POPULATION ANALYSIS AND MODELING OF THE WESTERN ARCTIC CARIBOU HERD WITH COMPARISONS TO OTHER ALASKAN *RANGIFER* POPULATIONS

A
Thesis

by
Joseph Doerr

University of Alaska
Fairbanks, Alaska
December 1979

POPULATION ANALYSIS AND MODELING OF THE
WESTERN ARCTIC CARIBOU HERD WITH
COMPARISONS TO OTHER ALASKAN *Rangifer* POPULATIONS

RECOMMENDED:

Dale Guthrie

David R. Klein

Samuel J. Harbo
Chairman, Advisory Committee

Samuel J. Harbo
Chairman, Program on Wildlife
and Fisheries

APPROVED:

Director, Division of Life Sciences

14 November 1979
Date

Dean, College of Environmental Sciences

3 December 1979
Date

Vice Chancellor for Research and Advanced Study

Date

POPULATION ANALYSIS AND MODELING OF THE WESTERN ARCTIC CARIBOU HERD WITH COMPARISONS TO OTHER ALASKAN *Rangifer* POPULATIONS

A

THESIS

Presented to the Faculty of the
University of Alaska in partial fulfillment
of the Requirements
for the Degree of

MASTER OF SCIENCE

Joseph Doerr, B.S.

December 1979

ABSTRACT

Elucidation of factors responsible for dramatic fluctuations in population levels of Alaskan *Rangifer* herds was undertaken through data analysis and modeling of two mainland and two introduced island herds. The pronounced decline of the Western Arctic Herd from 1970 to 1976 largely resulted from high hunting-induced mortality, including substantial waste by traditional subsistence hunters, and, secondarily, from wolf predation and relatively high overwinter natural mortality rates on calf and sub-adult cohorts. Recruitment of calves to the fall during the decline was relatively high; the role of increased natural adult mortality rates is uncertain. The effect of immigration and emigration was negligible. Population regulation mechanisms of the herds analyzed are presented. Increased overwinter natural mortality of calves appears to be the most important initial regulating mechanism for large herds. The reliability of numerous sampling techniques was evaluated and management implications and needs for future research discussed.

ACKNOWLEDGEMENTS

This study was made possible through a Research Fellowship from the Alaska Cooperative Wildlife Research Unit supported by the Alaska Department of Fish and Game. Logistic support for parts of this study was provided by the Alaska Department of Fish and Game and the Sierra Club Foundation. Many people contributed directly and indirectly to the ideas and data presented here. It is a pleasure to acknowledge the assistance I received from my committee members S. J. Harbo, Jr., and D. R. Klein; ADF&G personnel J. L. Davis, R. O. Stephenson, V. Van Ballenberghe, R. T. Shideler, H. R. Reynolds, Martha A. Robus, K. A. Neiland, Laurie Robertson, S. Eide, G. N. Bos, C. Lucier, and C. Grauvogel; and J. C. Shea, H. Thing, Brina Kessel, D. D. Gibson, P. C. Lent, E. Nygaard, Evelyn Kimbrough, Patty Dyer-Smith (typing), D. Borchet (figures), and Norma Milke. Special thanks is due to the numerous residents of northwestern Alaska who contributed to the 1975-76 WAH incisiform collection, especially Leonard Brown, Emma and Roland Norton, Wilbur and Elliot Sampson, Amos Lane, and the Flippo and McQueen families.

Two people deserve special recognition for their contribution to this thesis: Dr. Samuel J. Harbo, Jr., my committee chairman, for providing important direction regarding the scope and methodology of this thesis, offering important statistical advice concerning the analysis of the data, and carefully reading and editing the numerous drafts, and James L. Davis, ADF&G, for going far beyond his role as a cooperator in this study in arranging logistic and financial support for the WAH fieldwork and age-structure study and in unselfishly sharing his ideas and data on caribou population ecology.

TABLE OF CONTENTS

Table of Contents (continued) Page

Table of Contents (continued) Page

Table of Contents (continued) Page

Table of Contents (continued) Page

Table of Contents (continued) Page

Table of Contents (continued) Page

LIST OF FIGURES

List of Figures (continued)

LIST OF TABLES

List of Tables (continued) Page

List of Tables (continued) Page

List of Tables (continued) Page

LIST OF APPENDICES

When the last great herds
    have been slaughtered,
the last range divided;
    it will be lonely then,
the wind, *Eriophorum*,
    and legends.

CHAPTER 1. INTRODUCTION

The population size of a given species is the result of a multitude of factors, including mechanisms, intrinsic to the species (i.e., reproductive potential, longevity, territoriality) and regulating factors of the environment (i.e., weather, predation, food availability, nesting habitat) as well as the previous history of the species and its habitat. Ideally, a population study of a species should integrate knowledge of all these factors into a dynamic system that can explain observed population fluctuations. Ultimately, the test of our understanding of the population dynamics of a species is our ability to predict future population trends. Predictive ability usually hinges on obtaining sufficient demographic information upon which to base future population projections, but financial limitations restrict research, often producing insufficient data bases and precluding an adequate understanding of the population dynamics of a species in its habitat.

In Alaska, the State Constitution mandates management of wildlife populations on a sustained yield basis. Sustained yield management demands a thorough understanding of the population regulating mechanisms of the species as well as accurate and precise demographic data concerning the species. Wildlife management agencies, as caretakers of wildlife resources, must understand and monitor the wildlife populations sufficiently to prevent or minimize undesired declines. In Alaska, increasing human access and population have placed greater demands on the wildlife resources. Consequently, population dynamics studies attempting to construct descriptive as well as predictive population models are of paramount importance to wise management of our wildlife resources.

Caribou (*Rangifer tarandus granti*) inhabit a large portion of the tundra and taiga biomes of Alaska (Skoog 1968). The hunting of caribou is an important method of obtaining food by rural residents and has become a cultural tradition of many northern native people (Rausch 1951, Sonnenfeld 1957, Gidding 1961, Foote and Williamson 1966, Saario and Kessel 1966, Burch 1972, and others). Patterson (1974), for example, found that residents in eleven villages in the Northwest Alaska Native Association region harvested an average of 2,132,850 pounds of caribou meat, representing nearly 75 percent of the total subsistence meat obtained in those villages. As a game resource in Alaska, the harvest of caribou during the 1960's exceeded the harvest of all other big game species combined (Hemming 1971). Caribou are a unique and valuable component of the ecosystems in Alaska and the conservation of caribou resources should be a high priority of wildlife management.

Wide population fluctuations, rather than stability, have been the rule in Alaskan caribou herds (Murie 1935, Bee and Hall 1956, Lent 1966b, Skoog 1968, Bos 1975, Hemming 1975, LeResche 1975). The main factors influencing caribou numbers in Alaska are believed to be weather, predation, and emigration (Skoog 1968). Bergerud (1974c) emphasizes the role of hunting and wolf (*Canis lupus*) prediction in the decline of caribou in North America. Haber (1977) has hypothesized that exchange of animals among herds triggers population eruptions and declines. Presently, caribou are at relatively low numbers in Alaska (Hemming 1971, Bos 1975, LeResche 1975, Klein and White 1978), and in the barren-grounds of northwestern Canada (Kelsall 1968; Thomas 1969; Parker 1971, 1972; G. Calef, pers. corr.). Low caribou population levels, coinciding with increasing "development" of northern environments and increasing human populations have caused considerable concern for the future of large caribou herds.

The purpose of this study has been to elucidate the population dynamics of the Western Arctic Caribou Herd (WAH), which occupies a range of approximately 362,700 km^2 in the extreme northwestern region of Alaska (Hemming 1971), and to develop a model which would be useful in both analyzing and predicting that herd's population trends. The study entailed both evaluation and analysis of available demographic information on the herd as well as assisting the Alaska Department of Fish and Game (ADF&G) with its current population study of the herd. When the project was initiated in September, 1975, the WAH was considered to be the largest caribou herd in North America; in 1970 the herd was estimated to contain a minimum of 242,000 animals (Pegau and Hemming 1972). The need to critically analyze the available population data on the WAH and to develop a model explaining population fluctuations of the herd became evident when fall reconnaissance flights by ADF&G in 1975 indicated the herd was undergoing a rapid decline. The objectives of this study, pertaining to the WAH, were as follows:

1) To determine the principle factors responsible for the decline of the WAH, and
2) To simulate possible future trends of the WAh, given a range of management alternatives and population responses by the herd.

The paucity of demographic data on WAH caribou prevented the construction of an adequate population model of the herd. Consequently, review of other population studies of *Rangifer* to derive various population parameters was necessary. Some attributes, such as a single young per breeding female (Skoog 1968, Dauphiné 1976) and lack of a decline in conception rates with increasing age (Dauphiné 1976), were considered valid generalizations for caribou population models. Other characteristics, such as reproductive rates, post-natal survival of calves, rates of wolf predation, and age- and sex-specific natural mortality rates were either widely variable between studies, inadequately documented, or herd- and time-specific.

Review and analysis of population data from other herds was necessary in order to develop a model of caribou population dynamics and to determine important parameters of caribou population ecology.

Analysis of data was complicated by factors such as a lack of collection of demographic data, data collected using different classification categories, and the unreliability of accuracy and precision assessments of most of the survey data. As is shown later, some of the assumptions made in collecting the population data were often invalid. Consequently, some of the estimates of population characteristics were dangerously misleading. Simulation modeling was extremely useful in revealing discrepancies in the data. However, the problem of determining the reliability of the data constantly plagued the analysis and modeling attempts, and necessitated the third objective of this study:

3) To evaluate, whenever possible, the surveying techniques used to collect demographic data on caribou herds.

An evaluation of all caribou herds in Alaska was beyond the limitations of this study. In addition to the WAH, only the population dynamics of the Nelchina Caribou Herd (NCH) and two introduced island herds were analyzed and modeled. The NCH was chosen for four important reasons:

a) It is, by far, the most intensively studied caribou herd in Alaska from a population dynamics standpoint (Skoog 1968).

b) The wolf population on the herd's range has been investigated more intensively and over a longer period than in any other region of Alaska (Rausch 1967, 1968, 1969a; Stephenson 1978).

c) Various aspects of the population dynamics of the herd have been previously evaluated (Watson and Scott 1956, Skoog 1968, Bos 1975, Hemming 1975).

d) Since population studies were initiated on the NCH, the herd has increased, peaked, and declined (Bos 1975), a pattern of "boom and bust" exhibited by other Alaskan caribou herds.

Introduced herds of *Rangifer* on St. Matthew and Adak islands were chosen for analysis because they represented isolated, predator-free herds exhibiting a high intrinsic growth rate (Klein 1968, Burris and McKnight 1973). The simplified environments of these herds were useful for testing the population model developed for the NCH, and for evaluating the demographic data available on the herds. In addition, the population dynamics of those herds demonstrated important population characteristics of *Rangifer* under "ideal" environmental conditions. The latter point is especially valuable since the Adak Island Herd (AIH) originated from caribou obtained from the NCH (Jones 1966).

The objective of population evaluation and analysis of the NCH and the two island herds was

4) To critically analyze relevant population data available on these herds to obtain insight into the relationships between population fluctuations and parameters such as sex

ratios, age structures, and age-specific mortality and recruitment rates.

Before proceeding further, defining some terms used in this study is advisable. Caribou population is defined as all caribou in Alaska [see Skoog (1968)]. Caribou subpopulations are all caribou in six geographic regions of Alaska described as

> ...simply designated regions in which the subpopulations of caribou have been more or less discrete entities over the past 100 years and somewhat isolated as well. As will be shown later, there have been interchanges of animals between these regions on various occasions (Skoog 1968:205).

A herd is a group of caribou that repeatedly use a given area to calve, distinct from calving areas of other groups of caribou (Ibid.). Figure 1 illustrates important caribou herds in Alaska. The term "population" is also used in its more general sense, referring to any group of associated individuals with common reproductive and mortality rates, when using such terminology as "population dynamics" and "population modeling."

Calves and yearlings refers to animals zero to 12 months old and 12 to 24 months old, respectively, unless otherwise defined. Terms, such as 2+ and 3+, refer to animals 24 months of age and older and 36 months of age and older, respectively. Five year old caribou are caribou 60 to 72 months old, 5 to 6 year old caribou are caribou 60 to 84 months old.

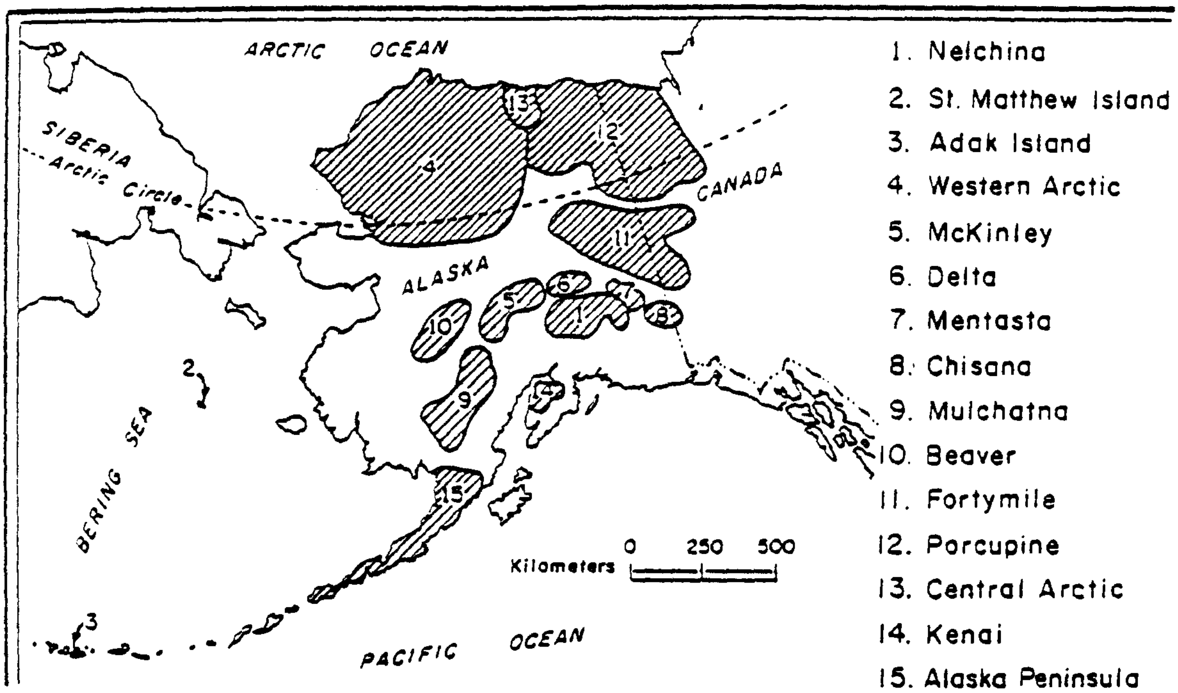

Figure 1. Approximate locations of *Rangifer* herds in Alaska. Sources are Skoog (1968), Hemming (1971), and Cameron and Whitten (in press).

It is important to realize that this study relied largely on population data collected by many other researchers, especially ADF&G personnel. Ideally, population modeling and data analysis should be done by the researchers involved, as was done in modeling the Kaminuriak barren-ground caribou herd of Canada (Bunnell et al. 1975). The urgency to evaluate our present knowledge of caribou population dynamics and sampling techniques justifies the "single-handed" approach of this study, and I accept sole responsibility for all conclusions made regarding the data.

CHAPTER 2. DATA ANALYSIS AND POPULATION MODELING OF THE NELCHINA CARIBOU HERD (1954-1977)

A. INTRODUCTION

The Nelchina Caribou Herd belongs to the southcentral subpopulation of the Alaskan caribou population and occupies a center of habitation located in the Nelchina Basin (Skoog 1968). The herd's traditional range (Figure 2) is bounded by the Alaska Range on the north, the Chugach Mountains on the south, the Parks Highway on the west, and the Wrangell Mountains on the east (Hemming 1971). Skoog (1968) estimated that the herd's range during the early 1960's totaled 45,000 km^2, of which 31,100 km^2 were considered suitable habitat for caribou. For a detailed description of the topography, climate, vegetation, and mammalian fauna of the Nelchina Basin, as well as seasonal movement patterns and habitat utilizations of the NCH, see Skoog (1968), Pegau and Hemming (1972), and Bos (1973, 1974b).

Research on the herd was begun in 1948 by the United States Fish and Wildlife Service (USFWS) and has continued since 1959 under the direction of the Alaska Department of Fish and Game (Skoog 1968). Because other herds in Alaska have not been well studied over an extended period, analysis of the demographic data from the NCH during its recent increase, peak, and decline is especially valuable in

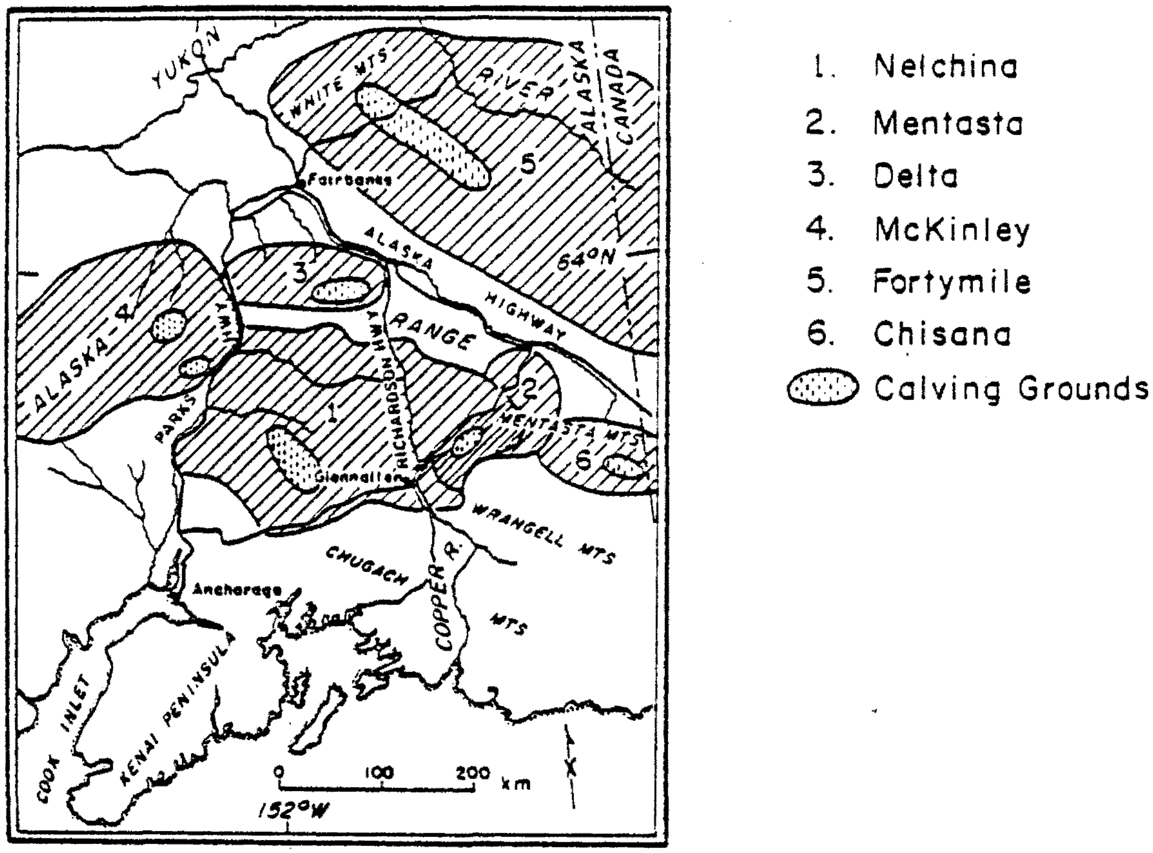

Figure 2. Approximate boundaries of Nelchina and adjacent caribou herds (1954-72).

providing insight into population trends in other caribou herds, as well as in evaluating various research techniques used in collecting population information.

B. RESULTS AND DISCUSSION

1. CRITICAL ANALYSIS OF THE NELCHINA CARIBOU HERD FALL COMPOSITION DATA (1954-72)

A critical analysis was made of the herd composition data for the NCH during its recent increase, peak, and decline, which extended from the late 1940's (Hemming 1975) to 1972 (Bos 1973), approximately 25 years. Because composition data were not collected until the mid-1950's (Skoog 1968), the analysis of the composition of the herd is restricted to the period of 1954-72. During the mid-1950's, intensive hunting of the herd and rather intensive monitoring of the human harvest began, the first accurate population estimate of the herd was obtained (Scott and Watson 1956, Skoog 1968), and wolf protection and research in the herd's range was initiated following the virtual elimination of wolves as a result of a federal control program (Rausch 1967). Population size, herd composition, and wolf and human predation are all necessary demographic parameters of the population dynamics of the herd.

Analysis of the composition data is complicated by the inconsistent method of classifying animals in different years or at different times of the year, the lack of data during many years within the time interval from 1954-72, and the fact that assumptions made in collecting the data may not have been valid due to varying segregational patterns of the caribou (see Chapter 4). Skoog (1968: 505-506) characterized the segregation of the NCH as follows:

> The basic segment of a caribou herd can be considered as being the "cows with calves" group. These animals have a tendency to remain more or less together during much of the year. To this group are attached most of the "cows without calves," although these frequently are found in greatest abundance on the peripheries, and tend to lag somewhat during major movements. Yearlings are associated more closely with the "cows without calves" group, and usually the males are not fully represented. Two-year-old bulls are rather common sometimes in the cow-calf segment of the herd, but older bulls are mostly absent, but to varying degrees. Evaluating data from aerial counts can be quite a problem without the benefit of more detailed ground segregation counts.
>
> During the rutting period, however, an aerial calf-count should reveal the actual proportion of calves in the herd at that time. In addition, one also can determine the proportion of bulls 3-years+, because these animals are identified readily from the air by body and antler size.

The following analysis considers four age groupings of animals: (a) 3+ males, (b) 3+ females, (c) yearlings and two-year-olds, and (d) calves.

a. 3+ Males

Because adult males are separated from the herd during most of the year (Skoog 1968), the first step in analyzing the composition of the herd is to build a representative picture of the 3+ males. This procedure is complicated by inconsistent classification of adult males. In 1967 and 1968, males 2 years and older were classified together (Hemming and Glenn 1968, 1969), and, since 1969, all males older than calves have been classified together (Bos 1973, 1974b). On 6 November 1962 an aerial composition count classified all 4+ males together (Skoog 1963). The percent of 3+ males in this count was estimated using the following equation:

$$P_{M3} = [N_{M4} + (R \cdot N_{M4})] / N_S , \qquad (1)$$

where

P_{M3} = estimated percent of 3+ males in the herd,

N_{M4} = number of 4+ males in the count,

N_S = total sample size of the composition count, and

R = ratio of three-year-old males to 4+ males obtained in a ground composition on 1-2 October 1962 (Skoog 1968).

Bos (1975) estimated that 6.7 percent of the herd in the early 1970's was 3+ males, based on the observed percentages of 1+ males in the fall (1971-72) and short yearlings in late winter (1970-72), and the assumptions that 80 percent of the non-calves in the late winter composition counts were 1+ females, that 45 percent of the short yearlings were females, that no differential mortality occurred between short yearlings and 2+ females from late winter to the following fall, and that the survival rate of males from 17 months to 29 months was 0.663. While verification of the assumptions used by Bos would be difficult, the fall percentages of 1+ males obtained in the 1971 and 1972 counts (20.6 and 20.7 percent, respectively) are indicative of a considerable decline in the portion of adult males in the herd (Bos 1973, 1974b). In lieu of other data during the early 1970's, I have used Bos's (1975) estimate of 6.7 percent to represent the percentage of 3+ males in the fall of 1972, when intensive hunting pressure on the adult male cohort was alleviated (Table 1), fully realizing this estimate is subject to error.

Figure 3 illustrates the results of a linear regression of the percent 3+ males in the herd and time, using all available fall composition data (Skoog 1963, 1968; Unp. data summarized by G. Bos, Caribou Files, ADF&G, Fairbanks). Figure 3 indicates no significant trend in the percentage of 3+ males over time, with wide flucuations between some years. The average percentage of 3+ males in the counts is 10.5 (S = 3.73), and a 95 percent confidence interval of the mean is 7.4 to 13.6 percent.

Skoog (1968), in reviewing the data prior to 1967, concluded that only the 20 October 1956 and the 1-2 October 1962 composition counts were representative of the 3+ male segments of the herd. Figure 4 shows the results of a linear equation of the percentage of 3+ males regressed on time, deleting all counts prior to 1966

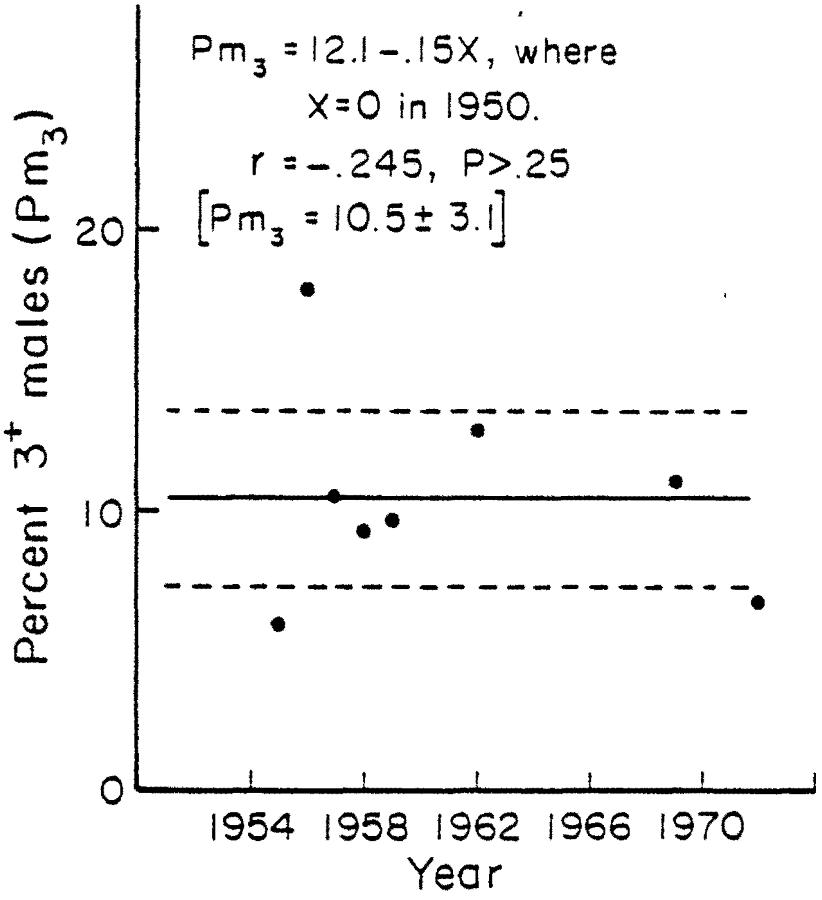

Figure 3. Results of linear regression of fall percentage of 3+ males in the Nelchina herd (1954-72), unselected composition data.

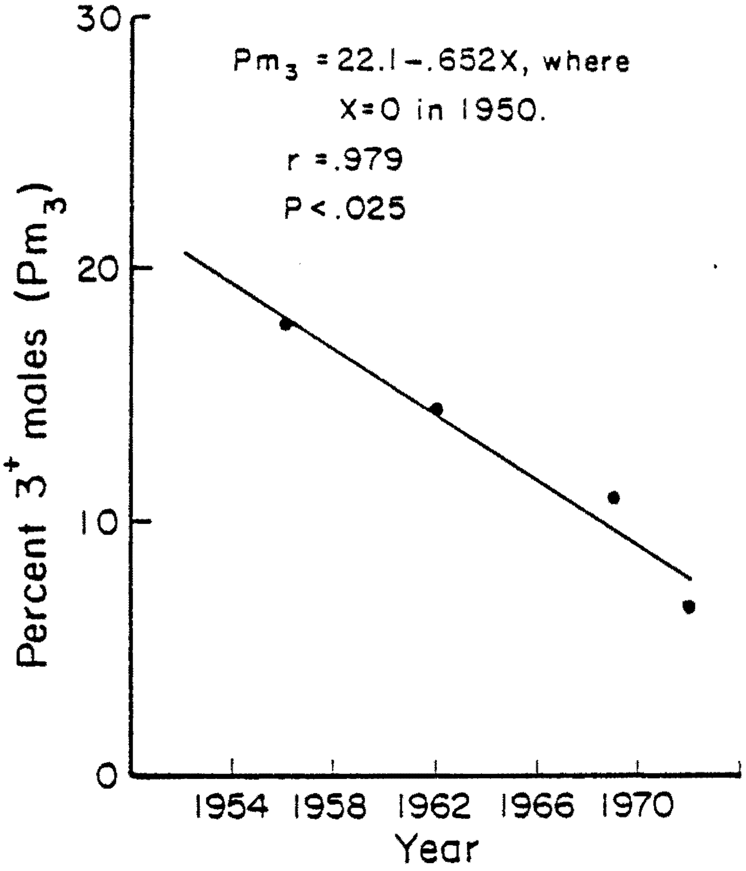

Figure 4. Linear regression of fall percentages of 3+ males in the Nelchina herd (1954-72), selected composition data.

except the two counts cited above. This linear regression model, referred to hereafter as Equation 2, indicates a significant decrease in the percentage of 3+ males from 1955 to the early 1970's ($b = -0.652$, $P < 0.025$) and "explains" 95.8 percent of the variance in the percentage of 3+ males in the fall composition counts. The differences between the percentages of 3+ males in the fall composition counts and the percentages predicted by Equation 2 were regressed on the data (number of days after 30 September) of the counts (Figure 5). Composition counts taken after 20 October had absolute differences of 2.7 to 12.8 percent from the values predicted by the linear regression model (Equation 2). The three "selected" counts, plus the fall composition counts on which Bos (1975) based his estimate, were all conducted within the period 1-20 October, which corresponds closely to the peak rutting period (early to mid-October) of the NCH (Skoog 1968).

Based on the arguments advanced above, as well as the fact that the selected data are from peak periods of rutting activity, Equation 2 (Figure 4) was used to generate the percentage of 3+ males used in the subsequent analysis of this section (Table 1). An assumption made in analyzing the remainder of the fall composition data was that the calves, yearlings, two-year-old males, and 2+ females were randomly mingled with each other during the rut and post-rut periods when the composition counts were obtained. Similar assumptions have been made by other workers analyzing the composition of the NCH (Skoog 1968, Bos 1975). Figure 5 suggests that 3+ males are often underrepresented

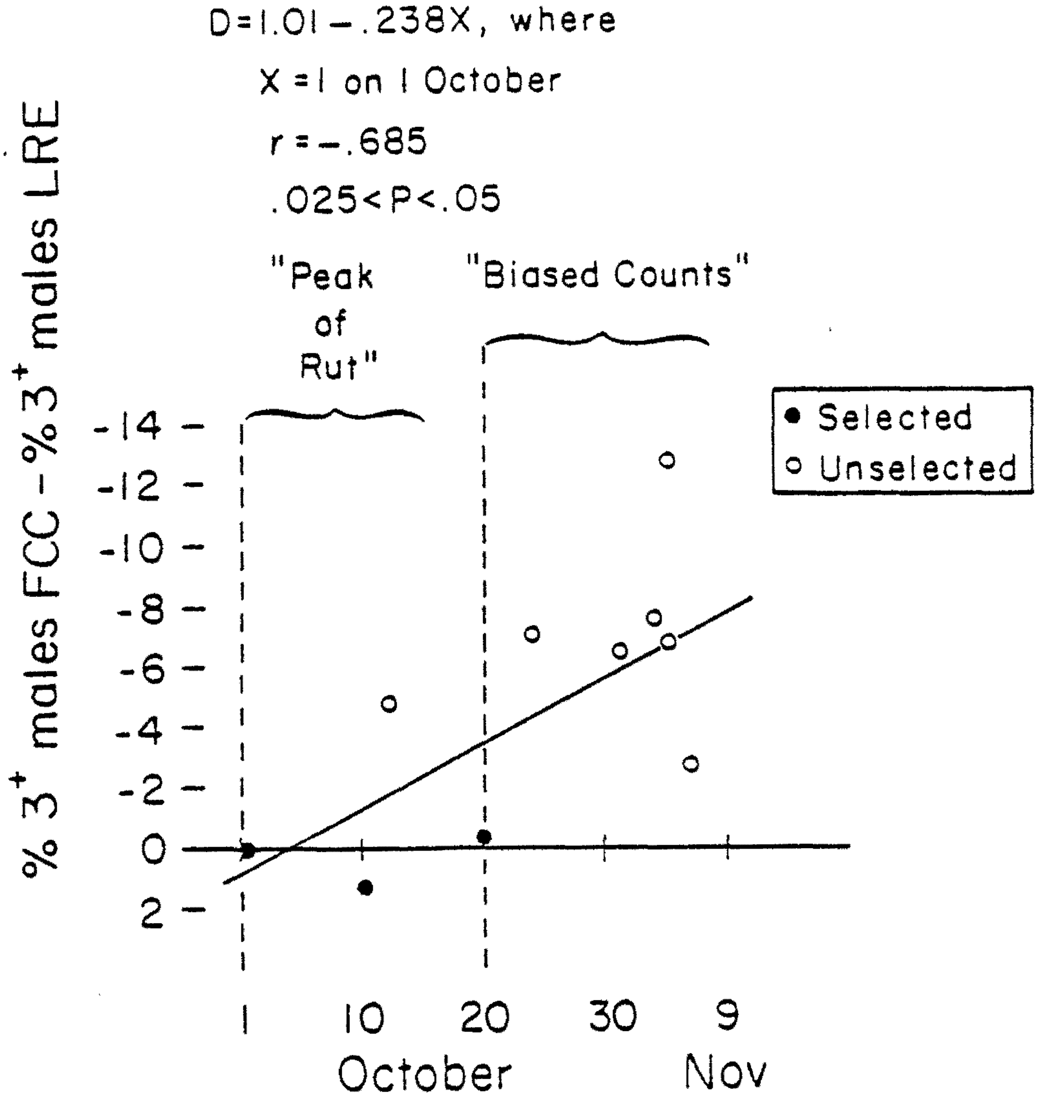

Figure 5. Difference between the percentage of 3+ males in the fall composition counts (FCC) and the percentage of 3+ males predicted by the linear regression equation (LRE) (Figure 4) regressed on date of composition counts.

in the fall counts; consequently the fall composition data were adjusted using the following formula:

$$Pa = Pc \times [(100 - P_{M3})/(100 - P_{M3C})] , \quad (3)$$

where

Pa = actual fall percentage of a given age-sex cohort (calves, yearlings, two-year-olds, 3+ females),

Pc = percentage of the given age-sex cohort in the composition count,

P_{M3} = fall percentage of 3+ males from Equation 2, and

P_{M3C} = percentage of 3+ males in the fall composition counts.

b. 3+ Females

Females 3 years of age and older were never directly classified in any of the composition counts, hence this proportion in the NCH had to be determined indirectly. In 1956, 1959, and 1962, ground-based composition counts separated one- and two-year-old males from 1+ females, while aerial-based counts classified these cohorts together (Skoog 1968; Unp. data summarized by G. Bos, Caribou Files, ADF&G, Fairbanks). The proportion of 3+ females (P_{F3}) in the fall composition counts in these years is estimated using the following formula and assuming a 50:50 sex ratio in the yearlings and two-year-olds combined:

$$P_{F3} = \left\{ (N_{F1}-N_{M12}) + \left(\left([(N_{F1}-N_{M12})/(N_{F1}+N_{M12})] \right) \times N_{S1} \right) \right\} / N_S , \qquad (4)$$

where

N_{S1} = number of one- and two-year-old males and 1+ females in the aerial-based counts,

N_{F1} and N_{M12} = number of 1+ females and one- and two-year-old males, respectively, in the ground-based counts, and

N_S = total number of animals classified in both the aerial and the ground based composition counts.

In 1971 and 1972, caribou were classified as calves, 1+ males, and 1+ females. Therefore, the following equation, which assumes a 50:50 sex ratio for yearlings and two-year-olds combined, is used to estimate the proportion of 3+ females in the herd in these years:

$$P_{F3} = (N_{F1} - N_{M1} + N_{M3}) / N_S , \qquad (5)$$

where

N_{M1} = number of 1+ males in the fall composition counts,

N_{M3} = estimated number of 3+ males in the fall composition counts obtained by multiplying the estimated percentage of 3+ males in the herd (Equation 2) times N_S, and P_{G3}, N_{F1}, and N_S are as defined in Equation 4.

The estimated percentages of 3+ females in the composition counts in 1956, 1959, and 1962 were adjusted to the estimated percentage in the herd using Equation 3. The results are listed in Table 1.

First, second, and third degree polynomial regressions were calculated for the estimated percentage of 3+ females and time. Both first and second degree polynomial regressions were significant ($P < 0.005$ and $P < 0.025$, respectively). Because the sum of squares of the quadratic term did not contribute significantly to the overall regression sum of squares ($F = 5.16$, $df = 1/2$, $0.10 < P < 0.25$), the linear regression was selected as the "best fit" of the data. The linear equation is:

$$P_{F3} = 19.4 + 1.33X , \qquad (6)$$

where

$X = 0$ in the year 1950.

Equation 6 accounts for 96.1 percent of the variance in the percentage of 3+ females in the fall composition counts and is useful in subsequent analysis of the composition data.

c. Yearlings and Two-Year-Olds

Skoog (1968) found a 1.24:1.00 ratio of male yearlings to male two-year-olds out of 360 one- and two-year-old males classified in the fall of 1962. These counts by Skoog are the only counts in which the ratio of yearlings to two-year-olds can be directly calculated. The

Table 1. Adjusted fall composition data of the Nelchina Herd (1954-72)[1]

Year	Percent Calves	Percent Yearlings	Percent 2-yr-olds	Percent 3+ Females	Percent 3+ Males	Predicted Percent 3+ Males[2]	Source
1954	20.5	19.5	15.8	24.7	--	19.5	[3]
1955	17.1(2,590)	--	--	--	6.0(2,590)	18.8	[4]
1956	21.5(5,178)	--	--	29.4	17.9(542)	18.2	Skoog (1968)
1957	18.8(2,919)	--	--	--	10.5(2,919)	17.5	[4]
1958	21.1(2,975)	--	--	--	9.3(2,975)	16.9	[4]
1959	22.2(2,091)	--	--	30.7	9.7(2,091)	16.2	[4]
1962	17.1(4,372)	19.9	16.1	32.5	14.4(2,057)	14.3	Skoog (1963, 1968)
1967	25.2(4,219)	9.7	--	--	20.8(4,219)[5]	11.0	Hemming and Glenn (1968)
1968	25.3(3,242)	9.5	--	--	6.2(3,242)[5]	10.4	Hemming and Glenn (1969)
1969	21.1(3,007)	15.4	--	--	11.0(3,007)	9.7	[4]
1971	18.4(3,540)	--	--	48.8	20.6(3,540)	8.4	Bos (1973)
1972	18.1(2,381)	15.6	11.3	48.3	6.7	7.8	Bos (1973, 1975)

[1] Sample size of composition counts in parentheses. See text for assumptions made in adjusting the data.

[2] Predicted percentage of 3+ males obtained from Equation 2 (Figure 4).

[3] Percentages of 3+ males and 3+ females in 1954 estimated from Equations 2 and 6, respectively. Percentages of calves in 1954 estimated from the average of 11 years of data. Percentage of yearlings and two-year-olds was calculated using a 1.24:1.00 ratio of yearlings and two-year-olds observed by Skoog (1968) in 1962.

[4] Source from unpublished data summarized by G. Bos, ADF&G, Caribou Files, Fairbanks.

[5] Includes two-year-old males.

percentages of yearlings and of two-year-olds are calculated from all the available 1962 fall data (Skoog 1963, 1968), modifying Equation 4 to calculate yearlings and two-year-olds instead of 3+ females and adjusting the results using Equation 3.

In 1969, two-year-old males were classified with 2+ females (Unp. ADF&G data summarized by G. Bos, Caribou Files, Fairbanks) and the following equation is used to estimate the percentage of two-year-olds (P_2) in the fall composition counts in that year:

$$P_2 = (100 - P_{M3} - P_{F3} - P_0 - P_1) \qquad (7)$$

where,

P_{M3} = percentage of 3+ males in the fall composition counts;

P_0 and P_1 = percentages of calves and yearlings, respectively, adjusted to the estimated percentage of 3+ males in the herd using Equation 3; and

P_{F3} = estimated percentage of 3+ females in the herd derived using Equation 6.

The estimated ratio of $P_1:P_2$ in 1969 is 1.66:1.00.

Because two-year-old males are classified with 3+ males in 1967 and 1968 (Hemming and Glenn 1968, 1969), it is not possible to directly adjust the data using Equation 3. To determine if adult males are representatively present in these counts, I estimated the percentage of 3+ males (P_{M3}) using the following equation:

$$P_{M3} = P_{M2} - (0.5 \times P_1 \times R) \ , \qquad (8)$$

where

P_{M2} = percentage of 2+ males in the counts,

P_1 = percentage of yearlings, and

R = average ratio of two-year-olds to yearlings in the 1962 and 1969 fall composition counts.

The calculated percentages of 3+ males in the composition counts in 1967 and 1968 are 17.4 and 2.6, respectively, compared to 11.0 and 10.4 percent predicted by Equation 2. The assumed R value used in Equation 8 is extremely tenuous given the limited data on which it is based and the rather wide differences in the yearling:two-year-old ratios calculated in 1962 and 1969. It seems apparent, however, that large numbers of adult males were missed in the 1968 composition counts, as suggested by the researchers conducting the counts (Hemming and Glenn 1969). Consequently, the percentage of yearlings in the 1968 count was adjusted using Equation 3. The 1967 count was not adjusted, since the above analysis suggested the male segment was not underrepresented in these counts. Table 1 summarizes the available composition counts and estimates for yearlings and two-year-olds. First through third degree polynomial regressions of the percent of yearlings and time were not significant, even at the 0.25 significance level. The average estimated fall percentage of yearlings is 14.0 (S = 4.4) with a 95 percent confidence interval of 8.5 to 19.5 percent.

d. Calves

The percentages of calves in the NCH are available directly from the data for more years from 1954-72 than for any other cohort since calves can be readily distinguished from 1+ adults from fixed-wing aircraft. The percentage of calves in 1968 was adjusted for missing adult males as described above for yearlings in that year; the percentages of calves in 1967, 1971, and 1972 fall counts were not adjusted due to reasons previously discussed; the percentages of calves in the remaining years were adjusted using Equation 3. Adjusting for the missing adult males lowers the percentage of calves an average of 1.5 percent, with the largest difference between observed and adjusted values equaling 2.7 percent. Table 1 summarizes the results.

First through fourth degree polynomial equations were calculated for the fall percentages of calves regressed on time. None of the equations were significant at the 0.25 significance level. The average fall percentage of calves in the NCH was 20.5 ($S = 2.93$) with a 95 percent confidence interval of 18.5 to 22.5.

e. Conclusions Regarding Fall Composition Data

Despite the limitations of the data, the detailed analysis presented was useful in detecting the presence or absence of trends in the proportion of various cohorts in the herd from 1954-72. The percentage of 3+ males declined from approximately 20 percent in 1954 to 8 percent in 1972, while the percentage of 3+ females increased at approximately twice the rate that the percentage of 3+ males declined. No trend was detected in the percentage of calves over time, indicating that the percentage of yearlings and two-year-olds combined declined from 1954 to 1972.

2. OBSERVATIONS OF THE COMPOSITION OF THE NELCHINA CARIBOU HERD AFTER ITS DECLINE

Since 1971, the NCH has been fairly regularly monitored by ADF&G. Changes in classification techniques make comparison of herd composition prior to 1970 with the herd composition since then more difficult. Recent researchers involved with population dynamics studies of the NCH believe that distinguishing yearlings or two-year-olds from older caribou during the composition counts is too subjective to provide useful information. Fall composition counts conducted within the first 20 days of October in 1973 and 1976 revealed low percentages of 1+ males comparable to the herd composition in 1971 and 1972 (Bos 1974b; S. Eide, Unp. ADF&G Data, Caribou Files, Fairbanks). Fall percentages of calves in 1973 and 1976 are 23.1 (Bos 1974b) and 17.8 (S. Eide, Unp. ADF&G Data, Caribou Files, Fairbanks), respectively, percentages comparable to the range of values found from 1955-72 (Table 1). Yearling recruitment has been estimated by comparing fall calf/1+ female ratios to late winter calf/1+ female ratios. Since 1972, late winter calf/1+ female ratios, ranging from 24 to 42 calves per 100 1+ females (Bos 1974b; Unp. ADF&G Data, Caribou Files, Fairbanks), indicate overwinter survival rates of calves similar to those estimated by Skoog (1968) during the herd's increase from 1955-62.

3. ANALYSIS OF TRENDS IN THE HARVEST DATA, NELCHINA HERD (1954-71)

Evaluating harvest data is useful for several reasons. First, hunting may be a significant mortality factor of the population and hence must be assessed. Second, various harvest parameters, such as age-sex structure and total harvest, may accurately reflect actual population parameters. This section places particular emphasis on assessing trends in the harvest data.

The following seven parameters from the harvests are analyzed: (1) total harvest, (2) percentages of males, (3) percentages of calves, (4) percentages of yearlings, (5) percentages of two-year-olds, (6) percentages of 3+ females, and (7) percentages of 3+ males. Total harvests and the sex ratio of the harvests were estimated from 1954-67 and 1954-68, respectively, by various USFWS and ADF&G personnel from information collected at roadside check stations and from interviews with guides and other hunters (Skoog et al. 1963, Skoog 1968). The estimates of total harvests prior to 1968 accounted for unreported kill and wounding loss, although the method of estimating these two values was not standardized (see Skoog 1957, 1963; Scott et al. 1958; Skoog et al. 1963; Lentfer 1965; McGowan 1966). Since 1968, total harvests have been estimated from the number of caribou reported killed by hunters returning harvest report tickets extrapolated to the total number of hunters obtaining harvest tickets. Wounding loss and illegal harvests have not been accounted for in the harvest estimates since 1967.

The sex ratios of the harvests since 1968 have also been estimated directly from the returned harvest report tickets. The accuracy of this estimate can be checked by comparing the sex ratio obtained from the harvest report tickets with the sex ratio of mandible collections obtained in the same year (Table 2). A significantly higher overall percentage of males is found in the harvest report tickets compared to the mandible collections from 1969 to 1972 ($P < 0.01$). One advantage of using the sex ratio based on harvest report tickets is that the harvest report tickets sample is 9.2 times larger than the sample size of the mandible collection. However, if hunters are incorrectly reporting the sex of the caribou taken, a correctly sexed mandible collection might then be more representative of the harvest than is the hunter report. Correlation between the sex ratio of the mandible collection and the estimated sex ratio of the harvest (Table 3) is highly significant ($r = 0.89$, $df = 14$, $P < 0.001$); hence, either sex ratio should be indicative of trends in the sex ratio of the harvest.

The remaining five harvest parameters are estimated from samples of aged and sexed caribou killed by hunters. Bos (1975) indicated that calves and yearlings are underrepresented in these samples, due to a bias in the collection process. Lacking other data for estimating age structure, I have ignored this bias, as did Skoog

Table 2. Comparison of the estimated sex ratios from harvest report tickets and from collections of caribou killed by hunters in the Nelchina Herd (1969-72).[1]

Harvest Season	Percent Males (Harvest Tickets)	Percent Males (Hunter-Killed Caribou)	P[2]
1969-70	49.3 (5,332)[3]	53.1 (439)	>0.10
1970-71	63.2 (4,018)	52.5 (386)	<0.01
1971-72	46.6 (6,743)	39.4 (885)	<0.01
1972	71.7 (541)	80.6 (98)	<0.02
Average weighted by estimated total harvest (Table 3)	52.9 (4,158)[4]	48.5 (452)[4]	<0.01

---

[1] Sources are Bos (1973, 1974b) and unpublished ADF&G data, Caribou Files, Fairbanks.

[2] Variance [V(p)] of the percentage of males (p) in the samples calculated using the following equation for the variance of a binomial distribution:

$$V(p) = \frac{N-n}{N} \cdot \frac{pq}{n},$$

where N represents the estimated harvest (Table 3), n represents the size of the sample, and q represents 1-p.

[3] Sample size in parentheses.

[4] Average sample size of 4 years.

Table 3. Seasons, bag limits, and estimates of total harvests and percentages of males in harvest, Nelchina Herd (1952-76).[1]

Year	Season	Bag Limit	Estimated Total Harvest	Estimated Percent Males
1952	10 Aug to 30 Sept 1 to 15 Dec	1 branch-antlered male	450	93.4
1953	10 Aug to 30 Sept 1 to 15 Dec	1 branch-antlered male	700	84.5
1954	10 Aug to 30 Sept 20 to 30 Nov	1 caribou except calves	2,000	71.8
1955	10 Aug to 30 Sept 20 to 30 Nov	2 caribou	4,000	72.5
1956	10 Aug to 31 Dec	2 caribou	3,500	71.8
1957	10 Aug to 31 Dec	3 caribou	2,500	75.0
1958	10 Aug to 31 Dec	3 caribou	3,500	--
1959	10 Aug to 31 Dec	3 caribou	4,000	68.8
1960	10 Aug to 31 Dec	3 caribou	5,500	66.1
1961	10 Aug to 31 Dec	3 caribou	8,000	58.0
1962	10 Aug to 31 Dec	3 caribou	3,500	68.7
1963-64	10 Aug to 31 Mar	3 caribou	6,300	60.8
1964-65	10 Aug to 31 Mar	4 caribou	8,000	66.0
1965-66	10 Aug to 31 Mar	3 caribou	7,100	67.0
1966-67	10 Aug to 31 Mar	3 caribou	5,500	71.0
1967-68	10 Aug to 31 Mar	3 caribou	4,000	65.0
1968-69	10 Aug to 31 Mar	3 caribou	6,000	57.1
1969-70	10 Aug to 31 Mar	3 caribou	7,800	49.3
1970-71	10 Aug to 30 Sept 1 Nov to 31 Mar	3 caribou	7,247	63.2
1971-72	10 Aug to 31 Mar	3 caribou	9,128	46.6
1972	10 Aug to 20 Sept	1 caribou	555[2]	71.7

---

[1] Sources are McKnight (1975) and unpublished data, ADF&G, Caribou Files, Fairbanks.

[2] Estimate considered low (McKnight 1975).

Table 3. continued

Year	Season	Bag Limit	Estimated Total Harvest	Estimated Percent Males
1973	10 Aug to 20 Sept	1 caribou	810	67.0
1974	10 Aug to 20 Sept	1 caribou	1,193	66.0
1975	5 Sept to 20 Sept	1 caribou	806	68.7
1976	5 Sept to 20 Sept	1 caribou	822	73.6

(1968) and Bos (1975), in estimating the proportion of various cohorts harvested by hunters in the NCH. I have assumed the proportion of calves and yearlings missed in these collections is small.

The hunting seasons and bag limits varied somewhat from 1954 to 1971 (Table 3) and may have influenced the harvest parameters. Although calves were not legal game in 1954, 14, or 2.3 percent, of 601 hunter-killed caribou collected in 1954 were calves (Unp. ADF&G Data, Caribou Files, Fairbanks). This value is included in the trend analysis of percentage of calves. Polynomial regressions of percentages with time were run; those not significant at the 0.05 level were rejected. If more than one regression equation is significant for a given parameter, the highest degree equation that had a significant ($P < 0.05$) increase in the total regression sums of squares is accepted as the "best fit" of the data. The regression sums of squares of the nth term over the residual mean square of the nth polynomial regression is used to test the significance of that increase.

The analysis of trends in the harvest data is divided into the following categories: (1) total harvest, (2) calves, (3) yearlings and two-year-olds, (4) males, and (5) 3+ females. Results are presented in Table 4.

Table 4. Summary of polynomial regressions of seven harvest parameters of the Nelchina Caribou Herd and time (1954-71).

Harvest Parameter[1]	Sig. of nth Degree Equation					"Best Fit"[2] Regression	"Best Fit" Equation[3]
	1st	2nd	3rd	4th	r		
Estimated total harvest (18)	<0.001	<0.005	<0.005	<0.005	0.749	1st	$H = 1{,}679+299x$ (9)[4]
Percent calves (16)	>0.500	>0.250	<0.050	<0.025	0.163	3rd	$H = -29.4+9.96x-0.787x^2 +0.0190x^3$ (10)[4]
Percent yearlings (16)	<0.100	<0.100	<0.250	>0.250	-0.493	none	$H = 13.3(\pm 2.9)$[5]
Percent 2-year-olds (16)	>0.250	>0.250	<0.100	<0.250	-0.281	none	$H = 14.7(\pm 2.6)$[5]
Percent yearlings and 2-year-olds (16)	<0.025	<0.100	<0.050	<0.100	-0.570	1st	$H = 37.2-0.736x$ (11)[4]
Estimated percentage of males (18)	<0.001	<0.001	<0.001	<0.005	-0.737	1st	$H = 78.7-1.11x$ (12)[4]
Percent 3+ males (16)	>0.250	>0.500	<0.250	<0.250	-0.220	none	$H = 41.3(\pm 5.1)$[5]
Percent 3+ females (16)	<0.001	<0.001	<0.001	<0.005	0.783	2nd	$H = 25.1-1.7x+0.108x^2$ (13)[4]

[1] Sample size in parentheses.

[2] See text for discussion of "best fit."

[3] H = harvest parameters in year x, where $x = 0$ in the fall-winter of 1950-51.

[4] Equation number in parentheses.

[5] ±95 percent confidence interval in parentheses.

a. Total Harvest

Total harvest increased from 1954 to 1971, despite a declining number of caribou in the late 1960's and early 1970's. The linear regression model (Equation 9:Table 4) accounted for 56.1 percent of the variance in the estimated total harvests.

b. Calves

The mean percentage of calves in the harvest mandible collection from 1954-71 was 7.0 ($S = 4.07$), with a 95 percent confidence interval of 4.8 to 9.2. A third degree polynomial equation (Equation 10: Table 4) of the percentage of calves in the harvest regressed on time produced the "best fit" of the data. In contrast, a third degree polynomial regression equation of the percentage of calves in the fall composition counts and time was not significant ($F = 1.31$, $df = 3/7$, $0.25 < P < 0.50$), suggesting that the calf proportions in the hunter harvest and in the fall composition counts do not show similar relationships with time.

c. Yearlings and Two-Year-Olds

None of the polynomial regressions of the percentage of yearlings or of two-year-olds in the harvest mandible collections and time were significant (Table 4). A linear regression of the combined cohorts (Equation 11:Table 4) was significant, however ($b = -0.736$, standard error of $b = 0.286$, $P < 0.025$). The slope of Equation 11 agrees closely with the annual decline of 0.68 in the percentage of yearlings and two-year-olds combined calculated from the fall composition data, with the latter calculation based on the assumptions that the percentage of calves is constant over time, that the percentage of 3+ females increases annually by 1.33 (Equation 6), and that a 0.65 annual decrease in the percentage of 3+ males occurs (Equation 2).

d. Males

A linear decline in the estimated percentage of males in the harvest was detected (Table 4) which corresponds to a similar decline in the percentage of various aged males in the fall composition data (Equation 2 and previous section on yearlings and two-year-olds). None of the polynomial equations of the percentage of 3+ males in the mandible collections regressed on time were significant, however. Thus harvest composition data did not indicate a decline in the proportion of adult males in the herd, similar to that evident from the evaluation of the fall composition data (Equation 2).

e. 3+ Females

All four polynomial regression equations of the percentage of 3+ females in the mandible collections and time were significant (Table 4). The slope of the linear regression equation ($b = 0.998$) was not significantly different than the slope of the Equation 6 ($t = 0.949$, $df = 17$, $0.25 < P < 0.50$). The critical difference in slopes (0.74) that can be detected at a 0.05 significance level, given the sample sizes and variances of the two linear regressions, is rather large, however.

4. ANALYSIS OF HUNTER SELECTIVITY OF NELCHINA CARIBOU HERD (1954-71)

Various authors have commented on the selectiveness of caribou hunters in Alaska (Rausch 1951, Saario and Kessel 1966, Skoog 1968, Bos 1975, and others); however, no one has analyzed hunter selectivity during an extended period of time or formulated mathematical equations defining hunter selectivity. Since the interpretation of harvest data in estimating sex and age structure of the population depends on an understanding of hunter selectivity, this section defines and analyzes hunter selectivity of caribou in the NCH.

The following equations are given for absolute (AHS_i), relative (RHS_i), and percentage (PHS_i) hunting selectivity of a given age-sex cohort (i):

$$AHS_i = (\text{\% ith age-sex group in hunting harvest}) - (\text{\% ith age-sex group in herd}), \qquad (14)$$

$$RHS_i = AHS_i \,/\, (\text{\% ith age-sex group in herd}), \qquad (15)$$

$$PHS_i = RHS_i \times 100. \qquad (16)$$

PHS for calves is calculated by using the percentage of calves in the mandible collection as an estimate of the percentage of calves in the hunting harvest and by using the adjusted percentage of calves in the fall composition counts (Table 1) as an estimate of the actual percentage in the herd. PHS for 3+ males and 3+ females are calculated using Equations 2 and 6, respectively, to calculate the estimated percentage in the herd and by using the percentages of these two respective cohorts in the mandible collections as an estimate of the percentages in the harvest. First through fourth degree polynomial regressions of PHS for calves, 3+ males, and 3+ females with time were calculated and analyzed as described in the previous section on trend analysis of the harvest data. The data on yearlings and two-year-olds is insufficient to allow estimating trends in hunter selectivity; hunter selectivity for these cohorts are estimated indirectly as described below. The results of the analysis of hunter selectivity is divided into four sections: (1) calves, (2) 3+ males, (3) 3+ females, and (4) yearlings and two-year-olds.

a. Calves

Second and third degree polynomial equations of PHS of calves and time are significant at the 0.05 level. The quadratic equation gives the "best fit" of the data and is shown in Figure 6. Hunters selected against calves more during increasing and declining phases of the herd and showed less selectivity against calves during the highest population levels of the herd. The greater selectivity against calves during the hunting seasons of 1955-56 and 1956-57 may have been partially influenced by the more restrictive bag limit of two caribou compared to three caribou in subsequent years (Table 3). Skoog (1968) believed that hunters in the Nelchina area were indiscriminant with regard to the sex of caribou calves taken, but his hypothesis has not been tested directly.

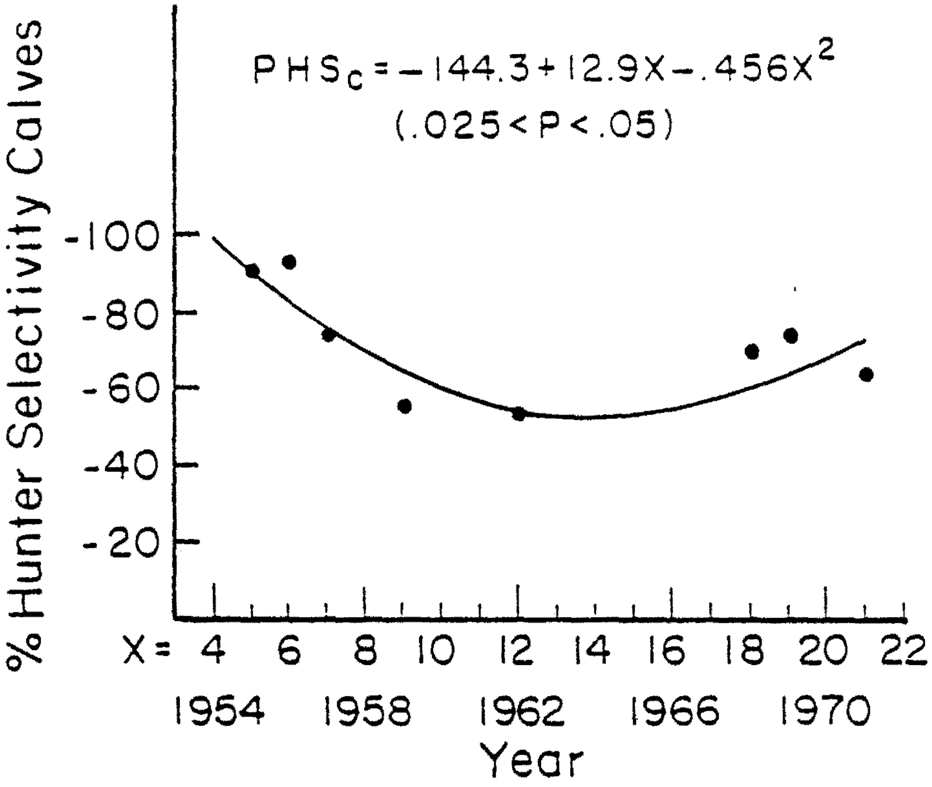

Figure 6. Quadratic regression of percentage hunter selectivity for calves and time in the Nelchina Caribou Herd (1954-71).

b. 3+ Males

All four polynomial equations of PHS of 3+ males over time are significant ($P < 0.025$). A third degree polynomial equation has the "best fit" and is shown in Figure 7. PSH of 3+ males declined slightly from 1954 to 1958, then increased nearly twofold by 1968 before declining again in the early 1970's. Hunters of the Nelchina herd from 1954 to 1971 were highly selective for 3+ males; moreover, hunters persisted in their desire to take adult males even after the total population and percent of 3+ males had apparently begun to decline. The estimated PHS for 3+ males ranged from 71.1 to 405.1.

c. 3+ Females

None of the polynomial regression equations of PHS of 3+ females and time are significant at the 10 percent level. The mean PHS of 3+ females is -35.7 ($S = 10.4$), and a 95 percent confidence interval is -30.1 to -41.3. Hunters selected against 3+ females, in all the years from 1954 to 1971, but no trend in the selectivity against 3+ females over the given time interval is evident.

d. Yearlings and Two-Year-Olds

Of the 868 yearlings and 1,010 two-year-olds from hunter-killed Nelchina caribou examined by USFWS and ADF&G from 1954-1971, 63.5 percent of the yearlings and 62.8 percent of the two-year-olds are males (summarized from unp. ADF&G Data, Caribou Files, Fairbanks). The sex ratio of yearlings from the hunter-killed animals is

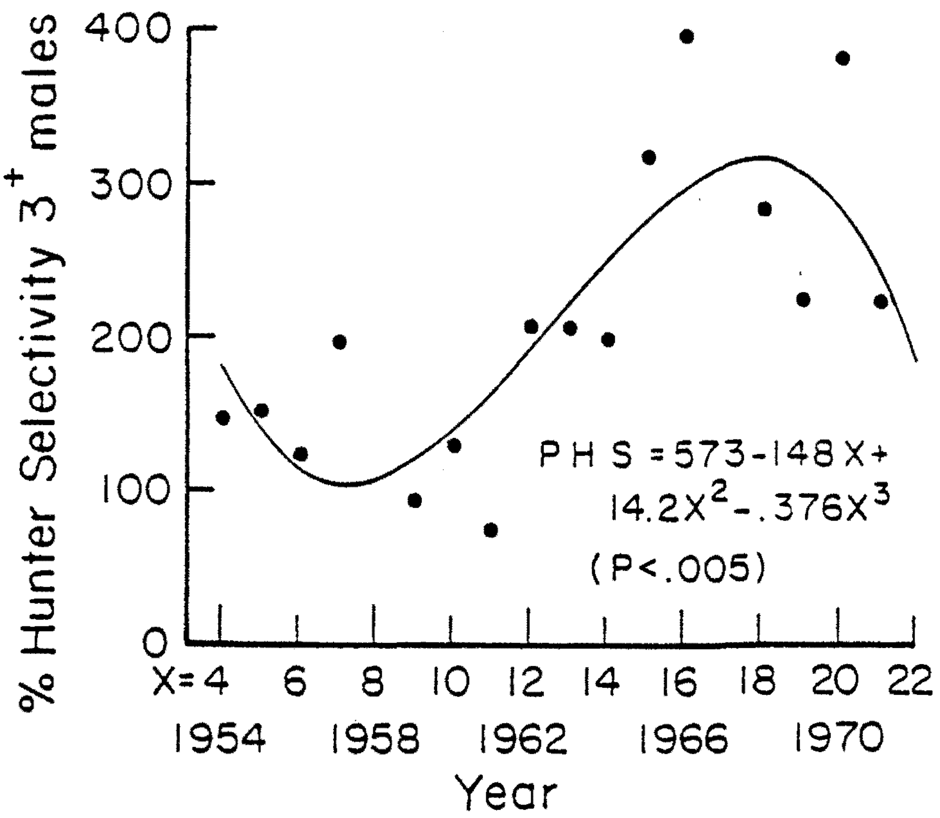

Figure 7. Third degree polynomial regression of percentage hunter selectivity for 3+ males and time in the Nelchina Caribou Herd (1954-72).

significantly different than a 50:50 sex ratio ($\chi^2 = 63.08$, df = 1, $P < 0.005$). The sex ratio of two-year-olds from the hunter-killed caribou is also significantly different than the 50:50 sex ratio postulated by Skoog (Ibid.) ($\chi^2 = 65.90$, df = 1, $P < 0.005$).

It is apparent that hunters in the Nelchina herd have a higher selectivity toward males than females in the one- and two-year-old age classes. Percentage hunter selectivity is not calculated for these age classes because of the extremely limited composition data available and its questionable reliability (discussed in later sections on population simulations in this chapter). However, some idea of hunter selectivity of the yearling and two-year-old age cohorts can be determined from a comparison of the percentages of one-, two-, and three-year-old animals in the harvest mandible collections.

In 8 (50 percent) of the 16 years of mandible collections from 1954-71, the number of two-year-old females exceeds the number of yearling females. In 8 (67 percent) of 12 years, the number of three-year-old females exceeds the number of yearling females in the collections. In 11 (92 percent) of 12 years, three-year-old females outnumber two-year-old females in the collections. Bos (1975:179) stated that for the NCH "age classes of females two years old and older are not differentiated by hunters and are probably taken in direct proportion to their abundance in the female population."

The proportions of one-, two-, and three-year-old females in the mandible collections mentioned above contradict this statement since, in most years, two-year-olds should outnumber three-year-olds in the actual population. In many years, hunters in the Nelchina area apparently discriminated against one- and two-year-old females in favor of three-year-old females. An aspect that can't be evaluated is whether or not hunters select against old females (i.e., 8+ years) in favor of younger females (i.e., 3 to 5 years); the data are confounded by the inability of the wear-age technique to accurately age-determine older animals to the year class (Skoog 1968), as well as the lack of knowledge of the actual age structure of the herd.

It is apparent that hunters also discriminate against harvesting one- and two-year-old males in favor of more mature bulls. The number of three-year-old males exceeded the number of yearling males and the number of two-year-olds in 9 (75 percent) of 12 years, while the number of two-year-old males exceeded the number of yearling males in 10 (62.5 percent) of 16 years of mandible collections from 1954-71. The greater selectivity for mature males versus younger males by NCH hunters is consistent with the findings of Skoog (1968) and Bos (1975). Selectivity of hunters for individual age classes of animals 3 years and older will be addressed with two independent models described in the sections entitled "Estimating age-specific survival of 3+ caribou in the NCH (1969-71)" (Chapter 2) and "Testing the accuracy of 3+ adult age structure data from village harvests by comparing the age structure of males and females" (Chapter 6).

5. AN EVALUATION OF THE USE OF THE AGE STRUCTURE OF THE HUNTER HARVEST TO ESTIMATE RECRUITMENT RATE

Age structure information is often used to directly estimate the recruitment of younger cohorts into a population. For example, Bos (1975) uses the ratio of two-year-old females to 1+ females in the hunter harvest in 1 year as an indice of calf production and survival 2 years earlier. Such a relationship between the initial recruitment of the cohort into the herd and the age structure of the harvest data in subsequent years would be extremely valuable for the purposes of modeling the NCH since age structure data is available for many years that lack composition data. However, before age-structure data can be validly used to extrapolate recruitment into the herd as suggested above by Bos (1975), the relationship between age structure and recruitment must be verified. The purpose of this section is to determine the correlation between the percentage of calves in the herd in the fall and the proportion of this cohort in the age structure of subsequent harvest samples.

Simple correlation coefficients were calculated between the adjusted percentage of calves in the fall composition counts (Table 1) and each of the following: 6 calf parameters from the harvest data in the same year, 13 yearling parameters from the harvest data 1 year later, and 13 parameters of two-year-olds from the harvest data 2 years later. The results are shown in Table 5.

Table 5. Simple correlation coefficients between adjusted percentages of calves in the fall composition data and various calf, yearling, and two-year-old parameters from mandible collections of hunter-killed caribou in the Nelchina Caribou Herd (1955-71).[1]

Parameters from Harvest Data	Percent Calves in the Fall Composition Counts (X)[2]	P
% female calves of total females (X)	0.125	>0.75
calves/3+ females (X)	0.061	>0.75
% yearlings (X+1)	0.046	>0.75
% yearlings of 1+ adults (X+1)	-0.070	>0.75
male yearlings/total males (X+1)	0.107	>0.75
female yearlings/total females (X+1)	-0.019	>0.75
yearlings/1+ females (X+1)	-0.095	>0.75
yearlings/2+ females (X+1)	-0.084	>0.75
yearlings/3+ females (X+1)	-0.126	>0.75
male yearlings/1+ females (X+1)	-0.131	>0.75
male yearlings/2+ females (X+1)	-0.112	>0.75
female yearlings/1+ females (X+1)	-0.014	>0.75
female yearlings/3+ females (X+1)	-0.048	>0.75
calves/1+ females (X)	0.260	>0.50
calves/2+ females (X)	0.173	>0.50
male yearlings/3+ females (X+1)	-0.161	>0.50
female yearlings/2+ females (X+1)	-0.237	>0.50
two-year-olds/2+ adults (X+2)	0.179	>0.50
male two-year-olds/total males (X+2)	0.151	>0.50
percent calves (X)	0.356	>0.25
percent male calves of total males (X)	0.308	>0.25
percent two-year-olds (X+2)	0.419	>0.25
two-year-olds/1+ females (X+2)	-0.439	>0.25
female two-year-olds/total females (X+2)	0.598	<0.25
two-year-olds/2+ females (X+2)	-0.552	<0.25
two-year-olds/3+ females (X+2)	-0.484	<0.25
male two-year-olds/1+ females (X+2)	-0.580	<0.25
male two-year-olds/2+ females (X+2)	-0.610	<0.25
male two-year-olds/3+ females (X+2)	-0.608	<0.25
female two-year-olds/1+ females (X+2)	0.561	<0.25
female two-year-olds/2+ females (X+2)	0.465	<0.25
female two-year-olds/3+ females (X+2)	0.490	<0.25

[1] Year in parentheses.

[2] Degrees of freedom = 6.

None of the correlations with the 6 calf parameters or the 13 yearling parameters from the harvest data are significant, even at the 0.25 level. Of 13 correlations with the various parameters of two-year-olds in the harvest collections 2 years later, only two-year-old females/2+ adults, two-year-old females/1+ females, two-year-old females/2+ females, and two-year-old females/3+ females had positive correlations significant at the 0.25 level; none were significant at the 0.10 level.

The negative correlations with the several harvest parameters involving the ratio of two-year-olds to females and two-year-old males to females (Table 5), probably result from the high inverse correlation between the percentage of two-year-old males in the harvest sample and the percentage of 3+ females in the same sample ($r = -0.676$, $df = 14$, $P < 0.01$), rather than any biological reasons concerning the survival of calves to 2 years of age. The highest positive correlation, which occurred between calves in 1 year and the two-year-old female/total female ratio 2 years later, accounted for only 35.8 percent of the variance in the calf percentages.

The lack of correlation between the proportion of animals in a given age class in the harvest in 1 year compared to the proportion of the same cohort in the harvest in subsequent years can be demonstrated further by the low correlations between the following: (1) percentage of calves in year X in the harvest sample and percentage of yearling females of total females in year X + 1 in the harvest sample ($r = 0.295$, df = 11, $0.25 < P < 0.50$), (2) percentage of calves in year X in the harvest sample and percentage of two-year-olds of total females in year X + 2 in the harvest sample ($r = 0.260$, df = 10, $0.25 < P < 0.50$), and (3) percentage of yearling females of total females in year X and percentage of two-year-old females of total females in year X + 1 in the harvest samples ($r = 0.242$, df = 10, $0.25 < P < 0.50$).

From the above, it can be concluded that *fall* percentages of calves in the herd cannot be accurately determined from the proportions of calves, yearlings, or two-year-olds in the harvest data, and that initially large or small cohorts of calves cannot be detected by the respective proportions of yearling or two-year-olds in collections of harvest age-structure data in the respective subsequent years.

6. REVIEW OF PERTINENT CARIBOU-WOLF PREDATION STUDIES

A review of the food habits of wolves in taiga and tundra ecosystems was made in order to establish a basis for estimating wolf predation in the model. From the literature available, the following conclusions were made regarding wolf predation on caribou.

1) Ungulates are the major food item of most wolves from September to April (Kelly 1954, Pimlott 1967, Rausch 1968) and generally provide from 60 to over 90 percent of their diet during the summer months (Murie 1944, Pimlott 1967, Clark 1971, Stephenson and Johnson 1972, Stephenson 1978).

2) Wolves require a daily mean of more than 3.2 kg of prey for successful reproduction (Mech 1977). Accounting for waste and loss to scavengers, Kuyt (1972) estimated the above rate amounts to a yearly minimum predation rate of 23 caribou/wolf, if caribou comprised the entire diet of wolves. Field studies suggest the individual wolf predation rate may be slightly higher (Burkholder 1959, Mech 1966).

3) The actual predation rate on caribou is influenced by the availability of other ungulate prey species (Murie 1944, Stephenson and Johnson 1972, Stephenson 1978).

4) Caribou calves are killed more readily than adults during the summer, although the degree to which calves are selected by wolves is highly variable (Murie 1944, Pimlott 1967, Clark 1971, Kuyt 1972, Parker 1972).

5) The selectivity of wolves for caribou calves over adults during the remainder of the year is highly variable, ranging from no selectivity to high selectivity for calves (Clark 1971, Kuyt 1972, Miller 1975, Davis and Valkenburg 1977, Stephenson 1978). Estimates of the percentage of calves among caribou in the yearly diet of wolves has ranged from 20 (Kuyt 1972) to 60 percent (Parker 1972).

6) No concensus has been reached regarding sex-specific selectivity of caribou by wolves (Kelsall 1960, Kuyt 1972, Miller 1975, Davis and Valkenburg 1977, Stephenson 1978); some evidence suggests older adults are preyed upon more heavily than younger adults (Pimlott 1967, Kuyt 1972, Miller 1975).

7. ESTIMATION OF WOLF PREDATION IN THE NELCHINA CARIBOU HERD

The number of caribou killed by wolves in the NCH was calculated by multiplying the estimated number of wolves and the estimated number of caribou killed/wolf/year, similar to the method used by Skoog (1968). Total wolf numbers were estimated from winter surveys in the Nelchina Wolf Study Area as described by Atwell (1964), Skoog (1968), and Rausch (1969a). The wolf population estimates are presented in Table 6. The Nelchina Wolf Study Area approximates the range of the Nelchina herd, although in some years portions of the herd have wintered outside the Study Area, notably to the east (Hemming 1971), while wolves have also undoubtedly moved in and out of the Study Area. McIlroy (1974) has also noted year-to-year variation in the area surveyed as well as variation in the size of the area to which extrapolation is made. The movement patterns of wolves and caribou and the lack of standardization in the wolf surveys among different years affect the estimate of wolf predation. However, lacking more refined data, the winter wolf surveys are useful as an index of relative wolf abundance; they were used by Skoog (1968).

Skoog (1968) summarized data and concluded that caribou comprised approximately half of the ungulates killed by wolves in the Nelchina Area, prior to the herd's precipitous decline. Determining the nature and extent of wolf predation during the decline is difficult.

Table 6. Estimated wolf populations in the Nelchina Basin.

Year	Estimated Population[1]	Source
1953-54	12	Atwell 1964
1954-55	23[2]	--
1955-56	35	Atwell 1964
1956-57	43	Skoog 1968
1957-58	53	Skoog 1968
1958-59	65	Skoog 1968
1959-60	80	Skoog 1968
1960-61	99	Skoog 1968
1961-62	123	Skoog 1968
1962-63	152 (145-160)	Atwell 1964
1963-64	226 ("increasing")[2]	Rausch 1967
1964-65	301[2]	--
1965-66	375 (350-400)	Rausch 1967
1966-67	300	McIlroy 1974
1967-68	300	Bishop and Rausch 1974
1968-69	350[2]	--
1969-70	400[2]	--
1970-71	450 ("peak abundance")[2]	McIlroy 1974
1971-72	350 ("reduced")[2]	McIlroy 1974
1972-73	200 ("reduced")[2,3]	McIlroy 1974
1973-74	200[2,3]	--
1974-75	250[2,3]	--
1975-76	300	R. Stephenson, pers. comm.

[1] Comments from sources in parentheses.

[2] Estimated population determined by author from extrapolation between "known" wolf populations.

[3] Estimate considered conservative (V. Van Ballenberghe, pers. comm.).

Computer simulations of the growth of the NCH from 1972-76 indicate that a decrease in wolf predation had to occur in order for the caribou population to stabilize (discussed in a later section). Since wolf numbers have remained high (Table 6), this implies a shift in the diet of wolves away from caribou. It should be noted that moose reached their peak abundance in the area about 1960, declined slowly to 25,000 to 30,000 in 1965, and then underwent a sharper decline of perhaps 30 to 50 percent by 1972-73 (Bishop and Rausch 1974).

The 1971-72 winter had the heaviest snowfall on record in the Nelchina Area, and overwinter moose mortality was high (Bishop and Rausch 1974). Stephenson and Johnson (1973) reported a high utilization of winter-killed moose by wolves during that winter. A similar high loss of caribou was not documented (Bos 1973); however, reconnaissance of the wintering area was light. Caribou comprised only 8 percent (n = 62) and 17 percent (n = 12) of "wolf-associated" ungulate deaths in the winters of 1971-72 and 1972-73, respectively (Stephenson and Johnson 1973, Stephenson and Sexton 1974), although such findings may have been biased by the area surveyed. Stephenson (1978) found 25 percent caribou in 100 "wolf-associated" ungulate deaths observed from April 1975 to June 1976 in areas occupied by 14 packs in the Nelchina Basin.

Based on the above, I postulate that since the 1971-72 winter, wolf predation has shifted away from caribou, due to the reduced number and restricted range of the NCH (Bos 1974b). I assume caribou comprised 50 percent of the ungulates killed by wolves from 1954-69, 17 percent from 1971 to the present, and 40 and 30 percent in the winters of 1969-70 and 1970-71, respectively. I also assumed, as Skoog (1968) did, that wolves eat 24 ungulates/year/wolf. Skoog (1968) excluded caribou calves from this estimate; however, in view of other caribou predation studies, I have included caribou calves in the estimate of 24 ungulates. Assuming that moose make up most of the remainder of the wolves' diet in the Nelchina area (Burkholder 1959, Stephenson and Johnson 1973, Bishop and Rausch 1974), the yearly kill per wolf is higher than previous estimates from food requirement studies. The February and March wolf surveys, which would tend to underestimate the average yearly wolf population, would help compensate for any overestimation of individual wolf predation rates. The above serves as a rough estimate of wolf predation which can be varied to test different hypotheses.

Skoog (1968) assumed 71 percent of all 1+ caribou killed by wolves in the NCH were males, but this assumption is without supporting field data. Various investigators disagree on the actual occurrence of calves in the composition of caribou eaten or killed by wolves, although the data in many studies indicate a high selectivity for calves. In my simulation, two different cases concerning the composition of wolf-killed caribou were assumed. In the first case, of caribou killed by wolves, 25 percent were calves from 0 to 5 months of age, 25 percent were calves from 5 to 17 months of age, and 50 percent were caribou older than 17 months of age. In the second case, 12.5 percent of the caribou killed by wolves were from 5 to 17 months of age and 75 percent were caribou older than 17 months. Caribou older than 17 months were assumed to be taken according to their proportions in the fall populations. No sex-specific selection for calves was assumed. The two cases outlined above attempt to simulate high and low selectivity for calves by wolves.

8. DEVELOPMENT OF A POPULATION MODEL FOR THE NELCHINA CARIBOU HERD

A simple model was constructed that could incorporate various information, such as caribou population size, composition and recruitment, wolf abundance, and human harvest, into a single system of the population dynamics of the Nelchina Caribou Herd. This model served several functions. First, it generated population statistics, such as hunting mortality, rates of wolf predation, and natural mortality rates. These population statistics are compared over time to detect changes and are used in modeling simulations of the WAH (Chapter 7) and the island herds (Chapter 3). Second, the model is used in "what if" simulations that are valuable for hypothesis testing. Finally the model was useful for revealing discrepancies among various sets of available data and hypotheses. Figure 8 illustrates a flow chart of the model. Various components of the model are discussed in five following sections.

a. Population Size and Composition

Estimates of the population size of the NCH from 1954-72 consist of an estimate of 40,000 animals from a systematic aerial census in February 1955 (Watson and Scott 1956), an estimate of 71,000 ± 11,867 caribou in February 1962 from a stratified-random survey (Siniff and Skoog 1964), and minimum counts of 27,054 2+ females in June 1967 (Hemming and Glenn 1968), and 4,954 1+ females

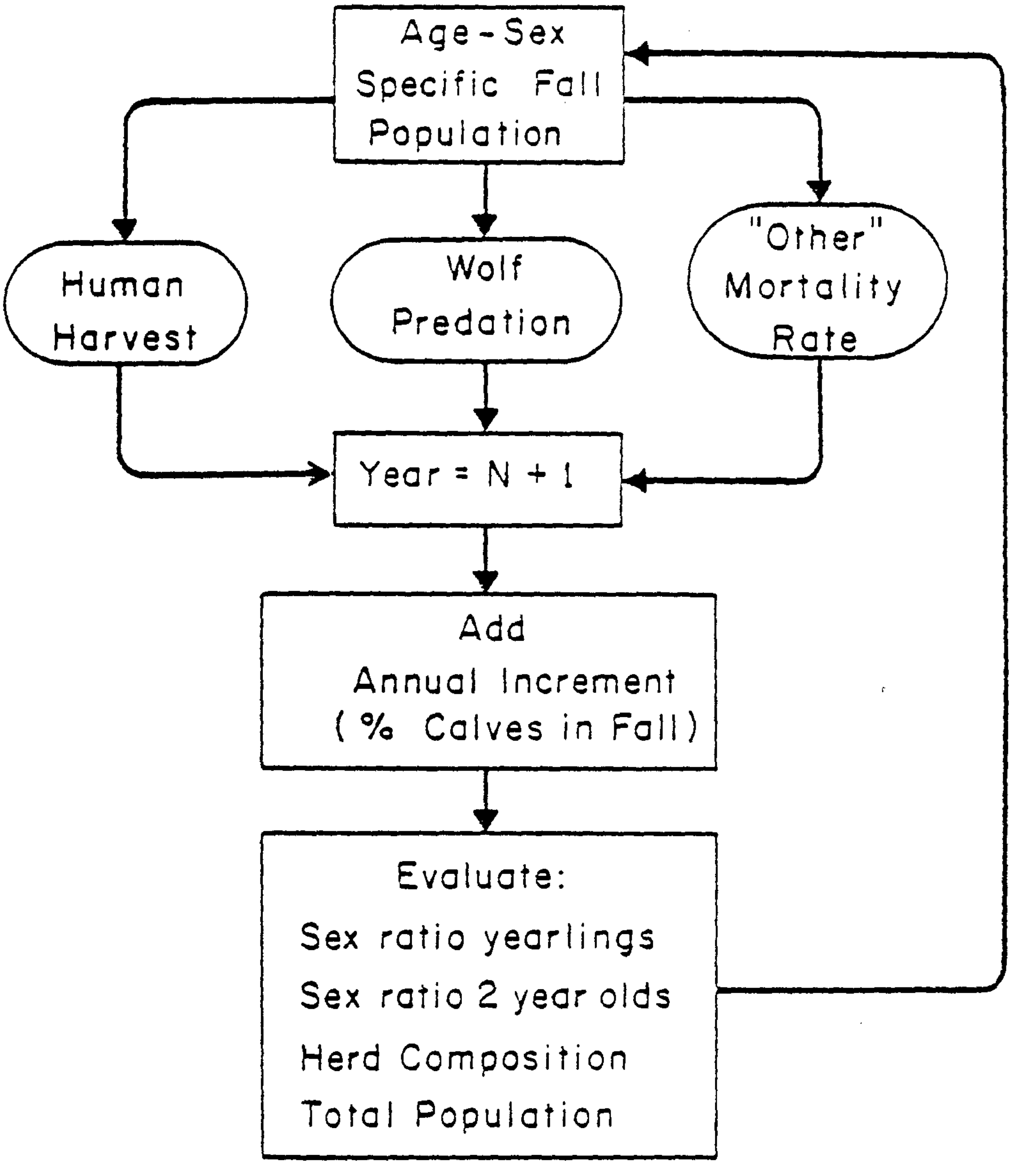

Figure 8. Flow chart of model used to analyze the population dynamics of the Nelchina Caribou Herd (1954-77).

in July 1972 (Bos 1973). An initial starting population for the fall of 1954 of 41,000 was extrapolated from the 1955 census and is well within the precision of the 1955 estimate (Watson and Scott 1956, Skoog 1968).

The "yearly" interval of the model started and ended in early October to correspond to the fall composition data which, as previously discussed, was assumed to best represent the actual herd composition. Table 1 gives the composition data used as starting and evaluating values in the model simulations. Starting percentages of male calves, male yearlings, and male two-year-olds of 54, 55, and 50 percent, respectively, as postulated by Skoog (1968), are used in preliminary model runs. Subsequent development of these statistics is discussed in connection with the actual modeling of the NCH in later sections.

b. Recruitment of Calves

Recruitment rate of calves is calculated using the estimated percentage of calves in the fall population (Table 1). The average value of 20.5 percent calves is generally used in the years in which data was lacking; however, other values were also used to test different hypotheses.

Post-calving composition counts of the NCH were obtained during the month of June in the years 1952, 1953, 1955, 1957, 1958, 1950, 1961, 1967, 1968, and various years in the 1970's (Skoog 1968; Unp. data summarized by G. Bos, ADF&G, Caribou Files, Fairbanks). These data are not used as initial recruitment in the model for two important reasons. First, adult females were either classified with two-year-old males, yearlings, or all animals older than calves in the post-calving composition counts, thereby preventing the direct calculation of post-calving calf/cow ratios. Second, data from the WAH (Table 36 and pp. 160-164) reveals a high degree of year-to-year variability in the proportions of yearlings and adult males in the post-calving composition counts. This same variability was present in the NCH with post-calving percentages of yearlings ranging from 4 percent in 1967 to 12 percent in 1958 and with post-calving percentages of adult males showing similar wide fluctuations (Unp. data summarized by G. Bos, ADF&G, Caribou Files, Fairbanks). Obtaining meaningful calf/adult female ratios from the composition data at calving time is likewise complicated by the tendency of pregnant females to separate from barren females as parturition nears (Skoog 1956, 1968; Kelsall 1957; deVos 1960; Pruitt 1960; Lent 1966a; Parker 1972; and others). Thus calf/adult female ratios obtained on the calving grounds often only reflect the calving female segment rather than the total female segment of the herd.

Based on the above, initial recruitment rates of calves and survival to fall are calculated and analyzed by indirect methods described in a later section of this chapter.

c. Natural Mortality and Wolf Predation

Yearly natural mortality and wolf predation rates are calculated for both sexes of calves (5 to 17 months), yearlings (17 to 29 months), and adults older than 29 months of age. The method of estimating wolf predation was discussed previously; the estimated numbers of calves less than 5 months of age killed by wolves are omitted from the model outlined in Figure 8. Natural mortality rates are used in the model in two ways. One, a given set of natural mortality rates is used to simulate "what if" situations for hypothesis testing. Second, while all other input variables are held constant, the natural mortality rates are manipulated by simple substitution and evaluation until a desired outcome is attained. The evaluating factors used are herd size, herd composition, and sex ratios of yearlings (17 months) and two-year-olds (29 months). In some runs, wolf predation and natural mortality rates are combined. Several important generalizations of the model are discussed in the following paragraphs.

Note that the above described model generates natural mortality rates that apply to all adults of a given sex older than 29 months of age. Various studies of wild *Rangifer* populations have indicated that natural mortality rates are not constant for all sex-specific adult age classes (Banfield 1955; Klein 1968; Skoog 1968; Bergerud

1971b; Miller 1974; E. Reimers, pers. comm.). In particular, most studies suggest a higher mortality rate for older adult animals, although Bergerud (1971b) found that fighting during the rut was the single greatest cause of mortality in adult males with the highest rate in the four- to six-year-old group. A relatively high mortality rate of mature stags from fighting during the rut has also been documented for Spitsbergen reindeer (Gossow 1974). Age-specific mortality rates of adults were not generally calculated in this model for several reasons. First, the wear-age method used to age caribou in the NCH prior to 1969 lumped various age classes together and wasn't consistent from year to year. Second, evidence suggests that present techniques used to age adult caribou to a single age class often result in incorrect ages being assigned to some of the caribou (Doerr, in prep.). Third, two independent models developed in this study suggest that the estimated age structure of collections of adult caribou killed by hunters do not accurately reflect the actual age structure of the adult segment of the herd (pp. 112-116, 207-208). The mortality rates calculated for adults in this model are real in the sense they apply to a single lumped cohort of animals older than 29 months of age. However, based on the above considerations, extrapolation of these mortality rates to single year cohorts should only be done with extreme caution.

An assumption made in this model, for reasons previously discussed, was that wolf predation was nonselective among cohorts older than 17 months of age, with the herd composition at the start of the year (fall) being used to determine the proportion of the various cohorts in that year. As long as the proportion of the cohorts older than 17 months of age remains constant throughout the year, the assumption will be correctly met by the model. As the proportions of the cohorts begin to alter throughout the model's year, some selective error is introduced. Comparing the proportion of the 17 month and older cohorts at the beginning of the model year with the proportion at the end of the model year, indicated that the magnitude of this induced error is inconsequential to the analysis of the population dynamics of the herd, given the resolution of the available data. This is true even when a fairly substantial change in herd composition occurs. More refined calculations of mortality rates integrated over smaller intervals is thwarted by the paucity of available data on the chronology of hunting and natural mortality as well as seasonal wolf abundance.

Only wolf predation is separated from other forms of natural mortality in this analysis; predation by other animals has generally been thought to be relatively minor on caribou in Alaska (Murie 1944, Kelsall 1968, Skoog 1968, and others). Grizzly bear predation on caribou is not analyzed in this study for several reasons. First, bear densities are poorly known in the NCH and the WAH for the time period in which the modeling was done. Second, much of the documented bear predation on caribou has suggested that bears primarily kill newborn calves (Murie 1944, Kelsall 1968, Davis and Valkenburg 1977, Stephenson 1978); such predation would not affect the results of the model illustrated in Figure 8 since calves are entered as a percentage in the fall. Third, the importance of grizzly bear predation on caribou in Alaska remains to be documented. Grizzly bears have been known to subsist in caribou range on a diet of vegetation, rodents, and carrion (Murie 1944, Kelsall 1968), and individual grizzly bears have been observed near the calving grounds over extended periods of time without making a successful ungulate kill even though caribou were present in the area (J. Gebhard, pers. comm.). Much of the recent evidence of the importance of bear predation has involved moose (Stephenson 1978).

d. Mortality Due to Hunting

Human harvest is calculated for the given cohorts using the estimated magnitude and sex ratio of the harvests (Table 3 and Appendix A) and the age composition of samples of animals killed by hunters.

Since the model year ran from early October to early October (to correspond to the fall composition data), it was necessary to adjust the harvest data accordingly. Skoog (1957) estimated that approximately 60 percent of the 1956 harvest occurred before mid-October, while an estimated 65 and 41 percent of the harvest occurred in the months of August and September in 1960 and 1961 respectively (Skoog et al. 1961, Skoog 1963). The availability of caribou along the road systems and the onset of the first deep snows and cold weather influenced the yearly chronology of the harvest, while the increasing use of snowmachines and prolonged hunting seasons encompassing nearly the entire winter in the later years (Table 3) shifted a larger proportion of the harvest toward the winter months. Harvest report tickets in 1969-70, 1970-71, and 1971-72 revealed 27.4, 36.2, and 18.9 percent, respectively, of the total reported harvest in those hunting seasons occurred in August and September, with caribou taken by hunters using snowmobiles as their primary mode of transportation comprising 26, 34, and 37 percent, respectively, of the total reported harvest (Bos 1973, Unp. ADF&G Data, Caribou Files, Fairbanks). Adjusting for the chronology of the harvest is further complicated by the tendency for hunters to take greater percentages of males in August and September than in later months (Skoog et al. 1963). Despite the difficulties mentioned above, the harvests were adjusted to fit the model year using the following assumptions.

1) 80, 60, 40, and 30 percent of the harvests by hunters in 1954-55, 1956-60, 1961-66, and 1967-72 hunting seasons, respectively, occurred between the opening of the season and early October.

2) The sex ratios and age distributions of the harvest prior to early October were assumed to be equal to those after early October.

The harvest data are entered in the model as the estimated total number of animals killed by hunters in each age-sex class, and the hunting mortality rate calculated as the number of animals killed by hunters in an age-sex cohort divided by the number of animals in the cohort at the beginning of the model year. The estimated number of calves killed by hunters before early October is excluded from the hunting mortality rates used in the model.

e. Immigration and Emigration

The population model constructed does not assume any immigration and classifies emigration with natural mortality. Skoog (1968), from a review of historical records, has hypothesized that herds frequently exchange animals. Usually emigration is believed to occur when a growing herd expands its winter range to the point that it overlaps with the winter range of another herd. Exchange of animals is then hypothesized to occur when animals from one herd follow animals from another herd to their calving ground in the spring (Skoog 1968, Hemming 1971). No interchange of animals involving the NCH has been documented during the time interval of this analysis, although emigration has been speculated to have occurred in various years since 1961 (Bos 1975). Implications of immigration and emigration are discussed in conjunction with specific modeling analysis.

9. COMPARISON OF MODEL SIMULATIONS OF THE POPULATION DYNAMICS OF THE NELCHINA CARIBOU HERD (1954-62) WITH A POPULATION ANALYSIS BY SKOOG (1968)

The period 1954-62 was a time of increasing growth for the NCH. Skoog (1968), who was involved with collecting much of the population data, has presented a rather extensive analysis of the population dynamics of the herd during this period. Simulations of the population model are compared with Skoog's analysis to provide greater insight into the reliability of the model.

a. Description of Analysis by Skoog (1968)

Table 7 lists some of the parameters used by Skoog (1968) to project the growth of the NCH from 1955 to 1963. The estimates of total harvest and the sex ratio of the harvests used by Skoog are nearly identical to those used in the present model (Table 7). However, Skoog assumed only 3 percent of the harvest was calves. Bos (1975) has previously discussed why the composition of the harvest samples would produce estimates slightly lower than those of Skoog's for hunter-caused mortality on caribou older than calves. Skoog assumed a natural mortality rate, excluding wolf predation, for 1+ adults of 4 percent, with 71 percent of the mortality comprised of males. This assumption, although poorly documented by field observation, closely fit the population growth of the herd. Skoog did not assess the possible uncertainty of the estimated wolf predation, human harvests, and natural mortality rates in his analysis, however.

Table 7. Comparison of some population variables used by Skoog (1968) with present analysis.

Parameter	Skoog (1968)	Present Analysis
Starting Date	1 May 1955	October 1954
Starting Herd Size	40,000	41,000
Starting Percent Calves (or short yearlings)	18	20.5
Starting 1+ Male:1+ Female	40:60	48:52[1]
Average "observed" fall percentage of calves (1955-62)	20.6	19.6
Total Harvest (1955-61)	31,030	31,000
% Males in Harvest (1955-61)	65.4	67.0
% Calves in Harvest (1955-61)	3.0	7.2
Sex Ratio of Natural Mortality (includes wolf predation)	2.5:1.0	1.9:1.0[2]
1962 Population	69,800 (1 May)	71,500 (1961 Fall)

[1] Calculated from Table 1, assuming 55:45 and 50:50 sex ratios of yearlings and of two-year-olds, respectively, as postulated by Skoog (1968).

[2] Calculated from Runs 1 and 2 (Table 8).

Skoog (1968) estimated recruitment and survival of calves from parturition to 12 months of age using the late winter composition counts and the following assumptions: (1) a 60 percent natality rate for 1+ females at parturition; (2) the 3 April 1960 composition count was not representative of the herd because most of the adult females and calves had already moved toward the calving grounds; (3) the late winter 1959 and 1961 composition counts of 1+ caribou contained 80 percent females; (4) only one portion of the late winter counts in 1957 and 1962 were representative of the herd; (5) the one- and two-year-old males were randomly distributed among the 1+ adult segment surveyed in the late winter counts except as noted in assumptions (2), (3), and (4); and (6) estimated mortality rates of females from parturition to early October, November, and April were 2, 5, and 8 percent, respectively.

Many of the assumptions used by Skoog (1968) concerning the late winter composition counts were not well substantiated by ground observations. The more recent use of the helicopter, with its greater manuverability and ability to land observers practically anywhere, allows observers to sex-determine 1+ adults and thus avoid many of the assumptions Skoog was forced to use. However, Skoog's evaluation of the late winter counts serve to illustrate the high degree of variability in late winter segregation of caribou, both among groups in the same year and between years.

Skoog also generated survival rates of calves from 0 to 5 months and from 5 to 12 months, using the above assumptions as well as additional assumptions concerning the fall composition counts (see Skoog 1968:623-624). To determine if differences between the fall composition data by Skoog (Ibid.) and that given in Table 1 significantly affect the calculated mortality rates for calves, overwinter mortality rates were calculated using the data in Table 1 and the above assumptions of Skoog. These calculations are described in detail in Appendix B. Average overwinter mortality rates calculated in this manner ranged from 6 to 17 percent lower than those calculated by Skoog (1968:624) for the corresponding years. In addition, the percentage of calves in the fall of 1955 (Table 1) compared to the late winter calf/cow ratio given by Skoog (Ibid.) for 1956 indicate survival rates greater than one (Appendix B). Skoog (Ibid.) did not use the 1955 fall composition count in his analysis, although it seems valid to question which count is more accurate. With the exception of the 1955 count, the overwinter mortality rates of calves calculated from the fall data in Table 1 are comparable to those calculated by Skoog (Ibid.).

b. Results of Simulations

Natural mortality rates that produced a close fit to the population and composition data using the population model described previously are shown in Table 8 (Runs 1 and 2). These natural

Table 8. Important input and output values of model runs of the Nelchina Caribou Herd (1954-52).

Model Run:	DEM[1]	1	2	SK1[2]	SK2
INPUT					
Herd Size (1954 Fall)	41,000	41,000	41,000	41,000	41,000
Average % Calves (1955-61)	20.3	20.3	20.3	20.3	21.0
Average Natural[3]/Hunting Mortality Rates					
Females (5 to 17 mo)	--	0.01/0.036	0.04/0.36	0.173/0.026	0.173/0.024
Males (5 to 17 mo)	--	0.01/0.063	-0.02/0.063	0.201/0.051	0.201/0.047
Females (17 to 29 mo)	--	0.00/0.037	-0.03/0.038	0.027/0.046	0.027/0.042
Males (17 to 29 mo)	--	0.06/0.099	0.09/0.096	0.093/0.124	0.093/0.106
Females (29 mo +)	--	0.06/0.043	0.06/0.043	0.027/0.043	0.027/0.042
Males (29 mo +)	--	0.15/0.136	0.15/0.137	0.093/0.140	0.093/0.132
OUTPUT					
Herd Size (1961 Fall)	ca. 73,000 ±11,000	71,567	71,558	63,430	69,170
Herd Composition (1962)					
% yearlings	19.9	18.5	18.5	16.1	15.7
% two-year-olds	16.1	15.4	15.4	13.4	13.0
% 3+ females	32.5	34.2	34.3	38.7	35.8
% 3+ males	14.4	14.7	14.7	14.7	14.5
Average % Males (1955-62)					
Yearlings	55.0	53.3	54.9	52.3	52.3
Two-year-olds	50.0	50.0	49.8	48.3	48.6

---

[1] DEM = Parameters used to evaluate model run. 41,000 = starting population from Watson and Scott (1956) extrapolated to the fall of 1954. 73,000 from Siniff and Skoog (1964) extrapolated to the fall of 1961. Herd composition from Table 1. Percent male yearlings and two-year-olds from Skoog (1968). See text for additional discussion.

Table 8. continued

Model Run:	SK3	SK4	SK5	SK6	SK7
INPUT					
Herd Size (1954 Fall)	41,000	41,000	41,000	41,000	41,000
Average % Calves (1955-61)	22.0	23.0	21.0	21.0	21.0
Average Natural[3]/Hunting Mortality Rates					
Females (5 to 17 mo)	0.173/0.022	0.173/0.020	0.173/0.024	0.193/0.024	0.223/0.023
Males (5 to 17 mo)	0.201/0.044	0.201/0.040	0.201/0.047	0.181/0.047	0.151/0.047
Females (17 to 29 mo)	0.027/0.040	0.027/0.037	0.057/0.042	0.037/0.044	0.007/0.045
Males (17 to 29 mo)	0.093/0.106	0.093/0.099	0.063/0.121	0.093/0.111	0.123/0.108
Females (29 mo +)	0.027/0.041	0.027/0.040	0.027/0.042	0.027/0.042	0.027/0.042
Males (29 mo +)	0.093/0.127	0.093/0.123	0.093/0.129	0.093/0.129	0.093/0.129
OUTPUT					
Herd Size (1961 Fall)	76,357	84,308	69,123	69,209	69,247
Herd Composition (1962)					
% yearlings	16.7	16.7	15.7	15.7	15.8
% two-year-olds	11.0	13.6	13.1	13.0	13.1
% 3+ females	34.0	32.0	34.8	34.8	34.7
% 3+ males	16.3	14.7	15.4	15.5	15.5
Average % Males (1955-62)					
Yearlings	52.3	52.4	52.3	53.6	55.5
Two-year-olds	48.8	49.0	50.3	50.4	50.5

[2] SK = natural mortality modified from Skoog (1968).

[3] Natural mortality rates include wolf predation. Wolf predation is estimated at 1.0 and 1.5 percent for caribou older than 17 months with wolves selective for calves and slightly selective for caribou than 17 months, respectively. The natural mortality rates for calves (5 to 17 months) modified from Skoog (Runs SKn) contain hunter-caused mortality for calves (5 to 12 months old), estimated at ca. 1.5 percent for both male and females calves.

mortality rates were assumed constant from 1954-62. In addition, "what if" simulations were run using natural mortality rates estimated by Skoog (1968). Skoog's calculated mortality rates for calves 5 to 11 months of age are adjusted to 5 to 17 months, in order to fit the model year, using the following equation:

$$M_{5-17} = 1. - [(1. - M_{5-11}) (\sqrt{M_a})] , \qquad (17)$$

where,

M_{5-17} = natural mortality rate of males (or females) 5 to 17 months of age,

M_{5-11} = natural mortality rate of males (or females) 5 to 11 months of age, and

M_a = annual natural survival rate of males (or females) older than 1 year of age estimated by Skoog (Ibid.).

Estimated mortality caused by hunters was subtracted from M_{5-11} when using natural mortality rates generated by Equation 17 in model simulations. The results of simulations of the population growth of the NCH from 1954-62 are shown in Table 8. Wolf predation is included with natural mortality in all these runs. Several important implications of these findings are discussed below.

(1) <u>Population growth of herd</u>

A simulation (Table 8--Run SK1) using Skoog's (1968) estimated mortality rates and an average of 20.3 percent calves in the fall predicted a lower population on October 1961 (63,430 animals) than Skoog calculated for 1 May 1962 (69,800). This results because Skoog's method of calculating recruitment produces slightly higher fall percentages of calves than the actual fall composition counts (Table 1, Skoog 1968:508). Increasing the fall percentage of calves to 21 percent predicts a 1961 population which falls slightly below Skoog's estimate (Table 8--Run SK2), while fall percentages of 22 and 23 (Runs SK3 and SK4) produce higher estimates, the latter slightly exceeding the upper confidence range of the February 1962 estimate.

(2) Herd composition

Natural mortality rates for 5 to 17 month old caribou used in the model that produced a close fit to the demographic data (Table 8--Run 1) are lower than the natural mortality rate of the adult cohorts. This contradicts the findings of other population studies which all indicate that overwinter calf mortality equals or exceeds mortality rates for other age classes, with the possible exception of old females and mature males (Bergerud 1967, 1971b; Kelsall 1968; Skoog 1968; Parker 1972). This suggests the natural mortality rates used in Run 1 are not realistic, which in turn implies that the proportion of yearlings in the 1962 fall data (Table 1) is too high, given the estimated proportion of calves and the projected growth of the herd. Runs SK2 and SK3, which approximate Skoog's (1968) projected growth for the NCH, similarly produce lower fall percentages of yearlings and two-year-olds than estimated in Table 1 and also lower than those estimated by Skoog (1968:488). Both Skoog's analysis and this modeling exercise indicate that calf recruitment and overwinter survival were relatively high and contributed greatly to the herd's increase.

(3) Sex ratio of yearlings and two-year-olds

Sex ratios of caribou in Alaska obtained from composition counts indicate slightly more males than females at birth (Lent 1960, 1961; Lent and Lønø 1962; Skoog 1968). Subsequent sex ratios of yearlings and two-year-olds have been poorly documented, however, due to the lack of composition data as well as lack of knowledge concerning the sex-specific segregational patterns of yearlings and two-year-olds.

In lieu of better data, Skoog estimated a 55:45 sex ratio of yearlings in the NCH, based on the percentage of yearling males per 1+ males in the 1962 counts, the percentage of yearling females in 1,259 1+ females killed by hunters, and an estimated 1+ adult sex ratio of 39.4:60.6. Skoog (1968) postulated the sex ratios went from 55:45 for yearlings to 50:50 for two-year-olds, and thereafter favored females, the latter point well documented by the fall composition data.

To produce these ratios, Skoog's (1968) calculated natural mortality rates for male and female yearlings were adjusted until a sex ratio for two-year-olds of approximately 50:50 was obtained (Table 8--Run SK5). Then Skoog's male and female mortality rates from 5 to 17 months were adjusted to produce a 55:45 sex ratio of yearlings (Table 8--Runs SK6 and SK7). Given the growth of the herd and the selectivity of hunters for male yearlings and two-year-olds, the ratio changes postulated by Skoog require that the natural mortality rate, including wolf predation, of male yearlings was approximately 17 times higher than the mortality rate of female yearlings (Table 8--Run SK7). A simulation obtaining a close fit to the demographic data (Table 8--Run 2) required negative mortality rates for male calves and female yearlings, in order to derive a 55:45 and 50:50 sex ratio of yearlings and two-year-olds. Since the analysis of hunter selectivity (pp. 42-45) showed that hunters select against female yearlings in favor of older females, the yearling sex ratio given by Skoog (1968) should underestimate the number of females as the results of the simulations suggest. Given the above considerations, subsequent model simulations assume 52:48 and 50:50 sex ratios of yearlings and two-year-olds as starting values.

10. MODEL SIMULATION OF THE NELCHINA CARIBOU HERD (1962-69)

Simulations for the period 1962-69 were used to test the hypothesis that (1) increasing wolf predation, (2) increasing hunting kill, and (3) lowered fall recruitment of calves were solely responsible for stopping the herd's growth. The simulations also served as the basis for estimating natural mortality rates, excluding wolf predation, for the various age and sex cohorts in the herd. Three starting fall 1962 populations of 63,000, 73,000, and 82,000 were used in the simulations to reflect the uncertainty in the 1962 population estimate (Siniff and Skoog 1964). The starting 1962 composition for the percentages of yearlings, two-year-olds, and 3+ males was taken from Skoog (1968:488), the percentage of calves was obtained from Table 1, and the percentage of 3+ females was estimated by subtracting the percentages of the above cohorts from 100.

Natural mortality rates estimated by Skoog (1968) from 1954-62 were modified to account for the estimated wolf predation and the estimated mortality caused by hunters on calves from 5 to 12 months of age (Table 8). These rates were then used to represent the natural mortality rates that were "operative" on the herd in "what if the natural mortality rates of the herd didn't change" simulations of the NCH after 1962.

Important input and output values of the simulations are given in Table 9 and implications of the simulations are discussed in the following sections.

a. Growth with High Natural Survival, Good Recruitment, and Increased Wolf Predation and Human Harvest

Results of simulations, using the estimated human harvest, wolf predation with high and low selectivity for calves, relatively high natural mortality rates modified from Skoog (1968), and an average of 21.3 percent calves in the fall are given in Runs SKWN 1-3 and Runs SKWS 1-3 (Table 9). Even with a starting 1962 fall population of only 63,000 animals, the herd size would have continued to increase, in spite of increased total harvests and wolf predation rates.

The effect of doubling the estimated wolf predation is shown in Runs SKWS 4 to 6 (Table 9). A 1962 fall population of 63,000 would have declined to ca. 48,041 by 1969; a population of 73,000 would have remained more or less stationary; and a population of 82,000 would have increased to 115,000 by 1969. Such a wolf predation rate would require an annual population of 600 to 750 wolves or a kill rate of 24 caribou/year/winter wolf or a combination of the two. This rate seems highly excessive given the wolf population estimates shown in Table 6 and the findings of the previously mentioned studies. The above indicates that increasing wolf predation and increasing human harvest of caribou

Table 9. Important input and output values of population simulations of the Nelchina Caribou Herd (1962-69).[1]

Parameters	DEM[2]	SKWS1	SWKS2	SKWS3
INPUT				
Starting Population (1962 fall)	ca. 73,000 (ca. 62-84,000)	63,000	73,000	82,000
Average Mortality Rates wolf/hunting (1962-69)				
Female (5 to 17 mo)	—	0.057/0.032	0.045/0.026	0.039/0.022
Male (5 to 17 mo)	—	0.057/0.037	0.045/0.030	0.039/0.026
Female (17 to 29 mo)	—	0.031/0.050	0.025/0.040	0.021/0.035
Male (17 to 29 mo)	—	0.031/0.094	0.025/0.068	0.021/0.058
Female (29 mo +)	—	0.031/0.051	0.025/0.042	0.021/0.036
Male (29 mo +)	—	0.031/0.214	0.025/0.162	0.021/0.134
Average Natural Mortality				
Female (5 to 17 mo) (1962-66, 1969-71)	—	0.130	same as SKWS1	same as SKWS1
Male (5 to 17 mo) (1962-66, 1969-71)	—	0.160		
Female (17 to 29 mo) (1962-68, 1969-71)	—	0.047		
Male (17 to 29 mo) (1962-68, 1969-71)	—	0.053		
Female (29 mo +) (1962-71)	—	0.017		
Male (29 mo +) (1962-71)	—	0.083		
Female (5 to 17 mo) (1966-67)	—	0.130		
Male (5 to 17 mo) (1966-67)	—	0.160		
Female (5 to 17 mo) (1967-68)	—	0.130		
Male (5 to 17 mo) (1967-68)	—	0.160		
Female (5 to 17 mo) (1968-69)	—	0.130		
Male (5 to 17 mo) (1968-69)	—	0.160		
Female (17 to 29 mo) (1968-69)	—	0.047		
Male (17 to 29 mo) (1968-69)	—	0.053		
Average % Calves (1962-69)	21.3	21.3	21.3	21.3
OUTPUT				
2+ Females (Fall 1967)	min. 27,054[3] (June 1967)	33,002	41,606	49,324
1969 Fall Population	—	88,297	123,511	155,197
1972 Fall Population	—	96,106	150,018	198,510
1969 Fall Composition				
% Yearlings	15.4	18.9	18.7	18.7
% Two-year-olds	9.3	14.2	14.1	14.1
% 3+ females	43.2	34.6	32.6	31.8
% 3+ males	11.0	11.2	13.2	14.4
% Yearlings (1967)	9.7	14.2	14.1	14.1
% Yearlings (1968)	9.5	17.6	17.5	17.5
Average % Males				
Yearlings (1963-69)	52.0	52.8	52.9	52.9
Two-year-olds (1963-69)	50.0	51.5	51.8	51.9

---

[1] Simulations run to evaluate 1962-69 population growth of NCH, but extended to 1972 for demonstrative purposes.

[2] DEM = demographic values used to evaluate model; SK = mortality rates modified from Skoog (1968), WS = wolf predation selective for calves, WN = wolf predation selective for 17 mo + adults. See text for discussion.

[3] From Hemming and Glenn (1968).

Table 9. continued

Parameters	SKWN1	SKWN2	SKWN3	SKWN4
INPUT				
Starting Population (1962 fall)	63,000	73,000	82,000	63,000
Average Mortality Rates				
Wolf/Hunting (1962-69)				
Female (5 to 17 mo)	0.029/0.032	0.023/0.026	0.019/0.022	0.034/0.036
Male (5 to 17 mo)	0.029/0.028	0.023/0.031	0.019/0.029	0.034/0.042
Female (17 to 29 mo)	0.047/0.049	0.037/0.040	0.031/0.034	0.050/0.053
Male (17 to 29 mo)	0.047/0.082	0.037/0.067	0.031/0.056	0.050/0.092
Female (29 mo +)	0.047/0.052	0.037/0.043	0.031/0.037	0.050/0.054
Male (29 mo +)	0.047/0.217	0.037/0.164	0.031/0.135	0.050/0.233
Average Natural Mortality				
Female (5 to 17 mo) (1962-66, 1969-71)	0.135	same as SKWN1	same as SKWN1	same as SKWN1
Male (5 to 17 mo) (1962-66, 1969-71)	0.163			
Female (17 to 29 mo) (1962-68, 1969-71)	0.042			
Male (17 to 29 mo) (1962-68, 1969-71)	0.048			
Female (29 mo +) (1962-71)	0.012			
Male (29 mo +) (1962-71)	0.078			
Female (5 to 17 mo) (1966-67)	0.135			
Male (5 to 17 mo) (1966-67)	0.165			
Female (5 to 17 mo) (1967-68)	0.135			
Male (5 to 17 mo) (1967-68)	0.165			
Female (5 to 17 mo) (1968-69)	0.135			
Male (5 to 17 mo) (1968-69)	0.163			
Female (17 to 29 mo) (1968-69)	0.042			
Male (17 to 29 mo) (1968-69)	0.048			
Average % Calves (1962-69)	21.3	21.3	21.3	20.2
OUTPUT				
2+ Females (Fall 1967)	31,797	40,609	48,501	29,802
1969 Fall Population	84,785	120,780	153,165	70,789
1972 Fall Population	90,095	145,758	195,223	68,569
1969 Fall Composition				
% Yearlings	19.5	19.1	18.9	19.8
% Two-year-olds	14.6	14.4	14.3	14.7
% 3+ female	33.8	32.2	31.4	35.6
% 3+ male	11.0	13.2	14.3	8.9
% Yearlings (1967)	14.6	14.5	14.4	12.1
% Yearlings (1968)	18.1	17.9	17.7	12.2
Average % Males				
Yearlings (1963-69)	52.9	52.9	52.9	52.8
Two-year-olds (1963-69)	51.5	51.8	52.0	51.3

Table 9. continued

Parameters	SKWN5	SKWN6	SKWS4	SKWS5
INPUT				
Starting Population (1962 Fall)	73,000	82,000	63,000	73,000
Average Mortality Rates				
Wolf/Hunting (1962-69)				
Female (5 to 17 mo)	0.027/0.029	0.022/0.025	0.137/0.037	0.104/0.028
Male (5 to 17 mo)	0.027/0.035	0.023/0.030	0.137/0.044	0.104/0.034
Female (17 to 29 mo)	0.040/0.043	0.033/0.037	0.076/0.060	0.057/0.046
Male (17 to 29 mo)	0.040/0.052	0.033/0.063	0.076/0.130	0.057/0.079
Female (29 mo +)	0.040/0.044	0.033/0.038	0.076/0.060	0.057/0.047
Male (29 mo +)	0.040/0.172	0.033/0.125	0.076/0.279	0.057/0.190
Average Natural Mortality				
Female (5 to 17 mo) (1962-66, 1969-71)	same as SKWN1	same as SKWN1	0.130	same as SKWS4
Male (5 to 17 mo) (1962-66, 1969-71)			0.160	
Female (17 to 29 mo) (1962-68, 1969-71)			0.047	
Male (17 to 29 mo) (1962-68, 1969-71)			0.053	
Female (29 mo +) (1962-71)			0.017	
Male (29 mo +) (1962-71)			0.083	
Female (5 to 17 mo) (1966-67)			0.130	
Male (5 to 17 mo) (1966-67)			0.160	
Female (5 to 17 mo) (1967-68)			0.130	
Male (5 to 17 mo) (1967-68)			0.160	
Female (5 to 17 mo) (1968-69)			0.130	
Male (5 to 17 mo) (1968-69)			0.160	
Female (17 to 29 mo) (1968-69)			0.047	
Male (17 to 29 mo) (1968-69)			0.053	
Average % Calves (1962-69)	20.2	20.2	21.3	21.3
OUTPUT				
2+ Females (Fall 1967)	38,184	45,686	25,182	33,942
1969 Fall Population	103,296	132,541	46,041	83,306
1972 Fall Population	118,912	164,168	24,795	78,934
1969 Fall Composition				
% Yearlings	19.3	19.0	18.7	18.6
% Two-year-olds	14.4	14.3	14.1	14.0
% 3+ females	33.6	32.5	39.2	35.0
% 3+ males	11.6	13.0	6.9	11.4
% Yearlings (1967)	11.9	11.9	12.5	13.7
% Yearlings (1968)	17.9	17.6	17.2	17.2
Average % Males				
Yearlings (1963-69)	52.9	52.9	52.6	52.8
Two-year-olds (1963-69)	51.7	51.8	51.0	51.5

Table 9. continued

Parameters	SKWS6	WN1	WN2	WN3
INPUT				
Starting Population (1962 Fall)	82,000	63,000	73,000	73,000
Average Mortality Rates				
Wolf/Hunting (1962-69)				
Female (5 to 17 mo)	0.086/0.024	0.033/0.035	0.025/0.028	0.028/0.030
Male (5 to 17 mo)	0.086/0.029	0.033/0.042	0.025/0.032	0.028/0.036
Female (17 to 29 mo)	0.047/0.039	0.054/0.070	0.042/0.055	0.046/0.064
Male (17 to 29 mo)	0.047/0.066	0.054/0.116	0.042/0.091	0.046/0.080
Female (29 mo +)	0.047/0.040	0.054/0.056	0.042/0.045	0.046/0.047
Male (29 mo +)	0.047/0.151	0.054/0.256	0.042/0.185	0.046/0.209
Average Natural Mortality				
Female (5 to 17 mo) (1962-66, 1969-71)	same as SKWS4	0.200	same as WN1	0.300
Male (5 to 17 mo) (1962-66, 1969-71)		0.230		0.330
Female (17 to 29 mo) (1962-68, 1969-71)		0.030		same as WN1
Male (17 to 29 mo) (1962-68, 1969-71)		0.070		
Female (29 mo +) (1962-71)		0.017		
Male (29 mo +) (1962-71)		0.083		
Female (5 to 17 mo) (1966-67)		0.450		
Male (5 to 17 mo) (1966-67)		0.480		
Female (5 to 17 mo) (1967-68)		0.570		
Male (5 to 17 mo) (1967-68)		0.570		
Female (5 to 17 mo) (1968-69)		0.370		
Male (5 to 17 mo) (1968-69)		0.360		
Female (17 to 29 mo) (1968-69)		0.000		
Male (17 to 29 mo) (1968-69)		0.000		
Average % Calves (1962-69)	21.3	21.3	21.3	21.3
OUTPUT				
2+ Females (Fall 1967)	41,748	29,107	37,449	33,931
1969 Fall Population	115,022	50,112	76,046	63,272
1972 Fall Population	127,538	33,482	71,638	48,055
1969 Fall Composition				
% Yearlings	15.5	15.7	15.3	15.4
% Two-year-olds	14.0	8.1	8.3	8.2
% 3+ females	33.2	46.0	42.4	44.6
% 3+ males	13.2	9.1	12.9	10.6
% Yearlings (1967)	13.7	9.8	9.7	9.7
% Yearlings (1968)	17.3	10.0	9.9	9.9
Average % Males				
Yearlings (1963-69)	52.8	52.9	53.0	52.9
Two-year-olds (1963-69)	51.8	50.1	50.6	50.2

Table 9. continued

Parameters	WN4	WN5	WS1	WN6
INPUT				
Starting Population (1962 Fall)	73,000	73,000	73,000	73,000
Average Mortality Rates				
Wolf/Hunting (1962-69)				
Female (5 to 17 mo)	0.029/0.032	0.031/0.033	0.061/0.033	0.032/0.034
Male (5 to 17 mo)	0.029/0.037	0.031/0.040	0.061/0.039	0.032/0.040
Female (17 to 29 mo)	0.049/0.069	0.053/0.077	0.034/0.073	0.049/0.068
Male (17 to 29 mo)	0.049/0.116	0.053/0.130	0.034/0.123	0.049/0.144
Female (29 mo +)	0.049/0.049	0.053/0.052	0.034/0.051	0.049/0.048
Male (29 mo +)	0.049/0.225	0.053/0.234	0.034/0.224	0.049/0.221
Average Natural Mortality				
Female (5 to 17 mo) (1962-66, 1969-71)	0.350	0.400	0.360	same as WN3
Male (5 to 17 mo) (1962-66, 1969-71)	0.380	0.430	0.390	
Female (17 to 29 mo) (1962-68, 1969-71)	same as WN1	0.030	0.040	
Male (17 to 29 mo) (1962-68, 1969-71)		0.070	0.080	
Female (29 mo +) (1962-71)		0.030	0.040	
Male (29 mo +) (1962-71)		0.070	0.080	
Female (5 to 17 mo) (1966-67)		same as WN1	0.410	
Male (5 to 17 mo) (1966-67)			0.440	
Female (5 to 17 mo) (1967-68)			0.530	
Male (5 to 17 mo) (1967-68)			0.530	
Female (5 to 17 mo) (1968-69)			0.330	
Male (5 to 17 mo) (1968-69)			0.320	
Female (17 to 29 mo) (1968-69)			0.000	
Male (17 to 29 mo) (1968-69)			0.000	
Average % Calves (1962-69)	21.3	21.3	21.3	20.2
OUTPUT				
2+ Females (Fall 1967)	32,252	28,681	29,942	32,137
1969 Fall Population	57,220	47,999	53,635	57,027
1972 Fall Population	37,666	22,590	31,310	39,503
1969 Fall Composition				
% Yearlings	15.5	15.9	15.9	15.5
% Two-year-olds	8.1	8.2	8.5	8.1
% 3+ females	46.0	45.6	44.7	46.1
% 3+ male	9.2	9.2	10.1	9.2
% Yearlings (1967)	9.7	9.8	9.8	9.9
% Yearlings (1968)	9.9	10.0	10.2	9.9
Average % Males				
Yearlings (1963-69)	52.8	52.7	52.7	52.9
Two-year-olds (1963-69)	50.0	49.6	49.8	50.1

Table 3. continued

Parameters	WN7	WN8	WN9
INPUT			
Starting Population (1962 Fall)	73,000	82,000	82,000
Average Mortality Rates			
Wolf/Hunting (1962-69)			
Female (5 to 17 mo)	0.037/0.037	0.026/0.027	0.029/0.030
Male (5 to 17 mo)	0.037/0.044	0.026/0.033	0.029/0.036
Female (17 to 29 mo)	0.055/0.083	0.042/0.063	0.048/0.068
Male (17 to 29 mo)	0.055/0.144	0.042/0.105	0.048/0.144
Female (29 mo +)	0.055/0.054	0.042/0.043	0.048/0.048
Male (29 mo +)	0.055/0.254	0.042/0.167	0.048/0.211
Average Natural Mortality			
Female (5 to 7 mo) (1962-66, 1969-71)	same as WN5	same as WN5	0.400
Male (5 to 7 mo) (1962-66, 1969-71)			0.430
Female (17 to 29 mo) (1962-68, 1969-71)			0.050
Male (17 to 29 mo) (1962-68, 1969-71)			0.090
Female (29 mo +) (1962-71)			0.050
Male (29 mo +) (1962-71)			0.100
Female (5 to 17 mo) (1966-67)			0.400
Male (5 to 17 mo) (1966-67)			0.430
Female (5 to 17 mo) (1967-68)			0.570
Male (5 to 17 mo) (1967-68)			0.530
Female (5 to 17 mo) (1968-69)			0.370
Male (5 to 17 mo) (1968-69)			0.360
Female (17 to 29 mo) (1968-69)			0.050
Male (17 to 29 mo) (1968-69)			0.090
Average % Calves (1962-69)	20.2	21.3	21.3
OUTPUT			
2+ Females (Fall 1967)	27,314	37,160	30,477
1969 Fall Population	41,686	71,089	51,315
1972 Fall Population	14,544	53,594	23,901
1969 Fall Composition			
% Yearlings	16.1	15.3	16.2
% Two-year-olds	8.0	8.3	7.9
% 3+ females	47.8	44.5	44.7
% 3+ males	6.9	10.8	10.0
% Yearlings (1967)	8.6	9.7	10.9
% Yearlings (1968)	10.0	9.9	10.2
Average % Males			
Yearlings (1963-69)	52.6	52.8	52.8
Two-year-olds (1963-69)	49.3	50.1	49.7

in the Nelchina Area could not have stopped the herd's growth given good fall recruitment of calves and high natural survival rates.

b. Growth with High Natural Survival Rates and Lowered Fall Recruitment of Calves in 1963-66

It is unfortunate that no population data were collected during the recent "peak" of the NCH. Bos (1975) and A. T. Bergerud (pers. comm.) have suggested that a decrease in the increment of calves during this time may have been partially responsible for stopping the herd's population growth and starting its decline. Previous analyses in this chapter have demonstrated no observable trend in the fall percentages of calves in the herd (Table 1) as well as poor correlations between the proportion of young cohorts in the harvest collections and the percentages of calves in the fall composition counts (Table 5). However, to simulate the possibility that fall percentages of calves were lower in the years with no data, the following linear regression equation was used to generate the fall percentages of calves (P_i) in the years 1963-66:

$$P_i = 15.6 + (0.389 \times R_{i+2}), \qquad (18)$$

where

R_{i+2} = the ratio of female two-year-olds to all females in the harvest sample in year i + 2, and

i = the year for which the percentage of calves is calculated.

Using values of R derived from harvest data (Unp. ADF&G Data, Caribou Files, Fairbanks), fall calf percentages of 20.9, 17.3, and 17.0 were calculated for the years 1963, 1964, and 1966, respectively. A value of 17.5 was used to represent relatively low fall percentages of calves in 1965 since Equation 18 could not be used to calculate the fall calf percentages in that year due to the lack of a harvest collection in 1967.

The results of simulations using the above values for fall calf percentages, good survival rates, and the estimated wolf predation and human harvests used are shown in Table 9 (Runs SKWN 4 to 6). These simulations suggest that lowered recruitment of calves in 1963-66 would stabilize the growth of NCH, given an initial starting population in 1962 of 63,000, while with starting populations of 73,000 and 82,000, the herd would have continued to increase.

c. Simulations Producing a "Good Fit" to the Composition Data

While some of the above simulations from 1962-69 produced herd levels which stabilized or began to decline, none of the simulations produced herd compositions which closely fit the estimated compositions for the herd given in Table 1. This is primarily because the natural survival rates of calves used in the above simulations are higher than those indicated in the data, as evidenced by the percent of yearlings observed in 1967-69. The above holds true even when the estimated overwinter wolf predation selective for calves was doubled (Table 9--Runs SKWS 4 to 6). The results of various simulations attempting to produce a close fit to both the population and composition data are given in Table 9 (Runs WN1 to WN9 and WS1). These runs suggest that natural mortality rates of calves from 5 to 17 months of age were roughly 0.45, 0.55, and 0.35 for the years 1966-67, 1967-68, and 1968-69, respectively. These values are well above the rates of approximately 0.13 to 0.17 modified from Skoog (1968) for the years 1954-62 suggesting an actual increase in overwinter mortality of calves in 1967-69. Overwinter wolf predation, selective for calves, was estimated at only 6 percent for this cohort (Table 9--Run WS1); thus wolf predation would have to be increased approximately 500 percent to account for this increased mortality rate. Such an increase seems unrealistic. In addition to the high overwinter mortality of calves in the years specified above, increased overwinter mortality rates of calves in the remaining years from 1962-69 of approximately 0.20, 0.40, and 0.40 (the latter two values in conjunction with increased natural mortality rates of caribou older than 17 months) would be required to reduce 1962 fall populations of 63,000, 73,000, and 82,000, respectively, to approximately 50,000 animals by 1969 and to produce a "close fit" to the composition data (Table 9--Runs WN1, WN5, and WN9). The hypothesis that increased natural mortality of calves during the winter played a major role in "checking" the growth of the NCH in the mid-1960's is supported by the following: (1) it can satisfactorily explain observed trends in herd size and composition, (2) late winter calf/adult female ratios were low in 1967 (Bos 1975), (3) the increased proportion of old females among 2+ females in the harvest collections since 1963 suggests lowered recruitment of animals to 2 years of age (Bos 1975), and (4) estimated wolf and human harvest does not appear to have been capable of stopping the herd's growth in the mid-1960's or explaining the estimated composition of the herd (Table 9). Egress of animals from the herd could have reduced its size to the point where it became more susceptible to wolf predation and hunting mortality and thus played a role in the decline of the herd. However, emigration cannot explain the herd composition data (Table 1) unless exceptionally high proportions of calves and/or short yearlings were included in the animals that emigrated.

It should be noted that even with zero natural mortality of 17 to 29 month old caribou in 1968-69, the estimated wolf predation and human harvests are such that the percentage of two-year-olds in 1969 is lower than predicted from the fall composition data (Table 1, Table 9--Runs WN1 to WN9, and WS1), suggesting some error in the composition data. These errors may have arisen because (1) the percentage of two-year-olds in 1969 is estimated from the linear regression equation of 3+ females over time minus the observed percentage of 2+ females; and (2) the 1968 fall composition count may not have fully represented the yearling cohort. Potential errors in the data set make conclusions based on the data seem less valid and reflect present difficulties regarding modeling and understanding caribou population ecology.

11. MODELING THE NELCHINA CARIBOU HERD (1969-72)

From 1969 to 1972 a drastic decline in the NCH occurred. Simulations were run and analyzed for this period in a manner analagous to that described in the previous section. Since population estimates of herd size are only available for the years 1967 and 1972, the results of model simulations from 1962-67 (Table 9) were used to determine starting herd sizes in the fall of 1969. Herd sizes of 48,000, 60,000, and 85,000 are chosen to represent the uncertainty of the 1969 fall population. Natural mortality rates for 1954-62 modified from Skoog (1968), as described previously, were used in simulations to test the hypothesis that good natural survival rates were still operative from 1969-72. Natural mortality rates were also selected to "fit" the composition data (Table 1) and population decline of the herd. The results are presented in Table 10 and discussed in following sections.

a. Population Response of the NCH with Good Natural Survival Rates

Simulations, using the natural mortality rates modified from Skoog (1968), estimated human harvest (Table 3), and wolf predation estimates discussed previously, generated 1972 herd sizes well above the 1972 census estimate of Bos (1973) (Table 10--Runs SKWN 7 to 9). Recall that the wolf predation estimates assume that at this time wolves were killing proportionately less caribou in favor of moose. However, simulations doubling the above estimated wolf predation

Table 10. Important input and output values of population simulations of the Nelchina Caribou Herd (1969-72).

Parameters	DEM[1]	SKWN7	SKWN8	SKWN9	SKWN10[2]
INPUT					
1969 Fall Population	?40,000-90,000?	45,000	60,000	85,000	48,000
Average % Calves (1969-72)	19.5	19.5	19.5	19.5	19.5
1969 Fall Composition					
% Yearlings	15.4	same as DEM	same as DEM	same as DEM	same as DEM
% Two-year-olds	9.3				
% 3+ females	43.2				
% 3+ males	11.0				
Average Mortality Wolf/Hunting (1969-71)					
Female (5 to 17 mo)	--	0.040/0.050	0.030/0.037	0.020/0.023	0.088/0.059
Male (5 to 17 mo)	--	0.040/0.075	0.030/0.055	0.020/0.036	0.088/0.089
Female (17 to 29 mo)	--	0.061/0.089	0.046/0.069	0.031/0.048	0.133/0.095
Male (17 to 29 mo)	--	0.061/0.116	0.046/0.090	0.031/0.061	0.133/0.125
Female (29 mo +)	--	0.061/0.142	0.046/0.108	0.031/0.072	0.133/0.161
Male (29 mo +)	--	0.061/0.529	0.046/0.358	0.031/0.220	0.133/0.675
Average Natural Mortality Rates (1969-71)					
Female (5 to 17 mo)	--	0.135	same as SKWN7	same as SKWN7	same as SKWN7
Male (5 to 17 mo)	--	0.165			
Female (17 to 29 mo)	--	0.042			
Male (17 to 29 mo)	--	0.048			
Female (29 mo +)	--	0.022			
Male (29 mo +)	--	0.078			
OUTPUT					
1972 Fall Population	?8,000-12,000?	33,200	52,134	91,578	22,044
1972 1+ Females	min 4,954 (July)[3]	20,249	31,527	50,072	14,314
1972 Fall Composition					
% Yearlings	15.6	14.8	14.4	14.0	15.6
% Two-year-olds	11.3	17.2	15.5	14.2	19.7
% 3+ females	48.3	45.4	43.1	41.2	47.5
% 3+ males	6.7	4.5	9.0	12.4	- 1.0
Average % Males (1970-72)					
Yearlings	52.0	52.1	52.5	52.7	51.8
Two-year-olds	50.0	51.2	51.5	51.9	50.8

[1] DEM = demographic parameters used to evaluate the model runs. SK = mortality rates modified from Skoog (1968). WN = wolf predation with low selectivity for calves. WS = wolf predation selective for calves. NoWP = wolf predation included in with natural mortality rates used.

[2] Wolf predation estimate is doubled.

[3] From Bos (1973).

Table 10. continued

Parameters	SKWN11[b]	SKWN12[b]	SKWN13[b]	NoWF1	NoWF2
INPUT					
1969 Fall Population	60,000	60,000	85,000	48,000	48,000
Average % Calves (1969-72)	19.5	19.5	19.5	19.5	19.5
1969 Fall Composition					
% Yearlings	|	|		|	
% Two-year-olds	same	same	same	same	same
% 3+ females	as	as	as	as	as
% 3+ males	DEM	DEM	DEM	DEM	DEM
Average Mortality Wolf/Hunting (1969-71)					
Female (5 to 17 mo)	0.064/0.041	0.036/0.100	0.022/0.055	0.000/0.079	0.000/0.073
Male (5 to 17 mo)	0.064/0.061	0.036/0.148	0.022/0.083	0.000/0.117	0.000/0.108
Female (17 to 29 mo)	0.098/0.072	0.055/0.147	0.034/0.098	0.000/0.123	0.050/0.117
Male (17 to 29 mo)	0.098/0.094	0.055/0.197	0.034/0.129	0.000/0.163	0.000/0.153
Female (29 mo +)	0.098/0.117	0.055/0.252	0.034/0.157	0.000/0.213	0.000/0.198
Male (29 mo +)	0.098/0.403	0.055/4.417	0.034/0.612	0.000/0.642	0.000/0.613
Average Natural Mortality Rates (1969-71)					
Female (5 to 17 mo)	|	|	|	0.44	0.42
Male (5 to 17 mo)	same	same	same	0.44	0.41
Female (17 to 29 mo)	as	as	as	0.57	0.54
Male (17 to 29 mo)	SKWN7	SKWN7	SKWN7	0.55	0.52
Female (29 mo +)	|	|	|	0.25	0.22
Male (29 mo +)	|	|	|	-0.02	-0.02
OUTPUT					
1972 Fall Population	40,981	20,752	60,199	8,201	10,842
1972 1+ Females	24,100	17,247	37,505	5,151	6,680
1972 Fall Composition					
% Yearlings	14.7	17.5	14.9	15.6	15.1
% Two-year-olds	16.5	27.0	17.6	12.3	11.9
% 3+ females	43.7	60.5	46.5	48.7	48.2
% 3+ males	7.0	-23.1	3.0	5.3	6.7
Average % Males (1970-72)					
Yearlings	52.3	51.0	51.1	51.7	52.1
Two-year-olds	51.4	49.0	51.0	50.8	51.3

---

[b] Estimated harvest (Table 3) is doubled.

Table 10. continued

Parameters	WS2	WS3	WS4[5]	WS5[5]	WS6[5]
INPUT					
1969 Fall Population	48,000	60,000	48,000	60,000	60,000
Average % Calves (1969-72)	19.5	19.5	19.5	19.5	19.5
1969 Fall Composition					
% Yearlings					
% Two-year-olds	same	same	same	same	same
% 3+ females	as	as	as	as	as
% 3+ males	DEM	DEM	DEM	DEM	DEM
Average Mortality Wolf/Hunting (1969-71)					
Female (5 to 17 mo)	0.101/0.074	0.086/0.067	0.101/0.098	0.085/0.083	0.083/0.081
Male (5 to 17 mo)	0.101/0.110	0.086/0.099	0.101/0.086	0.085/0.073	0.083/0.071
Female (17 to 29 mo)	0.050/0.117	0.044/0.101	0.051/0.129	0.043/0.106	0.042/0.104
Male (17 to 29 mo)	0.050/0.152	0.044/0.132	0.051/0.134	0.043/0.117	0.042/0.115
Female (29 mo +)	0.050/0.201	0.044/0.177	0.051/0.225	0.043/0.191	0.042/0.186
Male (29 mo +)	0.050/0.625	0.044/0.541	0.051/0.609	0.043/0.495	0.042/0.498
Average Natural Mortality Rates (1969-71)					
Female (5 to 17 mo)	0.31	0.38	0.31	0.350	0.340
Male (5 to 17 mo)	0.30	0.37	0.03	0.380	0.370
Female (17 to 29 mo)	0.52	0.57	0.52	0.555	0.545
Male (17 to 29 mo)	0.50	0.57	0.50	0.565	0.555
Female (29 mo +)	0.17	0.25	0.15	0.220	0.210
Male (29 mo +)	-0.08	0.04	0.00	0.09	0.100
OUTPUT					
1972 Fall Population	10,385	9,724	9,792	10,830	11,686
1972 1+ Females	6,427	6,096	6,065	6,650	7,282
1972 Fall Composition					
% Yearlings	15.6	15.8	16.2	15.8	15.8
% Two-year-olds	11.3	10.9	12.2	11.1	11.2
% 3+ females	48.7	49.4	49.6	48.7	49.6
% 3+ males	6.3	5.9	3.9	6.3	5.3
Average % Males (1970-72)					
Yearlings	52.6	52.6	55.3	53.2	53.1
Two-year-olds	51.6	50.0	54.3	50.2	50.3

---

[5] Sex ratio of harvest estimated from harvest collections (Table 2).

Table 10. continued

Parameters	WS7[5,6]	WS8[5,6]
INPUT		
1969 Fall Population	60,000	60,000
Average % Calves (1969-72)	19.5	19.5
1969 Fall Composition		
% Yearlings	same as DEM	same as DEM
% Two-year-olds		
% 3+ females		
% 3+ males		
Average Mortality Wolf/Hunting (1969-71)		
Female (5 to 17 mo)	0.084/0.099	0.085/0.102
Male (5 to 17 mo)	0.084/0.067	0.085/0.089
Female (17 to 29 mo)	0.042/0.128	0.043/0.219
Male (17 to 29 mo)	0.042/0.141	0.043/0.261
Female (29 mo +)	0.042/0.227	0.043/0.217
Male (29 mo +)	0.042/0.581	0.043/0.490
Average Natural Mortality Rates (1969-71)		
Female (5 to 17 mo)	0.25	0.61
Male (5 to 17 mo)	0.38	0.64
Female (17 to 29 mo)	0.53	0.26
Male (17 to 29 mo)	0.53	0.24
Female (29 mo +)	0.19	0.19
Male (29 mo +)	0.01	0.01
OUTPUT		
1972 Fall Population	10,332	10,127
1972 1+ Females	6,360	6,135
1972 Fall Composition		
% Yearlings	15.6	4.1
% Two-year-olds	11.9	7.6
% 3+ females	48.7	54.8
% 3+ males	5.7	15.4
Average % Males (1970-72)		
Yearlings	53.4	54.4
Two-year-olds	50.7	48.6

[6] Estimated magnitude of harvest (Table 3) is multiplied times 1.2.

also produce 1972 herd sizes more than twice the estimate of Bos (1973) (Table 10--Runs SKWN 10 and 11), although the magnitude of total mortality on adult males exceeds the number of adult males present in the herd when a starting 1969 fall population of only 48,000 is used (Run SKWN 10). Likewise, a model run using mortality rates with double the estimated human harvest (Table 3) and a starting population of 60,000 indicates negative numbers of adult males present in 1972, with a total herd size of over 20,000 animals (Table 10--Run SKWN 12). A starting 1969 fall population of 85,000, with good natural survival and double the estimated harvest, would have declined to approximately 60,000 by the fall of 1972, with only 3 percent of the remaining herd comprised of 3+ males (Table 10--Run SKWN 13). The poor agreement among output of the above simulations and estimated herd size and composition strongly indicates that different natural mortality rates were operative on the herd from 1969-72 compared to 1954-62.

b. Population Modeling of the NCH Producing a "Good Fit" to the Data

The natural mortality rates, which include wolf predation and produce a reasonable fit to the demographic data, given a 1969 fall population of 48,000, are listed in Table 10 (Runs NoWP1 and NoWP2). These mortality rates were relatively high for males 17 to 29 months old and for females older than 17 months; however, since the estimated human harvest of 3+ males alone exceeded the number of

3+ males in these runs, the natural mortality rates for the adult male cohorts were negative.

Runs WS2 and WS3 (Table 10) used natural mortality rates that gave a close fit to the demographic data, given that wolf predation is selective for calves. A starting 1969 fall population of 48,000 requires the addition of 1,310 2+ males, while 4,423 17- to 29-month-old males and 12,502 females older than 17 months died of causes other than hunters or wolves from the fall of 1969 to the fall of 1972 (Table 10--Run WS2). Wolf predation with less selectivity for calves would require even greater negative natural mortality rates for males older than 29 months in the simulations in order to closely fit the demographic data. Increasing the 1969 starting population can alleviate the need for negative mortality rates of males older than 29 months, but requires greater natural mortality rates for the other age and sex groups (Table 10--Run WS3).

Possible shortcomings of estimates of the magnitude and sex ratio of hunter-caused mortality on caribou has been discussed previously. The sex ratio from mandible collections of harvested animals (Table 2) from 1969-72 was substituted for the sex ratio from harvest report tickets in estimating the age and sex composition of the hunter harvests in the model. Simulations using the "revised" harvest data still required high natural mortality rates for 17- to 29-month-old males and for females older than 17 months and low natural mortality rates for males older than 29 months (Table 10--

Runs WS4 to WS7) in order to produce a close fit to the herd composition data.

The high mortality of 17 to 29-month-old caribou indicated in these simulations can be explained in part by possible error in the estimated 1972 fall composition of the herd. Lowering the natural mortality rate of 17- to 29-month old caribou implies an increased mortality rate in other age and sex groups for a similar population decline to occur, however. Run WS8 (Table 10) represents a run in which some of the natural mortality of the 17- to 29-month-old cohort shown in Run WS7 is transferred to the 5- to 17-month-old cohort. Such a shift in mortality rates would have produced a herd composition which was considerably different than that observed in the early 1970's (Bos 1973, 1974b, 1975).

c. Reasons for the Decline (1969-72)

The possible roles of emigration, hunting, wolf predation, and increased natural mortality rates in the decline of the NCH are discussed in three sub-sections given below.

(1) Emigration

No egress of animals from the NCH was documented in the late 1960's and early 1970's (Bos 1973, 1974b, 1975), nor have surrounding herds increased in size (J. Davis, pers. comm.). For emigration to explain the high natural mortality rates generated for many age-sex groups (Table 10) rather substantial numbers (13,500 to 22,000+

animals) of certain age-sex groups would have had to have emigrated from the herd (Table 11). Such large, conjectural immigrations of animals into surrounding herds would have substantially increased the size of the adjacent herds, since the largest of those herds had a maximum of only 10,000 animals prior to this time (LeResche 1975). It is doubtful that such an increase in herd size could have gone undetected.

(2) Wolf predation and human harvest

Undoubtedly, wolf predation and human-caused mortality played influential roles in the recent decline of the NCH. The decrease in adult males, for example, appears to be solely the result of excessive and selective hunting pressure. Also, the average hunting mortality rates of females older than 29 months are estimated at 18 to 23 percent (Table 10). Using the input in simulation WS3 (Table 10), the estimated hunting kill of all caribou older than 5 months and of male caribou older than 29 months is approximately 3.5 and 11 times higher than the estimated wolf predation on those same respective cohorts. Since the wolf predation rates in simulation WS3 assume wolves are beginning to switch to more moose and the hunting mortality rates do not take into account wounding loss or illegal kill, both wolf predation and hunting mortality estimates may be conservative. However, in lieu of increased natural mortality rates of the herd, wolf predation and/or hunting harvests are responsible for the rapid decline of the herd only if the estimates of the sex and age-specific numbers of caribou taken by hunters and wolves are considerably in error (Table 11). The need to evaluate the ability of harvest report tickets and harvest collections to accurately reflect the magnitude and age-sex composition of the actual human-caused mortality is indicated here. The level of wolf predation necessary to "account for" increased natural mortality rates observed in certain age and sex groups of animals older than 17 months (Table 11) seems highly unrealistic, given the previously discussed wolf predation studies.

(3) Natural mortality

It should be emphasized that virtually no natural mortality of caribou (excluding wolf predation) was documented during this time period (Bos 1973, 1974b, 1975); however, surveys of wintering areas were apparently not extensive and dead animals on summer range are often difficult to detect (Miller and Broughton 1974, pers. obs.). Much of the increased natural mortality indicated from the results of the population simulations (Table 10) may be due to the inability of harvest statistics to accurately portray the actual harvest. This point seems valid since the natural mortality rates generated by the model (Table 10) suggest virtually no natural mortality of adult males compared to adult females. This is contrary to findings of other *Rangifer* studies (Klein 1968, Skoog 1968, Bergerud 1971b) which all suggest a greater natural mortality rate of adult males. Likewise the high mortality rates on the 17 to 29

Table 11. Some assumptions producing a "reasonable fit" to the population and composition data of the NCH (1969-72).

Assumed Population Decline as In:[1]	Assumed Natural Mortality Rates[2]	Cause of Remaining Natural Mortality in Simulation	Implications
WS2	0.31, 0.30, 0.05, 0.05, 0.05, -0.08	Emigration	Egress of 3,981 males (17 to 29 mo) and 9,639 females (17 mo+) from fall 1969-72.
WS3	0.38, 0.37, 0.05, 0.05, 0.05, 0.04	Emigration	Egress of 5,420 males (17 to 29 mo) and 16,544 females (17 mo+) from fall 1969-72.
WS3	0.38, 0.37, 0.04, 0.04, 0.04, 0.04	Wolf Predation	Increase wolf predation (1969-72) used in model ca. 535 percent, 42 percent of caribou older than 17 mo killed by wolves are 29 mo old or younger, 3 percent are males older than 29 mo of age.
WS3	0.38, 0.37, 0.10, 0.10, 0.10, 0.04	Wolf Predation	Increase wolf predation used in model ca. 424 percent (1969-72), 45 percent of caribou older than 17 mo killed by wolves are 29 mo old or younger, 4 percent are males older than 29 mo of age.

---

[1] Input and output values of run given in Table 10.

[2] Natural mortality rates for females (5 to 17 mo), males (5 to 17 mo), females (17 to 29 mo), males (17 to 29 mo), females (29 mo+), males (29 mo+), respectively.

Table 11. continued

Assumed Population Decline as In:	Assumed Natural Mortality Rates	Cause of Remaining Natural Mortality in Simulation	Implications
WS2	0.31, 0.30, 0.04, 0.04, 0.04, 0.04	Hunting	Increase harvest estimate (Table 3) by 56 percent (1969-72), estimated percentage of males in harvest overestimated with an absolute error of 13, increase estimated number of 17 to 29-mo-old caribou in harvest by 348 percent.
WS3	0.38, 0.37, 0.04, 0.04, 0.04, 0.04	Hunting	Increase harvest estimate by 103 percent, estimated percentage of males in harvest overestimated with absolute error of 15, increase estimated number of 17 to 29-mo-old caribou in harvest by 462 percent.
WS2	0.31, 0.30, 0.10, 0.10, 0.10, 0.04	Hunting	Increase harvest estimate by 38 percent, estimated percentage of males in harvest overestimated by 9, increase estimated number of 17 to 29-mo-old caribou in harvest by 303 percent.
WS3	0.38, 0.37, 0.10, 0.10, 0.10, 0.04	Hunting	Increase harvest estimate by 82 percent, estimated percentage of males in harvest overestimated by 12, increase estimated number of 17 to 29-mo-old caribou in harvest by 410 percent.

month yearling cohort, indicated by the modeling exercise (Table 10), are difficult to explain. Wolves have not been shown to select for this cohort; NCH hunters tend to select against shooting yearlings in favor of larger adults. Dauphiné (1976) has shown that body fat reserves in late winter are lower in yearlings than older caribou in the barren-grounds of Canada; however, the vulnerability of this age class to natural mortality has not been demonstrated in previous population studies (Skoog 1968, Bergerud 1971b, Parker 1972, Gossow 1974). Natural mortality rates on caribou from 5 to 17 months of age used to produce a close fit to the composition data were comparable to those used for a close fit of the data in the time interval 1962-69. Apparently considerably higher average overwinter natural mortality of calves occurred since 1962 than during the increasing phase of the herd from 1954-62, supporting the hypothesis that such mortality played a role in halting the herd's growth as well as aiding in its rapid decline.

12. MODELING THE SURVIVAL OF CALVES TO FALL IN THE NELCHINA CARIBOU HERD (1954-72)

In modeling of the population dynamics of the NCH (1954-72), the fall percentages of calves were used for the recruitment rate of the herd, for reasons previously discussed. This section analyzes the initial productivity and survival of calves to the fall in the NCH, using, in part, the results of the previous modeling.

a. Estimating the Survival of Calves to the Fall

From an examination of 436 female carcasses from 1957 to 1962, Skoog (1968) determined fertility rates in the NCH of 0.00, 0.13, 0.61, and 0.89 for calves, yearlings, two-year-olds, and 3+ females, respectively. By assuming that these fertility rates represent parturition rates for the herd and by estimating the number of females in the herd at parturition, one can obtain an estimate of the number of calves born. By estimating the number of calves present in the fall, one can estimate the survival of calves from parturition to the fall. The number of females present at calving time and the number of calves in the fall are estimated from previous simulations (Tables 8, 9, and 10). Fall populations of female cohorts are converted to calving populations in the subsequent years using the following equation:

$$C_{i+1,j+1} = [F_{i,j} \times (1-M_{i,j})^{7/12}] - (W_{i,j} \times 7/12) - (H_{i,j}) \ , \qquad (19)$$

where

$F_{i,j}$ = number of females of age cohort i in the fall of year j,

$C_{i+1,j+1}$ = number of females of age i+1 at calving time in year j+1,

$M_{i,j}$ = natural mortality rate of females of age i from the fall of year j to the fall of year j+1,

$W_{i,j}$ = estimated wolf predation on the ith cohort from the fall of year j to the fall of year j+1, and

$H_{i,j}$ = estimated hunting kill on the ith cohort from the fall of year j to parturition in year j+1.

Seven months is used as an approximation of the time from fall to parturition (Skoog 1968). In simulations from 1954 to 1962, when wolf populations were relatively low, wolf predation is included with natural mortality.

Survival rates of calves from parturition to fall are only estimated for the years in which fall composition counts are available (Table 1). Since the population and composition estimates of the herd in any 1 year are subject to rather wide uncertainty, survival rates of calves are calculated for a number of simulations described in Tables 8, 9, and 10 and shown in Figure 9. Natural mortality rates were adjusted in all these simulations to "fit" the composition data.

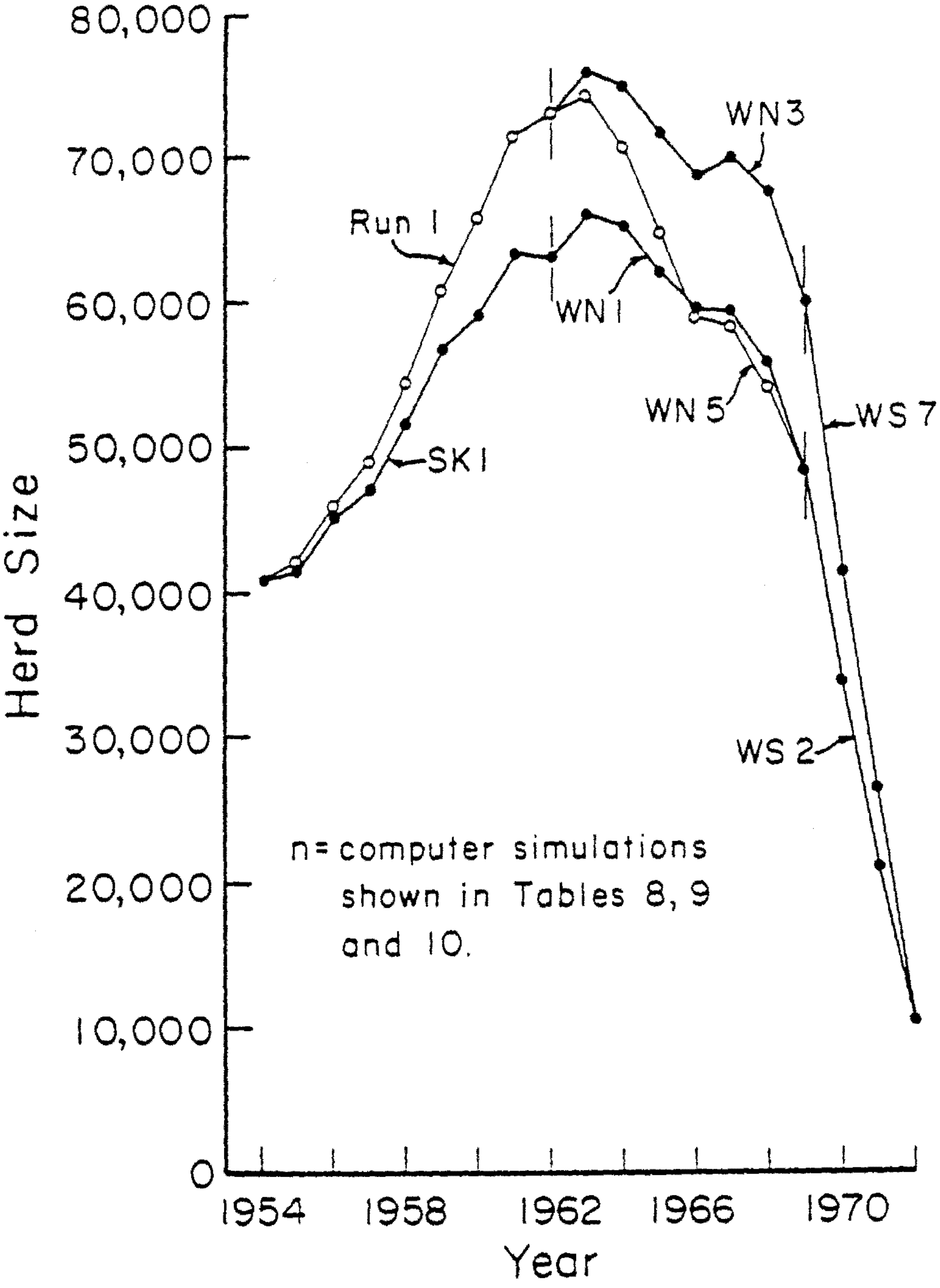

Figure 9. Projected fall herd size of the Nelchina Caribou Herd (1954-72).

b. Analyzing Trends in the Survival of Calves to the Fall

Using Equation 19 and the estimated herd sizes given in Figure 9, survival rates of calves from parturition to fall during the years 1955 through 1959 averaged 0.66, declining by 1972 to approximately 0.28. To determine if the decline in the calculated calf survival to the fall is solely the result of hunting and/or wolf predation, calf survival rates from parturition to fall are calculated taking into account: (1) the estimated hunting mortality on calves less than 5 months of age, (2) three assumed wolf predation rates of 1.5, 3.0, and 4.5 caribou younger than 5 months old/wolf/year, and (3) the above three wolf predation rates with the wolf predation rate declining by 20, 40, and 68 percent in the years 1969-70, 1970-71, and 1971-72, respectively, as described previously in the section on estimating wolf predation on the NCH. First through third degree polynomial equations were calculated for the estimated calf survival rates regressed on time, given the above conditions and the three simulation series. The results are shown in Table 12.

(1) Hunting mortality

Estimated hunting mortality on calves from parturition to 5 months of age ranged from 0.3 to 2.4 percent in the three simulation series. Polynomial equations of the survival rates of calves to the fall, excluding the mortality due to hunting, regressed on time are nearly identical to polynomial regressions

Table 12. Results of polynomial equations of the estimated "survival" of calves to fall regressed on time in the Nelchina Caribou Herd (1954-72).[1]

Simulation Series[2]		r	Degree of Polynomial with "Best Fit"[3]	Sig[4]	"Best Fit" Equation
(SK1-WN1-WS2)	1	-0.763	1st	<0.010	$y_x = 0.780 - 0.0174x$[5]
	2	-0.728	1st	<0.010	$y_x = 0.760 - 0.0142x$
	3	-0.734	1st	<0.010	$y_x = 0.780 - 0.0158x$
	4	-0.668	1st	<0.025	$y_x = 0.738 - 0.0110x$
	5	-0.699	1st	<0.025	$y_x = 0.765 - 0.0141x$
	6	-0.562	--	n.s.[6]	--
	7	-0.657	1st	<0.050	$y_x = 0.755 - 0.0125x$

---

[1] See text for additional discussion.

[2] Simulation series described in text and Figure 9. (1) = estimated calf survival from parturition to fall, (2) = estimated calf survival from parturition to fall excluding a predation rate of 1.5 caribou calves younger than 5 months old/wolf/year, (3) = same as (2) with wolves switching from caribou in 1969-72 (i.e., the wolves' diets are only comprised of 40, 30, and 17 percent caribou in the years 1969-72, 1970-71, and 1971-72, respectively, as described in the text), (4) and (6) = same as (2) with respective wolf predation rates of 3.0 and 4.5 caribou calves younger than 5 months/wolf/year, and (5) and (7) = same as (4) and (6), respectively, with wolves switching from caribou as described for (3).

[3] "Best fit" determined as described in the section on the analysis of trends in the harvest data.

[4] Number of observations = 11.

[5] $x = 0$ in 1950.

[6] Not significant at 0.05.

Table 12. continued

Simulation Series[2]	r	Degree of Polynomial with "Best Fit"[3]	Sig[4]	"Best Fit" Equation
(Run 1-WN5-WS2) 1	-0.817	1st	<0.005	$y_x = 0.795 - 0.0185x$
2	-0.826	1st	<0.005	$y_x = 0.860 - 0.0172x$
3	-0.821	1st	<0.005	$y_x = 0.825 - 0.0187x$
4	-0.797	1st	<0.005	$y_x = 0.800 - 0.0140x$
5	-0.803	1st	<0.005	$y_x = 0.820 - 0.0172x$
6	-0.738	1st	<0.010	$y_x = 0.770 - 0.0108x$
7	-0.776	1st	<0.005	$y_x = 0.810 - 0.0152x$
(Run 1-WN3-WS7) 1	-0.758	1st	<0.010	$y_x = 0.795 - 0.0183x$
2	-0.774	1st	<0.010	$y_x = 0.820 - 0.0174x$
3	-0.773	2nd	<0.005	$y_x = 0.445 + 0.0544x - 0.00273x^2$
4	-0.749	1st	<0.010	$y_x = 0.805 - 0.0147x$
5	-0.753	2nd	<0.005	$y_x = 0.450 + 0.0538x - 0.00266x^2$
6	-0.704	1st	<0.025	$y_x = 0.785 - 0.0119x$
7	-0.730	2nd	<0.025	$y_x = 0.454 + 0.0533x - 0.00259x^2$

of the survival rates with the hunting mortality included and are consequently omitted from Table 12. Unless the hunting mortality on calves younger than 5 months of age is many times greater than estimated, increased hunting is not responsible for the noted decline in the recruitment of calves to the fall.

(2) Wolf predation

Increasing the wolf predation played an important role in reducing the survival of calves to the fall from 1954 to 1972. In the years 1967-69, the estimated mortality rates of calves due to wolves ranged from 1.6 to 2.4 percent, 3.2 to 4.8 percent, and 4.8 to 7.4 percent for the three respective wolf predation rates of 1.5, 3.0, and 4.5 calves (0 to 5 months)/wolf. If wolves continued to prey on caribou calves less than 5 months of age at the same rate per wolf after the fall of 1969 as before, the estimated mortality rates due to wolves in 1972 would have increased to 7.5 to 8.1 percent, 14.9 to 16.3 percent, and 22.4 to 24.4 percent, given the above three respective wolf predation rates and the two simulations used to estimate calf survival to the fall. It was postulated previously that wolves reduced their take of caribou during the winters from 1969-72 as a response to the lower numbers of caribou and their reduced winter range. The calving and summering grounds of the NCH remained relatively fixed during this time, however (Hemming 1971, Bos 1973); therefore, if wolves switched from caribou during the summer months as the herd declined, it should be primarily a response to the lower density of caribou on the summer range.

(3) Natural mortality

All first degree polynomial regression equations of estimated calf survival from birth to 5 months of age and time are significant at the 0.05 level, except for one run (SK1-WN1-WS2:6, Table 12) which is significant at the 0.10 level. The additional significant decline in calf survival, even after wolf predation is considered, indicates that the decreased recruitment rate of calves to the fall was not solely the result of increased wolf predation. The "better fit" obtained by several second degree polynomial equations (Table 12) indicates that natural mortality of calves to the fall may have increased more rapidly during the drastic decline of the herd (1969-72); this possibility is more likely if proportionally fewer caribou calves were killed per wolf during the summer months in those years. The significant linear regression equations (Table 12) suggest a general trend of decreasing natural "survival" of calves to the fall from 1955 to 1972. Because of the lack of data mentioned earlier, it cannot be determined if this decrease in the "survival" rate of calves is primarily due to decreasing conception rates, increasing prenatal and natal mortality rates, or actual increasing mortality rates of calves from parturition to the fall. Clearly, however, reduced recruitment of calves to the fall contributed to the decline of the herd, especially in the later years.

13. ESTIMATING AGE-SPECIFIC SURVIVAL OF 3+ CARIBOU IN THE NELCHINA CARIBOU HERD (1969-71)

Because the wear-age technique, which was used to age-determine most of the harvest collections, classifies various age classes together, age-specific mortality rates could not be calculated in most years in the NCH. In 1969-71, however, the mandible collections of hunter-killed caribou were aged to the year by ADF&G personnel, using a technique developed by C. Lucier (Hemming and Glenn 1969, Bos 1973). The purpose of this section is to calculate age-specific survival rates for 3+ adults in the NCH and then compare mortality rates among the various cohorts.

Age-specific mortality rates are calculated for 1969-71 using the projected 3+ male and 3+ female populations in model simulations WS2 and WS7 (Figure 9) and the age structure of the 1969-71 harvest collections. The mortality rates calculated using the two simulated population declines are averaged and the results are shown in Table 13.

An important assumption on which the above calculations are based is that percentage hunting selectivity in any given year is constant for all age classes 3 years of age or older. Reimers (1975) had indicated that this assumption is probably correct for the female segment of wild reindeer killed by hunters in Norway since females there reach ultimate body size at 2 to 3 years of age.

The hunting mortality rates estimated from the population simulations (Table 10) for 3+ males are 0.38 and 0.55 in 1969-70 and 1970-71, respectively; for 3+ females the rates are 0.12 and 0.18, respectively. If percentage hunting selectivity is constant for all 3+ adults of a given sex in each year, then the estimated age-specific mortality rates should not be less than the above estimated hunting mortality rates. This is clearly not the case with the survival rates calculated for the 3 and 4 year old age classes from 1969-70 (Table 13). The above indicates that age-specific percentage hunting selectivity is not constant for adult males in at least the years 1969-70. Probably hunters tend to select large adult males (Skoog 1968, Bos 1975), thus invalidating the use of the age structure of the male segment of the harvest collection to estimate the age structure of the adult male population. The age-specific mortality rates for 3+ males from 1970-71 are roughly the same among individual age classes (0.72 to 0.88 for 3 to 9 year olds), an indication that hunters became less selective among adult males as the number of adult males substantially decreased.

The mortality rates of the adult male segment of the NCH during 1970-71 resembles the mortality rates of the excessively hunted male segment of the Rondane population (Reimers 1975). The survival of some Nelchina males to their fifth year of life in 1971 compared to none in the Rondane population probably results from the much larger population and range size of the NCH facilitating escape and avoidance

Table 13. Comparison of age-specific mortality rates of adult caribou in the Nelchina Herd (1969-71) with those in a hunted reindeer herd in Norway and a hunted caribou herd in the N.W.T., Canada.

	MALES							
	Nelchina[1]				Rondane[2]		Kaminuriak[3]	
	69-70		70-71		70-71		66-68	
Age	qx	1000 lx[4]	qx	1000 lx	qx	1000 lx	qx	1000 lx
3-4	0.104	1000	0.754	1000	0.75	1000	0.100	1000
4-5	0.188	896	0.719	246	1.00	250	0.424	900
5-6	0.595	728	0.736	69	--	0	0.263	518
6-7	0.738	295	0.881	18	--	--	0.293	382
7-8	0.462	77	0.722	2	--	--	0.495	270
8-9	0.641	42	0.814	1	--	--	0.500	136
9-10	0.731	15	0.499	0	--	--	0.500	68
10-11	-1.690	4	0.666	--	--	--	0.500	34
11-12	1.000	11	0.778	--	--	--	0.429	17
12-13	1.000	0	--	--	--	--	1.000	10
13-14	∞[5]	--	--	--	--	--	--	0
14-15	--	--	1.000	--	--	--	--	--
15-16	--	--	--	--	--	--	--	--
16-17	--	--	∞	--	--	--	--	--
17-18	--	--	--	--	--	--	--	--

[1] Qx values estimated as described in text from harvest collections by ADF&G (Bos 1973, Unp. Data, Caribou Files, Fairbanks) and population simulations WS2 and WS7 (Table 11).

[2] Qx values estimated to the nearest 5 percent from the age composition of hunter-killed animals in 1970 and 1971, given by Reimers (1975: 185), assuming the numbers of 3+ males and 3+ females in the population remained constant from 1970 to 1971.

[3] Taken from Miller (1974), who assumed a stationary population from 1966-68.

[4] 1000 lx values calculated applying the age-specific qx values from 1 year to the next to a single cohort over time.

[5] ∞ indicates animals in the i+1th age class were found in the harvest collections in year n+1, while no animals of age i were found in the harvest collections in year n.

Table 13. continued

	FEMALES							
	Nelchina				Rondane		Kaminuriak	
	69-70		70-71		70-71		66-68	
Age	qx	1000 lx	qx	1000 lx	qx	1000 lx	qx	1000 lx
3-4	0.600	1000	0.586	1000	0.40	1000	0.100	1000
4-5	0.700	400	0.358	414	0.45	600	0.043	900
5-6	0.745	120	0.218	266	0.45	330	0.037	861
6-7	0.231	30	0.406	208	0.05	182	0.073	829
7-8	-0.066	23	0.546	123	1.00	172	0.218	769
8-9	0.452	24	0.492	56	-0.85	(86)[6]	0.336	601
9-10	0.334	13	0.419	28	0.40	159	0.500	399
10-11	0.201	9	0.616	17	1.00	95	0.378	200
11-12	-0.998	7	0.597	6	--	0	0.274	124
12-13	0.112	14	0.340	3	--	--	0.324	90
13-14	0.667	13	0.450	2	--	--	0.360	61
14-15	∞	4	0.780	1	--	--	0.375	39
15-16	∞	0	1.000	0	--	--	0.600	24
16-17	--	--	0.894	--	--	--	1.000	10
17-18	--	--	--	--	--	--	--	0

[6] Estimated assuming a qx of 0.50 from 1970-71 for the 7-8 year old age class.

of hunting pressure. The large hunting mortality rate on adult males is undoubtedly responsible for reducing the average age of 3+ males in the harvest collections from 5.48 in 1969 to 4.45 in 1971.

Survival rates of adult female caribou in the NCH from 1969-71 (Table 13) were considerably lower than survival rates calculated for adult females from "stable" herds in Norway and Canada. The average age of 3+ females in the harvest collections increased from 6.08 in 1969 to 6.74 in 1971. This is suggestive of a lower recruitment rate of the younger age classes of females during the decline similar to that generated by the population model of the herd (Table 10).

Finally it should be noted that the unreal mortality rates shown in Table 13 for the less frequent aged individuals (i.e., negative mortality rates or spontaneous appearance of age cohorts) is probably the result of inaccuracies in the age-determining technique (Doerr, in prep.) as well as sampling variability.

14. RELATIONSHIPS BETWEEN HERD SIZE AND VARIOUS HARVEST STATISTICS IN THE NELCHINA CARIBOU HERD (1954-71)

In the analysis of harvest data earlier in this chapter the relationship between harvest statistics and the size of the herd was ignored. This was necessitated by the scant population data available on the herd. By integrating the various demographic data into a single system, it is possible to generate a number of simulations representing a range of possible population patterns of the herd's growth and decline (Figure 9). Using the yearly herd size from a number of these simulations, it is possible to examine the relationship between the size of the caribou herd and various population parameters. Correlation coefficients between herd size (Figure 9) and 14 harvest parameters are shown in Table 14 and are discussed below.

a. Total Harvest and Herd Size

No correlation was found between estimated herd size and total harvest of the NCH from 1954-71 (Table 14), a period of time when seasons and bag limits are comparable (Table 3). This lack of correlation is important; it should be emphasized that the harvest increased from 1969-71 (Table 3), despite a declining herd. In the NCH, human predation is not density dependent; this predator/prey relationship played a major role in rapidly depressing the herd to a low level. Reduced bag limits and shortened hunting seasons (Table 3)

Table 14. Simple correlation coefficients between estimated fall population in the Nelchina Caribou Herd and various harvest parameters (1954-71).

	Estimated Fall Populations[2]		
Harvest Parameters[1]	SK1-WN1-WS2	Run 1-WN5-WS2	Run 1-WN3-WS7
Total Harvest (18)	-0.040	-0.014	0.110
% males (17)	0.244	0.220	0.080
% calves (16)	0.356	0.447[3]	0.378
% yearlings (16)	0.350	0.373	0.254
% two-year-olds (16)	-0.312	-0.214	-0.359
% yearlings + two-year-olds (16)	0.049	0.135	-0.056
% 3+ females (16)	-0.466[3]	-0.491[3]	-0.304
% 3+ males (16)	0.152	-0.067	0.102
P.H.S. calves (8)	0.334	0.418	0.430
P.H.S. 3+ females (16)	-0.288	-0.343	-0.300
P.H.S. 3+ males (16)	-0.060	-0.150	-0.069
% male calves/calves (16)	-0.520[4]	-0.508[4]	-0.535[4]
% male yearlings/ yearlings (16)	0.187	0.137	0.036
% male two-year-olds/ two-year-olds (16)	0.166	0.137	0.010

[1] Degrees of freedom in parentheses.

[2] Fall populations illustrated in Figure 9.

[3] $P < 0.10$.

[4] $P < 0.05$.

were necessary to decrease the mortality due to hunting. It is uncertain whether large harvests at relatively low herd sizes from 1970-72 were the result of (1) increasing numbers of hunters, (2) increasing hunting effort on the part of the hunters, (3) greater access due to the increasing use of snow machines and other "all-terrain" vehicles (Bos 1973), (4) the particular accessibility of caribou to the hunters in those years, (5) the general vulnerability of caribou in Alaska to hunting, or (6) a combination of some or all of the above. Certainly, however, the role of hunting as a regulatory agent on caribou herds in Alaska is well documented by the decline of the NCH.

b. Harvest Composition and Herd Size

No significant correlations were found between three estimates of herd size and each of ten parameters of the composition of the harvest, except male calves as a percentage of total calves which is negatively correlated with herd size ($P < 0.05$). Paired t-tests of the number of males and the number of female calves in the harvest collections reveal significantly more male than female calves in 1954-60 ($P < 0.05$) and 1968-71 ($P < 0.01$) and more female than male calves in 1963-66 ($P < 0.025$). The male:female calf ratio of 48:53 found in the 1961 and 1962 harvest collections combined is not significantly different from 50:50 ($x^2 = 0.159$, df = 1, $0.05 < P < 0.75$). Significantly more male than female calves ($P < 0.05$) are found in individual harvest collections in the years of 1956 (n = 21), 1960 (n = 56), and 1970 (n = 11). Skoog (1968) has discussed why hunters would be unlikely to selectively take either male or female calves; moreover, there seems to be no reasonable explanation why hunter selectivity for one sex or the other would change over time. Other studies of ungulates (Klein 1970) have indicated that the sex ratio of calves produced by older females tend to favor females, and Baskin (1970) has demonstrated a similar sex ratio among older female reindeer in Siberia. This, however, would not explain the occurrence of more male calves from 1968-71 when large proportions of older age females were present (Bos 1975). Distorted sex ratios of calves also have been found in harvest collections of caribou in the WAH (Table 29). Whether such differences in sex ratios are due to variable neonate sex ratios, differential survival rates from parturition to fall between the sexes, sampling variability, biases in the harvest collections, or actual patterns in hunter-selectivity remains an enigma requiring future study. Obviously, changes in primary or secondary sex ratios could produce profound changes in adult sex ratios or mortality patterns in subsequent years.

The percentage of 3+ females was negatively correlated with herd size ($P < 0.10$) in two of the simulation series. This correlation is probably the result of the increasing proportion of females in the herd as the herd declined, since percentage hunter selectivity for 3+ females showed no significant trends with time.

The percentage of calves in the harvest collections was positively correlated with population size ($P < 0.10$) in one simulation series, but not in the other two.

c. Percentage Hunter Selectivity and Herd Size

No significant correlation was found between herd size and percentage hunter selectivity for calves, 3+ female, or 3+ males (Table 14).

d. Conclusions

Based on the above results, it seems unlikely that any harvest statistic is a good indicator of the size of the herd. The reasons for the occurrence of distorted sex ratios of calves in harvest collections requires further study.

15. TESTING THE ACCURACY OF THE POPULATION CENSUSES OF THE NELCHINA CARIBOU HERD (1972-77) THROUGH THE USE OF SIMULATION MODELING

Since 1970, the NCH has been censused on nearly an annual basis using a technique discussed in detail in Chapter 4. Simulations of growth of the NCH, using the previously described population model, were run in order to determine if yearly population estimates were compatible with projected simulations. In particular, the simulations were run to test the hypothesis that the NCH could increase from 8,000 in 1972 and 1973 (Bos 1973, 1974b) to approximately 14,000 caribou observed in the post-calving census in 1977 (S. Eide, Unp. ADF&G Data), given certain harvest and wolf predation levels.

Fall populations were estimated from counts of post-calving 1+ females assuming a natural survival rate (including wolf predation) of 0.98 for 1+ females from post-calving to fall, adjusting for the estimated hunting mortality on females prior to early October (Table 3), and then extrapolating a fall population from the fall composition ratio of caribou other than 1+ females/ 1+ females. In 1974, the fall population is estimated by simply subtracting the total harvest (Table 3) and a natural mortality of 2 percent from the number of animals counted in the post-calving aggregations since fall composition data is not available for that year.

Hunting mortality on caribou, used in the simulations, is obtained from the estimated magnitude and sex ratio of the harvests (Table 3) multiplied by 1.1 to account for wounding and illegal kill. The age structure of the harvest in 1972 (appendix B) is used to represent the age structure of the harvest in 1973-76, since harvest collections were not made in those years. Natural survival rates, excluding wolf predation, of 96, 93, 96, 95, 98.3, and 95 percent are used for females (5 to 17 months), males (5 to 17 months), females (17 to 29 months), males (17 to 29 months), females (29+ months), and males (29+ months), respectively. Two sets of fall calf recruitment are used for years lacking data (1974-75). One set uses the average observed percentage (19.7 percent) of fall calves in 1972, 1973, and 1976; the other uses a high value of 23.0 percent. Various starting populations in 1972 are used in the simulations along with different conditions of wolf predation. A comparison of some projected populations of the herd with fall census estimates are shown in Figure 10. Wolf predation is assumed to be highly selective for calves in these simulations, although similar results occur in simulations having wolf predation with low selectivity for calves.

Assuming no immigration from outside herds, the results of simulations using the above assumptions and a wolf predation rate of four caribou/year/wolf suggests that the 1972-76 caribou population censuses have accounted for only 60 to 70 percent of the total herd (Figure 10). The above wolf predation rate is felt to be the most realistic; however, even if the wolf predation rate is only one-half the above estimate, it is evident the census method has considerably underestimated the size of the herd in most years. Immigration from outside herds has not been noted since the decline (S. Eide, pers. comm.) and seems highly unlikely since adjacent herds are at very low population sizes (J. Davis, pers. comm.). Bos (1974b) felt the close herd estimates of the NCH in 1972 and 1973 were an indication of the reliability of the census method. Given the simulations discussed above and a detailed discussion of the census technique presented in Chapter 4, it seems very likely that the 1972 and 1973 estimates substantially underestimated the size of the herds in those years. It should be noted that the above assertion is made using simulations that assumed relatively high natural survival rates for caribou compared with findings from other studies (Skoog 1968, Bergerud 1971b, Parker 1972, Miller 1974, pp. 68-103) as well as assuming the 1977 post-calving count of 14,000 caribou contained most of the animals in the herd. If either of the above estimates is incorrect, the recent censuses of the NCH are even greater underestimates of herd size than the above discussion indicates.

Pegau and Hemming (1972), as well as others, have stressed that the present census method produces minimum estimates of herd size. However, the "minimum" estimates do not appear to represent a

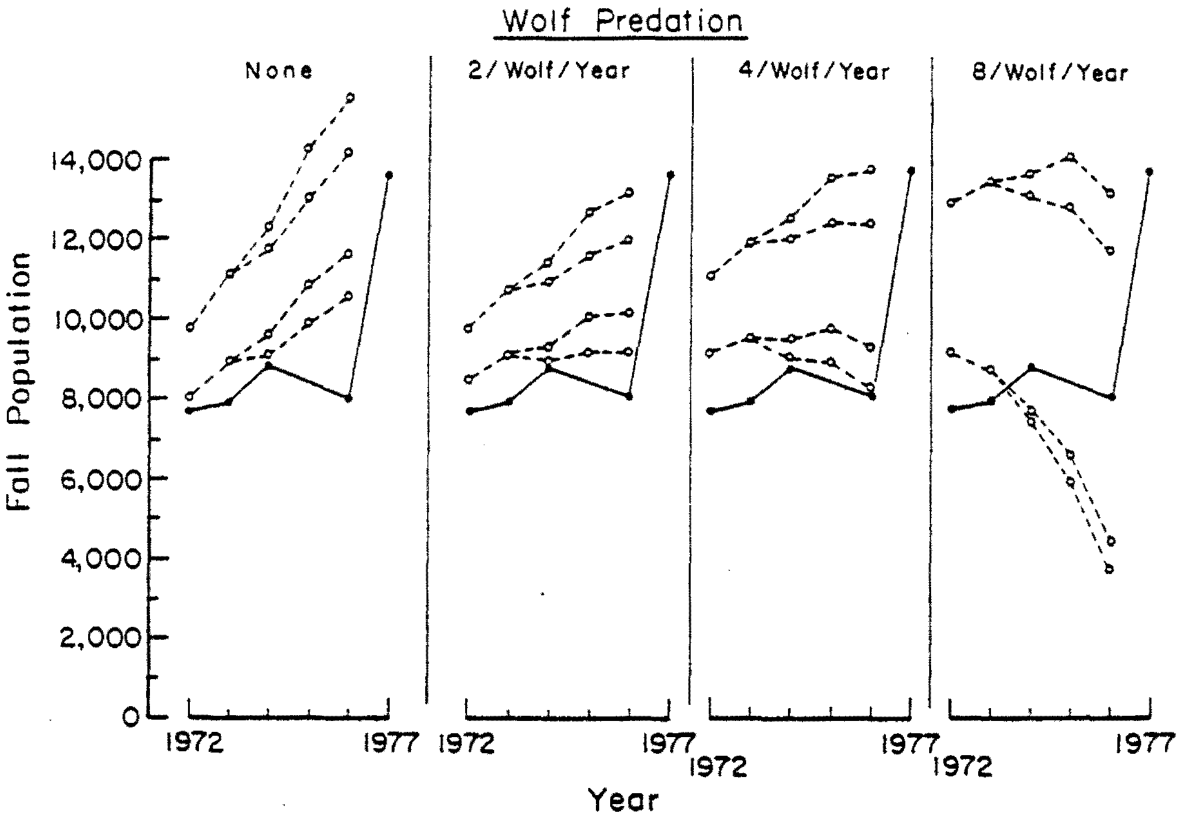

Figure 10. Simulations of the population growth of Nelchina Caribou Herd (1972-76).

— Solid line represents the minimum fall population estimates from census data of the ADF&G.

-- Dashed line represents computer simulations; the forked lines represent simulations using the average observed fall percentages of calves (19.7) and high fall percentages of calves (23.0) in the years with no fall composition data.

consistent portion of the herd from year to year and often seem to be such low estimates that subtle population trends in the herd may be difficult to detect (Figure 10).

Several other observations of the population dynamics of the NCH are worth mentioning here. First, Pegau (1975) has documented that lichens are in poor quality throughout the range of the NCH due to overutilization by caribou and trampling by caribou and moose. The recent indications of high calf recruitment and good natural survival in the NCH lends support to findings that caribou can do well in habitats largely devoid of lichens, possibly by switching to alternate foods such as sedges (Murie 1935, Skoog 1968, Bergerud 1972). Second, unless the herd estimates are considerably more conservative than suspected, it is apparent that the importance of caribou in the overall diet of wolves in the Nelchina Basin has been reduced (Figure 10). Wolf populations have remained relatively high, and caribou appear to be exhibiting good survival rates despite an "unbalanced" caribou/wolf ratio, possibly because wolves have concentrated on alternative prey, such as moose (Stephenson 1978). Finally, the dramatic effect various wolf predation rates are capable of exerting in simulations of the population dynamics of "small" herds (Figure 10) should be noted. Obviously the magnitude of wolf predation, as well as human harvest, is of extreme consequence to the future status of the NCH. The importance of high predator (humans included)/prey ratios to the management of other Alaskan caribou herds is discussed in more detail in Chapters 7 and 8.

C. SUMMARY

From 1954-62, the NCH increased in size by 50 to 100 percent. This increase was largely the result of high overwinter survival of calves (estimated at 85 percent or higher), low annual wolf predation (estimated at less than 2 percent for caribou older than 5 months of age), and high fall calf/adult female ratios compared to other caribou herds (Bergerud 1974a). Hunting mortality rates for 2+ males and 2+ females during this period were estimated at approximately 14 and 4 percent, respectively; natural mortality rates for these cohorts were estimated at between 7 and 14 percent and 1 and 5 percent, respectively.

From 1962-69, the NCH stopped increasing in size and began to decline. The main factors stopping the herd's increase are believed to be an increased overwinter natural mortality rate of calves of 20 to 40 percent, a decreased recruitment of calves to 5 months of age, and increasing wolf and human predation. Wolf predation on caribou older than 5 months of age was estimated at approximately 3 to 6 percent for that time. Hunting mortality rates on 2+ males and 2+ females were estimated at approximately 22 and 5 percent, respectively. The possible role of emigration or increased natural mortality of adults in stopping the herd's increase is uncertain.

From 1969-72, the NCH decreased to less than 20 percent its former size. The demographic data did not satisfactorily account for projected population trends of the herd during this time. Undoubtedly the rapidity of the herd's decline was largely the result of excessive hunting mortality on adults (estimated at approximately 50 and 20 percent annually for 2+ males and 2+ females, respectively), together with decreased recruitment of calves, yearlings, and two-year-olds and increased wolf predation rates estimated at 10 percent for caribou from 5 to 17 months of age and 5 percent annually for caribou older than 17 months of age. The decrease in the recruitment rate of animals to adult age was partially the result of relatively high natural mortality rates of caribou from 5 to 29 months of age during that time. There were also indications of an increased natural mortality rate for adult females during this time, while the estimated human harvest of adult males more than accounted for the estimated number of adult males in the herd.

A decrease in fall calf/adult female ratios from 1954-72 cannot be accounted for solely by increased wolf predation rates. Additional factors, which are believed to be related to the quality of the herd and range, such as decreased conception rates, increased natal and post-natal mortality rates, and decreased natural survival of calves from parturition to fall, are believed to have been operative on the herd.

Since the decline, the incidence of caribou in the diet of wolves in the Nelchina Basin has decreased and caribou appear to be exhibiting high natural survival rates comparable to the increasing phase of the herd from 1954-62. These observations seem to support the hypothesis that the herd would not have declined to such low levels except for hunting mortality.

A comparison of the composition of harvest data with the herd composition revealed that the estimated sex ratio of the harvest and the percentages of males, 3+ females, and yearlings and two-year-olds combined in the harvest mandible collections were useful in detecting trends in herd composition over an extended period of time, given rather liberal harvest seasons and bag limits. Trends in the percentages of calves and 3+ males in the harvest collections were not indicative of actual trends in the herd. The percentages of calves, yearlings, and two-year-olds in the harvest collections were poorly correlated with the initial fall calf percentages of these cohorts in the herd. Percentage hunter selectivity was found to vary for individual age classes of 3+ males in some years, invalidating the use of harvest collections for calculating survival rates of adult males in these years. No harvest parameter was found that could account for over 30 percent of the variability in herd size.

The need to develop techniques to estimate the accuracy and precision of survey data is indicated in the analysis of the NCH.

Population simulation suggested that the present census technique used by ADF&G often underestimates herd size by 30 to 40 percent or more.

The implications of the above findings for the management of caribou are discussed in Chapter 8.

CHAPTER 3. AN EXAMINATION OF THE POPULATION DYNAMICS OF *Rangifer tarandus* FOLLOWING INTRODUCTIONS TO TWO ALASKAN ISLANDS

A. INTRODUCTION

The introductions of reindeer and caribou to various islands in the Aleutian Chain and the Bering Sea have provided ready-made situations for studying the population responses of *Rangifer tarandus* in an isolated environment essentially free of natural predators. The purpose of this chapter is to examine the population dynamics of *Rangifer* following introductions on St. Matthew Island and Adak Island. These two island introductions were chosen because they are two of the best documented in Alaska and provide useful insight into the reliability of demographic data and modeling output. In addition, the growth of these herds, following introduction, serves to illustrate the reproductive potential of *Rangifer tarandus* and the rate of increase the species can obtain in certain environments.

The locations of the islands are shown in Figure 1. The introduction, increase, and subsequent crash of *Rangifer* on St. Matthew Island has been described in detail by Klein (1968). *Rangifer tarandus* were introduced to the island on 20 August 1944 when the U.S. Coast Guard released 24 yearling females and 5 yearling males that had been obtained from reindeer on Nunivak Island. During the subsequent build-up of the herd, the only known harvest on St. Matthew

Island, which has been uninhabited by man since 1944, consisted of 105 animals shot for either sport or scientific purposes from 1957 to 1963.

The introduction of caribou to Adak Island was a joint project of the National Military Establishment and USFWS (Jones 1966). Caribou, obtained from the NCH, were established on Adak Island through the introduction of ten calves (seven females and three males) in 1958 and fourteen calves (nine females and five males) in 1959 (Ibid.). One animal is believed to have died the winter following each introduction; the first newborn calves were produced on the island in 1960 (Ibid.). The Adak Herd's population has been censused nearly annually since then through the cooperative efforts of ADF&G, USFWS, and the National Military Establishment (Burris and McKnight 1973). Subsequent population increases and the initiation of annual hunting seasons beginning in 1964 have been documented by Burris and McKnight (Ibid.), as well as various survey and inventory reports of ADF&G.

B. MODELING THE POPULATION GROWTH OF THE ST. MATTHEW ISLAND REINDEER HERD (SMIH) FOLLOWING INTRODUCTION

The following demographic data available on the St. Matthew Island Herd are from Klein (1968) and are summarized.

1) The herd sizes in the summers of 1957 and 1963 were estimated at 1,350 and 6,000, respectively, based on complete ground surveys of the island in 1957 and complete coverage of the island in 1963 with two U.S. Coast Guard helicopters.

2) The summer calf/2+ female ratios in 1957 were 75/100 and 60/100 in 1963, based on composition counts of 910 and 1,652 animals, respectively.

3) The summer yearling/2+ female ratios were 45/100 in 1957 and 26/100 in 1963, based on composition counts of 218 and 705 animals, respectively.

4) The sex ratio of 1+ animals found from skeletal remains following the nearly complete die-off of the herd from starvation during the winter of 1963-64 was 57 males to 100 females (n = 193). The sex ratio of skeletal remains was essentially equal for all ages until 6 years old when the sex ratio shifted in favor of females.

5) Remains of 31 and 25 reindeer were found in 1957 and 1963, respectively. Animals 5 years old and older predominated, and males outnumbered females two to one, although some sampling biases between sexes may have existed (Klein 1968, pers. comm.).

6) Examination of ovaries collected from female reindeer in 1963 and 1966 suggested that some, but probably not all, females had bred during their first fall.

Modeling was used to calculate the growth of the herd, given certain natural survival and recruitment rates, and to simulate sets of recruitment and survival rates necessary for the herd to grow in the manner observed. The population model developed for the NCH in Chapter 2, with some modifications, was used to model the growth of the SMIH. Because the fall percentage of calves and herd composition on St. Matthew Island were totally unknown in most years, the fall increment of calves was calculated by multiplying the estimated age-specific conception rates times the estimated number of females in the various age cohorts times the estimated survival rate of calves from parturition to fall. Herd population and composition at calving time and at 5 months following calving were calculated in the model. Annual survival rates were adjusted to 5 and 7 month intervals. Human-induced mortality and, obviously, wolf predation were assumed to be zero; the sex ratio at birth was assumed to be 50:50.

Table 15 shows the results of simulations of the population growth of the SMIH given various reproductive and survival rates. Figure 11 illustrates the fall population sizes of some of the simulations over time. Run SMI1 shows the population growth of the herd using natural mortality and conception rates estimated for the increasing

Table 15. Results of simulations of the population growth of the St. Matthew Island Reindeer Herd.[1]

Population	SMI1	SMI2	SMI3	SMI4	SMI5[2]
INPUT					
1944 Population	29	29	29	29	--
Initial Calving Rates					
Yearling female	0.000	0.000	0.130	0.610	0.610
Two-year-old female	0.130	0.130	0.610	0.890	0.890
Three-year-old female	0.610	0.610	0.890	0.890	0.890
4+ female	0.890	0.890	0.890	0.890	0.890
Age-Specific Mortality Rates					
Calves (0 to 5 mo)	0.300	0.300	0.100	0.170	0.200
Female calves (5 to 17 mo)	0.140	0.050	0.100	0.050	0.100
Male calves (5 to 17 mo)	0.140	0.050	0.050	0.050	0.100
Female yearlings (17 to 29 mo)	0.050	0.040	0.040	0.040	0.040
Male yearlings (17 to 29 mo)	0.050	0.040	0.040	0.040	0.040
Female (29 mo +)	0.017	0.017	0.017	0.017	0.017
Male (29 mo +)	0.083	0.050	0.050	0.260	0.240
OUTPUT					
1957 Fall Population	277	338	983	1,354	1,350
1963 Fall Population	701	931	4,080	6,667	5,993
1957 Fall Calf/2+ cow	51.8	51.1	78.6	91.9	74.9
1957 Fall Yearling/2+ cow	38.3	41.1	59.0	66.9	45.2
1957 Fall 2+ Male/2+ cow	68.7	78.7	86.6	56.9	57.1
1963 Fall Calf/2+ male	51.8	51.1	78.6	91.9	87.6
1963 Fall Yearling/2+ female	38.3	41.1	59.0	66.9	61.6
1963 Fall 2+ Male/2+ female	72.3	83.8	89.0	56.9	56.7
1963 % Fall Calves	19.8	18.5	24.1	29.1	28.6
1963 % Fall Yearlings	14.6	14.9	18.1	21.2	20.1
1963 % Fall Two-year-olds	11.9	12.1	13.7	15.6	15.1
1963 % Fall 3+ Females	32.2	30.2	23.8	23.9	25.1
1963 % Fall 3+ Males	21.6	24.3	20.4	10.2	11.0

[1] See text for discussion.

[2] Population simulation from 1957 to 1963 only, using 1957 starting population and composition (listed under important output values), given by Klein (1968).

Table 15. continued

Population	SMI6	SMI7	SMI8
INPUT			
1944 Population	29	29	29
Initial Calving Rates			
Yearling female	0.61	1.00	1.00
Two-year-old female	0.89	1.00	1.00
Three-year-old female	0.89	1.00	1.00
4+ female	0.89	1.00	1.00
Age-Specific Mortality Rates			
Calves (0 to 5 mo)	0.20	0.20	0.00
Female calves (5 to 17 mo)	0.0,0.100[3]	0.00	0.00
Male calves (5 to 17 mo)	0.0,0.100	0.00	0.00
Female yearlings (17 to 29 mo)	0.0,0.040	0.00	0.00
Male yearlings (17 to 29 mo)	0.0,0.040	0.00	0.00
Female (29 mo +)	0.0,0.017	0.00	0.00
Male (29 mo +)	0.0,0.260	0.00	0.00
OUTPUT			
1957 Fall Population	1,366	3,791	9,323
1963 Fall Population	5,955	28,667	106,389
1957 Fall Calf/2+ cow	87.6	112.0	150.0
1957 Fall Yearling/2+ cow	61.6	80.0	100.0
1957 Fall 2+ Male/2+ cow	55.9	98.0	99.1
1963 Fall Calf/2+ male	87.6	112.0	150.0
1963 Fall Yearling/2+ female	61.6	80.0	100.0
1963 Fall 2+ Male/2+ female	54.9	99.9	99.9
1963 % Fall Calves	28.8	28.6	33.3
1963 % Fall Yearlings	20.3	20.4	22.2
1963 % Fall Two-year-olds	15.2	14.6	14.8
1963 % Fall 3+ Females	25.3	18.2	14.8
1963 % Fall 3+ Males	10.5	18.2	14.8

[3] First set of mortality rates are for the period 1944-51; second mortality rates are for the period 1951-63.

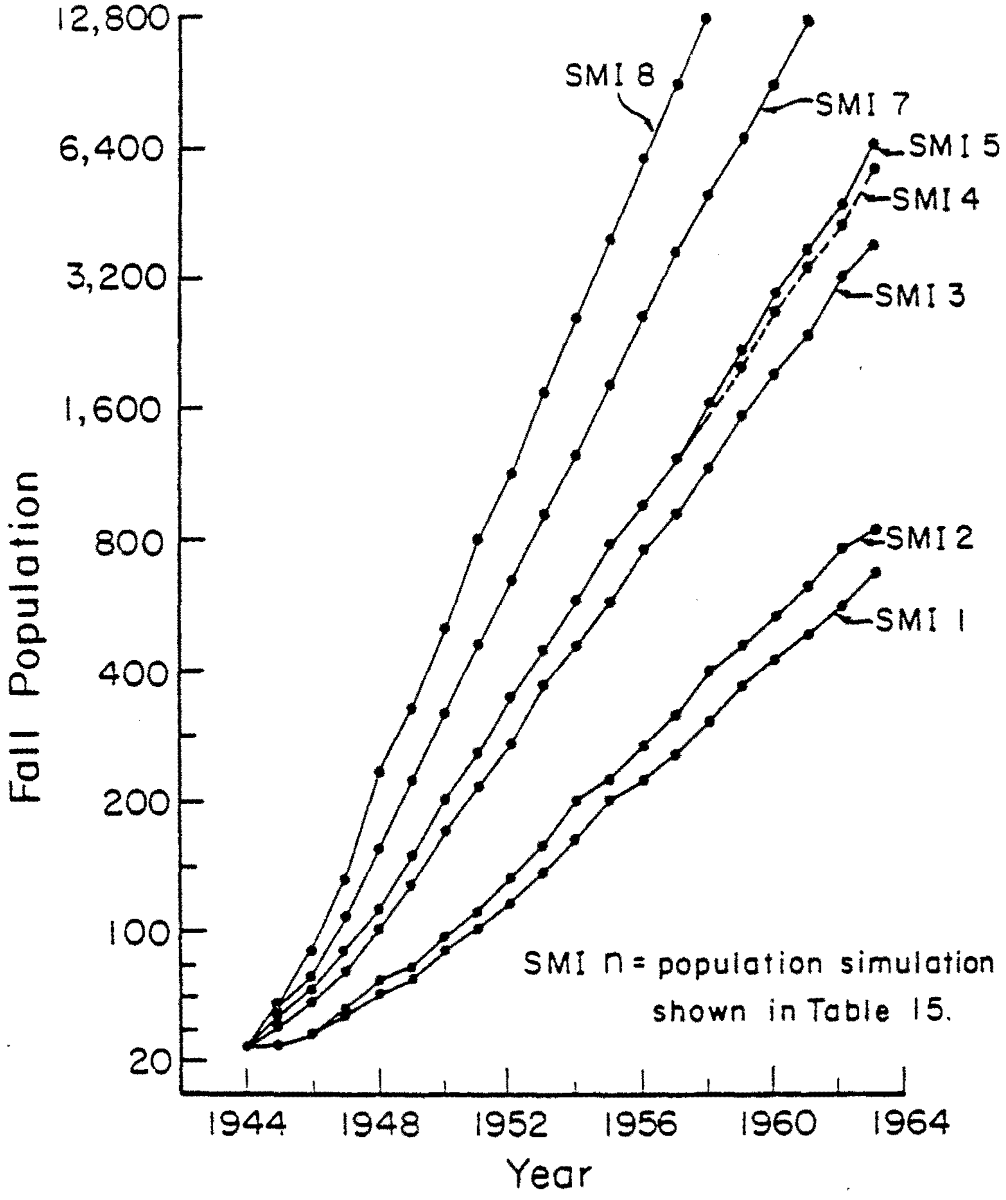

Figure 11. Simulated population growths of the St. Matthew Island reindeer herd. See text and Table 15 for description of input parameters used in simulations.

phase of the NCH, with the mortality rates adjusted to produce equal sex ratios of yearlings and two-year-olds. Run SMI2 simulates the growth of the herd using the same low natural mortality rates used in the 1972-76 computer simulations of the NCH, adjusted to produce equal sex ratios of yearlings and two-year-olds, together with the conception rates and survival rates of calves to 5 months of age used in Run SMI1. Run SMI3 simulates the growth of the herd using a mortality rate of 0.10 for calves from parturition to 5 months and assuming conception rates of 13 and 61 percent for female calves and yearlings, respectively. Run SMI4 demonstrates a set of conception and survival rates that produce a close fit to the observed growth of the herd from 1944-57 and subsequent growth of the herd from 1957-63. Run SMI5 shows conception and survival rates that produce a close fit to the observed population growth of the herd from 1957-63. Another set of conception and survival rates that also closely fit the observed population growth of the herd is presented in Run SMI6. The theoretical maximum increase of an ungulate species producing one young a year per female, with a 50:50 sex ratio at birth and mortality rates of 20 and 0 percent for calves from birth to 5 months of age are given in Runs SMI7 and SMI8, respectively.

The results of these simulations demonstrate the effect of an increased birth rate on the rate of increase of the herd. Even with no hunting mortality or wolf predation, the estimated reproduction and survival rates for the Nelchina Herd during its increasing phase in 1954-62 fall considerably short of producing the rate of increase observed by Klein (1968) for the St. Matthew Island Herd.

C. REEVALUATING THE COMPOSITION OF THE ST. MATTHEW ISLAND REINDEER HERD

It is assumed that the population surveys by Klein (1968) in 1957 and 1963 are reasonably accurate counts of the total population, since the entire island was either covered by foot or with helicopters. Accurate population data, along with the fact that the herd was isolated and subject to neglible predation, increases the validity of using population models to analyze the herd's growth. For example, the yearling/2+ female ratios predicted by Runs SMI4 to SMI6 (Table 15) are considerably higher and probably more representative of the herd during its increase than those observed by Klein (1968), as the following discussion will indicate.

The observed rate of increase (r) of a population from time zero to time t can be calculated from the following standard growth equation:

$$N_t = N_o e^{rt} , \tag{20}$$

where

N_o = population size at time zero, and

N_t = population size at time t.

Solving for r yields the following equation:

$$r = [\ln (N_o/N_t)]/t \quad . \tag{21}$$

Using Equation 21, the observed rates of increase calculated for the St. Matthew Island Herd in 1944-57 and 1957-63 are 0.295 and 0.249, respectively.

The rate of increase of a population can also be calculated from the herd composition and reproduction rate using the following equation derived from Buechner (1960);

$$r = \ln [1 - (P_f)(y)] \quad , \tag{22}$$

where

P_f = proportion of females in the adult population (here adult is defined to include all animals 12 months of age and older), and

y = average recruitment rate of young per female.

This equation assumes that no mortality occurs in the population other than that specified in y.

Three assumptions are necessary to use Equation 22 to calculate r values from the population data given by Klein (1968). First, the 2+ male to 2+ female sex ratio of 57:100 found after the die-off held for the herd in 1957 and 1963. Second, an equal sex ratio of yearlings existed in 1957 and 1963. Third, the yearling/2+ female ratios found by Klein (1968) in 1957 and 1963 represent y values as defined in Equation 22. The resulting rate of increase values calculated from the 1957 and 1963 composition data are 0.241 and 0.149, respectively, which is below the observed rate of increase of the herd from 1944-57 and 1957-63.

Table 16 illustrates r values calculated from Equation 22 for various P_f and y values. To obtain the rates of increase observed from 1944-57 and 1957-63, using the proportion of adult females described above and Equation 22, y values of 56.6/100 and 45.8/100 yearlings/2+ females, respectively, are necessary. If y equalled 0.45, Equation 22 predicts P_f values from 1944-57 and 1957-63 of 0.76 and 0.63, respectively. If y was 0.26, the predicted values of P_f required to match the observed rates of increase in the SMIH frim 1944-57 and 1957-63 are greater than one (1.32 and 1.09, respectively). In Runs SMI4 to SMI6 (Table 15), the mortality rate of 2+ males had to be approximately 14 to 15 times greater than the mortality rate of 2+ females in order to produce a 57:100 sex ratio of 2+ adults. The mortality rates of 2+ adults used in those three runs predict that approximately 8.8 times as many 2+ males died than did 2+ females during the period 1955-63. As indicated previously, Klein (1968) found only twice as many 2+ males compared to 2+ females among the remains of dead animals in 1957 and 1963. An assumption of the above runs is an equal sex ratio of yearlings.

Table 16. Rate of increase (r) values for various proportions of adult females (P_f) and reproductive rates (y).[1]

	P_f					
y	0.4	0.5	0.6	0.7	0.8	0.9
0.1	0.039	0.049	0.058	0.068	0.077	0.086
0.2	0.077	0.095	0.113	0.131	0.148	0.166
0.3	0.113	0.140	0.166	0.191	0.215	0.239
0.4	0.148	0.182	0.215	0.247	0.278	0.307
0.5	0.182	0.223	0.262	0.300	0.336	0.372
0.6	0.215	0.262	0.307	0.351	0.392	0.432
0.7	0.247	0.300	0.351	0.399	0.445	0.489
0.8	0.278	0.336	0.392	0.445	0.495	0.542
0.9	0.307	0.372	0.432	0.489	0.542	0.593

[1] Calculated from Equation 22, derived from Buechner (1960). See text for discussion.

This assumption has supportive data (Ibid.). Finally, it should be noted that any mortality occurring on the adult segment from time zero to time t requires higher P_f and/or y values to maintain the same rate of increase calculated by Equation 22. It seems unlikely that the lower r values calculated from the composition data, compared to the observed r values, are the result of underestimating the proportion of adult females, given the unequal mortality rates for 2+ males and 2+ females necessary to obtain the observed P_f values. More likely, the yearling/2+ female ratios observed by Klein (Ibid.) are not representative of the yearling/2+ female ratios found throughout the herd's increase. Klein's (Ibid.) yearling/2+ female ratios may be representative for the years observed; however, yearling/2+ females ratios undoubtedly were higher both before 1957 and during the time interval from 1957-63, or the herd could not have reached the population level it obtained. Runs SMI4 to SMI6 (Table 15) predict yearling/100 2+ female ratios ranging from 62 to 67 for the mid-1950's to 1963 in the St. Matthew Island Herd.

Klein (1968) demonstrated that the growth of the St. Matthew Island Herd could be explained by the observed summer percentages of calves; as shown above, however, his observed yearling/2+ female ratios indicated a lower growth potential. Many authors, such as Buechner (1960) and Bergerud (1971a), have calculated the rate of increase of a herd from Equation 22 using a y value based on observed summer or fall ratio of young to adult females. The use of this y value is only valid in estimating r if no mortality occurs on the young prior to productive age. In northern latitudes, where overwinter mortality of calves may be high or in environments with substantial predation, the use of accurate yearling/adult female ratios in estimating the recruitment rate of a herd, is far superior to calf/adult female ratios.

Discrepancies among the various population data, such as estimated sex ratio of yearlings, estimated sex ratio of adults, and estimated sex ratios of animals dying prior to the winter of 1963-64, are revealed here. This serves to illustrate the degree of difficulty involved with collecting representative demographic data, even on small, isolated herds. These difficulties become considerably magnified as herd size and range increases and factors affecting the herd's growth (i.e., immigration, predators) become more complex.

D. EXAMINING THE RATE OF INCREASE OF THE ADAK ISLAND CARIBOU HERD FOLLOWING INTRODUCTION

A reasonable assertion is that the high reproductive capability of the St. Matthew Island Reindeer Herd is not representative of the potential reproductive capabilities of wild caribou populations. Domestic reindeer have been selectively bred and, under good range conditions, have been known to conceive when calves (Klein 1968, Skuncke 1969). Reimers (1972, pers. comm.) has found that wild reindeer herds in Norway also breed as calves when on ranges with high forage production, but again such findings may not pertain to wild North American caribou. The purpose of this section is to determine if the age-specific conception rates found for the Nelchina Herd at the time of introduction remained constant in the very favorable Adak Island environment.

Population estimates of the herd, total harvest, and observations of natural mortality were derived from the following sources: Lentfer (1965), Jones (1966), McGowan (1966), Glenn (1967), Hemming and Glenn (1968), McKnight (1970, 1971, 1974, 1975, 1976), Pegau and Hemming (1972), Burris and McKnight (1973), and G. Bos (pers. comm.). The annual rate of increase of the herd was calculated from Equation 21. Human harvest and observed natural mortality from year zero to year t were added to N_t in Equation 21 so that r represents the rate of increase of the herd with no mortality, except undetected natural mortality. Figure 12 illustrates the r values calculated for the AIH from 1959-75. Some of the higher and lower values shown in Figure 12 may result from missing a portion of the herd in certain years in the aerial censuses. The censuses were probably quite accurate though, and repeated surveys of the herd during the same years have agreed closely. Because unobserved natural mortality of some animals undoubtedly occurred, the r values shown in Figure 12 are considered minimum values.

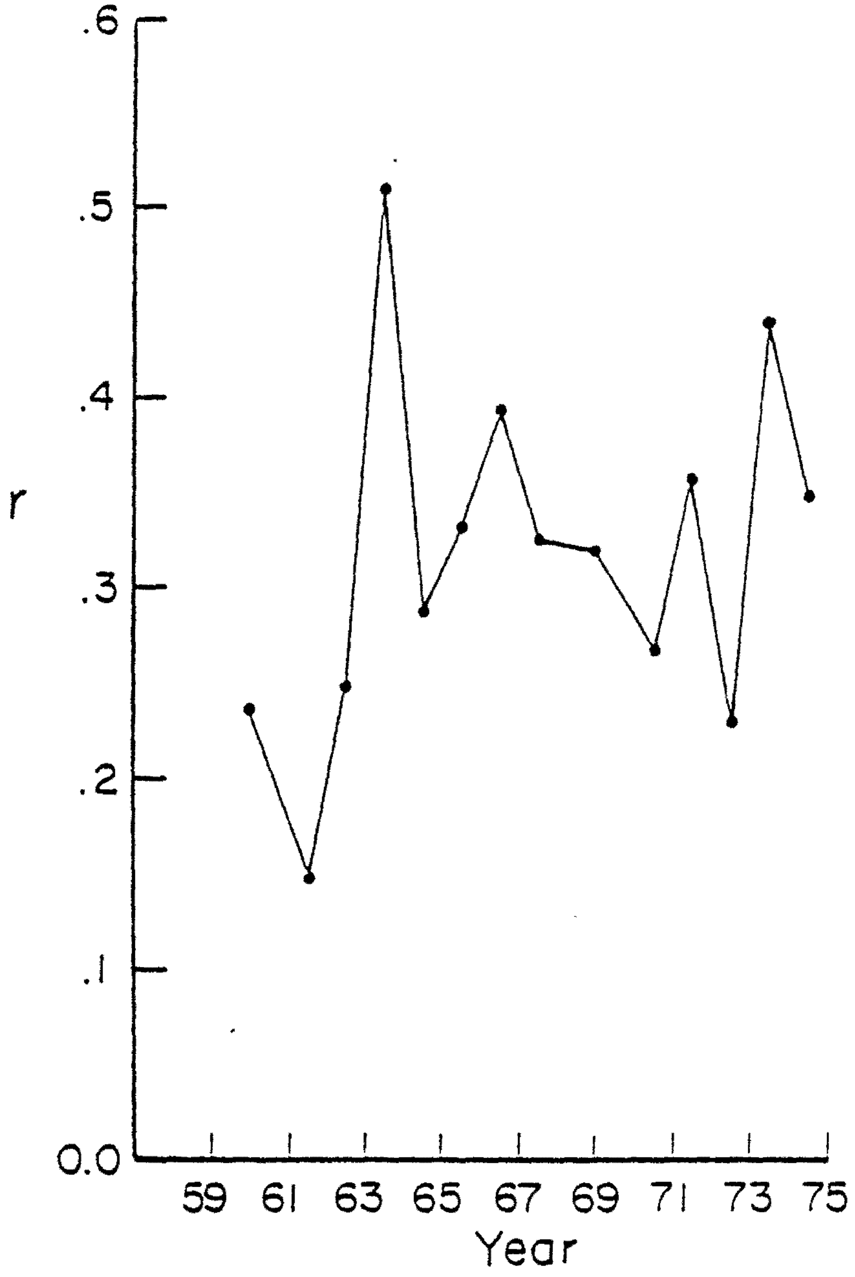

Figure 12. Estimated yearly exponential rates of increase of the Adak Island Caribou Herd from 1959-75 assuming no observed mortality.

The sex ratio of caribou killed by hunters and dying of natural causes in the AIH is approximately 50:50. Assuming an equal sex ratio at birth, this mortality ratio suggests approximately a 50:50 sex ratio in the adult breeding population. From Figure 12, it can be seen that average minimum rate of increase of the AIH since 1964 has exceeded 0.34. If the proportion of females in the adult population (P_f) equals 0.50, then y (the ratio of young surviving to adult age per adult female) must equal 0.7 for r to equal 0.3 and 0.9 for r to equal 0.372 (Table 16). Because the age-structure of the harvest is unknown, the female age structure of the population is difficult to estimate. The yearly increases of the population prior to the fall hunting season (estimated from the population after the hunting season and the known mortality) suggests the average summer percentage of calves from 1961-74 was 27.6 ($S = 6.7$) with a range from 16.3 to 40.2. Using the female composition in the fall of 1963 generated in Run SKI5 (Table 15) to represent the female age structure of a rapidly expanding *Rangifer* herd, the average number of young per female (y in Equation 22), given the rates of conception observed by Skoog (1968) for the NCH, would equal only 0.496, even if all calves born survived to reproductive age. If P_f equals 0.5 or 0.6, a y value of 0.496 would produce an r considerably below that observed in most years in the AIH (Table 16, Figure 12). Moreover, if hunters on Adak are more selective for older females than for calf, yearling, and two-year-old females, as was the case in the NCH, the proportion of younger females in the female segment of the herd would be higher than that generated in Run SMI5. All the above suggests that the conception rates of younger females are substantially higher on Akak Island than have been found in the NCH; given the rate of increase observed for the herd (Figure 12), the conception rates are probably as high or possibly higher than those found on St. Matthew Island.

Limited autopsy data from caribou killed by hunters on Adak Island has supported this idea of higher conception rates. One lactating 15-month-old female was shot in 1966 and most yearling females are suspected of breeding based on an unspecified number of 2+ females examined (Glenn 1967). Like the St. Matthew Island reindeer examined by Klein (1968), the Adak caribou have shown increased body weights compared to their "parent" herd, and an adult bull with an estimated live weight of 318 kilograms was killed in 1968 (Burris and McKnight 1973).

E. SUMMARY

Studies of the population dynamics of *Rangifer tarandus* following introductions to Alaskan islands are extremely valuable in demonstrating the increased reproductive capability of the species in a "favorable" environment. The rates of increase shown by the AIH strongly indicates that the age-specific conception rates of *Rangifer tarandus granti* are not genetically rigid, but, like domestic reindeer or wild reindeer in Norway, are strongly molded by the environment. The increased reproductive rates shown in some *Rangifer* herds results from higher proportions of the younger age classes of females successfully breeding; the rates of increase of the AIH suggests that over 90 percent of all females, including calves, may have bred in some years. Caughley and Birch (1971) have suggested that the population response of newly established populations is the best method of approximating the intrinsic rate of increase (r_m) of the population, an extremely valuable statistic for determining the "cropping rate" most likely to maintain a stable population at a reduced density. Klein's (1968) study on St. Matthew's Island and the work by ADF&G and others on Adak Island are useful in estimating r_m for *Rangifer* in certain environments. As stressed by Caughley and Birch (1971), r_m is not species-specific, but pertains only to the particular environment in which it was measured. Unfortunately, only very limited data is available on the reproductive potential, especially age-specific conception rates, of most mainland Alaskan caribou herds over extended periods of time.

CHAPTER 4. EVALUATION OF THE 1976 WESTERN ARCTIC HERD POPULATION AND COMPOSITION SURVEYS

A. INTRODUCTION

Data analysis and modeling in the previous two chapters indicated that accurate and precise estimates of herd size are of paramount importance to understanding the population dynamics of the herd. The purpose of this chapter is to critically evaluate the 1976 Western Arctic Herd population and composition estimate. It should be noted that the 1976 surveys were conducted during a time of wide speculation concerning the status and welfare of what had formerly been North America's largest caribou herd.

B. BRIEF DESCRIPTION OF THE HERD'S RANGE

The WAH occupies a range of approximately 362,700 km^2 in the extreme northwestern portion of Alaska (Hemming 1971). The bulk of the herd's range is contained in Game Management Units (GMU) 23 (119,430 km^2), 24 (72,383 km^2), and 26A (125,225 km^2), with the remainder of the range occupying portions of GMU 21, 22, 25, and 26B (Figure 13) (size of GMU from Stephenson 1976). GMU 26A and 26B comprise the portion of the WAH's range that is drained by river systems flowing northward into the Arctic Ocean. These areas contain the traditional calving grounds and summer range of the herd.

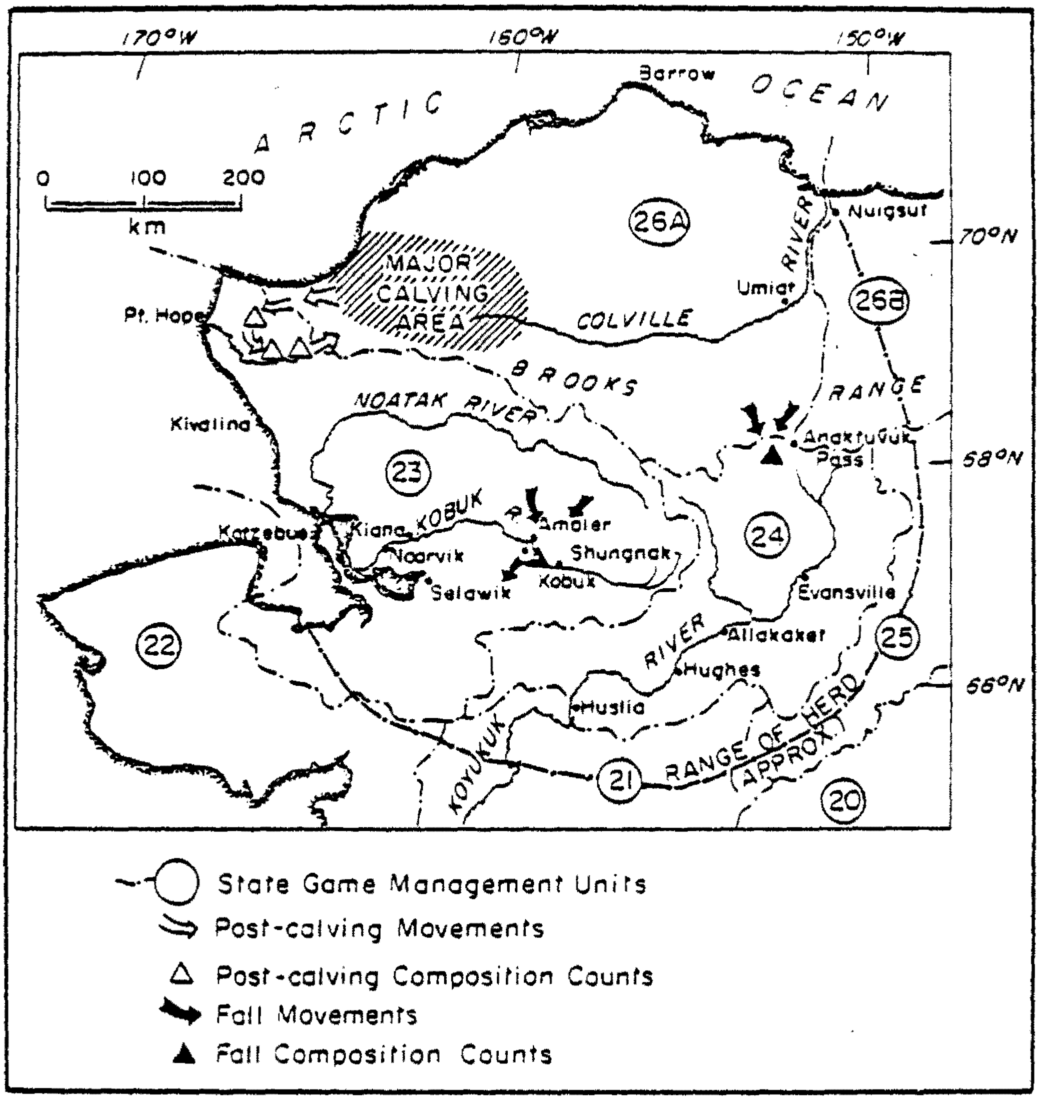

Figure 13. Approximate locations of important 1976 calving concentrations and movements, villages, game management units, and study areas in the Western Arctic Herd's range.

South of the Brooks Range lies important wintering areas of the WAH, largely drained by three major rivers: the Noatak, the Kobuk, and the Koyukuk. Major plant communities and physiographic provinces in the WAH's range have been described by Spetzman (1959), Lent (1966b), and Young (1974). Lent (1966b) discusses the significance of these communities to the seasonal movements of the caribou.

C. DESCRIPTION OF CENSUS TECHNIQUES

Ceribou herds have traditionally been censused using aerial strip transects or random plots of wintering or calving grounds (Bergerud 1963; Siniff and Skoog 1964; Parker 1972, 1975), as well as total counts of calving and post-calving aggregations. The tendency of a major portion of the adult females to concentrate, along with varying proportions of the remainder of the herd, on traditional calving and post-calving areas (Lent 1966b, Kelsall 1968, Skoog 1968, Parker 1972) has lead to the development of a censusing technique referred to as a direct aerial-count extrapolation census. This technique was originally developed by ADF&G personnel during the mid-1960's on the NCH (Hemming and Glenn 1968) and has since been widely used for inventorying caribou herds throughout Alaska, including the WAH in 1970 (Pegau and Hemming 1972), 1975 (Davis et al. 1976), and 1976.

The census technique requires three separate counts to determine population size:

1) A complete count, either ocular or with aerial photography, of all animals older than calves in the post-calving aggregation;
2) A ground-based composition count of these same animals to determine the proportion of adult females; and
3) A representative fall composition count of the entire herd during the rut to determine the proportion of various age and sex cohorts.

The estimate of the fall population is derived from the following equation:

$$FP = N_a \times P_f \times S_f \times (1 + R) \quad , \tag{23}$$

where

FP = estimated fall population;

N_a = number of animals in the post-calving aggregation;

P_f = proportion of adult females in post-calving aggregation;

S_f = survival of adult females from the time of the post-calving counts until the fall; and

R = ratio of caribou other than adult females to adult females in the fall.

Adult females have either been classified as females 12 months and older (Bos 1973, 1974b) or 24 months and older (Pegau and Hemming 1972).

Four basic assumptions have generally been made in estimating fall populations. The assumptions are:

1) Most or all of the adult females in the herd are counted in the post-calving census;
2) Mortality of adult females from post-calving to fall is zero;
3) The adult females are randomly distributed throughout the post-calving aggregations; and
4) The age and sex cohorts are randomly distributed throughout the herd during the fall.

Assumptions three and four have been necessitated by the classification methods employed. Animals have not been randomly selected for classification. Often only one portion of the herd has been classified or, if more than one group has been classified, the variance among the groups has not been analyzed and the data lumped without regard to group size. Because it is generally recognized that some adult females in the herd are missing in the census of the post-calving aggregations, the final estimate is usually considered a minimum estimate of the number of animals in the herd. One may obtain an estimate of the post-calving population, and avoid assumption two, by assuming no differential mortality between adult females and other caribou older than calves from post-calving until fall. The post-calving estimate is then derived from the following equation:

$$PP = N_a \times P_f \times (1 + R_1 + R_2) \quad , \tag{24}$$

where

PP = estimated post-calving population;

R_1 = post-calving ratio of calves to adult females;

R_2 = fall ratio of animals older than calves minus adult females to adult females; and

N_a and P_f = defined as in Equation 23.

1. DESCRIPTION OF 1976 SURVEY EFFORT

During June and July 1976, approximately 400 hours and 66,600 air kilometers were flown in the WAH's range by ADF&G personnel and various cooperators (J. Davis, pers. comm.). The herd's distribution, movements, and calving chronology were determined from these aerial surveys. I collected data on the chronology of calving, the herd's movements, and the composition of peripheral calving groups by ground observations in the vicinity of Noluck Lake (68°47'N × 160°00'W) from 31 May to 11 June and in the vicinity of Driftwood Creek (68°54'N × 161°10'W) from 11 to 27 June.

The population size of the post-calving aggregation was determined from ocular counts during intensive aerial surveys from 25 to 27 June by ADF&G. A follow-up photo census was performed during 17 to 18 July. Portions of the herd's range adjacent to the areas photographed were flown to locate additional animals at that time.

A Bell Jet Ranger 206B helicopter, provided by ADF&G, transported observers to the sites of the composition counts during post-calving and in the fall. Composition counts were made from the ground, using a variable spotting scope (15-60x) and a hand counter to tabulate the results. Animals were separated into calves, yearlings, 2+ females, and 2+ males. The presence or absence of the dark vulva patch was generally used to distinguish the adult sexes, although large antlers of mature males or distended udders of adult females were also used. Yearlings were usually separated from 2+ adults on the basis of their smaller body size and relatively shorter muzzle. Other characteristics that were used to distinguish the sex and age cohorts have been described previously by Skoog (1956, 1968), Bergerud (1961, 1964b), Lent (1965), and Parker (1972).

I assisted in composition counts of post-calving aggregations from 27 June to 2 July and composition counts of fall groups from 16 to 18 October. Reconnaissance flights by ADF&G personnel recorded caribou movements, numbers, and distribution during the fall and winter of 1976-77 (J. Davis, Unp. ADF&G Data).

The population and composition data were evaluated using standard statistical procedures, some of which are given in Appendix C.

2. EVALUATION OF THE 1976 POST-CALVING COUNT

The 1976 calving and post-calving movements followed traditional patterns described by Lent (1966b). The first calf was observed at Noluck Lake on 5 June and was estimated to be one day old based on descriptions by Lent (1966a). The majority of calving is believed to have occurred between then and 15 June (J. Davis, pers. comm.). Following calving the cow-calf segment of the herd began moving westward, reaching the headwater regions of the Pitmegea and Ipewik Rivers by 26 June (Figure 13).

Error may have arisen in the occular post-calving census taken during this westward movement because (1) large groups were estimated rather than counted, (2) cow-calf groups may have been missed in the areas surveyed, and (3) 2+ adult females may have occurred outside the area surveyed.

Watson and Scott (1956) felt that observers missed approximately 20 percent of the caribou counted during the winter aerial censuses in the NCH, with the error of estimation increasing with group size. Bergerud (1963) similarly estimated that an average of 20 percent of the caribou were overlooked during winter surveys in Labrador and

Newfoundland, with extreme values ranging from 10 to 40 percent. Controlled experiments have indicated that substantial portions of ungulates are missed in aerial surveys (LeResche and Rausch 1974, Caughley 1974, Caughley et al. 1976). The percentage missed is influenced by a host of factors such as topography of the terrain, lighting conditions, the type of aircraft used, the experience of the observers, snow conditions, and the group size of the animals. Parker (1972) estimated overlooking 20 percent of the caribou in a population survey in early summer on open tundra with approximately 30 percent snow cover. Parker's study most closely approaches the viewing conditions of the 1976 post-calving counts except that the area surveyed in this study was virtually snow-free.

The number of adult females that occurred outside the area surveyed is impossible to estimate, using the present census technique. Fixed-wing composition counts of 472 caribou south of the Delong Mountains on 11 June revealed 2 (0.4 percent) newborn calves, 2 (0.4 percent) adult females, 50 (10.6 percent) 2+ males, 180 (38.1 percent) yearlings, and 238 (50.4 percent) unclassified caribou older than calves, most of which were yearlings and adult males (J. Davis, Unp. ADF&G Data). Caribou calving over 300 km from the traditional calving grounds in the WAH has been documented by Lent (1966b), McGowan (1966), and Glenn (1967). It is possible that such groups were missed in the 1976 census.

Modeling the NCH (1972-76) suggests that the census technique substantially underestimates the size of the herd in most years (pp. 122-126). To simulate various probabilities of missing adult females, three different estimates of the mean and variance of the number of caribou in the 1976 post-calving aggregations are hypothesized. The "most probable minimum" is assumed to be 29,000 animals older than calves. This 29,000 is hypothesized to represent 60, 80, and 90 percent of three respective "most probably maximum" number of caribou older than calves. The hypothesized means are assumed to be halfway between 29,000 and the "most probable maximums," and the hypothesized variances of the means are assumed to be one-fourth the square of the differences between the "most probable maximums" and 29,000. The three respective means and variances attempt to simulate relatively low, moderate, and high probabilities of missing adult females and are used in estimating the population variance in subsequent sections.

3. POST-CALVING COMPOSITION COUNTS

The 1976 post-calving composition counts are given in Table 17. A 6 × 2 χ^2 contingency table revealed highly significant differences in the percentages of 2+ females of animals older than calves among the six post-calving groups classified ($\chi^2 = 95.80$, df = 5, $P < 0.005$). This clearly violates assumption three of Equations 23 and 24, and points out the necessity of randomizing the composition sample. Furthermore, since the composition of the post-calving aggregation is

Table 17. Composition counts of the 1976 Western Arctic Herd post-calving concentrations.

Date	Location[1]	Calves	Yearlings	2+ Females	2+ Males	Total	Observer(s)
June 27-29	1	1,141 (31.2)[2]	309 (8.5)	2,090 (57.2)	114 (3.1)	3,654	J. Doerr
June 29	2	276 (30.2)	52 (5.7)	561 (61.3)	26 (2.8)	915	J. Doerr
June 30	2	264 (33.8)	17 (2.2)	496 (63.6)	3 (0.4)	780	J. Doerr
June 30	2	152 (37.9)	9 (2.2)	234 (58.4)	6 (1.5)	401	J. Doerr
July 1-2	2	85 (32.7)	18 (6.9)	143 (55.0)	14 (5.4)	260	J. Doerr
July 2	3	743 (30.9)	188 (7.8)	1,343 (55.9)	128 (5.3)	2,402	J. Davis/ J. Doerr
TOTAL		2,661	593	4,867	291	8,412	

[1] Location 1: Headwaters of Ipewik River (68°35'N x 164°30'W); Location 2: Headwaters of Kukpuk River (68°27'N x 164°17'W); Location 3: West side of Mount Kelly (68°29'N x 163°40'W). See Figure 13.

[2] Percentage in parentheses.

in a state of flux, due to yearlings and adult males entering the aggregation, it is essential to conduct the composition counts at the same time as the aerial census of the post-calving grounds and to ensure than all animals counted in the post-calving census have an equal probability of being classified in the composition counts. The photo-census estimate of approximately 61,000, including calves, in July could not be used to estimate the population using Equations 23 and 24 since no composition data were obtained due to limited access (J. Davis, pers. comm.).

Randomization of the composition sample was ignored in this census and only the larger groups of animals counted on the post-calving grounds. Composition counts of peripheral groups on the calving grounds from 31 May to 26 June indicate a high portion of yearlings and barren females (ACWRU Unp. Data). If these smaller groups had not completely mingled with the main calving segment of the herd at the time of the post-calving composition counts, the percentage of adult females estimated from the post-calving composition counts (Table 17) may be biased. Additional problems that arose in the post-calving composition counts are that only a small portion of each group of caribou were classified in the composition counts and the aerial reconnaissance was not sufficient to ensure that ground observers did not sample some of the same animals at the three different locations (Table 17). By assuming equal sampling intensity among all groups with no replicate sampling, an estimate of the percentage of adult females of animals older than calves in the post-calving aggregation is generated, together with an estimate of the variance, using formulas given in Appendix C. The results are shown in Table 22.

4. FALL COMPOSITION COUNTS

Problems associated with conducting composition counts at post-calving are pertinent to the fall composition counts. In addition, two other serious problems arise. The animals are dispersed over a considerably larger area in the fall, and yearling females are more difficult to distinguish from 2+ females since the yearlings are approaching adult size. In 1976, fall composition counts were obtained from two distinct concentrations of caribou (Tables 18 and 19). North of the Nahtuk Mountains, the caribou were localized in groups ranging in size from several animals to over 200 and appeared relatively stationary. All groups encountered with the helicopter were censused and complete composition counts were obtained from all but the largest groups in which only a relatively small proportion of the animals were missed. Animals classified along the Kobuk River were migrating enmass in a south to southwesterly direction. "Group size" here was simply the number of caribou classified moving past two observers on the ground at one location for approximately 2 to 4 hours. In two locations the two

Table 18. 16 October 1976, Western Arctic Herd fall composition counts[1] from north of Nahtuk Mountain.[2]

Calves	Yearlings	2+ Females	2+ Males	Total
64	19	108	47	238[3]
34	16	43	47	140[3]
27	6	81	56	170[3]
16	4	24	6	50
11	3	21	8	43
4	2	24	22	52
11	3	36	18	68
17	15	26	24	82[4]
23	12	38	29	102[5]
18	7	30	16	71[6]
225	87	431	273	1,016

[1] J. Davis, observer; J. Doerr, recorder.

[2] Area of counts was from 67°35'N to 68°08'N and from 152°05'W to 153°20'W (Figure 13).

[3] Total does not equal group size since a few animals were not classified in these groups.

[4] Composed of 13 groups classified with ten or less caribou.

[5] Composed of 7 groups classified with 11-20 caribou.

[5] Composed of 2 groups classified with 21-40 caribou.

Table 19. 17 to 18 October 1977 Western Arctic Herd fall composition counts from the Kobuk River Valley.

Date	Location	Calves	Yearlings	2+ Females	2+ Males	Total	Observers
17 Oct	1	884	484	1,266	853	3,487	J. Davis/J. Doerr
17 Oct	2	55	57	151	61	324	R. Shideler/ H. Reynolds
18 Oct	2	19	16	69	37	141	R. Shideler/J. Doerr
18 Oct	3	139	73	297	219	728	R. Shideler/J. Doerr
18 Oct	4	298	170	653	327	1,448	J. Davis/H. Reynolds
TOTAL		1,395	800	2,436	1,497	6,128	

[1] Location 1: 0.8 km north of the Kobuk River between Ambler and Shungnak (67°01'N x 157°37'W); Location 2: 2.4 km south of the Kobuk River between Ambler and Shungnak (66°58'N x 157°43'W); Location 3: West of the Sheklukshuk Range (66°46'N x 157°58'W); Location 4: Southwest of the Sheklukshuk Range (66°44'N x 158°04'W).

observers classified the same animals; the results of these counts were averaged and treated as one count.

A 2 × 4 χ^2 contingency table revealed significant differences in the composition counts between the Kobuk River and the Nahtuk Mountain caribou concentrations ($\chi^2 = 18.81$, df = 3, $P < 0.005$). Significant differences in the composition of groups with 40 or less caribou compared with groups of over 40 caribou from the Nahtuk Mountain concentration also exist ($\chi^2 = 10.67$, df = 3, $P < 0.05$). On the basis of the above, the fall composition counts were initially divided into three strata: (1) caribou from the Kobuk River, (2) caribou from near Nahtuk Mountain in group sizes greater than 40, and (3) caribou from near Nahtuk Mountain in group sizes of 40 or less. Hereafter, these strata are referred to as Stratum 1, Stratum 2, and Stratum 3, respectively.

Chi-squared contingency tests reveal significant differences among the sex and age groups in Stratum 1 ($\chi^2 = 85.72$, df = 12, $P < 0.005$) and Stratum 2 ($\chi^2 = 49.84$, df = 18, $P < 0.005$). This demonstrates that the sex and age structure of the herd in the fall is not randomly mingled as has been assumed in many past studies. Furthermore, comparison of counts taken by observers in Stratum 1 reflect significant differences between the sex and age counts made by different observers on the same migrating portion of the herd (Table 20). Whether this significant difference is due to classification error among observers or actual segregation within

Table 20. Comparison of composition of caribou from the same group classified by different observers.

Observers	Degree of Overlap in Animals Classified	P[1]	Total Classified	Greatest Difference in Percentages[2]	
RS/HR	none	n.s.[3]	324	--	
JLD/HR	none	0.100	919	2+ Females	(10.0)
JLD/JGD	none	0.005	3,487	2+ Males	(4.8)
RS/JGD	80+%	n.s.	279	--	
RS/JGD	none	0.100	183	2+ Males	(10.6)
RS/JGD	ca. 15-20%	0.005	959	Yearlings	(7.1)

[1] 2x4 contingency table used to test for differences in composition of caribou classified by two observers. Composition of caribou divided into calves, yearlings, 2+ males, and 2+ females. Probability that differences are due to chance is given.

[2] Age and sex group with the greatest absolute difference between the composition counts of the two observers. Absolute difference between observers for this age and sex group shown in parentheses.

[3] Not significant at 0.10 level.

associated bands of caribou is uncertain; however, the results are instrumental in demonstrating that the WAH fall composition data cannot be treated as a simple random sample (assuming a binomial distribution to calculate variance). Instead variances of the various cohort/2+ female ratios were calculated for each stratum using standard ratio formulas (Appendix C), and the results are given in Table 21.

Since the age-sex cohorts are not randomly distributed in the fall and differences in composition occur among different concentrations of caribou, it is essential to obtain accurate population estimates of each major concentration of animals, as well as representative composition counts, in order to accurately estimate the fall herd composition. Reconnaissance flights do not generally provide very accurate or precise estimates of herd size. In 1976, the largest wintering concentration of caribou located north of 70° latitude wasn't sampled because the fall reconnaissance flights indicated the presence of only a few thousand caribou in widely scattered groups (J. Davis, pers. comm.). Subsequent aerial surveys in January 1977 revealed the presence of an estimated 20,000 to 35,000 animals (Davis and Reynolds 1977).

Stratum 1 and Strata 2 and 3 combined had estimated sizes of 12,500 and 5,000, respectively (Davis and Reynolds 1977). Both these estimates are subject to a wide range of uncertainty. For the purposes of calculating the variance of fall composition

Table 21. 1976 Western Arctic Herd fall composition ratios.

Ratio	Stratum 1 Kobuk River Valley		Stratum 2 Nahtuk Mt. Group Size >40		Stratum 3 Nahtuk Mt. Group Size ≤40		Total Herd	
	r	V(r)[1]	r	V(r)[1]	r	V(r)[2]	r	V(r)[3]
Calf/2+ female	0.573	0.00352	0.496	0.00468	0.617	0.00273	0.565	0.00407
Yearling/2+ female	0.328	0.00077	0.157	0.00119	0.362	0.00364	0.328	0.00103
2+ bull/2+ female	0.615	0.00142	0.605	0.00815	0.734	0.01214	0.617	0.00161
Non-cow[4]/2+ female	1.516	0.01409	1.258	0.01857	1.713	0.02968	1.492	0.01686
Groups classified	5		7		22		34	

---

[1] Finite population correction factor used assuming 20 percent of the stratum was classified.

[2] Finite population correction factor used assuming 50 percent of the stratum was classified.

[3] Finite population correction factor used assuming a post-calving population of 32,625 caribou older than calves, 84.6 percent of the post-calving animals older than calves are 2+ females, a fall non-cow/2+ female ratio of 1.492, and 98 percent survival of 2+ females from post-calving to the peak of rut. See text and Appendix C for additional discussion of the computations and assumptions used.

[4] Non-cow = all caribou except 2+ females.

ratios, the range of uncertainty is assumed to be zero; consequently, variances listed in Table 21 are probably conservative.

Given the wide variance of the fall composition ratios in the individual strata (Table 21), no significant differences are detected among strata for any of the ratios, except that the yearling/2+ female ratio in Stratum 2 is significantly lower than the combined yearling/2+ female ratio in Strata 1 and 3 ($t = 4.06$, $df = 32$, $P < 0.01$). Formulas used to estimate a total herd variance are given in Appendix C and the results are shown in Table 22.

5. SURVIVAL FROM POST-CALVING TO FALL

Mortality of adult females from post-calving to the fall has not been empirically tested, but is believed to be low due to the favorable environment at this time of year. Skoog (1968) estimated a natural mortality rate of 0.02 for adult females from post-calving to the fall. This estimate is used in Equation 23 for the 1976 WAH census since there was virtually little hunting prior to the fall composition counts that year and wolf predation during the summer is believed to be minor (Stephenson 1976, p. 228). The potential variance of the estimated survival rate is ignored in estimating the variance of the population since it is believed to be small.

Table 22. 1976 Western Arctic Herd estimates.

Source(s) of Variance	Estimate	Variance of Estimate	95% C.I. of Fall Population[1]
Fall calf/2+ female ratio[2]	0.565 (0.435-0.695)[3]	0.004066	11,766-18,799 calves
Fall yearling/2+ female ratio[2]	0.293 (0.233-0.353)[3]	0.000703	6,302- 9,548 yearlings
Fall 2+ male/2+ female ratio[2]	0.617 (0.535-0.699)[3]	0.001609	14,471-18,907 2+ males
Fall non-cow/2+ female ratio[2]	1.492 (1.228-1.756)[3]	0.016860	33,075-47,498 animals other than 2+ females
% 2+ females post-calving[4]	0.846 (0.806-0.886)[3]	0.000246	64,218-70,592
Animals older than calves in post-calving aggregation	"30,611" "32,625" "38,666"	"648,830" "3,285,156" "23,360,306"	"59,890-66,547" "59,890-74,865" "59,890-99,320"
% 2+ females post-calving x fall total/2+ female[5]	2.108 (1.870-2.346)[3]	0.013600	59-789-75,007
Animals older than calves in post-calving aggregation x % 2+ females post-calving x fall total/2+ female ratio	"63,244" "67,405" "79,887"	"14,927,266" "27,960,293" "119,954,808"	"55,355-71,133" "56,608-78,202" "57,524-102,250"
Post-calving calf/2+ female ratio	0.547 (0.525-0.569)[3]	0.000071	--

[1] Confidence intervals for fall populations including calves unless otherwise stated.

[2] Variance and confidence intervals calculated assuming 32,625 caribou older than calves on the post-calving grounds with 2+ females comprising 84.6 percent of these animals.

[3] 95 percent confidence interval of estimate in parentheses.

[4] Variance and confidence intervals calculated assuming 32,625 caribou older than calves on the post-calving grounds and assuming a fall ratio of 1.492 for caribou other than 2+ females to 2+ females.

[5] Variance and confidence intervals calculated assuming 32,625 caribou older than calves on the post-calving grounds.

High mortality of adult females prior to the fall could substantially affect the fall estimate and would be difficult to detect with the census technique.

D. RESULTS OF THE 1976 WAH ANALYSIS

Formulas for the exact variance of products of independent variables (Goodman 1960) were used to calculate the variances of various population estimates. Confidence intervals of 95 percent were estimated, weighing the t values of the variables, using a formula given by Steel and Torrie (1960:81). The results are shown in Table 22. While the variances are artificial for reasons previously mentioned, they nevertheless illustrate wide uncertainty in the population and composition estimates. The variance of the fall composition data alone produced a 95 percent confidence interval in the fall population estimate of approximately ±10.6 percent of the mean. The wide variance in herd composition ratios among different "groups" of caribou creates substantial uncertainty in survival rates estimated from the composition data and may explain survival rates calculated from survey data that are apparently greater than one (Table 22, Appendix B, Bente and Roseneau 1978).

The greatest problem with the present census technique is its inability to estimate an upper confidence limit for the size of the herd. If the post-calving census missed substantial portions of the herd, the 1976 fall population could have been as high as 100,000 animals or more (Table 22). Obviously, the need to develop more accurate and precise estimates of herd size and composition is evident, in order to improve our understanding of caribou population dynamics.

CHAPTER 5. ESTIMATING THE MAGNITUDE OF THE WESTERN ARCTIC CARIBOU HARVESTS (1950-1960)

A. INTRODUCTION

The importance of caribou to the lifestyle of people living within the Western Arctic Herd's range has been described in detail by Rausch (1951), Sonnenfield (1957), Giddings (1961), Foote and Williamson (1966), Saario and Kessel (1966), and others. Most hunting of caribou occurs within 100 km of villages within the herd's range (Foote and Williamson 1966, Saario and Kessel 1966, Glenn 1967). Although some hunting occurs during the summer and early fall months, especially along river systems, most hunting generally takes place during the winter when travel is facilitated by ice and snow. Since the late 1960's, the use of snowmobiles has virtually eliminated dogsleds as a source of transportation.

In many ungulate populations in North America, human harvest is an important mortality factor. Consequently the collection of harvest data is valuable since, together with population size, it yields an estimate of the hunting mortality rate. The purpose of this chapter is to summarize and evaluate data available on the magnitude of the WAH harvests from 1950 to 1976.

B. MATERIALS AND METHODS

The magnitude of hunter harvests prior to the fall of 1975 was estimated from a review of past literature, especially unpublished ADF&G reports. The 1975-76 harvest of the WAH was determined from estimates made by J. L. Davis and other ADF&G game biologists working in the area, and from observations made during trips to (1) Allakaket, Anaktuvuk Pass, Evansville (Bettles), Hughes, and Huslia from 14 to 22 January 1976; (2) Ambler, Evansville, Kiana, Kobuk, Kotzebue, Noorvik, Selawik, and Shungnak from 17 to 24 February 1976; (3) Kotzebue from 19 to 20 March 1976; (4) Kivalina, Kotzebue, and Point Hope from 29 March to 2 April 1976; (5) Barrow from 8 to 11 April 1976; (6) Anaktuvuk Pass and Evansville from 5 to 9 October 1976; and (7) Anaktuvuk Pass, Evansville, and Kobuk from 15 to 18 October 1976.

A chance to observe actual hunting practices and to estimate wanton waste occurred at a field research camp of the ACWRU, located south of the Kiana Hills (66°58'N × 161°08'W). An approximately 22 km^2 area in the vicinity of camp from 20 to 29 March 1976 was searched for evidence of hunting kills. Caribou carcasses found were examined in the field to determine their probable cause of death. Whether or not the animal had been eviscerated was recorded, and loss to scavengers was estimated visually. Remains of caribou that died previous to the fall of 1975 were not included in the kills examined. Femurs, mandibles, and incisiform teeth were taken from a portion of the carcasses found. The percentage of fat in the femur marrow was determined following Neiland (1970). Mandible measurements and age-determining of the incisiform teeth is described in Chapter 6 (section B. Materials and Methods). Actual hunting practices were observed whenever possible and surmised from the examination of caribou kill sites. Composition counts of caribou wintering in the area were also made. Additional notes were contributed by ACWRU personnel working out of the field camp on various aspects of caribou ecology and span a period of time from early March to early April 1976.

C. RESULTS AND DISCUSSION

1. ESTIMATES OF VILLAGE HARVEST

Both the total harvest and the composition of the harvest in a given village is the result of two nebulous factors: (1) the availability of caribou, and (2) the needs of the people (including both recreational and sustenance needs). These two factors encompass such items as the number and composition of caribou in proximity to the village, the season of the year and length of time the herd is in the vicinity of the village, the population size and economic base of the village, and the amount of available alternative food

Table 23. Estimates of total village harvests of Western Arctic Caribou Herd (1954-74).

Year	Estimated Harvest	Source
1953-54	15,000[1]	Woolford 1954
1963	20,000[2]	Lentfer 1965
1964	25,000[2]	Hemming and Glenn 1968
1965	29,000[2]	McGowan 1966
1966	24,000[2]	Glenn 1967
1967	26,000[2]	Hemming and Glenn 1968
1968	27,000[2]	Hemming and Glenn 1969
1969	<25,000[2]	Davis et al. 1976
1970	25,000[2]	Davis et al. 1976
1971	≤25,000[2]	Davis et al. 1976
1972	over 25,000[2]	Davis et al. 1976
1973	over 25,000[2]	Davis et al. 1976
1974	<25,000[2]	Davis et al. 1976
early 1970's	22,653[3]	Patterson 1974 and Davis et al. 1976

[1] Estimate considered low.

[2] Estimate by ADF&G personnel based on reported kill in villages, interviews with hunters, and personal observations. Estimates are considered conservative and do not account for wounding loss, wanton waste, and caribou taken by residents and nonresidents outside the villages.

[3] Average of several years data. Number reported in the villages within the WAH's range. Estimate believed minimum and does not account for wounding loss, wanton waste, and caribou taken by residents and nonresidents outside the villages.

resources, such as salmon, marine mammals, and moose. Legal restraints have not played an important role in regulating the magnitude of village harvests. From statehood in 1959 until the summer of 1976, there was no closed season or bag limit on caribou throughout most of the WAH's range. Restrictions on caribou hunting in arctic Alaska by the federal government prior to statehood were largely ignored (Woolford 1954). (It should be noted that, in retrospect, restrictions on subsistence hunting of caribou in the WAH in the 1950's were probably biologically unjustified, and the population of the herd increased despite widespread violations of the regulations.)

Table 23 summarizes harvest estimates of the WAH from 1954-74 based on the number of animals reportedly taken in the villages. Estimates by Patterson (1974) are comparable with estimates by ADF&G personnel. The estimates given suggest that annual village harvests of caribou in the WAH increased from the 1950's to the 1960's and have remained relatively constant since 1963. The average reported village harvest since 1963 is approximately 25,000 animals. The increasing harvest of caribou from the 1950's to the 1960's is probably the result of both an increasing human population in the villages (Alonso and Rust 1976) and greater numbers of caribou wintering south of the Brooks Range in the 1960's near existing settlements (Glenn 1967, Skoog 1968, Hemming 1971). It should also be noted that the per capita harvests of caribou in the villages have declined since the mid-1960's as the human population has steadily increased (Alonzo and Rust 1976). Two possible factors affecting this decline are the gradual implementation of a wage-base economy in the village as well as the decreased use of dogs since the advent of the snowmachine (Glenn 1967).

Table 24 presents estimated harvests in particular villages. Wide variation in the average number of caribou harvested per capita is evident both among villages and between different years in the same village. The higher per capita use of caribou at Anaktuvuk Pass, for example, is largely due to the lack of substantial alternative food resources (Rausch 1951). Subsistence needs at Anaktuvuk Pass largely depend on caribou (see Rodahl 1963).

Minimum village harvest estimates for the winter of 1975-76 are summarized in Table 25. The bulk of the herd that year migrated down the western coast and wintered in the lower Kobuk Valley and in the Selawik Flats (J. Davis, pers. comm.; pers. obs.). Hunters in the villages of Kiana, Kivalina, Kotzebue, Noatak, Noorvik, Point Hope, and Selawik had heavy harvests. The villages of Ambler, Kobuk, and Shungnak farther up the Kobuk River had moderate hunting success, while few caribou migrated near the villages in the upper Koyukuk drainage. Of all the villages I visited, Barrow undoubtedly had the highest village harvest. Most of the harvest in Barrow resulted from fall hunting and was concentrated on a group of at least 5,000

Table 24. Some estimates of individual village harvests in the Western Arctic Herd.

Year	Village	Estimated Harvest	Caribou/ Person	Source
1953-54	Selawik	150	0.50	Woolridge 1954[1]
	Noorvik	200	0.67	Woolridge 1954
	Kotzebue	1,000	1.22	Woolridge 1954
	Pt. Barrow	2,000	1.67	Woolridge 1954
	Shungnak	250	1.76	Woolridge 1954
	Noatak	750	2.59	Woolridge 1954
	Kivalina	500	3.79	Woolridge 1954
	Wainwright	1,000	4.44	Woolridge 1954
	Kiana	800	4.49	Woolridge 1954
	Point Lay	500	7.58	Woolridge 1954
	Anaktuvuk Pass	2,000-4,000	26.67-53.33	Woolridge 1954
1959-60	Kivalina	417	2.88	Saario and Kessel 1966[2]
1960-61	Kivalina	619	4.27	Saario and Kessel 1966
1960-61	Noatak	1,491	6.66	Foote and Williamson 1966[2]
1960-61	Point Hope	742	2.59	Foote and Williamson 1966
early 1970's	Barrow	3,500	1.84	Patterson 1974[3]
	Point Hope	750	2.03	Patterson 1974
	Kivalina	513	2.70	Patterson 1974
	Kiana	863	2.88	Patterson 1974
	Kotzebue	5,000	2.95	Patterson 1974
	Noorvik	1,381	2.99	Patterson 1974
	Shungnak	525	3.18	Patterson 1974
	Noatak	1,214	4.14	Patterson 1974
	Selawik	1,887	4.19	Patterson 1974
	Anaktuvuk Pass	1,000	10.31	Patterson 1974

---

[1] Estimates "considered low."   [2] Known reported harvests.   [3] Average of several years data.

Table 25. Estimated minimum village harvests of caribou in the Western Arctic Herd in the fall and winter 1975-76.

Village	Estimated Harvest	Caribou/ Person[1]	Source
Ambler	802[2]	4.64	ADF&G Unp. Data
Shungnak	676[2]	4.10	ADF&G Unp. Data
Buckland	369[3]	2.82	Davis 1976
Kivalina	1,175[3]	6.25	Davis 1976
Kiana	1,144[3]	4.09	Davis 1976
Noorvik	1,442[3]	3.12	Davis 1976
Kotzebue	2,000-3,300[4]	1.18-1.95	Davis 1976
Noatak	1,600-2,100[4]	5.46-7.17	Davis 1976
Point Hope	1,700[4]	4.57	Davis 1976
Kobuk	140[5]	2.37	Davis 1976
Selawik	1,200-2,000[6]	2.80-4.66	pers. obs.
Barrow	3,000-4,000[6]	1.43-1.90	pers. obs.
Nuiqsut	300-450[7]	?	Davis 1976
Point Lay	300[7]	?	Davis 1976
Wainwright	800[7]	2.33	Davis 1976
Meade River (Atkasook)	100[7]	?	Davis 1976
Anaktuvuk Pass	500[8]	4.03	Davis, pers. comm.
Unit 24	300[9]	0.61	Davis, pers. comm.
TOTAL	17,548-21,298	2.45-2.97	

[1] Village population estimates from Alonso and Rust (1976) using largest estimate of 1970 census estimate and 1974 Alaskan native population estimate.

[2] Based on numbers reported by paid village data collector from September 1975 through April 1976. Estimate considered known minimum.

[3] Based on numbers reported by paid village data collector from September 1975 through January 1976, plus estimates by J. Davis, ADF&G, from February through April. Estimates considered conservative.

[4] Based on estimates by ADF&G Area Biologists, from September 1975 through January 1976 and estimates by J. Davis from February through April 1976.

[5] Based on village meetings in February 1976, plus estimates by J. Davis from February through April. Estimates considered conservative.

[6] Based on personal observations and personal communication in the villages and estimates of "average" harvests for these villages from Patterson (1974).

[7] Number estimated killed from September 1975 through January 1976 by Area Biologist, ADF&G. More animals killed since January.

[8] Based on numbers reported by paid village data collector September 1975 through December 1975 plus pers. comm. with J. Davis. Estimate deemed conservative.

[9] Includes only the village of Evansville (Bettles), Allakaket, Hughes, and Huslia. Based on village meetings in January 1976 plus pers. comm. with J. Davis. Estimate considered known minimum.

caribou that wintered near the town (H. Reynolds, pers. comm.; J. Davis, Unp. ADF&G Data).

The harvest estimate for 1975-76 (Table 25) is considered a minimum estimate of the number of animals killed by people residing within the herd's range. Patterson (1974) estimated that the average harvests of caribou in villages not included in Table 25 (i.e., Elim, Galena, Koyuk, Shaktoolik) in the early 1970's was 616. If we assume 500 caribou were taken by residents in these villages plus people residing in the "bush" and 2,000 additional caribou were taken in the villages listed in Table 25, the estimated harvest for the winter 1975-76 is 20,000 to 23,800, excluding wounding loss, wanton waste, and caribou taken by sport hunters residing outside the herd's range.

2. ESTIMATES OF HARVESTS BY HUNTERS RESIDING OUTSIDE THE HERD'S RANGE

The number of caribou taken by both resident and non-resident hunters residing outside the WAH's range is unknown because hunters were not required to report the number of animals they killed. The number killed by these hunters is believed to be small. As McGowan (1966:9) states, "The caribou harvest in the Arctic consists almost entirely of subsistence hunting."

In lieu of other data, I would estimate the annual harvest by hunters from outside the herd's range has been in the neighborhood of 500 to 1,000 animals.

3. ESTIMATING THE MAGNITUDE OF WANTON WASTE

Wastage of caribou resources by native subsistence hunters in Arctic North America has been documented by Banfield (1954, 1957), Sonnenfield (1957), Kelsall (1968), Parker (1972), and many others and has probably played an important role in the decline of some herds (Sonnenfield 1957, Kelsall 1968, Parker 1972). Wastage of caribou in the WAH has, unfortunately, been poorly documented, outside of occasional notes taken by biologists and others working in the area. Woolford (1954) mentions a high wounding rate of caribou in arctic Alaska and the reluctance of hunters to pursue and dispatch wounded animals. Lent (1966b:514) noted:

> Unless the civilian population of the Alaskan Arctic increases far beyond its present level of approximately 5,000, there should be no necessity for placing restrictions upon subsistence hunting. However, my own observations have led me to believe that both educational and law enforcement programs may be useful in counteracting wasteful hunting practices and ensuring a more efficient utilization of the caribou population.

Grauvogel and Pegau (1976:37) write concerning the Western Arctic Herd:

> There is ample evidence that hunting practices have been poor and crippling loss is probably a significant mortality factor. Also, many animals that have been retrieved and cleaned have been left in the field to rot.

Davis (1976) summarized many observations regarding subsistence waste in the Western Arctic Caribou Herd at a special Alaska State Senate Resource Committee Hearing in Juneau, Alaska, on 17 May 1976. Davis (1976) classified wastage of caribou resources into the following categories:

1) Crippling loss;
2) Mistakenly killed caribou (i.e., bulls during and after the rut and calves during the winter);
3) Poor or abnormal caribou killed and not used;
4) Caribou killed and properly cleaned and cached in the field, but not retrieved;
5) Caribou killed for trap bait;
6) Wastage of caribou retrieved from the field but not properly cared for at home.

Observations concerning the above include: (1) an unspecified number of adult males killed during the 1975 fall migration near Kivalina and reportedly left on the tundra to "mellow" out by spring (pers. comm. with Kivalina resident on 30 March 1976); (2) an annual wastage of caribou that are shot and not retrieved at Noorvik (pers. comm. by a non-native residing in the village at the time); (3) a ca. 60-year-old native of Selawik who reported he shot and left two caribou out of "less than 35" he had shot that year because the animals had swollen joints and soft white abscesses ("like butter"), which "stunk" when cut open, in the pleural cavities and peritoneum; and (4) 12 caribou stacked in one pile and reportedly rotting at a residential home in Noorvik in early April 1976 (H. Thing, pers. comm.).

A minimum of 10,000 caribou wintered in the vicinity of the Kiana Hills. Composition counts in late March 1976 by J. Shea and myself, revealed 27.7 percent calves (n = 2,121), 13.1 percent yearlings (n = 1,149), and 8.0 percent unantlered (n = 746). Hunting in the area was primarily from residents of Kiana, Kotzebue, and Noorvik, as determined from conversations with people in those villages and hunters in the field. Detailed results of kill sites examined and hunting practices observed near the Kiana Hills are given in Appendices D and E and summarized in Table 26.

All kills listed in Table 26 are believed to be the result of local hunting. This was surmised from the arrangement of the carcasses, evidence of snow machine tracks and human litter near the carcasses, evidence of bullet holes and evisceration of the animals, and the level of hunting activity known to have occurred in the area (Appendices D and E).

Of 164 kills found, only 76 (46.3 percent) caribou had been retrieved from the field and 7 others (4.3 percent) were only partially utilized. Seventy-five percent (n = 80) of the caribou left were deemed unsalvageable when last observed. A salvageable carcass is defined as one that had been eviscerated after being shot and had a maximum estimated loss to scavengers of 12.5 percent

Table 26. Observations of hunting waste near the Kiana Hills, Northwest Alaska (1975-76).

	Kills Located[1]	Kills Observed[2]
Caribou retrieved from field	76/164 (46.3)[3]	21/24 (87.5)
Caribou partially used	7/164 (4.3)	0/24 (0.0)
Caribou left in the field	81/164 (49.4)	3/24 (12.5)
Caribou eviscerated of caribou left in the field	25/ 62 (40.3)	0/ 3 (0.0)
% over 1/8 scavenged of caribou left in the field	48/ 80 (60.0)	0/ 3 (0.0)
Salvageable[4]	20/ 80 (25.0)	0/ 3 (0.0)
% calves of caribou left	12/ 84 (14.3)	1/ 3 (33.3)

[1] All kills occurred prior to 20 March.

[2] Does not include animals that were wounded and escaped or observation number 2 in Appendix E. Kills occurred from 9 March to 2 April.

[3] Number having attribute/total number of observations (%).

[4] Salvageable are eviscerated carcasses with no more than 12.5 percent loss to scavengers.

This definition seems defensible since all caribou that had not been eviscerated had begun to putrify by mid-March despite the freezing temperatures. Furthermore, it seems doubtful that hunters would bother to retrieve carcasses that were scavenged due to the availability of living caribou and unscavenged, eviscerated carcasses, plus the large quantity of caribou meat present in the villages at that time (pers. obs.).

A few of the carcasses examined may have been wounded animals that escaped only to die later. However, since nearly all carcasses examined were lying adjacent to other carcasses or rumen piles (Appendix D), most were the result of animals killed by hunters and purposely left in the field.

It can be argued that the kills located are not representative of all kinds since whole piles of carcasses are considerably more visible than gut piles which may be buried under many inches of snow. While this is true, the kills located are not believed to be as biased a sample of the actual hunting practices in the area as it may seem for the following reasons:

1) Most of the kills were located in tundra areas. Some of these areas were windswept and the kills were highly visible.
2) The hunters have a tendency to drag all the animals killed to one place before eviscerating them. This practice was observed in the field (Appendix E), as well as being apparent from the arrangement of the carcasses.

3) Animals cleaned and retrieved from the field were often apparent from the remains of antlers, heads, forelegs, hides, and rumen piles.

4) Single rumen piles were occasionally found. Invariably the rumen piles had tell-tale signs of scavenging by ravens.

5) The number of animals taken from the field undressed is probably small, although I observed one hunter take six caribou he had shot from the field, after eviscerating only five of them (Appendix E).

It is very important to realize that the hunting practices of individuals are highly variable, and observations of hunting practices (Appendix E) described both instances of good hunting ethics and instances of reckless killing of animals. Much of the waste is believed to have occurred in association with caribou killed and legitimately utilized; with no daily bag limits, the hunters often shot more than they could haul back on their sleds and the surplus animals were wasted. Until the summer of 1976, there was no legal requirement against caching animals in the field. However, since approximately 60 percent of the caribou (n = 62) examined in the field in March were not eviscerated, it is apparent that hunters had no intention of returning for many of the animals "cached." In addition, loss to scavengers was substantial (Table 26).

Twelve of 84 carcasses left in the field were calves. This percentage was significantly greater than the percentage of calves (4.1) found in 362 hunter-killed caribou in the villages of Kiana and Noorvik combined ($x^2 = 10.37$, df = 1, $P < 0.005$), and indicates that calves were selectively wasted.

Table 27 shows the percentages of fat in femur marrows from a portion of the animals examined. The percentage of fat in femur marrows from animals left in the field compare very favorably with early winter percentages of fat in femur marrows from barren-ground caribou in Canada (Dauphiné 1976), suggesting that many healthy, breeding caribou were killed and wasted.

Time did not permit an opportunity to examine all the carcasses in the vicinity of camp. Aerial reconnaissance by ADF&G on 6 May 1976, after snowmobile travel was impossible and the chances of salvaging additional carcasses was unlikely, revealed a minimum of 423 carcasses in a relatively small portion of the total hunting area of the villages of Kiana, Kotzebue, and Noorvik (Davis 1976). While it is impossible to determine an exact estimate of the number of caribou killed and not used by village hunters, the data presented above indicates that the number was substantial. It should be emphasized that the waste documented here was not an isolated case, but occurred to some degree wherever caribou were taken in abundance in Northwest Alaska and constitutes an important source of human-induced mortality for the WAH (Davis 1976; pers. obs.; J. Davis, pers. comm.).

Table 27. Percent marrow fat in femurs collected from non-retrieved caribou carcasses near the Kiana Hills, Northwest Alaska (1975-76).

Number	Age[1]	Sex	Percent Marrow Fat
1	3-9 mo	Unknown	81.5
2	3-9 mo	Unknown	81.2
3	3-9 mo	Unknown	74.6
4	3-9 mo	Unknown	70.8
5	3-9 mo	Unknown	58.3
6	1-1/2 yr	Female	71.4
7	1-1/2 yr	Unknown	79.7
8	3-1/2 yr	Female	80.6
9	3-1/2 yr	Female	55.1
10	4-1/2 yr	Female	83.4
11	4-1/2 yr	Female	80.3
12	6-1/2 yr	Female	87.0
13	6-1/2 yr	Female	82.3
14	6-1/2 yr	Female	81.5
15	4-1/2 to 6-1/2 yr	Female	76.4
16	7-1/2 yr	Female	87.8
17	7-1/2 yr	Female	74.3
18	8-1/2 yr	Female	76.3
19	9-1/2 yr	Female	76.0[2]
20	11-1/2 yr	Female	86.3
21	11-1/2 yr	Female	71.2
22	12-1/2 yr	Female	47.6
23	2+ Adult	Female	74.0
24	2-1/2 yr	Male	77.7
25	3 yr 10 mo	Male	85.4
26	5-1/2 yr	Male	45.1[2], 48.0[3]
27	2+ Adult	Male	86.0
28	2-1/2 yr	Unknown	73.3
29	3-1/2 yr	Unknown	77.7
30	1+ Adult	Unknown	85.0
31	1+ Adult	Unknown	80.5
32	1+ Adult	Unknown	78.6
33	1+ Adult	Unknown	78.6

[1] All animals were killed between September 1975 and 20 March 1976. Most animals are believed to have been killed between January and March 1976.

[2] Femur marrow from epiphysial end of femur.

[3] Marrow taken from humerus.

4. WOUNDING LOSS

The gregarious nature of caribou probably subject them to a relatively high wounding loss since wounded animals may mingle with larger bands of animals and be lost to the hunter. From the observations of hunting in Appendices D and E, it is obvious that the hunting practices of many local people were extremely poor and wounding loss was probably high. Kelsall (1968) has suggested that 20 percent of the estimated or known kill be considered a conservative crippling loss for native people hunting caribou in the barren-grounds of Canada. This percentage is probably also a conservative estimate for the WAH.

D. CONCLUSIONS

Undoubtedly both wounding loss and wanton waste were a significant hunting mortality factor to caribou, although they vary greatly among villages and among years in the same villages in the WAH. There is some speculation that the use of snow machines increased the wastage of caribou, but documentation of waste prior to 1975-76 is too sparse to validate this assumption. The exact hunting mortality is impossible to estimate due to the lack of data. However, if we assume only 60 percent of the animals killed directly by hunters were retrieved, and 20 percent of the animals killed directly by hunters represents the number of animals that escaped and later died as a result of being wounded, the human-induced mortality in the Western Arctic Herd in the winter of 1975-76 could have been as high as 40,000 animals or more.

CHAPTER 6. ESTIMATING THE COMPOSITION AND AGE STRUCTURE OF THE WESTERN ARCTIC CARIBOU HERD HARVESTS (1950-1976)

A. INTRODUCTION

The importance of the composition of human harvests of caribou in modeling the population dynamics of the herd was discussed previously (Chapter 2, p. 29). The purpose of this chapter is to summarize and evaluate the data available on the composition and age structure of human harvests of caribou in the WAH from the 1950's to 1976.

B. MATERIALS AND METHODS

Two collections of animals killed by hunters were age-determined through a cooperative study between ADF&G and the ACWRU. One collection consisted of mandibles from caribou killed by hunters from the villages of Anaktuvuk Pass, Kivalina, Point Hope, and Noatak from 1959-61. A second collection, consisting of incisiform teeth from WAH caribou killed by hunters in the fall and winter of 1975-76, was collected from January through April 1976, during trips to the villages described previously in Chapter 5 (p. 175). J. Davis, ADF&G, also collected caribou teeth from Ambler and Kiana; teeth collected in the Kiana Hills (pp. 175-176) were included in the 1975-76 collection.

Calves and yearlings from the 1959-61 collection and calves from the 1975-76 collection were age-determined by eruption and wear methods (Skoog 1968, Miller 1972). The 1959-61 and 1975-76 collections of 2+ and 1+ animals, respectively, were age-determined by counting cementum annuli. The aging technique, described in detail by Davis (1978), is similar to one used by Miller (1974) for barren-ground caribou in Canada. Slides of stained cementum annuli were prepared and then read by at least two readers. Difficulties in age-determining the slides is described by Doerr (in prep.). Based on a comparison of ages assigned by two readers, Doerr (Ibid.) concluded that 80 percent or more of the ages assigned to the slides were within 1 year of the correct age of the animal.

Measurements of diastema lengths and mandible lengths were recorded for the 1959-61 collection and the few mandibles obtained while collecting incisiform teeth in 1975-76. Diastema length was measured as the distance between the alveolus of the canine and the first premolar (P2). Mandible length was measured as the distance between the posterior rim of the angle of the ramus and the anterior end of the process lateral to the canine alveolus, rather than the customary way described by Bergerud (1964a), due to the fact that the anterior portion of alveoli of the incisiform teeth of the 1959-61 collection were often severely eroded due to shipping and prolonged storage. Measurements were made to the nearest millimeter and were not recorded if damage to the specimen prevented making a proper measurement. Seven millimeters were added to the mandible lengths recorded to make them comparable to the mandible length measurements described by Bergerud (1964a) and used by Skoog (1968). A large percentage of the specimens in both collections were of unknown sex. An attempt to determine the sex of these animals on the basis of their mandible and diastema lengths was unsuccessful (Doerr, in prep.).

The composition of the WAH harvests was evaluated using the 1959-61 collection and the 1975-76 collection, together with other collections of WAH caribou killed by hunters and age-determined using the wear-age technique (Skoog 1968, Miller 1972). Analysis of trends in the harvest follows the methods used in Chapter 2 (p. 34-38).

C. RESULTS AND DISCUSSION

1. SEX RATIO OF CARIBOU KILLED BY HUNTERS IN THE WESTERN ARCTIC HERD

a. 2+ Adults

Saario and Kessel (1966:990) have summarized the selectivity of caribou hunters at Kivalina as follows:

> During approximately the first two-thirds of October, hunters concentrated their attention on the biggest bulls. The bulls are fat at this time of the year, and, by shooting a big bull, hunters can get more meat per shot than with a cow or calf. As the rutting season begins, the meat of the bulls has a strong and offensive

> odor and taste; so the hunters seek the cows. When the rutting season is over, about the middle of December, the hunters begin to hunt both bulls and cows with more or less equal emphasis.

Table 28 summarizes data on the sex ratio of 2+ adults in WAH harvests. No significant difference was found in the percentage of females taken during the months of November and December compared to the months of January to June when data from all years were combined ($\chi^2 = 0.788$, df = 1, $P < 0.50$). The percentage of females in the harvest during the months of August to October was significantly lower than the percentage of females in the harvest during the months from November to June ($\chi^2 = 418.1$, df = 1, $P < 0.005$). These findings are similar to Saario and Kessel's (1966), except that a shift back to the harvesting of adult males after mid-December was not detected. It is interesting to note that Parker (1972) documented the opposite trend in the sex ratio of caribou killed by native hunters in the Kaminuriak population. Hunters there took greater proportions of females from August to October and more males from January through April. The hunting practices in the WAH tend to concentrate on the animals with the highest relative amounts of fat (adult males in the fall, adult females in the winter). The chronology of the harvest is valuable in predicting the sex ratio of harvests. Approximately 70 percent of the village harvests in

Table 28. Chronology of the percentage of females in Western Arctic Herd harvests of 2+ caribou.

Number of Villages	Year	Percent 2+ Females of Total 2+ Caribou[1]				Source
		Aug-Oct	Nov-Dec	Jan-June	Aug-June	
1	1950-51	--	--	--	68(162)[2]	Lentfer 1965
1	1963-64	--	--	84(69)	--	Lentfer 1965
4	1959-61	52(44)[3]	62(139)[4]	54(338)[5]	57(537)[6]	Present study
not specified	early 60's	--	--	--	51(1,012)	Skoog 1968
9	1964-65	--	--	--	54(836)[7]	McGowan 1966
7	1965-66	--	--	--	49(365)[8]	Glenn 1967
1	1966-67	26(97)[3]	--	--	--	Hemming and Glenn 1968
4	1966-67	--	77(123)[9]	76(1,142)[9]	--	Hemming and Glenn 1968
7	1966-67	--	--	--	69(1,607)[10]	Hemming and Glenn 1968
1	1968-69	26(238)[11]	--	--	--	Hemming and Glenn 1969
5	1975-76	46(2,380)[9]	--	--	--	[ADF&G Unp. Data from village data collectors]
4	1975-76	--	72(325)[9]	--	--	
6	1975-76	--	--	65(1,014)[9]	--	
7	1975-76	--	--	--	52(3,972)[9]	[Same as above]
TOTAL		43(2,759)	71(587)	69(2,563)	56(8,491)	

[1] Sample size in parentheses.

[2] Does not include 55 2+ adults of unknown sex.

[3] Does not include 67 2+ adults of unknown sex.

[4] Does not include 70 2+ adults of unknown sex.

[5] Does not include 133 2+ adults of unknown sex.

[6] Does not include 358 2+ adults of unknown sex.

[7] Does not include 241 2+ adults of unknown sex.

[8] Does not include 36 2+ adults of unknown sex.

[9] Includes calves and yearlings also.

[10] Does not include 37 2+ adults of unknown sex.

[11] From a fall collection, months not specified.

1975-76 occurred after October (Davis et al. 1976, Table 25). Using the following equation, the percent of females in the harvest can be estimated:

$$P_f = H_1 (P_{f_1}) + H_2 (P_{f_2}) , \qquad (25)$$

where

P_f = percentage of females in the total yearly harvests (fall to spring);

P_{f_1} and P_{f_2} = percentages of females in the harvests from August through October and November through June, respectively, derived from Table 28; and

H_1 and H_2 = proportion of the total harvest in those time periods, respectively.

The estimate for the 1975-76 harvest is 39 males:61 females, approximately the same as the mean sex ratio estimated for 2+ adults in the 1976 fall composition counts (Table 22).

b. Calves

Table 29 shows the percentage of male calves killed by hunters in the WAH based on data from various studies. Like collections of hunter-killed animals from the NCH (pp. 119-121), wide yearly differences in the sex ratio of calves are apparent. A particularly striking example is the 1959-61 Cape Thompson collection (Table 29). That such a sex ratio for calves in 1959-61 was not representative of the population at that time is demonstrated by the tagging work

Table 29. Percentages of male calves in the Western Arctic Herd (1950-76).

Year	Percent Male Calves[1]	Collection	Source
1950-52	72.0 (25)[2]	Hunter-killed animals	Lentfer 1965
1959-61	10.6 (47)[3]	Hunter-killed animals	Present study
1960	58.1 (93)	Calves tagged 28 May to 3 June	Lent 1960
1960-61	68.8 (16)	Calves collected for biological studies 3 June to 3 April	Lent 1960, 1961
1961	58.3 (48)	Calves tagged 25 May to 24 June	Lent and Lønø 1962
1961-62	70.0 (33)[3]	Calves collected for biological studies during winter	Lent and Lønø 1962
1964-65	50.0 (16)	Hunter-killed animals	McGowan 1966
1965-66	33.3 (12)	Hunter-killed animals	Glenn 1967
1966-67	44.2 (104)	Hunter-killed animals	Hemming and Glenn 1968
1968	20.6 (34)[3]	Fall hunter-killed animals	Hemming and Glenn 1969
1975-76	52.0 (25)	Hunter-killed animals	Present study
TOTAL (1960-61)	58.2 (141)	Calves tagged in summer	
TOTAL (1950-76)	38.4 (263)[3]	Hunter-killed animals	

[1] Sample size in parentheses. Sample size does not include calves of unknown sex.

[2] Probability that the percentage of male calves equals 50 percent is less than 5 percent.

[3] Probability that the percentage of male calves equals 50 percent is less than 0.5 percent.

and specimen collecting done by Lent (1960, 1961) and Lent and Lønø (1962) (Table 29). It seems unlikely that the hunters could consciously select for female calves since it is difficult to determine the sex of calves in the field. Furthermore, I believe the sex of the calf is unimportant to local hunters in the WAH's range. While collecting incisiform teeth in the villages in 1976, I noted that hunters could seldom recall the sex of calves which they had harvested that year. An explanation for the biased sex ratio in 1959-61 may be that animals were incorrectly classified by the collector. Several other studies (Table 29) have also found the sex ratios of calves in WAH harvests slanted toward females, however. Hemming and Glenn (1968) commented that they knew of no satisfactory explanation for this phenomenon. R. L. Rausch found significantly ($P < 0.05$) more male than female calves among caribou killed by natives from Anaktuvuk Pass in 1950-52 (Lentfer 1965). I found a ratio of 13 males:12 females from an examination of 25 caribou calves killed by hunters in 1975-76 in the WAH. Overall, in the WAH, hunters appear to harvest significantly more female than male calves; the reason for this is unknown.

c. Yearlings and Two-Year-Olds

Significantly higher percentages of females than males are also found in WAH harvests of yearlings and two-year-olds (Table 30). There is little reliable composition data available from the WAH on the sex ratio of these cohorts (Table 30). Data from other

Table 30. Percentage of male yearlings and two-year-olds in the harvest of Western Arctic Herd caribou (1950-76).

Year	Age Class	Percent Males[1]	Collection	Source
1950-72	Yearlings	35.3 (17)	Hunter-killed animals	Lentfer 1965
	Two-year-olds	38.9 (36)	Hunter-killed animals	Lentfer 1965
1959-61	Yearlings	24.2 (62)[2]	Hunter-killed animals	Present study
	Two-year-olds	26.9 (52)[2]	Hunter-killed animals	Present study
1964-65	Yearlings	20.6 (34)[2]	Hunter-killed animals	McGowan 1966
	Two-year-olds	28.2 (85)[2]	Hunter-killed animals	McGowan 1966
1965-66	Yearlings	25.9 (27)[3]	Hunter-killed animals	Glenn 1967
	Two-year-olds	22.2 (36)[2]	Hunter-killed animals	Glenn 1967
1966-67	Yearlings	17.8 (163)[2]	Hunter-killed animals	Hemming and Glenn 1968
	Two-year-olds	13.1 (183)[2]	Hunter-killed animals	Hemming and Glenn 1968
1968	Yearlings	22.9 (48)[2]	Fall hunter-killed animals	Hemming and Glenn 1969
	Two-year-olds	36.4 (11)	Fall hunter-killed animals	Hemming and Glenn 1969
1976	Yearlings	31.7 (63)[4]	Composition counts	Present study
	Two-year-olds	32.4 (34)	31 May to 11 June[5]	Present study
1976	Yearlings	54.8 (73)	Composition counts 16 October	ADF&G Unp. Data
TOTAL	Yearlings	21.4 (351)[2]	Hunter-killed animals	
	Two-year-olds	21.8 (403)[2]	Hunter-killed animals	

[1] Sample size in parentheses. Sample size does not include yearlings and two-year-olds of unknown sex.

[2] Probability that the percentage of males equals 50 percent is less than 0.5 percent.

[3] Probability that the percentage of males equals 50 percent is less than 2.5 percent.

[4] Probability that the percentage of males equals 50 percent is less than 1.0 percent.

[5] These counts from the periphery of the calving area probably over represent females (see Lent 1966a).

studies (Klein 1968, Skoog 1968, Miller 1974, pp. 76-77), suggest that the sex ratio of yearlings and two-year-olds is close to 50:50. If such is the case in the WAH, then hunter selectivity favoring females in the one and two year age cohorts is the rule there. This selectivity is opposite the hunter selectivity demonstrated for the NCH (pp. 42-44).

2. TESTING FOR DIFFERENCES IN THE AGE STRUCTURE OF THE WESTERN ARCTIC HERD HARVESTS AMONG VILLAGES

The age composition of hunter-killed animals in the WAH was analyzed to determine if differences existed among villages. The data evaluated is contained in Appendices F and G. Chi-square analysis was used to test for differences; age classes were grouped so that no more than 20 percent of all expected values were less than five, following Cochran (1954). The results are shown in Table 31.

a. Calves

Significant differences ($P < 0.005$) in the percentage of calves of total animals killed by hunters were found among villages in 1960-61 and in 1975-76. The exact reason for the high degree of variation in the percentage of calves is unknown. Possibly the percentage of calves among caribou wintering in the vicinity of the villages is partially responsible for determining the percentage in the village harvest; in the NCH, however, no significant correlation

Table 31. Comparison of the age structure of Western Arctic Herd harvest data among villages.

Variable Tested	Villages Compared[1]	χ^2	df	P
Percent calves of total animals	1959-61 KV, NT, PH	5.704	2	<0.100
	1960-61 AP, KV, NT, PH	14.570	3	<0.005
	1975-76 B, KN, KV, NR, PH, SEL	19.850	5	<0.005
Percent yearlings of total 1+ animals	1959-60 KV, NT, PH	7.692	2	<0.010
	1960-61 AP, KV, NT, PH	4.228	3	<0.250
	1975-76 B, KN, KV, NR, PH, SEL	3.892	5	<0.500
Percent two-year-olds of total 2+ animals	1959-60 KV, NT, PH	3.203	2	<0.250
	1960-61 AP, KV, NT, PH	1.206	3	<0.900
	1975-76 B, KN, KV, NR, PH, SEL	3.639	5	<0.750
3-4, 5-6, 7+ Males	1960-61 AP, NT	4.577	2	<0.250
	1960-61 AP, KV-NT-PH	4.193	2	<0.250
	1975-76 KN, KV, SEL	8.759	4	<0.100
3-4, 5-6, 7+ Females	1960-61 AP, NT	0.336	2	<0.900
	1960-61 AP, KV-NT-PH	1.230	2	<0.750
3-4, 5-6, 7+ Unknown sex	1960-61 B, KV, NR, SEL	5.550	6	<0.500
3-6, 7+ Males	1960-61 AP, NT	0.075	1	<0.900
	1960-61 AP, KV-NT-PH	0.062	1	<0.900
	1975-76 B, KN, KV, SEL	4.704	3	<0.250
3-6, 7+ Females	1960-61 AP, NT	0.222	1	<0.750
	1960-61 AP, KV-NT-PH	0.121	1	<0.750
	1975-76 KN, NR	0.119	1	<0.750
3-6, 7+ Unknown sex	1975-76 B, KN, KV, NR, PH, SEL	7.919	5	<0.250

[1] AP = Anaktuvuk Pass
B = Barrow
KN = Kiana
KV = Kivalina
NR = Noorvik
NT = Noatak
PH = Point Hope
SEL = Selawik
KV-NT-PH means the data from these three villages were combined.

was found between the percentages of calves in the fall composition counts and the percentages in the overall harvests (Table 5).

b. Yearlings

The percentages of yearlings of total 1+ animals in the village harvests were significantly different ($P < 0.01$) among three villages in 1959-60, suggesting the yearling composition in the harvests may also vary among villages. No significant differences ($P > 0.10$) were detected in the percentage of yearlings of total 1+ animals in harvests among four and among six villages in 1960-61 and 1975-76, respectively.

c. 2+ Adults

No significant differences were found among villages in the percentage of two-year-olds of 2+ adults, the age structure of 3+ males, or in the age structure of 3+ females in collections of hunter-killed animals in 1959-60, 1960-61, and 1975-76. Consequently, the age structure data from all the villages were combined for 2+ adults. The results are shown in Tables 32 and 33.

Table 32. Age structure of hunter-killed caribou from the Western Arctic Herd (1959-61).[1]

	Number of Individuals (Percentages)			
Age	Male	Female	Unknown Sex	Total
2-3	14 (10.8)[2]	38 (21.6)	37 (17.1)	89 (17.0)
3-4	12 (9.2)	29 (16.5)	43 (19.9)	84 (16.1)
4-5	24 (18.5)	33 (18.8)	41 (19.0)	98 (18.8)
5-6	30 (23.1)	19 (10.8)	30 (13.9)	79 (15.1)
6-7	19 (14.6)	25 (14.2)	19 (8.8)	63 (12.1)
7-8	9 (6.9)	13 (7.4)	14 (6.5)	36 (6.9)
8-9	9 (6.9)	11 (6.2)	9 (4.2)	29 (5.6)
9-10	4 (3.1)	5 (2.8)	10 (4.6)	19 (3.6)
10-11	5 (3.8)	1 (0.6)	5 (2.3)	11 (2.1)
11-12	4 (3.1)	1 (0.6)	4 (1.9)	9 (1.7)
12-13	0 (0.0)	1 (0.6)	2 (0.9)	3 (0.5)
13-14	0 (0.0)	0 (0.0)	1 (0.4)	1 (0.2)
14-15	0 (0.0)	0 (0.0)	1 (0.4)	1 (0.2)
TOTAL	130	176	216	522

---

[1] Collected in the villages of Anaktuvuk Pass, Kivalina, Noatak, and Point Hope (see Appendix F).

[2] Percentages in parentheses.

Table 33. Age structure of hunter-killed caribou from the Western Arctic Herd (1975-76).[1]

	Number of Individuals (Percentages)			
Age	Male	Female	Unknown Sex	Total
2-3	17 (8.6)[2]	14 (11.7)	64 (15.3)	95 (12.9)
3-4	28 (14.2)	11 (9.2)	64 (15.3)	103 (14.0)
4-5	34 (17.3)	18 (15.0)	80 (19.1)	132 (17.9)
5-6	45 (22.8)	13 (10.8)	65 (15.5)	123 (16.7)
6-7	35 (17.8)	20 (16.7)	41 (9.8)	96 (13.0)
7-8	19 (9.6)	11 (9.2)	39 (9.3)	69 (9.4)
8-9	11 (5.6)	11 (9.2)	35 (8.4)	57 (7.7)
9-10	4 (2.0)	10 (8.3)	15 (3.5)	29 (3.9)
10-11	2 (1.0)	6 (5.0)	5 (1.2)	13 (1.8)
11-12	0 (0.0)	4 (3.3)	6 (1.4)	10 (1.4)
12-13	1 (0.5)	2 (1.7)	3 (0.7)	6 (0.8)
13-14	0 (0.0)	0 (0.0)	2 (0.5)	2 (0.3)
14-15	1 (0.5)	0 (0.0)	0 (0.0)	1 (0.1)
TOTAL	197	120	419	736

[1] Collected in the villages of Ambler, Barrow, Evansville, Kiana, Kivalina, Kotzebue, Noorvik, Point Hope, Selawik, Shungnak, and in the Kiana Hills (see Appendix G).

[2] Percentages in parentheses.

3. TESTING THE ACCURACY OF 3+ ADULT AGE STRUCTURE DATA FROM VILLAGE HARVESTS BY COMPARING THE AGE STRUCTURE OF MALES AND FEMALES

It is desirable to validate age structure data prior to the modeling effort, so that the data may be justifiably used as information input into the model. One method of testing the reliability of the 3+ adult age structure data is presented here.

As indicated previously, the number of male two-year-olds is approximately equal to the number of two-year-old females, while the sex ratio of adults tends to favor females in most North American caribou herds (Bergerud 1967, 1971b, 1974b; Klein 1968; Skoog 1968; Parker 1972; Table 1, 22; and others). If the sex ratio is approximately equal for males and females entering adulthood, then altered sex ratios in favor of females can only be explained through increased mortality of adult males compared to females. This implies a larger population ratio of "old" females to "young adult" females than of "old" males to "young adult" males.

Table 34 shows the results of comparisons of the age structure of 3+ males to 3+ females in hunter-killed collections of animals from the WAH. In most years significant differences between the age structure of adult males and adult females could not be detected. This suggests that the age structure of hunter-killed caribou often may not reflect the age structure of the population. Whether this is due to bias in the adult male sample, the adult female sample, or both, is uncertain from the above comparisons. The inability to detect significant differences between the adult age structure of males and females in the 1964-68 harvest collections may be partially due to the lack of precision in the wear-age technique used to age-determine animals in those years. To illustrate that significant differences between the male and the female age structures should have been detected given the sample sizes of the collections, I present the following: Miller (1974) estimated the male and female age structure of the Kaminuriak population from animals collected by biologists. Population studies of the herd during that time indicated equal sex ratios of two-year-olds and a 55:100 ratio of 3+ males:3+ females (Parker 1972). Assuming a sample size of 100 3+ males and 100 3+ females, dividing the cohorts into 3 to 5, 6 to 9, and 10+ years and testing for differences as in Table 34 produced a χ^2 of 16.4 (df = 2, $P < 0.005$). Repeating the above test with 50 3+ males and 50 3+ females (lumping age classes into 3 to 6 and 7+ years to avoid expected values of less than 5.0) still allowed detection of significant differences ($\chi^2 = 7.6$, df = 1, $P < 0.01$). The sample sizes of the yearly comparisons between males and females in the WAH (Table 34) generally exceeded 100 animals for both 3+ males and for 3+ females.

Table 34. Comparison of the age structure of 3+ males and females from village harvest data in the Western Arctic Herd.

Age Classes Tested	Data Source[1]	χ^2	df	P[2]
3-5, 6+	1950-52 AP[3]	4.830		0.050
3-6, 7+	1960-61 AP	0.078	1	0.900
3-4, 5-6, 7+	1960-61 AP	4.580	2	0.250
3-6, 7+	1960-61 KV-NT-PH	1.470	1	0.250
3-4, 5-6, 7+	1960-61 KV-NT-PH	1.810	2	0.500
3-6, 7+	1959-60 Total	0.106	1	0.750
3-4, 5-6, 7+	1959-60 Total	0.264	2	0.900
3-6, 7+	1960-61 Total	1.140	1	0.500
3-4, 5-6, 7+	1960-61 Total	5.050	2	0.100
3-6, 7+	1959-61 Total	1.080	1	0.500
3-4, 5-6, 7+	1959-61 Total	4.870	2	0.100
3-5, 6-9, 10+	1964-65 Total[4]	2.820	2	0.100
3-5, 6+	1965-66 Total[5]	0.097	1	0.900
3-5, 6-9, 10+	1966-67 Total[6]	4.500	2	0.250
3-5, 6-9, 10+	Fall 1968 AM[7]	1.580	2	0.500
3-4, 5-6, 7+	1975-76 KN	7.980	2	0.025
3-6, 7+	1975-76 KN	3.220	1	0.100
3-4, 5-6, 7+	1975-76 Total	9.840	2	0.010
3-6, 7+	1975-76 Total	5.630	1	0.025

[1] Unless otherwise specified, all tests compare proportions of 3+ males to proportions of females. AM = Ambler, AP = Anaktuvuk Pass, KN = Kiana, KV = Kivalina, NT = Noatak, PH = Point Hope. 1975-76 Total does not include data from the Kiana Hills. KV-NT-PH means the data from these three villages were combined.

[2] Less than or equal to the probability a higher ratio of "old" males to 3+ males than "old" females to 3+ females observed in harvest collection is due to chance.

[3] Raw data from Lentfer (1965).

[4] Raw data from McGowan (1966).

[5] Raw data from Glenn (1967).

[6] Raw data from Hemming and Glenn (1968).

[7] Raw data from Hemming and Glenn (1969).

4. AN ANALYSIS OF TRENDS IN THE AGE STRUCTURE OF THE WESTERN ARCTIC HERD HARVEST DATA

This section presents an analysis of trends in the WAH harvest data. First through fourth degree polynomial regression equations were calculated for twelve harvest parameters from 1950 to 1976 and were tested to determine the "best fit" polynomial regression models as described in Chapter 2 (p. 34). The results are summarized in Table 35 and Figure 14 and 15.

Third and fourth degree polynomial equations produced the "best fit" to most of the harvest parameters regressed over time. It is difficult to determine if such equations reflect actual trends in the harvest data or are simply spurious equations resulting from the variability in the data and the particular years in which the data were collected. Some parameters predicted by the models seem unrealistic (i.e., only 20 percent of the 1954-56 collection of 3+ adults are 3 to 5 years of age).

A second method for determining trends in the harvest data was to test the 1959-61 and 1975-76 collections to determine significant differences between the age structure of these two collections. The results of these tests are summarized in Appendix H. Two differences ($P < 0.05$) were indicated by these comparisons. One, the proportion of two-year-olds of 2+ adults was significantly higher in 1959-61 than in 1975-76 and, two, the proportion of females 7 years of age

Table 35. Summary of polynomial regressions of 12 harvest parameters of the Western Arctic Herd and time (1950-76).

Harvest Parameters[1]	Significance of nth Degree Polynomial Regression 1st	2nd	3rd	4th	r	Polynomial Regression with "Best Fit"[2]	"Best Fit" Polynomial Regress Equation[3]
Percent calves (9)	>0.50	>0.25	>0.25	<0.005	-0.220	4th	$Y_x = 0.578 + 12.0x - 2.21x^2 + 0.133x^3 - 0.00253x^4$
Percent yearlings (9)	>0.50	>0.50	>0.50	<0.010	0.198	4th	$Y_x = -3.73 + 13.9x - 2.40x^2 + 0.150x^3 - 0.00200x^4$
Percent two-year-olds (9)	<0.05	<0.10	<0.01	<0.050	-0.695	3rd	$Y_x = 15.6 + 1.93x - 0.274x^2 + 0.00753x^3$
Percent two-year-olds of 2+ adults (9)	<0.05	<0.10	<0.01	<0.050	-0.684	3rd	$Y_x = 19.3 + 2.33x - 0.341x^2 + 0.00949x^3$
Percent yearlings and two-year-olds (9)	<0.25	<0.25	<0.25	<0.010	-0.543	4th	$Y_x = 13.4 + 14.1x - 2.44x^2 + 0.139x^3 - 0.00252x^4$
Percent 3+ adults (9)	<0.25	<0.25	>0.25	<0.001	0.436	4th	$Y_x = 86.0 - 26.1x + 4.65x^2 - 0.272x^3 + 0.00506x^4$
Percent 3-5 year old males of 3+ males (7)	>0.50	>0.50	<0.25	<0.005	-0.305	4th	$Y_x = 131 - 54.9x + 8.50x^2 - 0.454x^3 + 0.00709x^4$
Percent 3-5 year old females of 3+ females (7)	>0.50	<0.25	<0.10	<0.010	-0.234	4th	$Y_x = 99.6 - 41.1x + 6.71x^2 - 0.363x^3 + 0.00620x^4$
Percent 6-9 year old males of 3+ males (5)	>0.50	<0.25	<0.25	--	0.273	none	$Y_x = 23.0$
Percent 6-9 year old females of 3+ females (5)	>0.50	<0.05	<0.10	--	0.306	2nd	$Y_x = 156 - 16.9x + 0.506x^2$
Percent 10+ males of 3+ males (5)	<0.25	<0.25	<0.01	--	-0.743	3rd	$Y_x = 70.3 - 13.1x + 0.741x^2 - 0.0135x^3$
Percent 10+ females of 3+ females (5)	<0.01	<0.10	<0.25	--	0.970	1st	$Y_x = -4.37 + 0.603x$

[1] Sample size in parentheses.
[2] See page 34 for discussion of "best fit."
[3] Y_x = harvest parameter in year x where x = 0 in the fall and winter of 1950-51.
[4] Data regressed over time period from 1960 (x = 10) to 1975-76 (x = 25).

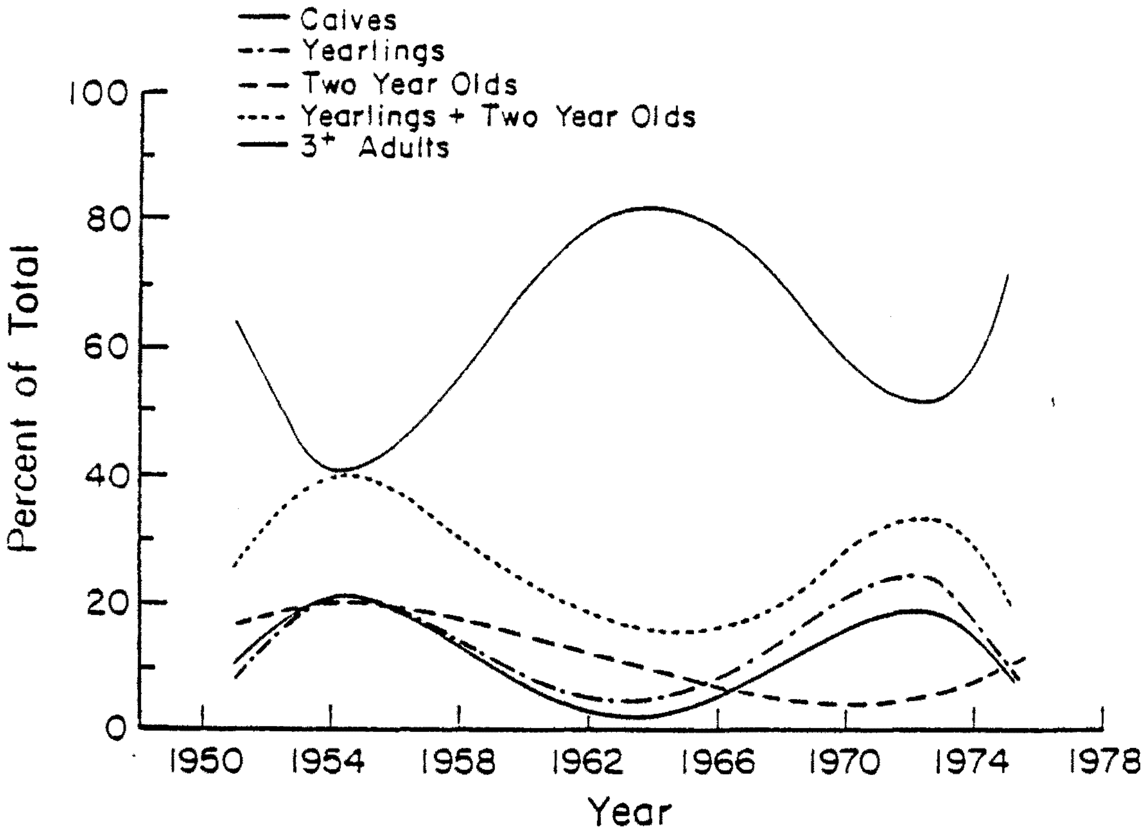

Figure 14. Polynomial regression models of the age composition of the Western Arctic Herd harvests over time.

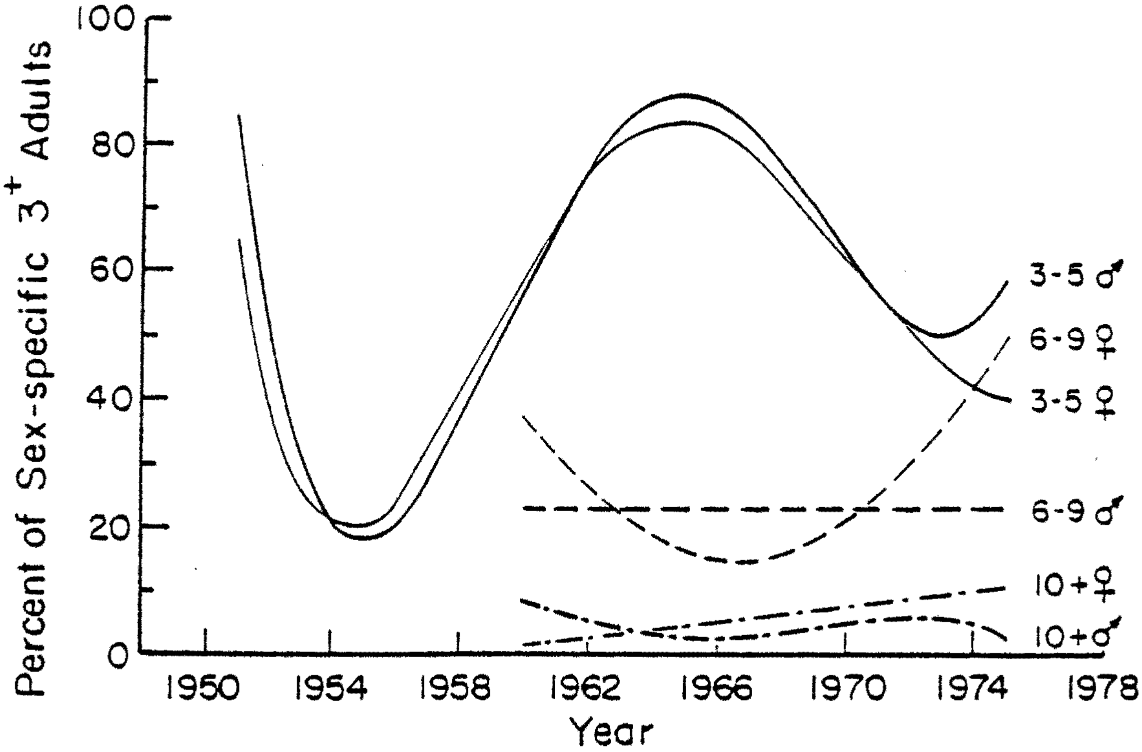

Figure 15. Polynomial regression models of the age structure of 3+ adults in the Western Arctic Herd harvests.

and older of total 3+ females was significantly higher in the 1975-76 collection. The significance of these findings is discussed in the following chapter in connection with the modeling effort on the WAH.

D. CONCLUSIONS

A comparison of the estimated age structure of 522 and 736 2+ adults collected from village harvests in the WAH in 1959-61 and in 1975-76, respectively, revealed significantly higher ratios of two-year-olds of total 2+ adults and lower ratios of 7+ females of 3+ females in the 1959-61 collection. It is uncertain if significant third and fourth degree polynomial equations of various harvest parameters regressed on time reflected actual trends in the harvests or were spurious results due to the collecting and age-determining techniques.

A model was constructed based on the assumption that the 3+ male and 3+ female age structures in the WAH are different, and, furthermore that differences in age structures can be readily detected at the 0.05 significance level with random samples as small as 50 adult males and 50 adult females. Age structure data from village harvests failed to show these significant differences in 5 of 7 years, suggesting that the age structure of the harvest collections in those years did not accurately reflect the actual adult age structure of the herd.

Hunters in the WAH take significantly higher percentages of adult males from August to October compared to the time period from November to June. Higher percentages of females than males were found among calves and yearlings in harvest collections, indicating sex-specific hunter selectivity favoring females in these cohorts.

CHAPTER 7. MODELING THE POPULATION DYNAMICS OF THE WESTERN ARCTIC HERD SINCE 1960

A. INTRODUCTION

The purpose of this chapter is to elucidate factors responsible for the rapid decline of the Western Arctic Herd and to simulate some future projections of the herd's growth, given a range of management alternatives and population responses by the herd. As in Chapters 2 and 3, simulation modeling is used to assess the role of human harvests, wolf predation, and other mortality factors on the population dynamics of the herd. The first five sections of this chapter are devoted to evaluating population estimates, available composition data, the magnitude of wolf predation, the magnitude of reindeer immigrations, and the condition or "quality" of the caribou in the WAH. These five sections, together with the analysis of harvest and census data presented in Chapter 4 through 6 and the results of analysis in Chapter 2, form the data base with which the population model is constructed, input parameters derived, and simulations validated in the remaining sections of this chapter.

B. RESULTS AND DISCUSSION

1. A REVIEW OF THE POPULATION STATUS OF THE WESTERN ARCTIC HERD

a. Prior to 1950

Reviews of historical data have indicated that caribou were abundant in northwestern Alaska from the 1830's to 1870's and then declined to a low population level in the early 1900's (Bee and Hall 1956, Sonnenfield 1957, Lent 1966b, Skoog 1968). The number of caribou in northwestern Alaska in the early 1900's is unknown. Caribou were plentiful at this time, however, along the upper Colville River from the Killik River to the Utukok River, just north of the Brooks Range, a region that includes a portion of the present calving grounds of the herd (Lent 1966b). A gradual increase in the caribou population was first noted in the early 1920's (Ibid.), although no extensive migrations were recorded along the northern coast or into the Baird and Schwatka Mountains to the south (Skoog 1968). In 1936-37, a concentration of caribou, estimated at 90,000, apparently wintered along the Cutler River, north of Ambler (Ibid.). By the 1940's, caribou were being hunted again along the coastal villages from Barrow to Kotzebue (Lent 1966b). In 1947, a large concentration of caribou, estimated at over 250,000 animals, was observed in the upper Noatak Valley, and by the late 1940's, caribou became abundant along the Kobuk River in increasing numbers

(Skoog 1968). Since then, the caribou herd has wintered primarily south of the crest of the Brooks Range, extending south and eastward throughout what is now considered its present winter range.

Because the increase of the WAH from 1920 to 1950 coincided with a dramatic decrease of caribou in the interior and northeastern portions of Alaska (Murie 1935, Skoog 1968), immigration has been implicated as an important cause of the increase (Scott et al. 1950, Lent 1966b, Skoog 1968), although no egress of animals from other herds has been documented. The uncertainty of the role of immigration, the lack of demographic data, and the lack of adequate census data confound attempts to estimate the population of the herd prior to 1950.

b. Since 1950

Scott et al. (1950) suggested the presence of four caribou herds in northwestern Alaska and estimated they contained a total of 119,000 animals. Later studies by USFWS and ADF&G revealed the presence of only one herd in the region (Lent 1966a, Skoog 1968, Hemming 1971). Lent (1966a), using aerial photos to census the post-calving aggregations, estimated the 1962 summer population (including calves) was between 175,000 and 200,000 animals. Skoog (1968) estimated a minimum population of 300,000 animals, excluding calves, for June 1964, based on the following:

> During the winter of 1963-64 large numbers of caribou moved through the lower Kobuk and Kotzebue Sound areas, accessible to many of the settlements in that area. An attempt was made by the Alaska Department of Fish and Game to obtain harvest figures for that period. The results indicated that at least 25,000 animals were killed between September 1963 and April 1964. If one were to assume that one out of every ten animals in the herd had been killed that winter, it would mean that the original population was approximately 250,000 animals. In view of the wide distribution of the movement of these caribou to the wintering grounds, especially since such a vast number of animals moved southward east of the main settlements, it seems quite doubtful that the people could possibly have killed 10 percent of the animals. This type of reasoning implied that there probably was a much greater population in the northwest arctic than had been supposed. As such, the writer placed the minimum estimate for this herd at 300,000 animals (calves excluded) for June 1964. It is not known at present whether or not the herd is continuing to increase; the relatively high incidence of morbidity found in recent years may indicate a reduced vitality and lowered annual increment.

In June 1970 a total of 179,843 caribou were counted on aerial photographs in addition to 10,380 counted in peripheral areas, and a minimum fall population of 242,000 caribou was estimated (Pegau and Hemming 1972). The 1976 population estimates of the WAH (approximately 60,000 to 100,000) was discussed in detail in Chapter 4.

c. Conclusions

The past estimates of herd size for the WAH present a conflicting picture of the population trends of the herd. This is probably largely the result of inaccuracy in many of the estimates.

Since 1950, however, the herd apparently increased to an unknown level, with an obvious sharp decline since 1970.

2. ESTIMATING THE COMPOSITION OF THE WESTERN ARCTIC HERD (1960-76)

Composition data from the WAH is extremely limited (Table 36). Furthermore, as indicated previously, assumptions on which the estimates are based (such as random mixing of various cohorts) may often be invalid; hence the reliability of the composition data is rather uncertain. Several of the fall composition counts of the WAH (Table 36) are believed to be unreliable. These are discussed as follows.

Lent (in litt.) felt that the 1961 fall composition counts were not representative of the herd due to the lower proportion of males in the fall composition counts compared to the post-calving composition counts. Lent (1966b) used the post-calving composition counts in estimating the composition of the WAH. By assuming the 1961 post-calving yearling/2+ female and 2+ male/2+ female ratios are representative of the herd, the fall percentage of calves can be calculated from the following formula:

$$P_c = [R_c/(R_c + R_y + R_m + 1)] \times 100 \; , \qquad (26)$$

where

P_c = percentage of calves in the fall,

Table 36. Summary of Western Arctic Herd post-calving and fall composition data (1961-76).

Date	Percentages of Total Sample				n	Source
	Calves	Yearlings	2+ Females	2+ Males		
Early July 1961	16.1(42)[1]	14.3(37)[2]	38.4	31.2(81)[3]	3,073	Lent 1966a
18-21 Oct 1961	18.6(37)	4.2(8)	49.8	27.4(55)	1,006	P. Lent in litt.
10-11 July 1968	17.8(41)	11.9(27)	43.5	26.7(61)	4,062	Hemming and Glenn 1969
21-28 Oct 1968	15.6(34)	10.6(23)	45.6	28.3(62)	2,217	Hemming and Glenn 1969
1-3 July 1970	19.7(48)	15.4(37)	41.1	23.8(58)	26,250	Pegau and Hemming 1972
Fall 1970	21.2	--	48.1[4]	30.8[4]	6,238	Pegau and Hemming 1972
2-5 July 1975	31.9(60)	7.8(15)	52.7	7.6(14)	5,075	J. Davis, Unp. ADF&G Data
18-19 Oct 1975	25.0(48)	7.0(13)	52.0	16.0(31)	2,231	J. Davis, Unp. ADF&G Data
27 June-2 July 1976	31.2(54)	7.9(14)	57.8	3.2(6)	8,412	Chapter 4, this study
16-18 Oct 1976	22.8(56)	11.8(29)	40.4	24.9(62)	7,143	Chapter 4, this study

[1] Number of calves per 100 2+ females in parentheses.

[2] Yearling/100 2+ females in parentheses.

[3] 2+ males/100 2+ females in parentheses.

[4] Includes yearlings.

R_c = fall calf/2+ female ratio, and

R_y and R_m = yearling/2+ female and 2+ male/2+ female post-calving ratios, respectively.

It should be noted that the post-calving calf/2+ female ratios in 1960 and 1962 were considerably higher than the 1961 post-calving calf/2+ female ratio (Lent 1966a,b). Consequently, the 1961 fall percentage of calves may be lower than the fall percentages of calves in other years during the yearly 1960's. Unfortunately, fall composition counts were not obtained in other years during that time.

In 1970, the yearling cohort was lumped with 2+ adults during the fall composition counts (Pegau and Hemming 1972) and the fall composition was estimated using the post-calving yearling/2+ female ratio (Ibid.). If one assumes an equal sex ratio of yearlings in the fall, a 2+ male to 2+ female sex ratio of 56:100 is generated from the 1970 data.

The 1975 fall composition counts by J. Davis, ADF&G, revealed a relatively low 2+ male to 2+ female ratio (31:100). The 1976 fall ratio (62:100) indicated a marked change in the adult sex ratios. Such a change in sex ratios in one year is considered unlikely for the following reasons.

1) Human harvest was undoubtedly the major adult mortality factor from 1975 to 1976. All available data indicates that the harvest of 2+ adults during that time was not selective for males (Chapter 6: p. 198).

2) A low percentage of yearlings was found in the 1975 fall composition counts (Table 36), suggesting that the increment of two-year-olds in 1976 was not large enough to alter the adult sex ratio substantially.

First and second degree polynomial equations were calculated for various composition parameters regressed on time from 1961 to 1976 and tested for "best fit" as described earlier. The results are shown in Table 37. The only significant trend ($P < 0.05$) in the composition data was a linear increase in the percentage of calves in the population from 1961-76 (Equation 27).

Table 37. Summary of polynomial regression of seven fall composition parameters of the Western Arctic Herd and time.

Composition Parameter[1]	Significance of Regression		r	"Best Fit"[2] Regression	"Best Fit" Equation[3]
	1st Degree	2nd Degree			
Calf/2+ female (5)	0.25	0.25	0.76	none	$y_x = 0.455$
Yearling/2+ female (5)	0.25	0.50	-0.56	none	$y_x = 0.279$
2+ male/2+ female (4)	0.25	0.25	-0.76	none	$y_x = 0.583$
% calves (5)	0.05	0.25	0.90	1st	$y_x = 12.9+0.687x$ (27)[4]
% yearlings (5)	0.25	0.50	-0.58	none	$y_x = 11.8$
% 2+ females (5)	0.50	0.75	0.45	none	$y_x = 43.6$
% 2+ males (5)	0.25	0.25	-0.79	none	$y_x = 24.8$

[1] Sample size in parentheses.

[2] See p. for discussion of "best fit."

[3] x = 0 in year 1960.

[4] Equation number in parentheses.

3. ESTIMATING THE MAGNITUDE OF WOLF PREDATION IN THE WAH

Perhaps the largest gap in our knowledge of factors affecting the population dynamics of the WAH is the role of predation. For the purposes of this model, only wolf predation is treated as a separate mortality factor on the herd. Predation by other vertebrates has been included in the general category of "natural mortality" for reasons discussed previously (pp. 63-64). This section reviews and summarizes information available on the densities and food habits of wolves in the range of the WAH and develops a method of estimating the magnitude of wolf predation.

a. Estimation of Wolf Densities

No wolf censuses have been conducted in northwestern Alaska until recently. The general trend of wolf abundance in the past has been a presumably high density of wolves in the early 1950's (Kelly 1954), a low density of wolves in the late 1950's and early 1960's (Rausch 1968), a reasonably large increase in wolf abundance peaking around 1965-67 (Rausch 1968, 1969b), and a sharp decline in wolf numbers to a low in the late 1960's and early 1970's (Rausch 1969b, Stephenson and Johnson 1973). Both declines in wolf numbers are generally believed to be due to large human harvests of wolves (Rausch 1968, 1969b; Rausch and Hinman 1977; Stephenson and Johnson 1973). On the North Slope where the open tundra terrain made wolves especially vulnerable to aerial hunting, wolves were reduced to extremely low numbers, prompting the State to close GMU 26 to wolf hunting from 1970-72. In 1972, aerial sport hunting of wolves was closed statewide when the Commissioner of ADF&G stopped the issuance of wolf permits (Rausch and Hinman 1977). Wolf populations in the area appeared to respond to the reduced hunting pressure. By 1973, Stephenson and Johnson (1973) estimated a late winter density of one wolf per 233 km^2 in a 9,326 km^2 area in the central portion of the Brooks Range around Anaktuvuk Pass, an apparent increase from an estimated late winter density of one wolf per 321 km^2 in 1971.

Aerial surveys in March and April of 1977 indicated densities of less than one wolf per 391 km^2 in GMU 26A (Stephenson 1977) and densities of one wolf per 145 km^2 and 161 km^2 in GMU 23 and 24, respectively (R. Stephenson, pers. comm.).

Using these estimated densities and extrapolating, I have estimated mid-winter densities in 1969-71 of one wolf per 265 km^2, 241 km^2, and 835 km^2 for GMU 23, 24, and 26A, respectively. Peak wolf densities (assumed to occur from 1965-67) were estimated at one wolf per 133 km^2, 121 km^2, and 228 km^2 for the above respective units; 1961 estimates were one wolf per 239 km^2, per 181 km^2, and per 391 km^2 in those same respective units. Wolf populations in other years were estimated by visually fitting a smooth curve to the number of wolves in each game management unit in the years specified and rounding the estimate to the nearest 50. In addition, I assumed a stable winter wolf population in GMU 24 and 26A from 1973 to 1976 and a stable winter wolf population in GMU 23 from 1974 to 1978. This assumption was based on the overall impression I obtained from conversations with local residents of the area, as well as wildlife biologists. Densities of wolves on the portion of the WAH's range south of GMU 23 and 24 were assumed to be the same as the average densities of GMU 23 and 24.

Estimated wolf harvests, obtained from bounty and sealing records, were of limited value in estimating wolf numbers in northwestern Alaska. On one hand, the estimates of harvests substantially underestimated the total human kill of wolves since some wolves taken were not reported and some wounded wolves were not retrieved (Stephenson 1976). On the other hand, wolves have a highly variable recruitment rate and fall percentages of pups can exceed the number of older wolves in the population when wolf populations are heavily exploited (Mech 1970). Rausch (1969b) used wolf harvest estimates to determine the period of high wolf numbers in northern Alaska; however, the relationship between wolf harvest statistics and actual wolf population levels may not necessarily be well correlated.

To avoid using projected wolf populations that could not sustain the estimating harvests, I used the following equation:

$$W_i \geq (W_{i+1}/1.92) + (1.2 \times H_i) \quad , \tag{28}$$

where

W_i = projected wolf population in year i,

H_i = reported harvest from year i to year i+1, and

1.92 = ratio of pups and adults to adults found in an examination of 1,196 wolf carcasses from the arctic region of Alaska from 1959-66 (Rausch 1967).

Before concluding the discussion of wolf densities, special attention should be given to the calving grounds of the WAH, where wolf densities have apparently been extremely low since at least 1960 (Stephenson 1976; J. Davis, pers. comm.; K. Keiland, pers. comm.). During the 1976 WAH studies, only three wolves were seen north of the Brooks Range during intensive aerial reconnaissance (J. Davis, pers. comm.). In addition, I observed a single wolf unsuccessfully chase a band of eight caribou near Noluck Lake on 1 June 1976 and found two separate sets of wolf tracks in mid-June along Driftwood Creek. More intensive work on the calving grounds in the summer of 1977 also revealed few wolf sightings (Davis and Valkenburg 1977). Relatively high apparent survival of calves from post-calving to fall (Table 36) lends further support to the hypothesis that wolf predation on the calving and summering ranges is low. This idea contrasts markedly with the findings of Parker (1972) and Miller and Broughton (1974) that wolf predation was a substantial mortality factor on the calving grounds of the Kaminuriak caribou population in Canada. The difference in the magnitude of wolf predation between the two areas is probably the result of the considerably higher summer wolf to caribou ratio in the Kaminuriak population (Parker 1972, 1973) as well as the availability of alternative ungulate species in the WAH.

b. Food Habits of Wolves in Northwest Alaska

Caribou and moose are believed to be the principal prey of wolves in the coastal regions of northwest Alaska, with caribou comprising over 70 percent of all incidences of ungulate food remains found in the stomachs of wolves there (Kelly 1954, Rausch 1968). From an analysis of scat remains, Stephenson and Johnson (1972) concluded that Dall sheep are the principal summer prey of wolves in the portion of the Brooks Range comprising the eastern part of the WAH's range. Moose and caribou are also substantial in the summer diet of some packs and are taken when available. During winter, all three ungulates are taken at comparable rates in the Brooks Range, with the dependency on caribou waning in the later months (Stephenson and Johnson 1972). The importance of WAH caribou to wolves south of the Brooks Range has not been well studied.

c. Effect of Migration on Wolf Predation

Kelly (1954) and Stephenson (1976) have suggested that the distribution, movements, and food habits of wolves in northwest Alaska are strongly influenced by the movements of caribou.

Following suggestions given by Stephenson (Ibid.), I have assumed caribou were available on a year-round basis in GMU 26A. On the remainder of the herd's range, I have assumed caribou were available to 50 percent of the wolves for six months of the year. In addition, I assumed 25 percent of the wolves in GMU 23 and 24 had caribou available for seven months and 15 percent of the wolves in these units had caribou available for eight months. Finally, I have assumed 10 percent of the wolves in GMU 23 and 24 had caribou available all year to account for the fact that varying numbers of WAH caribou summer in the Delong, Baird, Schwatka, and Endicott Mountains (Lent 1966b, Dean and Chesemore 1974, Gardner 1974, Stepehenson 1976). An examination of the year-to-year variability in the chronology of the WAH's southward fall migration (Lent 1966b; Hemming and Glenn 1968, 1969; Pegau and Hemming 1972; J. Davis, Unp. ADF&G Data) reveals that the above assumptions are extremely gross simplifications.

d. Estimating Caribou Killed per Wolf

In view of the previous discussion, I have assumed that 50 percent of the ungulates killed by wolves were caribou during the time caribou were available, and that the wolves in the WAH had the same annual kill rate of ungulates (24/wolf/year or 2/wolf/month) as in the NCH. The number of caribou killed by wolves in the WAH was estimated from the estimated number of wolves times the kill rate of caribou times the length of time caribou were available. Subtracting the estimated number of calves less than 5 months of age from this predation rate, I have estimated individual annual wolf predation rates, excluding calves less than 5 months of age to be:

1) GMU 26A: nine caribou,
2) 50 percent of the wolves in GMU 23 and 24 and all the wolves in the portions of range south of GMU 23 and 24: six caribou,
3) 25 percent of the wolves in GMU 23 and 24: seven caribou,
4) 15 percent of the wolves in GMU 23 and 24: eight caribou, and
5) 10 percent of the wolves in GMU 23 and 24: eleven caribou.

The above rates were used in the model as a rough estimate of wolf predation which could be increased or decreased to provide insight into possible effects of wolf predation on the herd.

4. INFLUENCE OF REINDEER ON THE POPULATION DYNAMICS OF THE WESTERN ARCTIC CARIBOU HERD

Lantis (1950) and Skoog (1968) have described the history of the reindeer industry in Alaska. During the precipitous decline of the reindeer industry from 1929 to the late 1940's, large numbers of reindeer were lost and possibly joined the WAH. Such large losses could have had a direct effect on the population dynamics of the WAH during that time.

During this study the presence of reindeer in the WAH was detected several times. At Shungnak, Lawrence Gray, a former reindeer herder, showed me three adult male "caribou" he had shot from the same group of animals in the fall of 1975. One "caribou," with considerably smaller antlers than the other two males, had a distinct V notched in one ear. This mark, Mr. Gray claimed, was his method of marking reindeer. The reindeer was estimated by cementum annulations to be in its ninth year of life at the time of its death and had survived in the wild since at least 1971 (Table 38). A native of Barrow reported her husband had shot two reindeer at Nuiqsut during the summer of 1975. While in the Kiana Hills, I observed an adult female with a marked "white-faced" pattern, a characteristic common amongst domesticated reindeer. Similar reports by hunters killing or observing reindeer among caribou in the WAH have been reported by Rausch (1951) and Lent (1960).

Table 38. Recent numbers of reindeer which were lost and possibly joined the Western Arctic Herd.[1]

Reindeer Herd	Years	Estimated Loss
Wilson-Weber	1944-56	2,500
Nome Demonstration	1948-64	4,800
Skin	1953-60	1,400
Gray	1953-71	6,300
Hadley	1954-76	500
Commack	1956-61	800[2]
Sheldon	1957-61	400
Skin	1960-61	800
Commack	1961-62	425
Sheldon	1961-62	700
Stalker	1965	400

[1] Based on information from E. Nygard (in litt.). The list is incomplete for the 1940's and early 1950's.

[2] Approximately 150 of these reindeer were later recovered and placed in the Nome Demonstration Herd (E. Nygard, in litt.).

Semenov-Tian-Shanskü (1975) has indicated that domestic reindeer which escape with wild reindeer in the USSR may be more susceptible to both human and natural predators. Consequently, escaped reindeer could theoretically enhance the growth of wild *Rangifer* populations by acting as a buffer to predation or as potential breeding stock. The genetic mixing of domesticated and wild stocks of *Rangifer* may not be desirable, however, as discussed by a number of authors (Murie 1935, Bee and Hall 1956, Skoog 1968). Estimated reindeer losses to caribou since the 1950's are shown in Table 38. In comparison with the population size of the WAH, the increment of reindeer to the herd since 1950 has been extremely small. Consequently, the effect of ingresses of escaped reindeer on the herd's growth since 1950 has probably been negligible and was not considered in the model.

5. QUALITY OF THE WESTERN ARCTIC HERD

This section summarizes data available on herd quality in the WAH. This information is useful in subsequent discussion in conjunction with modeling the herd, as well as useful in demonstrating the paucity of knowledge available on relationships between the population dynamics and the overall condition of the caribou. Placental retention, mandibular lesions, body fat reserves during winter, mandible lengths, and reproductive rates are five possible indices of herd quality.

a. Incidence of Placental Retention at Parturition

A relatively high incidence of placental retention during parturition was detected in the WAH during the early and mid-1960's (Neiland et al. 1968). While a multitude of factors may be involved, Neiland (1972) identified brucellosis, leptospirosis, and arboviruses as possible pathogens. Brucellosis was shown to be at epidemic portions in the WAH during this period (Neiland et al. 1968, Skoog 1968). Since a substantial proportion of calves are lost to females exhibiting placental retention (Neiland et al. 1968, Neiland 1972), outbreaks of such disorders could directly influence the population dynamics of the herd. Neiland et al. (1968) have suggested a relationship between poor nutrition and the high incidence of brucellosis and metritis-abortion in the WAH. Since 1968, the overall observed incidences of retained placentas have been less than 2 percent (Neiland 1978) compared to incidences of 3.4 and 5.0 percent in 1963 and 1965, respectively (Neiland et al. 1968).

b. Mandibular Lesions

Approximately 7 percent of the 1959-61 Cape Thompson mandible collection exhibited osseous lesions (Doerr and Dieterich, in press). This incidence compares closely with the occurrence reported in the WAH from 1961-64 (Skoog 1968) and is the highest known incidence of mandibular lesions reported for free-ranging caribou herds in North America. While Doerr and Dieterich (Ibid.) have postulated that the high incidence of lesions may be related to range or herd quality, this relationship remains to be verified and significantly lower incidences of mandibular lesions since 1964 have not been demonstrated (Ibid.).

Mandibular lesions found in WAH caribou are believed to be the result of dental abscesses, trauma, and periodontal disease and are generally chronic in nature (Ibid.). Since the incidence of lesions is highest in 7+ caribou (Ibid.), mandibular lesions may influence the mortality rate of old adults in the herd.

c. Body Fat Reserves during Winter

In the early and mid-1960's, hunters indicated that animal's taken during the fall and winter had low body fat reserves compared with the 1950's (Skoog 1963, 1968; Lentfer 1965; McGowan 1966; Glenn 1967). In 1967, hunters reported that animals were in better condition than previous years (Hemming and Glenn 1968). Winter femur fat percentages for 1975-76 shown in Table 27 indicate good fat reserves compared to other studies (Dauphiné 1976). No extensive overwinter mortality of caribou due to starvation has been demonstrated in the WAH; however, winter reconnaissance prior to 1975 has been extremely limited.

d. Mandible Length

The lengths of the mandible and the diastema in wild cervids are influenced in part by the quality of the animal's range, with longer mandible and diastema lengths occurring among animals on higher quality ranges (Klein and Strandgaard 1972, Reimers 1972). Skoog (1968) has shown that adult mandible lengths, as well as total body weight, total body length, hind foot length, antler length, and metacarpal and femur lengths, are smaller for WAH caribou than they are for other Alaskan caribou. The influence of heredity versus environment in influencing the size of caribou in the WAH is uncertain.

An additional phenomenon of the WAH is that considerable overlap is found between the mandible lengths of mature adult males and adult females (Doerr, in prep.) compared with virtually no overlap between sexes of caribou in the Nelchina Basin (Skoog 1968), Newfoundland (Bergerud 1964a), Labrador (Bergerud 1967), and the barren grounds of Canada (Miller 1974). Again, such a relationship may be related to heredity. E. Reimers (pers. comm.), however, has found indications that the difference between male and female mandible and diastema lengths in wild reindeer herds in Norway may vary with the quality of the range. There range conditions show greater influence on skeletal growth for males than is true for females. This phenomenon is supported by research on the SMIH (Klein 1968). There the body weights of the reindeer were larger than their parent stock by 24 to 53 percent among females and 46 to 61 percent among males in 1957, 13 years after the introduction to the island. By 1963, when the range had deteriorated considerably, the average body weights had decreased from 1957 by 38 percent for adult females and 43 percent for adult males. Similarly, the differences between 3+ male and 3+ female skeletal measurements, such as hind foot length, total length, and the length of the longest antler beam, decreased from 1957 to 1963 by 67, 72, and 15 percent, respectively. The greater increase in size of males relative to females among caribou on improved range can be explained by the following:

1) Under conditions of improved range quality, increased growth in body size among females is hampered somewhat by the increased energy requirements imposed by an earlier age of conception and lactation (Reimers 1972, pers. comm.).
2) A shorter length of time is required for skeletal growth in females than in males (Skoog 1968, Dauphiné 1976). Thus males can increase their body size relative to females over a longer period of time on high quality range. This idea is supported by the findings of Dauphiné (Ibid.) that the skeletal measurement with the least

> amount of overlap between males and female barren ground caribou are from bones which mature at a relatively late age.

Consequently, the overlap between adult male and female mandible lengths in the WAH (Doerr, in prep.) may be the result of a poor quality range.

Table 39 presents available data on mandible lengths in the WAH, grouped by age classes to be comparable with data from Skoog (1968). From Table 39, it can be seen that the absolute difference in average mandible lengths between 6 to 9 year old males and females is 2.1 times greater in the 1961-64 collection than it is in the 1959-61 collection. Also, the average mandible length of 3 to 4 year old males in the 1959-61 collection was as large as the average for 5+ males in the same collection (Doerr, in prep.). Since mandibles of males continue to grow until at least 6 years of age (Skoog 1968, Dauphiné 1976), the increase in adult mandible lengths may indicate that range conditions have improved since about 1956. If the body size of males actually increased during the late 1950's and early 1960's, it occurred in conjunction with high population levels. This would seem to support findings by Cowan and Wood (1955) and Klein (1964, 1968) that growth of wild ungulates are more influenced by qualitative and quantitative aspects of food supply rather than actual population densities. Since the mandible lengths of 3+ females in the 1959-61 and the 1961-64 collections are similar (Table 39),

Table 39. Comparison of mandible lengths from Western Arctic Herd caribou.

		1959-61[1]		1961-64[2]		1975-76[1]
Age		Male	Female	Male	Female	Female
2 yr	Mean ($\overline{x}$)	266	259	262	253	--
	Range	256/279	246/275	244/282	237/269	--
	n	10	21	51	66	--
	$V(\overline{x})$[3]	2.14	2.18	--	--	--
	95% C.I. of $\overline{x}$	(263-269)	(256-262)	--	--	--
3-5 yr	Mean ($\overline{x}$)	277	263	287	263	--
	Range	250/299	247/284	258/314	241/291	--
	n	45	37	338	236	--
	$V(\overline{x})$	4.17	2.72	--	--	--
	95% C.I. of $\overline{x}$	(273-281)	(260-266)	--	--	--
6-9 yr	Mean ($\overline{x}$)	280	264	301	267	268[4]
	Range	252/315	250/280	276/321	250/290	256/276
	n	34	31	87	83	9
	$V(\overline{x})$	8.37	2.27	--	--	5.52
	95% C.I. of $\overline{x}$	(274-286)	(261-267)	--	--	(263-273)
10+ yr	Mean ($\overline{x}$)	270	260	300	267	--
	Range	261/274	248/268	282/310	254/277	--
	n	7	3	9	16	--
	$V(\overline{x})$	3.51	36.12	--	--	--
	95% C.I. of $\overline{x}$	(265-275)	--	--	--	--

---

[1] Seven mm have been added to the 1959-61 and 1975-76 measurements to make the measurements equivalent to measurements in 1961-64 by Skoog (1968). See Materials and Methods (Chapter 7).

[2] From Skoog (1968).

[3] Sampling variance of the mean.

[4] Includes one 10 year old female.

improved range conditions (based on increased male mandible lengths) may indicate earlier average conception rates for females since 1956, given the arguments presented above. Unfortunately, data on body measurements and age-specific reproductive rates in the WAH are not available over an extended time period.

e. Reproductive Rate

Lent and Lønø (1962) estimated that 30 percent of the 3+ adult females were not pregnant during spring 1961, a year which they considered had an abnormally low calf crop. Skoog (1968) estimated a pregnancy rate for 4+ females at the start of the calving period of only 78 percent, based on late winter examinations of 130 animals in 1963 and 1964. McGowan (1965) found 83 percent of 196 2+ females examined during late winter in 1965 were pregnant, a proportion comparable to the increasing phase of the NCH (Skoog 1968). The average fall calf percentages observed since 1970 (Table 36) are higher than those for 13 other mainland North American caribou herds given by Bergerud (1974c). Since fertility and initial survival have been shown to be influenced by range conditions in many ungulate populations (Cheatum and Severinghaus 1950, Klein 1970, Reimers 1972, Chapter 3), range and herd quality in the WAH since at least 1970 should presumably be in good condition, based on the above.

f. Conclusions

An examination of a number of possible indices does not reveal a consistent pattern of herd quality over time in the WAH. This may be partially due to the limited data available. Placental retention and mandibular lesions occurred at relatively high incidences in the early to mid-1960's, the prevalence of the former declining in the late 1960's. The condition of the animals, based on hunter observations, is believed to have been relatively poor from 1960-66; however, no extensive die-offs of animals due to starvation were detected. The overlap in adult mandible lengths between males and females may be a reflection of poorer range quality in the WAH. The apparent increase in the length of adult male mandible lengths in the late 1950's and early 1960's suggest improved range conditions during a period of high population levels. Initial productivity for the herd in 1960, 1962, and 1965 (Lent 1966b, McGowan 1966) seems comparable with the increasing phase of the NCH, lower reproductive rates were found in 1961, 1963, and 1964, and calf production in the 1970's appears high in comparison with other mainland North American caribou herds. While some of the above indices suggest poorer range conditions in comparison to other herds, no evidence of a decrease in herd quality from 1960 to 1976 was found.

6. DEVELOPING A POPULATION MODEL FOR THE WESTERN ARCTIC HERD (1961-76)

The objectives of modeling the population dynamics of the WAH are: (1) to generate population statistics, such as natural mortality rates, to compare over an extended period of time; and (2) to determine the results of different assumptions and varying magnitudes of mortality and reproduction rates. The limited demographic data and their uncertainty seems to justify the use of the same simple population model as was used for the NCH (Figure 8). Specific components of the model are discussed below.

a. Population Size and Composition

Various starting populations were used for the fall of 1961 and 1970 (the beginning of the model's runs). Herd composition was estimated for 1961 and 1970 as described previously. Starting fall sex ratios of calves and yearlings in the WAH were assumed to be 50:50 (see pp. 76-77).

b. Recruitment of Calves

Recruitment of calves in subsequent years was entered in the model as a fall percentage either derived directly from Equation 27 or assumed to equal 20 percent. The latter assumption was used to simulate the possibility that the fall percentages of calves were higher from 1961-70 than the limited data suggested.

c. Natural Mortality and Wolf Predation

Natural mortality and wolf predation rates were generated as described previously (see pp. 61-62, 225-231). The wolf predation estimate was multiplied by different constants to invoke various assumptions regarding higher or lower wolf predation rates. Wolf predation nonselective for calves was simulated by assuming the proportion of 5 to 17 month old calves among caribou older than 5 months of age in the diet of wolves equaled the proportion of calves in the fall population. This assumption is supported by the findings of Davis and Valkenburg (1977). Calves from 0 to 5 months of age were not included in the wolf predation rate. The implications of overwinter wolf predation with selectivity for calves is discussed in connection with specific model runs.

d. Mortality Due to Hunting

The estimates of human harvest (Tables 23 and 25) were used as minimum estimates of the mortality in the WAH due to hunting; the estimates were increased by multiplying the "known" harvests by various constants to reflect wounding loss, waste, and unreported harvest. "Known" harvests for 1961-63 were assumed to equal 20,000. The composition of wounding loss, animals not retrieved from the field, and unreported kill was assumed to be the same as that of the harvest, except that 15 percent of animals killed and left in the field were assumed to be calves (Table 26). The following assumptions were made regarding the composition of the hunter-killed caribou:

1) One-third of the calves in the harvest were killed prior to the fall composition counts. This proportion was excluded from the model.
2) Harvest parameters for 1+ cohorts assumed all hunting mortality occurs after the start of the model's year (mid-October). This assumption was made since the composition data is extremely limited and the harvest chronology is poorly understood in most years.
3) Thirty-eight and 21 percent of the calves and yearlings, respectively, were males (Tables 29 and 30).
4) Six and 8 percent of the "known" harvests were calves and yearlings, respectively. (These figures were obtained by combining all harvest collections from the WAH.)
5) For those years with no available harvest collections, an estimated 56 percent of all 2+ animals in the "known" harvests were females (Table 28).

e. Immigration and Emigration

No evidence of immigration or emigration in the WAH has been documented from 1960-76, although some loss to or ingress of animals from other caribou herds, primarily the Porcupine Herd and the Central Arctic Herd, could have occurred undetected. Due to lack of evidence, immigration or emigration was not entered into the model. The simulation modeling of the WAH from 1961-76 was broken into two time periods--1961-70 and 1970-76. The results are given in the following two sections.

7. POPULATION MODELING OF THE WESTERN ARCTIC HERD FROM 1961-70

a. Results of Model Runs

The results of population simulations are given in Table 40. A starting population of 200,000 animals in 1961 would have declined far below the minimum estimate of 242,000 in 1970 (Pegau and Hemming 1972) (Runs WAH1 and WAH2). A starting population of 250,000 would have increased only if natural mortality rates were extremely low and calf percentages were higher than suggested by Equation 27 (Runs WAH3 through WAH6); in either case, higher fall yearling/2+ female ratios than were observed in the composition counts would occur (Run WAH5). Similarly, a starting population of 300,000 could only increase if wounding loss, waste, and "unreported" kill were relatively small, calf percentages were higher than predicted by Equation 27, and overwinter survival did not greatly exceed the values observed by Skoog (1968) for the NCH (Runs WAH7-8). Run WAH9 (Table 40) represents a run with a starting 1961 population of 300,000, "high" fall calf percentages, wolf and hunting mortality rates that are considered "realistic," and natural mortality rates, modified from Skoog (1968). This run fits the population data, but again the yearling/2+ female ratios generated are considerably higher than

Table 40. Important input and output values of model runs of the Western Arctic Herd (1961-70).

Parameters	WAH 1	WAH 2	WAH 3	WAH 4	WAH 5	WAH 6	WAH 7	WAH 8	WAH 9
INPUT									
Starting Population (1961 Fall)	200,000	200,000	250,000	250,000	250,000	250,000	300,000	300,000	300,000
Wounding Loss and Unreported Harvest/Waste	0.10/0.00	0.10/0.00	0.10/0.00	0.10/0.00	0.10/0.00	0.20/0.10	0.10/0.00	0.10/0.00	0.20/0.00
Wolf Predation[1]	X0.75NS	X0.75NS	X0.75NS	X0.75NS	X1NS	X1NS	X0.75NS	X1NS	X1NS
% Calves in Fall[2]	L.R.	20%	L.R.	20%	20%	20%	L.R.	20%	20%
Natural Mortality Rates (1961-70)									
Females (5 to 17 mo)	0.040	0.040	0.040	0.135	0.040	0.040	0.135	0.135	0.135
Males (5 to 17 mo)	0.070	0.070	0.070	0.165	0.070	0.070	0.165	0.165	0.165
Females (17 to 29 mo)	0.040	0.040	0.040	0.042	0.040	0.040	0.042	0.042	0.042
Males (17 to 29 mo)	0.050	0.050	0.050	0.048	0.050	0.050	0.048	0.048	0.050
Females (29 mo +)	0.017	0.017	0.017	0.012	0.017	0.017	0.012	0.012	0.012
Males (29 mo +)	0.050	0.050	0.050	0.070	0.050	0.050	0.070	0.078	0.070
OUTPUT[3]									
1970 Fall Population	EXT(1970)[4]	110,000	152,000	225,000	294,000	174,000	216,000	358,000	252,000
Average Wolf Predation Rate (1961-70)									
Calves (5 to 17 mo)	0.096	0.055	0.047	0.040	0.049	0.057	0.038	0.041	0.045
Adults (17 mo +)	0.096	0.055	0.047	0.040	0.049	0.057	0.038	0.041	0.045
Average Yearling/2+ Female (1962-70)	50.2	55.3	40.8	42.0	49.4	53.1	30.1	40.6	41.9
Average 2+ Male/2+ Female (1962-70)	95.3	93.0	87.0	75.2	86.0	90.9	71.7	74.6	75.2
Average Hunting Mortality (1961-70)									
Females (5 to 17 mo)[5]	0.082	0.039	0.040	0.020	0.026	0.040	0.032	0.021	0.031
Males (5 to 17 mo)[5]	0.050	0.024	0.025	0.017	0.016	0.024	0.020	0.013	0.019
Females (17 to 29 mo)	0.109	0.111	0.113	0.089	0.076	0.103	0.100	0.069	0.090
Males (17 to 29 mo)	0.050	0.030	0.030	0.024	0.026	0.028	0.027	0.019	0.025
Females (29 mo +)	0.413	0.224	0.169	0.141	0.130	0.190	0.122	0.106	0.141
Males (29 mo +)	0.298	0.196	0.156	0.148	0.129	0.176	0.133	0.112	0.148

[1] Wolf predation estimates described in text. NS = no selectivity toward calves. 0.75, 1.0, and 2.0 are constant multipliers of the baseline estimates.

[2] L.R. = % calves calculated from Equation 27. 20% = assumed values of 20% calves in all years except 1961. See text for additional discussion.

[3] Demographic parameters used to evaluate model runs are described in text. 1970 fall population is assumed greater than 240,000. See Tables 36 and 37 and text for herd composition information.

[4] EXT (1970) = population goes to zero in 1970.

[5] Does not include hunting mortality prior to the fall estimated at one-third the total harvest of calves.

Table 40. continued

Parameters	WAH 10	WAH 11	WAH 12	WAH 13	WAH 14	WAH 15	WAH 16	WAH 17	WAH 18
INPUT									
Starting Population (1961 Fall)	300,000	350,000	350,000	350,000	400,000	400,000	400,000	400,000	400,000
Wounding Loss and Unreported Harvest/Waste	0.20/0.10	0.20/0.10	0.10/0.00	0.20/0.10	0.20/0.10	0.20/0.10	0.20/0.10	0.20/0.10	0.20/0.10
Wolf Predation	X2NS	X0.75NS	X1NS	X1NS	X1NS	X1NS	X1NS	X1NS	X1NS
% Calves in Fall	20%	L.R.	L.R.	20%	L.R.	L.R.	20%	L.R.	20%
Natural Mortality Rates (1961-70)									
Females (5 to 17 mo)	0.040	0.135	0.135	0.300	0.135	0.250	0.400	0.135	0.135
Males (5 to 17 mo)	0.070	0.165	0.165	0.300	0.165	0.250	0.430	0.165	0.165
Females (17 to 29 mo)	0.040	0.042	0.042	0.042	0.042	0.042	0.042	0.042	0.042
Males (17 to 29 mo)	0.050	0.040	0.048	0.048	0.048	0.048	0.048	0.040	0.048
Females (29 mo +)	0.017	0.012	0.012	0.012	0.012	0.012	0.012	0.012	0.012
Males (29 mo +)	0.050	0.070	0.070	0.078	0.070	0.070	0.070	0.078	0.070
OUTPUT									
1970 Fall Population	89,000	279,000	305,000	245,000	367,000	259,000	248,000	104,651	365,000
Average Wolf Predation Rate (1961-70)									
Calves (5 to 17 mo)	0.115	0.032	0.041	0.041	0.035	0.039	0.030	0.098	0.067
Adults (17 mo +)	0.115	0.032	0.041	0.041	0.035	0.039	0.038	0.098	0.067
Average Yearling/2+ Female (1962-70)	55.9	32.1	31.6	33.3	31.5	27.8	26.3	33.1	40.2
Average 2+ Male/2+ Female (1962-70)	93.2	71.9	71.5	74.1	71.7	71.6	69.3	70.5	74.0
Average Hunting Mortality (1961-70)									
Females (5 to 17 mo)	0.042	0.035	0.026	0.029	0.029	0.033	0.026	0.042	0.023
Males (5 to 17 mo)	0.025	0.022	0.016	0.017	0.018	0.020	0.016	0.026	0.014
Females (17 to 29 mo)	0.105	0.098	0.082	0.099	0.083	0.106	0.105	0.119	0.068
Males (17 to 29 mo)	0.206	0.027	0.022	0.026	0.022	0.028	0.029	0.032	0.018
Females (29 mo +)	0.214	0.110	0.090	0.124	0.098	0.109	0.100	0.147	0.102
Males (29 mo +)	0.104	0.129	0.107	0.131	0.107	0.120	0.121	0.163	0.109

those suggested by the limited fall composition counts. Doubling the estimated wolf population with the above set of conditions would produce a rapidly declining population (Run WAH10).

Simulations WAH11-13 demonstrate population projections for the WAH that "approximate" the population and composition data available on the herd for that time. If 30 percent of the "known" village harvests of caribou equals the number of unreported caribou killed by hunters (i.e., wounding loss, non-retrieved animals, kill by nonresident hunters), and if the wolf predation estimates described previously are realistic, then a starting population of 350,000 animals in 1961 would decline below the observed population level in 1970 unless calf percentages from 1961-70 were higher than predicted by Equation 27. Run WAH13, based on assumptions that 20 percent of the herd in the fall are calves and that a natural mortality rate of 0.30 for calves from 5 to 17 months of age prevailed, closely fits the available demographic data, particularly the observed yearling/2+ female ratios for this time. If wolf predation for calves from 5 to 17 months of age is quadrupled in Run WAH13, natural mortality rates of 0.18 for the calf cohort would produce similar results.

A starting population of 400,000 animals would decline only slightly given natural mortality rates similar to the increasing phase of the NCH (Skoog 1968), calf percentages generated from Equation 27, and estimates of wolf predation and hunting mortality which are considered realistic (Run WAH14). Runs WAH15 and WAH16 represent "close fits" to the population and composition data, given respective low and high fall calf percentages. Runs WAH17 and WAH18 are simulations using natural mortality rates modified from Skoog (1968), together with a wolf predation rate twice as high as that described in the text and low and high fall calf percentages, respectively. These two respective simulations produce a rapidly declining and a slowly declining herd.

b. Discussion

Given the uncertainty of the demographic data, especially the fall herd size in 1961, the decline or stabilization in the population size of the WAH from 1961-70 can be explained by a number of different assumptions concerning various mortality factors or reproductive rates. However, if the estimate of wolf predation, human harvest, and the observed yearling/2+ female ratios (Table 37) used in the model are realistic, and if no ingress of animals into the WAH occurred, then Table 40 indicates that the herd size in the fall of 1961 was probably at least as high as 350,000 to 400,000 animals. This possibility becomes even more likely if Equation 27 reflects actual fall calf percentages for the years 1962-70. Such a population size is in agreement with the 1964 estimate by Skoog (1968:295-296).

Lent (in litt.) has noted that a population as large as 300,000 1+ adults would imply that only one-half of the herd was counted during the summer of 1962 (Lent 1966b) and that only one-fourth of the herd was counted during winter reconnaissance flights in the early 1960's (Lent and Lønø 1962). Since ADF&G estimates of caribou killed by hunters are low (Chapter 5), the actual wolf predation must have been considerably lower than estimated in the model, reproductive and natural mortality rates must have been high (invalidating the composition data), or immigration must have been substantial for Lent's (1966b) population estimate to be correct. The limited data presented earlier do not seem to support these requirements. Undoubtedly the actual herd size and population trend during the 1960's will remain an arguable point, depending on which of the various pieces of data one wishes to accept as reliable.

Runs WAH11, WAH13, WAH15, and WAH16 (Table 40) represent possible population projections of the WAH from 1961-70, assuming an early 1960 population close to that estimated by Skoog (1968). These runs suggest that the average wolf predation rate on caribou older than 5 months of age ranged from 3 to 4 percent, while the average annual hunting mortality rate on 2+ males and females ranged from 10 to 13 percent and 10 to 12 percent, respectively. The wolf predation rates in these runs are comparable to the 1962-69 period in the NCH; the hunting mortality rates on adult males are slightly less than the estimated 1954-62 hunting mortality rate in the NCH, while the hunting mortality rate on adult females is bounded by the estimated mortality rates for adult females in the NCH for the period 1962-69 and for the period 1969-72. Hunting mortality rates for male and female yearlings were approximately 2.8 and 10.5 percent, respectively. The estimated hunting mortality rate on calves older than 5 months of age in the WAH during this time is relatively small (2 to 4 percent).

It seems apparent from Table 40 that, if the herd composition data is reasonably accurate, then either the rate of initial calf production, the rate of calf survival to the fall, the rate of overwinter natural survival of calves, or a combination of the above rates were lower in the WAH from 1961-70 compared with the NCH during its increasing phase from 1954-62. As was the case in the NCH, wolf predation does not appear to be able to solely account for the observed yearling/2+ females ratios if reproduction and natural survival rates had been relatively high. For example, the average wolf predation rate in Runs WAH13 and WAH16 are 4 percent, whereas the average natural overwinter mortality rate of calves used in these runs to closely fit the observed yearling/2+ female ratios range from 30 to 43 percent. These natural survival rates are similar to the wide range of estimates for the NCH from 1962-69 (the period of the herd's peak and beginning of its decline). The data available on the WAH are insufficient for accurately calculating natural mortality rates of cohorts older than calves from 1961-70; the calf mortality rates given above for the WAH should not be greatly affected by the possible error in the natural mortality rates of adults used in the model runs providing the yearling/2+ females ratios used to validate the model represent the actual ratios in the herd.

Finally, it should be noted that model runs WAH11, WAH13, WAH15, and WAH16 suggest a declining herd size since 1961-63. This may partially result from the use of averaged natural survival rates for the period 1961 to 1970. However, since the magnitude of hunting and wolf predation apparently increased from the early to mid-1960's, the WAH may well have "peaked" during the early 1960's or perhaps earlier. Given the limited demographic data, the exact magnitude and timing of the "peak" of the WAH is uncertain.

8. POPULATION MODELING OF THE WESTERN ARCTIC HERD (1970-76)

The population dynamics of the herd during the period 1970-76 was modeled in the same manner as described in the previous section. The results of those model simulations from 1970-76 are given in Table 41. Model simulations using natural mortality rates modified from Skoog (1968) for the increasing phase of the NCH (Runs WAH19-26) could explain the observed population decline of the herd if the herd numbered only 250,000 animals in the fall of 1970 and the estimated wolf predation rate was doubled (Run WAH21) or the "known" harvest estimates were increased by 80 percent to account for wounding loss, waste, and unreported harvest (Run WAH25). Both of these requirements produce considerably higher percentages of yearlings and higher yearling/2+ female ratios than were observed in the composition counts. This suggests that the natural mortality rates of calves from 5 to 17 months of age in the WAH from 1970-76 were higher than the natural mortality rates during the increasing phase of the NCH. In addition, the percentage of two-year-olds in 1975 generated by these model runs are considerably higher than the percentage found in the 1975-76 harvest collection. Such a difference could be accounted for by percentage hunter selectivity of approximately -40 in 1975-76 (calculated using percentages of two-year-olds generated in Run WAH21). Whether or not hunter selectivity against two-year-olds is that high in the WAH is uncertain.

Table 41. Important input and output values of model runs of the Western Arctic Herd (1970-76).

Parameters	DEM[1]	WAH 19	WAH 20	WAH 21
INPUT				
Starting Population (1970 Fall)	ca. 250,000-300,000	250,000	275,000	250,000
Wounding Loss and Unreported Harvest/Waste	?	0.20,0.25/0.10/0.20[2]	0.20.0.25/0.10/0.20[2]	0.20,0.25/0.10,0.20[2]
Wolf Predation	?	1HS	1HS	2HS
Natural Mortality Rates (1970-76)				
Females (5 to 17 mo)	--	0.135	same as WAH 19	same as WAH 19
Males (5 to 17 mo)	--	0.165		
Females (17 to 29 mo)	--	0.042		
Males (17 to 29 mo)	--	0.048		
Females (29 mo +)	--	0.012		
Males (29 mo +)	--	0.070		
OUTPUT				
1976 Fall Population	60,000-100,000	205,000	202,000	67,000
Average Wolf Predation Rate (1970-76)				
Calves (5 to 17 mo)	--	0.040	0.041	0.129
Adults (17 mo +)	--	0.048	0.041	0.129
Average Yearling/2+ Female (1971-76)	26(13-37)	46.8	45.8	50.2
Average 2+ Male/2+ Female (1971-76)	50(31-62)	59.8	60.6	55.8
% Yearlings (1975)	7.0	17.4	16.9	18.9
% Yearlings (1976)	11.8	20.1	19.4	24.9
% Two-year-olds (1975)	10.0?	14.6	14.0	16.5
Average Hunting Mortality (1970-76)				
Females (5 to 17 mo)	--	0.036	0.030	0.046
Males (5 to 17 mo)	--	0.022	0.019	0.028
Females (17 to 29 mo)	--	0.105	0.090	0.129
Males (17 to 29 mo)	--	0.028	0.024	0.035
2+ Females	--	0.171	0.145	0.220
2+ Males	--	0.235	0.197	0.313

---

[1] DEM = demographic parameters used to validate model runs. Average yearling/2+ female and 2+ male/2+ female ratios given are from the years 1970, 1975, and 1976 only (ranges of these values are in parentheses). Percentages of two-year-olds in 1975 calculated from the percentage of two-year-olds in the 1975-76 2+ adult harvest collection (Table 33) multiplied by the percentage of 2+ adults in the 1975 fall composition counts (Table 36) and 1.1 (a factor to simulate some selectivity against two-year-olds). Thus, 12.9 x 0.68 x 1.1 = 10, the derived percentage of two-year-olds in the population. This percentage, although tenuous since percentage hunter selectivity of two-year-olds in 1975 in the WAH is unknown, reflects the findings of significantly fewer two-year-olds in the 1975-76 harvest collection compared to the 1959-61 collection. Fall percentages of calves derived from Equation 27.

[2] 1970-75, 1975-76.

Table 41. continued

Parameters	WAH 22	WAH 23	WAH 24	WAH 25	WAH 26
INPUT					
Starting Population (1970 Fall)					
Wounding Loss and Unreported Harvest/Waste	0.20,0.25/0.10,0.20^2	0.30/0.20	0.30/0.20	0.30/0.50	0.30/0.50
Wolf Predation	2HS	1HS	1HS	1HS	1HS
Natural Mortality Rates (1970-76)					
Females (5 to 17 mo)					
Males (5 to 17 mo)					
Females (17 to 29 mo)	same	same	same	same	same
Males (17 to 29 mo)	as	as	as	as	as
Females (29 mo +)	WAH 19	WAH 19	WAH 19	WAH 19	WAH 19
Males (29 mo +)					
OUTPUT					
1976 Fall Population	144,000	145,000	299,000	52,000	128,000
Average Wolf Predation Rate (1970-76)					
Calves (5 to 17 mo)	0.100	0.055	0.038	0.072	0.053
Adults (17 mo +)	0.100	0.055	0.038	0.072	0.053
Average Yearling/2+ Female (1971-76)	47.0	48.8	46.0	55.9	49.9
Average 2+ Male/2+ Female (1971-76)	58.7	58.4	60.5	52.7	57.4
% Yearlings (1975)	17.7	18.4	17.1	21.2	18.9
% Yearlings (1976)	21.0	21.3	19.4	29.6	22.4
% Two-year-olds (1975)	14.9	15.9	14.1	19.8	16.7
Average Hunting Mortality (1970-76)					
Females (5 to 17 mo)	0.036	0.047	0.034	0.084	0.065
Males (5 to 17 mo)	0.022	0.029	0.021	0.052	0.040
Females (17 to 29 mo)	0.106	0.128	0.095	0.180	0.146
Males (17 to 29 mo)	0.028	0.034	0.026	0.048	0.039
2+ Females	0.173	0.215	0.153	0.322	0.246
2+ Males	0.240	0.300	0.208	0.475	0.346

Table 41. continued

Parameters	WAH 27	WAH 28	WAH 29
INPUT			
Starting Population (1970 Fall)	250,000	275,000	275,000
Wounding Loss and Unreported Harvest/Waste	0.20,0.25/0.10,0.20[2]	0.30/0.50	0.30/0.30
Wolf Predation	1HS	1HS	1HS
Natural Mortality Rates (1970-76)			
Females (5 to 17 mo)	0.30,0.40,0.70,0.56[3]	0.135,0.40,0.60,0.60[3]	same as WAH 28
Males (5 to 17 mo)	0.30,0.40,0.70,0.56[3]	0.165,0.40,0.60,0.60[3]	
Females (17 to 29 mo)	0.042,0.250[4]	0.042,0.270[4]	
Males (17 to 29 mo)	0.040,0.250[4]	0.040,0.270[4]	
Females (29 mo +)	0.012	0.012	
Males (29 mo +)	0.070,0.030[5]	0.050	
OUTPUT			
1976 Fall Population	72,323	67,000	117,000
Average Wolf Predation Rate (1970-76)			
Calves (5 to 17 mo)	0.063	0.057	0.050
Adults (17 mo +)	0.063	0.057	0.050
Average Yearling/2+ Female (1971-76)	29.0	35.7	35.0
Average 2+ Male/2+ Female (1971-76)	55.4	61.2	63.0
% Yearlings (1975)	5.7	8.8	8.7
% Yearlings (1976)	11.3	10.3	9.8
% Two-year-olds (1975)	9.9	9.7	9.1
Average Hunting Mortality (1970-76)			
Females (5 to 17 mo)	0.045	0.069	0.049
Males (5 to 17 mo)	0.027	0.042	0.010
Females (17 to 29 mo)	0.222	0.211	0.162
Males (17 to 29 mo)	0.056	0.053	0.042
2+ Females	0.196	0.254	0.202
2+ Males	0.281	0.334	0.264

[3] 1970-73, 1973-74, 1974-75, 1975-76.

[4] 1970-74 and 1975-76, 1974-75.

[5] 1970-74, 1974-76.

Runs WAH27 and WAH28 (Table 41) represent simulations which "fit" the limited demographic data. These two simulations suggest a substantial natural mortality rate for caribou from 5 to 17 months of age of 0.30 to 0.70 percent, at least in the years from 1974-76 when herd composition data were available. Wolf predation can account for the apparently higher overwinter natural mortality rate of calves in the years 1974-76 compared to the rates modified from Skoog (1968) only if the estimated wolf predation on calves from 5 to 17 months of age is increased by over 490 percent in Runs WAH27 and 28. Similarly, if the significantly lower percentage of two-year-olds in the 1975-76 harvest collection is indicative of a lower percentage of two-year-olds in the herd, the natural mortality of yearlings from 17 to 29 months of age may have been relatively high during the rapidly declining phase of the WAH (Runs WAH27 and 28). The high average hunting mortality rates from 1970-76 for adult females (estimated at 19 to 25 percent) is comparable to the estimated average hunting mortality rates on adult females during the rapid decline of the NCH from 1969-72. Hunting mortality rates of adult males from 1970-76 in the WAH (estimated at averaging from 28 to 33 percent) are lower than the estimated hunting mortality rates of adult males from 1969-72 in the NCH; this results from high hunter selectivity for adult male caribou only during the early fall in the WAH. Such hunting practices should not produce widely distorted adult sex ratio as were observed in the NCH. Average wolf predation rates on caribou from 1970-76 were estimated at approximately 6 percent, or 29 percent of the average estimated hunting mortality rates (derived from Runs WAH27 and 28).

A tragic part of the decline of the WAH was the high incidence of human waste of healthy, productive caribou by some subsistence users. If 20 percent of the "known" harvest represents the number of caribou that were killed and not utilized by humans and that died as a result of wounding loss due to reckless hunting practices (i.e., shooting at moving groups of animals from long distances, reluctance to attempt to locate wounded animals), and if Run WAH28 represents the actual decline of the WAH from 1970-76, then Run WAH29 predicts that there would have been 75 percent more caribou in the fall of 1976 if the above waste had been avoided. It should be evident that the low population size of the WAH in 1976 was to some degree the result of the extremely poor hunting ethics on the part of certain subsistence users.

9. POPULATION MODELING OF THE WESTERN ARCTIC HERD (1976-1996)

Modeling in the previous section indicates that the sharp decline and present numbers of WAH caribou were created by excessive predation (primarily from hunters). Apparently, the range of the herd can support greater numbers of caribou than presently occupy it. Thus, if predation by humans and wolves is reduced to a low enough level, the herd presumably should begin to increase. The latter assumption has been supported by high calf production and survival in the summer of 1976 (p. 228), as well as apparently high survival of calves during the following winter (J. Davis, Unp. ADF&G Data). Allowing the WAH to recover to a higher herd size as rapidly as possible in order to provide greater sustained harvests seems to be the primary objective of management. The purpose of this section is to analyze the effect of various management alternatives on the population dynamics of the herd.

a. Difficulties with Predictive Modeling

The principal difficulties inherent in trying to predict future trends of the WAH are as follows:

1) The starting values are subject to a considerable degree of uncertainty;
2) Harvest strategies formulated may not in practice be met (i.e., illegal take, wounding loss);

3) Factors, such as recruitment of calves, wolf predation, natural survival, and immigration or emigration, are difficult to accurately determine and may vary from year to year;
4) Compensatory factors that may be operative on the herd are poorly, if at all, understood;
5) Validating the outcome of management strategies may be difficult, given the "state of the art" of estimating caribou numbers.

Thus the uncertainty of the input into the model creates a vast array of possibilities regarding the outcome of any one management strategy.

b. Simulating Future Trends

Mindful of the above mentioned difficulties, modeling of the WAH from 1976-1996 was done in a simplistic fashion by assuming a constant condition of natural mortality rates, of recruitment, and of wolf predation for each run and varying the starting population size in 1976. Compensatory factors were assumed to be negligible. Thus the model run "predicts" future trends only if the set of conditions used in the model are actually operative on the herd, the harvest strategies are correctly met, and the starting herd size is known. A series of such simulations is useful for giving insight into possible trends of the herd given various sets of input; intensive monitoring of the herd will be necessary to determine which set of conditions are actually operative on the herd from year to year. The same model used in the previous sections was used to simulate future trends of the WAH, except that recruitment was entered as a ratio of 55 calves to 100 2+ females rather than a fall percentage.

It should be obvious that, without compensatory factors and given a set of recruitment and natural survival rates that produce an increasing herd, the herd will increase most rapidly with zero mortality from predation. Consequently, if the objective is to allow the herd to increase as rapidly as possible, hunting should be stopped and wolf predation minimized until the desired herd size is reached. Such a strategy would provide larger total harvests over an extended period of time than management plans that allow some human harvest (see Bos 1974a).

To evaluate the effect of various harvest strategies on the herd, the following were considered: (1) no harvest, (2) 3,000 2+ males, (3) 6,000 2+ males, (4) 3,000 either sex, (5) 1,000 yearling males and 9,000 2+ males, (6) 6,000 either sex, and (7) 10,000 either sex. The composition of harvests of both sexes were assumed to equal the average harvest composition from 1970-76. The above harvest strategies are ranked in order of increasing effect on decreasing the rate of increase of the herd in the model runs (Table 42).

Table 42. Important input and output values of model runs of the Western Arctic Herd (1976-96).

Run	1976 Starting Population	Wolf Predation[1]	Natural Survival[2]	Harvest Strategy[3]	Herd Size[4]	Does the ratio of 2+ males/2+ females go below 0.30?[5]
WAH 30	65,000	1NS	High	1	D: Ext (1985)	no
WAH 31	75,000	1NS	High	1	D: Ext (1990)	no
WAH 32	90,000	1NS	High	1	I: 121,000 (1984)	no
WAH 33	90,000	1NS	High	2	I: 127,000 (1994)	no
WAH 34	90,000	1NS	High	3	D: Ext (1985)	yes (1981)
WAH 35	90,000	1NS	Good	1	S: 90,000 (1984)	no
WAH 36	90,000	1NS	Good	2	D: Ext (1990)	yes (1984)
WAH 37	90,000	1NS	Low	1	D: Ext (1987)	no
WAH 38	65,000	0.75NS	High	1	I: 122,000 (1991)	no
WAH 39	65,000	0.75NS	High	2	D: Ext (1991)	no
WAH 40	65,000	0.75NS	Good	1	D: Ext (1995)	no
WAH 41	75,000	0.75NS	High	1	I: 124,000 (1984)	no

NS = wolf predation estimate for 1974-76 described in text (13,492 caribou older than 5 months of age per year).

High = annual mortality rates of 0.04, 0.07, 0.04, 0.05, 0.017, 0.05 for female and male caribou from 5 to 17 months of age, female and male caribou from 17 to 29 months of age, and female and male caribou older than 29 months of age, respectively; Good and Low = mortality rates of 0.135, 0.165, 0.042, 0.048, 0.012, 0.078, and 0.35, 0.38, 0.042, 0.048, 0.012, and 0.078, respectively, for the above cohorts.

1 = no harvest, 2 = 3,000 2+ males, 3 = 6,000 2+ males, 4 = 3,000 either sex, 5 = 1,000 male yearlings, and 9,000 2+ males, 6 = 6,000 either sex, and 7 = 10,000 either sex.

I:, S:, and D: indicate increasing, stable, and declining populations, respectively. Ext (n) indicate extinct populations in year n. Population size and years for increasing herds indicate the first year the herd increases over 120,000 animals.

Yes (n) indicates the year in which the ratio of 2+ males/2+ females goes under 0.30 and then declines to zero. Yes (n/m) indicates the lowest 2+ male/2+ female ratio (m) the herd obtains.

Table 42. continued

Run	1976 Starting Population	Wolf Predation	Natural Survival	Harvest Strategy	Herd Size	Does the ratio of 2+ males/2+ females go below 0.30?
WAH 42	75,000	0.75NS	High	2	I: 120,000 (1987)	no
WAH 43	75,000	0.75NS	High	3	D: 64,000 (1995)	yes (1979)
WAH 44	75,000	0.75NS	High	4	D: Ext (1991)	no
WAH 45	75,000	0.75NS	Good	1	I: 124,000 (1988)	no
WAH 46	75,000	0.75NS	Good	2	D: 70,000 (1988)	yes (1984)
WAH 47	75,000	0.75NS	Low	1	D: Ext (1990)	no
WAH 48	90,000	0.75NS	High	1	I: 124,000 (1980)	no
WAH 49	90,000	0.75NS	High	2	I: 122,000 (1981)	no
WAH 50	90,000	0.75NS	High	3	I: 124,000 (1983)	yes (1980/0.27)
WAH 51	90,000	0.75NS	High	4	I: 126,000 (1984)	no
WAH 52	90,000	0.75NS	High	5	I: 126,000	yes (1978)
WAH 53	90,000	0.75NS	High	6	D: Ext (1989)	no
WAH 54	90,000	0.75NS	Good	1	I: 121,000 (1981)	no
WAH 55	90,000	0.75NS	Good	2	I: 121,000 (1983)	no
WAH 56	90,000	0.75NS	Good	3	I: 120,000 (1986)	yes (1979/0.15)
WAH 57	90,000	0.75NS	Good	4	I: 124,000 (1995)	no
WAH 58	90,000	0.75NS	Good	5	D: 6,000 (1995)	yes (1978)
WAH 59	90,000	0.75NS	Good	6	D: Ext (1987)	no
WAH 60	90,000	0.75NS	Low	1	S: 88,000 (1995)	no
WAH 61	90,000	0.75NS	Low	2	D: Ext (1993)	yes (1982)
WAH 62	65,000	0.50NS	High	1	I: 132,000 (1983)	no
WAH 63	65,000	0.50NS	High	3	I: 123,000 (1986)	yes (1978/0.10)
WAH 64	65,000	0.50NS	High	4	I: 127,000 (1990)	no
WAH 65	65,000	0.50NS	High	6	D: Ext (1986)	no
WAH 66	65,000	0.50NS	Good	1	I: 123,000 (1984)	no
WAH 67	65,000	0.50NS	Good	2	I: 121,000 (1986)	no
WAH 68	65,000	0.50NS	Good	3	I: 103,000 (1988)	yes (1978)
WAH 69	65,000	0.50NS	Good	4	D: 36,000 (1995)	no

Table 42. continued

Run	1976 Starting Population	Wolf Predation	Natural Survival	Harvest Strategy	Herd Size	Does the ratio of 2+ males/2+ females go below 0.30?
WAH 70	65,000	0.50NS	Low	1	I: 127,000 (1996)	no
WAH 71	65,000	0.50NS	Low	2	D: Ext (1995)	yes (1980)
WAH 72	75,000	0.50NS	High	1	I: 130,000 (1980)	no
WAH 73	75,000	0.50NS	High	2	I: 130,000 (1982)	no
WAH 74	75,000	0.50NS	High	3	I: 125,000 (1983)	yes (1979/0.23)
WAH 75	75,000	0.50NS	High	4	I: 129,000 (1984)	no
WAH 76	75,000	0.50NS	High	5	I: 122,000 (1985)	yes (1978)
WAH 77	75,000	0.50NS	High	6	D: Ext (1993)	no
WAH 78	75,000	0.50NS	Good	1	I: 129,000 (1982)	no
WAH 79	75,000	0.50NS	Good	2	I: 124,000 (1983)	no
WAH 80	75,000	0.50NS	Good	3	I: 128,000 (1985)	yes (1979/0.14)
WAH 81	75,000	0.50NS	Good	4	I: 125,000 (1987)	no
WAH 82	75,000	0.50NS	Good	6	D: Ext (1988)	no
WAH 83	75,000	0.50NS	Low	1	I: 123,000 (1987)	no
WAH 84	75,000	0.50NS	Low	2	I: 125,000 (1993)	yes (1982/0.24)
WAH 85	75,000	0.50NS	Low	3	D: Ext (1996)	yes (1978)
WAH 86	90,000	0.50NS	High	1	I: 129,000 (1979)	no
WAH 87	90,000	0.50NS	High	3	I: 124,000 (1980)	no
WAH 88	90,000	0.50NS	High	5	I: 135,000 (1982)	yes (1978/0.07)
WAH 89	90,000	0.50NS	High	6	I: 123,000 (1983)	no
WAH 90	90,000	0.50NS	High	7	D: Ext (1987)	no
WAH 91	90,000	0.50NS	Good	1	I: 121,000 (1979)	no
WAH 92	90,000	0.50NS	Good	3	I: 124,000 (1981)	yes (1980/0.26)
WAH 93	90,000	0.50NS	Good	5	I: 128,000 (1983)	yes (1981)
WAH 94	90,000	0.50NS	Good	6	I: 121,000 (1990)	no
WAH 95	90,000	0.50NS	Low	1	I: 126,000 (1982)	no
WAH 96	90,000	0.50NS	Low	2	I: 123,000 (1984)	no
WAH 97	90,000	0.50NS	Low	3	I: 120,000 (1987)	yes (1979/0.07)

Table 42. continued

Run	1976 Starting Population	Wolf Predation	Natural Survival	Harvest Strategy	Herd Size	Does the ratio of 2+ males/2+ females go below 0.30?
WAH 98	90,000	0.50NS	Low	4	I: 122,000 (1996)	no
WAH 99	90,000	0.50NS	Low	6	D: Ext (1988)	no
WAH 100	65,000	0.20NS	High	1	I: 121,000 (1980)	no
WAH 101	65,000	0.20NS	High	2	I: 128,000 (1981)	no
WAH 102	65,000	0.20NS	High	3	I: 134,000 (1982)	yes (1979/0.25)
WAH 103	65,000	0.20NS	High	4	I: 128,000 (1982)	no
WAH 104	65,000	0.20NS	High	5	I: 132,000 (1983)	yes (1977)
WAH 105	65,000	0.20NS	High	6	I: 123,000 (1986)	no
WAH 106	65,000	0.20NS	High	7	D: Ext (1986)	no
WAH 107	65,000	0.20NS	Good	1	I: 129,000 (1981)	no
WAH 108	65,000	0.20NS	Good	2	I: 134,000 (1982)	no
WAH 109	65,000	0.20NS	Good	3	I: 137,000 (1983)	yes (1978/0.18)
WAH 110	65,000	0.20NS	Good	6	I: 126,000 (1991)	no
WAH 111	65,000	0.20NS	Good	7	D: Ext (1985)	no
WAH 112	65,000	0.20NS	Low	1	I: 126,000 (1983)	no
WAH 113	65,000	0.20NS	Low	2	I: 120,000 (1984)	no
WAH 114	65,000	0.20NS	Low	3	I: 125,000 (1986)	yes (1978/0.01)
WAH 115	65,000	0.20NS	Low	4	I: 126,000 (1989)	no
WAH 116	65,000	0.20NS	Low	6	D: Ext (1990)	no
WAH 117	75,000	0.20NS	High	1	I: 121,000 (1979)	no
WAH 118	75,000	0.20NS	High	3	I: 120,000 (1980)	no
WAH 119	75,000	0.20NS	High	5	I: 121,000 (1981)	yes (1978/0.04)
WAH 120	75,000	0.20NS	High	6	I: 123,000 (1986)	no
WAH 121	75,000	0.20NS	High	7	D: Ext (1991)	no
WAH 122	75,000	0.20NS	Good	1	I: 132,000 (1980)	no
WAH 123	75,000	0.20NS	Good	3	I: 126,000 (1981)	yes (1979/0.25)

Table 42. continued

Run	1976 Starting Population	Wolf Predation	Natural Survival	Harvest Strategy	Herd Size	Does the ratio of 2+ males/2+ females go below 0.30?
WAH 124	75,000	0.20NS	Good	5	I: 125,000 (1982)	yes (1978)
WAH 125	75,000	0.20NS	Good	6	I: 120,000 (1984)	no
WAH 126	75,000	0.20NS	Good	7	D: Ext (1988)	no
WAH 127	75,000	0.20NS	Low	1	I: 122,000 (1981)	no
WAH 128	75,000	0.20NS	Low	2	I: 120,000 (1982)	no
WAH 129	75,000	0.20NS	Low	3	I: 129,000 (1984)	yes (1979/0.12)
WAH 130	75,000	0.20NS	Low	4	I: 128,000 (1984)	no
WAH 131	75,000	0.20NS	Low	6	D: 26,000 (1996)	no
WAH 132	90,000	0.20NS	High	1	I: 125,000 (1978)	no
WAH 133	90,000	0.20NS	High	3	I: 130,000 (1979)	no
WAH 134	90,000	0.20NS	High	5	I: 137,000 (1980)	yes (1978/0.17)
WAH 135	90,000	0.20NS	High	7	I: 121,000 (1983)	no
WAH 136	90,000	0.20NS	Good	1	I: 120,000 (1978)	no
WAH 137	90,000	0.20NS	Good	3	I: 122,000 (1979)	no
WAH 138	90,000	0.20NS	Good	5	I: 125,000 (1980)	yes (1978/0.10)
WAH 139	90,000	0.20NS	Good	6	I: 121,000 (1980)	no
WAH 140	90,000	0.20NS	Good	7	I: 123,000 (1992)	no
WAH 141	90,000	0.20NS	Low	1	I: 122,000 (1979)	no
WAH 142	90,000	0.20NS	Low	2	I: 124,000 (1980)	no
WAH 143	90,000	0.20NS	Low	3	I: 125,000 (1981)	yes (1980/0.22)
WAH 144	90,000	0.20NS	Low	6	I: 120,000 (1986)	no
WAH 145	90,000	0.20NS	Low	7	D: Ext (1988)	no

The effects of four levels of wolf predation and three sets of natural mortality rates on the herd's growth were simulated. Model runs were evaluated by whether the herd increased, decreased, or stabilized and whether or not the 2+ male to 2+ female ratio of the herd dropped below 30/100, a level which could potentially disrupt the breeding success of the herd. The results of model simulations from 1976-1996 are given in Table 42 and are discussed below under separate sections dealing with specific levels of wolf predation.

(1) "High" wolf predation

Given an annual wolf predation rate of 13,492 caribou older than 5 months, herds of 65,000 or of 75,000 animals would continue to decline, even with high natural survival rates and no harvests. A herd of 90,000 animals would increase or stabilize only with good natural survival rates and very limited hunting.

With an annual wolf predation rate of 10,119 caribou older than 5 months, a herd of 65,000 animals could increase only with very high natural survival rates and no hunting (a harvest of only 3,000 males would cause the herd to decline--Run WAH39). A herd of 75,000 animals would decline given the above wolf predation level and relatively low overwinter survival of calves (Run WAH47) or high survival rates and a human harvest of 6,000 adult males (Run WAH43). A herd of 90,000 animals would stabilize with relatively low overwinter survival of calves and no human harvest (Run WAH60) and increase with high overwinter natural survival rates of calves and a harvest of 3,000 animals of either sex (Run WAH49) or 6,000 adult males (Run WAH50); the latter harvest would cause the 2+ male/2+ female ratio to temporarily drop as low as 0.27.

(2) "Moderate" wolf predation

Given an annual wolf predation rate of 6,746 caribou older than 5 months of age, the possible combinations of initial herd sizes, natural mortality rates, and harvest strategies that allow the herd to grow are greatly increased. At this level of predation, the herd would increase in the absence of hunting, even with relatively high overwinter natural mortality of calves and a starting population of 65,000 animals (Run WAH70). Harvests of 3,000 males and 6,000 males, together with high overwinter natural mortality of calves, would cause herds of 65,000 (Run WAH71) and 75,000 (Run WAH85), respectively, to decline. Harvests, as high as 6,000 animals of either sex, would still allow the herd to increase given a starting herd of 90,000 animals and high overwinter natural survival rates (Run WAH89). With relatively low natural survival rates of calves, a harvest of 6,000 males would cause the 2+ male/ 2+ female ratio to drop to as low as 0.07 (WAH97), while a harvest of 6,000 animals of either sex would cause the herd to decline (WAH99).

(3) "Low" wolf predation

Given a wolf predation rate of only 2,698 caribou older than 5 months of age, a herd of only 65,000 animals would increase, even with low overwinter survival of calves and a harvest of 3,000 males (Run WAH113). With the above wolf predation level and high overwinter survival of calves, herd sizes of 65,000 and 75,000 caribou could support harvests as high as 6,000 animals of either sex (Runs WAH105 and WAH120) and still increase, while a herd of 90,000 caribou could support a harvest as high as 10,000 animals of either sex (Run WAH135). Such harvests would delay the time it takes a herd to reach a fall population of over 120,000 animals compared to no harvest, by 6, 7, and 5 years, given an initial starting population of 65,000, 75,000, and 90,000, respectively.

c. Conclusions

The future status of the WAH depends on the level of wolf predation, natural mortality, recruitment rates, and hunting mortality rates that are operative on the herd. Table 42 lists various combinations of the above that have increasing, decreasing, and stabilizing effects on the herd's growth. Under "high" levels of wolf predation and "good" natural survival rates, the herd could decline even in the absence of hunting. "Low" survival rates of calves with "moderate" wolf predation could likewise cause the herd to decline with only limited hunting pressure. The effect of limited hunting on the herd's growth could vary from causing an otherwise increasing herd to decline or accelerating the herd's decline to delaying the herd's increase to a given level by several years. The importance of accurate and precise population estimates in planning management strategies for the herd is evident when evaluating the effect of harvest strategies on herd sizes of 65,000, 75,000, and 90,000 (Table 42). Until the size of the WAH is better known, the lowest estimate of herd size should be used for management purposes. No hunting should be allowed until the rates of wolf predation, natural mortality, and recruitment have been measured precisely and are definitely high enough to support the hunting pressure and still allow the herd to increase (the management objective). A wolf predation level of only 2,700 and 6,700 caribou older than 5 months of age would greatly accelerate the herd's rate of increase compared to higher wolf predation levels. The decreased individual wolf predation rate could potentially result from wolves switching to alternative prey species (and hence maintaining their population numbers as in the NCH) and/or reducing their total food intake [and hence suffering reduced reproductive success and increased mortality of adults (Mech 1977)]. In the absence of "natural" controls on wolf predation, aerial hunting of wolves could be an effective, and perhaps necessary, method of allowing the herd to increase while still maintaining limited hunting.

C. SUMMARY

Modeling of the WAH suggested a gradual decline from approximately 350,000 to 400,000 animals in 1961 to approximately 250,000 to 300,000 animals in 1970 followed by an accelerated decline to 60,000 to 100,000 animals in 1976. A combination of natural survival rates of approximately 0.25 to 0.40 for caribou from 5 to 17 months of age, together with relatively "high" hunting mortality and "moderate" wolf predation, is a possible explanation for the herd's decline during the sixties. Reduced fall percentages of calves, believed to result from lower conception rates and/or natural survival of calves to 5 months of age, may also have contributed to the herd's decline during that period. From 1970 to 1976, the rates of hunting mortality and wolf predation increased; this predator-prey relationship caused the herd to rapidly decrease. Both the 1975 and 1976 composition data and the decreased proportion of two-year-olds in the 1975-76 harvest collection suggest relatively high natural mortality rates in the younger age classes of caribou during this time, an additional factor contributing to the herd's rapid decrease.

Fall calf percentages were high in the 3 years of data collection during the period 1970 to 1976, suggesting that mortality of animals older than 5 months of age was the chief dampening factor on the herd during this time. The estimated hunting mortality was over three times greater than the estimated wolf predation on animals older than 5 months of age.

The future of the herd will depend on its reproductive success, natural survival rates, wolf predation, and hunting mortality. Prediction of future trends and the possible effects of harvest strategies is hampered to a degree by the wide uncertainty of the herd's population size. Human harvest has been greatly limited since the 1975-76 season and a lower magnitude of wolf predation from that estimated in the model runs from 1970-76 may be necessary if the herd is to increase very rapidly in the immediate future.

CHAPTER 8. CONCLUSIONS

Specific conclusions of the individual chapters have been previously given in the chapter summaries. The following is a synthesis of those conclusions, some management implications, and future research recommendations.

A. POPULATION DYNAMICS OF ALASKAN CARIBOU HERDS

Despite the limitations of the available data, several conclusions regarding herd dynamics could be ascertained through deterministic modeling. The findings form the basis for the schematics of herd growth presented below.

1. CARIBOU WITHOUT PREDATION

Under conditions without predation, caribou and reindeer will presumably increase in numbers until external forces halt increases and possibly cause abrupt declines. On predator-free islands overwinter mortality related to the relative abundance of food has been the chief regulating factor of *Rangifer* populations (Klein 1968, Reimers 1977). The role of disease and parasites in regulating numbers is poorly known; some diseases and abnormalities, such as brucellosis and mandibular lesions which occurred at relatively high incidences in the WAH during its "peak," may be proximately associated with the quality of the range (Neiland et al. 1968; Doerr and Dieterich, in press). Thus range appears to be the ultimate regulating factor on caribou in predator-free environments.

As herd size increased (and presumably absolute forage abundance and quality deteriorated), a decrease in the production and/or natural survival of calves to mid-summer or fall occurred in the SMIH (Klein 1968) and the NCH (pp. 104-111). Possible factors responsible for this decrease include lower conception rates, increased neonatal mortality, increased incidence of abandonment, increased incidence of placental retention, increased social aggression, and smaller and weaker calves at parturition. Further evidence of the effect of the environment on calf production was shown by the increased rates of conception in younger females when Nelchina caribou were transplanted to Adak Island (Chapter 3). However, decreased calf production to the fall (excluding the effects of predation) appeared to have only a minor affect on decreasing the rates of growth of the NCH and the SMIH.

In the NCH, increased overwinter mortality of calves, excluding predation, was found to have an important effect on checking the herd's growth. Additional support for the role of overwinter natural calf mortality in regulating caribou populations may be found in the WAH where natural mortality rates of caribou from 5 to 17 months of age were estimated to range from 0.25 to 0.60 percent in many years since 1961 compared to estimated mortality rates of less than 0.15 in rapidly increasing herds. It is postulated here, that for large increasing herds, increased *overwinter* natural mortality of calves reflects deteriorating range and herd conditions and is an important *initial* regulating mechanism of herd growth. The role of increased natural mortality of adults is poorly understood due to limitations of the data base. However, evidence in both the WAH and NCH suggests increased natural mortality on the younger sub-adult age classes during the latter stages of the decline. The above implies that the condition of caribou entering the winter and the relative abundance and quality of winter forage are critical aspects of caribou population ecology. It should be emphasized that the ultimate role of increased natural mortality on regulating caribou herds could not be determined due to excessive predation in both the NCH and the WAH.

Skoog (1968) and Haber (1977) have emphasized the role of dispersal in regulating caribou numbers. This hypothesis could not be examined in the declines of the WAH and NCH because of the heavy influence of predation and because emigration could not be detected due to limited reconnaissance of the herds. If emigration did occur during the declines, it was of no apparent consequence as surrounding herds did not increase. Furthermore, modeling of the NCH showed that increased natural mortality rates and decreased production of calves will occur in spite of or prior to dispersal. Range conditions and social factors should presumably be the principle cause of dispersal.

2. CARIBOU AND WOLVES

If the estimates of wolf predation used in the model for the NCH and the WAH are at all realistic, wolf predation was only a minor mortality factor during the peak of the herds and contributed little to their initial declines. With low herd sizes, wolf predation can theoretically hold a population at a low level or contribute greatly to its decline. In the case of the NCH, it appears caribou have been able to increase, at least initially, since the decline in spite of "high" wolf numbers, due to the fact that wolves began taking greater proportions of moose. The effect of the altered wolf:caribou ratio on wolf predation in the WAH remains to be documented. Since aerial wolf hunting has been stopped and human hunting of caribou greatly limited, the WAH provides a test case in which to determine the effect of a substantial reduction of caribou on the wolf population.

It may be argued that the effect of wolf predation on a large herd cannot be assessed from the analysis of the WAH or NCH since humans were exerting some control on the wolf populations. However, wolves have a high reproductive capacity, are territorial, and can limit their numbers to some degree (Mech 1970). Moreover, wolf densities in the unexploited McKinley Park (Murie 1944, Haber 1977) are similar to wolf densities in the Nelchina Basin from 1964-72 (Table 6) and to the estimated peak wolf densities in the southern half of the WAH's range from 1965 to 1967 (pp. 226-227).

In systems without the influence of human hunting, wolves will presumably hold caribou at low densities until factors such as immigration, increased reproduction or natural survival rates, or numerical or functional responses on the part of wolves allow the herds to increase. Once the herd reaches a "critical level," wolf predation is no longer able to control the herd's growth. Under these conditions, other presumably range-related factors discussed in the previous section are necessary for control.

The above conclusions regarding the effect of wolves on caribou herds are essentially a repetition of Haber (1977). Several differences in the interpretation of the data and modeling of the herds need to be elaborated here, however. First, production of calves is not constant within the herds over time or between herds as assumed by Haber (1977). Second, low apparent survival rates of calves (especially from 5 to 12 months), in at least the NCH and the WAH, are more a reflection of environmental conditions, excluding wolves, than they are of increasing wolf predation. This assertion can be disproven by predation studies that show considerably higher incidences of caribou calves in the winter diet of wolves than those cited earlier (pp. 50-51) or those found by Haber (1977) in McKinley Park. A third point emphasized by Haber (1977) concerning the role of emigration in causing herds to increase is largely conjectural and dramatic changes in herd size in the literature may be related to the immense uncertainties in estimates of caribou numbers. The importance of the role of sudden changes in the regime of natural mortality and reproduction rates in caribou population eruption and declines also deserves attention.

3. CARIBOU AND MAN

Hunting mortality of 1+ caribou played a major role in the gradual declines of the NCH from 1962-69 and the WAH from 1961-1970, and was the major adult mortality factor in the subsequent rapid declines of both herds. It is concluded that the present low sizes of these herds are the result of overhunting, for it can hardly be argued that caribou have evolved the capacity to cope with hunters largely utilizing snowmachines, airplanes, motor boats, and all-terrain vehicles (Glenn 1967, Bos 1973) and capable of exerting an annual mortality rate exceeding 20 percent of the adult population. In addition, hunting harassment throughout the winter may be detrimental to the survival of caribou (Thomson 1971, 1973; Shea 1978). The suggested higher natural mortality rates of younger age classes during years in which harvests substantially reduced the size of the herds (1969-1972 in the NCH, 1974-76 in the WAH) may reflect to some degree the stress of harassment from hunting and the high orphaning of calves as a result of hunter selectivity for mature adults. During the rapid decline of both the NCH and the WAH, human hunting-induced mortality was estimated to be over three times higher than wolf predation on caribou over 5 months of age. Moreover, hunting mortality was shown in this study to be unaffected by the overall density of caribou as long as humans had access to the herds. Severely reduced bag limits and seasons are necessary to reduce human take and preserve the viability of caribou herds. The above findings are in agreement with those of Bergerud (1974c) and Haber (1977) that predation, especially human harvest, is the chief factor responsible for the low number of caribou in Alaska today.

4. CARIBOU, WOLVES, AND MAN

With the presence of two relatively effective predators, mortality on caribou is increased, and the herd sizes and the regimes of natural survival and reproduction rates under which the herd can increase are more limited. Haber (1977) has discussed many of the implications of the effect of wolves and man on caribou in Alaska. With the present low abundance of caribou in Alaska, predation has the greatest potential for controlling the size of many herds, and a substantial reduction in wolf and human predation should allow herds to obtain higher population levels.

B. SAMPLING TECHNIQUES

It is obvious from the analysis presented that understanding of caribou population dynamics will not progress far without both better techniques to obtain the required demographic data and a more intensive and representative sampling effort. Modeling showed conflicting discrepancies in many of the various sets of data and the wide uncertainty of the estimates makes the determination of accurate regimes of reproduction and natural survival rates (important statistics for wildlife management) practically impossible without subjective interpretation of the data (see Skoog 1968, Haber 1977, Chapters 2, 3, and 7). To a large degree, the problems involved with collecting data relate to limitations of manpower, funding, or physical phenomenon such as weather; on the other hand, much data (i.e., composition counts) have been collected for years largely ignoring basic principles of sampling design, such as those described by Cochran (1963) and Kish (1965). A critique of current data techniques is as follows:

1) The direct count extrapolation technique widely used in Alaska has limited value for detecting change in herd size and for establishing harvest quotas. Yearly fluctuations are lost in the potential variance of the population estimate; changes in herd size that may be significant to the welfare and management of the herd may not be readily detected. Population simulation suggests that four

of five estimates of the NCH since 1971 have underestimated the size of the herd by 30 to 40 percent or more.

2) Alternative methods of estimating caribou numbers through aerial sampling, although unbiased, have wide variances that similarly make understanding and management of caribou herds difficult (Siniff and Skoog 1964; Davis and Reynolds 1977; G. Calef, pers. corr.; Chapter 2).

3) It is the opinion of the author that aerial censuses of post-calving aggregations combined with aerial sampling of the remainder of the herd's range could, with good weather conditions, produce accurate and precise estimates of caribou numbers. The amount of aerial sampling necessary to obtain very precise estimates may be prohibitively costly in terms of money and manpower, however.

4) Assumptions that age and sex groups were randomly mixed during the fall and that the proportion of adult females were randomly distributed in the post-calving concentrations were shown to be invalid in the 1976 WAH composition counts. In the NCH, 3+ males showed distinct segregation from the calf-adult female groups shortly after the peak of the rut. The above suggests that much of the composition data may be unreliable. This was verified by discrepancies among sets of composition data revealed through simulation modeling and analysis.

5) The segregational patterns of the herd need to be well defined and representative sampling schemes adopted to assure that calving, post-calving, and late winter calf/adult female ratios are not biased.

6) Harvest statistics collected from 16 years in the NCH revealed trends similar to those shown by the fall composition data in the percentage of 3+ adult females, the percentage of yearlings and two-year-olds combined, and the percentage of total males. Thus, harvest statistics may have some utility for long-term trend analysis of herd composition when the harvest seasons and bag limits are relatively comparable over time. Accurate trends in the percentages of 3+ males could not be determined from the harvest data; this resulted from changes in hunter selectivity for 3+ males over time.

7) Proportions of calves, yearlings, and two-year-olds in the harvest mandible collections are biased by hunter selectivity and hence are not representative of the proportion of these cohorts in the actual herd. Fall percentages of calves in the herd could not be accurately determined from subsequent age classes in harvest mandible collections in the NCH.

8) The estimated total harvest was poorly correlated with herd size in both the WAH and the NCH.

9) Several models indicated that the 3+ adult age structure of harvest collections often do not accurately represent the 3+ adult

age and sex structure of the herd. It appears more accurate adult age structure information can be obtained by directly collecting animals for age-determination as was done by Miller (1974).

10) An evaluation of the influence of the age and sex of the animal, reader bias, the age of the collection, and which tooth is used for age determination using cementum annulations is presented elsewhere (Doerr, in prep.). A comparison of ages assigned by two readers suggested that over 80 percent of the ages assigned by each reader in this study were within 1 year of the correct age of the animal. Inaccuracies in the age-determining technique may prevent detection of missing age classes; however approximate age structures of the harvest collections can be determined.

11) Collection of total harvest and harvest composition data is valuable for estimating hunting mortality rates. Present estimates of total harvest allow estimation of minimum human-induced mortality; however, an obvious need exists to evaluate the magnitude of unreported harvest, wounding loss, and wanton waste in caribou herds throughout Alaska. The accuracy of sex ratios derived from harvest report tickets in predicting the actual sex ratio of the harvest needs to be evaluated. The chronology of the harvest may be useful in determining the sex ratio of the harvest in some herds.

12) Adult mandible lengths, commonly used to sex-determine caribou throughout North America, may not be a valid sex-determining technique in some Alaskan herds due to genetic or environmental factors.

C. MANAGEMENT IMPLICATIONS

In the declines of both the WAH and the NCH, a similar pattern of wildlife management practices by the State of Alaska was revealed: allow continual large harvests until the herds were reduced to low levels, whereupon greatly restricted harvests were necessary to assure the survival of these herds. Furthermore, problems with excessive waste of caribou resources by many subsistence users were ignored since at least the early 1960's in the WAH (Lent 1966b), although it was probably a relatively substantial (and certainly unnecessary) mortality factor on the herd during later stages of its decline. To a degree, the apparent lack of concern over the hunting mortality on the herds stemmed from a long-held belief that large caribou herds could not be overhunted (Lent 1966b, Glenn 1967). Such a belief is clearly wrong; as demonstrated in this study, caribou are exceptionally vulnerable to hunting. In fact, the WAH may have been declining since the early 1960's partially as a result of hunting. The increase in human population throughout Alaska (Alonzo and Rust 1976), together with greater access to "remote" places, makes the monitoring and regulation of <u>total</u> hunting mortality essential to the survival of caribou in Alaska.

It seems paradoxical that ADF&G developed a census technique that estimates "minimum" herd sizes (Pegau and Hemming 1972) which aid in planning conservative harvest strategies, yet two major herds have since declined to low levels, largely as a result of overhunting. It is my assertion that the declines of both the NCH and the WAH should have come as no surprise, given the herd size estimated for the NCH in 1967 (Hemming and Glenn 1968) and the WAH in 1970 (Pegau and Hemming 1972) and the literature available on wolf predation and natural mortality and reproduction rates in caribou (Bergerud 1967, 1971b; Rausch 1967, 1968, 1969a,b; Kelsall 1968; Skoog 1968; and others). The "unexpectedness" of the decline of both herds can be attributed largely to the fact that the mortality factors on the herds were not assessed and the population dynamics of the herds were not modeled. Obviously some sets of reproduction and mortality rates would have indicated declining populations in both herds. To avoid overhunting leading to similar declines in the future, it is essential that the demographic data be evaluated and all Alaskan caribou herds modeled. The simple models described in this text may be useful for this purpose; the sets of natural mortality rates given in Table 42, for example, can be used to represent different regimes of natural survival rates and to gain insight into possible trends in the herds. Henny et al. (1970) have presented an excellent discussion of the use of structural models for determining possible trends in populations. Additional population models have been developed or applied by Dean and Gallaway (1965), Bos (1974a), Bunnel et al. (1975), Walters et al. (1975), and Haber (1977).

Given the difficulties with present sampling techniques, as well as the lack of knowledge concerning range relationships, carrying capacity, and compensatory factors, maximum sustained yield is not a realistic management strategy. Harvests attempting to maintain stable, highly productive herds will probably "underharvest" or "overharvest" the herd in any given year due to the above difficulties. "Underharvesting" can be corrected by liberal bag limits and seasons in following years. "Overharvesting" can have serious consequences since it may reduce the herd to levels where natural mortality, predation, and other factors cause further decline and require severely restricted harvests before the herd can regain its former size. A further complicating factor to management is the findings of this text that overwinter natural mortality can be an important regulating factor of caribou. Thus the outcome of fall and winter harvests, in terms of the number of animals in the herd at parturition, cannot be assessed until survival through the winter is known. Since the relative availability of forage is influenced by weather (Bergerud 1974a, LaPerriere and Lent 1977) [an unpredictable factor], carrying capacity and the best harvest strategy in any given year may be difficult to assess. This is a common dilemma of wildlife management in northern ecosystems.

Survival of caribou seems best enhanced by a reduced harvest rate which allows herds to increase to relatively high population levels. Certainly large productive herds are desirable in that normal wolf populations can exist synchronously with relatively large human harvests. The feasibility of maintaining these large herds, in the face of possible range deterioration and reduced natural survival and reproduction, is uncertain. Short-term liberal harvests could be implemented to reduce the size of the herd if a reduction in range or herd quality becomes evident.

Obviously sustained yield management requires intensive (and expensive) monitoring. Haber (1977) has argued that single herd management is biologically unsound and the herds must be managed collectively. He asserts that some herds should be allowed to increase beyond range capacity, triggering immigrations into other smaller herds which will then subsequently increase following an evolved pattern of population regulation. Such alternative management strategies merit considerable attention.

It is extremely critical to evaluate the present role of predation and hunting in depressing small caribou herds throughout the state. A temporary reduction in the level of mortality by predators may be very beneficial in allowing certain herds to increase to larger population sizes.

A final important consideration is the need for greater communication between rural residents and game agencies. It is hoped, perhaps optimistically, that the excessive waste of caribou observed in the Kiana Hills, will not be repeated again. My worst suspicions are, however, that waste of game resources commonly occurs in many aspects of subsistence hunting and fishing. Such situations cannot be ignored. Game resources are finite in Alaska as elsewhere. All hunters should consciously utilize the animals killed and avoid unnecessary harassment of animals with motorized vehicles. The rapidity of the WAH's decline was largely caused by those people dependent on the herd for subsistence needs. These people now face long-term harvest reductions if the herd is to survive.

D. NEEDS FOR FUTURE RESEARCH

In order to better understand the population ecology of caribou in Alaska, gaps in the present knowledge of caribou ecology need to be researched. An analysis of the "state of the art" of population ecology and recommendations for future research were formulated during a workshop from 17 to 19 November 1977 at the University of Alaska, Fairbanks (Klein and White 1978). Several other important research needs are mentioned here.

Probably the greatest gap in understanding caribou population dynamics is the lack of knowledge concerning compensatory mortality and reproduction. The influence of compensatory factors on the effects of hunting and wolf predation can be presented as two questions: (1) What proportion of the animals killed would have died of other causes before producing young (in the case of females) or successfully breeding (in the case of males)? (2) What proportion of the animals killed are "replaced" through enhanced natural survival or reproduction by the remainder of the herd? These two questions must be answered to validly interpret the ultimate effects of hunting and predation. Some insight into the former question can be gained by examination of the animals killed; the latter question can only be answered by experimental conditions designed to test the effect of various herd sizes and predation and hunting levels on reproduction and natural survival of caribou.

Assessing the rate and composition of kill by wolves requires greater research. The seasonal chronology of kill rates and the abundance of wolves on summer and winter caribou ranges in herds throughout Alaska merits special consideration, especially in small herds exhibiting poor survival rates and herds with high wolf:caribou ratios. The effect of caribou migration on wolf predation needs to be clarified. Natural factors responsible for altering the functional and numerical responses of wolves are especially important to understanding the population ecology of caribou and better assessing the role of predation in caribou fluctuations.

The effect of hunting disturbance on caribou should be researched in lieu of findings in this study. Special emphasis should be given to delineating critical periods when disturbance may be most harmful and to determining the amount of harassment that commonly accompanies various methods of hunting, especially hunting with snowmachines.

The need for range evaluation of all herds is evident. Research is also needed to investigate the condition of the animals (i.e., conception rates, body fat reserves, body size) in various herds throughout Alaska. The relationships between range and herd quality and the demographic parameters of the herd, especially the regimes of reproduction and natural survival rates of the herds, should be the ultimate goal of such research. Similarly the importance of disease and parasites on the survival and reproduction rates of caribou needs to be evaluated more critically, as does the effect of weather. In particular, factors of weather which are most critical to the reproduction and natural survival rates of caribou need to be determined.

Sex ratios of calves, yearlings, and two-year-olds should be specifically investigated, in light of findings presented here. Accurate determination of natural survival rates of adults and changes in adult survival rates as herds flucuate in size is of paramount importance.

It is hoped that, through wise management and the protection of caribou habitat, large herds will roam the tundra and taiga biomes in the future and the integrity of northern ecosystems will be preserved.

APPENDIX A

ESTIMATING THE COMPOSITION OF THE NCH HARVESTS IN 1958, 1967, AND 1972

No aged collections of the NCH harvests were available for 1958 and 1967. Consequently, the age structure of the harvests in those years were estimated indirectly. The available information on the harvests in these years is summarized in Table 3 (Chapter 2). Percentage of males in the harvest in 1958 (69.8 percent) is estimated using Equation 12 (Table 4). The percentage of 3+ males in 1958 and 1967 is the average value (41.3 percent) of 16 years of harvest data (Table 4). Percentage of calves in 1958 and 1967 (9.6 and 5.8 percent, respectively) is calculated from Equation 10 (Table 4). Fifty-four percent of the calves were assumed to be males. The percentage of 3+ females in 1958 and 1967 (18.4 and 27.4 percent, respectively) is estimated from Equation 13 (Table 4). The percentage of male and of female yearlings and two-year-olds in 1958 and 1967 was obtained by subtracting the percentage of calves, 3+ males, and 3+ females from the estimated sex ratios of the harvests. An assumed yearling:two-year-old ratio of 13.3:14.7 (Table 4) was used to determine the individual percentages of yearling and two-year-olds in the harvests in those years. The above ratio was used for both males and females since the sex ratio of yearlings and of two-year-olds in the NCH harvest is nearly identical (pp. 42 -45). The results are:

APPENDIX A (continued)

1958 Harvest

Age	Male	Female	Total
0	182	154	336
1	388	122	510
2	430	133	563
3+	1,445	645	2,091
Total	2,445	1,054	3,500

1967 Harvest

Age	Male	Female	Total
0	128	104	232
1	388	96	484
2	432	104	536
3+	1,652	1,096	2,748
Total	2,600	1,400	4,000

In 1972, a sample of 79 male caribou killed by hunters is used to estimate the age structure of the male harvest (Bos 1973). Male:female sex ratios of 54.6:45.4, 63.5:36.5, and 62.8:37.2 for calves, yearlings, and two-year-olds, respectively, (the sex ratios from all harvest collections combined) were used, together with the estimated total number of females in the harvest (Table 3), to calculate the number of female calves, yearlings, and two-year-olds in the harvest. The number of 3+ females in the harvest was then estimated by subtracting the above from the estimated number of total females in the harvest. The results are:

APPENDIX A (continued)

1972 Harvest

Age	Male	Female	Total
0	10	8	18
1	20	11	31
2	40	24	64
3+	328	114	442
Total	398	157	555

APPENDIX B

CALCULATING OVERWINTER CALF MORTALITY IN THE NELCHINA CARIBOU HERD (1955-60)

Mortality rates for calves from October to April in the NCH were calculated for the years 1955-56 through 1959-60 using the fall composition data given in Table 1 and the late winter composition data calculated by Skoog (1968:623-624). The percentages of 3+ males in the fall were estimated using the observed value in 1956 and the predicted values from Equation 2 in the years 1955 and 1957 through 1959. The percentages of 3+ females in the fall were estimated from the observed values in 1956 and 1959 and from Equation 6 in the years 1955, 1957, and 1958. Subtracting the observed percentages of calves (adjusted for 3+ males not present in the counts) and the estimated percentages of 3+ males and 3+ females from 100 gave the estimated percent of yearlings and two-year-olds. The percentages of female one- and two-year-olds were estimated in two ways:

1) Assuming equal sex ratios of yearlings and two-year-olds; and
2) Assuming a ratio of yearlings:two-year-olds of 1.24:1.00 (Skoog 1968) and 45 and 50 percent of the yearlings and the two-year-olds, respectively, were females (Skoog 1968). Mortality of calves from October to April (M) were then calculated as:

APPENDIX B (continued)

$$M = [1 - (A/B)] \times 100,$$

where,

A = the calf/1+ female ratio in late winter from Skoog (1968:623), and

B = the calf/1+ female ratio in the fall derived above.

Both A and B were adjusted to the "original female base" assuming mortality rates of 5 and 8 percent for 1+ females from parturition to November and from parturition to April, respectively (Skoog 1968:623). The results of the computations are compared below with calculations by Skoog (Ibid.:624).

October-April Mortality Rate of Calves

Year	50:50 Sex Ratio Yearlings	55:45 Sex Ratio Yearlings	Skoog (1968)
1955-56	-16.0	-13.5	--
1956-57	18.5	20.0	21
1957-58	10.0	12.0	13
1958-59	11.0	13.0	15
1959-60	21.0	23.0	22
Ave. 1955-60	9.0	11.0	--
Ave. 1956-60	15.0	17.0	18

APPENDIX C

FORMULAS USED TO CALCULATE MEANS AND VARIANCES OF 1976 WESTERN ARCTIC HERD COMPOSITION DATA

Percentages of Post-Calving 2+ Females

The percentage of 2+ females in the post-calving aggregation is generated weighting each group classified by the sample size of the composition count (hence, assuming equal sampling intensity). The variance is calculated weighting the square of the differences between each group and the mean by the number of animals classified in the group, modifying an equation from Steele and Torrie (1960: 181) (S. Harbo, pers. comm.). The equations are as follows:

$$P_f = \left(\sum_{i=1}^{g} F_i \right) / \left(\sum_{i=1}^{g} N_i \right)$$

$$V(P_f) = [(N_T - \sum_{i=1}^{g} N_i)/N_T] \quad [S^2/g]$$

$$S^2 = \left(\sum_{i=1}^{g} N_i \, (P_{f_i} - P_f)^2 \right) / \left(\sum_{i=1}^{g} N_i \right) ,$$

where

P_c = estimated percentage of 2+ females of total 1+ caribou on the post-calving aggregation,

APPENDIX C (continued)

F_i = number of 2+ females classified in the ith group,

N_i = number of 1+ caribou classified in the ith group,

g = number of groups classified, and

N_T = estimated number of 1+ caribou in the post-calving aggregation.

Fall 2+ Female Composition Ratios

Individual Stratum

$$r_{y/f} = \left(\sum_{i=1}^{g} Y_i\right) / \left(\sum_{i=1}^{g} F_i\right)$$

$$V(r_{y/f}) = [(N-n)/N)] \cdot g \cdot \left(1/\left(\sum_{i=1}^{g} F_i\right)^2\right) \cdot s_q^{\,2}$$

$$s_q^{\,2} = \left(\sum_{i=1}^{g} (y_i - r_{y/f} \cdot F_i)^2\right) / (g - 1) ,$$

where

Y_i = number of animals other than 2+ females classified in the ith group,

F_i = number of 2+ females classified in the ith group,

g = number of groups in the stratum,

N = estimated number of total caribou in the stratum, and

n = number of caribou classified in the stratum.

APPENDIX C (continued)

Combined Stratum

(Assuming ratios among strata are equal and combining all groups to calculate ratios and variances)

$$r_{y/f} = \left(\sum_{j=1}^{h} \sum_{i=1}^{g_j} Y_{ij} \right) / \left(\sum_{j=1}^{h} \sum_{i=1}^{g_j} F_{ij} \right)$$

$$V(r) = [(N_T - n_T)/N_T] \cdot g_T \cdot \left(1 / \left(\sum_{j=1}^{h} \sum_{i=1}^{g_j} F_{ij} \right)^2 \right) \cdot s_q^{\,2}$$

$$s_q^{\,2} = \left(\sum_{j=1}^{h} \sum_{i=1}^{g_j} (Y_{ij} - r_{y/f} \cdot F_{ij})^2 \right) / (g_T - 1) \quad ,$$

where

Y_{ij} = number of animals other than 2+ females classified in the ith group of the jth stratum,

F_{ij} = number of 2+ females in the ith group of the jth stratum,

N_T = estimated fall population,

n_T = total number of caribou classified in the fall composition counts,

g_T = total number of "groups" classified,

h = number of strata, and

g_j = number of groups in the jth stratum.

APPENDIX C (continued)

The above formulas are used to calculate herd ratios and variances for calves/2+ females, 2+ males/2+ females, and all animals other than 2+ females/2+ females.

Combined Stratum

Assuming ratios among strata are unequal and weighting the variances of the individual stratum gives

$$r_{y/f} = \sum_{i=1}^{K} W_i \, r_{y_i/f_i} \quad \text{, and}$$

$$V(r_{y/f}) = \sum_{i=1}^{K} W_i \quad V(r_{y_i/f_i}) \text{ ,}$$

where

W_i = estimated number of caribou in the ith stratum over the estimated number of caribou in all strata,

r_{y_i/f_i} = ratio of the ith strata,

$V(r_{y_i/f_i})$ = variance of the ith strata, and

K = number of strata.

Only the yearling/2+ female ratio for the herd is calculated with the above equation. Strata 1 and 3 are combined into one stratum. The ratio and variance of the yearling/2+ female ratio in stratum 2

APPENDIX C (continued)

is assumed to represent 23 percent (4,000/17,500) of the entire herd and the ratio and variance of the ratio in strata 1 and 3 combined are assumed to represent the remainder of the herd.

APPENDIX D

DESCRIPTION OF CARIBOU KILLS EXAMINED IN THE KIANA HILLS, NORTHWEST ALASKA, 20 MARCH TO 3 APRIL 1976

The following is a description of caribou kills examined in a 22 km^2 area, ca. 5 km southwest of Deviation Peak. The extreme boundaries of the area searched are 66°57.5'N to 67°00'N and 161°05'W to 161°11'W. Not all the caribou carcasses within these boundaries were examined. Of the caribou kills examined, all are believed to be the result of human hunting. Most hunters hunting in this area were from Noorvik, Kotzebue, and Kiana (pers. obs., pers. comm. with people in those villages). All caribou examined had died since September 1975 and most deaths were believed to have occurred since 1 January 1976.

The dates listed below are the dates the kills were examined. All caribou kills in a "kill site" were lying within a 10 m radius circle unless otherwise stated. Only recent scavengers (Sc =) are listed. The first number of caribou is the minimum number of caribou killed at the kill site. Kill sites 1 to 58 were examined by the author; descriptions of kill sites 59 to 62 were from notes by J. Shea.

Foreleg, as used here, refers to the portion of the front and hindlegs distal to the radius and the tibia, respectively.

APPENDIX D (continued)

Date	Kill Site	Description
20 March	1	Four caribou. One rumen pile; three ungutted adults. Two adults of unknown sex were over 50 percent scavenged. Remaining adult was a two-year-old male with no scavenging loss, no back fat and 77.7 percent femur fat content. Sc = raven (*Corvus corax*).
20 March	2	Five caribou. Four rumen piles; one 11 year old eviscerated female; one ungutted 4 year old female; found ca. 100 m from (1). Eleven year old female was 25 to 50 percent scavenged and had a femur fat content of 86.3 percent. Four year old female was less than 10 percent scavenged, pregnant with 0.68 kg, 37 cm fetus, had little subcutaneous back fat, and a femur fat content of 86.3 percent. The 4 year old cow appeared to be a more recent kill than the 11 year old cow. Sc = ravens.
20 March	3	One very small calf with 13 cm velvet antlers found ca. 200 m from (2). Calf appeared to be an old kill, maybe from the fall, and was over 50 percent eaten by scavengers. Impossible to determine sex or if eviscerated. Femur fat content of 58.3 percent.
20 March	4	Two caribou. Found two caribou heads minus the lower mandibles, one foreleg, and one complete hide.
20 March	5	Four caribou. Found four rumen piles, nine forelegs, and one fetus (weight 0.45 kg, total body length = 33 cm).
20 March	6	One antlerless adult female. Ungutted, one side and back flank scavenged (25 to 50 percent loss). Femur fat content was 74 percent. Sc = ravens.
20 March	7	Three adult male caribou. Two males with both the front and hindquarters taken; one male with both hindquarters and one front quarter taken.

APPENDIX D (continued)

Date	Kill Site	Description
20 March	8	Three caribou. Two adults of unknown sex with only the heads left in the field. One 6 year old female, eviscerated, 25 percent scavenged, 0.6 cm subcutaneous back fat, 87.0 percent femur fat content.
20 March	9	One rumen pile. Sc = ravens.
		(1) through (9) were found within a 1.6 km^2 area, on wind-swept tundra with an average snow depth of ca. 6 cm.
21 March	10	One caribou leg hanging from a spruce tree with a steel trap set underneath it.
21 March	11	One yearling female, ca. 70 m south of camp, ungutted, little back fat, small 3 cm scavenger's hole in one side (former bullet hole?), viscera completely eaten inside carcass, possibly by shrew (*Sorex* spp.) or weasel (*Mustela* spp.). 71.4 percent femur fat content. Average snow depth ca. 25 cm.
21 March	12	One yearling caribou. Indeterminate sex. Ungutted. Over 75 percent loss to scavengers. 79.7 percent femur fat content. On the night of 20 March, five wolves visited this carcass, tore off three forelegs dragged them 7 to 15 m from the carcass, and chewed on the forelegs. One wolf urinated on the carcass. Sc = wolves, fox (*Vulpea fulva*), raven, and shrew.
21 March	13	Two caribou, ca. 45 m from (12). One 3 year old female, ungutted, propped on its back with its legs in the air. Small hole (bullet hole?) in one side; several holes in its other side were caused by a shrew(s). 55.1 percent femur fat content. Second caribou was a 7 year old female, largely scavenged on one side; one front and hind leg was missing; rump and back had been scavenged, rumen was intact. 74.3 percent femur fat content. Wolves had visited these carcasses the night before and eaten nothing on them. Sc = raven, shrew, and wolves.

APPENDIX D (continued)

Date	Kill Site	Description
22 March	14	One adult caribou. Either young male or adult female, ungutted, 50 percent loss to scavengers. Sc = ravens.
22 March	15	Three female adult caribou, ca. 100 m from (14). All gutted. One antlerless female, age 5 years, less than 10 percent scavenged, 0.6 cm thick layer of back fat. Near this cow was a 35.6 cm long fetus. Second female was 7 years old, 25 percent scavenged, and had a femur fat content of 87.8 percent. Third female was 4 years old, less than 10 percent scavenged, had almost no back fat, and a 80.3 percent femur fat content. Sc = ravens.
22 March	16	One caribou. Found four forelegs, one head, and one rumen pile. Either adult female or young male. Sc = ravens, shrew.
22 March	17	One female caribou. Age 9 years, ungutted, scavenged slightly on back flank. Epiphyseal femur fat content of 76.0 percent. Sc = raven, fox.
22 March	18	One male calf, ca. 70 m from (17). Ungutted, less than 10 percent loss to scavengers. Sc = raven.
22 March	19	One adult caribou. Indeterminate sex, ungutted 50 percent loss to scavengers. Snow depth of ca. 80 cm in vicinity of carcass. Sc = raven, foxes.
22 March	20	Five caribou, ca. 200 m from (19). Found four heads, three rumen piles, one carcass. 50 percent scavenger loss to carcass. One of the caribou taken was a calf; other four caribou were females or young males. Snow depth of ca. 60 cm. Sc = raven.

APPENDIX D (continued)

Date	Kill Site	Description
22 March	21	One caribou. Adult female head and small portion of the neck, ca. 140 m from (20). Average snow depth ca. 91 cm.
22 March	22	Three caribou; all ungutted. One male age 5 years, 25 percent scavenger loss, bullet hole(?) in abdomen, antlerless. 48.0 percent femur fat content. Second adult male, light scavenger loss, 86.0 percent femur fat content. 4 to 6 year old female, 25 percent scavenger loss, 76.4 percent femur fat content. Sc = raven.
23 March	23	One female caribou. Age 6, ungutted, 50 percent loss to scavengers, femur fat content of 81.5 percent.
23 March	24	Two caribou, ca. 200 m from (23), adult females or young males. One was ungutted, 25 to 50 percent scavenged, and had had its nose and incisiform teeth sawed off in the same manner I had sawed off incisiform teeth during my visits to Kiana and Noorvik on 17 to 18 February and 20 to 21 February 1976, respectively. The other caribou had only four forelegs, a rumen pile, and a head, minus the lower jaw, present. See description of kill site (25) for additional comments. Sc = raven.
23 March	25	Nine caribou, ca. 65 m from (24). Nine rumen piles, four heads with antlers attached, two pairs of antlers chopped off of caribou presumably taken from the field, and three adult caribou (two females and one male) eviscerated and stacked in one pile. One of the caribou was set on its back, with its legs in the air. Yellow line had been tied to the legs. The incisiform teeth from the four heads and three carcasses had been sawed off. Of the 11 caribou in kill sites (24) and (25), I believe 10 were shot since my visit to the villages of Kiana and Noorvik since the lower incisiform teeth were taken. The first caribou described in kill

APPENDIX D (continued)

Date	Kill Site	Description
		site (24) had probably been killed before the others since both the upper and lower portions of the front jaw were sawed off, indicating the upper and lower jaws had frozen together. The four heads and two antler pairs in group (25) were 1+ females or young males. At the time examined, the three carcasses had no loss to scavengers. H. Thing, who visited the site in early April, reported that the carcasses were still there, had begun to rot due to unseasonably warm weather, and had been largely scavenged by ravens.
23 March	26	Two caribou. Two heads and two rumen piles. Average snowdepth ca. 60 cm.
23 March	27	Four caribou, ca. 200 m from (26), all within a 20 m radius circle. One calf, ungutted, over 75 percent scavenged, 81.5 percent femur fat content. One adult, either adult female or young male, was eviscerated with less than 12.5 percent scavenging loss. Second adult, an old female, had 50 to 75 percent loss to scavengers; unable to tell whether or not this caribou had been eviscerated. Third adult was an antlerless male, scavenging loss and whether or not it was eviscerated was not recorded.
23 March	28	One caribou, ca. 50 m from (22). 12 year old female, eviscerated, over 75 percent scavenged, 47.6 percent femur fat content. Sc = raven.
23 March	29	One caribou. 3 year old female, intact skeleton with 75 percent loss to scavengers. 80.6 percent femur fat content.
23 March	30	20 caribou. 13 carcasses left in the field, and at least seven more were removed prior to my visit as evidenced by snow machine tracks and seven depressions in the snow made by caribou carcasses (three depressions had caribou heads near them). All 20 caribou were within a 20 m radius circle. Five of the above depressions

APPENDIX D (continued)

Date	Kill Site	Description
		were from caribou removed that same day (see Observation 6, Appendix E). Of the thirteen carcasses left in the field, there were two male calves, one female calf, one female yearling, four adult males, and three adult females (two antlerless). The remaining two carcasses and the three heads were from 1+ females or young males. All of the thirteen carcasses were eviscerated except the three calves. Scavenging loss to all 13 carcasses was 12.5 percent or less, with five carcasses virtually untouched. Several were propped on their backs to make the kill site more visible. This kill site was located ca. 3 km south of camp. Sc = raven.
25 March	31	Four caribou. Three rumen piles and one adult female that appeared to have been partially gutted. No scavenging loss to female.
25 March	32	One male calf. Ca. 25 percent loss to scavengers, unable to determine if eviscerated. Sc = raven.
25 March	33	One calf, ca. 120 m from (32). Indeterminate sex, over 50 percent scavenged, ungutted. Femur fat content of 81.2 percent. Sc = raven.
25 March	34	One caribou, ca. 100 m from (33). Age 3 years, indeterminate sex, 75 percent scavenged (all bones intact). Ungutted, 77.7 percent femur fat content. Sc = ravens.
25 March	35	Five caribou, ca. 100 m from (34). Two calves and two adults were completely scavenged. One caribou, older than calf, taken from field as evidenced by the antlers and forelegs left behind. One calf had a 74.6 percent femur fat content; one adult was an 8 year old female with a 76.3 percent femur fat content. Average snow depth ca. 20 cm.
25 March	36	One caribou, ca. 100 m from (35). Age 3 or 4 years. 25 to 50 percent loss to scavengers. Ungutted.

APPENDIX D (continued)

Date	Kill Site	Description
25 March	37	Two caribou. Two rumen piles and two pairs of antlers. Either young males older than calves or adult females.
25 March	38	Two caribou; both gutted and less than 12.5 percent scavenged. One carcass propped up in the snow. An empty .264 Win. Mag. box found near the carcasses. Sc = ravens.
25 March	39	Two caribou. Two rumen piles and eight forelegs found.
25 March	40	One calf. Indeterminate sex. Carcass intact and 50 to 75 percent lost to scavengers. 70.8 percent femur fat content. Sc = raven.
25 March	41	One caribou. Indeterminate sex. 25 to 50 percent scavenged. Average snow depth ca. 63.5 cm. Sc = fox, raven.
25 March	42	One female adult; ca. 100 m from (41). Ungutted, 25 percent loss to scavengers. Ravens had eaten on the mandibles, the neck (two holes present), the belly, the rump, the vagina, and the eyes; some of these spots may have been fed on previously by some carnivor. The neck of the caribou appeared to have been cut with a knife. Sc = raven, carnivor?
25 March	43	One yearling caribou. Indeterminate sex, ungutted. Propped on its back with its legs in the air. 50 percent loss to scavengers.
25 March	44	One caribou. Indeterminate sex, older than calf. Ca. 150 m from (43). Over 50 percent loss to scavengers, ungutted, carcass buried in snow. Sc = raven.

APPENDIX D (continued)

Date	Kill Site	Description
25 March	45	Four caribou, less than 100 m from (44). Three carcasses (young males or adult females). One-eighth to one-fourth scavenging loss to two carcasses; one carcass totally scavenged. Forelegs of fourth caribou. Deep, hard-packed snow (63+ cm) on kill site, may have hid other kills.
25 March	46	Four caribou. Found four heads and one hide. All young males or adult females.
25 March	47	One yearling caribou. Indeterminate sex. Ungutted, both hindquarters minus the forelegs taken. Deep snow (63+ cm) on kill site. Sc = fox.
25 March	48	One caribou. Either young male or adult female. 50 percent loss to scavengers. Ungutted. Ca. 110 m from (47). Sc = fox, raven.
25 March	49	One caribou calf. Indeterminate sex. 50 percent loss to scavengers.
25 March	50	Two adult male caribou. Found only two antler pairs and upper skulls. Deep snow on site (63+ cm).
25 March	51	One adult male caribou; ca. 200 m from (50). Found only one head.
25 March	52	One female caribou. Age 6. 75 percent scavenged, apparently ungutted. 82.5 percent femur fat content. Sc = shrew.
26 March	53	Seven caribou. Ca. 200 m from (25). Found seven heads and seven rumen piles. All young males or adult females.
26 March	54	13 caribou; 30 m from (53). Four ungutted carcasses and nine rumen piles. Four carcasses consisted of one adult male, two adults of indeterminate sex (young males or adult females) and one yearling of unknown sex. The respective percent loss to scavengers were 50, 100, 75, and 25.

APPENDIX D (continued)

Date	Kill Site	Description
26 March	55	Two caribou. One caribou older than calf, scavenged, ungutted. One rumen pile.
27 March	56	One adult male caribou. Ungutted, 25 percent scavenged. Sc = fox, raven.
27 March	57	Three caribou. One adult male with four quarters taken and the rest left. One 2 year old, indeterminate sex, 25 to 50 percent loss to scavengers, 73.3 percent femur fat content. One adult male, ungutted, one eighth loss to scavengers.
28 March	58	Two caribou. All four "hams" of the two carcasses were taken as well as one head. Rest left in field. Caribou were older than calves and the one with head attached was either a young male or adult cow. A fox had urinated on the head of the carcass. Sc = fox, shrew.
3 April	59	One male. Age 2 or 3. Eviscerated. Tongue taken and it was set on its back. Little scavenging loss. Sc = fox, raven.
3 April	60	Two male caribou. Both antlerless. One eviscerated, age 5 to 9, the other ungutted, age 5. Very little scavenging. Sc = raven.
3 April	61	Seven caribou. Seven rumen piles. One male carcass, age 3, 30 percent scavenged. One female head left, age 6. Sc = raven, wolf.
3 April	62	Two female caribou. Two heads and rumen piles left. Ages 6 and 8 years.

APPENDIX E

DESCRIPTION OF HUNTING PRACTICES OBSERVED IN THE KIANA HILLS, NORTHWEST ALASKA, 9 MARCH TO 5 APRIL 1977

The following is a description of actual caribou hunting practices observed in late winter in the vicinity of Noggin Mountain, approximately 5 km southwest of Deviation Peak. All of the hunters involved were local subsistence hunters primarily from Noorvik, ca. 18 km from Noggin; although hunters from Kiana and Kotzebue, ca. 37 and 64 km, respectively, from Noggin also hunted in this area. All hunters observed, except one, used snowmachines. Observations 1 and 7 were taken from notes by J. Shea. Observation 2 was taken from notes by D. Klein. Observation 3 was taken from notes by both J. Shea and D. Klein.

Date	Observation Number	Description
9 March	1	Saw hunters kill one animal after running it with two snowmachines for 5 to 10 minutes. Five to six animals were already downed after I heard about 50 shots in less than 1 hour. Four snowmachines and five to six hunters were involved in the hunt altogether.
10 March	2	Saw two snowmachines in area and heard ca. 60 rifle shots. One machine included two sleds and four people; the other machine pulled one sled and was driven by only one hunter. This hunter downed four caribou, one of which was a calf that he said he took by mistake. Later he pursued more caribou and shot seven more, one which later regained its feet and joined a large herd. The hunter made an attempt to locate the cripple but without success. Sled could probably haul eight or nine caribou at the most, so it is assumed that some caribou taken were left in the field.

APPENDIX E (continued)

Date	Observation Number	Description
13 March	3	Saw five limping adults and one limping calf. Saw and heard two hunters on a snowmachine pulling a sled shoot 13 shots and down three animals. Two caribou were killed 400 to 500 m apart; these were gutted and taken from the field. One hundred meters away, a downed female calf was still alive. Hunters passed within 20 m of the calf on their snowmachine and left it. Portions of the calf were salvaged by us the following day. Watched these same hunters shoot three shots at a group of moving caribou at least 300 m away. No hits were obvious and the hunters did not pursue the caribou. Observed a man and a boy hunting caribou with a sled pulled by 12 dogs kill one caribou which was presumably taken from the field. Located and approached to within 2 m of a wounded unantlered male caribou near the top of Noggin. Heard 40 to 50 shots today.
22 March	4	In the early morning, a native from Noorvik shot five caribou in five (?) shots with a .243 Win. All caribou were gutted in the field and taken back in a sled.
23 March	5	In the early morning, another native from Noorvik shot six caribou in six shots or so. The caribou were shot with a .243 Win. with a scope (the hunter's regular rifle was a scoped .270 Win.). All the caribou were hauled to one spot with the snowmachine, prior to being dressed out and taken from the field. Four cows, ages 3, 6, 9, and one male yearling were decapitated and eviscerated in the field. One male yearling was taken from the field without eviscerated. All the females were pregnant.

APPENDIX E (continued)

Date	Observation Number	Description
23 March	6	Forty meters from kill site 30, described in Appendix D, I found a fresh gut pile. Ca. 120 m from the gut pile I found four empty .270 Win. cartridges and one .30-.30 Win. cartridge adjacent to a fresh snowmachine trail. This same hunter(s) visited kill site 30 and retrieved five carcasses. Darkness prevented searching for signs of wounded animals. Only one set of fresh caribou tracks (the animal killed) were noted.
2 April	7	One hunter on a snowmachine killed two caribou and fired several other times at a moving group of animals 300 m away. Two wounded animals were observed in this group. The hunter did not pursue these animals, but moved to two other places and shot at least five more times. Over 3,000 caribou were disturbed in a 5.3 to 7.9 km^2 area. The two animals killed were left without being examined by the hunter. (They were both 3 year old males, one with a femur fat content of 85.4 percent.)

APPENDIX F

AGE STRUCTURE OF 2+ ADULT CARIBOU FROM THE 1959-61 WESTERN ARCTIC HERD COLLECTION OF MANDIBLES FROM HUNTER-KILLED ANIMALS

The age structure of 2+ adult caribou from the 1959-61 Western Arctic Herd is presented below with regards to village and year of collection. Ages given are based on the average age structure determined by two readers.

Anaktuvuk Pass (1960-61)

Age	Male	Female	Unknown	Total
2	3.0	3.8	11.5	18.3
3	3.0	3.2	13.5	19.7
4	3.6	8.5	11.9	24.0
5	10.8	5.0	7.1	22.9
6	9.1	4.0	6.0	19.1
7	2.5	5.3	3.2	11.0
8	5.5	2.2	0.5	8.2
9	1.5	0.0	2.7	4.2
10	0.0	0.0	1.7	1.7
11	0.0	0.0	2.0	2.0
12	0.0	1.0	1.0	2.0
TOTAL	39.0	33.0	61.0	133.0

APPENDIX F (continued)

Noatak (1959-60)

Age	Male	Female	Unknown	Total
2	5.0	5.0	1.0	11.0
3	1.5	3.5	1.0	6.0
4	5.6	6.8	0.0	12.4
5	3.7	4.2	0.0	7.9
6	5.7	1.5	0.5	7.7
7	3.0	1.5	0.5	5.0
8	1.0	1.5	0.0	2.5
9	1.5	0.5	0.0	2.0
10	1.5	0.5	0.0	2.0
11	0.5	0.0	0.0	0.5
TOTAL	29.0	25.0	3.0	57.0

Noatak (1960-61)

Age	Male	Female	Unknown	Total
2	2.0	13.9	0.0	15.9
3	4.5	13.6	0.0	18.1
4	8.5	9.0	0.5	18.0
5	7.5	5.5	0.5	13.5
6	3.0	9.5	0.0	12.5
7	2.5	3.5	0.0	6.0
8	2.0	3.5	0.0	5.5
9	0.0	3.5	0.0	3.0
10	2.0	1.0	0.0	3.0
11	2.0	1.0	0.0	0.0
TOTAL	34.0	64.0	1.0	99.0

APPENDIX F (continued)

Noatak (exact year unknown: 1959-61)

Age	Male	Female	Unknown	Total
2	0.0	1.0	0.0	1.0
3	0.0	0.5	0.0	0.5
4	0.0	0.5	0.0	0.5
5	0.0	0.0	0.0	0.0
6	0.5	0.0	0.0	0.5
7	0.5	0.0	0.0	0.5
TOTAL	1.0	2.0	0.0	3.0

Kivalina (1959-60)

Age	Male	Female	Unknown	Total
2	0.0	0.0	5.2	5.2
3	0.0	0.0	4.8	4.8
4	2.5	0.0	3.2	5.7
5	0.5	0.0	5.2	5.7
6	0.0	0.0	1.2	1.2
7	0.0	2.0	1.4	3.4
8	0.0	0.5	0.9	1.4
9	0.0	0.5	0.4	0.9
10	0.0	0.0	0.9	0.9
11	0.0	0.0	0.0	0.0
12	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0
14	0.0	0.0	1.0	1.0
TOTAL	3.0	3.0	24.0	30.0

APPENDIX F (continued)

Kivalina (1960-61)

Age	Male	Female	Unknown	Total
2	1.5	4.7	10.5	16.6
3	2.0	5.8	11.5	19.4
4	2.9	4.5	12.4	19.8
5	3.1	2.5	5.7	11.3
6	0.5	5.0	4.1	9.6
7	0.5	0.5	1.0	2.0
8	0.5	1.5	2.8	4.8
9	1.0	0.5	5.5	7.0
10	1.0	0.0	0.5	1.5
11	1.0	0.0	1.0	2.0
12	0.0	0.0	1.0	1.0
13	0.0	0.0	1.0	1.0
TOTAL	14.0	25.0	57.0	96.0

Kivalina (exact year unknown: 1959-61)

Age	Male	Female	Unknown	Total
2	0.0	0.0	4.0	4.0
3	0.0	0.0	5.0	5.0
4	0.0	0.0	5.7	5.7
5	0.5	0.0	6.5	7.0
6	0.5	0.0	4.9	5.4
7	0.0	0.0	4.5	4.5
8	0.0	0.0	4.0	4.0
9	0.0	0.0	1.5	1.5
10	0.0	0.0	0.5	0.5
11	0.0	0.0	0.5	0.5
TOTAL	1.0	0.0	37.0	38.0

APPENDIX F (continued)

Point Hope (1959-60)

Age	Male	Female	Unknown	Total
2	2.5	2.2	3.0	7.8
3	0.5	0.2	1.5	2.2
4	0.5	2.0	0.5	3.0
5	1.5	0.5	0.0	2.0
6	0.0	4.0	0.0	4.0
7	0.0	0.0	0.0	0.0
8	0.0	2.0	0.0	2.0
9	0.5	0.0	0.0	0.5
10	0.5	0.0	0.0	0.5
TOTAL	6.0	11.0	5.0	22.0

Point Hope (1960-61)

Age	Male	Female	Unknown	Total
2	0.0	6.5	0.6	7.1
3	0.0	2.0	4.9	6.9
4	0.5	1.0	6.0	7.5
5	2.5	0.5	5.0	8.0
6	0.0	1.0	2.5	3.5
7	0.0	0.0	2.5	2.5
8	0.0	0.0	0.5	0.5
9	0.0	0.0	0.5	0.5
10	0.0	0.0	1.5	1.5
TOTAL	3.0	11.0	24.0	38.0

Point Hope (exact year unknown: 1959-61)

Age	Male	Female	Unknown	Total
2	0.0	1.0	1.0	2.0
3	0.0	0.0	1.0	1.0
4	0.0	0.5	1.0	1.5
5	0.0	0.5	0.0	0.5
6	0.0	0.0	0.0	0.0
7	0.0	0.0	1.0	1.0
TOTAL	0.0	2.0	4.0	6.0

APPENDIX G

AGE STRUCTURE OF 2+ ADULT CARIBOU FROM THE 1975-76 WESTERN ARCTIC HERD COLLECTION OF INCISIFORM TEETH FROM HUNTER-KILLED ANIMALS

Ages given here were determined as in Appendix F.

Ambler, Evansville, Kotzebue, and Shungnak*

Age	Male	Female	Unknown	Total
2	2.0	0.0	2.0	4.0
3	1.0	0.0	4.5	5.5
4	1.0	0.0	3.5	4.5
5	1.0	0.0	0.5	1.5
6	2.0	0.0	1.5	3.5
7	0.0	0.0	1.0	1.0
8	1.0	0.0	0.0	1.0
TOTAL	8.0	0.0	13.0	21.0

---

*Includes eight males from Shungnak, three unknown sex animals from Kotzebue, three unknown sex animals from Evansville, and seven unknown sex animals from Ambler.

Barrow

Age	Male	Female	Unknown	Total
2	0.0	0.0	6.0	6.0
3	3.5	1.0	3.5	8.0
4	4.0	0.5	9.0	10.5
5	1.0	0.5	9.0	10.5
6	1.0	0.5	2.5	4.0
7	4.0	0.0	4.9	8.9
8	2.5	0.0	4.2	6.7
9	1.0	0.0	3.9	4.9
10	0.0	0.0	1.0	1.0
11	0.0	0.0	1.0	1.0
TOTAL	17.0	2.0	44.0	63.0

APPENDIX G (continued)

Kiana

Age	Male	Female	Unknown	Total
2	3.0	5.0	2.0	10.0
3	3.0	5.0	2.0	10.0
4	8.2	4.4	3.0	15.6
5	17.4	4.4	3.0	24.8
6	18.4	3.3	1.0	22.7
7	7.8	2.0	3.0	12.8
8	2.2	1.0	2.0	5.2
9	0.0	3.0	0.0	3.0
10	0.0	3.0	0.0	3.0
11	0.0	0.0	1.0	1.0
TOTAL	60.0	31.0	17.0	108.0

Kiana Hills

Age	Male	Female	Unknown	Total
2	3.2	1.2	10.0	14.4
3	6.4	1.7	9.0	17.1
4	1.6	5.2	0.0	6.8
5	5.2	5.4	0.0	10.6
6	0.0	13.7	0.0	13.7
7	1.1	7.1	0.0	8.2
8	0.0	6.6	0.0	6.6
9	0.5	3.5	0.0	4.0
10	0.0	2.0	0.0	2.0
11	0.0	2.0	0.0	2.0
12	0.0	0.5	0.0	0.5
TOTAL	18.0	49.0	19.0	86.0

APPENDIX G (continued)

Kivalina

Age	Male	Female	Unknown	Total
2	7.0	2.0	8.5	17.5
3	7.0	0.0	5.5	12.5
4	10.4	2.5	14.0	26.9
5	9.7	0.5	7.8	18.0
6	7.4	1.0	7.2	15.6
7	3.5	0.5	3.5	7.5
8	2.5	1.5	1.5	5.5
9	2.5	0.5	1.5	4.5
10	0.0	0.5	0.5	1.0
11	0.0	0.0	0.0	0.0
12	1.0	0.0	0.0	1.0
13	0.0	0.0	1.0	1.0
14	1.0	0.0	0.0	1.0
TOTAL	52.0	9.0	51.0	112.0

Noorvik

Age	Male	Female	Unknown	Total
2	0.0	4.0	25.2	29.2
3	0.0	3.0	20.8	23.8
4	1.0	4.7	35.1	40.8
5	3.0	1.2	33.5	37.7
6	2.0	1.2	18.4	21.5
7	1.0	1.0	16.5	18.5
8	0.0	2.0	15.9	17.9
9	0.0	2.0	6.6	8.6
10	0.0	0.0	2.1	2.1
11	0.0	0.0	4.0	4.0
12	0.0	0.0	3.0	3.0
13	0.0	0.0	1.0	1.0
TOTAL	7.0	19.0	182.0	208.0

APPENDIX G (continued)

Point Hope

Age	Male	Female	Unknown	Total
2	0.0	0.0	3.5	3.5
3	0.5	0.0	3.5	4.0
4	2.5	1.5	4.5	8.5
5	1.0	1.0	1.0	3.0
6	0.0	0.5	1.5	2.0
7	0.0	0.0	2.5	2.5
8	0.0	0.0	5.0	5.0
9	0.0	0.0	2.0	2.0
10	1.0	0.0	1.0	2.0
11	0.0	0.0	0.5	0.5
TOTAL	5.0	3.0	25.0	33.0

Selawik

Age	Male	Female	Unknown	Total
2	2.1	2.0	6.6	10.7
3	6.3	0.0	15.4	21.7
4	4.2	0.0	13.0	17.2
5	6.3	0.0	11.0	17.3
6	4.2	0.0	9.0	13.2
7	2.0	0.0	8.0	10.0
8	3.0	0.0	6.0	9.0
9	0.0	1.0	1.0	2.0
10	1.0	1.0	0.0	2.0
11	0.0	0.0	1.0	1.0
12	0.0	0.0	1.0	1.0
TOTAL	29.0	4.0	72.0	105.0

APPENDIX H

COMPARISON OF THE AGE STRUCTURE OF THE 1959-61 AND 1975-76 WESTERN ARCTIC HERD HARVEST COLLECTIONS

This appendix summarizes χ^2 contingency tests comparing the age structure of village harvests of the WAH in 1959-61 and 1975-76.

Year	Calves	1+	Total
1959-61	76	867	943
1975-76	64	720	784*
TOTAL	140	1,587	1,727

$\chi^2 = 0.006$, df = 1, $P < 0.95$

*Does not include the Kiana Hills collection.

Year	Yearlings	2+	Total
1959-61	92	775	867
1975-76	72	704	776*
TOTAL	164	1,479	1,643

$\chi^2 = 0.810$, df = 1, $0.25 < P < 0.50$

Year	Two-year-olds	3+	Total
1959-61	89	433	522
1975-76	95	641	736
TOTAL	184	1,074	1,258

$\chi^2 = 4.196$, df = 1, $0.025 < P < 0.05$

APPENDIX H (continued)

3+ Males

Year	3-6	7+	Total
1959-61	81	32	113
1975-76	129	36	165
TOTAL	210	68	278

$\chi^2 = 1.534$, df = 1, $0.10 < P < 0.25$

3+ Females

Year	3-6	7+	Total
1959-61	105	31	136
1975-76	37	22	59
TOTAL	142	53	195

$\chi^2 = 4.368$, df = 1, $0.025 < P < 0.05$

3+ Males

Year	3-4	5-6	7+	Total
1959-61	35	46	32	113
1975-76	54	75	36	165
TOTAL	89	121	68	278

$\chi^2 = 1.570$, df = 2, $0.25 < P < 0.50$

APPENDIX H (continued)

3+ Females

Year	3-4	5-6	7+	Total
1959-61	60	45	31	136
1975-76	23	14	22	59
TOTAL	83	59	53	195

$\chi^2 = 4.627$, $df = 2$, $0.05 < P < 0.10$

LITERATURE CITED

Alonso, W., and E. Rust. 1976. The evolving pattern of village Alaska. Federal-State Land Use Planning Commission for Alaska. Berkeley Planning Associates, Berkeley, Ca. No. 17. 70 pp.

Atwell, G. 1964. An aerial census of wolves in the Nelchina wolf study area. Proc. Alaska Sci. Conf. 14:79-83.

Baskin, L. M. 1970. Reindeer ecology and behaviour. Inst. Eval. Morph. and Ecol. of Animals. Acad. Sci., Moscow. Unpubl. English transl. by Foreign Lang. Div., Dept. of State, Ottawa. Original in Russian.

Banfield, A. W. F. 1954. Preliminary investigation of the barren ground caribou. Part II. Life history, ecology, and utilization. Can. Wildl. Manage. Bull., Ser. 1, No. 10 B. 112 pp.

Banfield, A. W. F. 1955. A provisional life table for the barren ground caribou. Can. J. Zool. 33:143-147.

Banfield, A. W. F. 1957. The plight of the barren-ground caribou. Oryx 4:5-20.

Bee, J. W., and E. R. Hall. 1956. Mammals of northern Alaska on the arctic slope. Univ. Kansas Mus. Nat. Hist. Misc. Publ. No. 8. 309 pp.

Bente, P. J., and D. G. Roseneau. 1978. An aerial photo-estimate of the 1977 Porcupine Caribou Herd population. Renewable Resources Consulting Services, Ltd. Unp. report to Foothills Pipe Lines (Yukon) Ltd., Alaska Dept. Fish and Game, and U.S. Fish Wildl. Serv., Fairbanks, Ak. 84 pp.

Bergerud, A. T. 1961. Sex determination of caribou calves. J. Wildl. Manage. 25:205.

Bergerud, A. T. 1963. Aerial winter census of caribou. J. Wildl. Manage. 27:438-449.

Bergerud, A. T. 1964a. Relationship of mandible length to sex in Newfoundland caribou. J. Wild. Manage. 28:54-56.

Bergerud, A. T. 1964b. A field method to determine annual parturition rates for Newfoundland caribou. J. Wildl. Manage. 28:477-480.

Bergerud, A. T. 1967. Management of Labrador caribou. J. Wildl. Manage. 31:621-642.

Bergerud, A. T. 1971a. Hunting of stag caribou in Newfoundland. J. Wildl. Manage. 35:71-75.

Bergerud, A. T. 1971b. The population dynamics of Newfoundland caribou. Wildl. Monographs No. 25. 55 pp.

Bergerud, A. T. 1972. Food habits of Newfoundland caribou. J. Wildl. Manage. 36:913-923.

Bergerud, A. T. 1974a. Relative abundance of food in winter for Newfoundland caribou. Oikos 25:379-387.

Bergerud, A. T. 1974b. Rutting behavior of the Newfoundland caribou. Pages 394-435 in The Behavior of Ungulates and its Relation to Management. IUCN Publ. N.S. No. 24, Vol. 1.

Bergerud, A. T. 1974c. The decline of caribou in North America following settlement. J. Wildl. Manage. 38:757-770.

Bishop, R. H., and R. A. Rausch. 1974. Moose population fluctuations in Alaska, 1950-1972. Nat. Can. 101:559-593.

Bos, G. N. 1973. Nelchina caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-4 and W-17-5. Juneau, Ak. 25 pp.

Bos, G. N. 1974a. Computerized population models for use in caribou management plans. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-3, W-17-4, and W-17-5. Juneau, Ak. 34 pp.

Bos, G. N. 1974b. Nelchina and Mentasta caribou reports. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor. Proj. W-17-5 and W-17-6. Juneau, Ak. 50 pp.

Bos, G. N. 1975. A partial analysis of the current population status of the Nelchina caribou herd. Pages 170-180 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildl. Monographs 4. 174 pp.

Bunnell, F., D. C. Dauphiné, R. Hilborn, D. R. Miller, F. L. Miller, E. H. McEwan, G. R. Parker, R. Peterman, G. W. Scotter, and J. C. Walters. 1975. Preliminary report on computer simulation of barren ground caribou management. Pages 189-193 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

Burch, E. S., Jr. 1972. The caribou/wild reindeer as a human resource. Am. Antiquity 37:339-68.

Burkholder, B. L. 1959. Movements and behavior of a wolf pack in Alaska. J. Wildl. Manage. 23:1-11.

Burris, O. E., and D. E. McKnight. 1973. Game transplants in Alaska. Alaska Dept. Fish and Game, Wildl. Tech. Bull. No. 4. 57 pp.

Cameron, R. D., and K. P. Whitten. In press. Seasonal movements and sexual segregation of caribou determined by aerial survey. J. Wildl. Manage.

Caughley, G. 1974. Bias in aerial survey. J. Wildl. Manage. 38:921-933.

Caughley, G., and L. C. Birch. 1971. Rate of increase. J. Wildl. Manage. 35:658-663.

Caughley, G., R. Sinclair, and D. Scott-Kemmis. 1976. Experiments in aerial survey. J. Wildl. Manage. 40:290-300.

Cheatum, E. L., and C. W. Severinghaus. 1950. Variations in fertility of white-tailed deer related to range conditions. Trans. N. Am. Wildl. Conf. 15:170-189.

Clark, K. R. F. 1971. Food habits and behavior of the tundra wolf on central Baffin Island. Ph.D. Thesis, Univ. of Toronto, Toronto. 221 pp.

Cochran, W. G. 1954. Some methods of strengthening the common χ^2 tests. Biometrics 10:417-451.

Cochran, W. G. 1963. Sampling techniques. John Wiley and Sons, New York. Second ed. 413 pp.

Cowan, I. McT., and A. J. Wood. 1955. The growth rate of the black-tailed deer (*Odocoileus hemoinus columbianus*). J. Wildl. Manage. 19:331-336.

Davis, J. L. 1976. Some aspects of human use of the Western Arctic Caribou Herd. Unp. ADF&G report presented to Alaska State Senate Resource Committee. Juneau, Ak. 29 pp.

Davis, J. L. 1978. Age structure of caribou populations in Arctic Alaska. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-9,10. Juneau, AK. 9 pp.

Davis, J. L., C. Grauvogel, and H. Reynolds. 1976. The western arctic caribou herd. Unp. Alaska Dept. Fish and Game staff report to Alaska Board of Game. 20 pp.

Davis, J. L., and H. Reynolds. 1977. Distribution of wintering caribou in northwest Alaska 1976-77. Unp. Interim Report, Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. Job IIIB-3.21R. Juneau, Ak. n.s.

Davis, J. L., and P. Valkenburg. 1977. NPR-A caribou studies. Unp. Interim Report, Alaska Dept. Fish and Game. 22 pp.

Dauphiné, T. C., Jr. 1976. Biology of the Kaminuriak population of barren-ground caribou. Part 4. Growth, reproduction, and energy reserves. Can. Wildl. Service Report Ser., No. 38. 69 pp.

Dean, F. C., and D. L. Chesemore. 1974. Studies of birds and mammals in the Baird and Schwatka Mountains, Alaska. Biol. Pap. Univ. of Alaska, No. 15. 80 pp.

Dean, C. F., and G. A. Gallaway. 1965. A FORTRAN program for population study with minimal computer training. J. Wildl. Manage. 29:892-894.

deVos, A. 1960. Behavior of barren ground caribou on their calving grounds. J. Wildl. Manage. 24:250-258.

Doerr, J. G. In prep. Notes on the reliability of age and sex determination of caribou from mandibles and teeth. ADF&G Final Report

Doerr, J. G., and R. A. Dieterich. In press. Mandibular lesions in the western arctic caribou herd. J. Wildl. Dis.

Foote, D. C., and H. A. Williamson. 1966. A human geographical study. Pages 1041-1107 in N. J. Wilimovsky and J. N. Wolfe, eds. Environment of the Cape Thompson Region, Alaska. U.S. Atomic Energy Comm., Washington. 1250 pp.

Gardner, A. L. 1974. Mammals of the Noatak River valley. Pages 224-251 in S. B. Young, ed. The environment of the Noatak River basin, Alaska. Contr. from the Center for Northern Studies, No. 1. Wolcott, Vt. 584 pp.

Giddings, J. L. 1961. Kobuk River people. Dept. Anthropology and Geography. Studies of Northern Peoples, Univ. of Alaska, Fairbanks, No. 1. 166 pp.

Glenn, L. P. 1967. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-15-T-1,2. Juneau, Ak. 36 pp.

Goodman, L. A. 1960. On the exact variance of products. Amer. Statistical Assoc. J. pp. 708-713.

Gossow, H. 1974. Natural mortality pattern in the Spitzbergen reindeer. Pages 103-106 in Proc. 11th Intl. Cong. of Game Biologists. Stockholm, 1973.

Grauvogel, C., and R. Pegau. 1976. Caribou survey-inventory progress report--1974: Game Management Units 23, 24, and 25--Arctic herd. Pages 36-37 in D. E. McKnight, ed. Annual report of survey-inventory activities. Part III. Caribou, brown bear, polar bear, and black bear. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-7. 157 pp.

Haber, G. C. 1977. Socio-ecological dynamics of wolves and prey in a sub-arctic ecosystem. Unp. Ph.D. Thesis, Univ. of British Columbia, Vancouver. 876 pp.

Hemming, J. E. 1971. The distribution movement patterns of caribou in Alaska. Alaska Dept. Fish and Game, Wildl. Tech. Bull. No. 1. 60 pp.

Hemming, J. E. 1975. Population growth and movement patterns of the Nelchina caribou herd. Pages 162-169 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

Hemming, J. E., and L. P. Glenn. 1968. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-15-R-2. Juneau, Ak. 41 pp.

Hemming, J. E., and L. P. Glenn. 1969. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-15-R-3 and W-17-1. Juneau, Ak. 37 pp.

Henny, C. J., W. S. Overton, and H. M. Wight. 1970. Determining parameters for populations by using structural models. J. Wildl. Manage. 34:690-703.

Jones, R. D. 1966. Raising caribou for an Aleutian introduction. J. Wildl. Manage. 30:453-460.

Kelly, M. W. 1954. Observations afield on Alaskan wolves. Proc. Alaska Sci. Conf. 5:35.

Kelsall, J. P. 1957. Continued barren-ground caribou studies. Can. Wildl. Serv., Wildl. Manage. Bull., Ser. 1, No. 12. 148 pp.

Kelsall, J. P. 1960. Co-operative studies of barren-ground caribou 1957-58. Can. Wildl. Serv., Wildl. Manage. Bull., Ser. 1, No. 15. 145 pp.

Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Queens Printer, Ottawa. 340 pp.

Kish, L. 1965. Survey sampling. John Wiley and Sons, Inc., New York. 643 pp.

Klein, D. R. 1964. Range-related differences in growth of deer reflected in skeletal ratios. J. Mammal. 45:226-235.

Klein, D. R. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. J. Wildl. Manage. 32:350-367.

Klein, D. R. 1970. Food selection by North American deer and their response to over-utilization of preferred plant species. Pages 25-46 in Animal populations in relation to their food resources. Brit. Ecological Society Symp. No. 10. Blackwell Scientific Publ., Oxford and Edinburgh. 447 pp.

Klein, D. R., and H. Strandgaard. 1972. Factors affecting growth and body size of roe deer. J. Wildl. Manage. 36:64-79.

Klein, D. R., and R. G. White, eds. 1978. Parameters of caribou population ecology in Alaska: Proceedings of a symposium and workshop. Biol. Papers Univ. of Alaska, Spec. Rep. No. 3. 49 pp.

Kuyt, E. 1972. Food habits of wolves on barren-ground caribou range. Can. Wildl. Serv. Report Ser. No. 21. 36 pp.

Lantis, M. 1950. The reindeer industry in Alaska. Arctic 3:27-44.

LaPerriere, A. J., and P. C. Lent. 1977. Caribou feeding sites in relation to snow characteristics in northeastern Alaska. Arctic 30:101-108.

Lent, P. C. 1960. Project Chariot. Phase III. Caribou investigations, northwest Alaska. Unp. progress report, AEC Contract No. AT(04-2)-310. 57 pp.

Lent, P. C. 1961. Project Chariot. Phase III. Caribou investigations, northwest Alaska. Unp. progress report, AEC Contract No. AT(04-2)-310. 14 pp.

Lent, P. C. 1965. Observations of antler shedding by female barren-ground caribou. Can. J. Zool. 43:553-558.

Lent, P. C. 1966a. Calving and related social behavior in the barren-ground caribou. Zeitschrift für Tierpsychologie 23:701-756.

Lent, P. C. 1966b. The caribou of northwestern Alaska. Pages 481-517 in N. J. Wilimovsky and J. N. Wolfe, eds. Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Comm., Washington, D.C. 1250 pp.

Lent, P. C., and O. Lønø. 1962. Terrestrial mammal investigation, Ogotoruk Creek-Cape Thompson and vicinity. Part C: Caribou investigation, northwest Alaska. Unp. manuscript, AEC Contract No. AT(04-2)-310. 46 pp.

Lentfer, J. 1965. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-6-R-5 and W-6-R-6. Juneau, Ak. 20 pp.

LeResche, R. E. 1975. The international herds: present knowledge of the Fortymile and Porcupine caribou herds. Pages 127-139 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

LeResche, R. E., and R. A. Rausch. 1974. Accuracy and precision of aerial moose censusing. J. Wildl. Manage. 38:175-182.

LeResche, R. E., R. H. Bishop, and J. W. Coady. 1974. Distribution and habits of moose in Alaska. Nat. Can. 101:143-78.

McGowan, T. A. 1966. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-6-R-6 and W-15-R-1. Juneau, Ak. 19 pp.

McIlroy, C. 1974. March 1974 wolf survey. Unp. memorandum, Alaska Dept. Fish and Game. 4 pp.

McKnight, D. E., ed. 1970. Annual report of survey-inventory activities. Part II. Caribou, brown bear, sheep, furbearers, marine mammals, bison, goat, wolf, and black bear. Alaska Dept. of Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-2. Juneau, Ak. 94 pp.

McKnight, D. E., ed. 1971. Annual report of survey-inventory activities. Part II. Caribou, brown-grizzly bear, sheep, furbearers, marine mammals, bison, goat, wolf, wolverine, and black bear. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-3. Juneau, Ak. 145 pp.

McKnight, D. E., ed. 1974. Annual report of survey-inventory activities. Part II. Moose, caribou, marine mammals, and goat. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-5. Juneau, Ak. 269 pp.

McKnight, D. E., ed. 1975. Annual report of survey-inventory activities. Part III. Caribou, marine mammals, mountain goat, wolf, and black bear. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-6. Juneau, Ak. 198 pp.

McKnight, D. E., ed. 1976. Annual report of survey-inventory activities. Part III. Caribou, brown bear, polar bear, and black bear. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-7. Juneau, Ak. 157 pp.

Mech, L. D. 1966. The wolves of Isle Royale. Nat. Parks Fauna Ser. No. 7. 210 pp.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, New York. 384 pp.

Mech, L. D. 1977. Population trend and winter deer consumption in a Minnesota wolf pack. Pages 55-83 in R. L. Phillips and C. Jonkel, eds. Proc. 1975 predator symposium. Montana Forest and Conservation Exp. Stn., Univ. of Montana, Missoula. 268 pp.

Miller, D. R. 1975. Observations of wolf predation on barren ground caribou in winter. Pages 209-220 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

Miller, F. L. 1972. Eruption and attrition of mandibular teeth in barren-ground caribou. J. Wild. Manage. 36:606-612.

Miller, F. L. 1974. Biology of the Kaminuriak population of barren-ground caribou. Part 2: Dentition as an indicator of age and sex; composition and socialization of the population. Can. Wildl. Serv. Rep. Ser. No. 31. 87 pp.

Miller, F. L., and E. Broughton. 1974. Calf mortality on the calving grounds of Kaminuriak caribou, during 1970. Can. Wildl. Serv. Rep. Ser. No. 26. 25 pp.

Murie, A. 1944. The wolves of Mount McKinley. U.S. Dept. Interior, Natl. Park Serv., Fauna Ser. 5. 238 pp.

Murie, O. J. 1935. Alaska-Yukon caribou. U.S. Bur. Biol. Survey, N. Am. Fauna No. 54. 93 pp.

Neiland, K. A. 1970. Weight of dried marrow an indicator of fat in caribou femurs. J. Wildl. Manage. 34:904-907.

Neiland, K. A. 1972. Caribou disease studies. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-2 and W-17-3. Juneau, Ak. 42 pp.

Neiland, K. A. 1978. Caribou disease studies. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-4 through W-17-10. Juneau, Ak. 67 pp.

Neiland, K. A., J. A. King, B. E. Huntley, and R. O. Skoog. 1968. The diseases and parasites of Alaskan wildlife populations. Part I: Some observations on brucellosis in caribou. Bull. Wildl. Disease Assoc. 4:27-36.

Parker, G. R. 1971. Trends in the population of barren-ground caribou of mainland Canada over the last two decades: a re-evaluation of the evidence. Can. Wildl. Ser., Occas. Papers No. 10. 9 pp.

Parker, G. R. 1972. Biology of the Kaminuriak population of barren-ground caribou. Part I: Total numbers, mortality, recruitment, and seasonal distribution. Can. Wildl. Ser. Rep. Ser. No. 20. 93 pp.

Parker, G. R. 1973. Distribution and densities of wolves within barren-ground caribou range in northern mainland Canada. J. Mammal. 54:341-348.

Parker, G. R. 1975. A review of aerial surveys used for estimating the numbers of barren-ground caribou in northern Canada. Polar Record 17:627-638.

Patterson, A. 1974. Subsistence harvests in five native regions. Joint Federal-State Land Use Planning Commission for Alaska. 48 pp.

Pegau, R. E. 1975. Analysis of the Nelchina caribou range. Pages 316-334 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

Pegau, R. E., and J. E. Hemming. 1972. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-2 and W-17-3. Juneau, Ak. 226 pp.

Pruitt, W. O., Jr. 1960. Behavior of the barren-ground caribou. Univ. of Alaska, Biol. Pap. No. 3. 44 pp.

Pimlott, D. H. 1967. Wolf predation and ungulate populations. Am. Zool. 7:267-278.

Rausch, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. Am. Zool. 7:253-265.

Rausch, R. A. 1968. Wolf studies. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-15-R-2 and W-15-R-3. Juneau, Ak. 51 pp.

Rausch, R. A. 1969a. A summary of wolf studies in southcentral Alaska, 1957-1968. Trans. N. Am. Wildl. Nat. Res. Conf. 34:117-131.

Rausch, R. A. 1969b. Statewide wolf population studies. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-1. Juneau, Ak. 36 pp.

Rausch, R. A., and R. A. Hinman. 1977. Wolf management in Alaska--an exercise in futility? Pages 147-156 in R. L. Phillips and C. Jonkel, eds. Proc. 1975 Predator Symposium. Montana Forest and Conservation Exp. Stn., Univ. of Montana, Missoula, Montana. 268 pp.

Rausch, R. L. 1951. Notes on the Nunamiut Eskimo and mammals of the Anaktuvuk Pass region, Brooks Range, Alaska. Arctic 4:147-195.

Reimers, E. 1972. Growth in domestic and wild reindeer in Norway. J. Wildl. Manage. 36:612-619.

Reimers, E. 1975. Age and sex structure in a hunted population of reindeer in Norway. Pages 181-188 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbanks, Ak. 551 pp.

Reimers, E. 1977. Population dynamics in two subpopulations of reindeer in Svalbard. Arctic and Alpine Research 9:369-381.

Rodahl, K. 1963. The last of the few. Harper and Row, New York. 208 pp.

Saario, D. J., and B. Kessel. 1966. Human ecological investigations at Kivalina. Pages 969-1039 in N. J. Wilimovsky and J. N. Wolfe, eds. Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Comm., Washington. 1250 pp.

Scott, R. F., E. F. Chatelain, and W. A. Elkins. 1950. The status of the Dall sheep and caribou in Alaska. Trans. N. Am. Wildl. Conf. 15:612-626.

Scott, R. F., S. T. Olson, R. O. Skoog, D. R. Klein, H. C. Hanson, A. Courtright, S. J. Harbo, Jr., H. Kantner, J. Whisenhant, and W. Miller. 1958. Caribou management studies. U.S. Fish and Wildlife Serv., Fed. Aid in Wildl. Restor., Proj. W-3-R-12. 118 pp.

Semenov-Tian-Shanskii, O. I. 1975. The status of wild reindeer in the USSR, especially the Kola Peninsula. Pages 155-161 in J. R. Luick, P. C. Lent, D. R. Klein, and R. G. White, eds. Proc. First Intl. Reindeer/Caribou Symposium, Univ. of Alaska, Fairbarks, Ak. 551 pp.

Siniff, D. B., and R. O. Skoog. 1964. Aerial censusing of caribou using stratified random sampling. J. Wildl. Manage. 28:391-401.

Skoog, R. O. 1956. Range, movements, population, and food habits of the Steese-Fortymile caribou herd. Unp. M.S. Thesis, Univ. of Alaska, Fairbanks, Ak. 145 pp.

Skoog, R. O. 1957. Alaska wildlife investigations, work plan B: Caribou management studies. U.S. Fish and Wildl. Serv., Fed. Aid in Wildl. Restor., Proj. W-3-R. Juneau, Ak. 132 pp.

Skoog, R. O. 1963. Caribou report. Alaska Dept. Fish and Game, Fed. Aid in Wild. Restor., Proj. W-6-R-4. Juneau, Ak. 31 pp.

Skoog, R. O. 1968. Ecology of the caribou (*Rangifer tarandus granti*) in Alaska. Ph.D. Thesis, Univ. of California, Berkeley, Ca. 699 pp.

Skoog, R. O., F. F. Jones, and S. J. Harbo, Jr. 1961. Caribou management investigations. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-6-R. Juneau, Ak. 128 pp.

Skoog, R. O., R. F. Batchelor, F. F. Jones, and R. L. Winters. 1963. Caribou investigations. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-6-R-3. Juneau, Ak. 89 pp.

Skuncke, F. 1969. Reindeer ecology and management in Sweden. Univ. of Alaska, Biol. Paper. 8. 81 pp.

Sonnenfeld, J. 1957. Changes in subsistence among the Barrow Eskimo. Ph.D. Thesis, John Hopkins Univ., Baltimore. 561 pp.

Spetzman, L. A. 1959. Vegetation of the Arctic slope of Alaska. U.S. Geol. Surv., Prof. Pap. No. 302-B. 58 pp.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Book Co., Inc., New York. 481 pp.

Stephenson, R. O. 1976. Wolves and caribou in northwestern Alaska. Unp. memorandum. Alaska Dept. Fish and Game. 14 pp.

Stephenson, R. O. 1977. NPR-A mammal studies. Wolf studies. Alaska Dept. Fish and Game. n.s.

Stephenson, R. O. 1978. Unit 13 wolf studies. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-8. Juneau, Ak. 75 pp.

Stephenson, R. O., and L. Johnson. 1972. Wolf report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-3. Juneau, Ak. 52 pp.

Stephenson, R. O., and L. J. Johnson. 1973. Wolf report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-4 and W-17-5. 52 pp.

Stephenson, R. O., and J. J. Sexton. 1974. Wolf report. Alaska Dept. Fish and Game, Fed. Aid in Wildl. Restor., Proj. W-17-5 and W-17-6. Juneau, Ak. 28 pp.

Thomas, D. C. 1969. Population estimates and distribution of barren-ground caribou in Mackenzie District, N.W.T., Saskatchewan, and Alberta--March to May, 1967. Can. Wildl. Ser. Rep. Ser. No. 9. 44 pp.

Thomson, B. R. 1971. Wild reindeer activity, Hardangervidda: July-December 1970. Statens viltundersøken Direktoratet for Jakt, Viltstell og Ferskvannsfiske and IBP Report from the grazing project at the Norwegian IBP Committee. 83 pp.

Thomson, B. R. 1973. Wild reindeer activity, Hardangervidda: 1971. Statens viltundersøken Direktoratet for Jakt, Viltstell og Ferskvannsfiske and IBP Report from the grazing project at the Norwegian IBP Committee. 76 pp.

Watson, G. W., and R. F. Scott. 1956. Aerial censusing of the Nelchina caribou herd. Trans. N. Am. Wildl. Conf. 21:499-510.

Walters, C. J., R. Hilborn, and R. Peterman. 1975. Computer simulation of barren-ground caribou dynamics. Ecological Modeling 1:303-315.

Woodford, R. 1954. Notes on village economics and wildlife utilization in arctic Alaska. Unp. report, U.S. Fish and Wildl. Serv., Fairbanks, Ak. 34 pp.

Young, S. B. 1974. Vegetation of the Noatak River Valley, Alaska. Pages 58-84 in S. B. Young, ed. The environment of the Noatak River basin, Alaska. Contr. from the Center for Northern Studies, No. 1. Wolcott, Vt. 584 pp.

OTHER REFERENCE SOURCES

A. T. Bergerud, Victoria, British Columbia

Gregory Box, Anchorage, Alaska

George Calef, Yellowknife, N.W.T.

James Davis, Fairbanks, Alaska

Sterling Eide, Glennallen, Alaska

James Gebhard, Fairbanks, Alaska

Lawrence Gray, Shungnak, Alaska

Samuel Harbo, Jr., Fairbanks, Alaska

David Klein, Fairbanks, Alaska

Peter Lent, Anchorage, Alaska

Kenneth Neiland, Fairbanks, Alaska

Edward Nygard, Juneau, Alaska

Eigil Reimers, Oslo, Norway

Harry Reynolds, Fairbanks, Alaska

Jack Shea, Sheffield, Massachusetts

Robert Stephenson, Fairbanks, Alaska

Henning Thing, Copenhagen, Denmark

Victor VanBallenberghe, Fairbanks, Alaska