census on 15 July before all radio-collared caribou had been located and before a portion of the census area known to contain several hundred caribou could be intensively searched. The entire study area was dominated by heavy clouds, fog, and rain on 16 July. On 17 July, J. Davis and V. Crichton flew the Scout to locate radio-collared caribou missed on 15 July and to reconnoiter the area that had not been intensively searched on 15 July.

On 29 June 1989 J. Davis located all radio-collared caribou and determined that aggregations were suitable for censusing. The census commenced on 30 June 1989 and was completed on 1 July 1989. Three aircraft were employed on 30 June. P. Valkenburg, J. Schoen, D. Reed, and R. DeLong crewed a DeHavilland Beaver aircraft and visually searched 100% of Area III (see Appendix A, Fig. 1 in Davis et al. 1990); M. McNay and R. Beasley crewed a Piper Super Cub aircraft and visually searched 100% of Area II; J. Davis and R. Boertje crewed a Bellanca Scout aircraft and visually searched 100% of Area I, located all radio-collared caribou in Areas I, II, and III, and photographed all aggregations in the 3 areas.

On 26 June 1990, we used a Bellanca Scout, PA-12, and Beaver aircraft to census the DCH. M. McNay and R. Beasley crewed the Bellanca Scout, located all radio-collared caribou, and took 35-mm photographs of all aggregations. P. Valkenburg, D. Reed, C. Smith, and L. Tutterrow crewed the Beaver, visually searched the area west of the Wood River including portions of the Yanert River drainage, and took large-format photographs of selected aggregations. J. Davis crewed the PA-12, searched the Upper Wood River and the tributaries draining the east side of the Wood River, and photographed groups over 50 in number with a 35-mm camera.

b. Determining if All Caribou Photographed During Censuses Appear as Discrete Images

This objective was never addressed because of insufficient funding and its relegation to a low-priority objective. Field evaluation was scheduled for June 1990, the final month of the study. Because June falls at the end of the ADF&G's fiscal year, reprioritization of regional budgets late in the fiscal year precluded conducting the field evaluation.

The proposed experimental design was to locate one or more postcalving aggregations of caribou under circumstances encountered in the actual photocensusing procedure. The subject aggregations would be enumerated by whatever procedure required to accurately ascertain the total number of caribou. We planned to land nearby in a helicopter and have 2 or more observers count the aggregations with spotting scopes until we judged that we had satisfactorily enumerated all individuals, including calves and older individuals. Photographs would then be taken from the ground when individuals in the aggregations were spaced so that all would appear as discrete images. After we had accurately ascertained the group sizes, we planned to communicate by radio with a crew in fixed-wing aircraft, which would then photograph the aggregations from the air, simulating conditions employed during aerial photocensusing. Different scales (altitude), photo angles, and film (including 35-mm and 9" x 9" formats) would be evaluated. Results would then be compared with the "ground truth" information.

c. Sex and Age Composition

Minor differences occurred among years in the field procedures used to sample sex and age composition of the herd. We classified caribou several times each year (Tables 2 and 3). During the time of calving, we frequently classified caribou on the calving grounds from a Super Cub or a Bellanca Scout to determine initial calf production and/or survival (calves:100 caribou older than calves). Sex and age composition surveys were conducted using a Bell 206B or other helicopter during the time of the rut. Caribou were classified as bulls, cows, or calves, and in some years bulls were classified as large, medium, or small. Also, calves were classified according to sex in some surveys.

Generally, for groups of more than 50 caribou and during most of the counts in early June, a helicopter was used to place observers in strategic locations from which they could classify caribou with spotting scopes. This technique was successful on the groups that were not densely aggregated, especially if the caribou were moving slowly; however, the technique can be difficult, especially if the postcalving aggregations occur on flat ground. In this situation the observer cannot view an entire large group. In large groups, composition counts may be biased, because it is difficult to count the entire group, and members of certain age or sex classes may be concentrated on the periphery. We do not presently have satisfactory methods to classify dense aggregations. Using a helicopter to count small groups is convenient and probably as accurate as counting them on the ground with a spotting scope. However, when classifying large calves during fall, we felt it advantageous to have a side view of the caribou to better observe their relative size and length of their rostrum.

During the composition counts conducted from the helicopter, the pilot sat in the right front seat with an observer in the left front one; a person recording data sat in the left rear seat. The pilot pursued the groups of caribou closely, and while the observer called out the sex and age of each caribou in the group, the recorder tallied the information with a 5-place mechanical counter. Experienced observers often recorded as they classified.

Observers based age determinations on body morphology and sex determinations on external genitalia. Because caribou generally run with their tails halfway down, it was usually possible to see the dark, vertical line of the vulva on cows; however, some cows ran with their vulva covered, and these were often difficult to distinguish from young bulls. An observer can be sure that a caribou showing the dark vulva is a cow, but when it is not seen the animal cannot be assumed to be a bull. Animals in question normally changed tail carriage if watched sufficiently long. Alternatively, viewing from a different angle frequently made sex determination possible.

We tried to sample caribou in as many different areas as possible to determine whether our counts were representative. To then calculate the average herd composition for each season, we weighted the samples from each area by the proportion of the herd that each count was thought to represent, rather than by the actual sample size. Weighting was often based on the distribution of the radio-collared caribou present within the herd. In many years the results differed little from those of the unweighted sample data.

d. Yearling Recruitment

In 1985 funding was insufficient to charter a helicopter to estimate yearling recruitment in April. However, J. Davis (observer) and W. Lentsch (pilot) flew a 2.1-hour sex and age composition survey of the DCH in a PA-18-150 Super Cub on 3 May 1985.

We monitored radio-collared cows to determine their natality rate and subsequent calf survival. Composition counts were also conducted during April on the herd at large. In 1986, 1987, and 1990 we attempted to obtain random, even-sized subsamples to facilitate evaluation of bias and calculation of a confidence interval for the ratio of short yearlings (i.e., 11 mos old):100

cows. Our sample design required classifying approximately (to ensure classification of entire groups) 100 caribou closest to each radio-collared caribou. This rationale for sampling assumes that the basic social structure of caribou consists of "temporary tenuous association(s) of individuals" (Lent 1965) or "open social units" (Bergerud 1974*b*), which have been validated for some Alaska caribou herds through radio-telemetry studies (Valkenburg et al. 1983). In short, this implies that the specific individual caribou in proximity of a collared caribou varies over time and space. Hence, we reasoned that the sample unit near the radio-collared caribou approximated a "random" sample (albeit the sample does not meet the statistical requirements for being random).

The 20 April 1986 composition survey of the DCH obtained 11 subsamples (n = 998), using a helicopter to classify approximately 100 caribou closest to each of 11 radio-collared caribou chosen randomly from the radio-collared cohort. To test the precision of our unadjusted ratio for short yearlings:100 cows, we used Cochran's (1977) ratio estimation formula to calculate a 95% confidence interval. We expected a 50:50 sex ratio of short yearlings:100 cows and adjusted our observed ratio on that basis. We repeated this procedure in 1987 and 1990.

On 2 May 1986, J. Davis located all radio-collared YCH caribou from a Bellanca Scout aircraft, and M. McNay and R. Bishop used a 206B helicopter to classify all associated caribou. All caribou observed were classified as male or female short yearlings (11.5 mos old), cows, or bulls.

e. Precision and Accuracy of Yearling Recruitment Surveys

We initially planned to test precision by conducting serial counts of the same sample area (e.g., on successive days, weeks, or months). However, inadequate project funding precluded that sampling scheme. Our measure of precision was therefore limited to calculating variance of subsamples as described in d. above.

f. Natality Rate

Annually from 1979 through 1990, calving distribution, success, and chronology of the DCH and YCH were monitored by fixed-wing aircraft surveys (primarily Super Cub or Bellanca Scout) conducted on several days in late May. The surveys monitored radio-collared and associated caribou. These surveys were augmented in some years by ground and/or helicopter surveys, including distended udder counts of the herd at large.

During the period 1986 to 1989, natality data were obtained primarily from radio-collared DCH caribou. In 1990 natality data were obtained from both the radio-collared caribou and from the herd at large via composition counts conducted from a helicopter, the ground, and several radio-collared caribou relocation flights.

g. Validity of Using Radio-collared Cows to Estimate Herd Natality

Empirical data from the herd at large and from the radio-collared cohort were compared.

h. Reproductive Cost of Birthing When 24-36 Months Old and/or for Several Successive Years

Davis et al. (1986) and Valkenburg et al. (1988) described the methods used to relocate caribou during the calving periods. We relocated caribou with Piper Super Cub or Bellanca Scout aircraft, and J. Davis and/or P. Valkenburg was an observer in all relocations. Each female >24 months old was located and observed a minimum of 1-3 times per calving season. For about 80% of the relocations, reproductive status was judged from the presence or absence of a distended udder (Bergerud 1964); in most remaining instances, a calf was present and appeared bonded to the female. Occasionally, the presence of hard antlers or subjective impressions by the observers was the basis for judging the female's parturition status. In 4 of 294 cases (all in 24-mo-old caribou) we were unable to judge reproductive status.

Denali Herd:

We collaborated with L. Adams, National Park Service research biologist, to investigate reproduction in subadult Alaskan caribou (Davis et al. 1990), so we will briefly describe the relevant methods from Adams' Denali study. During March 1987 and 1988, 24 10-month-old female caribou were captured and radio-collared. All caribou were immobilized by darting with Wildnil (Adams et al. 1988b) from a helicopter. During the years that they became ≥2 year olds, all instrumented animals were relocated daily from 6 to 31 May until reproductive status could be determined. Cows that were believed to be pregnant were located daily until their calves were born. The calves were captured and radio-collared within 2 days of birth (Adams et al. 1988a, ADF&G files). Radio-collared calves were located daily until the end of May and then periodically throughout the rest of their 1st year.

i. Cohort-specific Pregnancy Probabilities for Cows 24 or 36 Months Old

Same procedure as h. above.

j. Rutting Weight and Natality Rate in 24- and 36-month-old Cows

We initially planned to weigh 16-month-old females and correlate weight with subsequent natality. However, this is one of the objectives that was relegated to a low priority when operating funds were reduced for this project. What effort was expended on this objective was through the procedure for a. and b. above and in the literature review and synthesis discussed in Davis et al. (1990).

We used Reimers' (1983<u>b</u>) conversion formula of dressed weight = 52% of the total body weight to convert total body weights to dressed weights for calculations involving Reimers' (1983<u>a</u>) prediction equation:

$P = 1 - e^{[-0.169(W-21)]}$, where P = probability of pregnancy and W = dressed weight in kg.

In our testing of hypotheses about the relationship of rutting weight of females and their probability of being pregnant, we used an <u>index</u> to rutting weight. Most of our weights were obtained around late April, so we must infer a rutting weight from those data. In doing so, we are assuming that a significant between-year change in variables affecting weight gain over summer will be manifested in weights of that year's calf cohort when weighed in late winter. For example, we infer that if the $\bar{x}$ weight of females from the 1978 cohort was 62 kg and if the $\bar{x}$ weight of the 1979 cohort is also 62 kg, then the $\bar{x}$ rutting weight at 17 months should be the same for the 1978 and 1979 cohorts. A corollary inference is that the within-cohort weight variation in year No. 1 will be proportionally the same in year No. 2.

k. Harvest by Hunters

ADF&G's survey and inventory program has annually collected harvest information using several procedures. A statewide mandatory hunter harvest report card system for general hunting seasons has been used since 1968. Since 1981 some limited hunting of the DCH and YCH has occurred through drawing-permit hunts and/or permit registration hunts as well as the general seasons. Harvest estimates from permit hunts are probably good estimates of harvest, because all drawing permits must be returned and that requirement is rigidly enforced; although registration permits are less rigidly tracked, they still produce acceptably accurate estimates of the harvest. In contrast, the same cannot be said for general season hunts where the harvest is reported by mandatory harvest reports. In recent years budget constraints have precluded sending out reminder letters to hunters who fail to voluntarily return harvest report cards. Many ADF&G biologists have suspected that harvest reports have been increasingly producing gross underestimates of the actual harvest. Consequently, M. McNay initiated a program in 1987 to better estimate harvest. In regulatory years 1987-88 through 1989-90, M. McNay and others maintained check stations near primary access routes for hunters, contacting several hundred DCH and YCH hunters while they were in the field. McNay (1990) reported the procedure employed in 1988 as follows.

ADF&G personnel interviewed hunters during the 1st 2 weeks of September 1988 to determine the frequency of harvested caribou not being reported through the harvest ticket system. Hunters were not told the purpose of these interviews, because it could potentially bias reporting. Hunters were contacted daily at hunting camps and a check station on the Parks Highway near the Yanert River.

The interviews and harvest report data were treated as a mark-recapture sample to estimate actual hunter numbers and harvest. Confidence limits were determined from a binomial confidence limit computer program (J. Venable, ADF&G, Fairbanks, 1987). The interviewed hunters composed the marked sample; the harvest reports, the recapture sample. Total hunters were estimated from the following minimum bias mark-recapture formula:

$$N = \left[\frac{(n_1 + 1)\ (n_2 + 1)}{m_2 + 1}\right] - 1.$$

Total hunters were calculated using, n_{1t} = interviewed hunters (i.e., marked sample), n_{2t} = total harvest reports returned, and m_{2t} = interviewed hunters who also returned harvest reports (i.e., recaptured markers). Similarly, the number of successful hunters (i.e., harvest) was calculated using n_{1s} = interviewed successful hunters, n_{2s} = total successful harvest reports returned, and m_{2s} = successful interviewed hunters who also returned a harvest report.

The reporting rates for successful hunters and total hunters were calculated simply as m_{2s}/n_{1s} and m_{2t}/n_{1t}, respectively. Confidence limits around those proportions were based on the binomial distribution.

It is not possible to calculate the reporting rate of interviewed, nonsuccessful hunters from interview report data, because a hunter who was unsuccessful when interviewed could have later taken a caribou and failed to return the harvest report. Therefore, using the estimates of successful hunters and total hunters derived from hunter interviews, a nonsuccessful hunter reporting rate was calculated as follows:

$$\frac{\text{Total reported hunters - Reported successful hunters}}{\text{Total est. hunters - Total est. successful hunters}} = \frac{215}{488} \times 100\% = 44\%$$

To improve hunter reporting rates, 120 radio and 51 television advertising spots were purchased and aired by Fairbanks broadcasters between 5 and 14 October 1988. Additional advertising was purchased in the hunting supplement of the newspaper in early September, and a newspaper article requesting hunters to return harvest reports was published in late September.

l. Mortality

Data from radio-collared caribou and from serial composition counts were used to determine the chronology of calf mortalities. Survival rates of adult caribou were calculated from the radio-collared caribou.

Composition surveys that yielded calf:cow ratios were conducted in May, June, October, and April to estimate mortality of the zero to 5- and 5- to 12-month-old cohorts (MOC's). Details of the methods were presented or cited by Davis et al. (1987) and in c. above. Composition surveys in late May, following the peak of calving, included distended udder counts (Bergerud 1964) that provided an index of natality. Differences in calf:cow ratios over time served as an estimate of the magnitude and chronology of calf mortality.

An annual natality rate for radio-collared caribou was obtained by observing each radio-collared cow at least once at or near the peak of calving and noting the presence of a calf, udder distension, and antlers. We initially planned to compare the chronology and magnitude of calf loss of the radio-collared cows with the herd at large; however, we found it extremely difficult to ascertain calf bonds with cows after the calf was a few weeks old. This was primarily a problem because relocations were from fixed-wing aircraft and often involved large groups.

We estimated adult mortality rates for radio-collared caribou data using procedures described by Trent and Rongstad (1974). Previously, we compared and contrasted mortality rates using the Trent and Rongstad (1974) procedure with rates calculated using Gasaway et al.'s (1983) method and, like Edmonds (1987) who compared the procedure of Gasaway et al. (1983) with that of Heisey and Fuller (1985), found only minor differences (Davis and Valkenburg (1985a, 1985b).

No statistical tests were conducted to compare mortality rates among the various sex and age cohorts discussed; conclusions were qualitatively based. The mortality rates presented for the various age cohorts apply to unequal time intervals: 0-5 MOC = 5 months, 8-12 MOC = 4 months, 12-24 MOC = 12 months, and >24 MOC = 12 months (i.e., the mean annual rate).

m. Wolf:Caribou and Grizzly Bear:Caribou Ratios

These ratios were determined by using data from the annual caribou censuses, the caribou distribution surveys of radio-collared caribou, results of wolf (Canis lupus) surveys conducted in Subunit 20A (McNay 1990), and the results of a concurrent ADF&G study of grizzly bears (Ursus arctos) (Reynolds et al. 1987).

n. Wolf Abundance and Rate of Caribou Predation

Estimates of caribou population size and distribution, wolf abundance and distribution, and caribou mortality rates from wolf predation will allow this correlation to be tested. A University of Alaska graduate study class under the direction of R. T. Bowyer reported on this relationship (S. Amstrup, unpubl. data; J. Davis, ADF&G files).

o. Sex and Age Composition of Predator-killed Caribou

We compared the sex and age data for radio-collared caribou killed by predators with data from the total radio-collared sample. We did likewise for caribou in the population at large.

p. Seasonal Movements, Distribution, and Fidelity to Calving Grounds

Caribou Winter Distribution:

Fleischman (1990) discussed winter distribution as follows:

> I analyzed ADF&G data on locations of radio-collared caribou to determine winter distribution of the DCH. Most radio-collared caribou were initially captured at approximately 10 months of age, and collars were renewed every three years as batteries expired (Davis and Valkenburg 1985_a_). Collared caribou were tracked, on average, once every 1.5 months from October through April 1979-1987, and their locations recorded on 1:250,000 topographic maps. From 20 to 60 radio-collars were active at a given time.
>
> For a radio-collared sample to adequately represent population distribution, radio-collared caribou must quickly become interspersed among the population. This assumption appears to be well-founded (Valkenburg et al. 1983, Skogland 1986). However the reliability of ADF&G radio-location data as a measure of population distribution probably varied (i.e., increased) during the study, since the number of active collars and age-classes represented increased from 1979 to 1987.

Calving Distribution:

Davis et al. (1986) described the methods used to relocate caribou during the calving period from 1975 to 1985; methods used from 1986 to 1990 were similar (Valkenburg et al. 1988). We relocated caribou with a Piper Super Cub or a Bellanca Scout aircraft on 14, 15, 17, and 28 May 1986 and on 14, 15, 20, 27, and 31 May 1987. Each radio-collared female ≥24 months old was located and observed 1-3 times per year. Radio-collared males and yearling females were relocated at least once during the last 2 weeks of May each year. On 30 May and 2 June 1987 we used helicopters (Allouette A-star and Bell Jet Ranger) to obtain sex and age composition and pregnancy data. Procedures were similar for 1988-90.

Calving location is defined as the site where a female was first found with a newborn calf. In years when a pregnant female was never seen with a newborn (i.e., some newborns died before being observed), the calving site was defined as the location where the pregnant female had last been observed on the date closest to the peak of calving. Peak calving date was estimated as the day(s) when approximately half of the pregnant females in the herd had calved. Calving distribution was defined as the area within a convex polygon that connected the outermost calving locations for all radio-collared females in a given year.

During radio-tracking flights, locations of caribou were recorded on topographic maps (USGS scale 1:250,000). Subsequently, locations were electronically digitized by latitude and longitude and then transferred to a computer file (DBase III, Ashton-Tate, Torrance, Calif.). Other information was later entered into each record. We replotted location data, using a Hewlett-Packard 7475A plotter and a computer graphics program developed by J. Venable (ADF&G, Fairbanks). Statistical testing for nonindependent ratio estimates was by Student's *t*-test (Cochran 1977). Significance level is presented in the narrative.

q. Dispersal and Population Dynamics in the DCH and YCH

Movements of radio-collared caribou in the Delta and Yanert Denali (Adams et al. 1989), Nelchina (Pitcher 1987), Macomb (ADF&G files), and Fortymile (Valkenburg and Davis 1989) herds were monitored to detect dispersal. In addition, frequent censusing of these adjacent herds should identify inexplicable major increases or declines suggestive of measurable immigration or emigration having occurred.

r. Comparative Food Habits of the Delta, Yanert, Denali, and Fortymile Herds

Fecal pellets will be collected monthly for herds where data are currently unavailable. Analysis will be done at Colorado State University using the microhistological examination technique. The literature will be purused to locate existing data.

Fleischman (1990) contributed much of the knowledge about DCH diet composition and quality. The following excerpt from his thesis describes the methods he used:

> I collected 16 composite fecal samples (1 sample = 20-25 pellets, each pellet from a different pellet group) from several locations in the DCH winter range from March 1986 to March 1987. Plant composition of these samples, plus one ADF&G sample from 1984, was estimated microhistologically (Davitt 1979) by the Wildlife

> Habitat Management Laboratory at Washington State University (WSU) in Pullman. Relative cover of identifiable epidermal fragments, classified to major forage class, was recorded and summed for 300 fields of view per sample (10 slides, 30 fields/slide). Some leaf material could not be differentiated between forbs or shrubs; I grouped this with shrubs because caribou seldom obtain forbs in winter (Bergerud 1977, Boertje 1984, Russell and Martell 1984). I used multivariate analysis of variance (SAS GLM procedure, SAS Institute 1985) to test for differences in diet composition by forage class among areas.
>
> Duplicate material from 10 of the above fecal samples was analyzed for content of acid-detergent fiber, nitrogen, and nitrogen in acid detergent fiber residue at the University of Alaska Agricultural Experiment Station in Palmer. Ash content was also determined and all values were standardized to percent of ash-free dry weight (i.e., percent of organic matter).
>
> Results are also reported here from plant composition analysis of four fecal samples collected by ADF&G and analyzed by a slightly different method (Sparks and Malechek 1968) at the Composition Analysis Laboratory, Colorado State University (CSU), Fort Collins. Collection dates and locations of WSU and CSU samples overlapped, yet WSU reported much lower lichen percentages (e.g., 69% lichen for area WFH than did CSU (90%).
>
> Other studies have shown CSU analyses of R. tarandus winter diets, similar to those reported here, to be biased. However the biases with regard to lichen proportion were small and in different directions (Boertje 1981, Duquette 1984). I therefore used CSU fecal analysis results for crude approximations of dietary lichen percent in this thesis. I assumed that the WSU technique must underestimate lichens. To enable crude comparisons with other studies, I therefore developed correction factors to convert from WSU- to CSU-type results, using the paired data existing for areas WRH and GKB. I applied the corrections to WSU diets from feces collected in area EFH, from which there were no corresponding CSU samples.

In addition to the samples discussed by Fleischman (1990), we sent 20 fecal samples and 22 rumen samples from the DCH and YCH to CSU for analysis in summer 1990 with the intent of having the results to incorporate in this report. Analysis has not yet been completed, so the results will be published in manuscripts emanating from this study.

RESULTS

a. Census of the DCH and YCH

All population estimates discussed in this section include calves; the timing for all estimates is approximately 1 July. The 1985 census located 8,083 caribou in association with the radio-collared DCH and YCH. Hence, 8,083 is a minimum estimate for the combined size of the 2 herds (Fig. 2). During the 1986 census, the DCH and YCH were aggregated in the same general area, and distribution overlapped for radio-collared DCH and YCH caribou. The only population estimate available, 7,804, was for the 2 herds combined.

The 1987 census located 8,380 (the mean of the high and low number counted on photos) caribou in association with or in the proximity of the radio-collared DCH and YCH caribou. Hence, 8,380 is the mean of our high and low estimate for the combined size of the DCH and YCH.

The DCH and YCH were intermingled when censused in 1988. The total number of caribou enumerated was 8,338. A minimum of several hundred more caribou were present, but they were not enumerated. A conservative estimate would be >8,500.

The DCH and YCH were apparently partially intermingled when censused in 1989. The number of caribou enumerated during the census was 10,690. We suspect that the YCH contained approximately 600 caribou and the rest were members of the DCH.

The DCH and YCH were apparently partially intermingled when censused in 1990. Census results were unavailable in time for this report; they will be reported in subsequent survey and inventory reports.

b. Determining if all Caribou Photographed During Censuses Appear as Discrete Images

Because of inadequate project funding to adequately accomplish all study objectives, this and additional objectives were assigned low priorities and were not worked on at all.

c. Sex and Age Composition

The sex and age composition of the DCH and YCH are summarized in Tables 2 and 3, respectively. In 1988 and 1989 the ratios for calves:100 cows during the rut were 35 and 36, respectively (Table 2). In both 1988 and 1989 the DCH and YCH were sufficiently overlapped in distribution to preclude obtaining data that clearly represented just one of the herds.

In 1989 the DCH bull:cow ratio was 27:100, confirming an accelerated decline since bulls-only hunting had been initiated in the general season of 1987-88. The bull:cow ratio has been in continuous decline since the early 1980's, when hunting of the DCH was resumed. Annually, the number of bulls harvested has been larger than the number of females.

d. Yearling Recruitment

In a 2-hour fixed-wing survey on 3 May 1985, 759 caribou were classified, including 256 short yearlings and 503 older than short yearlings; only 5 obvious bulls were present in the 503 "older than short yearlings" category (Table 2).

Eleven subsamples were obtained (n = 998) during the 20 April 1986 composition survey of the DCH, totaling 649 cows, 145 bulls, and 204 short yearlings (Table 4). The observed short yearling:cow ratio was 31:100, but it was probably biased. The short yearling sex ratio in our sample was 39% males and 61% females (79:123). The 95% confidence interval about the ratio estimate of 31.4 short yearlings:100 cows was 21.6 to 41.2 short yearlings:100 cows.

The 2 May 1986 survey of the YCH yielded a short yearling:100 cow ratio of 49:100 (n = 182). During the April 1987 composition survey of the DCH 14 subsamples were obtained (n = 1,280), totaling 838 cows, 199 bulls, and 243 short yearlings (i.e., 11 mos old) (Table 4). During the April 1990 composition surveys of the DCH 10 subsamples were obtained (n = 974), totaling 774 cows, 118 bulls, and 161 short yearlings (Table 4).

e. Precision and Accuracy of Yearling Recruitment Surveys

See results for d. above.

f. Natality Rate

Natality data through 1988 were reported in Davis et al. (1988). Natality has remained relatively stable throughout the study and the rate has been fairly high (84 ± 4%) (Table 5).

g. Validity of Using Radio-collared Cows to Estimate Herd Natality

Natality rate of the radio-collared cows has been compared with the natality rate of the herd at large for several years (Table 5).

h. Reproductive Cost of Birthing When 24-36 Months Old and/or for Several Successive Years

The age-specific parturition records show that, of the 7 cows that produced a calf at 24 months of age and were followed during each calving season until 5 years of age, four did not produce a calf in one of the 4 potentially productive years. We found no apparent pattern to indicate "pregnancy resting" at 36 months of age for individuals that first reproduced at 24 months of age (Fig. 3). Only 1 of 8 females was nonparturient at 36 months of age, resulting in an 88% parturition rate at 36 months for those females that reproduced at 24 months of age. There is no indication that "pregnancy resting" at 36 months or alternate-year reproduction resulted from Delta caribou giving birth at 2 years of age. However, missed pregnancies occurred among some of these individuals between 3 and 5 years of age, and the role of early puberty is unknown. Missed pregnancies following initial parturition occurred with comparable frequency among females that first gave birth at 3 years of age (Fig. 4).

The age-specific parturition records of 21 Delta caribou cows with 7 or more years of known status suggest that cows that first calved when 3 years old were just as likely to have a calf the subsequent year (11 of 12, 92%) as were those that had calved first at 2 years old (7 of 8, 88%) (Fig. 4).

i. Cohort-specific Pregnancy Probabilities for Cows 24 or 36 Months Old

See results from h. above. Davis et al. (1988) investigated this question, and their conclusions are presented in the Discussion section.

j. Rutting Weight and Natality Rate in 24- and 36-month-old Cows

This objective was not explicitly studied because of inadequate project funding for all objectives in the original study proposal. The discussion presented is from review of the literature.

k. Harvest by Hunters

McNay (1990) discussed the harvest in detail, so we present only a summary of historical harvest data here (Table 6). We also present a tabular summary of historical hunting seasons and bag limits for the DCH and YCH (Table 7).

l. Mortality

Davis et al. (1988) summarized the data available on mortality through 1987. Observed changes in the calf:cow ratio indicated a mean natural mortality rate of 56% for the 0-5 MOC (Table 8). Data were inadequate to determine if mortality was similar among males and females within the 0-5 MOC. However, fall 1988 data showed a sex ratio of 41 males:59 females (we expected 50:50) among the 5-month-old calves, suggesting that males suffer higher mortality within the first 5 months of life. We observed no natural mortality among 8- to 12-month-old radio-collared females (Table 9). This is consistent with the low mortality rate of 5- to 12-month-old caribou (both sexes combined) calculated from the serial calf:cow ratios (Table 8). Limited data on radio-collared males 8-12 months old suggested a 34% natural mortality rate (the small sample makes the finding suspect), which contrasts sharply with the low mortality rate of females.

In the 12-24 MOC's, natural mortality rates were 2% and 19% for females and males, respectively (Table 9). For the >24 MOC's, natural mortality was 7% and 19% for females and males, respectively.

The mean rate of natural mortality in the DCH of 56% for the 0-5 MOC is consistent with Bergerud's (1978) conclusion that the calf cohort commonly experiences >50% natural mortality. However, in contrast to suggestions in the literature and conjecture among caribou workers, we found that the natural mortality rate during the 1st winter (i.e., 5-11 mos. of age) was relatively low, with the exception of 8- to 12-month-old radio-collared males. This statement applies for years 1979 to 1989. However, during the winter of 1989-90, calf mortality apparently was higher than that for adults.

m. Wolf:Caribou and Grizzly Bear:Caribou Ratios

R. Boertje (ADF&G files) compiled available information on the distribution and abundance of wolves in Subunit 20A (includes an area larger than the combined ranges of the DCH and YCH) for the fall of 1985 and spring of 1986. The data suggested a total fall wolf population of 195. This total is the sum of the wolves estimated to be in the 24 identified packs plus a 10% add-on factor to include single wolves (Fig. 5, Table 10). Juxtaposition of the range of the DCH and YCH and wolf pack distribution in Subunit 20A can be depicted by comparing wolf distribution (Fig. 5) with caribou seasonal distribution maps (Figs. 6-11). The wolf population in Subunit 20A ranges over about 16,500 km^2, compared with minimum herd ranges of 9,650 km^2 and 1,409 km^2 for the DCH and YCH, respectively, in 1986.

During the fall of 1985 there were at least 15 wolves in 3 packs in the range of the YCH, which contained 600-700 caribou. The wolf:caribou ratio, therefore, was 1:40-47 (15:600-700). There were probably 600 moose (Alces alces) in the range of the YCH during the fall of 1985 (W. Gasaway, pers. commun.). If we assume 1 moose = 3 caribou equivalents (Keith 1983) for the purposes of calculating predator:caribou equivalents, the probable wolf:caribou equivalents ratio during the fall of 1985 was 1:160-167. This calculated ratio should be considered a minimum estimate on the prey side, because Dall sheep are also abundant in the Yanert River drainage. There are >800 sheep in the Yanert River drainage (W. Heimer, ADF&G, pers. commun.). Available data suggest wolves infrequently prey on sheep in Subunit 20A (Heimer and Stephenson 1982, Gasaway et al. 1983), but because of their relative abundance they must be acknowledged as potential alternate prey for wolves. Sheep are clearly preyed upon by a number of wolf packs.

In 1986 Reynolds et al. (1987) estimated the minimum density in Subunit 20A study area at 1.27 grizzly bears/100 km^2 or 1.04 bears >2 years old/100 km^2. There is no reason to believe grizzly bear density is lower in the range of the YCH than in Reynolds et al.'s study area. So assuming a density of 1.27 bears/100 km^2 in the 1,409-km^2 YCH range, we calculated a minimum grizzly bear population of 18 in the YCH's range. The calculated grizzly bear:caribou ratio in the range of the YCH then was 1:33-39 (18:600-700); the grizzly bear:caribou equivalents for the caribou and moose combined ratio was 1:133-139.

Similar calculations of wolf:caribou and grizzly bear:caribou ratios for the DCH follow. The distribution of wolf packs in Subunit 20A suggested that caribou were probably not important prey for pack Nos. 1, 2, 4, 5, and 10 (Fig. 5). Excluding pack Nos. 1, 2, 4, 5, and 10 (and pack Nos. 18, 19, and 20 from the range of the YCH), we concluded that 150 (includes prorating to include single wolves) of the 195 wolves in Subunit 20A during the fall of 1985 were potential predators of DCH caribou. During the fall of 1985, the wolf:caribou ratio for the DCH was therefore 1:50 (150:7,500).

The moose population in Subunit 20A during the fall of 1985 was about 8,000-8,500; because about 5,000 of these moose were distributed in the DCH's range, a wolf:caribou equivalents ratio for that range would be 150:22,500 or 1:150. The DCH range (9,650 km^2) probably contained about 123 grizzly bears (by extrapolation based on data in Reynolds et al. [1987]), a ratio of 1 grizzly bear:61 caribou and a ratio of 1 grizzly bear:183 caribou equivalents when caribou and moose are combined as prey. The range of the DCH also contains 4,000-5,000 Dall sheep (W. Heimer, pers. commun.), including the Yanert drainage.

Predator:prey ratios were updated through 1988 (Table 11) by Davis et al. (1988). Data were available to update the ratios through 1989, which has been done in abbreviated form (Table 11). A wolf census of Subunit 20A was completed in 1989 (McNay 1990), the DCH and YCH were censused in 1989 (i.e., this report), the moose population in Subunit 20A was censused in 1988 (ADF&G files), and H. Reynolds (pers. commun.) has current grizzly bear estimates available. These updated ratios will be discussed in detail in forthcoming manuscripts prepared for journal publication.

n. Wolf Abundance and Rate of Caribou Predation

This will be the subject of a manuscript for journal publication that is currently being drafted. See o. below.

o. Sex and Age Composition of Predator-killed Caribou

Because the due date for this final report was moved forward 1 year because of retirement of the principal investigator, we were unable to fully analyze the available data for this objective in time for inclusion in this report. However, in the remaining 2 months of employment after this due date, these data along with all available wolf-caribou information from the study area will be included in several manuscripts submitted for journal publication.

p. Seasonal Movements, Distribution, and Fidelity to Calving Grounds

Caribou Winter Distribution:

The following is excerpted from Fleischman (1990):

> Distribution of radio-collared cow caribou during April and May (prior to calving) remained relatively constant from 1979 to 1989. In contrast, October-March distribution changed substantially (Fig. 2) [see Figs. 10 and 11 this report].
>
> During the winters of 1978/79 through 1980/81, caribou were found in the eastern foothills (EFH) throughout the entire winter. In addition many caribou were located on the Gold King Benches (GKB) in the center of the range, but beginning in March, most of the caribou on the GKB joined the others in the east. Movement of individual caribou between the EFH and the GKB occurred both among winters and within winters.
>
> Beginning in 1981/82, few caribou used the EFH from October through January. Instead, most of the herd remained west of the Wood River (areas GKB, UTC) [upper Tatlanika Creek] until moving east in February or later (Fig. 2) [see Figs. 10 and 11 this report].
>
> In October of 1983, for the first time in recent years, DCH caribou moved far west of the Totatlanika River nearly to the Nenana River (area WFH) [western foothills]. This was followed by a rapid retreat eastward so that by 9 November most of the herd was in the foothills and on the flats between Dry and Delta Creeks (areas EFH and ETF) [eastern Tanana Flats].
>
> Few data are available for 1984/85, however from 1985/86 through 1987/88 most caribou continued to use the WFH during and after the rut. They remained there until December or January, at which time they moved back to traditional winter ranges GKB and EFH. As in previous years, by 1 May nearly all cow and yearling caribou were in the EFH near the calving ground.
>
> An unprecedented movement of cow caribou onto the western Tanana Flats (including area LTC) [lower Tatlanika Creek] occurred in October of 1988.

> Approximately one-third of [the] radio-collared cows remained there until March 1989.
>
> Winter distribution of mature bulls is less well documented. Apparently, in most years, they were largely segregated from the rest of the herd, farther west and/or north. Bulls remained in the northwestern part of the range when cows and yearlings returned east in late winter.

The Calving Period:

From 1980 through 1987, 183 of 186 calves born to DCH and YCH females were found in 2 disjunct areas (<u>see</u> Figs. 2-9 in Valkenburg et al. 1988): the Little Delta River/Delta Creek area (Area No. 1; 2,020 km^2) and the Yanert/Wood River area (Area No. 2; 450 km^2). Two of the 3 calves found outside Area Nos. 1 and 2 were produced by primiparous DCH cows (age 36 months) in an area used by the herd during the preceding winter. The 3rd calf was with a YCH female on a plateau south of the Yanert River.

Between 1980 and 1987, the total range of the DCH increased from 8,000 km^2 to 10,800 km^2. Range of the YCH was about 1,500 km^2, overlapping that of the DCH.

From 1980 to 1987 over 98% of all parturient radio-collared DCH females calved within Area Nos. 1 and 2; however, a majority (>50%) of the radio-collared females have not calved within the MCA (the MCA is essentially the traditional calving area described in the Study Area section, <u>see</u> Valkenburg et al. 1988 for greater detail) in any year after 1983. In 1982 and 1983, deep snow (>10 cm) for that time of year covered the MCA throughout May, and most caribou calved on the northern periphery of the area where snow was patchy or absent. In 1986, 12 of 29 parturient DCH females calved within the MCA, and at least five more moved onto the MCA within several days after they had calved. In 1987 about 50% of the collared parturient DCH females calved on the Upper Wood River within the area normally used by YCH females (Area No. 2).

We first detected calving by DCH caribou in Area No. 2 in 1983, when 2 parturient and 2 nonparturient radio-collared females (>24 mos. old) used Area No. 2 (note: numbers differ slightly from those reported by Davis et al. [1986] because of slight changes in definition of calving date and areas for this paper). From 1982 through 1987, Area No. 2 was frequented during the calving period by both radio-collared and uncollared 12- to 24-month-old DHC caribou.

The 8 YCH females usually calved in Area No. 2, but there were notable exceptions. In one year a YCH female calved on a high plateau south of the Yanert River. A 2nd YCH female (No. 102368) calved in Area No. 2 in 1981 and 1982 and then calved in Area No. 1 from 1983 through 1987. A 3rd YCH female (No. 102366) calved in Area No. 2 and remained year-round in the Yanert River drainage from 1981 through the summer of 1985. She did not produce a calf in 1986, and from November 1985 through 2 May 1987 she remained south of the Alaska Range in the upper Nenana and Susitna River drainages with about 200 caribou assumed to be members of a discrete resident herd (Pitcher 1987). Between 2 and 15 May 1987, she traveled >70 km across the crest of the Alaska Range and returned to Area No. 2 where she calved.

We verified affinity to a specific calving site by one DCH female, but we may have underestimated birthing site affinity because our surveys were too infrequent to ascertain most birth sites. However, most workers experienced with barren-ground caribou behavior believe that affinity for birth sites is low.

Calving Distribution of Primiparous, Multiparous, and Nonparturient Females and Males:

Within Area No. 1, primiparous DCH females were no more likely to calve outside the MCA than multiparous females ($\underline{P} > 0.1$, $t = 0.33$, $df = 44$). Excluding replicates, 13 of 37 (35%) of the primiparous females calved outside the MCA and 14 of 37 (38%) of the multiparous females calved outside the MCA.

During the peak of calving from 1979 through 1987, 82% of the 99 locations of nonparturient radio-collared DCH females >12 months old were within Area Nos. 1 and 2. Yearling DCH females were no more likely to be outside (36 inside vs. 43 outside) Area Nos. 1 and 2 than nonparturient DCH females older than yearlings (45 inside vs. 56 outside) ($\underline{P} > 0.1$, $t = 0.43$, $df = 57$). In contrast, 4 of 6 locations of nonparturient YCH females were outside Area No. 2 in the Yanert River valley in the lowland spruce forest.

Eight of 30 locations of radio-collared DCH males during May were within Area No. 1, and none were within Area No. 2. Until June most males remained on winter ranges at lower elevations (often in spruce woodland or muskeg habitat) to the north and northwest of Area No. 1; YCH males also remained on their winter range, occupying similar habitats in the lower Yanert Valley. Furthermore, the sex ratio from composition samples on the calving areas never exceeded 5 males:100 females in late May, whereas samples during the rut indicated 40-50 males:100 females in the DCH and 70:100 in the YCH.

q. Dispersal and Population Dynamics in the DCH and YCH

In terms of demographically measurable emigration or immigration, no dispersal was detected from monitoring radio-collared caribou in the study and adjacent herds. However, dispersal is presently a vague concept in caribou ecology, even though it is central to population dynamics theory.

r. Comparative Food Habits of the Delta, Yanert, Denali, and Fortymile Herds

Samples sent to CSU for analysis were unavailable for this report. These data will be included in manuscripts emanating from this report that will be submitted for journal publication.

DISCUSSION

a. Census of the DCH and YCH

Yanert caribou were first collared in April 1981, and censusing in 1981 and 1982 indicated that our methods could provide acceptable population size estimates for both herds as discrete entities. However, from 1985 through 1990 overlapping distribution of the DCH and YCH in May and June confounded census results for either one as discrete populations. Rather, the censuses best estimated the combined population for the 2 herds.

A census of caribou closely associated with the radio-collared Yanert caribou located 335 caribou in 1985. Davis and Valkenburg (1983) reported that a census of caribou associated with 7 radio-collared YCH caribou in 1982 resulted in a count of 244 caribou. In contrast, a census consisting of an intensive visual search of the entire range of the YCH located 680 caribou. It is possible that the 1982 visual search located some DCH caribou in the range of the YCH, even though the distribution of radio-collared DCH suggested that this was unlikely. Two possible conclusions from the above discussion are that (1) an intensive visual search of the YCH's range during the 1985 census would have located more than 335 caribou in the YCH's range, which would imply a larger minimum population estimate for both the YCH alone and the DCH and YCH combined and (2) the YCH population size could have exceeded 335 because some YCH caribou were located with DCH caribou outside the range of the YCH and were widely separated from the radio-collared YCH caribou. The latter conclusion would imply a larger minimum population for the YCH but probably no change in the combined population size estimate of the DCH and YCH. We believe the 2nd conclusion is less likely.

When we compared the 1985 and 1986 census results, the data suggested a minimum decline of 279 caribou (8,083 vs. 7,804) in the DCH and YCH combined. However, past experience has shown that we cannot accurately detect population size trends by comparing 2 consecutive herd-size estimates. For example, Davis and Valkenburg (1985a) reviewed census data that suggested a lower combined herd size in 1984 (6,260) than in 1983 (6,800-7,229) and 1982 (7,335). For the 1984 population to have increased to 8,083 in 1985 is inconsistent with recruitment and harvest data. In retrospect, the most plausible explanation is that the 1984 census results underestimated the population.

It should not be inferred that herd growth ceased or became negative from 1985 to 1986 solely on the basis of the 1985 and 1986 census results. Census results from 1987 and population modeling using empirical harvest, recruitment, and natural mortality data suggest otherwise. Our census methodology is insufficiently refined to permit calculating a statistical confidence interval for each of the census estimates. We believe that "realistic" confidence intervals would probably be sufficiently broad to preclude demonstrating population size changes between any 2 consecutive years.

When we considered just the YCH alone, the June 1986 census contributed little to an improved estimate of population size; however, on 22 October 1986, 570 caribou were classified according to sex and age in the YCH's range. The area sampled contained all radio-collared Yanert caribou, except one that was in the range of the Nelchina Caribou Herd, and no radio-collared DCH caribou; so we believe that 570 constitutes a known minimum estimate of the YCH's size. A critical reexamination of past estimates of the size of the YCH, which included estimates ranging up to 900, suggests little concrete evidence that the YCH ever contained more than 600 caribou. Insights about seasonal mixing of the DCH and YCH in recent years have caused us to suspect that DCH caribou may have been present on the few occasions in the past when we had estimated more than 600 caribou in the range of the YCH.

During the 1987 census, distribution of the radio-collared DCH caribou overlapped that of the YCH caribou; this factor made it difficult to estimate the number of caribou in either the DCH or YCH alone. We attempted to estimate the YCH population size during the rut, but we aborted the attempt because approximately one-third of the radio-collared DCH caribou were within the YCH distribution at the time.

Estimated herd size of >8,500 for 1988 was clearly conservative. Before all radio-collared caribou had been located and a portion of the census area could be searched, a huge storm prematurely terminated the census. Consequently, several hundred caribou known to be in the area between Cody Creek and Mystic Mountain at the time of the census on 15 July were never counted. Also, at least 1 radio-collared caribou (apparently associated with many others) was at the head of Dry Creek at the time of the census but was not located because of the storm.

The DCH and YCH were apparently partially intermingled when censused in 1989. The number of caribou enumerated during the census was 10,690. We suspect that the YCH contains approximately 600 caribou; the rest are members of the DCH.

The history of population size changes for the DCH dates to the late 1940's and early 1950's, when the herd contained no more than several hundred caribou (Scott et al. 1950, Olson 1957). Caribou rapidly increased during the late 1950's (Olson 1957,

1958) and through the mid-1960's (Skoog 1963, 1968). P. Shepherd observed approximately 1,500 and 3,000 caribou in 1957 and 1959, respectively (Gasaway et al. 1983). Between 1963 and the late 1960's approximately 5,000 caribou resided year-round in the range of the DCH, including the present range of the Macomb herd (Skoog 1968). The herd apparently began declining in about 1970. A population estimate in 1973 indicated 2,400 caribou. In 1976 the herd numbered approximately 1,500-2,000, based on aerial surveys and extrapolations from recruitment rates. The population probably began to increase when recruitment increased during 1976. This change coincided with wolf removal and began 3 years after hunting had ended. The 1979 population estimate was 4,191.

Bergerud (1980) has calculated that the theoretical maximum growth rate for caribou is r = 0.30. Annual herd growth has approached this only in transplanted herds, and growth of much over 20% is uncommon, even under highly favorable circumstances. Herds with good recruitment (>20% calves in the fall) and adult survivorship (>90% annual survivorship) can obviously sustain harvests of >10%. Harvests of herds with moderate or high predator:caribou ratios must be restricted to perhaps <5% and bulls only, or the herd will decline.

There were no censuses of the DCH between 1973 and 1979, so conjecture becomes involved in discussing the rate of population change during the period. However, frequent censusing since 1979 allowed for data-based calculations of rate of change. The exponential growth rate between 1979 and 1982 was r = 0.18. After hunting increased, growth rate slowed and the r for 1979 to 1989 was 0.10 (Fig. 2).

b. Determining if All Caribou Photographed During Censuses Appear as Discrete Images

As stated earlier, no field work was accomplished on this objective because of lack of funding. This question remains of high importance, given the widespread and increasing use of aerial photocensusing techniques, particularly the use of oblique-angle 35-mm photographs of large herds that necessitate small-scale images.

c. Sex and Age Composition

Sex and age composition was estimated annually and showed several expected trends. The bull:cow ratio declined continuously in response to the selective harvest of males. The cow:calf ratio in the fall declined concurrently to increases in population densities and wolf abundance during the study.

d. Yearling Recruitment

For the 3 May 1985 fixed-wing survey data, the ratio of 51 short yearlings:100 older than short yearlings suggested excellent overwinter calf survival. However, the entire sample was obtained near Iowa Ridge and may have contained the portion of the herd with the highest short yearling:older caribou ratio. No late-winter herd composition data were obtained for the YCH in 1985.

The 20 April 1986 composition survey of the DCH that resulted in a short yearling:cow ratio of 31:100 was probably biased. Although we attempted to obtain a representative sample based on locating radio-collared caribou, we clearly did not obtain unbiased data. For example, radio collars were not proportionately distributed among all sex and age components of the DCH. No radio-collared males or short yearlings were present in the herd, and we believe that male short yearlings were underrepresented among the caribou associated with the adult females. The short-yearling sex ratio in our sample was 39% males and 61% females. We expected a 50:50 sex ratio, so we concluded that we undersampled male short yearlings. When we adjusted our observed short yearling:cow ratio (assuming a 50:50 sex ratio of short yearlings), the ratio was elevated from 31:100 to 38:100. Based on subsequent analysis, it is probably unrealistic to expect a 50:50 ratio; apparently mortality is disproportionately higher for males throughout the 1st year of life than for females (Davis et al. 1988).

e. Precision and Accuracy of Yearling Recruitment Surveys

McLean and Heard (1988) investigated the best way to define a sample unit and the best method for estimating the precision of calf:cow ratios. They also tested for sampling biases by comparing calf:cow ratios from arbitrarily selected sample units with sample units based on caribou spatially close to radio-collared cows. Calf:cow ratios were calculated from field classifications of caribou in the Bluenose herd from 7-17 March 1986 and 3-14 March 1987. Estimates of calf:cow ratios and their standard deviations were compared, using cluster analysis procedures and the jackknife technique.

In 1986 the estimate for the calf:cow ratio in groups associated with radio-collared cows was significantly lower than the estimate for arbitrarily selected groups. In 1987 the opposite was true. In 1986 the difference between estimates could not be attributed to observer bias or the effects of group size, location, or the proportion of males in the group; however, in 1987 location and percentage of males in the group had a significant effect on the calf:cow ratio.

McLean and Heard (1988) concluded that about 30 sample units (i.e., representative groups of about 100 caribou), provided an acceptable estimate of the mean and standard deviation of the calf:cow ratio. The significant differences between the ratios from the 2 methods of group selection were not fully explainable. The radio collars led the sampling team to locations that would not have been sampled by arbitrary group selection. The data suggested that groups sampled farther from their winter range and groups with fewer bulls had lower calf:cow ratios, probably because some calves stayed behind with the bulls when their mothers began migrating to the calving ground. It was therefore recommended that spring composition counts be conducted before spring migration begins.

f. Natality and Rate

Graphic depiction is the most concise way to present our concept of the relationship of population density to natality for Alaska caribou. We contrast the classic textbook relationship of natality for white-tailed deer (*Odocoileus virginianus*) (McCullough 1979), which is linear and inversely density-dependent (Fig. 12), with what we envision for Alaska caribou, which does not appear to be either linear or sensitively density-dependent throughout the density ranges for which credible data are available.

The birth rate is the product of the litter size times the pregnancy rate. Because caribou seldom have twins, the birth rate is simply the pregnancy rate. In caribou the pregnancy rate is mostly influenced by the age of puberty, which may be related to condition, but it is not simply a function of body weight (Davis et al. 1990).

Birth rates have varied less than the natural mortality rates through both the decline and growth phases of the Alaska populations. Caribou generally come into estrus at about 29 months of age, but with good nutrition some can conceive at 17 months of age. Natality rates in Alaska seem to follow the generalizations from the literature.

The fertility and birth rates in caribou are usually about the same from year to year (Skoog 1968, Parker 1972, Dauphine 1976, Bergerud 1971). Bergerud (1980) reported that the average pregnancy rate for 8 herds of caribou 2-1/2 years and older was 82%. The average percentage of parous females in 7 herds was 86%. However, in some years disease or poor nutrition can cause high intrauterine mortality in some herds (McGowen 1966, Neiland et al. 1968, Skoog 1968), and the birth rate drops relative to the fertility rate. There is a limit to the ability of caribou to maintain relatively constant fertility and birth rates (Thomas 1982).

The number of females reaching sexual maturity governs the potential rates of natality within a population. Free-ranging caribou calves are seldom bred. It is unlikely that females bred as calves could produce and rear young successfully, because they are physiologically and probably psychologically unsuited for the task. Even the yearling females in many populations are not ready to be mothers. They usually lack the necessary fat reserves, and they are still growing during the 2nd winter of life. Also, young, primiparous mothers may lack the psychological adjustment for calving, and the subsequent mother-young bond either does not develop or is weak (Skoog 1968, Miller and Broughton 1974). Most females have to live at least 3 years before they successfully produce and rear their young. Although the reproductive rate fluctuates only moderately, annual yearling increments to the population often fluctuate markedly (Miller 1982).

g. Validity of Using Radio-collared Cows to Estimate Herd Natality

In using a sample of radio-collared cows to estimate herd natality, the implied assumption is that the age distribution of the radio-collared sample is identical to that of the population at large. Estimated natality from as few as 22 radio-collared cows produced estimates that were not significantly different from estimates from samples of the herd ranging from 482 to 2,052 (Table 5). A major appeal of using already collared cows to estimate natality is only the several hours of fixed-wing monitoring that is required, compared with a costly helicopter survey of the herd at large. Also, knowing the age distribution of the radio-collared sample can help circumvent the biases often encounterd by segregation (often by age and parturition status) of caribou at calving time; for example, large numbers of apparently subadult caribou (i.e., 24 to 36 mos. of age) are often clumped during calving. Parturition rate is characteristically quite low for such aggregations.

h. Reproductive Cost of Birthing When 24-36 Months Old and/or for Several Successive Years

The following discussion is from Davis et al. (1988). Although the data in Figs. 3 and 4 do not provide a clear evaluation of "pregnancy resting" in the Delta Herd, it is unlikely that this phenomenon is important if lactation cost over summer, rather than merely producing a calf, is the mechanism resulting in insufficient body condition to breed during the fall rut. In herds such as the Delta and Denali, early calf mortality is high, resulting in few cows that support a calf through the summer.

The likelihood of having a calf survive in successive years is the product of the annual calf survival rate times the number of years. If calf survival to fall is only 0.5, then the likelihood of having a calf survive in 2, 3, or 4 successive years is 0.25, 0.12, and 0.06, respectively. If sequential successful calves are necessary to induce pregnancy resting, then it is unlikely to occur in the Delta and Denali herds. We did, however, detect considerable variation in parturition frequencies among individuals. For females ≥ 3 years old, the mean parturition rate was 87 ± 13% and ranged from 0% to 100%. Even if pregnancy resting is important, individual variation may be so great as to mask its effects on productivity.

Working with bison (Bison bison), Lott and Galland (1985) employed known reproductive histories of individuals to test the hypothesis that a commonly observed reproductive rate was the result of each cow calving for 2 successive years, skipping a year, then repeating that 3-year cycle. Their records revealed large individual differences in fecundity, and they concluded that the commonly observed reproductive rate could be alternatively explained by some cows calving several successive years while others calved rarely or never.

That fecundity can vary among individuals has important implications for modeling. For simplicity, many demographic and nutritional models implicitly assume that individuals are identical (i.e., clones). This assumption does not appear tenable, given the huge and increasing evidence for polymorphism in practically all species, including caribou (Davis et al. 1986). It is entirely possible that fecundity could vary by phenotype (or genotype) partially independent of nutritional status. Alternatively, a large-skeletoned individual (e.g., a dispersal phenotype in sensu [Geist 1983]) could weigh more than a smaller skeletoned (maintenance phenotype) individual in the same population but be in poorer body condition, which would confound using weight as an index to condition. Geist's (1983) dispersal and maintenance phenotypes present one mechanism by which the relative proportions of different phenotypes might occur in a given population over time.

i. Cohort-specific Pregnancy Probabilities for Cows 24 or 36 Months Old

This objective was discussed in Davis et al. (1990). In the Delta Herd, the proportion of 24-month-old radio-collared females that were parturient varied as follows: 67% (8/12) for the 1978 and 1979 cohorts, 5% (2/37) for the 1980 through 1983 cohorts, and 0% (0 of 17) for the post-1983 cohorts.

We did not determine any relationship between live weight at 7-12 months and the probability of being pregnant at 24 months of age. The mean weight of all calves (7-12 months of age) that became pregnant at 24 months of age was $\bar{X}$ = 62.3 kg (n = 7, SD = 5.4), compared with $\bar{X}$ = 61.2 kg (n = 83, SD = 5.4) for all calves in the sample (Table 12). Further, in the highly parturient 1978 cohort, the $\bar{X}$ weight of the cohort was 61.3 kg (n = 11, SD = 3.7), not significantly different from the entire sample mean (Table 12). The range of weights of the parturient females was 55.9 to 68.2 kg. Thirty nonparturient females equaled or exceeded the mean weight of 62.3 kg for parturient females. Also, 9 nonparturient females were heavier than the heaviest parturient female (i.e., 68.2 kg).

Given that our data do not indicate a relationship between weight at 7-12 months and the probability of being parturient in 24-month-old females, we decided to look for other variables present when early puberty was highest. We looked at the relationship between total population size, density, and the relative abundance of adult males for the Denali (not in Table 11) and Delta herds when the rate of early puberty had been high and for the Delta herd after the rate had become zero (Table 11). We also looked at wolf and grizzly bear:caribou ratios. Early puberty occurred in the Delta herd at 67% frequency when the population density was $<0.5/\text{km}^2$; it occurred at 40% frequency in the Denali herd at a density of $\leq 0.3/\text{km}^2$. Unfortunately, the quantity and quality of forage present was not quantified for the periods when early puberty occurred.

Bergerud (1980:557) commented as follows regarding early puberty:

> With caribou the age of puberty varies little between years within established populations (Bergerud 1971, Dauphine 1976). However, when animals have been introduced into new ranges with longer growing seasons, invariably more yearlings reach puberty than on established ranges. Preobrazhenskii (1968) states that reindeer fawns reach puberty if there is good nutrition in autumn. These data suggest that nutrition during the first summer-of-life makes the main contribution to early puberty. Thus the growing season would be more important than the winter diet in attaining puberty.

j. Rutting Weight and Natality Rate in 24- and 36-month-old Cows

This objective was discussed in Davis et al. (1990). Reimers (1983*b*) concluded the following:

> The pregnancy status of a female may be predicted once her rutting weight is known. In wild reindeer, when a female dressed weight (W) increased from 25 to 30 kg, her probability (P) of being pregnant increases from 0.49 to 0.78 (i.e., 49% to 78%) according to the equation: $P = 1 - e^{[-0.169(W-21)]}$ (Reimers 1983*b*). Therefore, from knowledge of the weight distribution of females in a population, its pregnancy rate may be calculated.

Predictions from Reimers' equation did not compare well with our field data. Reimers' original data (1983*a*:213, Table 2) resulted in an estimated pregnancy rate of 0.88 for reindeer ≥ 3 years old at the time of calving, the same as our observed rate for Delta caribou in that age group. The mean dressed weight of Reimers' reindeer in this age category was 33.4 kg or 0.57 that of Delta caribou. When the 0.57 correction factor was applied to mean dressed weights for Delta caribou that were 17 or 29 months old during the rut, the subsequent predicted pregnancy rates were 0.0 and 0.22, respectively, which generally agrees with field data. Therefore, Reimers' (1983*a*) prediction equation may apply for other than Norwegian reindeer, if a "correction factor" is applied to account for herd-specific differences in *Rangifer* body weights. Additional herd- and time-specific correction factors may be required to consider genetic effects, phenotype ratios, and environmental variables.

While reviewing Reimers' (1983a, Table 2) original data, we arrived at 2 conclusions that differed from those of the author. First, age may be an important influence on pregnancy rates. For the range of overlapping in dressed weight (18-26 kg) between calves and older animals, zero of 32 and 13 of 31, respectively, were pregnant. Hence, calves did not get pregnant, regardless of body weight at the time of the rut. Parallel comparisons of yearlings and older reindeer over the range of overlapping (27-47 kg dressed weight) also indicated that yearlings had a lower probability of becoming pregnant (14 of 32) than did older reindeer (175 of 215), regardless of body weight. We suspect that age plays an important role, in addition to body weight, in determining pregnancy probabilities.

Reimers (1983a: Table 2 footnote) reported that only calves from Rondane, Hardangervidda, and Snøhetta were weighed. He implied that calves from North and South Ottadalen were heavier. Reimers (1983b) reported that domestic reindeer have influenced both the North and South Ottadalen herds. "The domestic reindeer company. . .discontinued its activity in 1964. . . . Some animals were left behind in South Ottadalen and some (402 animals) were moved to North Ottadalen and given the status wild reindeer." So the variable of domestic vs. wild reindeer must also be considered if the argument is raised that the heavy calves from North and South Ottadalen might differently affect the data in Table 2. Bergerud (1980) reported that, "Jackson (1892-1908) suggests there has been some selection for early breeding in reindeer. Preabrazhenskii (1968) states that early breeding in reindeer fawns has a hereditary basis."

We believe that the prediction of 100% pregnancy at 48+ kg carcass weight is less tenable than a model showing no significant difference in pregnancy rates above 30 kg carcass weight. Reimers' (1983a) own data indicate an 88% pregnancy rate for this weight range and no reason to believe that pregnancy rates reach 100% for heavy reindeer. Reimers (1983a) reported 100% pregnancy for small samples of the large-bodied North and South Ottadalen reindeer, but interpretation of these data is confounded by influences of the domestic reindeer that founded these populations (i.e., possible selective breeding).

Although weight may often be a good index of reproductive condition for cervids, there are exceptions in the literature. Dusek et al. (1987) showed a higher reproductive level in a herd of white-tailed deer with smaller body weights than in another herd with larger female body weights.

In summary, weight may reasonably predict pregnancy in some populations of Rangifer (e.g., Reimers 1983a). However, we believe that one or more additional variables must be considered in conjunction with weight to create a predictor that might universally predict pregnancy probability in all Rangifer populations.

k. Harvest by Hunters

Data collected from hunters in the field from 1986 through 1988 indicated that the reporting rate by successful and unsuccessful hunters via the hunter report card-harvest ticket system grossly underestimated the total harvest (McNay 1988, 1989, 1990).

In 1988 the reported harvest in Subunit 20A from both the general season and permit hunts was 441 caribou by 698 reporting hunters. However, reporting rates have been low in recent years for both successful and nonsuccessful hunters. The total estimated harvest of 555 caribou by an estimated 1,085 hunters during 1988 was derived from harvest reports and from 186 caribou hunters who had been interviewed in the field between 1 and 15 September. Seventy-six of 103 interviewed successful hunters (74%) returned harvest reports. During 1986 and 1987, when there was no effort to encourage hunter reporting through advertising, the estimated reporting rates by successful hunters were 56% and 57%, respectively. Based on his experiences during hunter interviews, McNay (1990) believed that caribou that are crippled and not recovered by hunters contributed an additional 10-20% to the mortality induced by hunters during September. Modelers must be aware of the need to adjust reported harvest rates to more accurately reflect total hunter-induced mortality in the study population.

l. Mortality

Bergerud (1979) offered the following summary, which roughly applies to the Alaska caribou situation as we know it:

> In contrast to a consistent birth rate the mortality rate of caribou calves in many herds in North American caribou was variable and exceeded 50 percent and was frequently as high as 80-90 percent. Most of the mortality occurred in the first few months of life and the greatest mortality factor was predation. In two herds monitored for more than 10 years some calves probably starved in two and possibly six winters. This starvation was not due to an absolute shortage of food but resulted from deep snows and ice conditions. The annual adult mortality rate is estimated to vary from 7 to 13 percent (mean 10 percent) if predators are common and 5 to 6 percent if predators are rare. In general, herds without predators showed rapid population growth approaching the ^{r}m of the species of 0.30; whereas, populations coexisting with predators showed little or no growth and if also hunted usually show population decline.

Detailed demographic data have been obtained for Alaska caribou primarily during the mid-1970's and 1980's, a period characterized by low and increasing phases of populations. During that time, natural mortality and human-induced mortality have varied more and have influenced caribou herd demographics more than have natality changes.

Serial calf:cow ratios measure only relative change in the proportion of calves, so they are only an index of the rate of calf mortality. Determining the actual mortality rate of calves requires ascertaining the change in absolute numbers of calves over time. Calf mortality rates estimated from serial calf:cow ratios can be refined by adjusting for the loss of cows during the interval between acquiring ratios. For our data set, the adjustment for overwinter calf mortality, estimated from October and April calf:cow ratios, would amount to only a couple of percentage points.

An additional complication is that some calves, particularly males, separate from the females during late winter and remain with the adult males, which do not migrate to the calving grounds. Our April composition data always show that bulls are underrepresented, so it follows that calves may be as well. We have no means of objectively correcting for the missed calves, but even a modest increase in the calf:cow ratio would suggest little difference in overwinter mortality between calves and older cohorts.

Our data from radio-collared caribou suggest that natural mortality of Delta caribou was similar among the 8-12, 12-24, and >24 MOC's. Natural mortality of all cohorts was higher for males than for females, which is consistent with the literature (Bergerud 1978) and our expectations. In contrast, similar mortality rates among >5-month-old calves, yearlings, and adults was unexpected and is inconsistent with the literature on cervids, especially that on moose. When we extrapolate to caribou from the literature, particularly for age-specific mortality and predator-prey relationships, we rely most on the moose literature. We believe this is common among caribou biologists. The mean mortality rate for moose <24 months old is clearly higher than that for adults (Peterson et al. 1984a, Ballard et al. 1987).

It is imperative to consider our findings on rates and patterns of natural mortality in proper context. Extrapolating too broadly from our results may prove counterproductive. Our mortality rates were obtained from a herd that is part of a multi-prey/multi-predator system. Also, during the period of study, growth rate of the herd varied from rapid increases to near stability, resulting from increasing harvests and predation. Nutrition and weather appeared to be favorable during the study period.

Although there may be some utility in extrapolating to caribou from the conceptual models of moose ecology, we believe the practice may be counterproductive, particularly with regard to patterns of mortality and predator-prey relationships. Clearly, there is no substitute for empirical data.

m. Wolf:Caribou and Grizzly Bear:Caribou Ratios

In a past progress report, Davis et al. (1987) presented the data base and rationale for calculating and discussing wolf:caribou and grizzly bear:caribou ratios in both the DCH and YCH. Although we have obtained additional caribou census data and updated estimates of wolf abundance, the general discussion in our last report does not warrant updating. Wolf numbers, pack distribution, harvest rates, necropsy data, radio-cesium 135 burdens, and food habits will be reported in manuscripts prepared for journal publication.

In 1985 the wolf:caribou and wolf:caribou equivalents ratios of the YCH and DCH were similar enough to justify considering the 2 herds as 1 entity to simplify iterations regarding predator:prey ratios. A comparison of the wolf:caribou equivalents ratio for all of Subunit 20A prior to wolf control in 1976 with the comparable ratio in the fall of 1985 follows:

1975: 239 wolves, 2,900 moose, 2,000 caribou = 1 wolf:45 caribou equivalents

1985: 195 wolves, 8,500 moose, 8,000 caribou = 1 wolf:172 caribou equivalents

Keith (1983) presented a model (i.e., equation) that allows calculation of the annual ungulate kill per wolf that would stabilize an <u>unhunted</u> ungulate population as follows:

$K = \underline{N}\,(L - 1)$
where, K = ungulate kill per wolf annually
$\underline{N}$ = ungulate numbers per wolf in spring before births
L = finite rate of ungulate increase annually (assuming no wolf predation)

For the DCH and YCH combined, assume:

$\underline{N} = 40$ to 44 (for caribou only)
$L = 1.20$ to 1.25
therefore, best case scenario is $K = 44\,(1.25-1)$; or $K = 11.0$
therefore, worst case scenario is $K = 40\,(1.20-1)$; or $K = 8.0$

The above calculations suggest that if all wolves in the range of the YCH and DCH each killed 8 caribou annually, then wolf predation would stabilize the size of the DCH and YCH. This conclusion assumes no hunting of the caribou and no predation by other predator species. Another way of looking at this calculation is that 150 wolves, each killing 8 caribou per year, would kill 1,200 caribou annually.

If we assume that each wolf in the range of the DCH and YCH eats an average of 8 caribou per year, this equates to an assumption that one-third of the annual diet of wolves consists of caribou (Kuyt 1972). Gasaway et al. (1983) reported that the stomach contents of 156 wolves taken from 1975 through 1979 throughout Subunit 20A revealed frequencies of occurrence as follows: 55% for moose and 12% for caribou. It is difficult to equate the frequency of occurrence data to differential rates of consumption between moose and caribou for reasons such as differences in size of prey and caribou not being present in much of the area where the 156 wolves were killed. When the 156 wolves were collected, Subunit 20A contained a mean of about 3,300 moose (the 1977 level) and about 2,000 caribou, a ratio of 0.61 caribou:1 moose. In 1985 the ratio was about 1 caribou:1 moose (8,000 caribou:8,500 moose). It seems reasonable to expect a higher proportion of the diet of wolves to be caribou in 1985 than in 1976.

The role of predation on Subunit 20A caribou by grizzly bears and predators other than wolves is not well understood. Our study of mortality rates of radio-collared caribou and ongoing grizzly bear research (Reynolds et al. 1987) should elucidate the relative importance of predation by grizzlies and wolves. Results will be discussed in manuscripts prepared for journal publication.

n. Wolf Abundance and Rate of Caribou Predation

The following discussion speaks tangentially to the specific subject of wolf abundance and caribou predation; the discussion is based on our literature review and synthesis of wolf-caribou relationships. While there seems to be little dispute that under natural conditions wolf predation is the major process that suppresses caribou herds at low densities, additional field information will be required to fully resolve questions about what role predation, food limitation, and dispersal play at high densities.

Because the relative rate of predation on caribou may increase when caribou populations are at low levels (if predators have not declined proportionally), management to increase caribou may well involve predator control and more restrictive harvests. Suffice it to conclude that predator management is an integral part of caribou population management in many areas, which further increases its complexity.

Predator Pit:

The term "predator pit" was introduced into caribou ecology through discussion of multiple equilibria theory. The predator pit involves the theoretical concept that an upper-level stable equilibrium exists (e.g., from intraspecific competition for food) until disruption by "catastropy" occurs. For example, densities can be lowered by events such as emigration, severe weather, or excessive hunting. Because of a lowered density, a population would crash because of heavy predation, despite high natality. Theoretically, a lower, stable equilibrium (the predator pit) would occur as predators switched to alternate prey. Unfortunately, use of the term predator pit has been expanded to include situations where caribou populations are low or reduced and predation identified as a significant limiting factor.

While it has been conjectured (Skoog 1968, Haber and Walters 1980) that dispersal (immigration) from another herd may, in the past, have been the most important mode of release for Alaska-Yukon caribou herds at low densities, this was not likely the only mechanism in operation. In many cases release probably involved a combination of events. Following are 3 additional possibilities, each of which involves a reduction in the level of wolf predation (Haber and Walters 1980): (1) wolf numerical response via territory adjustments, (2) wolf functional response via social adjustments, and (3) caribou migrational changes.

Conceptual Models of Predator-Caribou Relationships:

Van Ballenberghe (1987) succinctly summarized what is currently known about moose-predator interactions as follows: "The question is no longer whether controlling effects occur but rather under what conditions they occur and how long such conditions last." That summary statement applies equally well to caribou.

Time lags come into play in many aspects of animal ecology, and in no aspect is the phenomenon more pronounced than in conceptual models of caribou-predator relationships. The model available to most of the lay public, and the most common one in the minds of professional ecologists not current on caribou ecology, is a generalized model for predator-ungulate relationships. At best the popular conceptual model is a general cervid-predator relationships model, most likely extrapolated from outdated information from Isle Royale moose-wolf relationships.

Until the mid-1980's, what have most influenced people's unarticulated conceptual models of predation and caribou population dynamics were results of intensive studies of ungulate ecology and population dynamics that had been conducted where predation had little or no impact (Caughley 1976, Sinclair 1977, McCullough 1979, Clutton-Brock et al. 1982, Houston 1982). Recently, it has become evident that predation may profoundly influence ungulate demography; studies of moose have contributed importantly to this understanding.

Two ecological concepts have probably influenced past conceptual models of caribou-predator relationships more than any others: compensatory mortality and differential prey vulnerability. Whether mortality from predation supplements (i.e., is additive) or replaces (i.e., is compensatory to) other natural mortality and hunting losses has been debated frequently in the literature. Haber (1977) and Peterson (1977) clearly felt that much predation on moose was compensatory, but Gasaway et al. (1983:36) concluded that "In most cases, mortality from predation, hunting, and severe weather has noncompensatory components."

Recent studies have demonstrated that survival of both calf and adult caribou may be severely depressed when predators are abundant. Available data suggest that predation on calf caribou is most likely to be additive, while predation on adults may be mainly compensatory, with the various mortality factors tending to substitute more for each other as moose population densities increase. Clearly, at low caribou densities when predators are abundant, many calves and some adults die that would have survived in the absence of predators, but these relationships may change as caribou densities increase.

Murie (1944) pioneered the concept of differential prey vulnerability in his early studies of wolf-prey relationships. This concept was stressed by Mech (1966), who found that wolves killed only 7.8% of the moose they encountered; none of these moose were 1 to 6 years old. Subsequent studies by Peterson (1977) revealed that snow conditions in winter influenced vulnerability; during a 5-year period of several severe winters, 53% of the wolf-killed moose at Isle Royale, Michigan, were 1 to 5 years old. Calves born following severe winters had reduced growth rates and were thought to be more vulnerable as young adults than calves born after more favorable winters.

Peterson et al. (1984a) recently reviewed data from 10 studies where age had been determined for 702 wolf-killed moose. About 25% of these were 1 to 5 years old. Data from Isle Royale suggested that 26% of 484 wolf-killed moose were in this age interval, but it constituted 58% of the living population (Peterson 1977). Gasaway et al. (1983) showed that predation on adults ≥6 years old declined markedly following a wolf control program, but mortality rates for 1- to 5-year-old moose were zero before and after control. Clearly, young adult moose are not killed by wolves in proportion to their occurrence in the population on a long-term basis.

Peterson et al. (1984b:1351) summarized the interplay between moose vulnerability and moose and wolf population dynamics as follows:

> An increasing moose population is characterized by large, vigorous animals that are less vulnerable to wolves until they are at least 7-8 years old, when age-related skeletal pathology begins to increase. This is the time lag before food supplies for wolves can increase. A longer lag, which will be rather site-specific, is the time required for an increasing moose population to reach a food-limited density, when a major increase in vulnerability to wolves occurs. Functional responses (increased kill rates) and numerical responses of wolves can prompt a prey reduction. Wolves increase to a high plateau, but face a dwindling food supply as culling of the prey population becomes complete.

Many predator species prey on caribou in Alaska. Skoog (1968) stated that predation was the greatest single mortality factor in most wild populations of caribou. The wolf is frequently the predator of greatest impact in most Alaska caribou herds. Although Crisler (1956) and Kelsall (1968) stated that caribou, except the incapacitated and calves, could normally outrun single wolves, Murie (1944), Banfield (1954), Skoog (1968), and other field workers observed that wolves are capable of overtaking healthy caribou. Such feats are not always necessary, as wolves often take prey by surprise or ambush. When in pursuit, wolves also take advantage of any tactical mistakes the caribou may make; for example, leaving areas with hard snow and attempting to cross ones with soft snow. The most interesting aspect of wolf hunting tactics is their ability to run relays and involve several members of the pack in herding and ambushing prey (Miller 1982). Skoog (1968) suggested that wolves can obtain their prey as needed from whatever caribou are available, and that the final selection is made more by chance than by design. Sick and lame animals may be selected, if available, but if the caribou population is healthy and there are few incapacitated individuals, the wolves will take healthy ones. Wolves can and sometimes do control or depress caribou populations (Miller 1982).

The following is paraphrased and adapted for caribou from Connolly's (1978) discussion about predation on ungulates. Predators eat caribou on most ranges where the two coexist. Predation can limit ungulate numbers and is most likely to do so when the ratio of predator-to-prey numbers is high. Mortality studies of big game populations may show predation to be a major cause of loss, but such findings do not necessarily prove that predation actually limits prey numbers. Predators frequently kill young, old, diseased, or other classes of caribou at disproportionate rates, relative to their incidence in the population. However, predation is not restricted to surplus or sick individuals whose death is imminent; healthy animals are taken as well. Carnivores perpetuate a number of parasites that may cause debilitation or death in ungulates, but the role of such parasites in ungulate population dynamics has received little study.

A number of studies have shown that predators limit ungulate numbers, but others have found them to have little effect. The theory that predators stimulate ungulates to maintain higher densities than would be possible without predation is not well-documented. Predation by humans and wolves appears to have limited certain caribou herds in Alaska.

Because of conflicting public attitudes over ungulate and objectives for managing predators, as well as the increasing costs of predator control, careful biologic and economic justifications are required for exercising predator control. In general, predator control is justified in big game management only when it will produce substantial increases in ungulates at reasonable costs and without undue damage to other environmental values. In some cases, control may produce long-range benefits for the predators.

Van Ballenberghe (1987) contributed a good summarization and critique of prevalent conceptual models of moose-predator interactions. His review applies equally well to caribou and is presented, with our elaboration, in the following 5 subheadings.

<u>Single Stable Equilibrium</u>. In essence this view is the balance of nature concept applied to predator-prey relationships; it implies that predation is density dependent over a limited range of caribou densities. The percentage of the population killed by wolves increases with caribou density, until recruitment and mortality are balanced; equilibrium occurs when the finite rate of increase is 1.0. Fluctuations may occur, but the population tends to return to equilibrium; time lags have minimal effect.

Empirical evidence that caribou-wolf equilibria occur is weak, as is evidence that wolf predation is density dependent. Bergerud (1974<u>b</u>) has argued that migration to calving grounds is a strategy of spacing away from wolves, and in essence, the calving grounds constitute refugia from wolves. Hence, theoretically a mechanism is present to allow for stable equilibria; however, the empirical data do not substantiate this.

<u>Multiple Equilibria</u>. Haber and Walters (1980) proposed a conceptual model for caribou interactions featuring multiple equilibria. Caribou were viewed as fluctuating about an upper equilibrium produced by density-dependent reductions in caribou birth rates and predation. This equilibrium was close to that produced by intraspecific competition for food and would persist unless the caribou population density was reduced because of emigration, severe weather, or excessive hunting. At this lowered density, the population would collapse because of heavy predation, despite high natality. Theoretically, a lower stable equilibrium would occur, as predators switch to alternate prey. Van Ballenberghe (1980) criticized Haber's (1977) conceptual

model as it applied to moose and questioned whether multiple equilibria models were appropriate for moose population dynamics.

Connell and Sousa (1983) critically reviewed empirical evidence for alleged multiple stable states in a wide variety of populations and communities. They concluded that all published examples had various shortcomings and that there was no evidence of multiple stable states in unexploited or natural situations. The multiple equilibrium model for moose is alluring because part of it accounts for inversely density-dependent predation during moose declines, but its contribution to a general theory of predation on caribou seems severely limited.

Stable Limit Cycles. These are known to most biologists as "natural cycles." Caughley (1981) stated that stable limit cycles caused by ungulate-forage interactions were an uncommon occurrence. Crete et al. (1981) demonstrated that cyclic moose-wolf interactions were possible for model populations only with constant reproductive rates. Hunting tended to enhance the oscillations. Peterson et al. (1984b) suggested that wolves and moose at Isle Royale may cycle with a period length of about 38 years, and the pattern observed thus far suggested recurring oscillations reminiscent of cyclic fluctuations observed in certain small animals. Whether the Isle Royale interactions are cyclic or merely recurrent fluctuations remains to be demonstrated.

Recurrent Fluctuations. Keith (1983) recognized that time lags in functional and numerical responses of wolves would generate recurrent fluctuations of moose and wolf populations. These would have variable periods and amplitudes, in contrast to the more uniform properties of cycles, and would be characterized by long-term mean densities, rather than equilibrium densities to which the populations would tend to return. Van Ballenberghe (1987) believed that long-term mean densities reflect underlying relationships of wolves and moose to their environment; these include moose-weather-forage interactions and fluctuations of alternate prey. Thus average moose densities in naturally regulated environments may vary spatially and temporally, and efforts to characterize them with one typical density expected to prevail throughout the boreal forest would be unwarranted.

Although theoretical arguments strongly suggest that recurrent fluctuations should occur in naturally regulated moose-wolf systems, empirical data are limited. Few such systems are available for study. The Isle Royale case history indicated that 1 major fluctuation occurred there during the past 30 years. The stage now seems set for this pattern to recur at Isle Royale.

Summary. Most caribou herds are significantly influenced by humans. Behavior of such populations may mimic stable equilibria, multiple equilibria, stable limit cycles, or recurrent fluctuations, depending on the extent of human interference. Nearly any outcome is possible. Similarly, naturally regulated moose-predator interactions in small, confined ecosystems (including small islands) defy prediction. Here, initial conditions and random events play an important role in determining how the predator-prey system behaves, which is a central lesson from chaos theory (Gleick 1987).

Empirical data from individual case histories suggest that recurrent fluctuations are the only model supported. It can be argued theoretically that this is an artifact of several of the models working interactively. The empirical evidence suggests that low, relatively stable equilibria densities of caribou are frequent for periods of time, but there is growing evidence that caribou frequently escape predation and attain high densities.

o. Sex and Age Composition of Predator-killed Caribou

See n. above. We obtained interesting data on this subject that will appear in forthcoming manuscripts for journal publication.

p. Seasonal Movements, Distribution, and Fidelity to Calving Grounds

Winter Distribution:

As the DCH population nearly tripled from 1979 to 1989, cow and calf caribou discontinued early winter use of the eastern half of their range, moving instead farther west and north. Cows and short yearlings consistently returned to the eastern foothills by late winter, whereas mature bulls remained in the west and north until after calving. Heaviest winter use was in the western and central foothills (Figs. 10 and 11).

Fidelity to Calving Areas:

The discussion that follows was presented in Valkenburg et al. (1988) and requires familiarity with the DCH's MCA. Intensive monitoring of calving distribution in the late 1970's and early 1980's seemed to confirm the fidelity of the DCH to the MCA (Davis and Preston 1980; Davis and Valkenburg 1981, 1983, 1984; Davis et al. 1982). Investigators estimated that 75-90% of all calving occurred within the boundaries of the MCA in 1979, 1980, and 1983, and failure of the DCH to calve within the MCA in 1981 and 1982 was attributed to late snow melt. From the late 1950's through 1980, calving apparently occurred annually within the MCA, with little or no calving elsewhere.

Clearly, the 640-km^2 MCA has remained an important calving area for the DCH. Furthermore, during the 8-year study period, the vast majority of parturient DCH females has calved in the 2,020-km^2 of Area No. 1 that encompasses the MCA. That most DCH females did not calve within the MCA between 1980 and 1987 may reflect a change in calving distribution, an increase in herd size, improved knowledge resulting from the use of radio collars, or a combination of these factors. Between the late 1950's and

1979 the DCH was considerably smaller (2,500-5,000) than it was in 1985-87 (7,000-8,000). Prior to 1980 major shifts in calving distribution (e.g., 1984 and 1987) could have gone undetected because surveys were relatively infrequent.

The major shifts in calving distribution of the DCH contrast with conventional concepts of calving tradition and herd identity (Skoog 1968, Davis et al. 1986, Gunn and Miller 1986). In reporting the 1984 shift in calving distribution, Davis et al. (1986) noted that most females returned to Area No. 1 in 1985 and 1986. Most of these females again used Area No. 2 in 1987 when snowmelt was particularly early, although virtually all DCH females were present on (or in close proximity to) Area No. 1 during early May. The caribou that eventually calved in Area No. 2 moved there along the route used since the early 1980's for postcalving movements. In addition, many females that had never previously used Area No. 2 for calving went there in 1987. A "Yanert" female (No. 102368) that "moved" to the DCH in 1982 was not one of those.

A possible explanation for the 1987 shift in distribution during calving may be that caribou concentrated near the retreating snow line, perhaps minimizing predator contact while allowing access to emerging Eriophorum spp. buds. Snowmelt was indeed early in 1987, which could partially explain why caribou that calved in Area No. 1 concentrated farther south than had been observed before (i.e., closer to high mountains). The conditions sought by calving caribou presumably present in southern Area No. 1 were probably also present in Area No. 2 (albeit Area No. 2 has more low-elevation forest and a greater abundance of alternative prey for wolves and bears than the southern portion of Area No. 1). Wolf and grizzly bear densities appeared to be comparable in both areas.

The pronounced difference in the distribution of radio-collared bulls and cows during the calving period suggests that the sex of individuals has the greatest influence on their distribution. More than 98% of the parturient females and 82% of the nonparturient females (regardless of age and calving tradition) went to Area Nos. 1 and 2 during calving; this contrasts with less than 30% for the males. Reproductive status is apparently the next most important influence on calving distribution; over 98% of the parturient radio-collared females were found in Area Nos. 1 and 2. Previous pregnancy may also influence calving distribution of individuals; 2 of 3 radio-collared pregnant caribou that did not calve in Area Nos. 1 and 2 were primiparous 3-year-olds.

The observed distribution of pregnant and nonpregnant females supports the premise that, as parturition approaches, pregnant females forego feeding in areas of high phytomass of nutritious plants in favor of higher elevation and more open habitat to avoid predation. Five of 10 locations of nonparturient YCH females during calving time were in the Yanert River Valley, which was not used by pregnant radio-collared females during calving. In the Yanert valley (elevation about 900 m), dwarf birch and willow leaves emerge by about 25 May in most years, in contrast to emerging 10 days later at calving locations (1,500-2,500 m) chosen by YCH cows.

Perhaps most nonparturient Delta females were in the same areas as parturient females because of the greater availability of lowland tundra in Area No. 1 than in Area No. 2. However, some nonparturient females used the highest parts of Area No. 1, and none were found in the lowest parts (300-400 m) frequented by radio-collared adult males and male yearlings. Presumably, quantity, quality, and diversity of new plant growth were greatest at the lowest elevation.

The preference of DCH females for open habitats, regardless of their reproductive status, could have a phylogenic basis or be a conditioned response to predators. Bergerud (1974b) hypothesized that predator harassment acts as an environmental trigger that causes barren-ground caribou to seek open habitats and form large groups during calving. Observations from the Fortymile Caribou Herd (FCH) may or may not be consistent with this hypothesis. Calving distribution of the FCH has varied annually during the past 10 years, and calving has not consistently occurred in the most open habitat (Valkenburg and Davis 1986). Because there may be no area within or adjacent to the range of the FCH where predator numbers are low, it suggests no advantage to a specific calving area; however, open habitat should still enhance predator detection. Present data are insufficient to critically test the hypothesis for either the DCH of FCH.

Radio-collared DCH and YCH females apparently did not exhibit as much affinity to birthing sites as has been reported for woodland caribou (R. t. caribou) (Edmonds and Bloomfield 1984, Hatler 1986, Pare and Huot 1985, Edmonds 1987). Only 1 DCH female clearly exhibited site affinity; however, it is possible that others exhibited such affinity undetected. Apparently, individuals with different behavioral tendencies may exist within a herd (Davis et al. 1986). Whether these tendencies are inherent in individuals or are facultative responses to the environment is an interesting question. A changing calving strategy by individuals (i.e., from site affinity to nonaffinity or vice versa) could be construed as evidence of facultative responses.

Because of progressive development in the North, it has become increasingly important that we learn how and why caribou select calving areas. It has proven difficult to learn what motivates caribou, because both environmental and phylogenic factors are likely involved as well as variation in individual behavior. With more data on the movements of radio-collared caribou, it has become increasingly apparent that short-term and perhaps long-term shifts in calving distribution are to be expected. Calving grounds are less easily delineated than previously believed, and infidelity of individual females to a designated calving area may be more frequent than implied in the literature. The above observations have important management implications. For example, census techniques may have major limitations, if based on the assumption that all females in a herd use a traditional calving area or that all calving occurs in a continuous distribution. Also, recognition that calving distribution may shift appreciably between years should be considered in formulating strategies to mitigate the impacts of development on caribou. For instance, moderate protection of calving habitat over a large and/or discontinuous area may prove more beneficial to caribou than inviolate protection of a relatively small area.

It is important to maintain access to larger areas for calving than those that may be identified at a narrow time interval. Empirical evidence is mounting to show that changes in snow condition and population size are only two of many possible variables that are apt to affect calving distribution.

g. Dispersal and Population Dynamics in the DCH and YCH

During the late 1960's and early 1970's, many caribou managers in Alaska strongly believed that dispersal (i.e., immigration or emigration) was a frequent and unpredictable influence on caribou herd abundance and distribution. This belief caused management philosophy to seemingly regard caribou as being unmanageable and not responding as predictably to the balance of births and deaths as do moose or other cervids. Hopefully, all managers now recognize that caribou herds most frequently increase and decline as a result of changes in birth and death rates and not necessarily or frequently from dispersal (at least under the conditions present in the 1970's and 1980's).

In the past, dispersal from another herd was thought to have been the most important mode of release for Alaska-Yukon caribou herds at low density (Skoog 1968, Haber and Walters 1980). Dispersal was not likely the only mechanism that operated (if in fact it was involved at all). Following are 3 additional possibilities, each of which involves a reduction in the level of wolf predation: (1) wolf numerical response via territorial adjustments, (2) wolf functional response via social adjustments, and (3) caribou migration changes.

Bergerud's (1980) conceptual model of how dispersal influences caribou populations (Fig. 13) is based on the available literature. It is the most concise model of caribou dispersal that we are aware of. The model can be considered a consensus because the 3 authors who have most discussed dispersal in caribou (i.e., Skoog 1968, Bergerud 1980, and Haber and Walters 1980), have all offered similar interpretations. However, all 3 sets of authors also have proposed that undocumented dispersal have occurred when densities were well below the dispersal threshold in Fig. 13.

In a recent review of the population dynamics of caribou in Alaska, Davis and Valkenburg (In press) concluded that dispersal played no measurable role in the population declines or increases in Alaska caribou herds that were documented with demographic data. They further concluded that during the 1970's and 1980's, the period when quantitative data have been available, observations of dispersal or the lack thereof have been inconsistent with predictions in the literature. For example, the Southern Alaska Peninsula Herd reached a density of >5 caribou/mi^2, and dispersal did not occur. Instead, the population declined, apparently from forage resource limitation (Pitcher and Johnson 1989).

Until additional data accrue, management programs for caribou herds in Alaska should assume that there are few, if any, demographically significant exchanges (dispersals) of caribou among herds under natural conditions. This assumption contrasts sharply with management thinking in the 1960's and early 1970's, when the consensus was that caribou were not "manageable" because of frequent and unpredictable dispersal.

Mass emigrations are not predictable, and it is not known why they occur; i.e., none have ever been conclusively documented. Dispersal may be density related; i.e., a threshold density triggers social intolerance and leads to dispersal of some segment of the population. It is difficult, however, to perceive how a density concept works, because the clumping behavior of caribou on winter feeding sites and postcalving aggregations suggests that caribou are tolerant of high densities (Miller 1982).

For the relative importance that has been placed on dispersal as an important factor in regulating caribou population dynamics, surprisingly little from the theoretical literature has been discussed by caribou workers. Also, the distinction between dispersal and migration in the theoretical literature is often hazy.

Dingle (1982:260) concluded that, "No single factor theory of migration is thus ever likely to be adequate." Cohen (1967) examined migration as a problem of optimal choice between alternatives with randomly varying outcomes. Migration can occur as a "pure strategy" with all individuals migrating or as a mixed strategy with only a portion doing so. Conversely, remaining sedentary is also a possible strategy. A pure migratory strategy is favored when the variance in the viability coefficient of nonmigrants increases; i.e., risks of remaining sedentary become greater and vice versa. If viability coefficients for migrants and nonmigrants are independent, then a mixed strategy is more likely; for example, where the variability in winter survival between years is high. When some environmental cue allows prediction of unfavorability, the population will be expected to respond to that cue by emigrating. Seasonal migration in response to photoperiod is an example. As a final conclusion, Cohen's (1967) model indicates that migration can only be optimumal when survival and reproduction at any one place do not remain constant; if they do, organisms gain no advantage by changing habitats. However, while agreeing that migration is clearly advantageous where habitats are transient and patchy, Hamilton and May (1977) demonstrated that constancy is not necessarily a constraint and that dispersal in stable habitats can also be selectively advantageous.

Parker and Stuart (1976) devised models that consider emigration thresholds from resource patches encountered by given search strategies. They used the concept of evolutionarily stable strategies (ESS's) (Maynard-Smith 1974) and considered optimal investment durations, gain accumulated, and search costs between patches. Various pure and mixed strategies are possible, depending on factors such as competition or resource sharing and ability to access resources. As an example, for patches with decreasing returns and increasing investment, the ESS is usually for all to stay until a critical threshold is reached. Whereupon, individuals should leave at a rate that balances the value of staying and of leaving.

Roff (1975) found that increasing environmental stability did not always decrease dispersal, nor was increased dispersal necessarily the result of an increase in dispersal genotypes. The influence of environmental stability was dependent on the nature of the genetic mechanism influencing dispersal (polygenic or "simple"), the type of dispersal strategy (density dependent or independent), and the form of the environmental changes occurring. The models also demonstrated a major role for sexual reproduction in determining genotype frequencies. In heterogeneous environments, dispersers are generally at an advantage when environmental variance is high, but with long-term stability there is a continuous loss of dispersal genotypes that are not replaced; the presence of dispersers permits colonization of new areas and persistence of the population as a whole.

In summary, dispersal as 1 of the 3 determinants (births, deaths, and dispersal) of population dynamics has clearly been the least studied, documented, and understood. Heightened emphasis in caribou ecology is clearly needed. As a starting point, consensus of definitions of dispersal, emigration, immigration, and migration must be established. We have concluded that no "dispersal" (in the sense of mass emigration or immigration) was documented in this study. However, dispersal was documented for individuals from the YCH to the DCH and to the Upper Susitna Sub-Herd (Pitcher 1987) of the Nelchina herd. In addition, this study documented range expansion of the DCH into the range of the YCH and the Nelchina herd. This discussion will be expanded in forthcoming manuscripts prepared for publication.

Population Closure and Range Delineation:

Defining population closure or delineating a herd range is particularly problematic for free-ranging mainland caribou herds. This more than any other consideration is what confounds any attempt to scientifically determine the optimal population level for any given caribou herd.

Despite decades of study of caribou herd movements, distributions, habitat use, and demographics, caribou biologists are still incapable of predicting if population growth in any given herd will result in elevated population densities and subsequent resource-limited declines before substantial range expansion occurs. At one extreme is the possibility of herd growth causing irreparable range damage and subsequent lower standing crops of caribou for protracted periods. On the opposite end is the possibility of limiting herd growth through management and precluding incredible herd growth and range expansion with all of its attendant benefits.

For example, who in the 1920's would have predicted that the Steese-Fortymile herd would number only 4,000 to 6,000 in the early 1970's and be reduced in distribution from >100,000 mi^2 to <20,000 mi^2. Alternatively, without the benefit of history, who looking at the Fortymile herd in the early 1970's would believe that the herd could conceivably number >500,000 as it did in the 1920's?

Mainland caribou herds in Alaska have historically exhibited extreme range distribution over time. This suggests that human value judgments may be as valid as scientific knowledge for delineating herd ranges to attain management goals, depending upon the specific goals.

r. Comparative Food Habits of the Delta, Yanert, Denali, and Fortymile Herds

Results from Fleischman's (1990) thesis regarding diet composition and quality of the DCH were reported as follows:

> Composition of fecal samples...varied considerably among areas ($P<0.0001$), but little among replicate samples collected from the same area during the same season (Table 7). Winter feces collected in the foothills ($n=15$) showed decreasing lichen content and increasing moss and shrub content from west to east. WFH samples contained 69% lichen, 15% moss, and 10% shrubs, while EFH samples had 30% lichen, 38% moss, and 19% shrubs. GKB samples were more variable and were intermediate in lichen, moss, and shrub content (49%, 29%, and 14%, respectively). Graminoid content did not vary among winter samples (mean of 5%) but was higher in one sample from the calving ground in late May (22%). One composite sample collected in February 1987

> on the western Tanana Flats (near LTC), then used exclusively by mature bulls, had high lichen (70%), horsetail (4%), and forb content (4%); and little moss (7%). . . .
>
> Chemical analysis of caribou feces showed that acid detergent fiber (ADF) varied (P=0.003) among areas, and increased from west to east (LTC < WFH < GKB < EFH) among winter samples (Table 8). This is consistent with the results of microhistological analysis; apparently caribou on western and northern peripheral ranges obtained the most digestible winter diet, and cow caribou on traditional eastern winter range the least. Neither nitrogen nor ADF nitrogen (ADFN) varied significantly among areas (P>0.05). However, widely disparate results for ADFN in two LTC samples indicate possible laboratory error. If these observations are excluded, estimated error variance is greatly reduced and feces collected from the WFH have significantly lower ADFN than those collected elsewhere in the foothills (P=0.02).

Additional food habits information from fecal and rumen analysis were delayed because of tardy lab analysis. These results will be included and discussed in forthcoming manuscripts for publication.

CONCLUSIONS

a. Census of the DCH and YCH

A comparison of annual DCH census results from 1979 through 1989 (Fig. 2) to mortality and recruitment estimates suggests that census precision was inadequate to accurately predict population change over a 1- or 2-year interval. However, censuses at 3-year intervals consistently detected continuous population increase. Annual censuses suggested finite growth rates ranging from 1.38 to 0.92; we believe 1.38 is unrealistically high and 0.92 is unrealistically low. Exponential growth rates of 0.18, 0.11, and 0.10 were calculated, respectively, for the 1979-82, 1979-85, and 1979-89 periods.

b. Determining if All Caribou Photographed During Censuses Appear as Discrete Images

No data were obtained during this study, but it remains an important question in need of research.

c. Sex and Age Composition

Sex and age composition was estimated annually and showed several expected trends. The bull:cow ratio declined continuously, in response to the selective harvest of males. The calf:cow ratio in the fall declined concurrently to increases in wolf abundance and to increasing population densities during the study.

d. Yearling Recruitment

Although yearling recruitment estimates (based on fall calf:cow ratios) showed a declining trend during the study, they remained high enough to allow continued population growth, despite considerable mortality from hunting and predation.

e. Precision and Accuracy of Yearling Recruitment Surveys

Calculation of confidence intervals around the sample mean for April calf:cow ratios showed that the estimates were not precise. Although known biases in existing sampling techniques suggest that the estimates are inaccurate, the degree of inaccuracy is unknown.

f. Natality Rate

Annual natality estimates suggest that natality has remained at a relatively high rate (84 ± 4%). From available evidence for Alaska caribou, we concluded that natality does not operate in a sensitive, linear, or curvilinear manner throughout the population density range monitored to date.

g. Validity of Using Radio-collared Cows to Estimate Herd Natality

Natality estimates from as few as 22 radio-collared cows were similar to natality estimates from samples of the herd ranging in size from 482 to 2,052.

h. Reproductive Cost of Birthing When 24-36 Months Old and/or for Several Successive Years

We found no apparent pattern to indicate "pregnancy resting" at 36 months of age for individuals that first reproduced at 24 months of age. Cows that first calved when 2 or 3 years old were just as likely to have a calf in subsequent years as the mean for the calving population as a whole.

i. Cohort-specific Pregnancy Probabilities for Cows 24 or 36 Months Old

We detected cohort-specific differences in pregnancy probabilities for 24-month-old caribou, but not for 36-month-old caribou. We detected considerable variation in parturition frequencies among individuals.

j. Rutting Weight and Natality Rate of 24- and 36-month-old Cows

Reimers (1983b) concluded that pregnancy in *Rangifer* was determined by the female's weight during the rut and developed a prediction equation. We concluded that although weight may reasonably predict pregnancy in some populations, one or more additional variables must be additionally considered to create a predictor that might universally predict pregnancy probability in all Rangifer populations.

k. Harvest by Hunters

Harvest varied tremendously, ranging from a closed season to limited bulls-only hunting by permit to open general seasons for either sex. Reported harvest were as high as 694. However, there is good evidence that reported harvests in recent years may constitute only 56-57% of the total. In addition, a wounding rate of 10-20% is not included in the harvest estimates.

l. Mortality

Mean rates of natural mortality, estimated from serial calf:cow ratios, for the 0-5 and 5-12 MOC's, respectively, were 56% and 5.5%. Estimates of natural mortality rates from radio-collared caribou were as follows: among the 8-12 MOC, 0% for females and 34% for males; among the 12-24 MOC, 4% for females and 19% for males; and among the >24 MOC, 7% for females and 19% for males. From available evidence for Alaska caribou, we concluded that mortality does not operate in a sensitive, linear, or curvilinear manner throughout the population density range monitored to date.

m. Wolf:Caribou and Grizzly Bear:Caribou Ratios

Caribou:predator ratios changed during the study from about 1 wolf:101 caribou and 1 grizzly bear:31 caribou in 1979 to about 1 wolf:50 caribou and 1 grizzly bear:61 caribou in 1989.

n. Wolf Abundance and Rate of Caribou Predation

Throughout the history of the DCH there has been a negative correlation between wolf abundance and recruitment rate of caribou; the correlation has been positive between wolf abundance and the natural mortality rate of caribou. Determining if this relationship is one of cause and effect is confounded because of unknown density-dependent relationships within the caribou population.

o. Sex and Age of Predator-killed Caribou

This is the subject of a manuscript for journal publication that will emanate from this study.

p. Seasonal Movements, Distribution, and Fidelity to Calving Grounds

Concurrent to population growth of the DCH, total range use has expanded; winter distribution has expanded to the west and north into the Tanana Flats. Profound changes in calving distribution and social organization were documented. During the period of study, the DCH expanded into the range of the previously discrete YCH; the expansion included overlapping distribution at calving. In 1990 the range expansion continued, and the DCH extended its calving distribution into the range of the Nelchina herd.

q. Dispersal and Population Dynamics in the DCH and YCH

No dispersal was documented in the sense of mass emigration or immigration; however, individuals dispersed from the YCH to the DCH and to the Nelchina herd. From available evidence for Alaska caribou, we concluded that dispersal does not operate in a sensitive, linear, or curvilinear manner throughout the population density range monitored to date.

r. Comparative Food Habits of the Delta, Yanert, Denali, and Fortymile Herds

Available information is from Fleischman (1990) who concluded that mean lichen abundance in the DCH range was relatively low at 10-85 g/m^2 but that even on relatively heavily used range caribou ate only 7% of lichen standing crop annually.

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PREPARED BY:

James L. Davis
Wildlife Biologist III

Patrick Valkenburg
Wildlife Biologist II

Mark E. McNay
Wildlife Biologist III

Robin M. Beasley
Wildlife Biologist II

V. Leigh Tutterrow
Wildlife Technician II

APPROVED BY:

W Lewis Pamplin Jr.
W. Lewis Pamplin, Jr., Director
Division of Wildlife Conservation

Wayne L. Regelin
Wayne L. Regelin, Deputy Director
Division of Wildlife Conservation

SUBMITTED BY:

Daniel J. Reed
Regional Research Coordinator

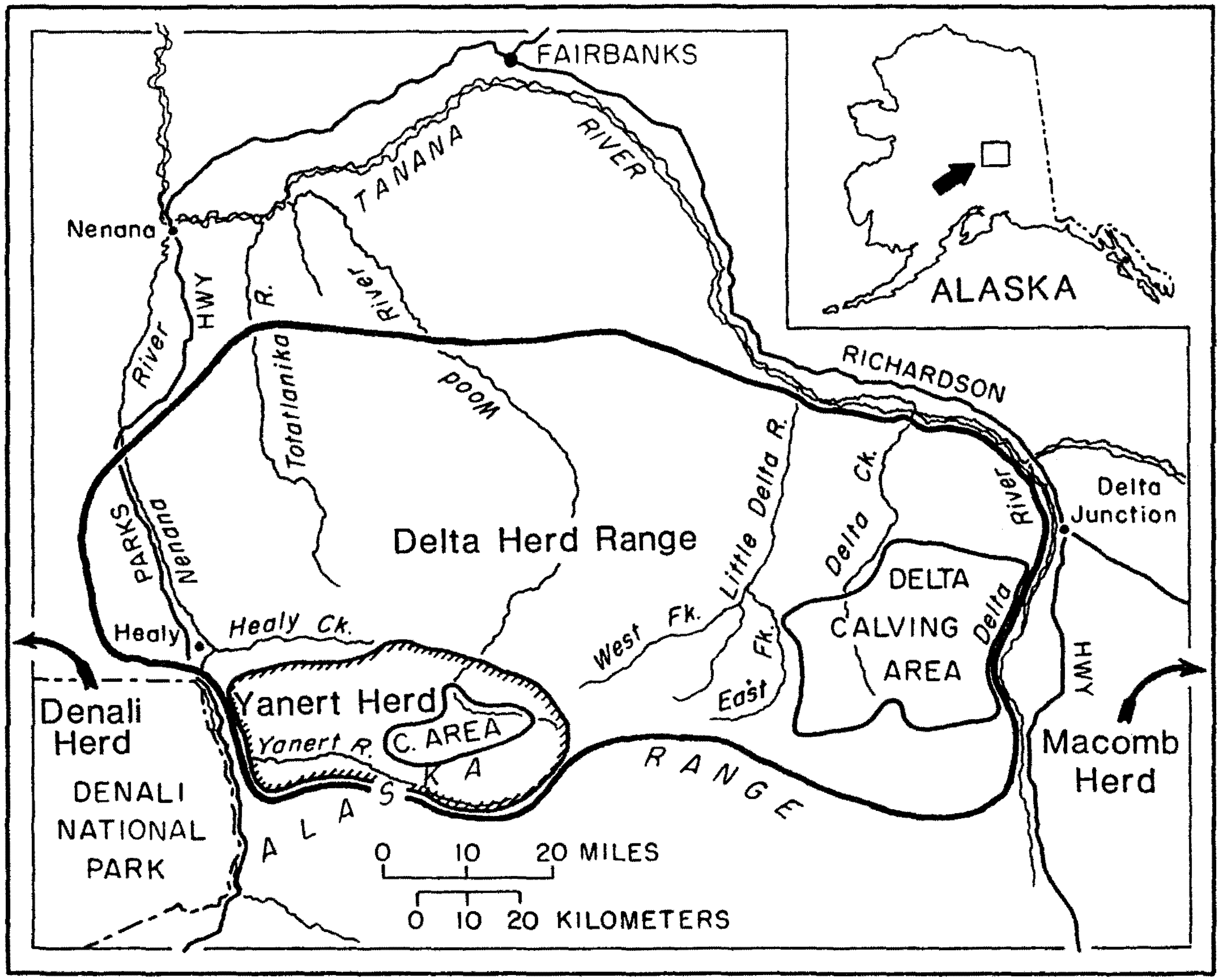

Fig. 1. The study area and caribou distribution as known at the onset of this study.

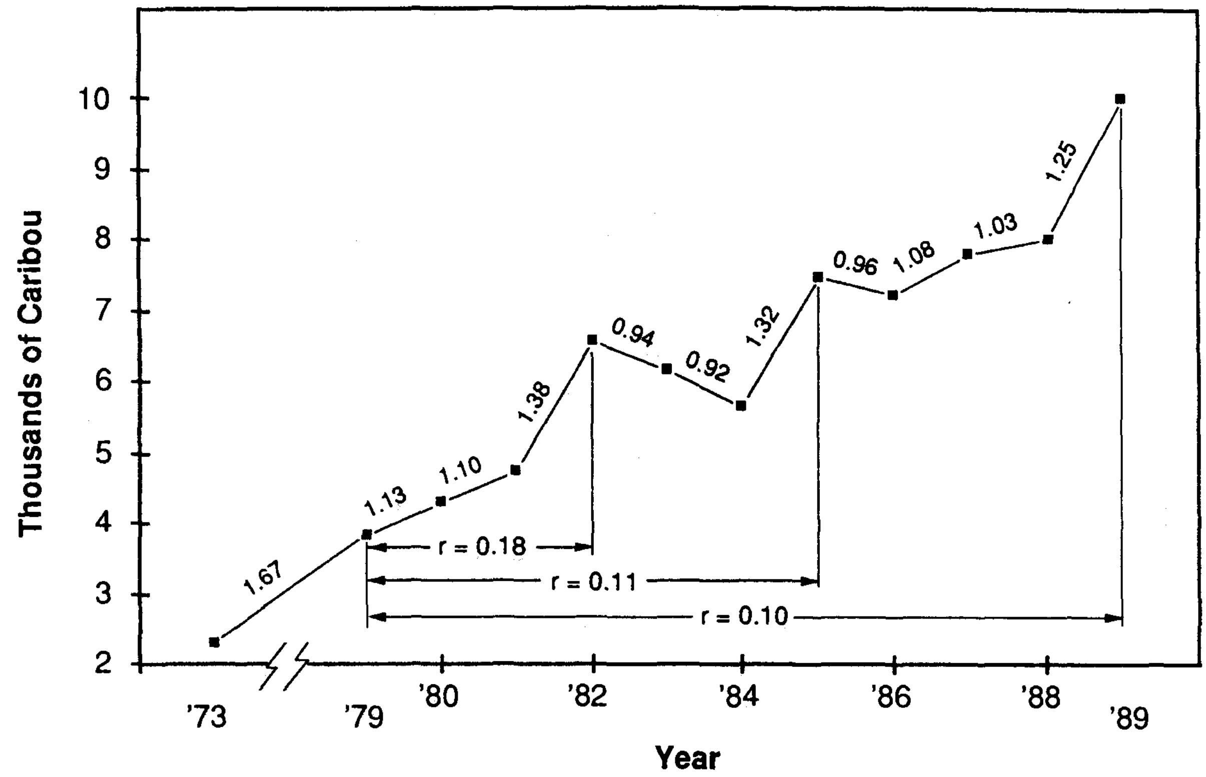

Fig. 2. Population trend of the Delta Caribou Herd determined from censuses, 1973-89. Values above the population line are estimates of the annual finite rate of increase, and the (r) values below the line are estimates of the exponential rate of increase.

Birth Year	Age in Years 1	2	3	4	5	6	7	8	9	10	11	Parturition frequency ›2 yrs ›3 yrs
1978	○	●	●	●	●							100/100
	○	●	●	●	●	●	●	●	●			100/100
	○	●	○									50/0
	○	●	●	○	●	●	●	●	●	●	●	90/90
	○	●	●							●	●	100/100
	○	●	●	●	○	●	●	●	○	●	●	80/78
1979	◌	●	◌	●	●	●	●					100/100
	○	●	●	●	●	●	●		●	●		100/100
1981	○	●	●	○	●							75/67
1983	○	●										100/N.A.

$\overline{x}$ = 90/82
SD = 17/33

○ = No
● = Yes
= Unknown

Fig. 3. Age-specific parturition status for 10 Delta Herd caribou that were first parturient at 24 months of age, 1978-89

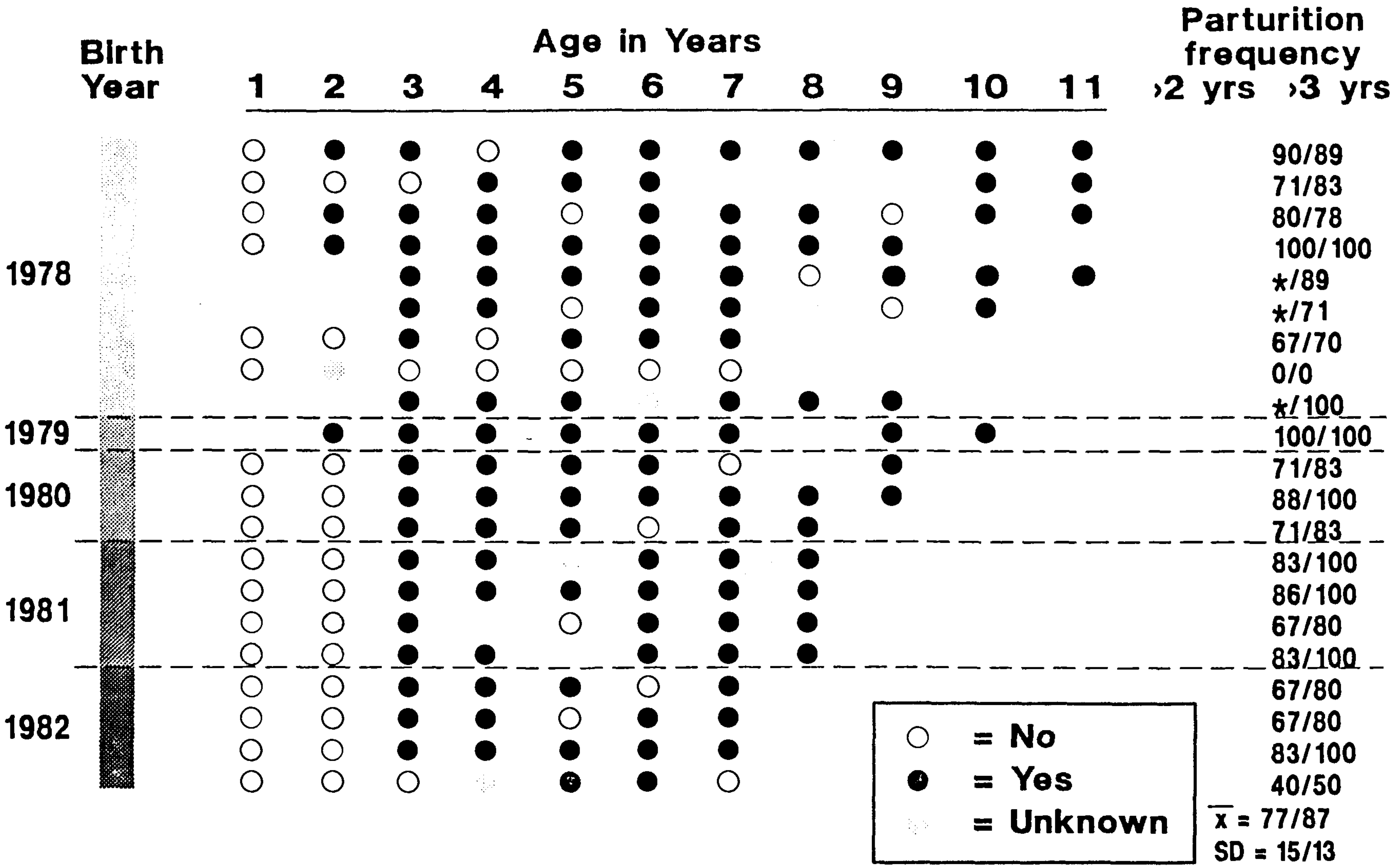

Fig. 4. Age-specific parturition status for 21 Delta Herd caribou with 6 or more years of known status, 1978-89.

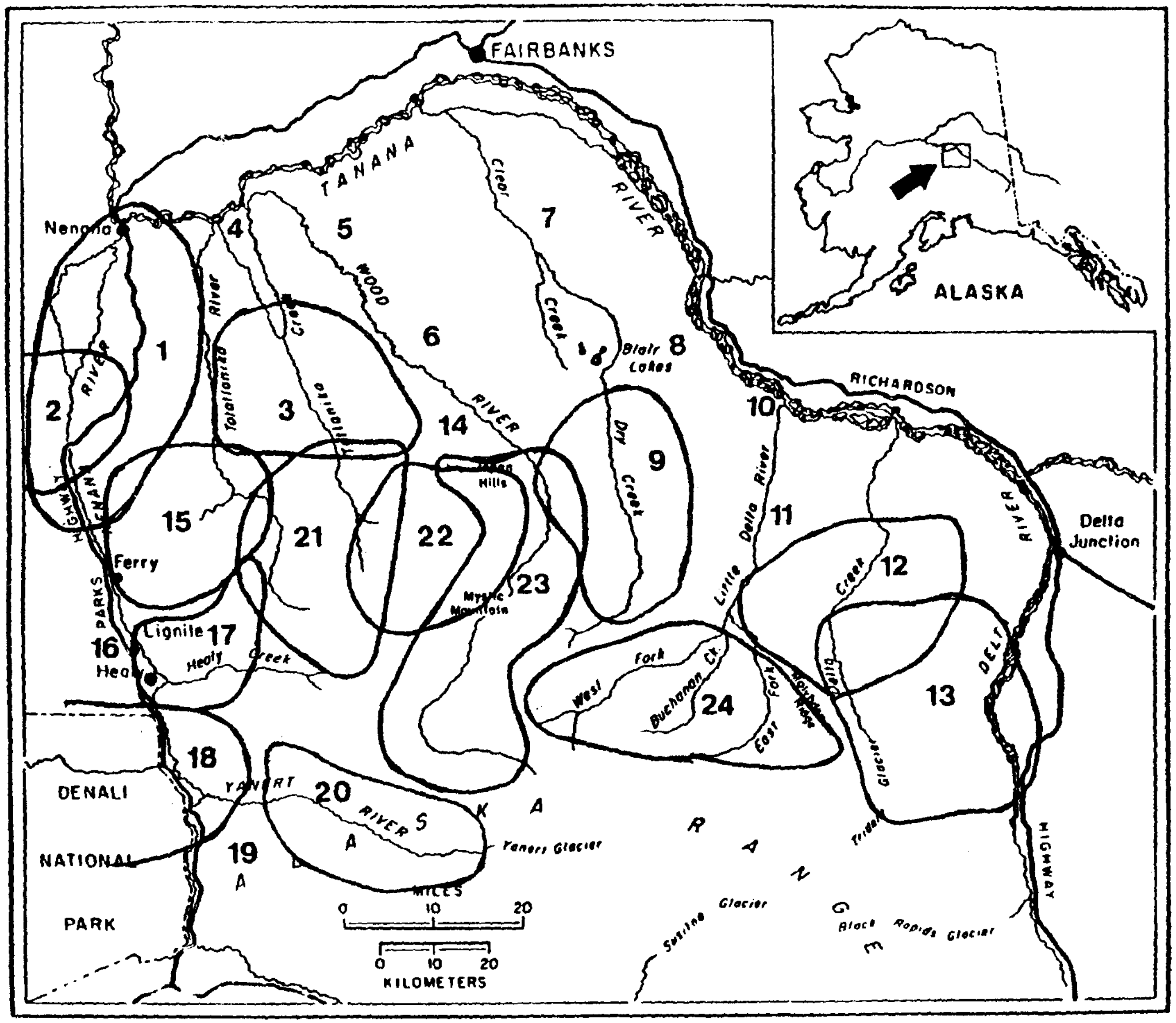

Fig. 5. Distribution of wolf packs in GMU 20A during 1985-86. Numbers correspond to pack numbers in Table 9; home ranges were delineated only for packs whose sign or members were observed in ≥3 locations and/or where tracking of the pack was extensive. Packs 3, 15, 17, 18, and 23 contained radio-collared wolves.

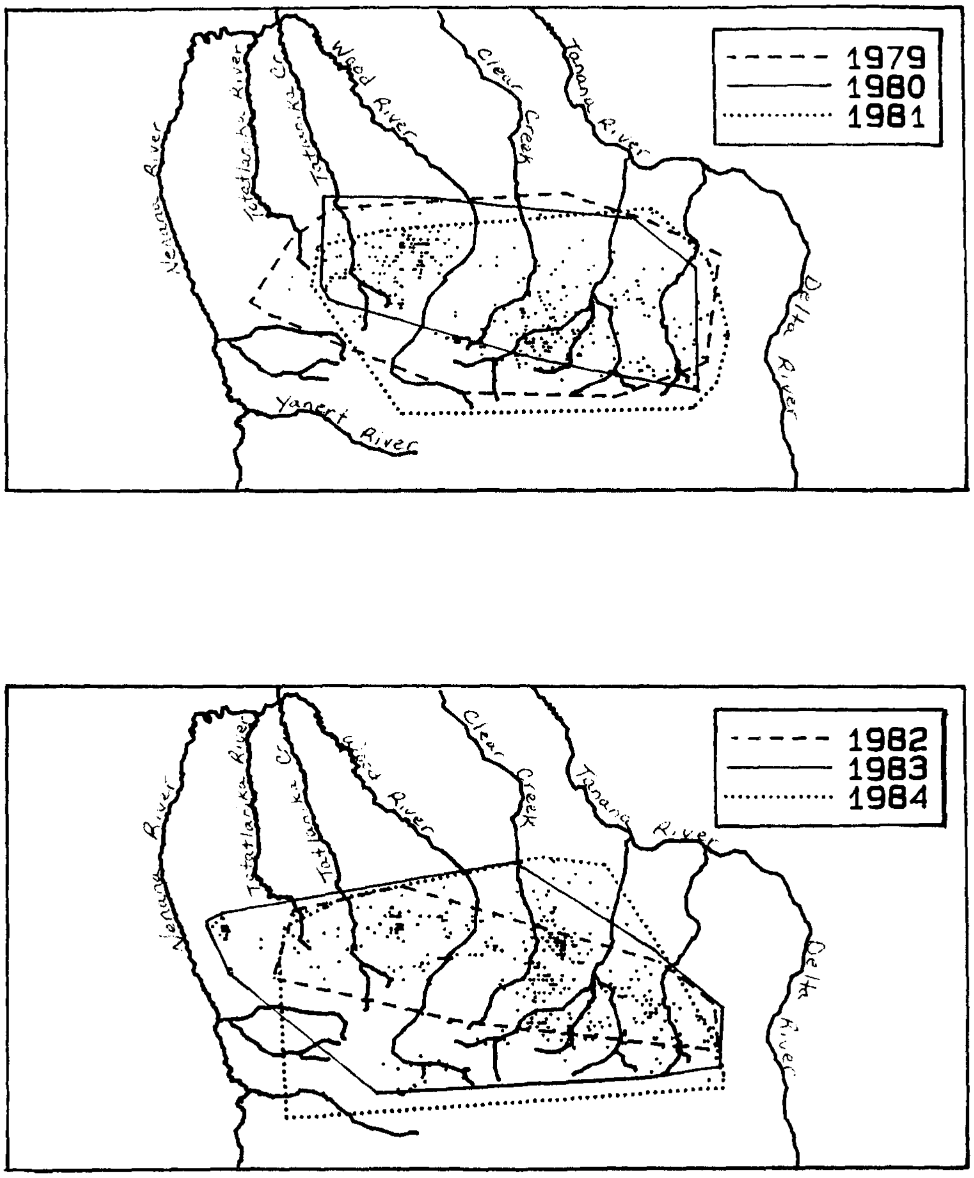

Fig. 6. Delta Caribou Herd distribution as delineated by convex polygons based on locations of radio-collared caribou, 1979-84

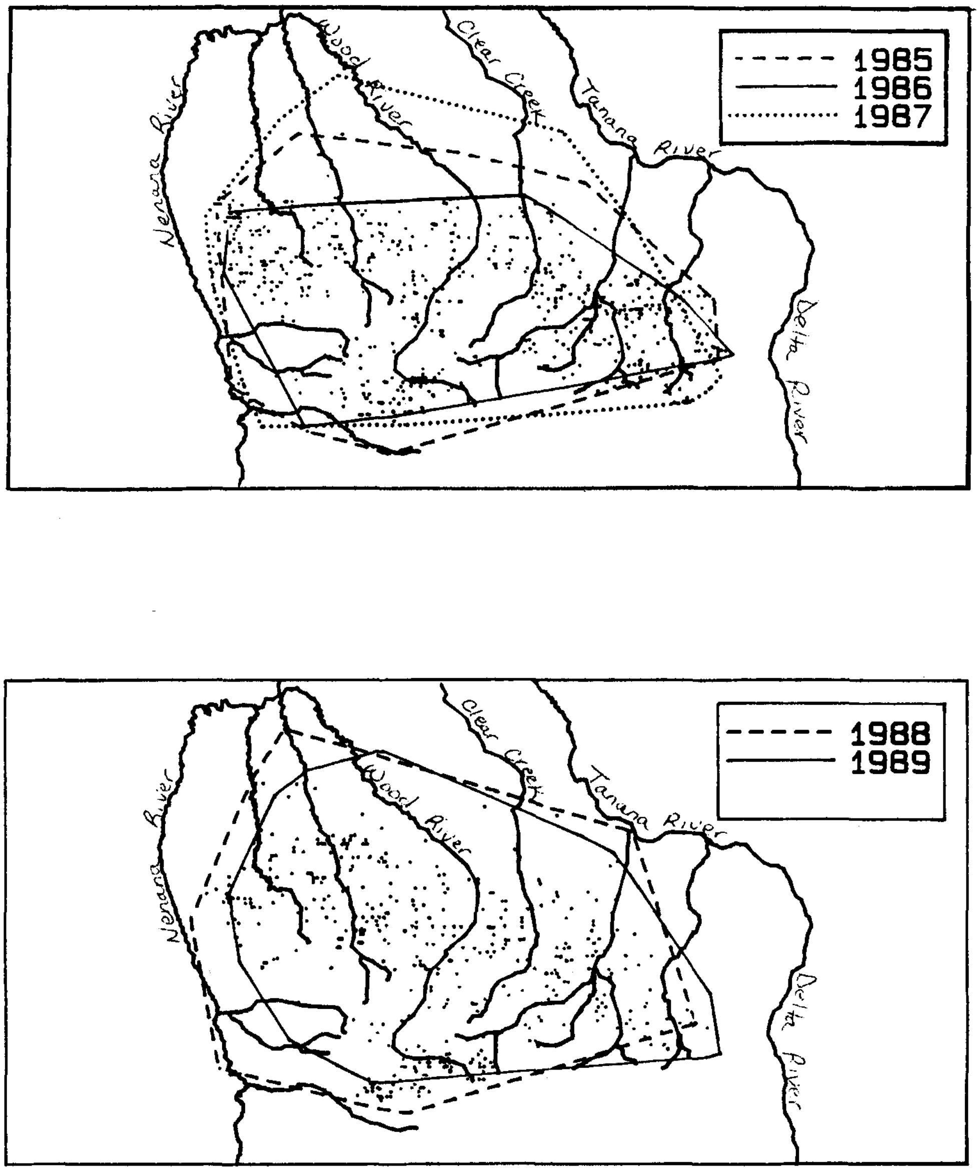

Fig. 7. Delta Caribou Herd distribution as delineated by convex polygons based on locations of radio-collared caribou, 1985-89.

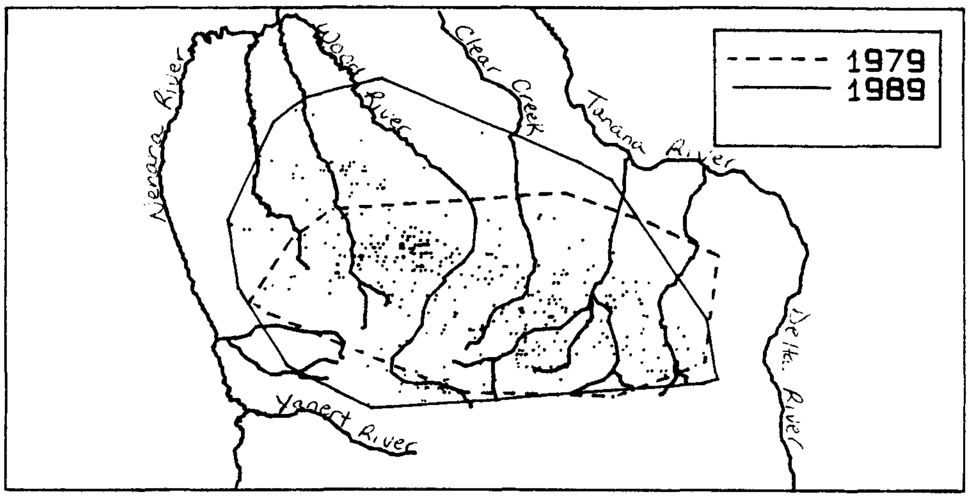

Fig. 8. Comparative herd range size for the Delta Caribou Herd based on convex polygons from relocations of radio-collared caribou 1979 and 1989.

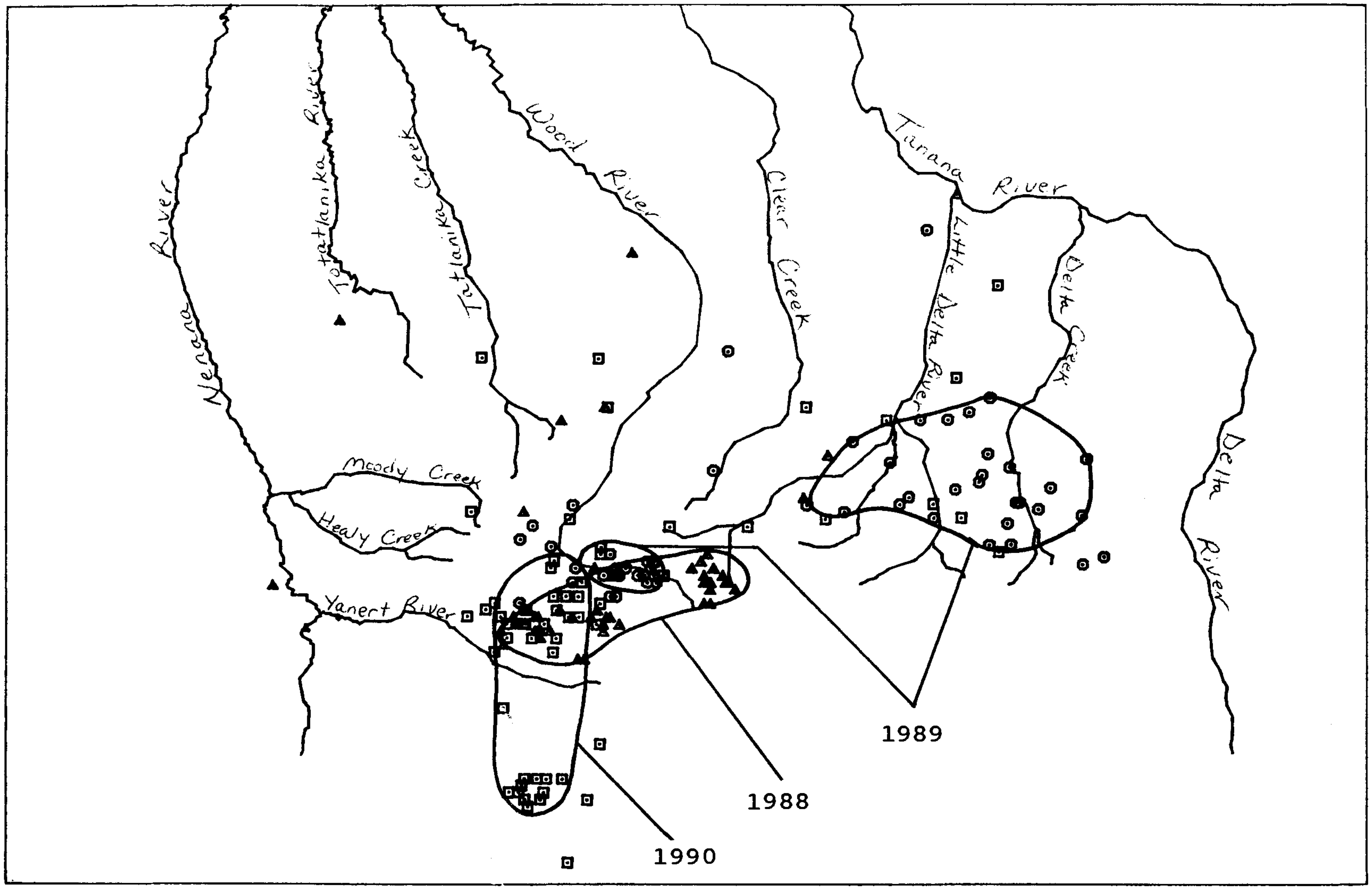

Fig. 9. Location of radio-collared Delta Caribou cows during calving (15-31 May), 1988-1990. Solid lines are subjective delineations of calving concentrations.

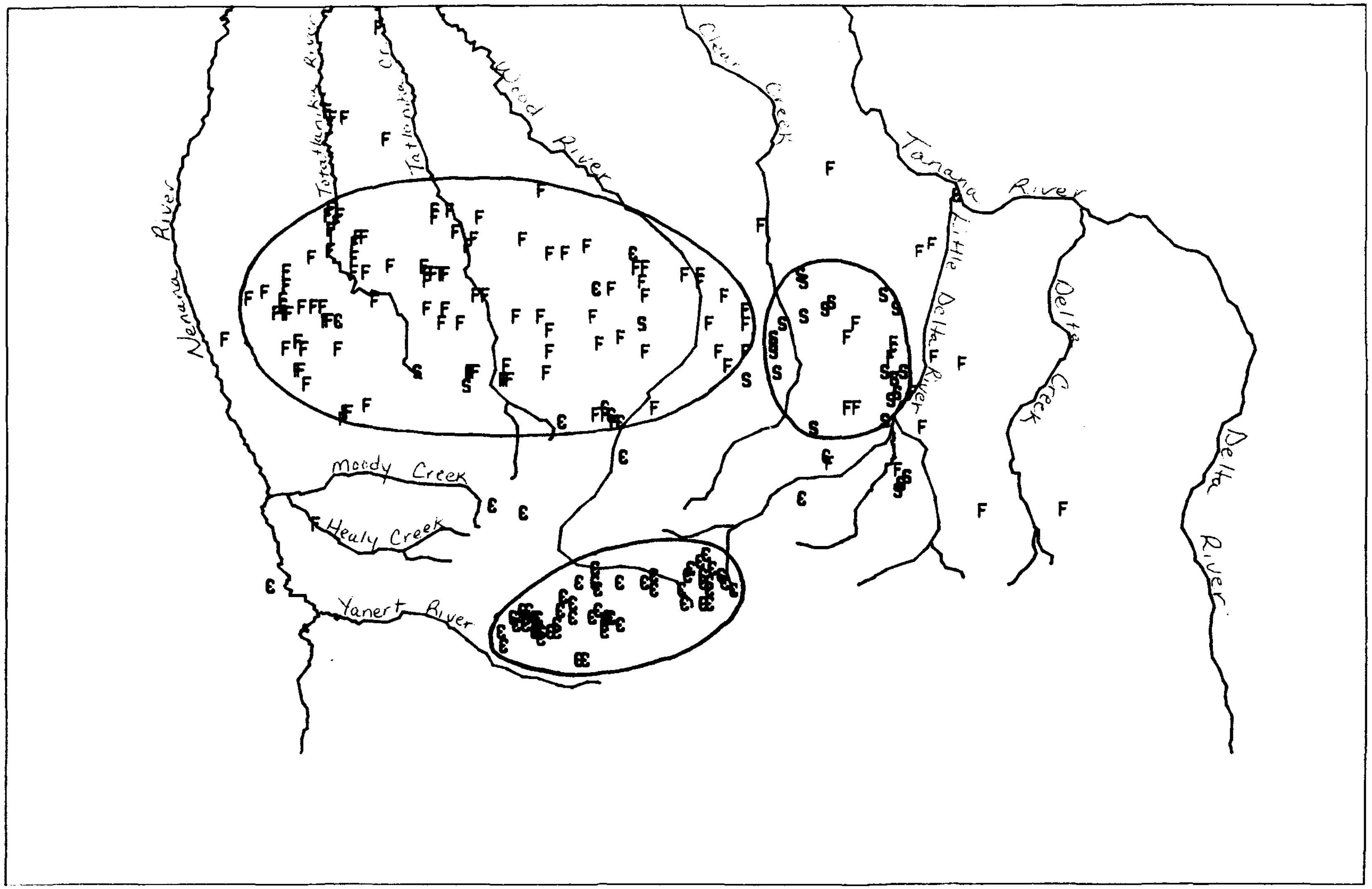

Fig. 10. Calving, fall/winter, and summer distribution of radio-collared Delta caribou, 1988 (includes males and females, but over 90% of locations are of females).

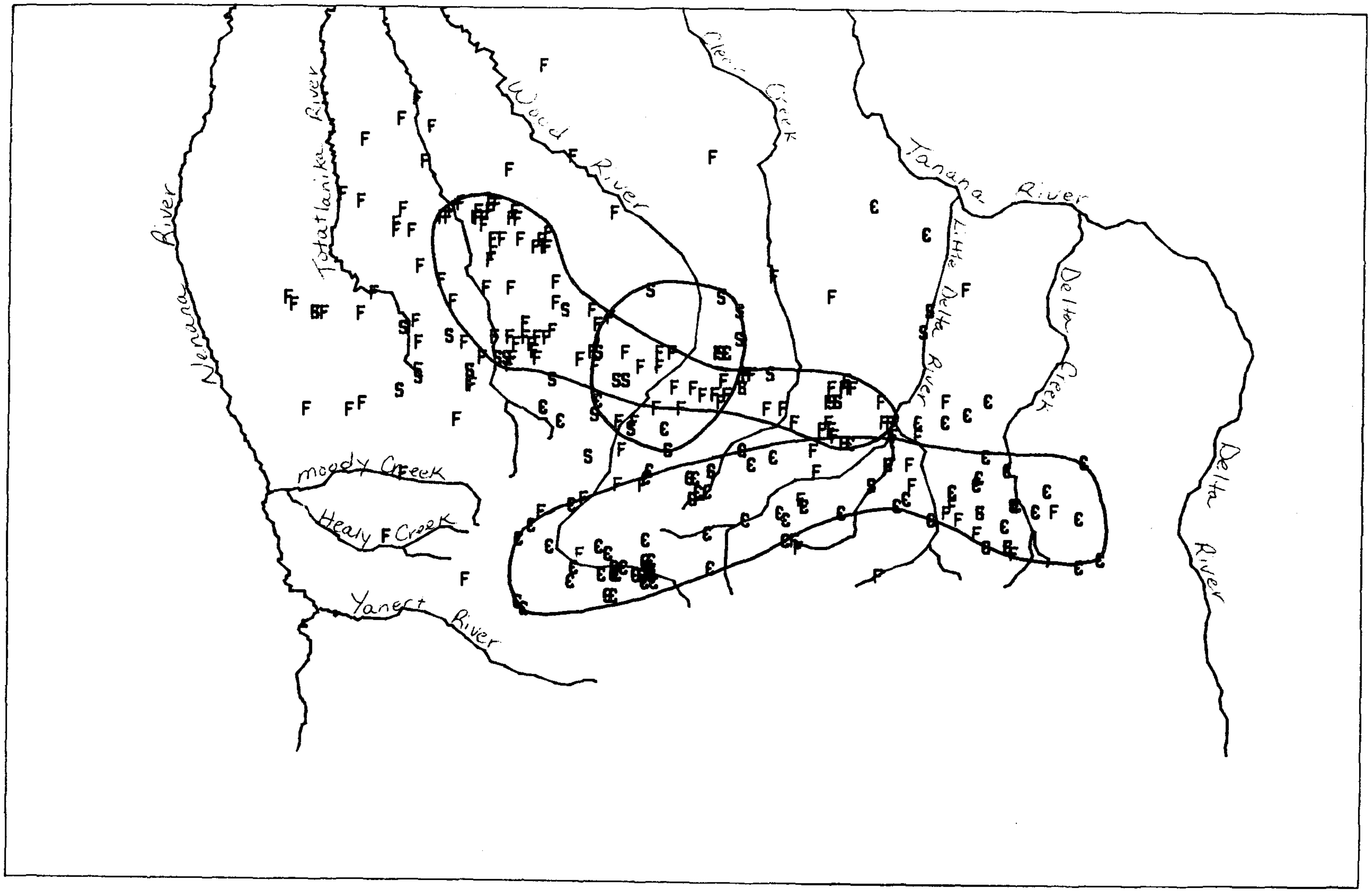

Fig. 11. Calving, fall/winter, and summer distribution of radio-collared Delta caribou, 1989 (includes males and females, but over 90% of locations are of females).

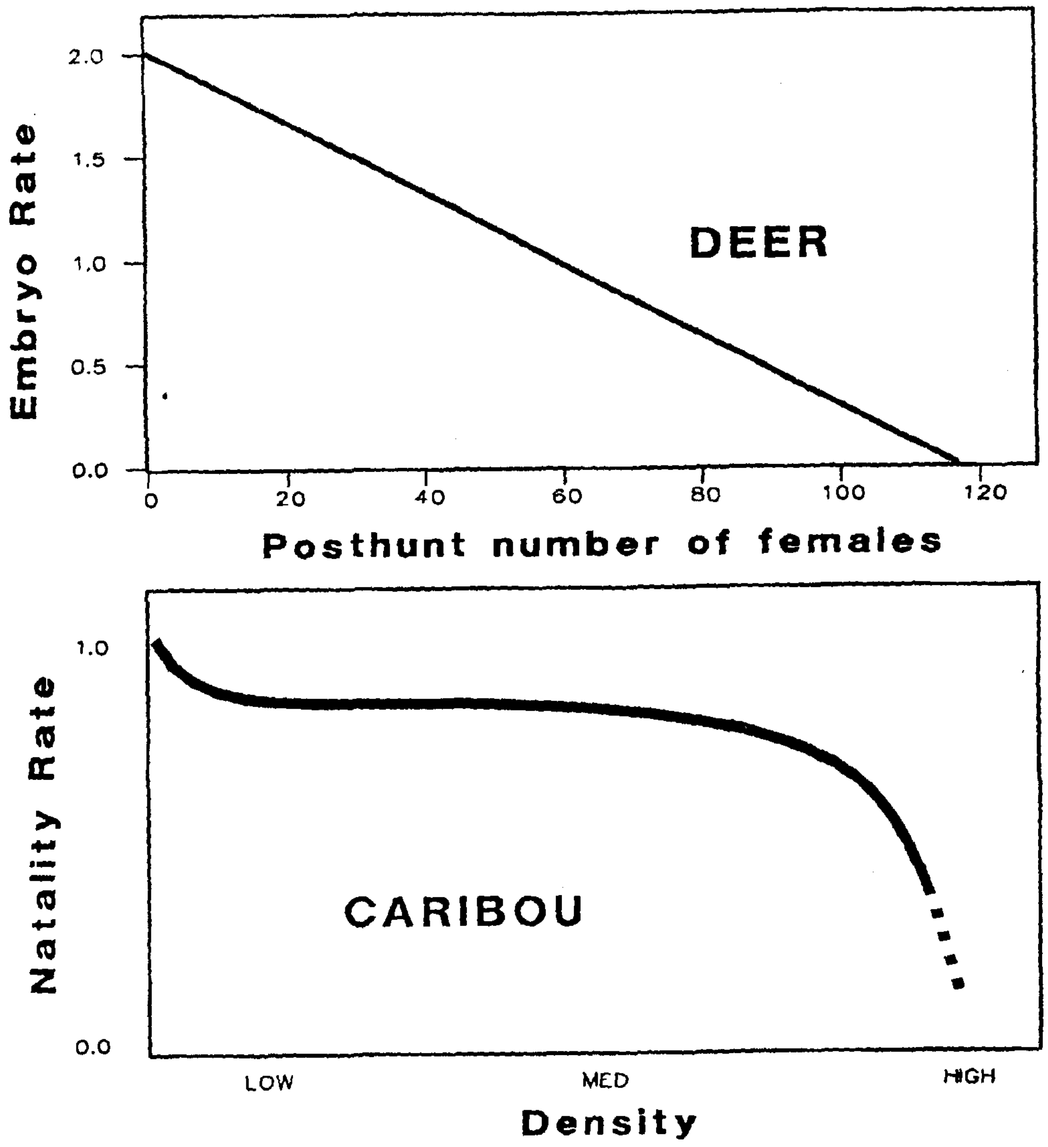

Fig. 12. Comparison of the natality/density relationship for white-tailes deer (after McCullough 1979) with that envisioned for caribou.

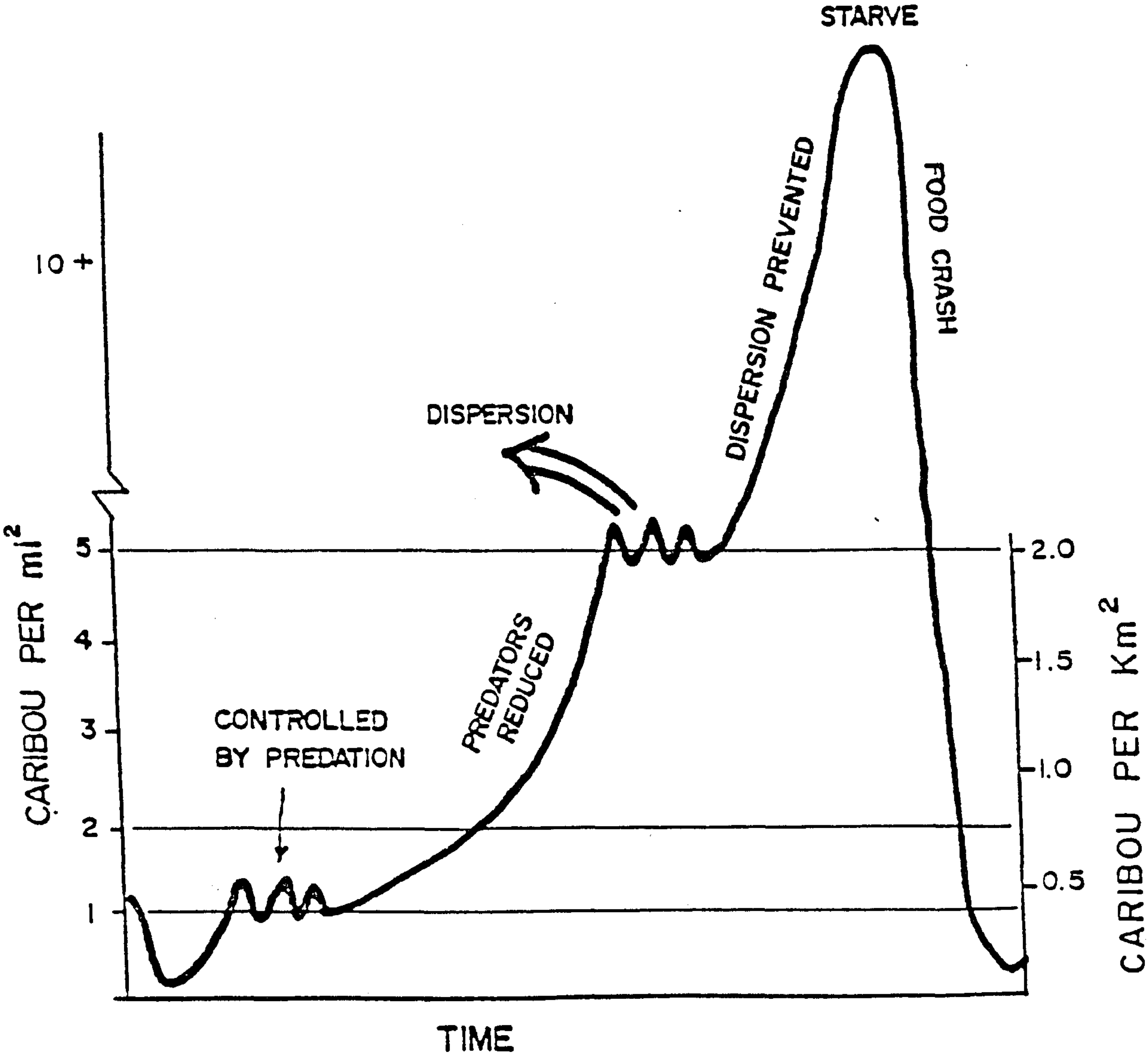

Fig. 13. The population growth limits of caribou envisioned as a staircase of limits imposed by predation and dispersion and a crash-decline caused by density-dependent food shortage (from Bergerud 1980).

Table 1. Permanent accession numbers and other pertinent information for Delta and Yanert Herd caribou, 1979-89.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
101972	R57	1978	F	1/4/79	D	Recollared 2/11/82
101972	Y36	1978	F	2/11/82	D	Dead unknown cause 1/84
101973	R53	1978	F	1/4/79	D	Recollared 2/11/82
101973	Y28	1978	F	2/11/82	D	Possible bear kill 9/11/85
101974	R88	1978	F	1/8/79	D	Recollared 2/11/82
101974	Y37	1978	F	2/11/82	D	Recollared 11/21/85
101974	B 3	1978	F	11/21/85	D	Shot 9/87
101975	B62	1978	M	1/9/79	D	Probable wolf kill 2/16-19/79
101976	R17	1978	M	1/9/79	D	Missing after 4/79
101977	R78	1978	F	1/9/79	D	Recollared 2/26/82
101977	Y49	1978	F	2/26/82	D	Probable capture mortality 3/82
101978	Y57	1978	M	1/9/79	D	Died unknown cause 3/79
101979	R18	1978	M	1/4/79	D	Shot 11/80
101980	Y58	1978	M	1/10/79	D	Missing 2/79
101981	R59	1978	F	1/10/79	D	Recollared 5/30/81
101981	Y20	1978	F	5/30/81	D	Capture mortality
101982	R52	1978	F	1/10/79	D	Recollared 2/11/82
101982	Y78	1978	F	2/11/82	D	Radio failed 5/27/85
101983	Y59	1978	M	1/10/79	D	Bear kill 8/80
101984	R54	1978	F	1/11/79	D	Recollared 2/26/82
101984	Y47	1978	F	2/26/82	D	Recollared 11/21/85
101984	057	1978	F	11/21/85	D	
101985	Y56	1978	M	1/11/79	D	Recollared 3/30/79
101985	R58	1978	M	3/30/79	D	Recollared 2/11/82
101985	Y79	1978	M	2/11/82	D	Shot 10/3/83
101986	Y69	1978	M	1/11/79	D	Missing 2/79
101987	R19	1978	M	1/8/79	D	Dropped collar 1/79
101988	R56	1978	F	1/4/79	D	Recollared 2/26/82

Table 1. Continued.

Accession No.	Collar color^a and No.	Birth year	Sex	Capture date	Herd name	Comments
101988	Y25	1978	F	2/26/82	D	Recollared 11/22/85
101988	B 9	1978	F	11/22/85	D	
101989	Y47	1978	M	1/11/79	D	Dropped collar 6/79
101990	Y58	1978	F	1/8/79	D	Capture mortality 1/8/79
101991	Y79	1978	M	1/10/79	D	Radio failed 9/80
101992	B63	1978	M	1/11/79	D	Radio failed 3/79
101993	R76	1978	F	3/30/79	D	Recollared 2/26/82
101993	Y26	1978	F	2/26/82	D	Probably shot 8/84
101994	R79	1978	F	3/30/79	D	Radio failed fall 1980
101995	Y67	1978	M	3/30/79	D	Missing 7/17/79
101996	B62	1978	M	3/30/79	D	Radio failed 3/79
101997	R77	1978	F	3/30/79	D	Recollared 2/26/82
101997	Y20	1978	F	2/26/82	D	Recollared 11/20/85
101997	O69	1978	F	11/20/85	D	Died unknown cause 7/28/89-5/17/90
102341	Y15	1980	F	2/8/81	D	Recollared 11/3/84
102341	Y53	1980	F	11/3/84	D	Recollared 4/14/87
102341	B 4	1980	F	4/14/87	D	Died winter 1988-89
102342	Y86	1979	M	2/8/81	D	Probable wolf kill 2/81
102343	Y13	1980	F	2/8/81	D	Recollared 11/3/84
102343	Y54	1980	F	11/3/84	D	Wolf kill 4/15/86
102348	Y14	1980	F	2/27/81	D	Recollared 10/30/84
102348	Y68	1980	F	10/30/84	D	Recollared 4/15/87
102348	O46	1980	F	4/15/87	D	
102349	Y12	1979	F	2/27/81	D	Radio failed 11/84
102350	Y22	1978	F	2/27/81	D	Recollared 4/22/86
102350	O47	1978	F	4/22/86	D	Missing 5/86
102360	Y16	1980	F	3/22/81	D	Recollared 10/12/85
102360	O62	1980	F	10/12/85	D	Capture mortality 10/15/85

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
102361	Y21	1980	M	3/22/81	D	Recollared 11/2/84
102361	046	1980	M	11/2/84	D	Dropped collar or died 7/85 or 8/85
102362	Y18	0	F	3/22/81	D	Recollared 11/3/84
102362	074	0	F	11/3/84	D	Killed by wolves 7/22/86
102363	Y29	0	F	4/17/81	Y	Recollared 11/2/84
102363	049	0	F	11/2/84	Y	Killed by predators 6/86
102364	Y30	0	F	4/18/81	Y	Recollared 10/31/84
102364	051	0	F	10/31/84	Y	Died 2/87
102365	Y31	0	F	4/18/81	Y	Recollared 10/31/84
102365	064	0	F	10/31/84	Y	
102366	Y32	0	F	4/18/81	Y	Recollared 11/2/84
102366	061	0	F	11/2/84	Y	Missing 6/89
102367	Y33	0	F	4/18/81	Y	Recollared 10/30/84
102367	060	0	F	10/31/84	Y	
102368	Y34	0	F	4/18/81	Y	Recollared 11/2/84
102368	Y11	0	F	11/2/84	Y	Probable wolf kill 10/5/87-12/4/88
102369	Y35	0	F	4/18/81	Y	Recollared 11/22/85
102369	B 7	0	F	11/22/85	Y	Wolf kill 11/25/85
102370	Y70	0	F	4/18/81	Y	Recollared 11/2/84
102370	065	0	F	11/2/84	Y	Died winter 1988-89
102411	Y19	1980	F	5/30/81	D	Recollared 11/3/84
102411	066	1980	F	11/3/84	D	Died unknown cause 8/86
102412	Y23	1980	F	5/30/81	D	Recollared 10/30/84
102412	063	1980	F	10/30/84	D	Died unknown cause ca. 10/7/86
102413	Y27	1980	F	5/30/81	D	Recollared 10/30/84
102413	Y51	1980	F	10/30/84	D	Recollared 4/14/87
102413	030	1980	F	4/14/87	D	
102546	Y 9	1981	F	5/3/82	D	Died unknown cause 8/83
102547	Y10	1981	F	5/3/82	D	Possible bear kill 5/5/82

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
102548	Y 7	1981	F	5/3/82	D	Recollared 11/21/85
102548	Y52	1981	F	11/21/85	D	
102549	Y 6	1981	F	5/3/82	D	Recollared 10/20/85
102549	047	1981	F	10/20/85	D	Snared 1/26/86
102560	Y 1	1981	F	5/3/82	D	Recollared 10/20/85
102560	052	1981	F	10/20/85	D	Died unknown cause 7/28/89-10/10/89
102561	Y 4	1981	F	5/3/82	D	Recollared 12/13/85
102561	B 6	1981	F	12/13/85	D	Died summer 1989
102562	Y 2	1981	F	5/3/82	D	Recollared 11/21/85
102562	B 5	1981	F	11/21/85	D	Shot 9/86
102563	Y 5	1981	F	5/3/82	D	Recollared 11/21/85
102563	044	1981	F	11/21/85	D	Capture mortality ca. 11/25/85
102564	Y 3	1981	F	5/3/82	D	Died unknown cause ca. 10/82
102565	Y 0	1981	F	5/3/82	D	Recollared 11/21/85
102565	B 4	1981	F	11/21/85	D	Probable wolf kill 3/86
102566	Y 8	1981	F	5/3/82	D	Recollared 11/20/85
102566	053	1981	F	11/20/85	D	
102803	Y40	1982	F	4/1/83	D	Recollared 4/7/86
102803	043	1982	F	4/7/86	D	
102804	Y43	1982	F	4/1/83	D	Recollared 4/7/86
102804	B10	1982	F	4/7/86	D	Died winter 1988-89
102805	Y41	1982	F	4/1/83	D	Recollared 4/22/86
102805	B 0	1982	F	4/22/86	D	
102806	Y42	1982	F	4/1/83	D	Recollared 4/21/86
102806	021	1982	F	4/21/86	D	Missing 6/30/89
102807	Y39	1982	F	4/1/83	D	Died unknown cause ca. 8/83
102808	Y48	1982	F	4/1/83	D	Recollared 4/21/86
102808	023	1982	F	4/21/86	D	Died winter 1988-89
102809	Y10	1982	F	4/1/83	D	Recollared 4/22/86

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
102809	B11	1982	F	4/22/86	D	Predator kill 10/5-11/27/87
102810	Y45	1982	F	4/1/83	D	Recollared 4/21/86
102810	B 8	1982	F	4/21/86	D	Died unknown cause 5/87
102811	Y44	1982	F	4/1/83	D	Died unknown cause 5/85
102812	Y17	1982	F	4/1/83	D	Recollared 4/7/86
102812	025	1982	F	4/7/86	D	Shot 9/9/86
102813	None	1982	F	4/1/83	D	
102814	Y46	1982	F	4/1/83	D	Recollared 4/7/86
102814	024	1982	F	4/7/86	D	
102815	Y 3	1982	F	4/1/83	D	Recollared 4/21/86
102815	B 1	1982	F	4/21/86	D	Probable wolf kill 7/28/89-5/19/90
102816	None	1982	F	4/1/83	D	Capture mortality
102982	076	1983	F	3/30/84	D	Recollared 4/14/87
102982	050	1983	F	4/14/87	D	
102983	074	1983	F	3/30/84	D	Capture mortality
102984	075	1983	F	3/30/84	D	Recollared 4/14/87
102984	020	1983	F	4/14/87	D	
102985	079	1983	F	3/30/84	D	Recollared 4/14/87
102985	052	1983	F	4/14/87	D	
102986	Y49	1983	F	3/30/84	D	Dropped collar ca. 4/1/84
102988	078	1983	F	3/30/84	D	Recollared 4/14/87
102988	051	1983	F	4/14/87	D	
102989	072	1983	F	3/30/84	D	Recollared 4/14/87
102989	033	1983	F	4/14/87	D	
102990	070	1983	F	3/30/84	D	Recollared 4/14/87
102990	Y47	1983	F	4/15/87	D	Died unknown cause 3/8/90-5/17/90
102991	067	1983	F	3/30/84	D	Recollared 4/15/87
102991	032	1983	F	4/15/87	D	

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
102992	077	1983	F	3/30/84	D	Recollared 4/14/87
102992	062	1983	F	4/14/87	D	
102993	Y50	1983	F	3/30/84	D	Recollared 4/14/87
102993	044	1983	F	4/14/87	D	Died unknown cause 1/25/90-3/8/90
102994	Y49	1983	M	4/13/84	D	Shot 9/84
103042	Y62	0	M	10/30/84	D	Dropped 11/84
103043	Y63	0	M	10/30/84	D	Dropped early 3/85
103044	Y66	0	M	10/30/84	D	Shot 9/2/85
103045	Y64	0	M	10/30/84	D	Dropped collar 11/1/84
103046	Y61	0	M	10/30/84	D	Dropped collar ca. 4/85
103047	Y67	0	M	10/30/84	D	Dropped collar ca. 1/85
103048	Y60	0	M	10/31/84	Y	Missing 6/87
103049	Y65	0	M	10/31/84	Y	Dropped collar 3/85
103050	Y52	0	M	10/31/84	D	Dropped collar 12/84
103051	Y59	0	M	10/31/84	D	Wolf/wolverine kill 12/4/87-1/13/88
103052	Y55	0	M	10/31/84	D	Shot 9/10/86
103054	O59	0	M	11/2/84	Y	Shot 9/3/85
103055	O50	0	M	11/2/84	Y	Shot 9/9/86
103074	Y66	0	M	11/21/85	D	Wolf kill 10/5/87
103094	O97	0	M	10/23/86	D	Wolf kill ca. 11/15/86
103095	O96	0	M	10/23/86	D	Dropped collar 10/28/86
103096	O95	0	M	10/23/86	D	Died 10/28/86
103097	O45	0	M	10/23/86	D	Shot Iowa Ridge/Portage 9/6/87

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
103111	094	0	M	2/27/87	D	Missing 5/18/88
103112	092	0	M	2/27/87	D	Dropped collar 2/87
103113	091	0	M	2/27/87	D	Wolf kill 12/4/87-1/13/88
103114	090	0	M	2/27/87	D	Shot 1/13/88
103115	096	0	M	2/27/87	D	Shot 9/88
103130	031	1986	F	4/15/87	D	
103131	042	1986	F	4/15/87	D	
103132	035	1986	F	4/15/87	D	
103133	036	1986	F	4/15/87	D	
103134	039	1986	F	4/15/87	D	
103135	038	1986	F	4/15/87	D	Predator kill 10/5/87-1/30/88
103136	034	1986	F	4/15/87	D	
103137	041	1985	F	4/15/87	D	
103138	037	1984	F	4/15/87	D	
103139	040	1986	F	4/15/87	D	Shot 11/87
103141	None	1986	F	4/15/87	D	Not collared
103142	None	0	F	4/15/87	D	Not collared
103143	None	1985	F	4/14/87	D	Not collared
103144	None	1985	F	4/15/87	D	Not collared
103284	049	1987	F	4/20/88	D	
103285	011	1987	F	4/20/88	D	
103286	0 4	1987	F	4/20/88	D	
103287	010	1987	F	4/20/88	D	

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
103288	013	1987	F	4/20/88	D	
103289	0 3	1987	F	4/20/88	D	
103290	059	1987	F	4/20/88	D	
103291	093	1987	F	4/20/88	D	
103292	043	1987	F	4/20/88	D	
103293	012	1987	F	4/20/88	D	
103294	095	1987	F	4/20/88	D	
103295	0 8	1987	F	4/20/88	D	
103296	None	1987	F	4/20/88	D	
103395	0 9	1988	F	4/30/89	D	
103396	014	1988	F	4/30/89	D	
103397	075	1988	F	4/30/89	D	
103398	074	1988	F	4/30/89	D	
103399	015	1988	F	4/30/89	D	
103400	B 5	1988	F	4/30/89	D	
103401	090	1988	F	4/30/89	D	Died unknown cause 10/10/89-1/25/90
103402	056	1988	F	4/30/89	D	
103403	049	1988	F	4/30/89	D	Died unknown cause 7/28/89-10/10/89
103404	025	1988	F	4/30/89	D	
103634	None	1988	F	4/20/90	D	Not collared
103635	None	1989	F	4/20/90	D	Not collared

Table 1. Continued.

Accession No.	Collar color[a] and No.	Birth year	Sex	Capture date	Herd name	Comments
103636	None	1989	F	4/20/90	D	Not collared
103637	None	1989	F	4/20/90	D	Not collared
103638	None	1989	F	4/20/90	D	Not collared
103639	None	1989	F	4/20/90	D	Not collared
103640	None	1989	F	4/20/90	D	Not collared
103641	None	1989	M	4/20/90	D	Not collared
103642	None	1989	F	4/20/90	D	Not collared
103643	None	1989	F	4/20/90	D	Not collared
103644	None	1988	F	4/20/90	D	Not collared
103645	None	1989	F	4/20/90	D	Not collared

Table 2. Sex and age composition of Alaska's Delta Caribou Herd, 1969-89.

Date	Bulls: 100 cows	Yrlgs: 100 cows	Calves: 100 cows	Yrlg % in herd	No. yrlgs	Calf % in herd	No. calves	Cow % in herd	No. cows	Bull % in herd	No. bulls	Sample size
<u>Fall/Rut</u>												
10/13-15/69	40	21	28	11	85	15	116	53	410	21	166	777
10/21-23/70	77	23	34	9	88	14	129	42	383	33	296	896
10/29-31/71	29	11	16	7	78	9	109	64	738	18	214	1,139
10/27-31/72	32	6	10	4	46	7	85	67	795	21	259	1,185
10/23-24/73	28	4	10	3	29	7	76	70	735	20	210	1,050
10/23-25/74	27	2	2	1	16	1	17	76	868	21	240	1,141
10/29-31/76	38	1	45	1	5	24	258	54	572	20	220	1,055
10/26-31/77	32	6	42	3	44	23	319	55	756	18	246	1,365
10/26/78	75	10	39	5	33	17	126	44	324	33	242	725
10/80	85	NA	49	NA	NA	21	288	43	585	36	496	1,369
10/2/81	59	NA	41	NA	NA	21	319	50	776	29	458	1,553
10/8/82	54	NA	29	NA	NA	16	215	55	736	30	398	1,349
12/7/79	39	NA	65	NA	NA	32	115	49	177	19	69	361
11/26/82	60	NA	38	NA	NA	19	65	51	173	30	104	342
10/4/83	54	NA	41	NA	NA	23	307	50	665	27	361	1,333
10/17/84	42	NA	36	NA	NA	20	222	56	613	24	258	1,093
10/9-12/85	49	NA	36	NA	NA	20	228	54	630	26	306	1,164
10/22/86	41	NA	29	NA	NA	17	330	59	1,136	24	468	1,934
10/5/87	32	NA	31	NA	NA	19	323	61	1,030	20	329	1,682
10/14/88	33	NA	35	NA	NA	21	620	60	1,790	20	593	3,003
10/10/89	27	NA	36	NA	NA	22	431	62	1,210	16	324	1,965
<u>Spring</u>												
4/20/83	23	NA	29	NA	NA	19	205	66	708	15	166	1,079
4/10/84	10	NA	49	NA	NA	31	194	63	396	6	38	628
4/20/86	21	NA	29	NA	NA	19	302	67	694	14	145	1,041
4/6/88	22	NA	29	NA	NA	19	285	66	976	14	212	1,473
4/18/90	15	NA	17	NA	NA	13	129	76	781	11	116	1,026

Table 2. Continued.

Date	Bulls: 100 cows	Yrlgs: 100 cows	Calves: 100 cows	Yrlg % in herd	No. yrlgs	Calf % in herd	No. calves	Cow % in herd	No. cows	Bull % in herd	No. bulls	Sample size
<u>Calving</u>												
5/23/82	0	NA	72	NA	NA	42	108	58	151	0	0	259
5/21/83	0	7	80	7	275	41	1,629	52	2,052	0	26	3,982
5/20/84	0	NA	82	NA	NA	0	0	0	482	0	0	877
5/3/85	0	NA	0	NA	NA	34	256	66	503	0	0	759
5/30/87	1	30	60	16	325	31	649	52	1,080	1	12	2,066
5/22-23/90	6	12	72[a]	9	114	13[a]	168	73	922	5	57	1,261
<u>Postcalving</u>												
6/11-12/75	3	1	12	1	3	11	108	86	839	2	26	976
6/3/76	1	NA	41	NA	NA	28	395	70	955	1	15	1,365
6/6-22/76	1	NA	55	NA	NA	35	390	63	699	1	10	1,099
6/16-19/77	9	12	34	8	95	22	269	64	784	6	76	1,224
6/13-14/78	12	8	23	6	52	16	157	69	661	8	81	951
6/23/79	12	18	45	10	76	26	189	57	424	7	49	738
6/14/80	18	NA	43	NA	NA	27	324	62	748	11	137	1,209
6/17/81	13	16	34	NA	87	21	182	62	543	8	68	880
6/15/83	4	NA	51	NA	NA	33	522	64	1,021	3	44	1,587
6/22/84	17	NA	56	NA	NA	32	837	58	1,508	10	259	2,604

[a] Calves:100 cows value is the percentage of cows ≥24 months old with distended udders.

Table 3. Sex and age composition of Alaska's Yanert Caribou Herd, 1982-90.

Date	Bulls: 100 cows	Yrlgs: 100 cows	Calves: 100 cows	Yrlg % in herd	No. yrlgs	Calf % in herd	No. calves	Cow % in herd	No. cows	Bull % in herd	No. bulls	Sample size
11/26/82	59	NA	36	NA	NA	18	56	51	156	30	92	304
4/13/84	22	NA	44	NA	NA	26	44	60	101	13	22	167
10/12/85	65	NA	40	NA	NA	19	152	49	383	32	252	787
5/2/86	21	NA	49	NA	NA	29	53	59	107	12	22	182
10/22/86	70	NA	38	NA	NA	18	105	48	274	34	191	570
10/5/87[a]	41	NA	38	NA	NA	21	192	56	505	23	209	906
10/14/88[b]	(see Delta Herd)											
10/10/89[b]	(see Delta Herd)											
4/18/90	(see Delta Herd)											

[a] Sample contains many Delta Herd caribou. Distribution of radio-collared caribou from the Delta and Yanert Herd confirmed overlap of the 2 herds at the time these data were obtained.

[b] No caribou were located in traditional rutting areas within the Yanert Herd's range. All radio-collared Yanert caribou that were located during the rut were totally intermingled with the Delta Herd caribou. The Delta and Yanert radio-collared caribou were largely intermingled during the rut in the Moody Creek drainage during October 1989.

Table 4. Sex and age composition within caribou sample units, and identity of radio-collared female caribou present in each sample, surveyed to estimate the ratio of 11-month-old calves:100 cows in the Delta Caribou Herd, 20 April 1986, 6 April 1988, and 18 April 1990.

Sample		Calves						Radio-collared
unit	Cows	Male	Female	Unknown	Total	Males	Total	caribou present
1986								
1	11	--	3	--	3	1	15	072
2	34	13	20	--	33	38	105	074
3	79	8	12	--	20	20	119	076
4	86	11	11	1	23	28	137	Y45, Y50
5	14	1	0	--	1	1	16	079,075
6	65	10	16	--	26	20	111	066
7	45	2	6	--	8	1	54	Y10
8	88	11	14	--	25	7	120	067
9	79	7	14	--	21	4	104	B5
10	80	11	5	1	17	14	111	Y41, 057
11	68	5	22	--	27	11	106	B9, 0536
Total	649	79	123	2	204	145	998	
1988								
1	81	9	15	--	24	4	109	033
2	90	3	16	--	19	15	124	050
3	73	13	12	--	25	18	116	034
4	91	14	13	--	27	19	137	B 9
5	115	8	12	--	20	18	153	B 0,052
6	88	8	16	--	24	20	132	032
7	19	4	1	--	5	12	36	057,062
8	65	18	24	--	42	24	131	Y47
9	11	1	1	--	2	9	22	024
10	29	1	5	--	6	5	40	B 4
11	31	0	5	--	5	0	36	B10
12	10	2	3	--	5	1	16	Y52
13	85	15	14	--	29	38	152	039
14	50	5	5	--	10	16	76	036
Total	838	101	142	--	243	199	1,280	
1990								
1	63	1	6	--	7	18	95	Y47
2	85	2	7	--	9	21	124	BO
3	28	4	11	--	15	3	61	056
4	87	2	2	--	4	9	104	?
5	87	2	2	--	4	9	104	?
6	9	0	0	--	0	0	9	033
7	21	3	6	--	9	8	47	049
8	118	7	9	--	16	10	160	034
9	87	2	2	--	4	9	104	?
10	82	2	5	--	7	19	115	057
Total	667	25	50	--	75	106	923	

Table 5. Estimates of natality in the Delta Caribou Herd, 1981-90.

Year	Sample from aerial survey of calving ground % parturient for cows ≥24 mo old (n)	Radio-collared caribou % parturient for cows ≥36 mo old (n)
1981	N.A.	77 (13)
1982	72 (151)	70 (10)
1983	79 (2,052)	77 (22)
1984	82 (482)	90 (31)
1985	N.A.	93 (41)
1986	82 (N.A.)	83 (40)
1987	60 (1,080)	89 (28)
1988	83 (891)	88 (32)
1989	N.A.	83 (30)
1990	72	
	$\bar{X}$ = 75.7 (8.3 S.D.) 90% C.I. = 75.7 ± 4.5	$\bar{X}$ = 83.8 (7.2 S.D.) 90% C.I. = 83.8 ± 4.1

Table 6. Harvest from the Delta Caribou Herd and Yanert Caribou Herd, 1968-89.[a]

Year	Males n (%)	Females n (%)	Sex unk n (%)	Total	Extrapolated total
1968-69	119 (81)	25 (17)	3 (2)	147[b]	160
	--	--	--	205[c]	NA
1969-70	169 (75)	54 (24)	2 (1)	225	324
1970-71	198 (72)	68 (25)	9 (3)	275	428
1971-72	387 (62)	226 (36)	12 (2)	624	740
1972-73	372 (72)	132 (25)	13 (3)	517	NA
1973-74	158 (70)	67 (30)	8	233	301
1974-75 through 1979-80		No open season			
1980-81	104 (100)			104	
1981-82 (fall)	78	9		87	
1981-82 (winter)	113	64	4	181	
1981-82 (total)	191	73	4	268	
1982-83 (fall)	92	11	1	104	
1982-83 (winter)	101	65	3	169	
1982-83 (total)	193	77	4	274	
Delta 1983-84	576	98	20	694	
Yanert 1983-84	40	12	2	54	
Delta 1984-85	258	153	24	435	
Yanert 1984-85	77	22	0	99	130
Delta 1985-86	251	63	0	317	
Yanert 1985-86	53	11	0	64	
Delta 1986-87	350	94	4	448[d]	Combined[d] 841 (646-1,139, 90% CI)
Yanert 1986-87	54	16	2	72[d]	

Table 6. Continued.

Year	Males n (%)	Females n (%)	Sex unk n (%)	Total	Extrapolated total
Delta 1987-88	325	36	1	362	Combined[d] 664
Yanert 1987-88	66	2	0	68	(503-890, 90% CI)
Delta 1988-89	350	21	4	375	Combined[d] 555
Yanert 1988-89	64	0	0	64	(490-643, 90% CI)

[a] Harvest from Subunit 20A and part of 20C.

[b] From 1969 Alaska Department of Fish and Game Survey and Inventory Progress Report.

[c] From J. Sexton memo 3 December 1970.

[d] Extrapolated totals are based on field interviews compared with harvest reports (McNay 1990).

Table 7. Hunting seasons and bag limits for Subunit 20A (includes Delta and Yanert Caribou Herd, 1968-89).[a]

Year	Season	Bag limit
1968-69	10 Aug-31 Mar	3 caribou
1969-70	10 Aug-31 Mar	3 caribou
1970-71	10 Aug-31 Mar	3 caribou
1971-72	10 Aug-31 Mar	3 caribou
1972-73	10 Aug-31 Mar	3 caribou
1973-74[b]	10 Aug-31 Dec	1 caribou
1974-75[c]	10 Aug-20 Sep	1 caribou
1975-76 through 1979-80	No open season	
1980-81	1 Sep-30 Sep	1 male by drawing permit. 200 permits issued.
1981-82	10 Aug-30 Sep 15 Nov-31 Dec	1 caribou by drawing permit from 10 Aug-30 Sep; 150 permits issued, up to 25 will be issued to nonresidents. Antlered caribou may be taken from 15 Nov-31 Dec by registration permit. A total of 400 caribou may be taken.
1982-83	10 Aug-30 Sep 1 Dec-31 Mar	1 caribou by drawing permit from 10 Aug-30 Sep; 175 permits issued, up to 30 will be issued to nonresidents. Antlered caribou may be taken from 1 Dec-31 Mar by registration permit. A total of 500 caribou may be taken.
1983-84[d]	10 Aug-31 Mar	1 caribou

Table 7. Continued.

Year	Season	Bag limit
1984-85[e,f]	20 Aug-20 Sep	1 caribou by registration permit only. 600 caribou may be taken. The 20 Aug-20 Sep season will be closed when 300 caribou have been taken; the 1 Feb-31 Mar season will be closed when the total harvest reaches 600 caribou.
	10 Aug-31 Mar	1 caribou
1985-86[g] Alaskan Residents	10 Aug-31 Dec Unit 20(A) north of the Yanert Controlled Use Area, west of Wood River Controlled Use Area, and south of the Rex Trail	1 caribou by Tier II hunting permit only. 200 permits will be issued.
	1 Sep-15 Sep Remainder of Unit 20(A)	1 caribou
1985-86 Nonresidents	No Open Season Unit 20(A) north of the Yanert Controlled Use Area, west of Wood River Controlled Use Area, and south of the Rex Trail	
	1 Sep-15 Sep Remainder of Unit 20(A)	1 caribou
1986-87	6 Sep-31 Dec Unit 20(A) north of the Yanert Controlled Use Area, west of Wood River Controlled Use Area, and south of the Rex Trail	1 caribou by drawing permit only. 200 permits will be issued.
	1 Sep-15 Sep Remainder of Unit 20(A)	1 caribou

Table 7. Continued.

Year	Season	Bag limit
1987-88, 1988-89, and 1989-90	10-25 Aug 21 Sep-31 Dec Unit 20(A) north of the Yanert Controlled Use Area, west of Wood River Controlled Use Area, and south of the Rex Trail	1 caribou by drawing permit only. 200 permits will be issued.
	1-15 Sep Remainder of Unit 20(A)	1 bull
1990-91	10 Aug-10 Sep Unit 20(A) within the Ferry Trail Management Area	1 caribou by drawing permit only. 100 permits will be issued.
	1-28 Feb	1 antlered caribou by registration permit only. 75 Permits will be issued.
	Remainder of Unit 20(A)	
	1-10 Sep	1 bull
	1-28 Feb	1 antlered caribou by registration permit
	1-31 Mar	1 antlered caribou by registration permit. 75 permits will be issued.

[a] Subunit 20A and part of 20C in early years.

[b] Amended by emergency announcement to close 20 September.

[c] Amended by emergency announcement to No Open Season.

[d] Amended by emergency announcement to close 28 October, except the Yanert River drainage which remained open through 31 March.

[e] Amended by emergency announcement to close 5 September, except the Yanert River drainage.

[f] Amended by emergency announcement to close the Yanert River drainage on 8 February 1985.

[g] The 1985-86 seasons and bag limits which for the 1st time (at least since 1968) differentiated between residents of Alaska and nonresidents was the result of a judicial ruling which said the State Subsistence Bill had not been properly implemented.

Table 8. Annual percent change in calf:cow ratio, birth to fall, and fall to spring in Alaska's Delta Caribou Herd, 1981-87.

Date	Sample size	Calves: 100 cows	% change in the ratio of calves:100 cows	
			Birth to fall	Fall to spring
Late May 1981	13RC[a]	77	-47	N.A.
10/2/81	1,095	41		
Late May 1982	10RC	70		
10/8 & 11/26/82	1,189	31		
4/20/83	913	29	-56	-6
Late May 1983	22RC	77		
10/4/83	972	46		
4/10 & 13/84	735	48	-40	+4
Late May 1984	31RC	90		
10/17/84	835	36	-60	N.A.
Late May 1985	41RC	93		
10/9 & 12/85	630	36		
4/20/86	853	38	-61	-14
Late May 1986	40RC	83		
10/6/86	1,576	29	-65	N.A.
Late May 1987	32RC	84		
10/5/87	1,682	31		
4/16/88	1,473	29	-63	-6
			$\bar{x}$ = -56.0 (9.2 S.D.) 90% C.I. = -56.0 ± 6.7	$\bar{x}$ = -5.5 (7.4 S.D.) 90% C.I. = -5.5 ± 8.7

[a] RC = Radio-collared caribou.

Table 9. Calculated mean mortality rates for male and female caribou, based on radio-collared caribou, in the 8-12, 12-24, and >24-month-old cohorts, Delta Herd, 1979-87 (after Trent and Rongstad 1974).

Age cohort	No. radio-collared (no. collar-months)	No. man-caused deaths (% mortality)	No. natural deaths (% mortality)	No. total deaths (% mortality)
8-12 mo	Female 61 (109.5)	0	0	0
	Male 10 (23.8)	0	2(34)	2(34)
12-24 mo	Female 62 (659)	0	2 (2)	2 (4)
	Male 7 (63.3)	1(19)	1(19)	2(38)
>24 mo[a]	Female 64 (2,861)	6 (3)	17 (7)	23(10)
	Male 18 (308)	8(31)	5(19)	13(50)

[a] Percent mortality represents a mean annual rate.

Table 10. Wolf survey data for Subunit 20A[a], Alaska, fall 1985 and spring 1986 (ADF&G files, data compiled by R. Boertje).

Pack name	Estimated numbers Fall 1985	Estimated numbers Spring 1986	Number harvested	Colors of wolves if seen	Evidence	Observers
Tanana Flats						
1 Nenana	8	8	0	6 grays, 2 blacks	Seen	Karczmarczyk-ADF&G; Myers, Carter, Lord-public
2 Clear	3	2	1[b]	2 blacks	Seen	Morris, Myers-public
3 Lower Tatlanika River	9	8	1	6 blacks, 2 grays	Seen spring	Valkenburg-ADF&G 1985, tracks 1986
4 Lower Wood River	8	0	8[c]	7 grays, 1 black	Seen	Hodnik-public
5 Crooked Creek	4	3	1	--	Tracks seen	Crain-ADF&G; Argall-public
6 Wood River Buttes	6	6	0	--	Tracks seen	Grangaard, Valkenburg-ADF&G
7 Clear Creek Buttes	3	3	0	--	Tracks seen	Long-public
8 Blair Lakes	16	14	2	--	Tracks seen	Long, Nystrom, Thompson-public
9 Dry Creek	6	6	0	--	Tracks seen	Grangaard, Quimby-ADF&G
10 Harding Lake	3	2	1	--	Tracks seen	Parrish-public
11 Little Delta Creek	7	4	3	--	Tracks seen	Bares, Thompson-public
12 Delta Creek	14	6	8	--	Tracks seen	Dorhorst, Thompson-public
13 100-mile Creek	6	5	1	4 grays, 1 black	Seen	Bunselmier-F&WP
14 Lower Bonnifield Creek	6	3	3	--	Tracks seen	Stephenson-ADF&G; Smith, Boltz-public
Subtotal	99+10[d] =109	70+7[d] =77	29			

Table 10. Continued.

Pack name	Estimated numbers		Number harvested	Colors of wolves if seen	Evidence	Observers
	Fall 1985	Spring 1986				
Foothills						
15 Rex Dome	6	6	0	6 blacks	Seen	Myers, Dabney-public
16 Healy	2	2	0	1 silver, 1 black	Seen	Winkleman, Sorenson-public
17 Lignite	7	6	1	5 grays, 2 blacks	Seen; 2 radio-collared	Davis, Grangaard, Valkenburg-ADF&G
18 Lower Yanert River	6	5	1[e]	6 grays	Seen; 2 radio-collared	National Park Service
19 Revine Creek	2	2	0	--	Tracks seen	Grangaard-ADF&G
20 Upper Yanert River	7	7	0	6 grays, 1 black	Seen fall and spring	Karczmarczyk, Grangaard-ADF&G
21 Upper Tatlanika	24	22	2	15 grays, 9 blacks	Seen fall and spring	Valkenburg-ADF&G; Graham, Smith-public
22 Gold King Creek	8	6	2	--	Tracks seen	Boertje-ADF&G; Smith-public
23 Snow Mountain	9	9	0	5 grays, 4 blacks	Seen; 2 radio-collared	Davis, Grangaard-ADF&G
24 Buchanan Creek	7	5	2	7 grays	Seen fall and spring	Bunselmier-F&WP; Quimby-ADF&G
Subtotals	78+8[d] =86	70+7[d] =77	8			
Totals	195	154	37[f]			

Percent change = -21[g]

Table 10. Continued.

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[a] Data collected prior to July 1984 were collected in part from a portion of Subunit 20C, since then they are included in Subunit 20A. Also, some wolf packs spend less than 50% of their time outside Subunit 20A.

[b] Wolf was trapped in Subunit 20C.

[c] Wolves were snared in Subunit 20B.

[d] Added 10% for single wolves.

[e] Wolf was killed by 1 or more wolves in Subunit 20C.

[f] Only 27 wolves were harvested in Subunit 20A; 10 additional wolves (that were apparently part-time residents of 20A) were harvested in Subunits 20C and 20B adjacent to Subunit 20A.

[g] This change assumes natural morality, dispersal, and/or unreported harvest totals 10% of reported harvest.

Table 11. Range size, population size, density, predator:caribou ratios, and bull:cow ratios of the Delta Caribou Herd, 1978-89.

Cohort year	Size of range km^2	Population size	% cohort parturition rate at 24 mos	Population density caribou:km^2	Wolf: caribou	Grizzly:[a] caribou	Bulls: 100 cows	Large[b] bulls: 100 cows
1978	8,023	3,200	67	0.40	1:84	1:26	75	NA
1979	8,023	3,831	67	0.48	1:101	1:31	39[c]	NA
1980	8,023	4,321	0	0.53	1:98	1:35	85	NA
1981	8,023	4,750	11	0.59	1:93	1:39	59	23
1982	8,023	6,545	0	0.83	1:111	1:53	54	24
1983	9,339	6,170	10	0.67	1:78	1:50	54	13
1984	10,007	5,660	NA	0.56	1:58	1:46	42	17
1985	10,339	7,483	0	0.71	1:63	1:61	49	9
1986	10,786	7,204	0	0.67	1:50	1:61	41	9
1987	10,786	7,780	0	0.71	1:47	1:61	32	8
1988	10,786	>8,000	NA	0.74	1:42	1:65	33	4
1989	10,786	10,000	NA	0.93	1:51	1:81	--	--

[a] Assumes 123 grizzlies in 1986 and ≥123 prior to 1986.
[b] Assumed to be ≥5 years old.
[c] Biased; real value probably about 75-80.

Table 12. Weight-related statistics for 7- to 12-month-old female caribou from Alaska's Delta Caribou Herd by cohort year.

Cohort year	Sample size	$\bar{x}$	SD	Minimum	Maximum
1978	11	61.3	3.7	58.8	63.7
1980	5	63.4	7.5	54.1	72.7
1981	11	62.4[a]	5.6	58.6	66.2
1982	14	64.8[a]	7.1	60.7	68.9
1983	12	58.6	2.2	57.1	60.0
1986	9	56.1[a]	3.8	53.2	59.0
1987	12	60.9	4.6	57.9	63.8
1988	9	61.9	3.7	59.0	64.7
Total	83	61.2[b]	5.4	60.0	62.4

[a] A Kruskal-Wallis non-parametric ANOVA and Student, Newman-Keuls multiple comparison on ranks test were combined to determine that the only significant ($\alpha = 0.05$) difference in cohort weights was that the 1981 and 1982 mean cohort weights were greater than in 1986.

[b] For comparison, $\bar{x} = 61.2$ kg ($n = 14$) for 11-month-old females from the Denali Herd for the 1986 and 1987 cohorts combined.

APPENDIX A

Citations of publications contributed to by P-R Federal Aid in Wildlife Restoration funded study of the Delta and Yanert Caribou Herds, 1979-90.

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