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

# DEMOGRAPHY OF THE DELTA CARIBOU HERD UNDER VARYING RATES OF NATURAL MORTALITY AND HARVEST BY HUMANS

by
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**Project W-23-2**
**Study 3.33**
**April 1990**

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# PROGRESS REPORT (RESEARCH)

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(Includes data through October 1989)

## SUMMARY

This report summarizes recent progress on a long-term demographic study of the Delta Caribou (*Rangifer tarandus granti*) Herd (DCH) initiated in 1979. Distribution of the DCH and Yanert Caribou Herd (YCH) probably overlapped somewhat during the census of postcalving aggregations on 30 June and 1 July 1989, but several hundred caribou were in the range of the YCH; only 2 radio-collared Yanert caribou are still alive. Including calves, there was a minimum of 10,690 caribou in the 2 herds when censused (Appendix A). The YCH probably contains about 600 caribou; the rest are part of the DCH. Sex and age composition in 1989 showed a continuing decline in the bull:cow ratio (predictable from the males-only hunting season). Natality data that were obtained primarily from monitoring radio-collared females remained relatively high in 1989 (i.e., 88%). Two manuscripts entitled "Relationships between body weight, early puberty, and reproductive histories in central Alaskan Caribou" (Appendix B) and "A review of caribou population dynamics in Alaska emphasizing limiting factors, theory, and management implications" (Appendix C) were presented at the 4th North American Caribou Workshop and will be published in the proceedings.

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

## CONTENTS

## BACKGROUND

The Alaska Department of Fish and Game's (ADF&G) goal for some caribou (Rangifer tarandus granti) herds, as stated in various draft wildlife management plans, is to stabilize them at specific levels. For other herds, the goal is to ensure that they do not decline below set minimum populations. However, few caribou herds in Alaska have remained stable for more than a few years; it has been particularly rare for a heavily harvested herd to remain stable. If the above goals are to be accomplished and any caribou management program is to be successful, understanding the mechanisms involved in caribou population dynamics is essential. Although the factors determining population dynamics for all wildlife species are the same (i.e., births, deaths, and emigration/immigration), the specific variables affecting these 3 factors can differ greatly.

A quantitative assessment of the demography of an Alaskan caribou herd has never been conducted over a period of greatly varying rates of natural mortality and human harvest. During a past workshop (Klein and White 1978), leading caribou researchers in North America identified the need for an intensive demographic study of one or more caribou herds in Alaska.

Proximity of the Delta Caribou Herd (DCH) to Fairbanks, considerable background information on the herd, and options for intensively managing (i.e., manipulating) the herd make it ideal for long-term demographic study. Hypotheses regarding many aspects of general caribou ecology may be more feasibly tested on the DCH than on larger herds, such as the Western Arctic and Porcupine herds. Intensified study of the DCH (Davis and Preston 1980) revealed that herd demography was 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, 1985), 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 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 caribou 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).

Since study of the DCH was intensified in 1979, considerable data on herd movements and distribution have been collected that are incidental to our major objectives. 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. If the DCH continues to increase, any change in movements and distribution will be better interpreted if earlier patterns are well documented.

Opposing views are emerging among caribou biologists regarding their basic social organization, including herd identity, herd 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 and calf survival 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 1985) still had functioning radio collars and were available for this project. Although pertinent information was summarized in Table 1 of Davis et al. (1988) for all radio-collared Delta and Yanert caribou studied through 1987, we have updated that list to include all caribou radio-collared to date for this project (Table 1).

## GOAL

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

## OBJECTIVES AND PROCEDURES

1. Objectives 1a through 1g will be addressed over a 5-year period (1986-90). Procedures for 1a through 1g have been described or cited in Davis and Valkenburg (1985). The following objectives will be accomplished by the ADF&G survey and inventory program and/or by this research project.

a. To census the DCH and the YCH in 1986, 1987, 1988, 1989, and 1990. We will use the modified aerial photo-direct/count-extrapolation (APDCE) technique, a radio-search technique, or a total-count technique (using 2 helicopters) to annually census the 2 herds.

On 29 June, 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 (Appendix A, Fig. 1); 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.

b. To determine the annual natality rates and calving chronologies of the 2 herds. Monitoring about 50 radio-collared cows and sampling the herd at large will enable us to determine the natality rate. Other supporting information will be obtained by using a helicopter to aid in obtaining composition counts and udder counts. Documenting annual calving distribution is a priority.

c. To determine yearling recruitment in the DCH and the YCH. We will monitor the radio-collared cows to determine their natality rate and subsequent calf survival. Composition counts will be conducted during April on the herd at large. We will attempt to obtain random, even-sized subsamples to facilitate evaluation of bias and calculation of a confidence interval for the data. Our sample design requires 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 1974b), which have been validated for some Alaskan caribou herds through radiotelemetry studies (Valkenburg et al. 1983). In short, this implies that the number of individual caribou in the proximity of a collared individual varies over time and space, constituting a "random" sample (albeit the sample does not meet the statistical requirements of being random).

d. Measure harvest by hunters. The existing survey and inventory program will collect harvest data through various reporting procedures. During the 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.

e. To determine when major mortality occurs to both calves and adults and to characterize caribou mortality from natural causes. Data from radio-collared caribou and from composition counts will determine the chronology of calf mortality. Survival rates of adult caribou will be calculated from the radio-collared caribou. Carcasses of caribou dying from natural causes will be collected and examined.

f. To determine caribou:predator ratios in the range of the DCH and YCH. These ratios will be determined 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 by management staff (augmented by our surveys when required), and the results of a concurrent ADF&G study of grizzly bears (Ursus arctos) (Reynolds et al. 1987).

g. To determine the seasonal movements, distribution, and fidelity to respective calving grounds of radio-collared caribou. We will locate all radio-collared caribou monthly and monitor all female radio-collared caribou 2 or more times during the calving period.

2. Objectives 2a through 2k will be addressed by collecting data during 1 or more years of this 5-year study.

a. 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. We will keep active radio collars on about 50 cows to determine their reproductive history.

b. To determine if there are any differing cohort-specific pregnancy probabilities for cows 24 or 36 months old. Same procedure as 2a.

c. To determine if the natality rate of 24- and 36-month-old cows is determined by their weight at the time of the rut. We will collar ten 12-month-old females in each cohort to determine natality rate at 24 months. We will weigh 16-month-old females and correlate weight with subsequent natality.

d. To determine if caribou killed by predators are taken in proportion to their representation in the population in terms of sex and age. We will compare the sex and age data of radio-collared caribou killed by predators with data from the total radio-collared sample. We will do likewise for caribou in the population at large.

e. To determine the correlation between wolf abundance and the number of caribou killed by wolves. To test this correlation we must know the size of the wolf and caribou populations and the number of caribou killed by wolves. These data will be determined from field studies and from modeling.

f. To determine if DCH and YCH caribou are faithful to their traditional calving grounds. We will determine this by monitoring radio-collared cows and by conducting aerial surveys of the respective calving areas. Once an animal is collared and calves on a given calving ground, subsequent calving on any other calving ground is judged as being "unfaithful."

g. To determine if dispersal is important to the population dynamics of the DCH and YCH. Movements of radio-collared caribou in the Delta, Yanert, Denali, Nelchina, Macomb, and Fortymile herds will be monitored. Also, annual censuses should identify inexplicable major increases or declines that suggest immigration or emigration has occurred.

h. To compare food habits of the Delta, Yanert, Denali, and Fortymile Herds. Fecal pellets will be collected monthly for herds where data are currently unavailable.

i. To determine if all caribou photographed during censuses appear as discrete images and are enumerated during photo interpretation. Ground counts will be made to determine the exact number of calves and older caribou in groups that will subsequently be photographed . Different scales (altitude), photo angles, and film will be evaluated.

j. To determine if yearling recruitment is precisely and accurately estimated by conducting herd composition surveys in April. Precision will be tested by conducting serial counts of the same sample area (e.g., on successive days, weeks, or months). Evaluating accuracy will involve modeling for cross-checking recruitment data.

k. To identify the limits of validity in using a small sample of radio-collared cows to estimate herd natality and recruitment. Empirical data from the herd at large and from the radio-collared cohort will be compared with results derived from simulation models. The validity of judging calf recruitment by monitoring radio-collared females will be evaluated by determining when the cow-calf bond breaks and by determining the sex and age of caribou that unbonded calves associate with.

## 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. The DCH currently encompasses about 9,600 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. 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 temperature range is approximately 29 C to -51 C. Annual precipitation averages about 30 cm; snow accumulation averages 0-50 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 more radio-collared caribou were on the flats in winter 1988-89 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 have been used as the traditional core calving areas since before the 1950's. 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.

In this report, all references to the DCH prior to 1980 include the Delta and Yanert Herds.

## RESULTS AND DISCUSSION

### Census of the DCH and YCH

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

### Sex and Age Composition

In 1988 and 1989 the ratios for calves:100 cows 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. The bull:cow ratio further declined to 27:100, representing a continuing trend since bulls-only hunting had been initiated in the general season of 1987-88. The bull:cow ratios have been in continuous decline since the early 1980's when hunting of the DCH was liberalized.

## Natality Rate

During this reporting period, the natality rate from radio-collared DCH caribou was 88% (Table 4). Natality has remained relatively stable since 1984.

## Yearling Recruitment in the DCH and YCH

Recruitment was last discussed in Davis et al. (1989), and it will be summarized in the upcoming final report in 1990.

## Harvest by Hunters

The 1988 harvest from the DCH and YCH combined was estimated to be 490-643 (Table 5). Data collected from hunters in the field indicate that the reporting rate by successful and unsuccessful hunters via the hunter report card/harvest ticket system grossly underestimated the total harvest (McNay 1988). Historical harvest data for the DCH and YCH are summarized in Table 5. Historical hunting seasons and bag limits are summarized in Table 6 and 7 for the DCH and YCH, respectively.

## Mortality

Mortality was last discussed in Davis et al. (1989), and it will be summarized in the 1990 final report.

## 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 (Appendix B), the general discussion in our last report does not warrant updating. Wolf numbers, pack distribution, harvest rate, necropsy data, and radio-cesium 137 burdens and food habits will be reported in the final report in 1990.

## Seasonal Movements, Distribution, and Fidelity to Calving Grounds

Throughout the study period, we monitored radio-collared caribou to document seasonal movements and distribution. A University of Alaska, Cooperative Wildlife Research Unit Master of Science project by Steve Fleischman is contributing toward collation, analysis, and interpretation of movements and distribution data.

The draft thesis is in review and will be defended in February 1990.

Data to be Collected During 1 or More Years to Test Hypotheses

Some field data pertaining to several of the 2a-k objectives (see Objectives and Procedures, p.3) were collected. Because no in-depth analysis was conducted, reporting will occur in the 1990 final report.

## ACKNOWLEDGMENTS

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

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 101972 | R57 | 1978 | F | 1/04/79 | D | Recollared 2/11/82 |
| 101972 | Y36 | 1978 | F | 2/11/82 | D | Dead unknown cause 1/84 |
| 101973 | R53 | 1978 | F | 1/04/79 | 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 | O57 | 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 |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 101987 | R19 | 1978 | M | 1/08/79 | D | Dropped collar 1/79 |
| 101988 | R56 | 1978 | F | 1/4/79 | D | Recollared 2/26/82 |
| 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 | |
| 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 died 11/84 |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 102350 | Y22 | 1978 | F | 2/27/81 | D | Recollared 4/22/86 |
| 102350 | 047 | 1978 | F | 4/22/86 | D | Missing 5/86 |
| 102360 | Y16 | 1980 | F | 3/22/81 | D | Recollared 10/12/85 |
| 102360 | 062 | 1980 | F | 10/12/85 | D | Capture mortality 10/15/85 |
| 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 |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 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 |
| 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 | |
| 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 | |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 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 |
| 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 | |
| 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 |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 102987 | 071 | 1983 | F | 3/30/84 | D | Wolf kill 2/86 |
| 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 | |
| 102991 | 067 | 1983 | F | 3/30/84 | D | Recollared 4/15/87 |
| 102991 | 032 | 1983 | F | 4/15/87 | D | |
| 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 | |
| 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 |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 103052 | Y55 | 0 | M | 10/31/84 | D | Shot 9/10/86 |
| 103054 | 059 | 0 | M | 11/2/84 | Y | Shot 9/3/85 |
| 103055 | 050 | 0 | M | 11/2/84 | Y | Shot 9/9/86 |
| 103074 | Y66 | 0 | M | 11/21/85 | D | Wolf kill 10/5/87 |
| 103094 | 097 | 0 | M | 10/23/86 | D | Wolf kill ca. 11/15/86 |
| 103095 | 096 | 0 | M | 10/23/86 | D | Dropped collar 10/28/86 |
| 103096 | 095 | 0 | M | 10/23/86 | D | Died 10/28/86 |
| 103097 | 045 | 0 | M | 10/23/86 | D | Shot Iowa Ridge/Portage 9/6/87 |
| 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 | |

Table 1. Continued.

| Accession No. | Collar color and No. | Birth year | Sex | Date collared | Herd name | Comments |
|---|---|---|---|---|---|---|
| 103138 | 037 | 1984 | F | 4/15/87 | D | |
| 103139 | 040 | 1986 | F | 4/15/87 | D | Shot 11/87 |
| 103140 | None | 1986 | F | 4/15/87 | D | Not collared |
| 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 | |
| 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 | |

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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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 |
| 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 |
| 10/29-31/76 | 38 | 1 | 45 | 1 | 5 | 24 | 258 | 54 | 572 | 20 | 220 | 1,055 |
| 6/16-19/77 | 9 | 12 | 34 | 8 | 95 | 22 | 269 | 64 | 784 | 6 | 76 | 1,224 |
| 10/26-31/77 | 32 | 6 | 42 | 3 | 44 | 23 | 319 | 55 | 756 | 18 | 246 | 1,365 |
| 6/13-14/78 | 12 | 8 | 23 | 6 | 52 | 16 | 157 | 69 | 661 | 8 | 81 | 951 |
| 10/26/78 | 75 | 10 | 39 | 5 | 33 | 17 | 126 | 44 | 324 | 33 | 242 | 725 |
| 6/23/79 | 12 | 18 | 45 | 10 | 76 | 26 | 189 | 57 | 424 | 7 | 49 | 738 |
| 12/7/79 | 39 | NA | 65 | NA | NA | 32 | 115 | 49 | 177 | 19 | 69 | 361 |
| 6/14/80 | 18 | NA | 43 | NA | NA | 27 | 324 | 62 | 748 | 11 | 137 | 1,209 |
| 10/80 | 85 | NA | 49 | NA | NA | 21 | 288 | 43 | 585 | 36 | 496 | 1,369 |
| 6/17/81 | 13 | 16 | 34 | NA | 87 | 21 | 182 | 62 | 543 | 8 | 68 | 880 |
| 10/2/81 | 59 | NA | 41 | NA | NA | 21 | 319 | 50 | 776 | 29 | 458 | 1,553 |
| 5/23/82 | 0 | NA | 72 | NA | NA | 42 | 108 | 58 | 151 | 0 | 0 | 259 |
| 10/8/82 | 54 | NA | 29 | NA | NA | 16 | 215 | 55 | 736 | 30 | 398 | 1,349 |
| 11/26/82 | 60 | NA | 38 | NA | NA | 19 | 65 | 51 | 173 | 30 | 104 | 342 |
| 4/20/83 | 23 | NA | 29 | NA | NA | 19 | 205 | 66 | 708 | 15 | 166 | 1,079 |
| 5/21/83 | 0 | 7 | 80 | 7 | 275 | 41 | 1,629 | 52 | 2,052 | 0 | 26 | 3,982 |
| 6/15/83 | 4 | NA | 51 | NA | NA | 33 | 522 | 64 | 1,021 | 3 | 44 | 1,587 |
| 10/4/83 | 54 | NA | 41 | NA | NA | 23 | 307 | 50 | 665 | 27 | 361 | 1,333 |
| 4/10/84 | 10 | NA | 49 | NA | NA | 31 | 194 | 63 | 396 | 6 | 38 | 628 |
| 5/20/84 | 0 | NA | 82 | NA | NA | 0 | 0 | 0 | 482 | 0 | 0 | 877 |

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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 6/22/84 | 17 | NA | 56 | NA | NA | 32 | 837 | 58 | 1,508 | 10 | 259 | 2,604 |
| 10/17/84 | 42 | NA | 36 | NA | NA | 20 | 222 | 56 | 613 | 24 | 258 | 1,093 |
| 5/3/85 | 0 | NA | 0 | NA | NA | 34 | 256 | 66 | 503 | 0 | 0 | 759 |
| 10/9-12/85 | 49 | NA | 36 | NA | NA | 20 | 228 | 54 | 630 | 26 | 306 | 1,164 |
| 4/20/86 | 21 | NA | 29 | NA | NA | 19 | 302 | 67 | 694 | 14 | 145 | 1,041 |
| 10/22/86 | 41 | NA | 29 | NA | NA | 17 | 330 | 59 | 1,136 | 24 | 468 | 1,934 |
| 5/30/87 | 1 | 30 | 60 | 16 | 325 | 31 | 649 | 52 | 1,080 | 1 | 12 | 2,066 |
| 10/5/87 | 32 | NA | 31 | NA | NA | 19 | 323 | 61 | 1,030 | 20 | 329 | 1,682 |
| 4/6/88 | 22 | NA | 29 | NA | NA | 19 | 285 | 66 | 976 | 14 | 212 | 1,473 |
| 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 |

Table 3. Sex and age composition of Alaska's Yanert Caribou Herd, 1982-89.

| 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 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 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) | | | | | | | | | | | |

[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. Natality rates of the Delta Caribou Herd, estimated from calf:cow ratios and the proportion pregnant among radio-collared females $\geq 3$ years old, 1981-89.

| | Calf counts (late May or early June) | | | Radio-collared caribou $\geq 36$ months | | |
|---|---|---|---|---|---|---|
| Herd and year | No. calves counted | No. cows counted | Calves: 100 cows | No. pregnant | Total | Natality rate (%) |
| Delta 1981 | -- | -- | -- | 10 | 13 | 77[a] |
| Delta 1982 | 108 | 151 | 72 | 7 | 10 | 70[a] |
| Delta 1983 | 1,629 | 2,052 | 79 | 17 | 22 | 77[a] |
| Delta 1984 | 395 | 482[b] | 82 | 28 | 31 | 90 |
| Delta 1985 | -- | -- | -- | 38 | 41 | 93 |
| Delta 1986 | -- | -- | -- | 33[c] | 40 | 83 |
| Delta 1987 | 649 | 1,080 | 60 | 25 | 28 | 89 |
| Delta 1988 | -- | -- | -- | 28 | 32 | 88 |
| Delta 1989 | -- | -- | -- | 28 | 32[d] | 88 |

[a] These natality rates are possibly biased underestimates because the age structure of our radio-collared sample contained a large percentage of adult females that were 36 months old. It remains unclear if natality at 36 months is significantly lower than at older age (at least for the Delta Herd).

[b] Includes some yearlings.

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

[d] Sample size was actually 33 including one of unknown pregnancy status.

Table 5. 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 | 13 | |
| 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]<br>841 |
| Yanert 1986-87 | 54 | 16 | 2 | 72 | (646-1,139, 90% CI) |

Table 5. Continued.

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

Table 6. Hunting seasons and bag limits for Alaska's Delta 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<br>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<br>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 6. 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 6. Continued.

| Year | Season | Bag limit |
|---|---|---|
| 1987-88,<br>1988-89,<br>and<br>1989-90 | 10-25 Aug<br>21 Sep-31 Dec<br>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<br>Remainder of Unit 20(A) | 1 bull |

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

[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 7. Hunting seasons and bag limits for Alaska's Yanert Caribou Herd, 1984-89.[a]

| Year | Season | Bag limit |
|---|---|---|
| 1984-85[b] | 10 Aug-31 Mar<br>Unit 20(A), that portion within the Yanert River drainage | 1 caribou |
| 1985-86[c] | 1 Sep-28 Feb<br>Unit 20(A) within the Yanert Controlled Use Area | 1 caribou |
| 1986-87[d] | 1 Sep-28 Feb<br>Unit 20(A) within the Yanert Controlled Use Area | 1 caribou |
| 1987-88[e] | 1 Sep-15 Sep<br>1 Jan-28 Feb<br>Unit 20(A) within the Yanert Controlled Use Area | 1 bull |
| 1988-89 and 1989-90 | 1 Sep-15 Sep<br>Unit 20(A) within the Yanert Controlled Use Area | 1 bull |
| | 1 Jan-28 Feb<br>Up to 25 permits will be issued | 1 caribou (by permit only) |

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[a] The 1st year that the Yanert Herd caribou season was not included as part of the Delta Herd season was 1984-85.

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

[c] Amended by emergency announcement to close the Yanert River drainage on 19 February 1986.

[d] Amended by emergency announcement to close the Yanert River drainage on 14 January 1987.

[e] Amended by emergency announcement to close the Yanert River drainage on 14 January 1988.

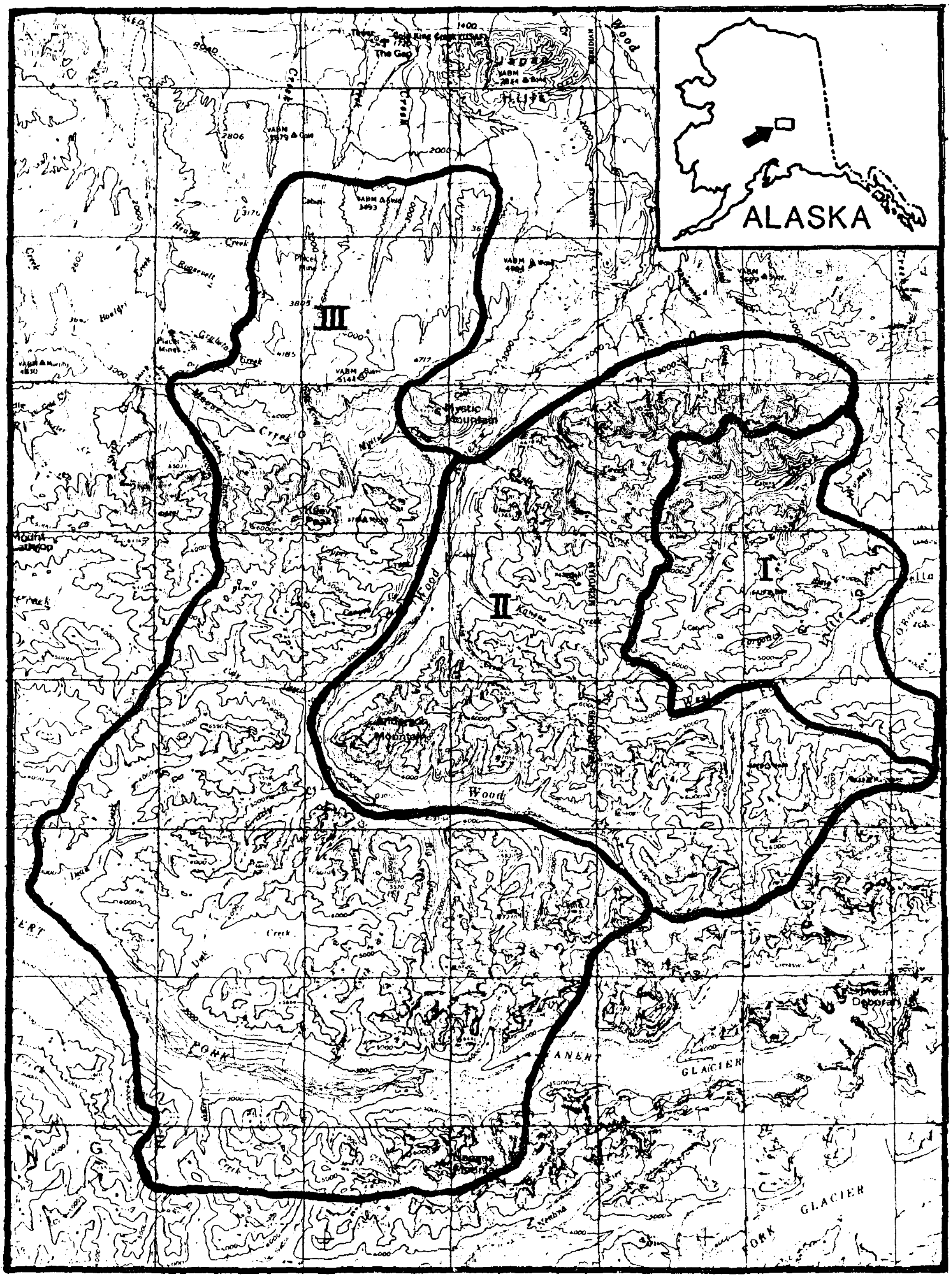
Appendix A. Distribution and size of caribou groups and distribution of radio-collared caribou from the Delta and Yanert Caribou Herds during the 30 June-1 July 1989 census (see Appendix A, Figs. 2 and 3).

| Group No. | Number of caribou on photos | Number of caribou visually enumerated | Number of radiocollars in group |
|---|---|---|---|
| 1 | 218 | 26 | 1 |
| 2 | 920 | | 8 |
| 3 | 150 | | 1 |
| 4 | 531 | 11 | 0 |
| 5 | 123 | | 0 |
| 6 | 143 | 9 | 0 |
| 7 | 1,654 | | 16 |
| 8 | 546 | 10 | 0 |
| 9 | 437 | | 1 |
| 10 | 0 | 73 | 1 |
| 11 | 2,016[a] | | 10 |
| 12 | 84 | 10 | 0 |
| 13 | 1,286 | | 5 |
| 14 | 237 | | 1 |
| 15 | 72 | | 1 |
| 16 | 145 | 3 | 1 |
| 17 | 266 | | 1 |
| 18 | 429 | | 1 |
| 19 | 586 | | 1 |
| 20 | 199 | | 0 |
| 21 | 103 | | 0 |
| 22 | | 7 | 0 |
| 23 | | 2 | 0 |
| 24 | | 1 | 0 |
| 25 | | 22 | 0 |
| 26 | | 25 | 0 |
| 27 | | 2 | 0 |
| 28 | | 12 | 1 |
| 29 | 295 | | |
| 30 | | 1 | 0 |
| 31 | | 4 | 0 |
| Subtotal 30 Jun 1989 | 10,440 | 218 | 50[a] |
| A | | 3 (all male) | 0 |
| B | | 2 (both male) | 0 |
| C | | 1 (unknown) | 0 |
| D | | 2 (both females) | 0 |
| E | | 4 (all male) | 0 |
| F | | 15 (1 calf, mostly females) | 0 |
| G | | 3 (unknown) | 0 |
| H | | 2 (1 cow, 1 calf) | 0 |

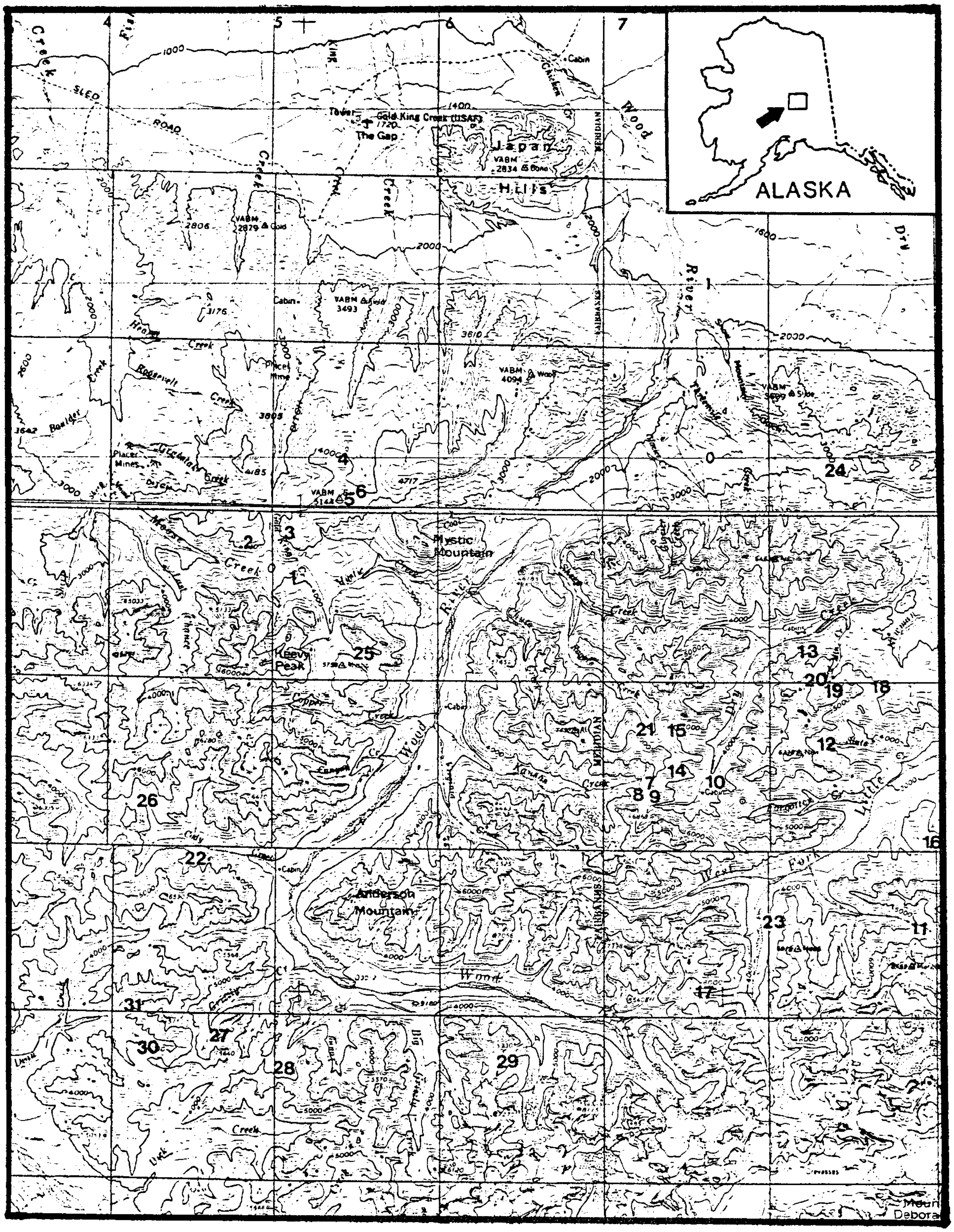
Appendix A. Continued.

| Group No. | Number of caribou on photos | Number of caribou visually enumerated | Number of radiocollars in group |
|---|---|---|---|
| Subtotal 1 Jul 1989 | | 32 | 0 |
| Total | 10,690 | | |

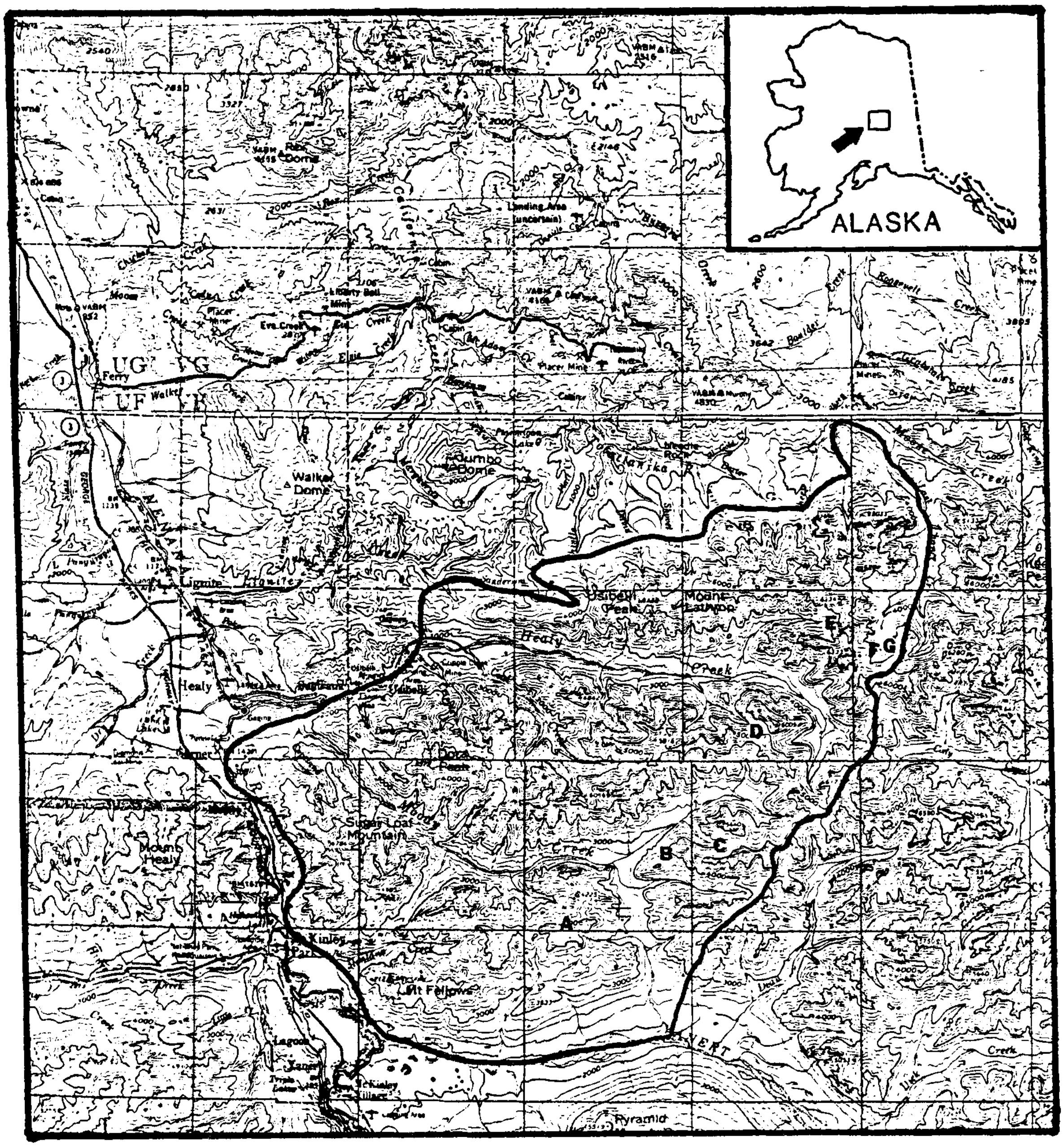
[a] A radio-collared Yanert caribou, 064, was between Dick and Dean Creeks in the Yanert drainage; caribou 042 was on the Tanana flats; and caribou 041 was not located all summer or during the census but was later located during the rut.



Appendix A, Fig. 1. Areas covered by 100% visual searches during the 1989 Delta/Yanert census, 30 June 1989.



Appendix A, Fig. 2. Locations of aggregations of Delta and Yanert Herd caribou during the census, 30 June 1989.



Appendix A. Fig. 3. Area covered by 100% visual search and locations of caribou observed during the Delta/Yanert census, 1 July 1989.

## APPENDIX B.

# RELATIONSHIPS BETWEEN BODY WEIGHT, EARLY PUBERTY, AND REPRODUCTIVE HISTORIES IN CENTRAL ALASKAN CARIBOU

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ABSTRACT: Reproductive histories were determined for known-age radio-collared caribou (Rangifer tarandus granti) in the Delta Caribou Herd from 1979 to 1989. During this time, herd size grew from <4,000 to >10,000. Live weights were obtained in most years from 11-month-old females (as an index of cohort condition). No significant change in mean body weight of cohorts occurred over time, but the parturition rate of 24-month-old females dropped from 67% in 1980 to 0% after 1983. Corroborating data from the adjacent Denali Herd are included. Discussion focuses on the hypothesis that the main factor relating to pregnancy in caribou is female body weight at rut. In addition, we discuss (1) effect of early puberty on pregnancy resting and alternate-year reproduction, (2) pregnancy resting in non-early puberty females, and (3) conditions associated with and demographic consequences of early puberty in female caribou.

## INTRODUCTION

When we began intensive research on the Delta Caribou Herd in the late 1970s, data were limited on the variables affecting reproduction in Alaska's caribou. Also, opinions were diverse regarding the relative importance of nutrition to caribou reproduction and hence population dynamics. For example, at a symposium and workshop on caribou population ecology in Alaska (Klein and White 1978:22-23), E. Reimers suggested that a close relationship exists between pregnancy rate and body weight of females at the time of rut. Based on Norwegian data, where predators were unimportant sources of mortality to caribou, Reimers concluded that, "...herd productivity was highly dependent on individual animal growth."

In contrast, A. T. Bergerud (Klein and White 1978:23) stressed that reproductive rates in North American caribou herds remain constant at 70-85% despite a wide diversity in range conditions. Also, he stressed that the major influences on caribou numbers, and in particular what brings their numbers down, are predator-prey interactions.

Lacking specific knowledge of the variables affecting reproduction in North America, there has been a tendency to extrapolate from the Scandinavian literature on domestic and wild reindeer (e.g., R. G. White, pers. commun.; Klein and White 1978:37) with considerable emphasis on Reimers' (1983a,b) work. Also, lacking empirical data from females of known reproductive histories and sequential annual weights at rut, several popular hypotheses have emerged and gone untested for a decade or more. Examples include Reimers' (1983a) hypothesis that from the weight distribution of females in a population the population's pregnancy rate can be calculated by the following equation: $P = 1 - e^{[-0.169\ (W-21)]}$, where P = probability of pregnancy, and W = dressed weight in kg (dressed weight = total body weight minus viscera, head, skin, and lower legs).

A second hypothesis is that repeated pregnancy and lactation will eventually result in a "pregnancy resting" year (Dauphine 1976, Reimers 1982). A third hypothesis is that early puberty could result in a developmental setback, leading to a temporary barren status the next breeding season (Reimers 1983a), or 2 seasons (Lenvik 1981 cited in Reimers 1983a), or even to a pattern of alternate-year reproduction (R. G. White, pers. commun.).

In addition, interest remains high in the management implications of early puberty in caribou herds. Early breeding has the potential to greatly increase herd growth because young-age cohorts are relatively large in populations with a "normal" age structure (i.e., stable or increasing herds). However, the actual contribution depends on survivorship of the offspring and whether producing a calf at 2 years of age will cause the female to "pregnancy rest" in some subsequent year or years.

Radio-collaring of Delta caribou females <12 months old began in 1979. The primary objective of the radio-collaring was to ascertain age-specific mortality and reproduction. In addition, the project allowed us to collect serial whole body weights and total reproductive histories of individuals. Similar work began on the adjacent Denali Caribou Herd in 1986. We believe that the data from the Delta and Denali studies can be used to evaluate the hypotheses stated above and/or as evidence for alternate hypotheses.

## OBJECTIVES

1. To test the hypothesis that pregnancy rates are predictably related to fall body weights of females (Reimers 1983a).

2. To ascertain if early puberty increased the probability of alternate year reproduction or "pregnancy resting" at 3 years of age in Delta caribou.

3. To review and discuss the evidence for pregnancy resting in caribou.

4. To identify the conditions associated with early puberty in the Delta and Denali Herds and to evaluate the demographic consequences of early puberty in the population dynamics of caribou herds.

## STUDY HERDS AND AREAS

The Delta and Yanert Caribou Herds currently range over about 11,000 km$^2$ on the north slopes of the Alaska Mountain Range between the Nenana River on the west and the Delta River on the east and seasonally overlap in distribution (Fig. 1). The Denali Herd inhabits an area of approximately 10,000 km$^2$

bounded by the Nenana River on the east and the Herron River on the west. The area inhabited by these herds lies approximately 110 km south of Fairbanks. The Alaska Range consists of rugged, glaciated ridges, 1,830-2,740 m in elevation, interspersed with glacier-capped mountains exceeding 3,660 m. The northern foothills of the Alaska Range are flat-topped ridges, 610-1,370 m in elevation, separated by rolling tussock tundra, muskegs, and lowlands dominated by spruce (Picea spp.). North of the foothills lies the predominantly spruce-covered Tanana Flats. The entire area is drained by the Tanana River.

The area is largely snow-free from May until October. Annual temperature range is approximately 29°C to -51°C. Annual precipitation averages about 30 cm; snow accumulation averages 0-50 cm and rarely exceeds 80 cm. In the foothills and mountains, ground vegetation is frequently exposed during winter by strong winds.

Large predators in the study areas include wolves (Canis lupus), black bears (Ursus americanus), and grizzly bears (Ursus arctos). Additional predators capable of preying on caribou include coyotes (Canis latrans), wolverines (Gulo gulo), Lynx (Lynx canadensis), golden eagles (Aquila chrysaetos), and possibly red fox (Vulpes fulva). Major prey species present include moose (Alces alces), caribou, Dall sheep (Ovis dalli), beavers (Castor canadensis), snowshoe hares (Lepus americanus), and ground squirrels (Citellus parryi).

Population status and history of the Delta and Yanert Herds was last reported by (Davis et al. 1988). During the past 2 decades, the Delta Caribou Herd has varied dramatically in size and population density, declining from 5,000 (0.6/km$^2$) in 1969 to about 2,000 (0.31/km$^2$) in 1975 and increasing from about 2,000 in 1975 to 7,000 (0.8/km$^2$) in 1982. Since 1982, herd growth has been slowed by hunting (and perhaps other factors) reaching >10,000 (1.0/km$^2$) in July 1989. The Yanert Herd was first recognized as a discrete herd in 1980. It has numbered about 600±200 since 1982 and seasonally overlaps the distribution of the Delta Herd.

Davis et al. (1983) surmised that nutritional status was high in the Delta Herd based on nutritional indices such as rapid growth, large body size, early sexual maturity, high pregnancy rates, high natality and calf survival rates, and early parturition. Because the Delta and Yanert Herds have shared seasonal ranges since 1984, we assume similar nutritional status, so data are pooled and hereafter referred to as Delta Herd data.

The population status and history of the Denali Herd has been reported by Boertje (1981), Singer (1987), and Adams et al. (unpubl. ms.). The herd numbered around 1,000 animals in the mid-1970s after a major decline from about 9,000 animals in the early 1960s. Historically, the Denali Herd may have numbered over 20,000 in the late 1930s-early 1940s. Boertje (1981) characterized the herd during the early 1980s as a reduced population with high nutritional status and a population density of around 0.08 to 0.12 caribou per km$^2$. Recent work by Adams et al. (unpubl. ms.) suggests that the population grew to over 3,000 animals by 1989 (0.3 caribou/km$^2$) and apparently has continued high nutritional status.

## METHODS

### Delta Caribou Herd

From January 1979 through April 1989, we captured and radio-collared 85 different female caribou from the Delta Herd. These females were collared primarily at 8-12 months of age. Collars were replaced every 3-4 years prior to battery exhaustion in the radio transmitters. We used a helicopter to immobilize most caribou by darting with M99 (Valkenburg et al. 1983) or Wildnil (Adams et al. 1988b). The remaining caribou were captured with a shoulder-held net gun (Valkenburg et al. 1983) or a net gun mounted on the skids of a helicopter and 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).

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 in addition to subjective impressions by the observers was the basis for judging the female's parturition status. In 4 of 294 cases (all in 24-month-old caribou), we were unable to judge reproductive status.

### Denali Caribou Herd

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 years old, all instrumented animals were relocated daily during 6-31 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, unpubl. files). Radio-collared calves were located daily until the end of May and then periodically throughout the rest of their first year.

### Weight Conversions

We used Reimers' (1983b) conversion formula of dressed weight = 52% of the total body weight to convert total body weights to dressed weights for calculations involving Reimers' (1983a) prediction equation: $P = 1 - e^{[-0.169(W-21)]}$, where P = probability of pregnancy and W = dressed weight in kg.

## Weights

In our testing of hypotheses about the relationship of rutting weight of females and their probability of being pregnant we used an index to rutting weight. Most of our weights were obtained around late April, so we must infer a rut weight from those data. In doing so, we are assuming that 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 and 1980 cohorts 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 1 will be proportionally the same in year 2.

## RESULTS AND DISCUSSION

### Objective 1: Body Weight - Pregnancy Relationships

Reimers (1983a) reviewed and summarized the literature regarding the main factors that relate to pregnancy in *Rangifer* as follows:

> "Skunke (1969) suggested that pregnancy rates relate to stocking rates and Movinkel and Prest-bakmo (1969) indicate a dressed weight relationship in domestic reindeer. Varo (1964, 1976), also working with domestic reindeer, found that pregnancy rate correlated to both age and weight. Skoog (1968), Kelsall (1968), and Parker (1982) found an age-dependent pregnancy rate in caribou. Dauphine (1976), although reporting an age-dependent pregnancy rate in caribou, found that pregnancy was clearly related to body weight and fat content.... Thomas (1982) shows that fertility in Peary caribou (*Rangifer tarandus pearii*) is related to the fat reserves."

Reimers (1983a) went on to conclude that reproduction data from wild and domestic reindeer in Norway indicate that pregnancy rates are related predictably to body weights of the females. Reimers (1983b) amplified the view from his 1983a paper as follows:

> "Recently Hamilton and Blaxter (1980) for red deer...Lenvik (1981) for domestic reindeer, Thomas (1983) for Peary caribou...and Reimers (1983) for wild reindeer, have found that reproduction in these species or sub-species is a function of weight rather than age. This means that 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 1983b). Therefore, from knowledge of the weight distribution of females in a population, its pregnancy rate may be calculated."

We believe that much "conventional wisdom" on the relationship between body weight and its influence on reproduction stems from Reimers (1983a,b), discussion in Klein and White (1978:31), and R. G. White (pers. commun.).

If Reimers' predictive equation applies universally, the implications are important and many. Although it is unclear whether Reimers meant for his equation to apply throughout R. tarandus, we applied it to body weight data from the Delta Herd. Predictions from the equation did not compare well with our field data (Table 1).

However, Reimers' original data (1983a:213, Table 2) resulted in an estimated pregnancy rate of 0.88 for reindeer $\geq$3 years old at the time of calving, the same as our observed rate for Delta caribou in that age group (Fig. 2). 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 1 or 2 years old at calving, the subsequent predicted pregnancy rates were 0.0 and 0.22, respectively, which generally agrees with field data. Therefore, Reimers' (1983a) 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-specific 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 overlap in dressed weight (18-26 kg) between calves and older animals, 0 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 overlap (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) footnoted his Table 2 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) did report 100% pregnancy for small samples of the large-bodied North and South Ottadalen reindeer, but interpretation of these data, similarly to in the case of calves, 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) wrote as follows: "...body weight has been shown to be directly correlated with, and may be used to predict, reproductive rates in female whitetails (Sauer 1984)...our recent analyses suggest that this traditional interpretation may need further qualification."

Dusek et al. (1987) showed a higher reproductive level in a herd with smaller body weights than in a second herd with larger female body weights.

As food for thought, Geist (1983) commented that, "...in red deer size differences in extremes are five-fold (Beninde 1937)." We may have taken Geist's quote out of context, but this great size range implies great plasticity in pregnancy-weight relationships.

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.

## Objective 2: Evaluation of Pregnancy Resting in Females First Reproducing at 24 Months of Age

Reproductive histories of females that first reproduced at 24 months of age appear in Fig. 3. We found no apparent pattern to indicate "pregnancy resting" at 36 months of age for these individuals. 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.

Of the 7 cows that were followed during each calving season at least to 5 years of age, 4 did not produce a calf in 1 of the 4 potentially productive years. 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 did occur 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).

## Objective 3: Evidence of Pregnancy Resting in Older Caribou

The age-specific parturition records of 21 Delta caribou cows with 7 or more years of known status are summarized in Fig. 4. 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 calved first at 2 years old (7 of 8, 88%).

Although the data in Fig. 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 the 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, 0.13, and 0.06, respectively. If sequential successful calves are necessary to induce pregnancy resting, then in herds such as Delta and Denali it is unlikely to occur.

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 1 mechanism by which the relative proportions of different phenotypes might occur in a given population over time.

## Objective 4: The Relationship Between Early Puberty and Demographic Variables in the Delta and Denali Herds

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 $\underline{x}$ = 62.3 kg ($\underline{n}$ = 7, SD = 5.4) compared with $\underline{x}$ = 61.2 kg ($\underline{n}$ = 83, SD = 5.4) for all calves in the sample (Table 2). Further, in the highly parturient 1978 cohort, the $\underline{x}$ weight of the cohort was 61.3 kg ($\underline{n}$ = 11, SD = 3.7) not significantly different from the entire sample mean (Table 2). The range of weights of the parturient females was 55.9 to 68.2 kg. Of nonparturient females, 30 equaled or exceeded the mean weight of parturient females of 62.3 kg. Also, 9 nonparturient females were heavier than the heaviest parturient female that weighed 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, population density, and the relative abundance of adult males for the Denali (not in Table 3) and Delta Herds when the rate of early puberty was high and for the Delta Herd after the rate became 0 (Table 3). 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 1971a, 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."

Young age classes are significantly larger than older age classes in most stable or increasing caribou populations. The implication of this general rule is that early puberty can potentially influence herd productivity greatly. What role does early puberty play in irruptions of caribou populations? More specifically, what was the role in the irruption of the Delta Herd and in the current growth of the Denali Herd? What are the implications of early puberty to managers who want to maximize the number of caribou that can be produced annually from a caribou herd?

Reimers (1982) reported that 2-year-old females constituted about 25% of all females $\geq 2$ years old in his 5 study herds. Messier (1988) reported that 2-year-old females made up 21% of females $\geq 2$ years old in a 1984 sample from the expanding George River Herd.

An approximate parturition rate of 50% (the approximate mean of 67% [8/12] in the Delta Herd in 1978 and 1979 and 42% [10/24] in the Denali Herd in 1988 and 1989) appears to be a high rate for 24-month-olds in established North American herds (Bergerud 1980). A scenario involving a high rate of early puberty will allow assessing the contribution to total calf production added by early puberty. Assuming 0.5 pregnancy in 2-year-olds, 0.9 pregnancy for ≥3-year-olds, and an age structure as in Messier (1988): (0.79) (0.9) + (0.21) (0.5) = 0.71 + 0.11; 82 calves/100 cows would be produced.

In this scenario, 13% of the total calf production came from 2-year-old females. However, data from the Delta, Denali, and Porcupine (K. Whitten, this workshop) Herds suggest that survival of calves produced by 2-year-old females is lower than for calves produced by older cows. For example, Davis and Valkenburg (1981) determined that at least 2 of 6 calves born to 2-year-old cows in the Delta Herd survived to October in 1980, i.e., ≥33% survival compared with 58% for calves born to older females. In the Denali Herd in 1989, 1 of 4 calves born to 2-year-old cows survived 10 days postpartum compared with 54% (37/68) of calves born to older females. K. Whitten (this workshop) reported that the 2 calves born to 2-year-old Porcupine Herd cows died within 24 hours of birth versus 71% survival until 1 July for calves born to older cows. L. Adams (unpubl. data) determined that birth weights were 25% lower for calves (n = 4) of 2-year-olds versus weights of calves born to ≥3-year-old cows, suggesting a possible explanation for the lower survival rate of the former calves. Hence an "adjustment" to the scenario assuming a survival rate of 0.5 for calves ≥3-year-olds and 0.25 to 0.13 for calves of 2-year-olds follows: (0.79) (0.9) (0.5) + (0.21) (0.5) (0.25) or (0.13) = 0.36 + 0.03 or 0.01. Therefore, 39 or 37 calves/100 cows would have survived, of which 8% or 3% were produced by 2-year-olds. In these scenarios, it is unlikely that early puberty would contribute more than 8% to the rate of herd growth (e.g., if r = 0.20 in an irrupting herd with high early puberty then r would = 0.18 without the contribution).

## ACKNOWLEDGMENTS

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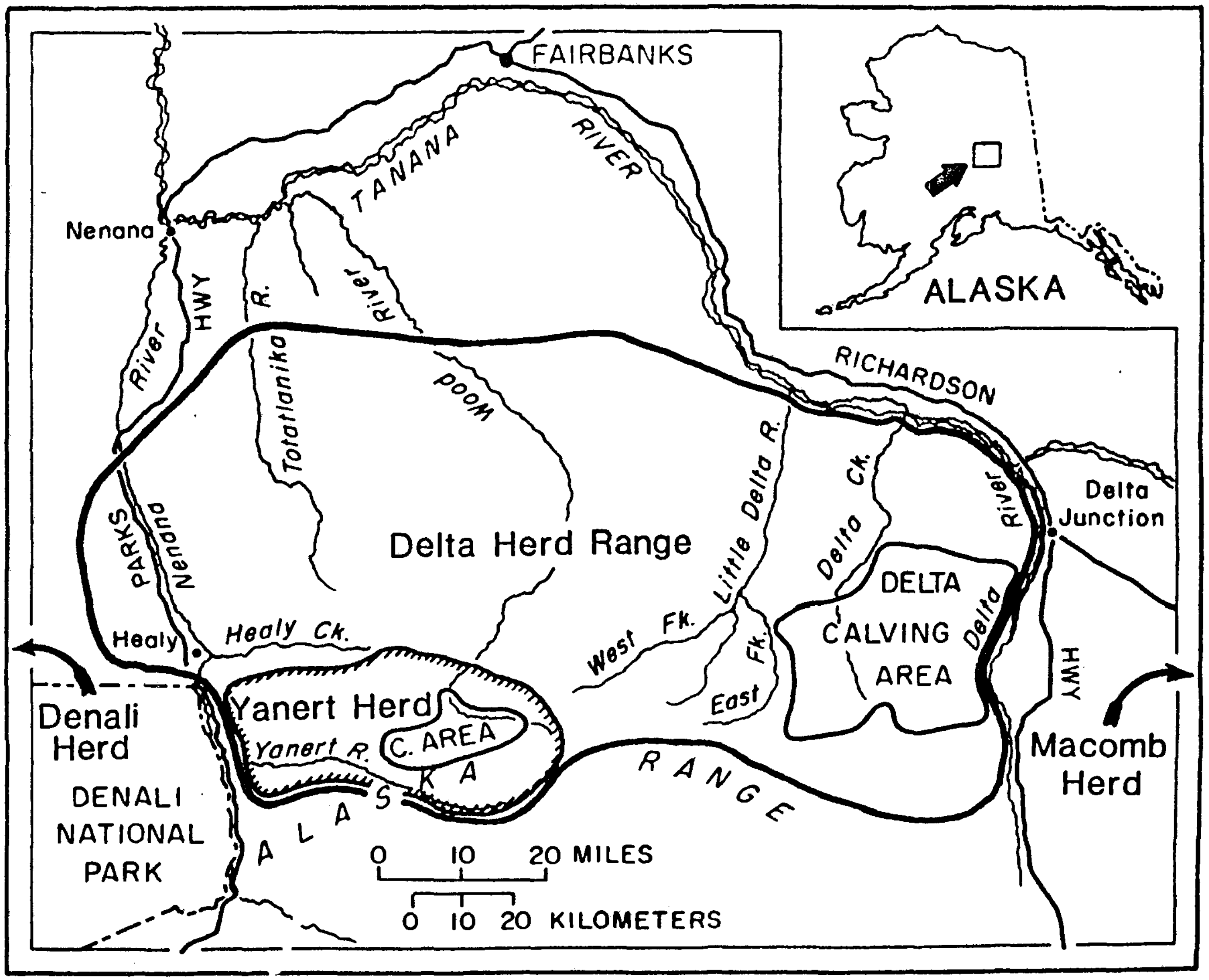

Fig. 1. The Delta and Denali study areas.

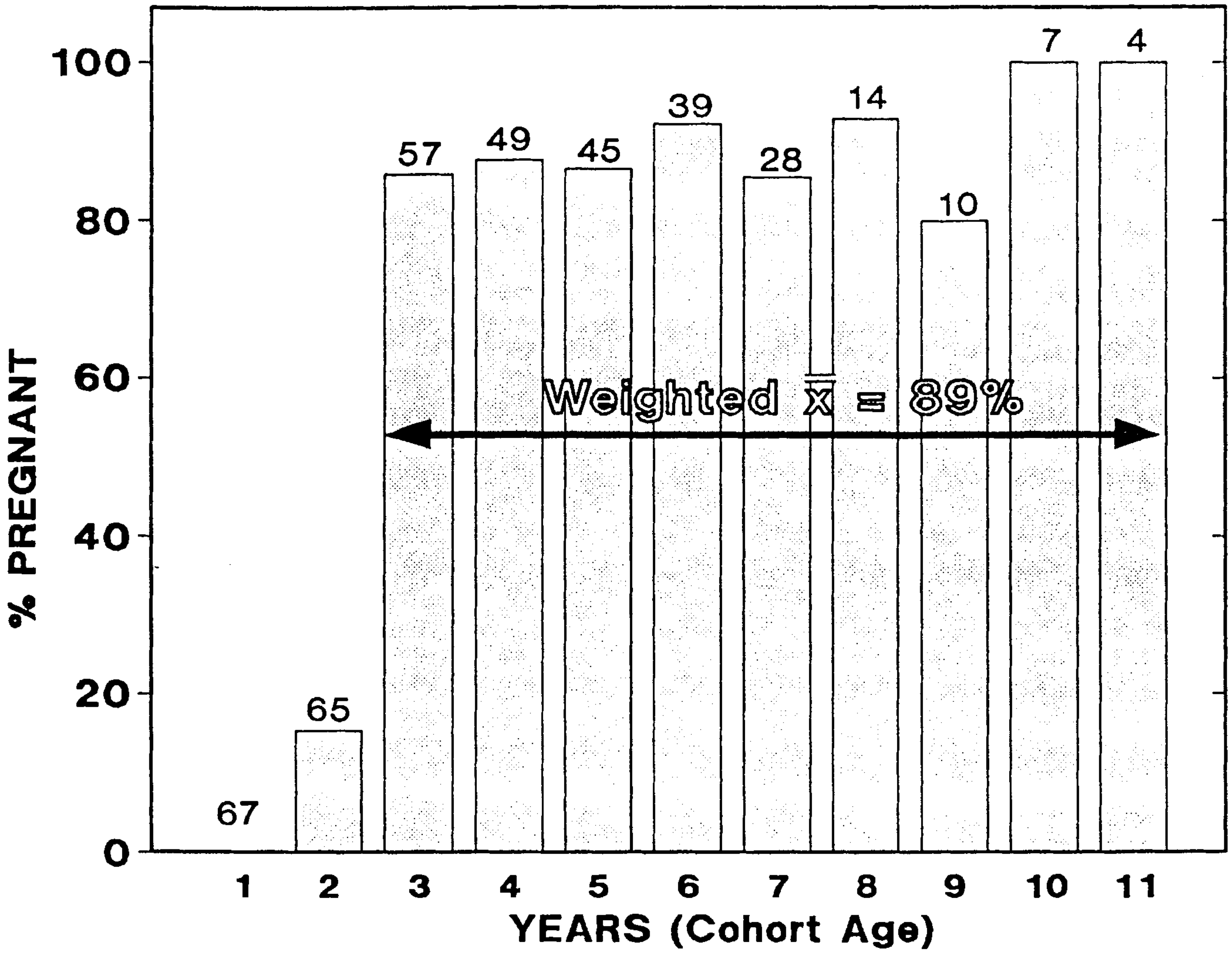

Fig. 2. Cohort specific pregnancy rate of known age Delta Herd caribou for ages 1-11 (sample size) 1979-1989

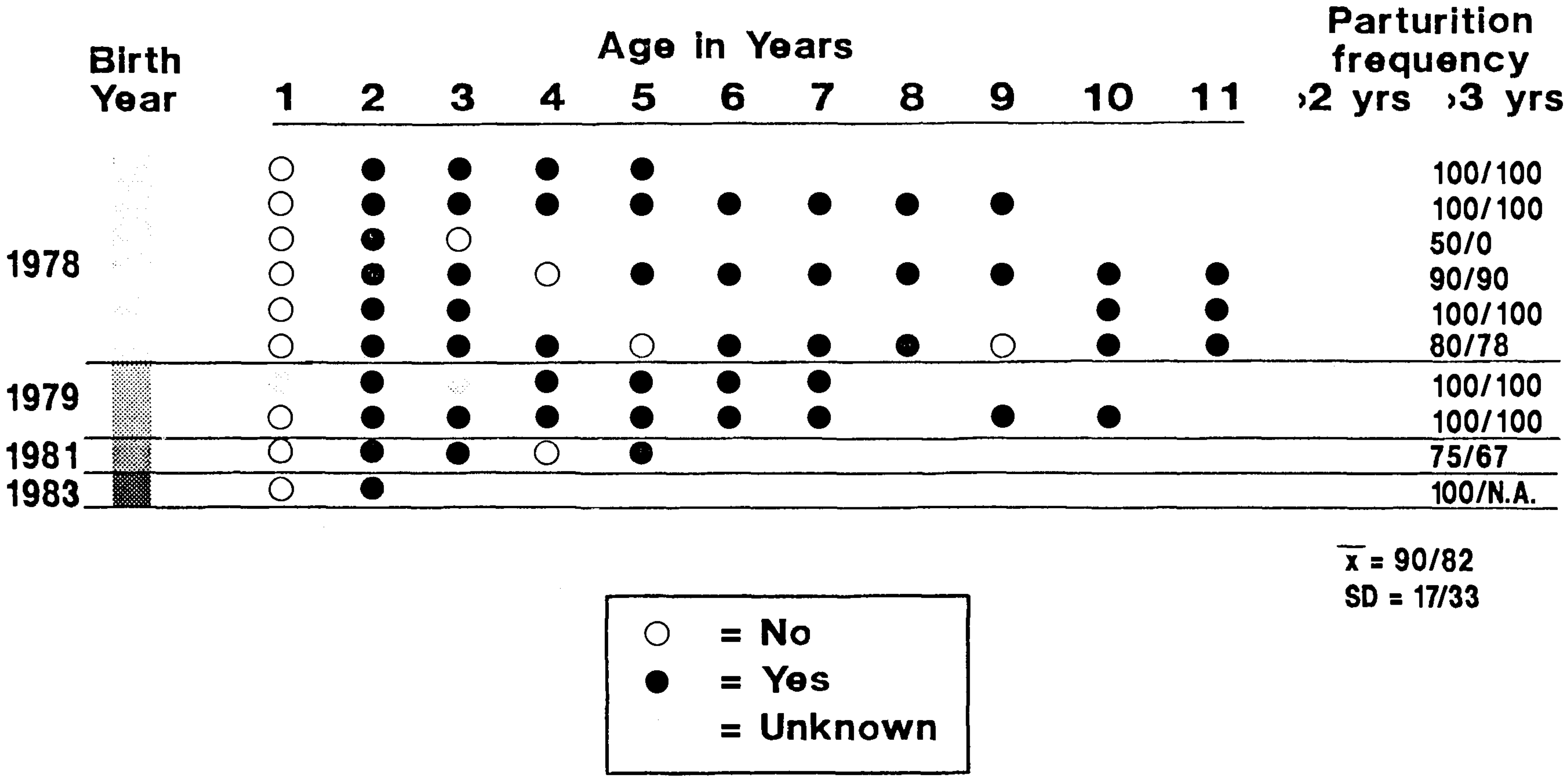

Fig. 3. Age-specific parturition status for 10 Delta Herd caribou that were first parturient at 24 months of age, 1978-89

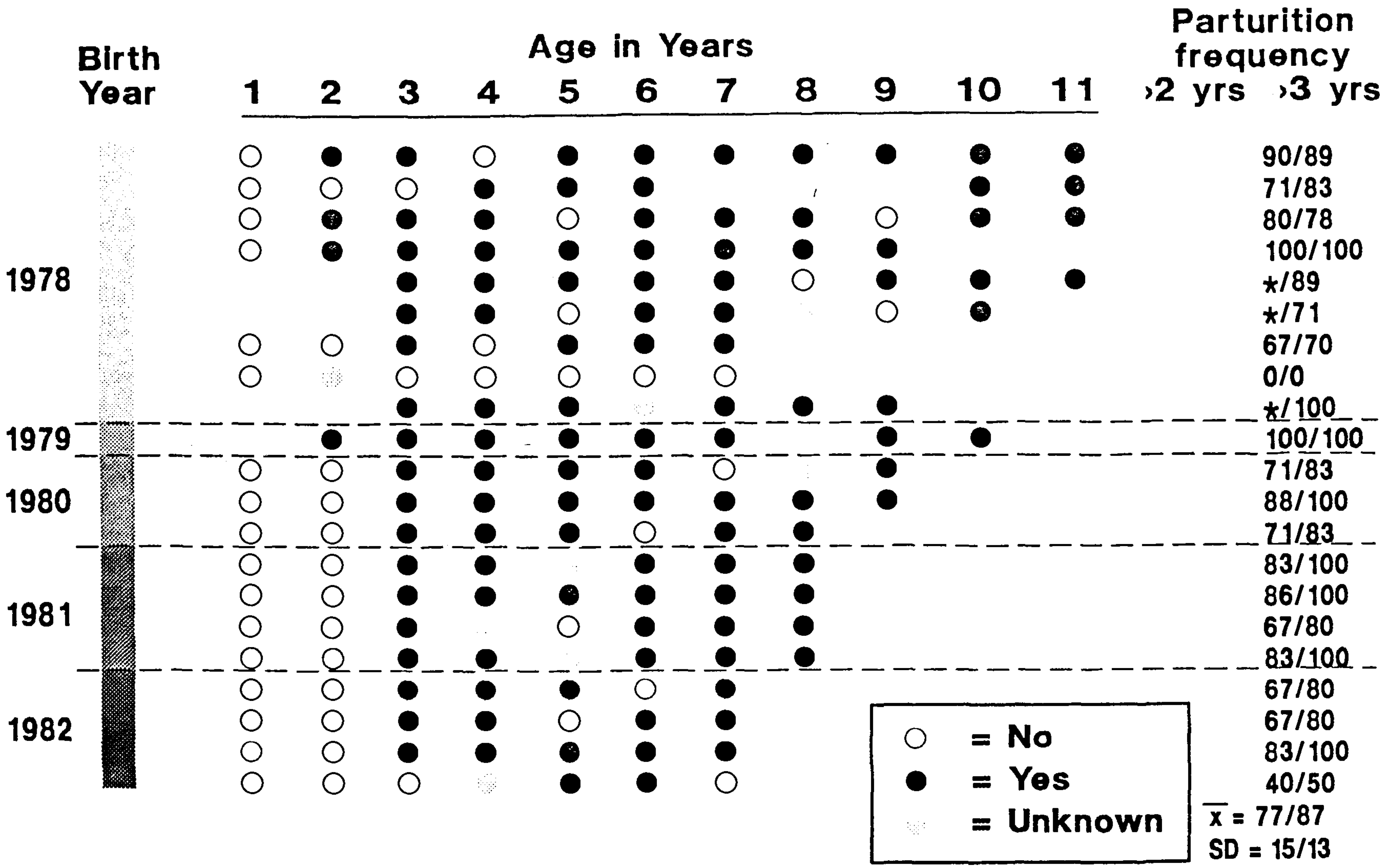

Fig. 4. Age-specific parturition status for 21 Delta Herd caribou with 6 or more years of known status, 1978-89.

Table 1. Comparison of Delta Caribou Herd body weights and pregnancy rates with predictions based on Reimers' (1983a) equation.

| Age (years) | Weight in kg |  |  |  | Actual pregnancy rate | (n) | Reimers' predicted rate | Adjusted[a] predicted rate (90% CI) |
|---|---|---|---|---|---|---|---|---|
|  | x live | x dressed | n | SD |  |  |  |  |
| 1 | 61.4 | 31.9 | 82 | 5.4 | 0.0 | 84 | 0.84 | 0.0 |
| 2 | 75.8 | 39.4 | 4 | 15.5 | 0.15 | 65 | 0.90 | 0.22 (0.0-0.69) |
| ≥3 | 112.5 | 58.5 | 46 | 10.4 | 0.89 | 253 | 1.00 | 0.88 (0.86-0.88) |

[a] An adjustment factor was calculated from the x weight of ≥3-year-old cows from this study (58.5 kg) and Reimers (1983a) (33.4 kg) as follows: 33.4/58.5 = 0.57. See text.

Table 2. Weight-related statistics for 7- to 12-month-old female caribou from Alaska's Delta Caribou Herd by cohort year.

| Cohort year | Sample size | $\underline{x}$ | 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 ( = 0.05) difference in cohort weights was that the 1981 and 1982 mean cohort weights were greater than in 1986.

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

Table 3. Range size, population size, density, predator:caribou ratios, and bull:cow ratios of the Delta Caribou Herd, 1979-87.

| 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.

APPENDIX C.

# A REVIEW OF CARIBOU POPULATION DYNAMICS IN ALASKA EMPHASIZING LIMITING FACTORS, THEORY, AND MANAGEMENT IMPLICATIONS

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ABSTRACT: Alaska's 29 recognized caribou (Rangifer tarandus granti) herds are classified to identify those that are both migratory and inhabit areas where moose (Alces alces) (or other ungulates) are important alternate prey. During the time that detailed demographic data have been obtained (i.e., 1960s-1980s), natural mortality and human-induced mortality have varied more and have more influenced Alaska's caribou herd demographics than have natality changes. Dispersal has not significantly influenced population dynamics during this time and has not been consistent with theory in the caribou literature. Detailed demographic data have been obtained primarily during low and increasing phases of populations. Recent conclusions regarding limiting and regulating factors are compared and contrasted with past reviews of Alaskan caribou population dynamics.

## INTRODUCTION

For discussion at the 4th North American Caribou Workshop, caribou in North America were envisioned as comprising 3 ecotypes (F. Messier, pers. commun.): ecotype 1 - woodland caribou (R. t. caribou) living in association with alternate ungulate prey (e.g., British Columbia caribou); ecotype 2 - migratory caribou herds that inhabit areas also used by alternate ungulate prey (particularly moose) (e.g., Alaska caribou); and ecotype 3 - migratory caribou herds having limited contact with alternate ungulate prey (e.g., the George River Herd in Quebec/Labrador).

This paper discusses population dynamics in the Alaskan caribou ecotype. The theory and empirical data for Alaska caribou population dynamics through the 1970's have been previously and intensively reviewed (e.g., Skoog 1968, Bergerud 1980, and others). Hence, we will only summarize recent changes in population size and trend for Alaska caribou herds. In discussing limiting versus regulating factors, we will summarily review the 3 components of population dynamics--natality, mortality, and dispersal--as they relate to the population dynamics of Alaska caribou. In addition, we will (1) discuss some existing theories of caribou population dynamics, (2) discuss how recent empirical findings relate to these theories, (3) evaluate the most tenable extension of the theories into management practices, and (4) attempt to identify factors currently limiting our understanding of caribou population dynamics.

## DEFINITIONS

For standardization at this workshop, we use definitions proposed by F. Messier (pers. commun.) for limiting factors, regulating factors, and population control. In addition, we define population dynamics.

Population dynamics - The process by which births, deaths, and dispersal change population size over time.

Limiting factors - Any processes that quantifiably affect [restrict] population growth. They induce year-to-year changes in the rate of population growth and, by extension, in animal abundance. They may be stochastic or with reproducible density relationships.

Regulating factors - Any density-dependent processes that ultimately keep populations within normal density ranges. Thus, regulating factors are a subset of limiting factors characterized by negative-feedback mechanisms, that depress population growth as animal abundance increases.

Population control - Connotes a planned attempt by humans to manipulate population size through hunting or culling.

## POPULATION DYNAMICS AND LIMITING FACTORS

During the early and mid-1970s, most Alaskan herds declined (Fig. 1, Table 1, 2, 3). The statewide population declined from 415,000 in 1970 to 255,000 in 1977 (a decline of 39%, $r = -0.08$). In contrast most herds increased from 1977 to 1989. The statewide population grew from 240,000 in 1977 to 729,000 in 1989 (200%, $r = 0.09$). The historical records and prehistorical evidence suggest that frequent and dramatic population changes have always occurred in Alaskan caribou herds.

The most important factors that explain changes in caribou abundance in Alaskan herds from $t$ (year 1) to $t + 1$ (year 2) have varied over time and among herds within any given time. Reasons for the declines during the 1970s have been reported, discussed, and debated repeatedly (e.g., Bergerud 1978, Doerr 1980, Gasaway et al. 1983). There is general consensus that exploitation by humans and predation increased mortality rates and lowered recruitment rates commonly during the declines of the 1970s. There is less consensus over the role of weather and nutritional limitation. Debate continues over the role of predation as a proximate versus ultimate limiting factor. Also, serious debate continues over the role of density-dependent factors in the declines and increases. However, little compelling evidence for density dependent regulation has accrued for the range of population densities that have been monitored. Albeit, evidence of density-dependent responses in Alaskan caribou have been reported (see Valkenburg et al., Davis et al., this workshop).

During the post-1977 population increase in Alaskan caribou, preclusion of excessive exploitation of caribou by humans has undoubtedly contributed to the rate of caribou population growth. Also, in general wolf populations were low or at moderate levels and weather has been favorable during the increases of the 1980s. Birth rate has varied less than natural mortality rate through both the decline and growth phases of the Alaskan population. Apparently dispersal played no measurable role in the recent population declines or increases.

## REGULATING FACTORS

To date, it appears that limiting factors have influenced population dynamics of Alaska caribou more than have regulating factors. Assuredly, caribou in Alaska show signs of resource limitation (i.e., negative feedback to nutritional limitation) that correlate with population size (density). However, these responses have not been demonstrated to create measurable population regulation. From available evidence for Alaska caribou, we conclude that neither natality, mortality, nor dispersal operate in a very sensitive, linear, or curvilinear manner throughout the population density range we have monitored.

Graphic depiction is the most concise way for us to present our view of the generalized relationship of density to natality, mortality, and dispersal for Alaska caribou. We contrast the classic textbook relationship of natality (Fig. 2), for white-tailed deer (McCullough 1979), which is linear and inversely density-dependent with that we envision for Alaska caribou. We did not graphically depict what we envision as the density/mortality relationship for caribou. We envision the general curve for that relationship as approaching a reflection of the natality/density curve in Fig. 2. Mortality appears to be low and relatively constant at low and medium density with a sharp inflection occurring at some point in the high-density range.

Regarding dispersal, we use Bergerud's (1980) model [which is similar to that of Skoog (1968) and Haber and Walters (1980)] to depict a consensus model for dispersal based on the literature (Fig. 3). There is little empirical data available for evaluation of the dispersal model. Since the 1960s, only Alaska's southern Alaska Peninsula Herd (SAPH) has reached or exceeded the model's dispersal threshold density. The SAPH apparently exceeded a density of 2/km$^2$, did not disperse, and declined by ≥50%, apparently from resource limitation (Pitcher and Johnson 1989; Johnson, in press). We have never verified density-dependent dispersion in Alaska caribou in the context of mass emigration/immigration (albeit anecdotal literature abounds with references, e.g., Skoog 1968). Davis et al. (1978) reviewed the circumstantial evidence for the assumed mass emigration from the Fortymile Herd in 1957 and 1964 (Skoog 1968) and concluded that there was no evidence to conclude that any net emigration had occurred. Similarly, the presence of radio-collared individuals has helped demonstrate that no measurable net emigration/immigration has occurred when several herds (e.g., Delta, Porcupine, Nelchina, Mentasta) have made major incursions into adjacent herd ranges and overlapped in seasonal distribution (primarily in winter). Similar incursions had been considered evidence for net emigration in the past.

Because population regulation is central to much general population dynamics theory, it seems logical to hypothesize that regulating factors must operate in caribou population dynamics. Caribou managers in Alaska have gone much further than that in the past. During the 1960s and early 1970s, management philosophy and policy in Alaska incorporated much general population regulation theory that proved to be inappropriate for caribou. This, and other factors, led to overharvest of caribou and decline of the statewide population.

Bergerud (1978) opined that 3 points contributed to the Alaskan caribou decline: (1) the belief that large herds would not be overharvested, (2) underestimating the extent of calf mortality when predators were abundant, and (3) the belief that food supplies set carrying capacity for caribou populations which, consequently, had to be hunted heavily to prevent the animals from overgrazing habitat and declining in number. These 3 points certainly contributed to the decline, and intertwined in all 3 points was the belief of density-dependent compensatory mortality and inversity (in terms of productivity and survival).

## ALASKA CARIBOU AS AN ECOTYPE

To consider all caribou herds in Alaska as 1 ecotype assumes that all herds are more similar to one another than to herds identified as separate ecotypes. We subjectively categorized caribou herds in Alaska as being part of predator-prey systems where the major prey was either caribou, moose/caribou, or sheep (Ovis dalli)/moose/caribou (Fig. 1). Herds characteristic of the moose/caribou system, i.e., the "Alaskan ecotype" number 16 of 29 total herds (Fig. 1). Hence, 55% of Alaska's herds fit the Alaska ecotype definition, but these herds contain only 15% of the statewide population.

Inferring the existence of different ecotypes of caribou implies to us that the systems to which the ecotypes are a part have been evolutionarily divergent from one another. Also implied is that the ecotypes have existed as they are for sufficient time for system "norms" to have evolved. We believe these implied assumptions about 1 caribou ecotype for Alaska may be largely invalid. The "tundra herds" in Alaska (i.e., those whose distributions reach the coastline) prior to the 1900s apparently never had significant moose as alternate prey in the past several thousand years. Most predator/prey systems associated with Alaska caribou herds today have existed no longer than a century, many only since the 1930s. Much of the present moose distribution has existed for only 50-100 years.

Biologists studying moose systems in Interior Alaska (e.g., Van Ballenberghe 1987; Gasaway, pers. commun.) have inferred that historically much of Interior Alaska was characterized by a low moose-low predator equilibrium with caribou appearing as secondary alternate prey.

From circumstantial evidence we have inferred an opposing model which considers caribou as the predominant prey during the pre-history past (i.e., prior to written records) in most of Alaska. This model was derived from a review of the archaeologic evidence for the relative importance of moose and caribou to Natives in Alaska during late pre-historic times and assumes that the relationships between wolves (Canis lupus) and bears to ungulate prey paralleled that of man.

Yesner (1989) recently reviewed the archaeological evidence from Interior and Southcentral Alaska (largely the Pleistocene refugium in east-central Alaska and adjacent Yukon). His archaeological evidence showed overwhelmingly that caribou and not moose were the predominant prey of native people in Interior Alaska throughout late pre-history and early historical times. Yesner (1989) succinctly outlined the background of and warranted reconsideration for native peoples' dependence on moose in late pre-history times. By inserting [predators] each time Athapaskan appears, in its general sense, in Yesner's (1989) summary, one can conjecture the character of the large mammal predator/prey systems in the past:

> "Many descriptions of lifestyles [including those of predators] in the western subarctic region have been built on the premise that the hunting and use of moose was a central feature of those lifestyles. While this may be true, it is worthwhile to question the time depth that underlies this adaptation and the degree to which it may have applied to former societies [predator populations] inhabiting the boreal forest region. Any such effort must include an analysis of available faunal remains from archaeological sites in that region. A consideration of the faunal record suggests that the intensive utilization of moose is relatively new in the western boreal forest, or at least was not widely characteristic of the late Holocene period. Thus it cannot be assumed that the archaeologically designated late prehistoric "Athapaskan tradition" [low wolf/moose equilibrium] was isomorphic with modern subsistence regimes [predator/prey systems].
>
> "To the degree to which large game played a central role in Athapaskan lifestyles [predator population systems], it was caribou, rather than moose, that seems to have dominated the northern ecotonal region.... Historical factors, primarily involving widespread fires, habitat disturbance and impacts on predators, seem to be most responsible for the increase in moose numbers during the past century."

The relevance of Yesner's (1989) findings to this paper is two-fold. First, much of the literature on Alaska caribou population dynamics may be more characteristic of caribou ecotypes 1 or 3 than the Alaska ecotype (ecotype 2). Secondly, even for the Alaska ecotype, the ecotype may be very young (no more than 50 to several hundred years old) in terms of moose being the significant prey in the ecotype predator/prey system that they are at present. Hence, it is unlikely that any tendency toward a "normal" predator-prey equilibrium would have had time to "evolve."

Further, classifying a caribou herd as fitting the Alaska ecotype may largely be a function of herd size. For example, the Western Arctic Herd, numbering 342,000 in 1989, was subjectively excluded from the Alaska ecotype. However, if it numbered only 50,000, we would likely have included it in the Alaska ecotype. This observation illustrates that theory is not without its complications.

## THEORY

If one concludes that caribou ecotypes are abstracts, considering them as substantive realities would be termed reifying (Geist 1983). This is but one of several complications often encountered in the theory of caribou population dynamics. Geist (1983) identified ambiguous formulation of hypotheses (as did Bergerud 1980), semantic problems, and reifications as being systematic difficulties with population biology that preclude decisive testing of hypotheses. Much population dynamics theory, with management implications, revolves around and includes reifications. For example, we believe that carrying capacity is clearly not a substantive reality but is frequently perceived as such. Arguably, density-dependent population regulation may be a parallel. What additional complications confound our reaching collective understanding and agreement about limitation of caribou populations?

Certainly, caribou management in Alaska has erred in the past by applying general theory in lieu of specific knowledge, which is not unique to Alaska caribou management nor to caribou management in general.

Geist (1983:84) commented on a parallel regarding mountain goat management as had Smith (1980). "To substitute general theory for specific knowledge is very dangerous in wildlife management. The demise of mountain goats is in good part due to hunting seasons based on wrong population biology theory. Kuck (1977) showed how territoriality by female goats falsified the common assumption that compensatory reproduction follows increased mortality."

In attempting to understand caribou population dynamics (both the general theory and specific knowledge), are we considering all possible or tenable hypotheses? Bergerud (e.g., 1980) has taken a leadership role during the past decade in identifying and testing high order hypotheses that relate to the underlying life history strategies of caribou (i.e., identifying ultimate limiting factors). Bergerud's focus in the past decade has been on "either-or" options between predation or food limitation hypotheses. Bergerud (1980) wrote that theoretically a food limitation exists but at much higher densities than are seen in the real world of observed values for herds free to disperse. In contrast, Bergerud (1980:556) concluded that, "Predation is considered the chief limiting factor to population growth and sets the level of stocking commonly at one to two animals per $mi^2$ (0.4-0.8/$km^2$) or less. Limits imposed by dispersion or food supplies occur at much higher densities."

We applaud Bergerud's (1980:556) leadership in focusing on hypothesis testing in caribou research and for emphasizing the utility of the hypothetico-deductive approach of the scientific method as follows:

> "This review is an attempt at a synthesis. At the risk of error and oversimplification, I have always sought to elucidate common underlying properties and life history strategies between populations and sub-populations. I believe the scientific method is largely deductive (Hempel 1966, Platt 1964); that is that we hypothesize from the general to the specific--there is predictive power there. The plurality-of-causes approach is self defeating. It provides no further synthesis or insight. An a posteriori catalog of causes becomes descriptive and untestable. We proceed by hypothesis--we state what we will accept as disproof of our hypotheses so others can test them, disprove them, and formulate new hypotheses. By such a course we leave old ideas behind. Very clearly in North America in caribou research we have not followed the scientific method: hypotheses are seldom stated or tested;

> disproofs never mentioned. We have been descriptive and <u>ad hoc</u> and today we are wrestling with the same ideas as 25 years ago."

Bergerud's (1980) hypothetico-deductive approach to caribou research is clearly a good approach for identifying common underlying properties and life history strategies (i.e., ultimate limiting factors) as confirmed by Romesburg (1981). However, in the day-to-day business of the practical wildlife manager, identification of proximal (point in time) limiting factors may have practical management implications. And in the frame of reference of the wildlife manager, the plurality-of-causes approach may be relevant and practical.

We favor a plurality-of-causes hypothesis to explain what is limiting given caribou herds at any point in time. Bergerud (1980) argued that such an approach is self-defeating because it provides no further synthesis or insight. Again we believe Bergerud's argument was in the context of ultimate limiting factors, i.e., "elucidating common underlying properties and life history strategies." We acknowledge that a plurality of causes approach can contribute to formulation of ambiguous hypotheses and may provide less predictive power, but it does not necessarily provide little insight or synthesis.

Peek and Eastman (1983) offered a "plurality-of-causes" type hypothesis for moose population limitation/regulation. We have modified it to serve as a discussion starter for a viable (testable?) and hopefully unambiguous hypothesis for caribou, as follows:

> Factors which serve to limit/regulate caribou numbers in any population vary with population density and through time and space. Population growth (negative or positive) is determined by a variety of factors, such as predation, insects, disease, parasites, weather-snow conditions, and intraspecific competition interacting to affect births, deaths, and dispersal.

Peek and Eastman (1983) also reported approaching the subject of natural control of moose numbers through Poore's (1962, cited in Peek and Eastman 1983) method of "successive approximations." The method draws inferences from data and they are judged for validity as far as the data allow. Peek and Eastman (1983) observed that all hypotheses are flexible and subject to modification as new or contradictory evidence becomes available. Field investigations of large ungulates may best be considered in this light, since conclusive, refined evidence is not yet available. If this approach is valid, then induction may be a fruitful scientific approach. We contend that deduction can only follow induction. We believe there is merit/validity in both inductive and deductive approaches and that they need not be mutually exclusive.

In fact, we endorse the scientific approach advocated by R. May at the International Congress of Game Biologists in Norway in 1989 as presented to us by R. O. Stephenson (pers. commun.) as follows:

> "Dr. May's point was that wildlife biologists spend too much time quarreling about the best methods when, in fact, we need to employ a wide range of approaches if we are to progress. These include long-term ("boring") monitoring, acute observation of natural history, observational and correlative field studies, natural experiments, manipulative experiments, as well as ideas and theory. These tools are equally important, and their application should be driven by a feel for the most appropriate method useful in dealing with a given problem."

Our closing comment regarding theory and its relevance to caribou population dynamics is about chaos theory. We make no pretense of understanding chaos theory and its relevance to caribou, but we believe there is compelling evidence that it may provide profound insight into existing unsatisfactory models of caribou population dynamics. As food for thought we have excised several short quotes from Gleick (1987) regarding chaos theory and its potential applicability to caribou population dynamics (Appendix A).

## MANAGEMENT IMPLICATIONS

What are the management implications of the general theory and specific knowledge available for caribou?. That of course depends on how accurate our knowledge is. Long overdue is evaluation of the progression, consistency, and validity of ideas, and data that have lead to our existing management programs. How clearly does any administrative jurisdiction transform scientific information into management practice? We attempt to graphically depict (Fig. 4) the stepdown process used in Alaska, as we see it, to get from theory and knowledge to management practice. Clearly, there is no institutionalized mechanism to assure that assessment and incorporation of new knowledge is timely.

We believe that an exhaustive, critical review is in order to clearly identify the valid ecological basis for caribou management. For example, does recognizing carrying capacity as a reification change its relevance as the foundation to base population size goals upon? Carrying capacity is only one of many confusing concepts (Dhondt 1988) that are central to the current theory and practice of caribou management.

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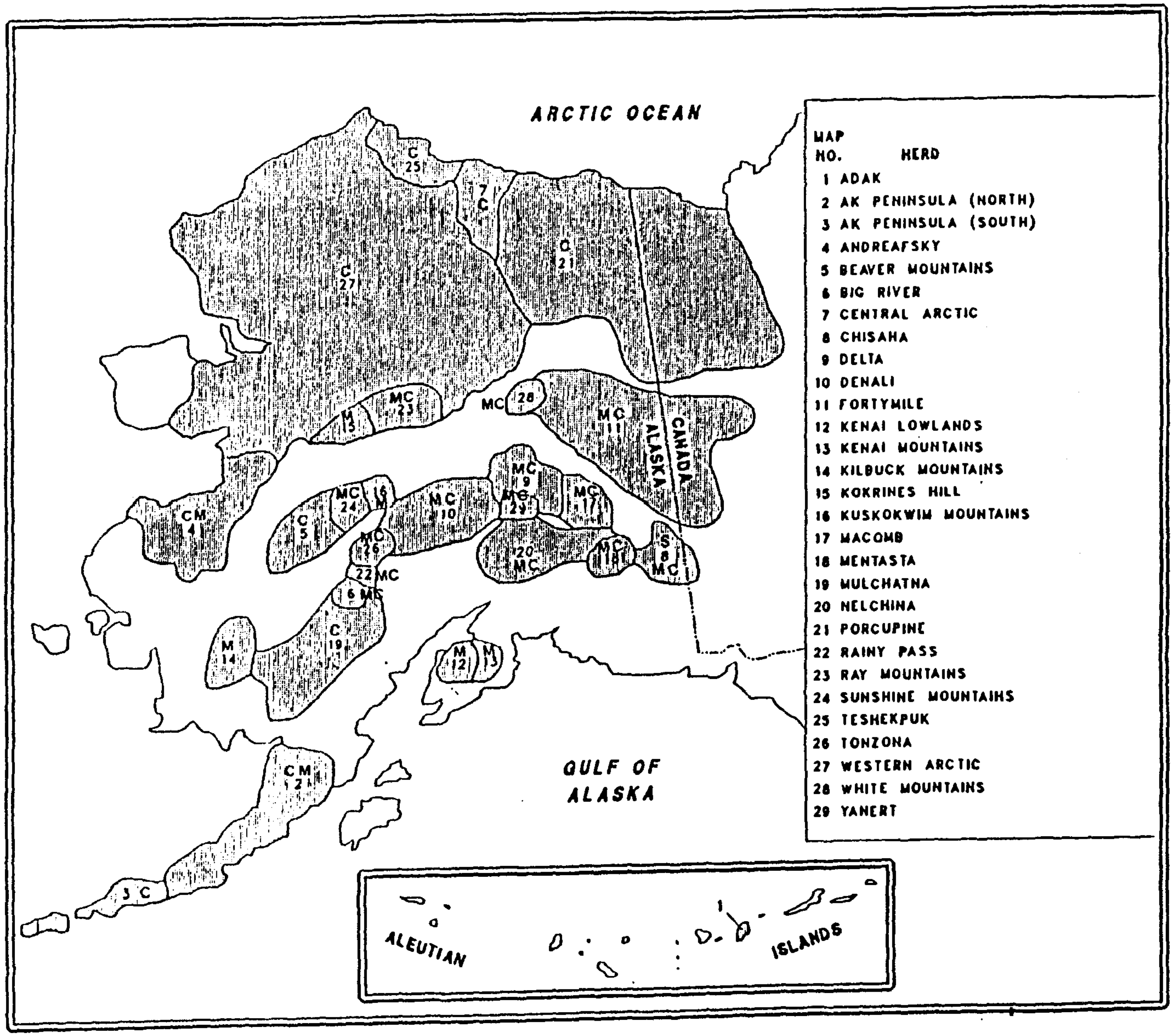

Fig. 1. Distribution of caribou herds in Alaska and major prey species in herd ranges (C = caribou, M = moose, S = sheep).

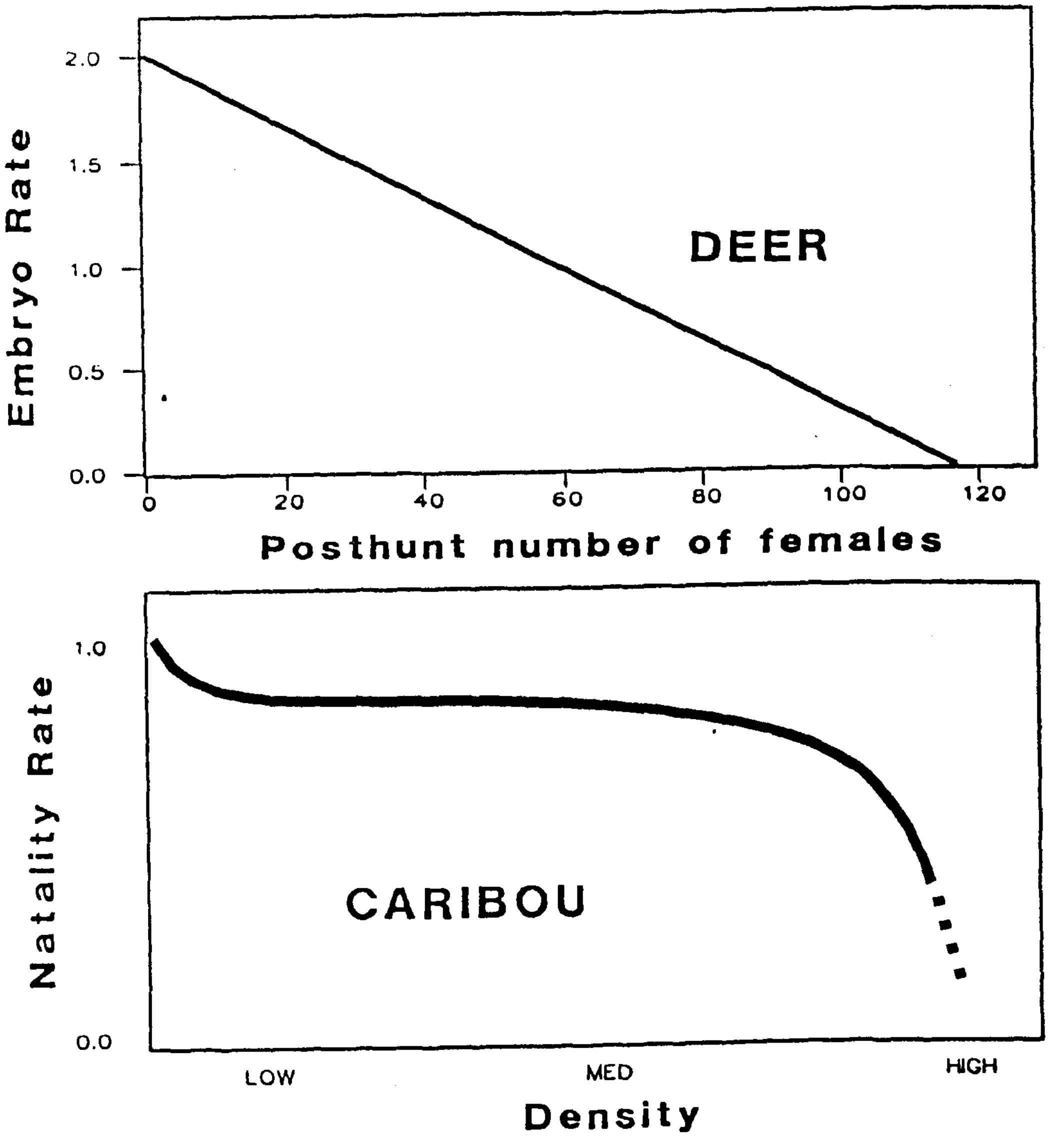

Fig. 2. Comparison of the natality/density relationship for white-tailed deer (after McCullough 1979) with that envisioned for caribou.

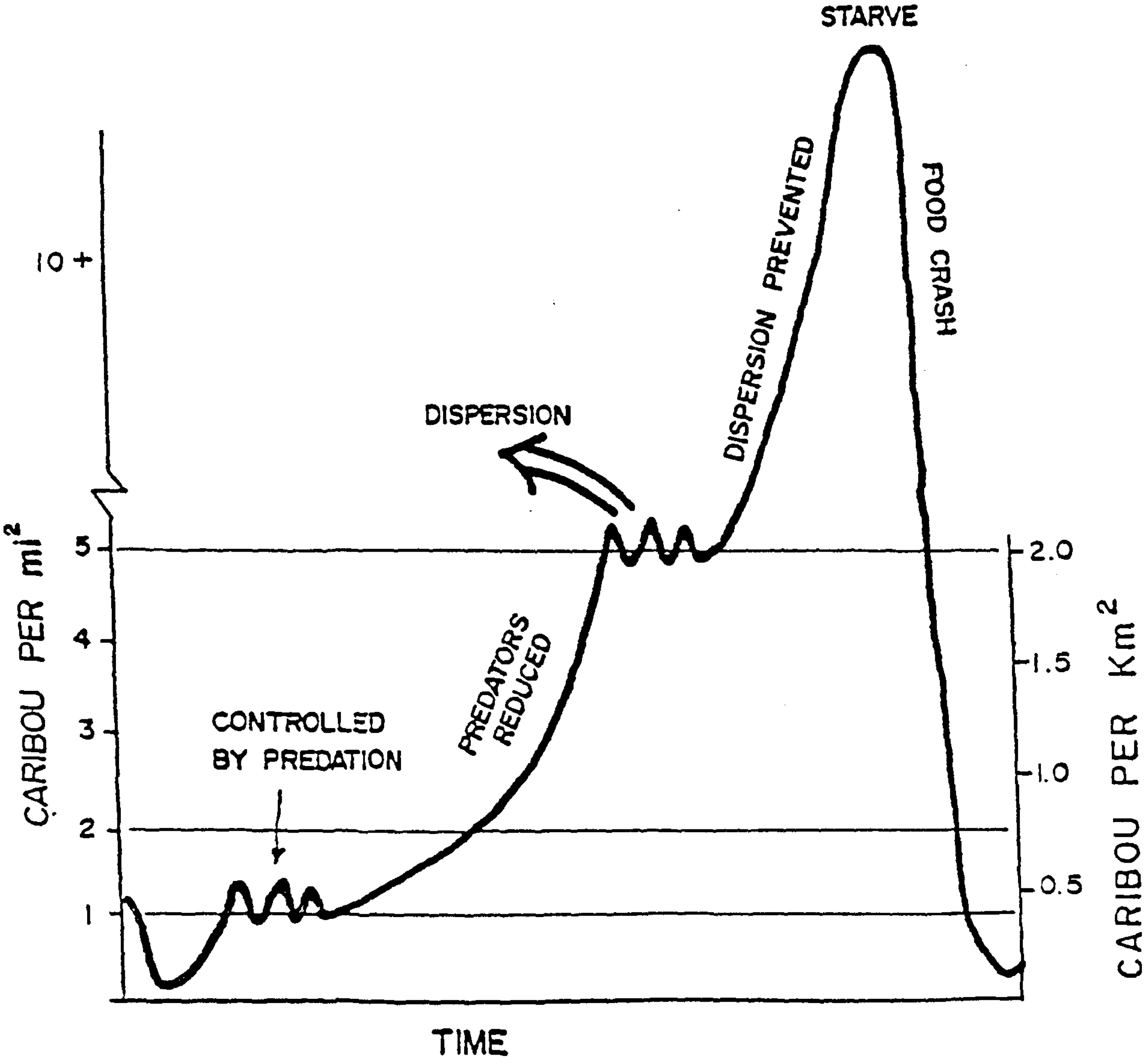

Fig. 3. The population growth limits of caribou envisioned as a staircase of limits imposed by predation and dispersion and a crash-decline caused by density-dependent food shortage (from Bergerud 1980).

Fig. 4. The institutionalized framework for caribou management in Alaska.

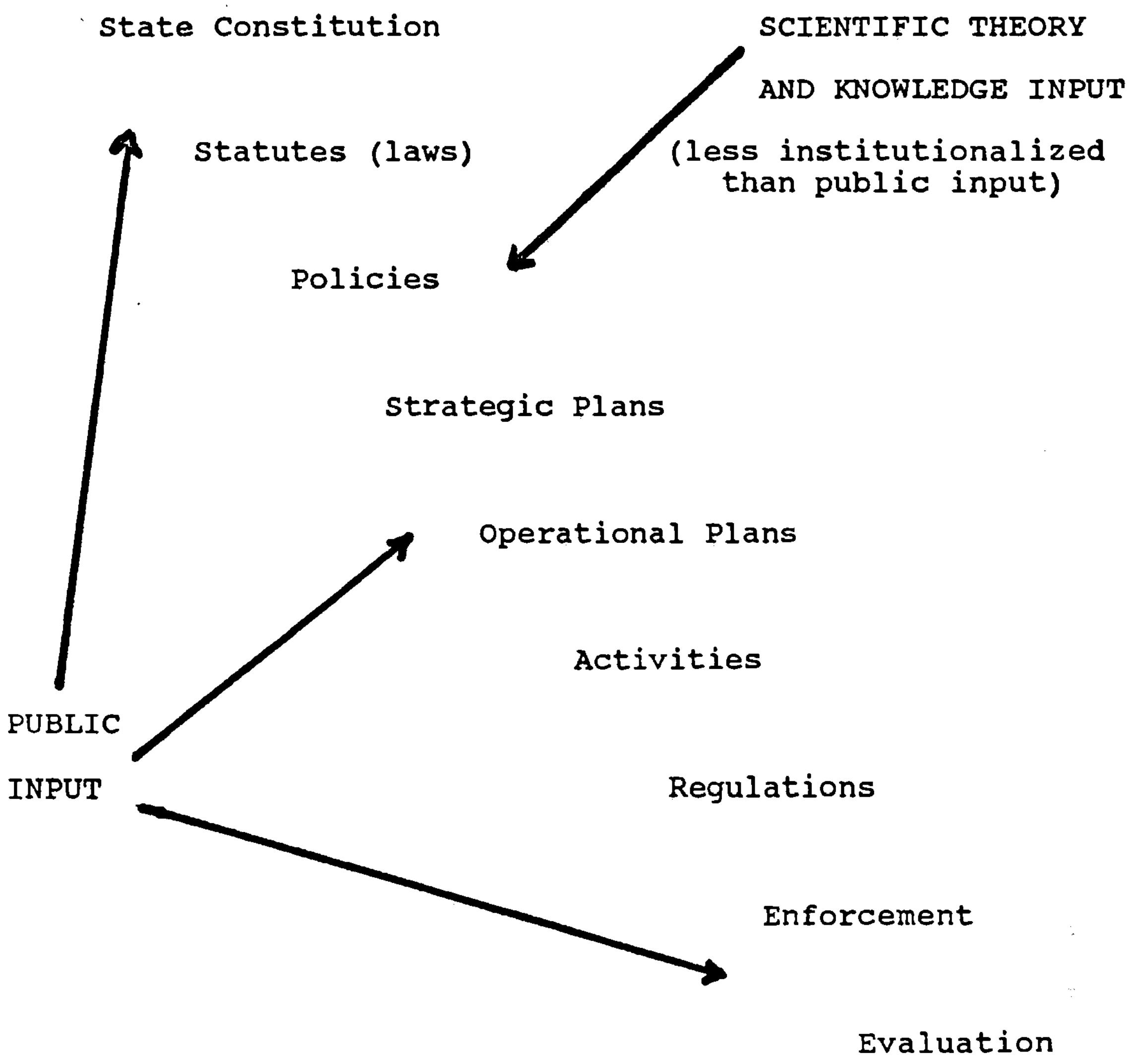

Table 1. Recognized caribou herds in Alaska and population size in 1970, 1977, and 1989.

| Herd | Population size<br>1970 | 1977 | 1989 |
|---|---|---|---|
| Adak | 110 | 250 | 500 |
| Alaska Peninsula (N) |  | 10,400 | 20,000 |
| Alaska Peninsula (S) |  | 7,600 | 5,500 |
| Alaska Peninsula (Total) | 14,000 | 18,000 | 26,000 |
| Andreafsky |  | 3,000 | 250 |
| Beaver Mountains | 2,000 | 2,000 | 2,000 |
| Big River |  |  | 750 |
| Central Arctic |  | 5,000 | 16,000 |
| Chisana | 1,500 | 1,500 | 1,700 |
| Delta | 5,000 | 2,500 | 10,200 |
| Denali | 4,500 | 1,000 | 3,000 |
| Fortymile | 10,000 | 6,000 | 22,500 |
| Kenai Lowlands |  | 80 | 100 |
| Kenai Mountains | 300 | 300 | 400 |
| Kilbuck Mountains |  | 1,000 | 950 |
| Kokrines Hills |  |  | 800 |
| Kuskokwim Mountains |  |  | 300 |
| Macomb Plateau |  | 900 | 800 |
| Mentasta | 2,500 | 2,500 | 2,000 |
| Mulchatna | 8,000 | 10,000 | 66,000 |
| Nelchina | 25,000 | 14,000 | 40,000 |
| Porcupine | 100,000 | 100,000 | 175,000 |
| Rainy Pass |  | 3,000 | 2,500 |
| Ray Mountains |  | 200 | 700 |
| Sunshine Mountains |  | 750 | 500 |
| Teshekpuk |  | 8,000 | 11,000 |
| Tonzona |  |  | 1,000 |
| Western Arctic | 242,000 | 75,000 | 343,000 |
| White Mountains |  |  | 1,000 |
| Yanert |  | 600 | 600 |
| Total | 414,910 | 255,580 | 729,050 |

Table 2. A comparison of exponential herd growth for Alaskan caribou herds from 1970 to 1977 and 1977 to 1989.

| Herd | 1970-77<br>r | 1977-89<br>r |
|---|---|---|
| Adak | 0.12 | 0.06 |
| Alaska Peninsula (Total) | 0.04 | 0.03 |
| Alaska Peninsula (N) | | 0.05 |
| Alaska Peninsula (S) | | -0.01 |
| Andreafsky[a] | | -0.21 |
| Central Arctic | | 0.10 |
| Delta | -0.10 | 0.12 |
| Denali | -0.21 | 0.09 |
| Fortymile | -0.13 | 0.14 |
| Kenai (lowlands) | | 0.03 |
| Kenai (mountains) | 0.00 | 0.02 |
| Kilbuck Mountains[a] | | -0.03 |
| Macomb Plateau | | -0.01 |
| Mentasta | 0.00 | 0.00 |
| Mulchatna | 0.03 | 0.16 |
| Nelchina | -0.08 | 0.09 |
| Porcupine | 0.00 | 0.05 |
| Rainy Pass | | -0.02 |
| Ray Mountains | | 0.10 |
| Teshekpuk | | 0.26 |
| Western Arctic | -0.17 | 0.13 |
| Total population | -0.08 | 0.09 |
| Mean of all herds | -0.05+0.10(SD) | 0.06+0.09(SD) |

[a] Census data are probably not reliable.

Table 3. Population size, trend, range size, and density of Alaska caribou herds, 1989.

| Herd No. | Herd name | Herd size | Population trend | Harvest in 1987-88 | Range km$^2$ | Density caribou/km$^2$ |
|---|---|---|---|---|---|---|
| 1 | Adak | 464-497 | Stable | 121 | 750 | 0.6 |
| 2 | Alaska Peninsula (N) | 20,000 | Stable | 2,300 | 23,000 | 0.9 |
| 3 | Alaska Peninsula (S) | 5,500 | Declining | 300 | 5,000 | 1.1 |
| 4 | Andreafsky | 250 | Unknown | Unknown | | |
| 5 | Beaver Mountains | 2,000 | Unknown | 17 | | |
| 6 | Big River | 750 | Unknown | 43 | | |
| 7 | Central Arctic | 16,000 | Increasing | 575 | 40,000 | 0.4 |
| 8 | Chisana | 1,700 | Stable | 82 | 4,000 | 0.4 |
| 9 | Delta | 10,200 | Stable | 667 | 11,000 | 0.9 |
| 10 | Denali | 3,000 | Increasing | 0 | 8,000 | 0.4 |
| 11 | Fortymile | 22,500 | Increasing | 260 | 50,000 | 0.5 |
| 12 | Kenai Lowlands | 100 | Stable | 4 | | |
| 13 | Kenai Mountains | 400 | Increasing | 50 | | |
| 14 | Kilbuck Mountains | 950 | Increasing | 75 | | |
| 15 | Kokrines Hills | 800 | Unknown | 5 | | |
| 16 | Kuskokwim Mountains | 300 | Unknown | Unknown | | |
| 17 | Macomb Plateau | 800 | Stable | 57 | 1,500 | 0.5 |
| 18 | Mentasta | 2,000 | Declining | 112 | 4,000 | 0.5 |
| 19 | Mulchatna | 66,000 | Increasing | 2,000 | 78,000 | 0.9 |
| 20 | Nelchina | 40,317 | Increasing | 1,747 | 40,000 | 1.0 |
| 21 | Porcupine | 175,000 | Increasing | 3,500 | 259,000 | 0.7 |
| 22 | Rainy Pass | 2,500 | Unknown | 85 | | |
| 23 | Ray Mountains | 700 | Unknown | 5 | 6,500 | 0.1 |
| 24 | Sunshine Mountains | 500 | Unknown | 2 | | |
| 25 | Teshekpuk | 11,000 | Unknown | 750 | 16,500 | 0.7 |
| 26 | Tonzona | 1,000 | Unknown | 45 | | |
| 27 | Western Arctic | 343,000 | Increasing | 10,000 | 360,000 | 1.0 |
| 28 | White Mountains | 1,000 | Increasing | 10 | 5,000 | 0.2 |
| 29 | Yanert | 600 | Stable | 113 | 1,950 | 0.3 |

Appendix C.

Appendix A. Quotes regarding chaos theory excerpted from Gleick (1987).

> Anyway, if the population kept bouncing back and forth, ecologists assumed that it was oscillating around some underlying equilibrium. The equilibrium was the important thing. It did not occur to the ecologists that there might be no equilibrium.

> Textbooks showed students only the rare nonlinear systems that would give way to such techniques. They did not display sensitive dependence on initial conditions. Nonlinear systems with real chaos were rarely taught and rarely learned. When people stumbled across such things--and people did--all their training argued for dismissing them as aberrations.

> Within ecology itself, as May saw it, a central controversy in the early 1970s dealt with the nature of population change.... Some read the message of the world to be orderly: populations are regulated and steady--with exceptions. Others read the opposite message: populations fluctuate erratically--with exceptions.... Those who believed that populations were steady argued that they must be regulated by some deterministic mechanisms. Those who believed that populations were erratic argued that they must be bounced around by unpredictable environmental factors, wiping out whatever deterministic signal might exist. Either deterministic mathematics produced steady behavior, or random external noise produced random behavior. That was the choice.
>
> In the context of that debate, chaos brought an astonishing message: simple deterministic models could produce what looked like random behavior. The behavior actually had an exquisite fine structure, yet any piece of it seemed indistinguishable from noise.

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