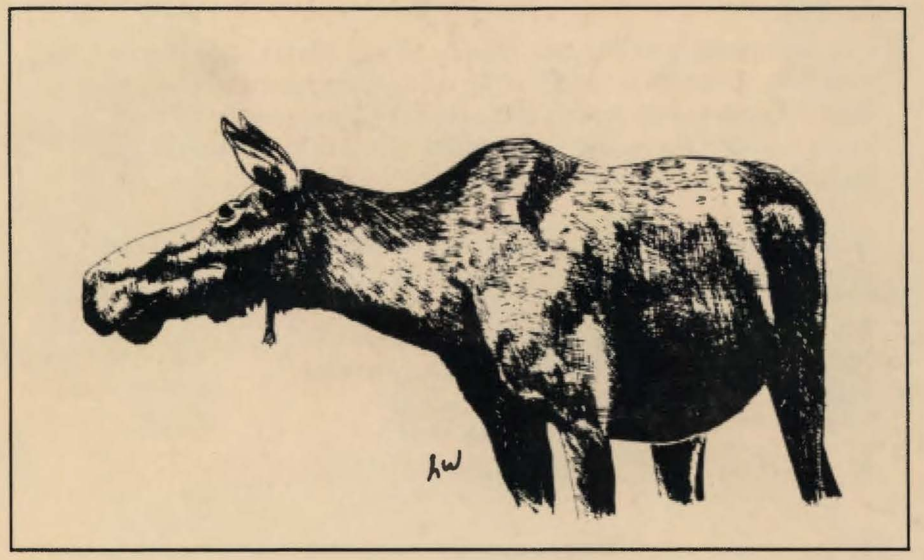
Alaska Department of Fish and Game
Division of Wildlife Conservation
Federal Aid in Wildlife Restoration
Research Final Report

FACTORS LIMITING MOOSE POPULATION GROWTH IN SUBUNIT 20E



by
William C. Gasaway
Rodney D. Boertje
Daniel V. Grangaard
David G. Kelleyhouse
Robert O. Stephenson
Douglas G. Larsen
Projects W-22-3 to W-23-4
Study 1.37
August 1990

STATE OF ALASKA
Steve Cowper, Governor

DEPARTMENT OF FISH AND GAME
Don W. Collinsworth, Commissioner

DIVISION OF WILDLIFE CONSERVATION
W. Lewis Pamplin, Jr., Director
W. Bruce Dinneford, Acting Planning Chief

Persons intending to cite this material should obtain prior permission from the author(s) and/or the Alaska Department of Fish and Game. Because most reports deal with preliminary results of continuing studies, conclusions are tentative and should be identified as such. Due credit will be appreciated.

Additional copies of this report, or reports on other species covered in this series may be obtained from:

Publications Technician
ADF&G, Wildlife Conservation
P.O. Box 3-2000
Juneau, AK 99802
(907) 465-4190

FINAL REPORT (RESEARCH)

State: Alaska

Cooperators: None

Project No.: W-22-3, W-22-4, W-22-5, W-22-6, W-23-1, W-23-2, and W-23-3 Project Title: Big Game Investigations

Job No.: 1.37R Job Title: Factors Limiting Moose Population Growth in Subunit 20E

Period Covered: 1 July 1983-30 June 1989

SUMMARY

A manuscript entitled "Predation Limiting Moose at Low Densities in Alaska and Yukon and Implications for Conservation" was submitted to Wildlife Monographs in June 1990. It covers work done for Job 1.37 and is submitted with minor format changes as the appendix for this final report.

Key Words: Alaska, conservation, grizzly bears, limiting factors, management, moose, mortality, population dynamics, predation, wolves.

APPENDIX.

PREDATION LIMITING MOOSE AT LOW DENSITIES IN ALASKA AND YUKON AND IMPLICATIONS FOR CONSERVATION

WILLIAM C. GASAWAY, Alaska Department of Fish and Game, 1300
College Road, Fairbanks, AK 99701

RODNEY D. BOERTJE, Alaska Department of Fish and Game, 1300
College Road, Fairbanks, AK 99701

DANIEL V. GRANGAARD, Alaska Department of Fish and Game,
PO Box 355, Tok, Alaska 99780

DAVID G. KELLEYHOUSE, Alaska Department of Fish and Game,
PO Box 355, Tok, Alaska 99780

ROBERT O. STEPHENSON, Alaska Department of Fish and Game,
1300 College Road, Fairbanks, AK 99701, AND

DOUGLAS G. LARSEN, Wildlife Branch, Box 2703, Whitehorse,
Yukon Territory, Canada Y1A 2C6

Abstract: We help resolve 3 major problems facing wildlife managers and wildlife users of northern ecosystems: (1) defining what factors limit moose (Alces alces) at low densities in lightly exploited systems, (2) achieving consensus on potential moose harvest yields, and (3) developing conservation plans that reduce the controversy over intensive management of moose, wolves (Canis lupus), and bears (Ursus arctos and U. americanus). We assessed the role that nutrition, snow/nutrition, harvest, disease, and predation played in limiting moose densities in a 9,700-km^2 area in east-central Alaska during 1948-88. Our intensive study occurred during 1981-88, and we reviewed and reanalyzed historical data. We also present published and unpublished moose, wolf, and bear inventory data and moose harvest data from 35 other areas, and we present conclusions on factors limiting moose density and moose harvest in Alaska and Yukon.

We identified predation by wolves and bears as the major factor limiting moose densities in the experimental area during the low-density phase. Moose irrupted coincidental with a predator reduction program (1948-60) that included poisoning. The subsequent decline of moose ended about 1976, at which time wolves declined and survival of moose increased. During the mid-1980's and after the recent wolf reduction (1981-83), we estimated predators annually killed 31% of the postcalving moose population, compared with 6% killed by nonpredation causes and 1.5% by humans. We concluded mortality from predation had a substantial additive component during the low-density phase and wolf predation on adult moose was less additive than grizzly bear predation.

Data from throughout Alaska and Yukon indicate that where wolves and bears are near K carrying capacity (KCC) and moose are the primary prey, moose populations remain at a low-density equilibrium ($\bar{x} = 153$ moose/1,000 km^2 of moose habitat). Moose attained higher densities ($\bar{x} = 647$ moose/1,000 km^2) where humans held wolves and/or bears below KCC. These elevated moose populations yielded sustainable harvests of 20-130 moose/1,000 km^2 compared with 0-18/1,000 km^2 in systems with predators near KCC.

We make recommendations to help resolve the controversy over managing predators for increased harvest of moose. Implementing these recommendations could provide agreement on where, how, and when moose-wolf-bear systems will be managed and, in intensively managed areas, provide elevated harvests of moose while ensuring the security of predator populations. This controversy needs to be reduced if conservationists are to unite in addressing the most serious long-term threat to these systems--the loss of wilderness.

CONTENTS

INTRODUCTION

Predation is now well recognized as a major factor affecting the dynamics of moose (Alces alces) populations. During the 1980's, ecologists demonstrated that predation could strongly depress rates of moose population growth and accelerate declines to low densities through antiregulatory processes, i.e., processes that increase mortality rates as densities decline (Lidicker 1978, Gasaway et al. 1983, Keith 1983, Messier and Crete 1985, Ballard and Larsen 1987, Crete 1987, Van Ballenberghe 1987, Bergerud and Snider 1988, Page 1989). In addition, growing evidence indicates the combined predation of wolves (Canis lupus) and bears (grizzly bears, Ursus arctos and/or black bears U. americanus) can limit moose populations at a low-density equilibrium, well below K carrying capacity (KCC), for extended periods in unexploited and lightly exploited systems (Messier and Crete 1985; Ballard and Larsen 1987; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988; Larsen et al. 1989a). KCC is conceptually the maximum number of animals that can be supported at equilibrium in a steady environment and in the absence of time lags, harvest, and predation (McCullough 1979:85).

The purpose of this monograph is to: (1) describe what factors limited moose at low densities in our intensive study area in Alaska, (2) use evidence from Alaska and Yukon Territory (Yukon) to provide additional support for the above concept that combined wolf and bear predation limits moose at densities below KCC where predators are lightly exploited, (3) describe how predation affects moose harvest yields for humans, and (4) recommend conservation objectives that help reduce the controversy over intensively managing predation to increase the harvest of moose.

To accomplish the above objectives, we: (1) report results of our field studies in east-central Alaska; (2) present published and unpublished data on moose, wolf, and bear densities and moose harvest from 35 other areas in Alaska and Yukon with lightly exploited and manipulated predator populations; and (3) review published literature from North America. For field studies, we chose an area that: (1) was typical of the large, sparsely populated wilderness of central and eastern Alaska and Yukon and which had predator species similar to most of Alaska and Yukon; (2) had a history of low moose densities temporarily interrupted by an irruption coinciding with an intense multi-species predator reduction program; and (3) had low harvest rates of moose and predators by hunters and trappers. We used inductive and hypothetico-deductive reasoning to evaluate the role nutrition, snow/nutrition, harvest, disease, and predation played in limiting moose at low densities in the experimental area. Data on moose, predators, and moose harvest rates in areas where predator populations were manipulated versus lightly exploited was presented and reanalyzed to extend our conclusions outside the experimental area. We used man-caused perturbations to help interpret the role of specific processes in lightly exploited systems, as suggested by Sinclair (1979) and Caughley (1981).

We use the term "lightly exploited" to describe systems where harvests of moose, wolves, and bears occur but harvests are not the primary factors shaping relationships between moose and predators; consequently, wolves and bears are near KCC. In contrast, in "manipulated" systems, moderate to high exploitation of wolves, bears, or moose largely shape predator-prey relationships and determine the abundance of wolves, bears, or moose relative to KCC. Consequently, wolves and/or bears are well below KCC or have recently increased as a result of decreased harvests. We deem predator populations below KCC if significant population growth could be expected following cessation of harvest. Humans today influence all ecosystems containing moose; therefore, we focus on understanding effects of minor (lightly exploited) and major (manipulated) human intervention.

Although most moose, wolf, and bear populations in systems classed as lightly exploited have had low harvest rates during the past 15-30 years, humans had strong impacts on these populations previously. For example, market hunting of ungulates and use of poisons for trapping occurred early in this century and government programs reduced wolf and bear numbers during the late 1940's and 1950's in Alaska (Harbo and Dean 1983). We acknowledge, therefore, that characteristics of lightly exploited systems described herein may, in part, result from historical manipulations (Van Ballenberghe 1987). Denali National Park is the least exploited studied area in Alaska and Yukon and, therefore, we often compare Denali with other lightly exploited areas. However, Denali Park's history also included market hunting and wolf removal and recently the harvest of ungulates, wolves, and bears along its boundaries (Singer and Dalle-Molle 1985, Singer 1987).

The management focus of this monograph is intended to help wildlife managers and wildlife users resolve the controversy over predator conservation and management in moose-wolf-bear systems. We make recommendations that promote coexistence between humans and large predators in intensively managed systems. This management contrasts with management that largely extirpated wolves and grizzly bears in the continental United States and southern Canada. We are not so naive to believe the controversy can be fully resolved, but we believe an understanding of the apparent biological realities and some options that accommodate diverse sets of values can begin to reduce the controversy among conservationists.

We define here our usage of several terms that have ambiguous connotations. "Conservation" is the protection, planned management, and wise use of natural resources, thus protection is just one of several conservation options. A "conservationist" is a person who advocates conservation. "Limiting factors" retard the rate of increase in population size by density-dependent (stabilizing) and density-independent (potentially destabilizing) processes. In contrast, "regulating factors" affect population growth rate only in a density-dependent manner (Watson and Moss 1970; Messier, in review). We generally describe the effects of factors on the moose population in the context of limitation rather than regulation for 3 reasons. First, limiting factors by definition include regulating factors. Second, population size and trajectory are functions of the sum of density-dependent and density-independent effects. Third, some factors are density-dependent at some densities and density-independent or inversely density-dependent (antiregulatory and destabilizing) at other densities; e.g., wolf predation (Messier and Crete 1985).

Acknowledgments.--We are indebted to many people who contributed to this study. S. DuBois and D. Preston assisted with the calf mortality study, browse-use assessment, and the adult moose movement and mortality study; J. Hechtel and E. Crain assisted with daily radio-tracking of grizzly bears to estimate predation rates; and P. Valkenburg assisted in locating, capturing, and radio-collaring grizzly bears. Pilot R. Warbelow provided helicopter and fixed-wing aircraft support throughout the study. The U.S. Army 172nd Infantry Brigade (Alaska) and J. Kerns provided helicopter support during spring 1985. T. Bowyer, M. Crete, F. Messier, S. Miller, J. Schoen, and V. Van Ballenberghe provided valuable comments on previous drafts. Financial support was provided by Federal Aid in Wildlife Restoration Projects, the Alaska Department of Fish

and Game (ADF&G), and Mutual of Omaha's "Wild Kingdom" program.

STUDY AREA

We conducted the study in an experimental area (9,700 km^2) where research and predator removal were undertaken, and 2 control areas (Washington Creek, 1,200 km^2, and North Ladue, 1,150 km^2) where predator numbers were not reduced (Fig. 1). The study area (experimental and control areas) is in Game Management Unit (GMU) 20E in east-central Alaska, except for a portion of the North Ladue control area in Yukon. The study area is centered around 64°N latitude and 142°E longitude.

The experimental area consists of hills covered with black spruce (*Picea mariana*) interspersed with subalpine and alpine areas, shrub-dominated burned areas, and creeks and rivers bordered by willow (*Salix* spp.), birch (*Betula nana*, *B. glandulosa*, *B. papyrifera*), alder (*Alnus* spp.), and white spruce (*P. glauca*). Subalpine shrub vegetation consists primarily of birch (*B. nana*, *B. glandulosa*) and willow (*Salix* spp.). Subalpine areas are used extensively by moose during September-December. Poorly drained lowlands occur most notably in the Mosquito Fork drainage (Mosquito Flats) and upper Middle Fork and are dominated by shrub birch, willow, and sedge (*Carex* and *Eriophorum* spp.) meadows. The Mosquito Flats is an important moose wintering and summering area. An extensive wildfire occurred during 1966 north and northeast of Mt. Fairplay and produced excellent moose habitat dominated by willow and birch. Elevation mostly ranges from 600 m to 1,000 m near treeline, although mountain peaks extend to 1,750 m. Vegetation nomenclature follows Viereck and Little (1972).

Excellent moose habitat dominates the 2 control areas. Wildfires burned much of the control areas during 1969, and willow (*Salix* spp.) and birch (*B. papyrifera*, *B. nana*, *B. glandulosa*) predominate. The unburned uplands support predominantly willow, birch, and scattered black spruce; unburned lowlands support predominantly black spruce interspersed with birch and willow. Elevations are 600-1,650 m in the North Ladue control area and 250-1,100 m in the Washington Creek control area.

The climate is subarctic and continental. "Winter" includes the months of October-April. Leaves emerged on most shrubs during 1-7 June 1983-86, and leaf senescence occurred during the last 2 weeks of August. The total annual precipitation averages 24 cm at Tok (National Climatic Data Center 1986; Fig. 1). Snow depths are usually <60 cm, and snow usually remains loosely packed except where windblown at high elevations.

Large carnivores inhabiting the study area include wolves, black bears, and grizzly bears. Their prey include moose, caribou (Rangifer tarandus), beaver (Castor canadensis), snowshoe hares (Lepus americanus), and hoary marmots (Marmota caligata). Snowshoe hare populations are cyclic; recent peak populations occurred about 1962, 1970, and 1979, with relatively low numbers during the last peak. About 100-150 Dall's sheep (Ovis dalli) occur along the northwest border of the experimental area. Seasonal distribution of the Fortymile Caribou Herd fluctuates among years (Valkenburg and Davis 1988), but in most years caribou spend more time in the experimental area (usually portions of spring, autumn, and winter) than in control areas (portions of autumn and winter).

METHODS

Moose Population Status

Estimating Moose Abundance and Population Trend.--Moose population size was estimated in a 7,700-km^2 portion of moose habitat in the experimental area during October 1981 and 1988 using stratified random sampling (Gasaway et al. 1986). Moose habitat includes all the area, exclusive of large lakes and glaciers, below the upper limits of vegetation characteristically used by moose. Randomly selected sample units from each stratum were searched at an intensity averaging 1.7 min/km^2 from a Super Cub or Citabria aircraft flying at 105-120 km/hr and 60-120 m above ground. When moose were seen by the pilot or observer, the aircraft was diverted from the flight path to circle the moose while observers searched for additional moose. Snow depths ranged from 10 to 40 cm, and tracks in snow were used as clues in locating moose. During 1988, a sightability correction factor (SCF) for under-counting bias was estimated and applied to the density estimate. During 1981, procedures to estimate a SCF had not been developed for low-density populations. Consequently, to test for changes in density, we used a 2-tailed Student's t-test using density estimates uncorrected for sightability (Gasaway et al. 1986). We estimated actual density during 1981 by applying the 1988 SCF to the uncorrected 1981 estimate. We approximated a 90% CI for the corrected 1981 estimate by using the variance of the 1988 SCF and standard formulas to calculate a 90% CI (Gasaway et al. 1986); we refer to this 90% CI as a "probable range" because it uses a value from a different survey.

Relative abundance of moose and population trend in the experimental area during 1949-88 were reconstructed from several sources. For the period 1949-55, we relied on observations of long-term residents. For the period 1956-

64, we estimated λ (finite rate of population change) using recruitment data from aerial winter composition surveys and an estimate of adult mortality from Gasaway et al. (1983) (see formulas below). We deemed these aerial composition surveys unsuitable for estimating trends in number of moose because of variation in timing and areas flown. Finally, for the period 1966-88, we used aerial trend surveys from 5 areas. Number of moose observed/hour during surveys, rather than number of moose observed, was used as the trend indicator during this period because the size of the area searched varied among years and boundaries were not exactly defined. Trend in each of the 5 areas was estimated by smoothing curves with a moving 3-point median (i.e., the central value of the 3 values was selected so that an observed data point was used in calculations; Bowyer et al. 1988). A composite of the 5 curves was then produced to reflect overall moose population trend. To do this, we annually plotted the median value of the 5 survey areas. Missing annual values in each of the 5 individual trend areas were estimated by interpretation before constructing the composite curve. Missing values occurred during 1981 and 1983, when no trend surveys were flown, and in 24% of the other cases.

Survey specifications for aerial trend and composition surveys were similar to those in the above estimates of population size; however, search intensity was about 50% lower. Transects were flown over flats, and contours were flown near timberline in the mountains.

Three surveys were flown annually in the control areas during 1982-87 to evaluate moose population trends. One survey was flown in the Washington Creek control area and two in the North Ladue control area. Numbers of moose observed in each survey area were regressed against year; trends were significant if the 90% CI for the slope of the regression line did not include 0. The 3 survey areas were precisely defined and ranged in size from 119 to 162 km^2. Survey methods were similar to those used to estimate population size (Gasaway et al. 1986).

Estimating Recruitment, Adult Mortality, and Rate of Population Change.--Sex and age of moose observed during early winter aerial surveys from 1956-88 were used to estimate calves or yearlings/100 cows and the proportion of recruits (yearlings) among yearlings and adults. Moose observed were classified as a calf, yearling bull, adult bull, or cow. Number of total yearlings in the sample was assumed equal to twice the number of yearling bulls. We estimated the number of cows $\geq$29 months old in a sample by subtracting the number of yearling bulls observed from the total cows observed; i.e., we assumed numbers of yearling bulls and yearling cows were equal (Gasaway et al. 1983).

Adult mortality was estimated using several methods; citations and assumptions are given in text except for the time periods below. For 1966-76 and 1976-81, mean adult mortality (M) was estimated from annual mortality estimates using the following formula from Bergerud and Elliott (1986):

$$M = 1 - \lambda(1 - R)$$

where

M = number dying during a year/number starting the year,
R = yearlings/yearlings and adults, in the annual sample of moose seen during aerial surveys, and
λ = the finite rate of population change based on the overall number of moose seen/hour during surveys.

We calculated M as the mean of annual mortality estimates, which accounts for the annual change in R resulting from changing numbers of bulls/cow due to selective hunting on bulls and the prohibition of hunting. In doing so, λ was held constant during the particular period and equal to the mean annual change.

We estimated the annual moose harvest rate in the experimental area during 1965-76 as follows: (1) the 1976 posthunt population was assumed equal to the 1981 moose population, (2) posthunt moose numbers were extrapolated from 1976 to 1965 using the mean estimated finite rate of change in moose observed/hour of survey as an annual index of abundance (Gasaway et al. 1983), (3) prehunt population size was estimated by adding annual reported harvest x 1.77 (to adjust for unreported harvest; Gasaway et al. 1983) to the annual posthunt population projections, and (4) we assumed 62% of the total GMU 20E harvest came from the experimental area as during 1983-88.

For the 1980's, adult mortality (M) was estimated assuming hunting mortality (M_h) and nonhunting mortality (M_n) were additive (Bergerud and Elliott 1986), as

$$M = 1 - (1 - M_h)(1 - M_n).$$

Hunting mortality during the 1980's was based on the reported harvest x 1.177 and estimates of population size. Nonhunting adult mortality was estimated during 1984-87 using data from 33 cow and 5 bull radio-collared moose and the computer program "SURVIVE" (White 1983). Radio-collared moose were located visually or audibly at least once a month during March 1984 through March 1987 to estimate mortality rates. Pulse rate of radiocollars doubled (150 beats/min) when motion ceased for 4 hours.

We estimated λ in several ways. Mean annual λ during 1956-59 and 1981-88 was calculated from annual estimates of λ using the following formula (Bergerud and Elliott 1986):

$$\lambda = \frac{1 - M}{1 - R},$$

where M was a constant mortality rate estimate and R was the annual estimated proportion of recruits. The mean of annual estimates of λ was used to account for the annual change in R resulting from varying numbers of bulls/cow, even though low harvest rates during these periods had little effect on sex ratios. Also, λ and its CI were estimated from the 1981 and 1988 moose density estimates in 7,700 km^2 of moose habitat (Gasaway et al. 1986). Lambda was also estimated for the periods 1966-76, 1976-80, and 1982-88 by regressing the $\log_e$ of overall moose observed/hour of survey against year.

Estimating Moose Physical Status, Population Age Structure, Pregnancy Rates, and Twinning Frequency.--Five parameters were estimated using data from 40 immobilized (Gasaway et al. 1978a) adult moose ($\geq$22 months old) in the experimental data: body form and composition based on a subjective 1 to 10 class ranking, with 10 being the best fleshed-out (Franzmann et al. 1977); packed cell volume in blood as an index of condition (Franzmann et al. 1987); total length of moose measured along the dorsal body contour from the small hairless patch on the nose to tip of the tail bone (Franzmann and Schwartz 1983); age from cementum annuli in an extracted central incisor (Gasaway et al. 1978b); and pregnancy by rectal palpation (Arthur 1964). Immobilization procedures were described by Boertje et al. (1987). Percent fat in marrow of long bones of dead moose (Neiland 1970) was used as an index of severe malnutrition. Twinning frequency was estimated by observing all radio-collared cows daily during 15-24 May 1984 and at 3- to 7-day intervals thereafter until 15 June 1984. Moose were located from an aircraft (Bellanca Scout or Piper Super Cub) equipped with radio-telemetry equipment (Telonics, Mesa, Ariz.).

Estimating Chronology and Causes of Mortality of Radio-collared Calf Moose.--Mortality parameters for calves were estimated from radio-collared calves during May 1984 through April 1985. Thirty-five neonates were radio-collared during 16-24 May 1984 in the experimental area; 33 remained bonded to their mother. During capture operations, cow-calf groups were located from an aircraft or a Hughes 500 helicopter. The helicopter hovered over the calf or calves, forcing the cow away. In low shrub areas, we exited the helicopter when it landed or hovered near the calf. In forested areas, we descended on a rope to the calf(s); after collaring the calf, the capture crew was slung away on the rope. We wore sterilized latex gloves and held calves away from our clothing to reduce human scent on the calves (Ballard et al. 1979).

Radio transmitters and expansion collars made of elastic bandages were similar to those described by Schwartz et al.

(1983). If radio transmitters remained motionless for 1-2 hours, the pulse rate doubled. Transmitters were rinsed in alcohol to remove scent before being sewn into the washed and well-rinsed collars. Subsequently, we handled collars with sterilized gloves and stored them in a plastic bag.

To estimate chronology of calf mortality during May 1984 through April 1985, we observed radio-collared calves daily (except 3 days) from aircraft beginning on the date of collaring to 4 July. After 4 July, we located calves on 11 July, 20 July, and on a monthly basis through April 1985.

To assess causes of calf mortality, we examined all carcasses or carcass remains from the ground. Death sites were reached by helicopter or aircraft. Descriptions of carcass remains, locality, and signs of predators were recorded following Ballard et al. (1979). We necropsied calves that were sufficiently intact.

<u>Estimating Browse Use</u>.--We estimated browse use at 100 points along 29 500-step transects during May and June 1982 and 1984. Sixteen transects were in the Mosquito Flats, an area of relatively high winter moose density; four were in high-concentration rutting areas near the Mosquito Flats; four were in an 18-year-old burn with excellent moose habitat; and five were in moose habitat along the Taylor Highway. Use of current growth of the nearest available browse plant was categorized as none (0%), low (1-25%), moderate (26-75%), and high (76-100%). Mean percentage of twigs browsed was estimated by multiplying the number of plants in each browse category by 0%, 13%, 50%, or 88%, depending on the use category, and dividing by the total number of plants being considered.

Wolf Population Status

<u>Estimating Wolf Abundance</u>.--Wolf distribution and abundance in the experimental area was primarily estimated by counting wolves or wolf tracks in snow from the air during October-April (Gasaway et al. 1983). To assist in these estimates during winters 1980-81 through 1988-89, 1-3 wolves in 9 of 16 study packs were immobilized with darts or captured in leghold traps or locking snares and then radio-collared. Radio-collared wolves were present in 1-6 packs annually. We administered 12.5 mg Sernylan (50 mg phencyclidine hydrochloride/ml; Bio-Ceutic Laboratories, St. Joseph, Mo.) using a jabstick, or 2.5 mg M99 via darts.

Wolf densities are based on our best estimate of wolf numbers in a 15,500-km^2 area, which encompassed all the wolf pack territories in, or partially in, the experimental area. Population size during late winter was the sum of observed wolves in packs, additional wolves enumerated based on tracks, plus 10% of the early winter population to account for single wolves not associated with packs (Mech 1973). Early winter population size, which was used to calculate prey/wolf ratios and population trend, was estimated using early winter counts, when available, or late winter counts plus the number of wolves harvested before late winter surveys. Early winter population size occasionally was underestimated because wolves dying from nonhuman causes before late winter surveys could not be included unless they were counted during early winter.

Aerial wolf surveys in the experimental area were conducted during winters 1981-82 through 1988-89; approximately 80, 70, 170, 30, 40, 50, 45, and 25 flight hours, respectively, were spent surveying, radio-collaring, and radio-tracking wolves. Total flight hours during which wolf survey data were gathered numbered 2-4 times the above figures when including flight hours for wolf removal, moose surveys, and radio-tracking moose and grizzly bears. Information was also obtained each winter from local trappers and pilots.

Harvest and Removal of Wolves.--The number and location of wolves harvested by trappers and hunters was obtained from a mandatory reporting program during 1972-89. In addition, during winters 1981-82, 1982-83, and October 1983, ADF&G killed some wolves that ranged fully or in part in the experimental area. Also, during winter 1980-81, ADF&G killed wolves from 2 packs (Mansfield Creek and Billy Creek) that had territories extending into the experimental area. Most wolves killed by ADF&G were shot from a helicopter or aircraft; the remainder were trapped or snared.

Determining Food Habits.--Wolf food habits in and adjacent to the experimental area were determined from: (1) examination of wolf stomach contents; (2) radiocesium (Cs-137) levels in muscle from wolves, caribou, and moose (Holleman and Stephenson 1981); (3) scat analysis (Floyd et al. 1978); and (4) observations of the carcasses of large prey during the monitoring of a radio-marked pack. Hunters and trappers contributed wolf carcasses. Radiocesium levels in 1-kg samples of fresh skeletal muscles from wolves (*n* = 108), caribou (*n* = 9), and moose (*n* = 10) were used to estimate the percent caribou in the wolves' winter diet (Y) during the month before the wolves' deaths (Holleman and Stephenson 1981), as follows:

$$Y = 100[\underline{\bar{x}}_w/(\underline{\bar{x}}_c-\underline{\bar{x}}_m)]\cdot[(A\cdot C)/(B\cdot D)],$$

where $\underline{\bar{x}}_w$, $\underline{\bar{x}}_c$, and $\underline{\bar{x}}_m$ are the mean concentration of Cs-137 in wolf, caribou, and moose muscle tissue, respectively; A = $\underline{\bar{x}}$ wolf weight (38 kg, *n* = 142); B = 28 days; C = 0.80 (proportion of caribou carcass consumed by wolves; J. Davis and A. Allaye-Chan, unpubl. data); and D = total estimated consumption rate by wolves (3.0-4.1 kg/wolf/day; Peterson et al. 1984, Sumanik 1987, Fuller 1989). All Cs-137 samples were corrected to a single data based on a half-life of 8.2 years (Holleman and Stephenson 1981), and wolf Cs-137 samples were weighted by pack size. We assumed the lichen component of the diet of caribou was constant during 1981-88, and that the explosion of the Chernobyl reactor in the Soviet Union added 15% Cs-137 to the study area during late April 1986 (D. Holleman, unpubl. data).

Assessing Productivity.--Examination of female wolves ≥1 year old killed in the experimental area during March or April 1980-88 provided data on wolf productivity. Wolves less than 1 year old were identified by tooth development and wear and by the uncalcified epiphysis at the distal end of the radius-ulna (Rausch 1967). Reproductive status was classed as active (i.e., in estrus or pregnant) or inactive based on size and thickness of the uteri and sectioning of ovaries. Ovaries were hardened in 10% formalin for at least 2 weeks, and then hand-sectioned at 1-mm intervals to count corpora lutea. Reproductive indices were compared using 2-tailed Student's *t*-tests, and proportions of females in estrus or pregnant were compared using Chi-square tests.

PREY AND PREDATOR POPULATIONS IN THE EXPERIMENTAL AREA

Moose Population Status

Population Trend and Density.--The moose population irrupted from about 1950 through the early 1960's and then rapidly declined (Fig. 2). No systematic trend surveys describe the irruption; however, biologists and long-term residents observed a marked increase in the moose population from the early 1950's through 1964-65 (Appendix 1). The high yearling recruitment during 1956-59 (Table 1) was typical of irrupting populations (Pimlott 1959, Gasaway et al. 1983), and the young age structure of this lightly hunted population during 1965-66 indicated the population had recently grown rapidly (Fig. 3). During the irruption, we estimated λ at 1.18 using recruitment and mortality estimates (Table 2). The moose population throughout the area rapidly declined ($\lambda = 0.85$, Table 2) from the mid-1960's through 1976 (Fig. 2), based on surveys in 5 widely distributed areas (Fig. 4).

Following the irruption and decline, a low-density population again prevailed (Fig. 2). Numbers of moose observed/hour remained largely unchanged during 1976-81. During 1981, density was estimated at 88 moose/1,000 km^2 (probable range = 65-112/1,000 km^2, an approximation of the 90% CI) in the 7,700 km^2 of moose habitat west of the Taylor Highway. Moose density in this area significantly increased to 157 moose/1,000 km^2 (90% CI = 127-188) between 1981 and 1988 (*P* < 0.001, 2-tailed Student's t-test on densities uncorrected for sightability). Estimates of annual rates of increase in the early winter population during 1981-88 are: (1) 4% and 5% based on models using mortality and recruitment estimates (*see* Causes and Extent of Calf and Adult Moose Mortality; Table 2), (2) 9% calculated by regressing the number of moose observed/hour of survey against years 1982-88 (Fig. 2), and (3) 9% (90% CI = 5-13%) using 1981 and 1988 moose population estimates. We suggest the actual rate of increase was likely in the lower half of the CI (5-9%) because models using recruitment and adult mortality rates indicate low potential growth rates. Similarly, we reason the 1981 density was likely in the upper half of the 1981 probable range (i.e., 88-112 moose/1,000 km^2) and the 1988 density was in the lower half of the 1988 CI (i.e., 127-157/1,000 km^2). Later, we use these ranges for calculations.

Moose Production and Mortality.--Calf production was high (138 calves/100 cows $\geq$24 months old during May in the experimental area during spring 1984 compared with many other North American moose populations (Pimlott 1959; Simkin 1965, 1974; Blood 1974). Our estimate is based on a proportion of 13 24-month-old cows/100 cows $\geq$36 months old (estimated by the $\bar{x}$ for 1981-87 cohorts at 18 months of age, Table 1), 100% pregnancy of 27 radio-collared cows $\geq$36 months old during 1984, assumed 30% pregnancy for 24-month-old cows (Blood 1974), 52% twinning frequency during 1984 (n = 27 cows $\geq$36 months old with calves), and 0% twinning frequency for 24-month-old cows (Blood 1974).

Increased calf mortality reflected in significantly fewer calves/100 cows after 1965 ($P < 0.001$, 2-tailed Mann-Whitney U test) coincided with the population decline and subsequent low-density phase (Table 1). Estimated calf mortality averaged 55% by 5 months of age during the 1956-60 portion of the irruption {[1 - ($\bar{x}$ calves per 100 cows $\geq$29 months old/138 calves produced by these cows)] x (5 month adult survival rate in Table 2) x 100}, compared with 89% mortality during the 1966-75 portion of the decline and 87% during the recent low-density phase (1976-88). These estimates assume a constant annual production of 138 calves/100 cows $\geq$24 months old. Even assuming time lags maintained strong density-dependent effects during much of the decline, the mean mortality rate would have remained high (82%) during the decline. This scenario is based on a hypothetical calf production of 80/100 cows derived from populations at or near KCC in Table 3 [(1 + $\bar{x}$ proportion of twin births) x ($\bar{x}$ percent pregnant)]. Our mortality study using 33 radio-collared calves during 1984 indicated most mortality occurred shortly after birth--76% of calves died within 8 weeks of birth and 76-79% by 5 months after birth (Fig. 5).

Estimated mortality rates of adult moose were highest during periods of population decline and lowest during periods of population growth (Table 2). Total adult mortality rates averaged 22% annually during the precipitous decline during 1966-76, of which approximately 3% was from hunting (see Harvest as a Limiting Factor). In contrast, estimated nonhunting and total mortality rates during the slow increase phase were 6.8% (95% CI = 1.6-12.0%) and 8.7% (2.9-14.5%), respectively, for 38 radio-collared adult moose during March 1984 through March 1987. Cow moose in this sample had a mean age of 8.5 years (SD = 3.4, n = 31) and a moderately old age distribution resulting from prolonged low recruitment (Fig. 6; Table 1). Our estimated rates for nonhunting mortality were similar to estimates for radio-collared adult moose during a precipitous decline (20%) and subsequent irruption (6%) in another interior Alaska population (Gasaway et al. 1983).

The major population fluctuations appear to coincide with changes in both adult mortality and recruitment rates (Table 2). For example, the rapid decline phase coincided with higher adult mortality and significantly lower recruitment ($P < 0.002$, 2-tailed Mann-Whitney U test) compared with the irruption phase (Table 2). The transition from a declining phase to nearly stationary and slowly increasing phases occurred following increased adult survival and possibly improved recruitment; however, recruitment was not significantly greater ($P > 0.1$, 2-tailed Mann-Whitney U test) than during the decline phase (Table 2).

Caribou Population Status

The Fortymile Caribou Herd numbered about 50,000 during the period 1953-63 but declined to about 6,600 caribou by 1973 (Skoog 1956, 1964; Davis et al. 1978; Fig. 2). Numbers subsequently increased to about 20,000 by June 1988 (Valkenburg and Davis 1989). Harvest hastened the decline, particularly during 1970-72 when harvest exceeded yearling recruitment (Davis et al. 1978). Nevertheless, Davis et al. (1978) concluded harvest likely contributed less to the decline of caribou than did predation. From 1973-86, annual harvest rates averaged 2% (range = 1-3%) and were a minor influence on herd growth (Davis et al. 1978, Valkenburg and Davis 1989).

Wolf Population Status

Historical Wolf Abundance and Harvest, 1940-81.--The high density of wolves in the region (Murie 1944) was rapidly reduced by a federal predator reduction program during 1948-60 (Kelly 1950a, 1957; Olson 1959a cited in Davis et al. 1978; Fig. 2). Wolves were killed by strychnine-laced baits dropped from aircraft, cyanide guns (coyote-getters), shooting from aircraft, and year-round trapping and snaring (Kelly 1950b, 1953, 1958). Bounties encouraged the public to harvest wolves using the above methods, except for poisoning.

After predator removal ceased in 1960, wolves again became abundant, but precipitously declined during the mid-1970's after prey became scarce (Fig. 2). One author, D. Grangaard, observed that wolf numbers declined during winter 1974-75 and especially during winter 1975-76. Grangaard trapped an average of 32 wolves (SD = 12) annually during winters 1971-72 through 1975-76 on the same line he currently traps in the experimental area. His annual catch declined to 15 wolves during winter 1976-77 and remained low ($\underline{\bar{x}}$ = 6, SD = 4) through spring 1980, despite similar effort among years. During early winter 1981, ADF&G began a wolf reduction program and population monitoring.

The wolf population was lightly exploited in and adjacent to the experimental area for at least 3 years before the 1981-83 wolf removal (Table 4). The mean annual wolf harvest rate for wolves was 11%, assuming wolf numbers were similar to the 1981 estimate preceding wolf removal (Table 4). This harvest rate is below sustained harvest rates ($\geq$20%) that have precluded wolf population growth in the experimental area and elsewhere (Keith 1983, Ballard et al. 1987, Fuller 1989, present study).

Population Size, Harvest, and Land Tenure System, 1981-88.--ADF&G wolf removal and public harvest during 1981-83 reduced the wolf population, and subsequent harvest by public hunters and trappers maintained the population below pre-removal size (Table 4). From 1983 to 1988, annual kill rates of 28%, 18%, 20%, 27%, and 32%, respectively, resulted in no net change in wolf numbers (Table 4). These data indicate the reduced wolf population can sustain harvests of about 25% of early winter population given low to moderate prey abundance relative to wolves (15-39 moose equivalents/wolf, Table 5).

Wolf packs had a residential territorial system. Radio-collared wolves associated with packs (Appendix 2) did not abandon their territory to follow caribou migrations, as observed in areas where migratory caribou are the primary prey available (Stephenson and James 1982).

Wolf Productivity.--Wolf productivity in 3 Alaska studies was directly proportional to ungulate biomass available/wolf. The 3 measures of productivity were lowest when prey biomass/wolf was lowest (Table 5). After wolf removal increased prey biomass/wolf, corpora lutea production increased significantly ($\underline{P}$ < 0.1, 2-tailed Student's $\underline{t}$-test) in both central and east-central Alaska populations, and the percentage of reproductively active females increased significantly ($\underline{P}$ < 0.01) in central Alaska, where prey biomass/wolf increased the most

(Table 5). The highest wolf productivity occurred during 1957-64 (Rausch 1967; Table 5), a period of extremely high prey biomass and, until 1960, low wolf numbers resulting from predator reduction programs (1948-60) (Gasaway et al. 1983; Fig. 2). Significantly ($\underline{P} < 0.1$) more corpora lutea and blastocysts or fetuses occurred during 1957-64 than when prey biomass/wolf was at moderate levels.

Although functional responses may alter relationships between wolf productivity and ungulate biomass, our data imply a relationship between wolf productivity and ungulate biomass. The data may also indicate, in part, the mechanism by which productivity varies. As per capita ungulate biomass declined, the number of corpora lutea/adult female decreased. Additional declines in per capita ungulate biomass decreased the percentage of females entering estrus, further reducing the number of corpora lutea produced by the wolf population.

We conclude that low wolf productivity in the experimental area immediately before wolf removal indicates wolves were, in part, nutritionally limited by the low prey density (Table 5), i.e., wolves were near KCC.

Grizzly Bear Population Status

Abundance of Grizzly Bears, 1950-86.--Density of grizzly bears was low in the experimental area during the 1940's and 1950's but increased by the mid-1970's (Fig. 2). Low densities occurred for 3 reasons: (1) miners were more abundant than after the 1950's, and they shot bears to minimize conflicts; (2) bears were killed in snares that were set year-round to catch wolves for bounty (O. Burris, ADF&G biologist, pers. commun.); and most importantly, (3) the wolf reduction program during 1948-60 killed grizzly and black bears incidental to killing wolves (P. Shepherd and D. Jones, predator removal officers, pers. commun.).

During 1986 grizzly bear density in a 4,000-km^2 portion of the experimental area was estimated to be 16 bears of all ages/1,000 km^2 on 1 May and 12 bears/1,000 km^2 on 1 November (Boertje et al. 1987). Approximately 65% of the spring bear population was $\geq$2 years old.

Harvest.--The grizzly bear population was lightly exploited in the experimental area during 1961-81 and moderately exploited during 1982-88. During 1961-81, annual harvests of 0-6 grizzly bears ($\bar{x}$ = 2, $\underline{n}$ = 21, SE = 0.3) were reported; this is an average of about 1% of the population, assuming a density similar to the spring 1986 estimate of 16 bears/1,000 km^2. Hunting regulations were liberalized for grizzly bears during 1981 and for caribou and moose during 1982 to, in part, stimulate more hunting in the area and thereby increase the incidental and intentional harvest of grizzly bears. During 1982-88, reported harvests increased to 6-14 grizzly bears ($\bar{x}$ = 12, n = 7, SE = 1.1) in the experimental area. These harvests indicate an average annual harvest rate of 8% during 1982-88, assuming spring grizzly bear densities were comparable with densities in the 4,000-km^2 grizzly bear study area (16 bears/1,000 km^2). An 8% harvest rate appears sufficient to cause the population to decline slowly. For example, Reynolds (1990) reported an 8-9% annual harvest rate resulted in a 2% annual decline in a central Alaska grizzly bear population during an 8-year study. However, immigration into our experimental area may have occurred from lightly hunted adjacent areas, since harvest rates of grizzly bears in the remaining 18,800-km^2 GMU 20E (Fig. 1) averaged only 2% annually during 1982-88.

Black Bear Population Status and Harvest

Black bears were scarce in the experimental area during the 1980's. We observed only 12 different black bears while capturing and monitoring grizzly bears in a 4,000 km^2 portion of the experimental area during 150 days during 1985-86 (Boertje et al. 1988).

Black bears were lightly exploited in the experimental area during 1974-88. Reported annual harvest averaged only 3 black bears during this period (range = 0-6), and a majority of this harvest occurred along the Taylor Highway.

FACTORS LIMITING MOOSE DENSITY IN THE EXPERIMENTAL AREA

In this section, we assess the role nutrition, snow/nutrition, harvest, disease, and predation played in limiting moose at low densities in the experimental area. We used inductive and hypothetico-deductive methods to build arguments for the importance of each factor, and we acknowledge the limitation of inductive methods to identify the causes of an event. Inductive methods provide knowledge on correlations between facts. In contrast, hypothetico-deductive methods help explain why events occur by using predictions about facts that are confirmable by data (Romesberg 1981).

Nutrition as a Limiting Factor

Nutritional stress sufficient to strongly retard population growth should be accompanied by low reproductive rates (Blood 1974, Albon et al. 1983, Albright and Keith 1987), reduced recruitment (Verme 1967, 1969; McCullough 1979; Skogland 1983), retarded body growth, poor physical condition of animals (Peterson 1977, Skogland 1983, Messier and Crete 1984), physiological stress indicated by low packed cell volume (PCV) (Franzmann et al. 1987), starvation before old age (Bergerud et al. 1983), and/or high browsing rates on preferred food species (Albright and Keith 1987).

Low-density Phases--Before 1949 and During 1976-88.--We suggest nutrition probably was not limiting moose at low densities immediately before the 1950's population irruption (Fig. 2). Irruptions occur when moose are well below KCC or when given significant habitat improvement (Peek and Eastman 1983). Wildfire creates most habitat improvements in the study area. Burned areas are easily identified 50 years after a fire in this area. Our observations, beginning in 1968, indicated no wildfires occurred during the 1930's and 1940's that produced extensive young seral stands during the late 1940's and 1950's. Therefore, moose were likely well below KCC before the irruption.

The size and condition of moose in the experimental area were inconsistent with predicted values for a nutrition-limited population during the recent low-density phase, 1976-88. First, the mean total length of adult cow moose born after 1975 was among the largest for Alaska moose (Table 6), indicating nutritional status during the period of skeletal growth (to 36 months old for cows) was excellent (Palsson and Verges 1952, Franzmann et al. 1978). Second, PCV in captured moose was greater than ($\underline{P} < 0.005$, 1-tailed Student's $\underline{t}$-test) the 36.5% value Franzmann and Schwartz (1983) reported for a population in poor condition (Table 7) and was in the range indicating average condition for late winter. Third, a physical body condition index (Franzmann 1977) estimated during late winter indicated captured moose were in average condition for that season ($\bar{x} = 7.0$, $\underline{n} = 39$, SE = 0.2). Fourth, only 4 of 42 adult moose dying from predation and other non-human causes during 1981-87 had <20% marrow fat, a fat level indicating severe malnourishment (Peterson et al. 1984). These 4 moose may have been in poor condition because they were old--12 and 13 years for 2 bulls and 17 years each for 2 cows. Few bulls live past 13 years (W. Gasaway, unpubl. data) and few cows live past 17 (Peterson et al. 1984). Finally, we observed no large-scale starvation of moose during 1975-88, despite at least one winter (1978-79) with relatively deep snow (Fig. 7, 8).

High twinning and pregnancy rates also indicate the moose population was not nutritionally stressed, i.e., well below KCC (see Blood 1974, Franzmann and Schwartz 1985). Our observed 52% twinning and 100% pregnancy rates were well above the values reported from populations near or above KCC (Table 3).

Low competition for browse indicated nutrition was not an important limiting factor for moose during 1976-88 in the experimental area. During winters 1981-82 and 1983-84, moose browsed only 6% of the total twigs on 1,652 plants of preferred willow species (Table 8). Also, within the high moose density area, only 7% of twigs were browsed on the 1,451 willows. Preferred willow species in this and other areas of Alaska were *Salix planifolia*, *S. arbusculoides*, and *S. alaxensis* (Coady 1974*a*, Risenhoover 1987). We discontinued sampling browse when these and other field observations indicated browsing rates were lower than in areas where investigators concluded food was not preventing moose population growth in interior Alaska. For example, moose browsed 16% of the twigs on the 3 most preferred willow species in Denali National Park (Risenhoover 1987), and about 31% of twigs on the 3 most preferred willow species on the Tanana Flats (Coady 1974*a*, Gasaway et al. 1983).

Because indicators of strong nutritional stress were not observed, we conclude nutrition was a minor factor limiting moose population density during the low-density periods and that moose densities were well below KCC.

Peak Density and Decline Phase.--Nutrition could have been one of the major factors limiting moose at peak density and during the early decline. Intense browsing of preferred willow species during 1968 (L. Jennings, ADF&G biologist, pers. commun.) and reduced recruitment and adult survival early in the decline are suggestive of a nutritionally limited population (Figs. 2, 9; Tables 1, 2, 3; McCullough 1979). Reduced recruitment and adult survival, however, are equivocal indicators of nutritional stress. Predation (Gasaway et al. 1983, Larsen et al. 1989*a*) and deep snow (Rolley and Keith 1980) can similarly reduce recruitment and adult survival.

By the latter half of the moose population decline (1970-76), 2 lines of reasoning suggest nutrition was likely not a major factor limiting moose population growth. First, mean total length of adult cow moose born during the latter half of the decline was the longest measured in Alaska (Table 6). Second, only a few moose were observed to have starved during 1 winter among winters 1969-70 through 1975-76 (D. Grangaard, pers. obs.; B. Roberts, pers. commun.), yet this period included 3 winters with relatively deep snow (Figs. 7, 8).

Snow/Nutrition as a Limiting Factor

Correlations indicate deep snow and accompanying reduced nutritional status were probably not major factors limiting moose at low densities immediately before the irruption (Fig. 2). No extremely deep snows were reported in interior Alaska during the several years before the irruption. Compared with snowfall during the irruption, snow was not significantly deeper at Fairbanks during 13 winters preceding the irruption or in Northway during at least 7 winters preceding the irruption ($\underline{P} > 0.2$, Mann-Whitney U test). Although no records exist for snow conditions before 1950 in the experimental area, snow depth at Mt. Fairplay (1970-85) in the experimental area (Fig. 7) was significantly correlated with snowfall in Fairbanks ($P < 0.01$, $r = 0.65$), 200 km to the west, and in Northway ($P < 0.05$, $r = 0.49$), 50 km southeast of the experimental area. Also, snow depth at Chicken (1965-85) in the experimental area was significantly correlated with snowfall in Fairbanks ($P < 0.001$, $r = 0.76$) and in Northway ($P < 0.05$, $r = 0.47$). However, Chicken snow depths were significantly shallower than in Fairbanks ($P < 0.001$, paired Student's t-test).

We found no evidence deep snow precipitated the decline of moose during the mid-1960's, or played a major role in maintaining the decline and subsequent low densities (Fig. 2). When moose were near peak densities, snow depths in the experimental area did not exceed 90 cm (Fig. 7), a depth above which substantial mortality has been observed in interior Alaska when moose densities were moderate to high (Bishop and Rausch 1974, Coady 1974*b*, Gasaway et al. 1983). Additionally, declines in relative cohort strength and calves or yearlings/cow preceded the first relatively deep snowfall (Tok 1966-67, Figs. 7, 8, 9), and the 1966-67 snowfall had little apparent effect on calf survival. For example, yearling/cow ratio for the 1966 cohort was greater than for the next 4 cohorts, which lived through winters of shallower snow (Fig. 8). During the decline and low-density phases, measured snow depths exceeded 70 cm 4 times, a depth that impedes movements of moose, but snow did not reach the critical 90 cm depths (Coady 1974*b*; Fig. 7). Only a few calves dying from nonviolent causes were observed during 1 winter (1970-71), and yearling abundance (relative to calves of the same cohort) in early winter appears unexpectedly low only following winter 1978-79 (Fig. 8). Also, snow depth experienced by pregnant cows from 1956-85 was not correlated ($P > 0.1$, $r = <0.14$ for 3 correlations) with calves/100 cows $\geq$29 months old the following early winter. Additionally, no correlations ($P > 0.1$, $r = <0.15$ for 3 correlations) were found between yearlings/100 cows $\geq$29 months old and snow depth during the calf's first winter. Snow data were the sum of March and April snow depths at individual snow stations (Fig. 7).

Three factors may have reduced the effect of snow depth in our study area compared with areas where snow depth has clearly affected moose population dynamics. First, maximum snow depth was lower in our study area than in areas of Alaska where snow depth affected calf survival (Bishop and Rausch 1974, Gasaway et al. 1983, Ballard et al. 1990). Second, effects of weather seem density-dependent (Picton 1984), and moose density was low except during the irruption and early in the decline. Third, the effect of snow on calves may have been masked by predation that, at least during the 1980's, killed most of the calves before winter (*see* Predation as a Limiting Factor).

Harvest as a Limiting Factor

Harvest increased early in the irruption phase compared with pre-irruption harvests (Fig. 2), and was therefore not an important factor limiting moose just before the irruption. Increased harvest resulted from construction of the Taylor Highway (1946-56), which provided access and brought increased numbers of hunters to this wilderness. Most of the moose harvest occurred along the highway from 1946 until 1972, when the scarcity of bull moose encouraged hunting in remote areas (Olson 1959*b*; Fig. 10).

Moose harvest apparently was a minor factor limiting growth of the population at peak density and during the decline, although harvest accelerated the decline. Few cows were harvested (Table 9), and total harvest rates were approximately 2% in 1965 and 2-5% ($\bar{x} = 3\%$) through 1976. Given that several assumptions affect estimated harvest rates (*see* Methods), we suggest these rates be viewed as conservative. By contrast, moose populations sustain harvest rates of 23-37% where moose are below KCC and predators are absent or substantially reduced in number (Messier and Crete 1984, Crete 1987, Nygren 1987). Thus, the 2-5% harvest rate on our study population was a small influence growth rate relative to other potential limiting factors. Harvests of primarily bulls, however, did cause significantly lower bull/cow ratios in the 2 survey areas <13 km of the Taylor Highway compared with ratios in the 3 offroad survey areas (>13 km) both before (1956-60; $P < 0.0005$, 1-tailed Mann-Whitney U test) and during (1966-76; $P < 0.05$, 1-tailed paired Wilcoxon tests) the decline (Fig. 10, Table 9). Lowered bull/cow ratios likely did not impair breeding based on pregnancy rates of about 90% in portions of Alaska with only 4-20 bulls/100 cows (Bishop and Rausch 1974).

Harvest of caribou probably hastened the decline in the moose population by lowering alternate prey numbers and increasing the antiregulatory effects of predation on moose. Caribou declined from about 50,000 to 6,600 during 1963-73 (Fig. 2). Harvest rapidly accelerated this decline during 1972-74 (Davis et al. 1978). Wolves, however, remained abundant and grizzly bears increased in numbers during most of the period when moose and caribou declined (Fig. 2).

Harvest had little influence on the low-density moose population during 1976-88. Moose hunting was prohibited during 1977-81 (Table 9) and bull/cow ratios recovered (Fig. 10), yet moose remained at low densities (Fig. 2). High bull/cow ratios during 1982-87 ($\bar{x}$ = 82/100 near and offroad, Fig. 10) indicated resumption of bull-only harvests had a negligible impact. The average annual harvest of 31 moose during 1983-88 (Table 9) was a 2.6% harvest rate, assuming a population of 1,200 moose (the average of the 1981 and 1988 early winter densities extrapolated to the 9,700 km^2 experimental area). Additionally, in our modeled moose population (<u>see</u> Predation as a Limiting Factor), hunting accounted for only 1.5% of the total annual mortality during the mid-1980's compared with 37% mortality from other causes.

Disease as a Limiting Factor

We found no evidence indicating disease was a limiting factor for moose in the experimental area. Several studies have concluded that Alaska moose are largely free of infectious diseases and parasites that seriously affect survival (Kocan et al. 1986, Lankester 1987, Zarnke 1988). Antibody tests of 35 sera samples from moose immobilized in the experimental area during 1984 and 1986 provided no conclusive evidence of exposure to brucellosis, Q fever, leptospirosis, contagious ecthyma, infectious bovine rhinotracheitis, bovine viral diarrhea, epizootic hemorrhagic disease, bluetongue, parainfluenza III, or respiratory syncytial virus (Zarnke 1988). The high reproductive rates observed among moose in the experimental area during the mid-1980's also indicates moose were free of diseases that lower reproduction (Table 3).

Predation as a Limiting Factor

The hypothesis that predation was a primary factor limiting moose at low densities is supported, in part, by the irruption of moose following an intense wolf and bear removal program in the experimental area beginning during 1948. This was the only known irruption of moose in this area during the 1900's (Appendix 1). Irruptions of moose also followed similar programs in central and south-central Alaska during the 1950's (Bishop and Rausch 1974, Gasaway et al. 1983, Ballard et al. 1990). Likewise, during the 1970's intense wolf and bear removal in south-central Alaska and intense wolf removal in central Alaska again contributed to the growth of moose populations (Gasaway et al. 1983, Ballard et al. 1990). Because these intense predator removal programs consistently resulted in moose population increases, predation was likely a significant limiting factor.

The following sections present evidence that predation was the primary factor limiting moose at low densities during the 1980's.

<u>Predator Food Habits and Ratio of Prey to Predators</u>.--Moose were the primary ungulate prey of wolves and grizzly bears in the experimental area during the 1980's, based on 4 types

of data. First, radiocesium analyses indicated caribou composed approximately 24-32% of the wolf's winter diet (Nov-Apr) during winters 1981-82 and 1985-86 through 1987-88. The majority of the winter diet, 68-76%, was presumably comprised mainly of moose, the only other ungulate. Second, stomach contents of wolves indicated moose were a major component of the winter diet; of 143 stomachs examined from spring 1981 through spring 1988, 30% contained caribou, 29% contained moose, 4% contained small mammals or birds, and 37% were empty. Third, analysis of 91 wolf scats collected at a den indicated adult and calf moose composed about 74% of the prey biomass consumed during spring and summer 1981; the remainder of the diet was 3% caribou, 16% snowshoe hares, and 7% rodents and birds. Fourth, daily observations of radio-collared predators indicated moose composed about 75% of the observed biomass consumed by 1 study wolf pack from 30 April to 10 June 1986, and moose composed 92% of prey biomass killed by grizzlies during 1985-86 (Boertje et al. 1988).

The low number of moose and caribou/predator in the experimental area indicates predation could have strongly influenced the moose population during 1981 (Tables 10, 11) and the late 1970's given similar predator and prey populations (Fig. 2). We summarized prey/predator ratios from North American moose populations where predation had been shown to be or was highly suspected of being a major limiting factor (Table 12). The number of prey/predator in the experimental area in 1981 is among the lowest reported in North America. Furthermore, when the number of wolves in our area is adjusted downward to compensate for approximately 28% caribou in the winter diet, the number of moose/wolf (15-19 in 1981, Table 11) remained within the range where wolf predation can strongly affect moose population growth (Gasaway et al. 1983).

<u>Causes and Extent of Calf and Adult Moose Mortality</u>.--Predation was the primary cause of high moose calf mortality. Mortality of 33 radio-collared calves born during 1984 was 79-82% by 11 months of age; 52% of the calves were killed by grizzly bears, 12-15% by wolves, 3% by black bears, and 12% drowned. Thus, predators killed 67-70% of calves. The relative importance of wolf and grizzly bear predation, however, may have differed when wolves were more abundant. The 1984 calf mortality study occurred in an area where the spring wolf population was reduced to approximately 40% of the early winter 1981 density.

Predation by grizzly bears and wolves was also the primary cause of nonhunting deaths for uncollared yearling and adult moose. Cause of death was determined for 46 yearling and adult moose during 1981-87; 41 (89%) were killed by predators, 4 (9%) died from antler wounds or locked antlers, and 1 (2%) drowned.

A model using natality and mortality data indicates predation was the major factor influencing moose population dynamics in the experimental area during 1981-88. Predators killed approximately 31% of the hypothetical population that included 1,685 neonate and older moose, whereas hunting and other factors accounted for only 1.5% and 6% of the population, respectively. This simulated adult and yearling population increases at 4% annually.

Additive and Compensatory Nature of Mortality When Moose Are Well Below KCC.--Although predators caused most mortality of moose in the experimental area, support for predation limiting the moose population below KCC depends on evidence that predation is largely additive to other sources of mortality, i.e., predators killed many moose that otherwise would have lived to reproduce. We considered predation compensatory when a moose was killed that likely would have died from another cause before reproducing.

McCullough (1979, 1984) presented a model that indicates mortality is mostly additive when ungulates are near or below maximum sustained yield levels (about 60-70% of KCC for moose, Crete 1987) and increasingly compensatory as populations approach KCC. We concluded that our study population was well below KCC, thus our prediction is that mortality would be mostly additive. We assess this prediction below.

Age and nutritional status of predator-killed adult moose indicated predation on adults was largely additive. We classed mortality as follows: (1) largely additive if moose were neither severely malnourished ($\geq$20% fat in marrow, Peterson et al. 1984) nor very old (bulls >12 and cows >15 years old), (2) largely compensatory if moose were very old, and (3) compensatory if moose were severely malnourished or severely malnourished and very old. Most (24 of 37) predator-killed moose were in the largely additive class (Fig. 11); only 4 of 37 were classed wholly compensatory.

Grizzly bear predation on adult moose was more additive than wolf predation when moose were at low densities. Ages of grizzly bear-killed uncollared cow moose were not significantly different ($P > 0.5$, 2-tailed Student's t-test) from living cow moose ($\bar{x} = 10.1$ years, $n = 8$, SE = 1.8 versus $\bar{x} = 8.5$ years, $n = 31$, SE = 0.6, respectively); whereas wolf-killed uncollared cow moose ($\bar{x} = 12.8$ years, $n = 15$, SE = 1.0) were significantly older ($P < 0.01$). Also, only 3 of 15 grizzly bear-killed adult moose were classed as very old and none of 16 were severely malnourished (Fig. 11). In contrast, 11 of 24 wolf-killed moose were very old and 4 of the very old were severely malnourished. Grizzly bears are powerful predators capable of killing moose more quickly than wolves (Boertje et al. 1988). We suggest the protection of young calves brought young and middle-aged adult cows in contact with grizzly bears. Most adult moose killed by grizzly bears were cows killed during and shortly after calving (Boertje et al. 1988, Larsen et al. 1989a). Wolves selecting very old adult moose when moose density was low and wolves were nutritionally stressed (see Wolf Productivity; Table 5) strengthens the concept that food availability for wolves varies with the age structure of the moose population (Peterson et al. 1984, Van Ballenberghe 1987).

Assuming other mortality sources remain unchanged, a direct test for additive mortality involves reducing predation and subsequently evaluating moose survival and population growth (Bergerud 1971, Gasaway et al. 1983). Although few data sets are available, we suggest the high calf survival and population irruption following the start of wolf and bear removal during 1948 indicates predation was strongly additive during that period.

We believe predation was not adequately reduced during the 1980's to fully evaluate the additive nature of predation. Planned sequential wolf and bear removal experiments were prematurely terminated during 1983. Nevertheless, the findings are as follows. Three factors probably contributed to a small reduction in total predation in the experimental area: (1) moderate wolf reduction (Tables 4, 11), (2) a probable small reduction in grizzly bear numbers from increased harvest (1982-88), and (3) increased caribou as alternate prey (Fig. 2). Of these factors, only the increase in caribou influenced predation in control areas. Moose numbers increased ($P < 0.001$, 2-tailed Student's t-test) in the experimental area between 1981 and 1988 but at a low rate ($\lambda = 1.04$-1.09) based on population estimates, indices, and models (Figs. 2, 12; Table 2). Although no significant trends occurred in control areas (slopes of regression lines not different from 0, $P > 0.1$; Fig. 13), positive slopes on regression lines lead us to speculated that moose in the control areas may have also increased. Because these data are equivocal, we draw no conclusions on the effects of the small reduction in predation on population growth. Problems relating to interpretation of results from small predator reductions are discussed by Connelly (1978) and Crete and Jolieoeur (1987).

The 1981-83 wolf removal in a portion of the experimental area allowed us to conclude that wolf predation on calves was not a detectable source of additive mortality when grizzly bears were abundant. Reducing wolf numbers from 85 during early winter 1981 to 19 during April 1982 in and around the Mt. Veta-Mosquito Flats survey area produced no treatment effect on calf or yearling/cow ratios for the 1982-86 cohorts (Table 13). Failure of the calf/cow ratio to increase during the 1980's wolf removal indicates either grizzlies were the predominant predator on young calves before and after wolf numbers were reduced, or increased grizzly bear predation compensated for reduced wolf predation. Lowered wolf predation likely was not compensated for by factors other than grizzly bear predation, e.g., drowning.

By severely reducing numbers of the predominant predator, other experiments demonstrated that predation on moose calves is largely additive when moose are well below KCC (Gasaway et al. 1983, Stewart et al. 1985, Ballard and Larsen 1987, Van Ballenberghe 1987, Ballard and Miller 1989). We speculated that if grizzly bears, the predominant predators on calves during 1984, had been severely reduced along with wolves, we may have observed increased calf survival. In lieu of a combined bear and wolf reduction program, we manipulated the food habits of predators by air-dropping 12-15 tons of train-killed moose and scrap meat during May and June 1985 in and around the Mosquito Flats calving area (Fig. 1). We observed grizzly bears, black bears, and wolves consuming much of this meat. The 1985 early winter calf/cow ratio in the Mosquito Flats increased to 53/100 females ($\underline{n}$ = 17 females) compared with a range of 11-15/100 ($\underline{n}$ = 26-39) during the preceding 3 years and 26-36/100 ($\underline{n}$ = 25-27) during the following 2 years. The 1985 response was not observed in 2 partially treated adjacent areas (11-12/100, $\underline{n}$ = 17-65) or 3 untreated areas in the experimental area (10-19/100, $\underline{n}$ = 25-70). Thus, total predation appears partially additive.

We conclude that data, aside from results of the inadequate predator removal experiment during the 1980's, indicate predation had an additive component, as predicted for ungulate populations that are well below KCC (McCullough 1979).

Conclusions on Factors Limiting Moose Density in the Experimental Area

Predation by lightly exploited bear and wolf populations was the primary factor limiting moose at low densities relative to KCC. Nutrition, snow/nutrition, and harvest were minor limiting factors when moose were at low densities. Disease was not identified as a limiting factor.

WOLF AND BEAR PREDATION LIMITING MOOSE AT LOW DENSITIES IN NORTH AMERICA

Increasing evidence suggests predation by wolves and 1 or 2 species of bears is the primary factor limiting moose at densities well below KCC where moose are primary prey and predators and moose are lightly exploited. Examples exist in Quebec, Ontario, Yukon, and Alaska (Bergerud et al. 1983;

Messier and Crete 1985; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988). The common conceptual model for moose population regulation in these lightly exploited multi-predator systems is a single, low-density equilibrium (LDE) (K4 of model 4, Fig. 14) where moose densities fluctuate over time, but in a range well below KCC (Messier and Crete 1985; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988). We use the term "equilibrium" to refer to a dynamic state that is influenced by many environmental factors. Messier and Crete (1985) and Bergerud and Snider (1988) indicate this fluctuating equilibrium is maintained within limits by density-dependent (regulating) processes. We concur and add that density-independent processes play a major role in determining the set point for an equilibrium and the relative range of densities over which populations fluctuate. For example, black and grizzly bear predation on low- to high-density moose populations may be density-independent, yet bear predation can be the major source of mortality to a population (Ballard and Larsen 1987, Crete and Jolicoeur 1987, Boertje et al. 1988, Larsen et al. 1989a, Schwartz and Franzmann 1989). Removing or reducing bear predation would allow the moose populations to stabilize at higher densities largely through density-dependent processes.

We provide further support for this predator-limited, LDE model using case histories in a large area with lightly exploited predator populations in Alaska and Yukon (Fig. 15). The following conditions are common to most of this area: (1) moose occur at low densities; (2) moose are primary prey; (3) predators include wolves, grizzly bears, and black bears (Table 14) and these populations are lightly exploited; and (4) most moose populations are lightly exploited and moose harvest removes primarily bulls (Table 14). Moose harvest rates averaged 5% of the prehunt population ($\underline{n}$ = 18, range 0-13%, SD = 4) and about 3% of the derived postcalving population. The mean of 20 moose density estimates in this area was 155/1,000 km^2 (range = 45-417/1,000 km^2, SD = 86). The mean and range were unchanged ($\bar{x}$ = 153/1,000 km^2, SD = 104) when only the 13 sites with harvests of ≤7% ($\bar{x}$ = 3%) of the prehunt population were included. Furthermore, moose density was only 190/1,000 km^2 in Denali National Park where moose hunting is prohibited and moose were below KCC (Risenhoover 1987, Table 14). Intensive studies within this region support the hypothesis that predation is the primary factor limiting moose density (sites 90, 190, 249, and 776 on Fig. 15; Gasaway et al. 1983, Van Ballenberghe 1987, Larsen et al. 1989a, present study). One study in site 190 (Fig. 15) presented an opposing view (Haber 1977), although subsequent studies in site 190 supported the LDE model (Risenhoover 1987, Van Ballenberghe 1987).

Additional support for the predator-limited LDE model comes from areas where predators were chronically or periodically held below KCC by harvests. Moose densities in these areas reach higher levels ($\underline{\bar{x}}$ = 647/1,000 km^2, $\underline{n}$ = 16, range = 169-1,447, SD = 389) compared with densities in lightly exploited regions ($\underline{P}$ = 0.02, Mann-Whitney U test; Fig. 15). Similar wolf densities exist in the lightly exploited (low prey biomass/wolf) and manipulated areas (high prey biomass/wolf) (Figs. 16, 17), which demonstrates that wolves were held below KCC in manipulated areas. The extent to which wolves were held below KCC is indicated by the difference between the predicted and observed wolf density. Reviews by Keith (1983) and Fuller (1989) regress wolf density on prey biomass (Fig. 16) and conclude that wolf density increases with prey biomass, unless harvest prevents wolves from increasing. In our region of light exploitation, wolf density was correlated ($\underline{r}$ = 0.75, $\underline{P}$ < 0.01) with moose density and wolf densities were close to Keith's and Fuller's predictions. In contrast, wolf densities in our region of manipulated predator populations did not increase significantly with moose density ($\underline{r}$ = 0.3, $\underline{P}$ > 0.1) and wolf densities were well below Keith's and Fuller's predictions (Fig. 16). In the manipulated region, case histories of high exploitation of wolf populations exist for sites 750, 776, 1220, and 816-1447 on Figure 15 (Gasaway et al. 1983, Ballard et al. 1987, Peterson et al. 1984, Schwartz and Franzmann 1989), and case histories of high grizzly bear exploitation exist for sites 750 and 776 (Reynolds and Hechtel 1988; Miller, in press).

Habitat studies and circumstantial evidence from predator removal and predation studies indicate that the LDE is not primarily a function of habitat. For example, habitat studies in Denali National Park (site 190 on Fig. 15; Risenhoover 1987) and in our experimental area (site 88) concluded moose were below KCC. Also, responses to predator removal in 2 sites demonstrated that habitat in interior Alaska can support elevated moose densities. For example, during and after an intense wolf removal program (1976-82) in site 776 (Fig. 15), moose increased from 200/1,000 km^2 in 1975 to 776/1,000 km^2 in 1988 (Gasaway et al. 1983; McNay 1990). Earlier, moose irrupted to high moose densities following multi-species predator reductions (site 776, Gasaway et al. 1983; site 88, present study).

The occasional overlap in moose density between the areas of lightly exploited versus manipulated predator populations (Fig. 15) can be accounted for, in part, by variation in the recency and magnitude of predator reductions, habitat differences, or moose harvest rates. For example, the moose density in the area immediately north of Fairbanks (site 280 on Fig. 15) is currently increasing following recent wolf removal. Also, moose densities in predator-manipulated areas in northwest Alaska (sites 169, 348, 407, and 438) are underestimated compared with other sites, because in these cases "moose habitat" includes a high proportion of tundra (non-moose habitat). In contrast, the highest moose density observed in areas with lightly exploited predators (site 417) occurred in uniformly good moose habitat (a large 26-year-old burn). We attempted to increase the comparability of study sites by disregarding study areas <2,000 km^2, where moose can be highly concentrated during surveys and habitat influences can be large. Finally, high but unknown local harvests reduced moose density in one of the sites with manipulated predator densities (site 269; K. Taylor, ADF&G, pers. commun.).

In contrast to the single LDE model above, a multiple-density equilibria model has been proposed (model 3, Fig. 14; Haber 1977). This model was based mainly on studies in Denali National Park (1,100 km^2 of moose habitat). Van Ballenberghe (1980, 1987) and Crete (1987) challenged the model based largely on qualitative flaws, and Van Ballenberghe (1987) questioned whether the multiple-density equilibria concept is appropriate for natural moose-predator systems.

To help resolve debate over the appropriateness of the LDE model versus the multiple-density equilibria model in moose-wolf-bear systems, Messier and Crete (1985), Crete (1987), and Van Ballenberghe (1987) suggested the following test: reduce predation on a moose population held at a low density by wolf and bear predation and allow moose to increase. Moose should continue to increase to KCC after surpassing 0.6-0.7 KCC. If the moose population maintains an equilibrium near KCC after cessation of predator removal, the multiple-density equilibria model would be supported. Alternatively, if the moose population returns to a density well below KCC, the LDE model would be supported. Ideal data sets for this test are lacking because areas have some exploitation of moose and predators following cessation of predator removal. Nevertheless, moose and predator population dynamics in our experimental area support the single LDE model. Moose increased to a high density following 12 years of reduced wolf and bear numbers and declined within 15 years to low, predator-limited densities where nutrition was a minor limiting factor (<u>see</u> Nutrition as a Limiting Factor; Fig. 2). Also, moose populations in central and south-central Alaska did not remain at high densities for long following cessation of predator removal (Bishop and Rausch 1974, Gasaway et al. 1983, Ballard et al. 1990).

In certain areas of North America, at least 3 circumstances allow moose to achieve and maintain moderate to high-density populations without continued predator management. These circumstances further support the LDE model as the appropriate model for lightly exploited moose-wolf-bear systems where moose is the primary prey.

First, moose remain abundant in areas where only a single predator species exists (Messier and Crete 1985; Crete 1987, 1989; Bergerud and Snider 1988; Messier 1989). To our knowledge, single predator systems, except Isle Royale, exist because of regional extirpation of the wolf. For example, in black bear-moose systems, moose density is about 2,000/1,000 km^2 in Quebec (Crete 1989) and commonly 1,100-2,400/1,000 km^2 on good range when lightly exploited in Newfoundland (Bergerud and Manuel 1969, Mercer and Manuel 1974, Fryxell et al. 1988). Crete (1987, 1989) suggested a single high-density equilibrium model (model 2, Fig. 14) for black bear-moose systems, which may also apply to grizzly bear-moose systems. Grizzly bears are the only major predator on moose on the Seward Peninsula, Alaska; despite moderate harvest rates, moose increased to 438 moose/1,000 km^2 by 1987 after first appearing during the 1950's (Fig. 15; Table 15). The only wolf-moose system we are aware of is on Isle Royale. There, moose have fluctuated widely (1,000-3,000 moose/1,000 km^2) during 20 years (Peterson 1988), but the lowest density on Isle Royale was more than double the highest density in lightly exploited wolf-bear-moose systems (Crete 1987, Bergerud and Snider 1988; Fig. 15).

Second, moose populations can sustain high densities (K2 of model 2, Fig. 14) where black and grizzly bears exist (wolves extirpated), with or without alternate ungulate prey. Examples are found in Jackson Hole, Wyoming (Houston 1968) and the Kenai Peninsula, Alaska (Bailey 1978). Kenai studies show that moose can fluctuate near KCC for long periods and occasionally attain high densities (1,570/1,000 km^2) when wolves are absent (early 1900's-1960's) and predation is restricted to that by black and brown bears (Bailey 1978, Peterson et al. 1984, Schwartz and Franzmann 1989).

Third, where moose are minor prey in wolf-bear-multiprey systems, moose can become at least moderately abundant (Crete 1987, Bergerud and Snider 1988). This occurs primarily in the southern portion of the moose's range and possibly in mountainous western Canada where other ungulate species are more important to wolves. Examples are Algonquin Provincial Park, Ontario (400-700 moose/1,000 km^2, Wilton 1987) and Riding Mountain National Park, Manitoba (800 moose/1,000 km^2, Carbyn 1983). The role that high caribou densities play in northern moose-wolf-bear systems requires further study, but moose apparently are major prey when caribou are at low densities (Ballard et al. 1987, present study).

Acceptance of the single, LDE model suggests that in much of northern North American moose range, sustaining moose densities above the LDE will require predator-prey management. Management will be needed because moose, wolves, grizzly bears, and/or black bears are sympatric in most of the moose's range (Burt and Grossenheider 1976) and moose are commonly the primary prey of these predators and of humans (Ballard and Larsen 1987, Van Ballenberghe 1987, Boertje et al. 1988).

HARVEST RATES OF MOOSE IN LIGHTLY EXPLOITED AND MANIPULATED SYSTEMS IN ALASKA AND YUKON

Developing conservation plans that allow hunters and predators to share moose resources requires an understanding of the potential yield from moose populations. Therefore, in this section we report and review harvest rates of moose and describe how predation and predator management alter harvest rates.

Harvest rates of moose increased rapidly with moose density and were, in part, a function of the type of predator management. Disregarding sustainability, harvest rates were low ($\underline{\bar{x}}$ = 9 moose/1,000 km^2, $\underline{n}$ = 18, SE = 2; Fig. 18) in Alaska and Yukon where moose populations were preyed on by lightly exploited predator populations. In contrast, harvest rates were significantly greater ($\underline{\bar{x}}$ = 55 moose/1,000 km^2, $\underline{n}$ = 13, SE = 15; $\underline{P}$ = 0.02 Mann-Whitney U Test) where moderate to heavy harvest of predators kept predators below KCC, although not always at low absolute densities (Figs. 15, 16, 18).

Maintaining moose densities above the LDE through moderate to heavy harvest of predators increased the approximate sustainable yield of moose in Alaska and Yukon study sites from about 0-18 moose/1,000 km^2 to about 20-130 moose/1,000 km^2 (Fig. 19). This approximate sustainable yield curve has limitations. It was derived from impirical data from 22 populations (Tables 14, 15) at varying densities rather than from one population varied over a range of densities (e.g., McCullough 1979). Also, the populations have differing KCC's, which produces a family of sustained yield curves. This is most important at the higher densities where the curves end at differing KCC's; therefore, we place less faith in predicted yields for high densities. Despite these limitations, we believe the empirical yield curve is a useful first approximation of sustained yields from low- and moderate-density moose populations in Alaska and Yukon.

The shape of the approximate sustainable harvest curve for Alaska and Yukon study sites differs from the sustainable harvest curve for ungulates in predator-free areas (Caughley 1976, Crete 1987; Fig. 20). Differences in the shape of these yield curves are largely attributed to some additive mortality from predation reducing the sustainable yield to humans (McCullough 1979) and the degree to which humans reduced predation. Yield will always be low at the left side of the Alaska-Yukon curve when predators are lightly exploited (Fig. 20). At densities above the LDE, we suggest that the impact of predation diminishes with increasing moose density, based on increasing moose/wolf ratios (Fig. 17). This diminishing predation increases net moose population growth rate until strong density-dependent competition for food occurs. The result is an accelerating yield curve, due in part to increased harvest of cows, followed by a sharp decline in yield (Fig. 20).

For moose populations at a LDE, we give 2 examples where predators killed most of the potential sustainable yield that could be shared between hunters and predators, i.e., predation was largely additive mortality. After the 1980's wolf removal in our experimental area, wolves and bears killed an estimated 54 moose/1,000 km^2 (31% of the postcalving population). This predation restricted potential sustainable harvest by humans to about 6 moose/1,000 km^2 (the sum of postcalving harvest rate [1.5%] and predicted postcalving population growth rate [2%]; Fig. 12). In a comparable Yukon study area, predators killed 120 moose/1,000 km^2 and humans killed at least 12 moose/1,000 km^2; however, the predicted sustainable harvest for humans was zero because the population was predator-limited and declining (Larsen et al. 1989a).

Messier and Crete's (1984) and Crete's (1987) harvest model for low-density, predator-limited moose populations in Quebec also predicted greater yields than we observed in Alaska and Yukon predator-limited populations (Fig. 20). In Quebec, the lightly exploited LDE is about 370 moose/1,000 km^2 in systems with only wolves and black bears. By lowering moose densities to 200-300 moose/1,000 km^2 through intensive harvesting, their sustained yield increased from 13 moose/1,000 km^2 to about 54 moose/1,000 km^2, compared with <18 moose/1,000 km^2 in lightly exploited Alaska and Yukon systems. At these reduced moose densities in Quebec, wolf numbers and predation rates declined, resulting in increased recruitment and harvest of moose (Messier and Crete 1984). Increased harvest of black bears by moose hunters may have also contributed to the increased recruitment of moose (M. Crete, pers. commun.). In contrast, moose densities as low as 45/1,000 km^2 in Alaska and Yukon have not consistently been associated with increased moose recruitment (calves/100 cows during early winter, Fig. 21). Grizzly and black bears and wolves remain effective predators on calves at very low moose densities in these northern areas (e.g., Boertje et al. 1988, Larsen et al. 1989a, present study). We predict, however, that at moose densities somewhere below 45/1,000 km^2 and where alternate ungulate prey are rare, the killing rate by bears and wolves will rapidly decline and eventually the wolf population will disappear. This will cause the moose recruitment rate to increase, as in Quebec (model 4, Fig. 14); however, these densities are too low to be useful for managing moose and predation.

REDUCING CONTROVERSY OVER MANAGING MOOSE-WOLF-BEAR SYSTEMS IN ALASKA AND YUKON

In the 2 preceding sections, we conclude that moose densities and harvests by humans will remain low for long periods in Alaska and Yukon where moose are the primary prey of both wolves and bears and these predators are lightly exploited. This situation has caused a divisive controversy among conservationists across North America. On one side are advocates for managing predation to increase prey densities and harvests; on the other side are advocates for maintaining more natural, lightly exploited and protected systems at a LDE. Substantial common ground exists among these conservationists: they are all concerned about the perpetuation of wildlife resources and most of them support management providing some lightly exploited and protected systems. It is the management for enhanced wildlife densities and harvests that is most divisive and that we address in this section. Here, controversy focuses on which, if any, lands should be intensively managed for enhanced densities, the appropriate share or allocation of moose for humans and predators, and how those shares will be maintained given society's concerns for the treatment and welfare of the remaining large predator populations in North America. Reducing this controversy appears essential if conservationists are to unite in addressing the most serious threat to moose-wolf-bear systems--loss of wilderness. In an effort to reduce the divisiveness, we offer management approaches that accommodate some of the major values and desires of conservationists with divergent objectives.

1. Following the lead of citizens in British Columbia (Archibald 1989), we recommend the public and wildlife conservation agencies construct mutually agreed on conservation plans that outline where wolves and bears and their ungulate prey will be managed for specific uses. Options could range from protection to high harvest rates of wildlife. Society is demanding that administrative decision-making processes involve the public and, where possible, satisfy a variety of public interests (Tipple and Wellman 1988). We suggest the formalized conservation plans define by specific area: (1) the priority uses of wildlife, (2) a commitment to the long-term welfare of large predators, (3) if management of predation can be used to elevate prey density and harvest, and (4) the types of predator management that are acceptable. Without formal

goals and accountability for specific areas, many people will remain convinced that the extirpation of large carnivores observed in much of North America will also occur in Alaska.

2. Given that area-specific management goals are sanctioned for sustained moose harvests larger than those obtained in the LDE, we suggest a conceptual conservation plan that maintains moose densities well above the LDE and maintains long-term wolf and bear densities approximately equal to mean densities in lightly exploited systems.

Biological components of this conceptual conservation plan are described below. First, areas selected for this management should have a relatively high KCC for moose. A high KCC will allow high moose/predator ratios, which will simplify maintaining long-term wolf and bear densities equal to the mean values in lightly exploited populations.

Second, to allow moose to initially increase in density when at a LDE, predation must initially undergo a large reduction; subsequently, total predation can return to levels found in lightly exploited systems. Both field experiments and simulation models indicate that large reductions in predation and low moose harvest rates are required if low-density, predator-limited moose populations are to increase to high densities at annual rates that exceed 10% (i.e., a 7-year doubling time) (Gasaway et al. 1983; Crete and Jolicoeur 1987; Larsen et al. 1989a, 1989c; present study). The intensity of predation reduction programs can be determined after the public and wildlife managers decide if the initial growth phase of low-density moose populations is to be short and swift or long and slow. At a 5% growth rate, a moose population will double in about 14 years; at 20% it will double in 4 years. Commonly, low-density moose populations will require 2 to 4 doubling periods to reach optimal densities.

Third, maintaining moose densities above those at the peak of the total yield curve (Fig. 22), but below KCC, will reduce the risk of rapid population declines resulting from short-term increased predation or harvest (Van Ballenberghe and Dart 1982; McCullough 1979, 1984). Predation and harvest are largely additive mortality factors at densities below those at the peak of the yield curve, whereas they become increasingly compensatory as density approaches KCC (McCullough 1979). Maintaining density below KCC helps avoid low moose reproductive rates (Table 3), high mortality from deep snow (Gasaway et al. 1983), and low potential harvest rates (McCullough 1979; Fig. 22). These elevated densities of moose should satisfy many consumptive and nonconsumptive needs of humans for moose, while ensuring enough moose to support long-term densities of wolves (about 9/1,000 km^2, Fig. 16) and bears (Table 14) similar to those in lightly exploited systems. Defining bear densities, however, is a problem because affordable census techniques are not available for large areas; therefore, conservative long-term harvest strategies will help maintain bears near KCC.

Fourth, the long-term number of moose killed by predators will have to be held near levels observed in systems where prey are scarce and wolves are food-limited. This is necessary, in part, because wolf numbers tend to linearly increase with prey density (Keith 1983, Fuller 1989; Fig. 16). Harvest of moose by hunters will also require close control.

Implementing this conservation plan should: (1) maintain sufficient wildlife use and value to compete more effectively with alternative land uses destructive of wildlife habitat or populations; (2) assure the long-term security of wolves and bears in intensively managed areas; and (3) provide sufficient wildlife to satisfy many nonconsumptive and consumptive users of moose, wolves, and bears. We envision that management following this plan will help fulfill wildlife desires of people living in adjacent lightly exploited and protected areas.

The plan we have offered is one of many variations on the theme of sharing an elevated moose population among hunters, bears, and wolves. This plan varies the long-term density of principally one species, moose. Where desired, other allocations among hunters and predators can be made. For example, the share to wolves could be increased or decreased with appropriate changes in harvest of moose by humans.

3. Plans for manipulating predation should consider altering wolf and bear predation simultaneously rather than intense management of 1 predator species. Attempting to increase moose numbers by reducing only numbers of 1 predator species may require large, unacceptable levels of reduction (Ballard and Larsen 1987, Larsen et al. 1989_a_, present study). Additionally, managing predation by manipulating only black or grizzly bear populations is not desirable because: (1) bear populations have low recovery rates due to low reproductive and immigration rates (Bunnell and Tait 1981, Reynolds and Hechtel 1988), (2) bears are often managed for large trophies, and (3) the greater difficulty in censusing bears makes measuring the effects of management actions on bear populations more costly than in the case of wolves (Miller, in press). Finally, reducing predation of only 1 species may result in compensatory predation by another species, hence diminishing the effects of intense single species management (Schlegel 1976; M. Schlegel, unpubl. data cited in Ballard and Larsen 1987).

4. We recommend development of and greater reliance on more socially acceptable alternatives to intense, lethal government-sponsored predator removal for increasing prey populations that are in a LDE or maintaining elevated prey populations. Although lethal predator removal is currently the most effective means of reducing predation, recent history indicates intense, lethal predator removal is socially unacceptable as a widespread, routine management technique. Developing more acceptable alternatives would reduce the controversy over predator-prey management (Kellert 1985).

To begin the search for a more socially acceptable management system, we suggest 5 nonlethal and 1 lethal alternatives that are either functional or in developmental stages. First, diversionary feeding of predators on or near moose and caribou calving areas for 4-5 weeks may reduce predation on neonates. Our preliminary test indicates moose calf survival can increase during years that feeding occurs. Also, diversionary feeding has reduced damage by black bears to forest plantations in Washington (Flowers 1987). Second, increased alternate prey (caribou) may reduce predation on moose populations (Bergerud and Elliott 1986, Crete 1987, Wilton 1987). Third, habitat enhancement (e.g., through fire management) may increase moose numbers through immigration of moose causing increased moose/predator ratio (Peek 1974, Gasaway et al. 1989) or improved moose physical condition and reproductive rate (Franzmann and Schwartz 1985). Fire management may also increase moose density by reducing bear density or bear predation rates during several years following the fire. Schwartz and Franzmann (1989), however, reported no difference in black bear densities and black bear predation rates (as a percentage of the moose population) in a 13-year-old versus a 31-year-old burn on the Kenai Peninsula, Alaska. Fourth, chemically, surgically, immunologically, or hormonally reducing birth rates in predators can reduce growth rates of predator populations (Orford et al. 1988, Stelflug and Gates 1988). Fifth, the relocation of grizzly bears just before calving can improve moose calf survival in small areas (Ballard and Miller 1989).

Finally, conventional public hunting and trapping of predators effectively limits some Alaskan wolf and bear populations (Peterson et al. 1984; Reynolds and Hechtel 1988; Schwartz and Franzmann 1989; Miller, in press). Trapper and hunter education programs and liberalized seasons, bag limits, and methods of harvest are integral to increasing the effectiveness of this method. The potential effects of public hunting and trapping on wolf and bear populations in Yukon and portions of Alaska are less significant because of low human populations and reduced access. In some of these areas, the public may choose more controversial methods such as baiting of bears or use of aircraft to hunt wolves, an effective means of manipulating wolf densities in some parts of Alaska and Yukon (Ballard et al. 1987).

These alternatives may substitute for intense, lethal predator removal in Alaska and Yukon if applied over long periods and/or in combination; each method may have a small or delayed effect on predator-prey relationships. Alternate methods such as these may also be insufficient to initiate growth of populations in a LDE or prevent prolonged declines of high-density moose populations, particularly in forested areas where predators are not vulnerable to capture, hunting, or trapping. In such areas, lethal, government-sponsored predator removal programs may be the only effective option to assist in achieving a management goal of elevated moose densities and harvests.

We believe that cooperation among wildlife users can produce conservation plans that will reduce the divisiveness of intensive predator-prey management. Area-specific plans can address wildlife values and uses, ranging from natural densities with little or no harvest to increased abundance and higher harvests of wildlife. Conservation plans can define what is acceptable management in specific areas and, where necessary, can spur development of acceptable techniques.

By making some concessions, conservationists on both sides of the controversy have much to gain in Alaska and Yukon. First, the long-term security of large predator populations can be assured in most intensively managed areas--a departure from trends in predator conservation worldwide and in local areas of Alaska. Second, diverse human uses of wildlife can be provided. Third, in those areas where elevated moose abundance is sanctioned, opportunities will increase (1) for consumptive uses of moose and associated predators and scavengers and (2) for nonconsumptive uses of moose, scavengers of moose, and occasionally wolves. Increased wildlife use will result in significant economic advantages from tourism and hunting. Fourth, on lands not already protected by Park or Refuge status, elevated moose densities accompanied by relatively abundant predators and increased use of wildlife may strengthen the case for protecting wildlife habitat from competing land uses. Finally, by moving past the predator-prey management controversy, a united conservation effort can work to retain the wilderness ecosystems that are necessary for maintenance of wolf-bear-moose systems.

CONCLUSIONS

1. Low wolf reproductive rates and low harvest of wolves suggested the wolf population was near KCC in our

experimental area before the 1981-83 wolf reduction program. Harvests of grizzly and black bears were also low.

2. The recent increase in the early winter moose population in our experimental area (4-9% annually during 1981-88) may have resulted, in part, from the combined effects of a wolf reduction program, elevated public harvest of grizzly bears and wolves, and an increase in alternate prey (caribou). However, the possibility exists of concurrent increases in moose density within control areas. If increases occurred, the small reduction in numbers of predators may have had little effect on the experimental moose population.

3. Despite the recent increase in the early winter moose population, moose density remained low (127-157 moose/1,000 km^2) during 1988. Predation by wolf and bear populations was the primary factor limiting moose at low densities for extended periods in our experimental area. By comparison, nutrition, snow/nutrition, and harvest were minor limiting factors, and disease appeared inconsequential.

4. Predation by lightly exploited wolf and grizzly or black bear populations appears to limit lightly exploited moose populations at a LDE for extended periods in much of Alaska and Yukon. In these systems, densities averaged 153 moose/1,000 km^2, 9 wolves/1,000 km^2, and bears were common. We suggest these lightly exploited systems typify conditions people can expect in the absence of programs that strongly manipulate predation. Average moose and wolf densities in lightly exploited systems were similar to densities in Denali National Park.

5. High-density moose populations in Alaska appear to be products of predator management. We found no recent evidence indicating that long-term high-density equilibria naturally occur over large areas for moose, although exceptions may occur. Moose have attained elevated densities ($\bar{x}$ = 647 moose/1,000 km^2) only in portions of Alaska (>2,000 km^2) where humans have reduced predators below KCC. Also, habitat studies and circumstantial evidence from predator reduction programs and predation studies indicate that moose are not at LDE's because of habitat limitations in most of Alaska and Yukon.

6. Recent data indicate predator management is needed to maintain elevated moose abundance where moose, wolves, and bears are sympatric and moose are the primary prey. Moose appear to persist at higher densities without special long-term predator management only in areas where moose are: (1) preyed on by only 1 predator species, (2) preyed on by black and grizzly bears (wolves absent), or (3) minor prey of wolves and bears in multi-prey systems. Extirpation of

predators by humans, however, has created circumstances for numbers (1) and (2) above, except for Isle Royale.

7. In Alaska and Yukon, elevating the sustainable moose harvest above levels common to populations at a LDE required manipulating predation to increase moose density. This management has caused a divisive controversy among wildlife conservationists. We believe this controversy and the accompanying environmental, social, and economic costs can be reduced. Cooperation and compromise among conservationists can produce conservation plans in Alaska and Yukon that ensure long-term predator densities in intensively managed areas are equivalent to those in lightly exploited systems, while benefiting most wildlife users. Also, predator management techniques with wider social acceptability should be developed and used. Reducing the predator management controversy will allow conservationists to unite in addressing more serious threats to the existence of moose-wolf-bear systems in the North--the loss of wilderness ecosystems.

LITERATURE CITED

ALBON, S. D., B. MITCHELL, AND B. W. STAINES. 1983. Fertility and body weight in female red deer: a density-dependent relationship. J. Anim. Ecol. 52:969-980.

ALBRIGHT, C. A., AND L. B. KEITH. 1987. Population dynamics of moose, _Alces alces_, on the south-coast barrens of Newfoundland. Can. Field Nat. 10:373-387.

ARCHIBALD, W. R. 1989. Wolf management in British Columbia. Pages 170-180 _in_ Wolf-Prey Dynamics and Management. British Columbia Ministry of Environment, Wildl. Working Rep. No. WR-40, Victoria.

ARTHUR, G. H. 1964. Wright's veterinary obstetrics. 3rd ed. Williams and Williams Co., Baltimore, Md. 549pp.

BAILEY, T. N. 1978. Moose populations on the Kenai National Moose Range. Proc. North Am. Moose Conf. Workshop 14:1-20.

BALLARD, W. B., AND D. G. LARSEN. 1987. Implications of predator-prey relationships to moose management. Swedish Wildl. Res. Suppl. 1:581-602.

__________, AND S. D. MILLER. 1989. Effects of reducing brown bear density on moose calf survival in southcentral Alaska. Proc. Int. Congr. Game Biol. 18. In press.

__________, AND K. P. TAYLOR. 1980. Upper Susitna Valley moose population study. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-17-10 and W-17-11. 102pp.

__________, J. S. WHITMAN, AND C. L. GARDNER. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98. 54pp.

__________, __________, AND D. J. REED. 1990. Dynamics of moose populations in south-central Alaska. Wildl. Monogr. In press.

__________, C. L. GARDNER, J. H. WESTLUND, AND J. R. DAU. 1982. Susitna hydroelectric project. Phase I Final Rep., Big Game Studies, Vol. V, Wolf. Alaska Dep. Fish and Game, Anchorage. 220pp.

__________, K. E. RONEY, D. N. LARSEN, AND L. AYRES. 1988. Demographhpy of Noatak grizzly bears in relation to human exploitation and mining development. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5 and W-22-6. 100pp.

__________, A. W. FRANZMANN, K. P. TAYLOR, T. H. SPRAKER, C. C. SCHWARTZ, AND R. O. PETERSON. 1979. Comparison of techniques utilized to determine moose calf mortality in Alaska. Proc. North Am. Moose Conf. Workshop 15:362-387.

__________, L. AYRES, S. FANCY, D. LARSEN, D. REED, K. RONEY, AND M. SPINDLER. 1990. Demography and movements of wolves in relation to Western Arctic caribou herd of Northwest Alaska. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-1 and W-23-2. In press.

BERGERUD, A. T. 1971. The population dynamics of Newfoundland caribou. Wildl. Monogr. 25. 55pp.

__________, AND J. P. ELLIOT. 1986. Dynamics of caribou and wolves in northern British Columbia. Can. J. Zool. 64:1515-1529.

__________, AND F. MANUEL. 1969. Aerial census of moose in central Newfoundland. J. Wildl. Manage. 33:910-916.

__________, AND J. B. SNIDER. 1988. Predation in the dynamics of moose populations: a reply. J. Wildl. Manage. 52:559-564.

__________, W. WYETT, AND B. SNIDER. 1983. The role of wolf predation in limiting a moose population. J. Wildl. Manage. 47:977-988.

BISHOP, R. H., AND R. A. RAUSCH. 1974. Moose population fluctuations in Alaska, 1950-1972. Nat. Can. (Que.) 101:559-593.

BLOOD, D. A. 1974. Variation in reproduction and productivity of an enclosed herd of moose (*Alces alces*). Trans. Int. Congr. Game Biol. 11:59-66.

BOER, A. H. 1987. Reproductive productivity of moose in New Brunswick. Alces 23:49-60.

BOERTJE, R. D., AND E. L. YOUNG. 1982. Stikine River moose study; wildlife evaluation of Stikine-Iskut dams. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-21-1. 20pp.

__________, W. C. GASAWAY, D. V. GRANGAARD, AND D. G. KELLEYHOUSE. 1988. Predation on moose and caribou by radio-collared grizzly bears in east-central Alaska. Can. J. Zool. 66:2492-2499.

__________, _________, D. V. GRANGAARD, D. G. KELLEYHOUSE, AND R. O. STEPHENSON. 1987. Factors limiting moose population growth in Subunit 20E. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5. 86pp.

BOWYER, R. T., S. C. AMSTRUP, J. G. STAHMANN, P. E. REYNOLDS, AND F. A. BURRIS. 1988. Multiple regression methods of modeling caribou populations. Proc. 3rd North Am. Caribou Workshop. Alaska Dep. Fish and Game. Wildl. Tech. Bull. No. 8:89-118.

BUCHHOLTZ, M. J., AND L. JENNINGS. 1974. Moose survey-inventory progress report, 1972. Pages 146-153 *in* D. McKnight, ed. Annual report of survey-inventory activities. Vol. IV. Part II. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-17-5.

BUNNELL, F. L., AND D. E. N. TAIT. 1981. Population dynamics of bears--implications. Pages 75-98 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of Large Mammal Populations. John Wiley and Sons, New York.

BURT, W. H., AND R. P. GROSSENHEIDER. 1976. A field guide to the mammals. Houghton Mifflin Co., Boston. 289pp.

CARBYN, L. N. 1983. Wolf predation on elk in Riding Mountain National Park, Manitoba. J. Wildl. Manage. 47:963-976.

CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. Adv. Appl. Biol. 1:183-247.

__________. 1981. Comments on natural regulation of ungulates (what constitutes a real wilderness?). Wildl. Soc. Bull. 9:232-234.

COADY, J. W. 1974_a_. Interior moose studies: evaluation of moose range and habitat utilization in interior Alaska. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-17-6. 12pp.

__________. 1974_b_. Influence of snow on behavior of moose. Nat. Can. (Que.) 101:417-436.

CONNOLLY, G. E. 1978. Predators and predator control. Pages 369-394 _in_ J. L. Schmidt and D. L. Gilbert, eds. Big Game of North America. Stackpole Co., Harrisburg, Pa.

CRAIN, E. B., AND D. A. HAGGSTROM. 1985. Moose survey-inventory progress report. Pages 86-90 _in_ A. Seward, ed. Annual report of survey-inventory activities. Vol. XV. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-3.

__________, and __________. 1986. Moose survey-inventory progress report. Pages 77-86 _in_ B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVI. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-4.

__________, and __________. 1987. Moose survey-inventory progress report. Pages 87-96 _in_ B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5.

CRETE, M. 1987. The impact of sport hunting on North American moose. Swedish Wildl. Res. Suppl. 1:553-563.

__________. 1989. Approximation of K carrying capacity for moose in eastern Quebec. Can. J. Zool. 67:373-380.

__________, AND H. JOLICOEUR. 1987. Impact of wolf and black bear removal on cow:calf ratio and moose density in southwestern Quebec. Alces 23:61-87.

DAVIS, J. L., R. E. LERESCHE, AND R. T. SHIDELER. 1978. Size, composition, and productivity of the Fortymile caribou herd. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Final Rep. W-17-6 and W-17-7. 69pp.

DALLE-MOLLE, J. 1987. Denali National Park moose trend survey 1987. Natural Resources Survey and Inventory Report. AR-87-11. U.S. Natl. Park Serv., Anchorage. 13pp.

DEAN, F. C. 1987. Brown bear density, Denali National Park, Alaska and sighting efficiency adjustment. Int. Conf. Bear Res. and Manage. 7:37-43.

EDWARDS, R. Y., AND R. W. RITCEY. 1958. Reproduction in a moose population. J. Wildl. Manage. 22:261-268.

FARO, J. B., AND A. W. FRANZMANN. 1978. Alaska Peninsula moose productivity and physiology study. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Final Rep. W-17-9 and W-17-10. 29pp.

FLOWERS, R. 1987. Supplemental feeding of black bear in tree-damaged areas of western Washington. 1987-88 Annual Report. Washington Forest Protection Association, Olympia.

FLOYD, T. J., L. D. MECH, AND P. A. JORDAN. 1978. Relating wolf scat content to prey consumed. J. Wildl. Manage. 42:528-532.

FRANZMANN, A. W. 1977. Condition assessment of Alaskan moose. Proc. North Am. Moose Conf. Workshop 13:119-127.

__________, AND C. C. SCHWARTZ. 1983. Moose productivity and physiology. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Final Rep. W-17-9, W-17-10, W-17-11, W-21-1, and W-21-2. 131pp.

__________, and __________. 1985. Moose twinning rates: a possible population condition assessment. J. Wildl. Manage. 49:394-396.

__________, __________, AND D. C. JOHNSON. 1987. Monitoring status (condition, nutrition, health) of moose via blood. Swedish Wildl. Res. Suppl. 1:281-288.

__________, R. E. LERESCHE, P. D. ARNESON, AND J. L. DAVIS. 1976. Moose productivity and physiology. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Final Rep. W-17-2 through W-17-7. 87pp.

__________, __________, R. A. RAUSCH, AND J. L. OLDEMEYER. 1978. Alaskan moose measurements and weights and measurement-weight relationships. Can. J. Zool. 56(2):298-306.

FRYXELL, J. M., W. E. MERCER, AND R. B. GELLATELY. 1988. Population dynamics of Newfoundland moose using cohort analysis. J. Wildl. Manage. 52:14-21.

FULLER, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105. 41pp.

__________, AND L. B. KEITH. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44:583-602.

GASAWAY, W. C., A. W. FRANZMANN, AND J. B. FARO. 1978_a_. Immobilizing moose with a mixture of etorphine and xylazine hydrochloride. J. Wildl. Manage. 42:686-690.

__________, D. B. HARKNESS, AND R. A. RAUSCH. 1978_b_. Accuracy of moose age determinations from incisor cementum layers. J. Wildl. Manage. 42:558-563.

__________, S. D. DUBOIS, D. J. REED, AND S. J. HARBO. 1986. Estimating moose population parameters from aerial surveys. Biol. Pap. No. 22, Univ. Alaska, Fairbanks.

__________, __________, R. D. BOERTJE, D. J. REED, AND D. T. SIMPSON. 1989. Response of radio-collared moose to a large burn in central Alaska. Can. J. Zool. 67:325-329.

__________, R. O. STEPHENSON, J. L. DAVIS, P. E. K. SHEPHERD, AND O. E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84. 50pp.

GRAUVOGEL, C. A. 1989. Moose survey-inventory progress report. Pages 122-131 _in_ S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XIX. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-1.

HABER, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. Thesis, Univ. British Columbia, Vancouver. 817pp.

HAGGSTROM, D. A., AND T. O. OSBORNE. 1981. Moose survey-inventory progress report. Pages 146-149 _in_ R. A. Hinman, ed. Annual report of survey-inventory activities. Vol. XII. Part II. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-19-1 and W-19-2.

HARBO, S. J., AND F. C. DEAN. 1983. Historical and current perspectives on wolf management in Alaska. Pages 51-65 in L. N. Carbyn, ed. Wolves in Canada and Alaska. Can. Wildl. Serv. Rep. Ser. 45. Ottawa.

HAUGE, T. M., AND L. B. KEITH. 1981. Dynamics of moose populations in northeastern Alberta. J. Wildl. Manage. 45:573-597.

HAYES, R. D., AND A. BAER. 1986. Wolf population research and management studies in the Yukon Territory. Yukon Dep. Renewable Resour. Annu. Rep. 76pp.

__________, and __________. 1987a. Wolf inventory, Nisutlin River area January 1987. Pages 1-8 in R. Hayes, ed. Wolf population research and management studies in the Yukon Territory, population inventories - 1985-87. Yukon Dep. Renewable Resour. Annu Rep. 28pp.

__________, and __________. 1987b. Wolf inventory, Nisling River area March 1986. Pages 1-10 in R. Hayes, ed. Wolf population research and management studies in the Yukon Territory, population inventories - 1985-87. Yukon Dep. Renewable Resour. Annu. Rep. 28pp.

__________, P. MERCHANT, AND A. BAER. 1985. Wolf population research and management studies in the Yukon Territory. Yukon Dep. Renewable Resour. Annu. Rep. 26pp.

HOLLEMAN, D. F., AND R. O. STEPHENSON. 1981. Prey selection and consumption by Alaskan wolves in winter. J. Wildl. Manage. 45:620-628.

HOUSTON, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Grand Teton Nat. Hist. Assoc., Tech. Bull. No. 1. 110pp.

JAMES, D. D. 1984. Moose survey-inventory progress report. Pages 128-135 in J. A. Barnett, ed. Annual report of survey-inventory activities. Vol. XIV. Part IV. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-2.

__________. 1986. Moose survey-inventory progress report. Pages 122-128 in B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVI. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-4.

JINGFORS, K. 1988. Moose population research and management studies in Yukon. Yukon Dep. Renewable Resour. Annu. Rep. 35pp.

__________, AND R. MARKEL. 1987. Abundance and composition of moose in Whitehorse south, Nisutlin, and Liard east areas, November 1986. Yukon Dep. Renewable Resour. Annu. Rep. 25pp.

JOHNSTON, W. G., AND C. A. MCEWEN. 1984. Moose abundance and habitat use in Liard west, Yukon during early winter 1983. Northern Biomes Ltd. for Yukon Dep. Renewable Resour. Annu. Rep. 43pp.

__________, AND H. A. MCLEOD. 1983. Moose population dynamics in the Dromedary Mountain Area, Central Yukon Territory. Northern Biomes Ltd. for Yukon Dep. Renewable Resour. Annu. Rep. 31pp.

KEITH, L. B. 1983. Population dynamics of wolves. Pages 66-77 <u>in</u> L. N. Carbyn, ed. Wolves in Canada and Alaska: their status, biology, and management. Can. Wildl. Serv. Rep. Ser. 45. Ottawa.

KELLERT, S. R. 1985. Public perceptions of predators, particularly the wolf and coyote. Biol. Conserv. 31:167-189.

KELLY, M. W. 1950<u>a</u>. Predator control. Annual report, Branch of Predator and Rodent Control. U.S. Fish and Wildl. Serv. 10pp.

__________. 1950<u>b</u>. Predator control. Second quarter report, Branch of Predator and Rodent Control. U.S. Fish and Wildl. Serv. 26pp.

__________. 1953. Predator control. Annual report, Branch of Predator and Rodent Control. U.S. Fish and Wildl. Serv. 14pp.

__________. 1957. Predator control. Annual report, Branch of Predator and Rodent Control. U.S. Fish and Wildl. Serv. 31pp.

__________. 1958. Predator control. Annual report, Branch of Predator and Rodent Control. U.S. Fish and Wildl. Serv. 26pp.

KOCAN, A. A., A. W. FRANZMANN, K. E. WALDRUP, AND G. J. KUBAT. 1986. Serologic studies of select infectious diseases of moose (<u>Alces</u> <u>alces</u> L.) from Alaska. J. Wildl. Dis. 22:418-420.

LANKESTER, M. W. 1987. Pest, parasites, and diseases of moose (<u>Alces</u> <u>alces</u>) in North America. Swedish Wildl. Res. Suppl. 1:461-490.

LARSEN, D. G. 1982. Moose inventory in the southwest Yukon. Alces 18:142-167.

__________, AND R. MARKEL. 1989. A preliminary estimate of grizzly bear abundance in southwest Alaska. Yukon Dep. Renewable Resour. Final Rep. 52pp.

__________, D. A. GAUTHIER, AND R. L. MARKEL. 1989_a_. Causes and rate of moose (_Alces alces_) calf mortality. J. Wildl. Manage. 53:548-557.

__________, R. MARKEL, AND R. M. P. WARD. 1989_b_. Moose population characteristics in the Mayo and Pelly crossing areas, 1988-89. Yukon Dep. Renewable Resour. Annu. Rep. 33pp.

__________, D. A. GAUTHIER, R. L. MARKEL, AND R. D. HAYES. 1989_c_. Limiting factors on moose population growth in the southwest Yukon. Yukon Dep. Renewable Resour. Final Rep. 105pp.

LARSEN, D. N. 1987. Moose survey-inventory progress report. Pages 134-140 _in_ B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5.

LEROUX, P. A. 1973. Moose survey-inventory progress report. Pages 88-94 _in_ D. E. McKnight, ed. Annual report of survey-inventory activities. Vol. III. Part I. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-17-4.

LIDICKER, W. Z. 1978. Regulation of numbers in small mammal populations--historical reflections and a synthesis. Pages 122-141 _in_ D. P. Snyder, ed. Populations of small mammals under natural conditions. Vol. V, Spec. Publ. Ser., Pymatuning Lab of Ecol., Univ. of Pittsburgh, Pittsburgh, Pa.

MARKEL, R. L., AND D. G. LARSEN. 1983. Southwest Yukon moose survey results, November 1982. Yukon Dep. Renewable Resour. Annu. Rep. 17pp.

__________, and __________. 1988. Moose population characteristics in the Casino trail area, November 1987. Yukon Dep. Renewable Resour. Annu. Rep. 18pp.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd. Univ. Mich. Press, Ann Arbor. 271pp.

__________. 1984. Lessons from the George Reserve, Michigan. Pages 211-242 _in_ L. K. Halls, ed. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pa.

MCNAY, M. 1990. Moose survey-inventory progress report. In S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XX. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-2. In press.

MECH, L. D. 1973. Wolf numbers in the Superior National Forest of Minnesota. U.S. Dep. Agric. For. Serv., Res. Pap. NC-97, Northcentral For. Exp. Stn., St. Paul. 10pp.

__________. 1987. Demography and distribution of wolves, Denali National Park and Preserve, Alaska - progress report. Natural Resour. Prog. Rep. AR-87/14. U.S. Natl. Park Serv., Anchorage. 30pp.

MEIER, T. J. 1987. 1986 aerial moose census - Denali National Park and Preserve. Natural Resources Survey and Inventory Rep. AR-87/10, U.S. Natl. Park Serv., Anchorage. 15pp.

MERCER, W. E., AND F. MANUEL. 1974. Some aspects of moose management in Newfoundland. Nat. Can. (Que.) 101:657-671.

MESSIER, F. 1989. Towards understanding the relationship between wolf predation and moose density in southwestern Quebec. Pages 13-25 in Wolf-Prey Dynamics and Management. British Columbia Ministry of Environment, Wildl. Working Rep. No. WR-40. Victoria.

__________. In review. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. J. Anim. Ecol.

__________, AND M. CRETE. 1984. Body condition and population regulation by food resources in moose. Oecologia (Berlin) 65:44-50.

__________, and __________. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia (Berlin) 65:503-512.

MILLER, S. In press. Detection of differences in brown bear density and population composition caused by hunting. Int. Conf. Bear Res. and Manage. 8.

MITCHEL, W. L. 1982. The opening of Alaska, 1901-1903. Cook Inlet Historical Society, Anchorage. 111pp.

MURIE, A. 1944. The wolves of Mount McKinley. U.S. Dep. Interior, U.S. Natl. Park Serv., Fauna Ser. 5. 238pp.

MYTTON, W. R., AND L. B. KEITH. 1981. Dynamics of moose populations near Rochester, Alberta, 1975-1978. Can. Field-Nat. 95:39-49.

NATIONAL CLIMATIC DATA CENTER. 1986. Climatological data annual summary, 1986. Vol. 72, No. 13. U.S. Dep. Commerce, Natl. Climatic Data Center, Asheville, N.C.

NEILAND, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. J. Wildl. Manage. 34:904-907.

NELSON, R. R. 1988. Moose survey-inventory progress report. Pages 152-159 <u>in</u> S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XVIII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6.

__________. 1989. Moose survey-inventory progress report. Pages 314-323 <u>in</u> S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XIX. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-1.

NOWLIN, R. A. 1984. Moose survey-inventory progress report. Pages 140-145 <u>in</u> J. A. Barnett, ed. Annual report of survey-inventory activities. Vol. XIV. Part IV. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-2.

__________. 1985. Moose survey-inventory progress report. Pages 139-143 <u>in</u> A. Seward, ed. Annual report of survey-inventory activities. Vol. XV. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-3.

__________. 1986. Moose survey-inventory progress report. Pages 132-136 <u>in</u> B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVI. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-4.

__________. 1988. Moose survey-inventory progress report. Pages 169-174 <u>in</u> S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XVIII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6.

__________. 1989. Moose survey-inventory progress report. Pages 342-352 <u>in</u> S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XIX. Part VIII.

Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-1.

NYGREN, T. 1987. The history of moose in Finland. Swedish Wildl. Res. Suppl. 1:49-54.

OLSON, S. T. 1959a. Management studies of Alaska caribou--movements, distribution and numbers. Pages 58-70 in Alaska Wildl. Invest. Caribou Management Studies. U.S. Fish and Wildl. Serv., Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep., Proj. W-3-R. U.S. Fish and Wildl. Serv.

__________. 1959b. Herd composition in Interior Alaska. Pages 43-52 in Alaska moose management studies. U.S. Fish and Wildl. Serv., Fed. Aid in Wildl. Restor. Proj., Job Completion Rep. W-3-R-13.

ORFORD, H. J. L., M. R. PERRIN, AND H. H. BERRY. 1988. Contraception, reproduction, and demography of free-ranging Etosha lions (Panthera leo). J. Zool., Lond. 216:717-733.

OSBORNE, T. O. 1987. Moose survey-inventory progress report. Pages 113-115 in B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5.

__________. 1988. Moose survey-inventory progress report. Pages 136-140 in S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XVIII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6.

__________. 1989. Moose survey-inventory progress report. Pages 303-313 in S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XIX. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-1.

PAGE, R. E. 1989. The inverted pyramid: ecosystem dynamics of wolves and moose on Isle Royale. Ph.D. Thesis, Mich. Tech. Univ., Houghton. 62pp.

PALSSON, H., AND J. B. VERGES. 1952. Effects of the plane of nutrition on the growth and the development of carcass quality in lambs: Part I--the effects of high and low planes of nutrition at different ages. J. Agric. Sci. 42:1-92.

PEEK, J. M. 1974. Initial response of moose to a forest fire in northeastern Minnesota. Am. Midl. Nat. 91:435-438.

__________, AND D. S. EASTMAN. 1983. Factors which naturally control moose populations. Pages 175-193 in F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds. Symposium on Natural Regulation of Wildlife Populations. For., Wildl., and Range Exp. Stn., Univ. Idaho.

PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Natl. Park Serv. Sci. Monogr. Ser. 11. 210pp.

__________. 1988. Ecological studies of wolves on Isle Royale. Annual Report 1987-88. Mich. Tech. Univ., Houghton. 14pp.

__________, and R. E. Page. 1983. Wolf-moose fluctuations at Isle Royale National Park, Michigan, USA. Acta Zool. Fenn. 174:251-253.

__________, J. D. WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. 88. 52pp.

PICTON, H. D. 1984. Climate and the prediction of reproduction of three ungulate species. J. Appl. Ecol. 21:869-879.

PIMLOTT, D. H. 1959. Reproduction and productivity of Newfoundland moose. J. Wildl. Manage. 23:381-401.

PITCHER, K. W. 1987. Susitna hydroelectric project. Final Report Big Game Studies Vol. 4. Alaska Dep. Fish and Game, Anchorage. 59pp.

QUIMBY, R. L., AND D. D. JAMES. 1985. Moose survey-inventory progress report. Pages 124-135 in A. Seward, ed. Annual report of survey-inventory activities. Vol. XV. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-3.

RAUSCH, R. A. 1959. Some aspects of population dynamics of the railbelt moose population, Alaska. M.S. Thesis, Univ. Alaska, Fairbanks. 81pp.

__________. 1967. Some aspects of the population ecology of wolves, Alaska. Am. Zool. 7:253-265.

REYNOLDS, H. V. 1990. Population dynamics of a hunted grizzly bear population in the northcentral Alaska Range. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-23-2. 63pp.

__________, and J. L. Hechtel. 1988. Population dynamics of a hunted grizzly bear population in the northcentral Alaska Range. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6. 52pp.

__________, __________, AND D. J. REED. 1987. Population dynamics of a hunted grizzly bear population in the northcentral Alaska Range. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5. 59pp.

RISENHOOVER, K. L. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats. Ph.D. Thesis, Mich. Tech. Univ., Houghton. 108pp.

ROLLEY, R. E., AND L. B. KEITH. 1980. Moose population dynamics and winter habitat use at Rochester, Alberta, 1965-79. Can. Field-Nat. 94:9-18.

ROMESBURG, H. C. 1981. Wildlife science: gaining reliable knowledge. J. Wildl. Manage. 45:293-313.

SCHWARTZ, C. C., AND A. W. FRANZMANN. 1989. Bears, wolves, moose, and forest succession, some management considerations on the Kenai Peninsula, Alaska. Alces 25:1-11.

__________, __________, AND D. C. JOHNSON. 1983. Black bear predation on moose (bear ecology studies). Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Final Rep. W-17-10, W-17-11, W-21-1, W-21-2, and W-22-1. 135pp.

SCHLEGEL, M. 1976. Factors affecting calf elk survival in northcentral Idaho--a progress report. Proc. 56th Annu. Conf. West. Assoc. State Game Fish Comm. 56:342-355.

SIMKIN, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Manage. 29:740-750.

__________. 1974. Reproduction and productivity of moose. Nat. Can. (Que.) 101:517-525.

SINCLAIR, A. R. E. 1979. Dynamics of the Serengeti ecosystem: process and pattern. Pages 1-30 in A. R. E. Sinclair and M. Norton-Griffiths, eds. Serengeti: dynamics of an ecosystem. Univ. Chicago Press.

SINGER, F. J. 1987. Dynamics of caribou and wolves in Denali National Park. Pages 117-157 in F. J. Singer, ed. Conference on Science in the National Parks, Vol. 2. George Wright Society and the U.S. Natl. Park Serv., Washington, D.C.

__________, AND J. DALLE-MOLLE. 1985. The Denali ungulate-predator system. Alces 21:339-358.

SKOGLAND, T. 1983. The effects of density dependent resource limitation on size of wild reindeer. Oecologia (Berlin) 60:156-168.

SKOOG, R. O. 1956. Range, movements, population, and food habits of the Steese-Fortymile caribou herd. M.S. Thesis, Univ. Alaska, Fairbanks. 145pp.

__________. 1964. Alaska wildlife investigations, work plan C: caribou management investigations. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-6-R. 44pp.

SPRAKER, T. H. 1985. Moose survey-inventory progress report. Pages 56-58 in A. Seward, ed. Annual report of survey-inventory activities. Vol. XV. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-3.

__________. 1986. Moose survey-inventory progress report. Pages 46-47 in B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVI. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-4.

__________. 1987. Moose survey-inventory progress report. Pages 49-50 in B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5.

__________. 1988. Moose survey-inventory progress report. Pages 64-66 in S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XVIII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6.

STELFLUG, J. N., AND N. L. GATES. 1987. Antifertility research. Pages 5-9 in J. S. Green, ed. Protecting livestock from coyotes: A synopsis of research of the Agricultural Research Service. U.S. Agricultural Research Service, Beltsville, Md.

STEPHENSON, R. O., AND D. D. JAMES. 1982. Wolf movements and food habits in northwest Alaska. Pages 26-42 in F. H. Harrington and P. C. Paquet, eds. Wolves of the world. Noyes Publications, Park Ridge, N.J.

STEWART, R. R., E. H. KOWAL, R. BEAULIEU, AND T. W. ROCK. 1985. The impact of black bear removal on moose calf survival in east-central Saskatchewan. Alces 21:403-418.

SUMANIK, R. S. 1987. Wolf ecology in the Kluane region, Yukon Territory. M.S. Thesis, Mich. Tech. Univ., Houghton. 102pp.

TAYLOR, K. P. 1983. Moose survey-inventory progress report. Pages 73-76 <u>in</u> J. A. Barnett, ed. Annual report of survey-inventory activities. Vol. XIII. Part III. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-1.

__________. 1984. Moose survey-inventory progress report. Pages 65-68 <u>in</u> J. A. Barnett, ed. Annual report of survey-inventory activities. Vol. XIV. Part IV. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-2.

__________. 1987. Moose survey-inventory progress report. Pages 68-70 <u>in</u> B. Townsend, ed. Annual report of survey-inventory activities. Vol. XVII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5.

__________. 1988. Moose survey-inventory progress report. Pages 87-89 <u>in</u> S. O. Morgan, ed. Annual report of survey-inventory activities. Vol. XVIII. Part VIII. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6.

TIPPLE, T. J., AND J. D. WELLMAN. 1988. Life in the fishbowl, public participation rewrites public foresters' job descriptions. J. For. 86:24-30.

VALKENBURG, P., AND J. L. DAVIS. 1988. Population status of the Fortymile Caribou Herd and identification of limiting factors. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-5 and W-22-6. 17pp.

__________, and __________. 1989. Population status of the Fortymile Caribou Herd and identification of limiting factors. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Final Rep. Proj. W-23-1. 33pp.

VAN BALLENBERGHE, V. 1980. Utility of multiple equilibrium concepts applied to population dynamics of moose. Proc. North Am. Moose Conf. Workshop 16:571-586.

__________. 1987. Effects of predation on moose numbers: a review of recent North American studies. Swedish Wildl. Res. Suppl. 1:431-460.

__________, AND J. DART. 1982. Harvest yields from moose populations subject to wolf and bear predation. Alces 18:258-275.

VERME, L. J. 1967. Influence of experimental diets on white-tailed deer reproduction. North Am. Wildl. Conf. 32:405-420.

__________. 1969. Reproductive patterns of white-tailed deer related to nutritional plane. J. Wildl. Manage. 33:881-887.

VIERECK, L. A., AND E. L. LITTLE. 1972. Alaska trees and shrubs. U.S. Dep. Agric., Washington, D.C. Agric. Handb. No. 410. 265pp.

WATSON, A., AND R. MOSS. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. Pages 167-221 in A. Watson, ed. Animal populations in relation to their food resources. Blackwell Sci. Publ., Oxford, England.

WHITE, G. C. 1983. Numerical estimation of survival rates from band recovery and biotelemetry data. J. Wildl. Manage. 47:506-511.

WILSON, R. W. 1951. Steel Creek. Alaska Sportsman 17:12-17.

WILTON, M. L. 1987. How the moose came to Algonquin. Alces:89-106.

ZARNKE, R. L. 1988. Serologic survey for microbial pathogens. Alaska Dep. Fish and Game, Fed. Aid in Wildl. Restor. Proj., Job Prog. Rep. W-22-6. 19pp.

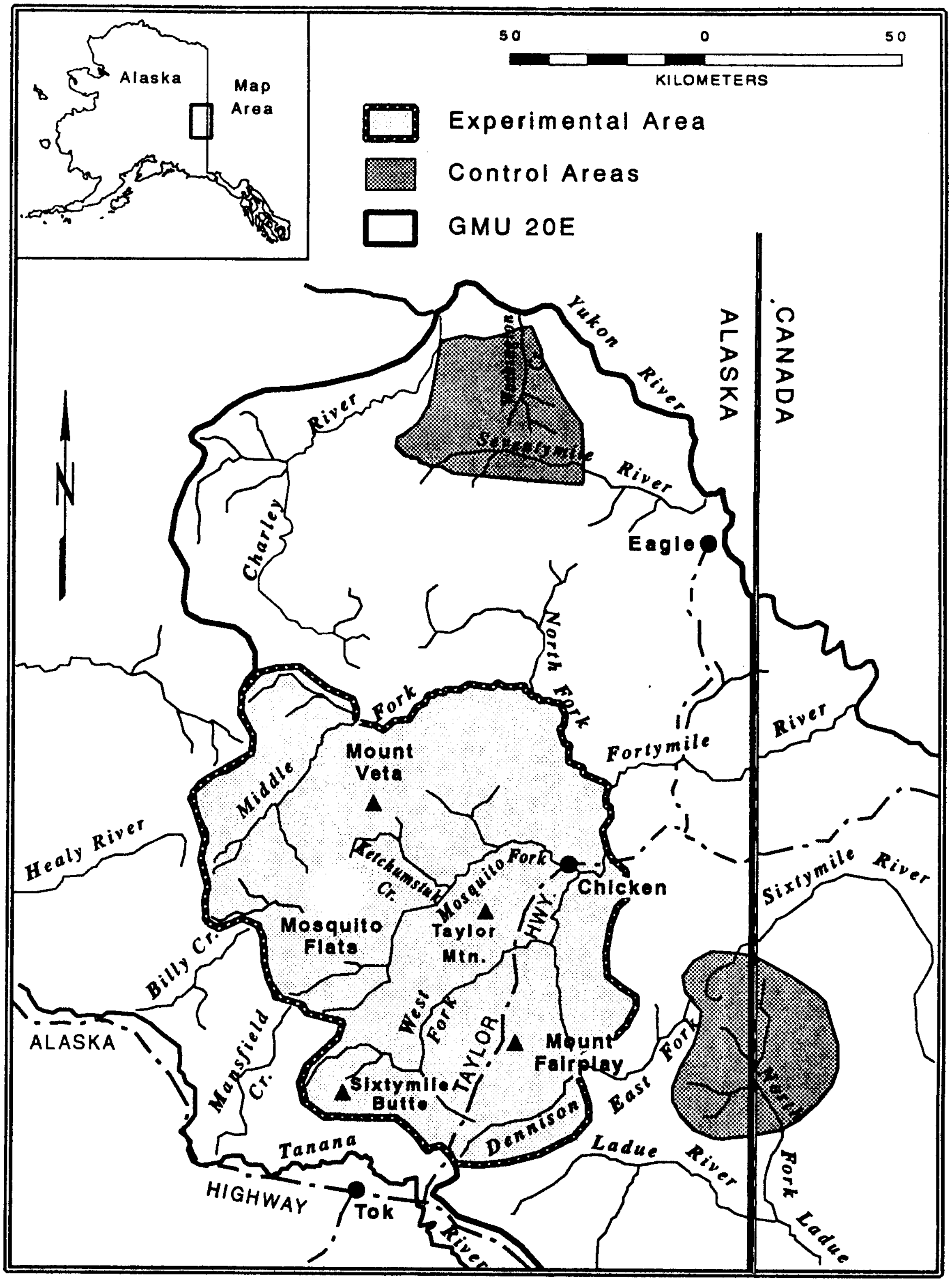


Fig. 1. Experimental area (with wolf removal) and 2 control areas (without wolf removal) in Game Management Unit (GMU) 20E, Alaska, and adjacent Yukon.

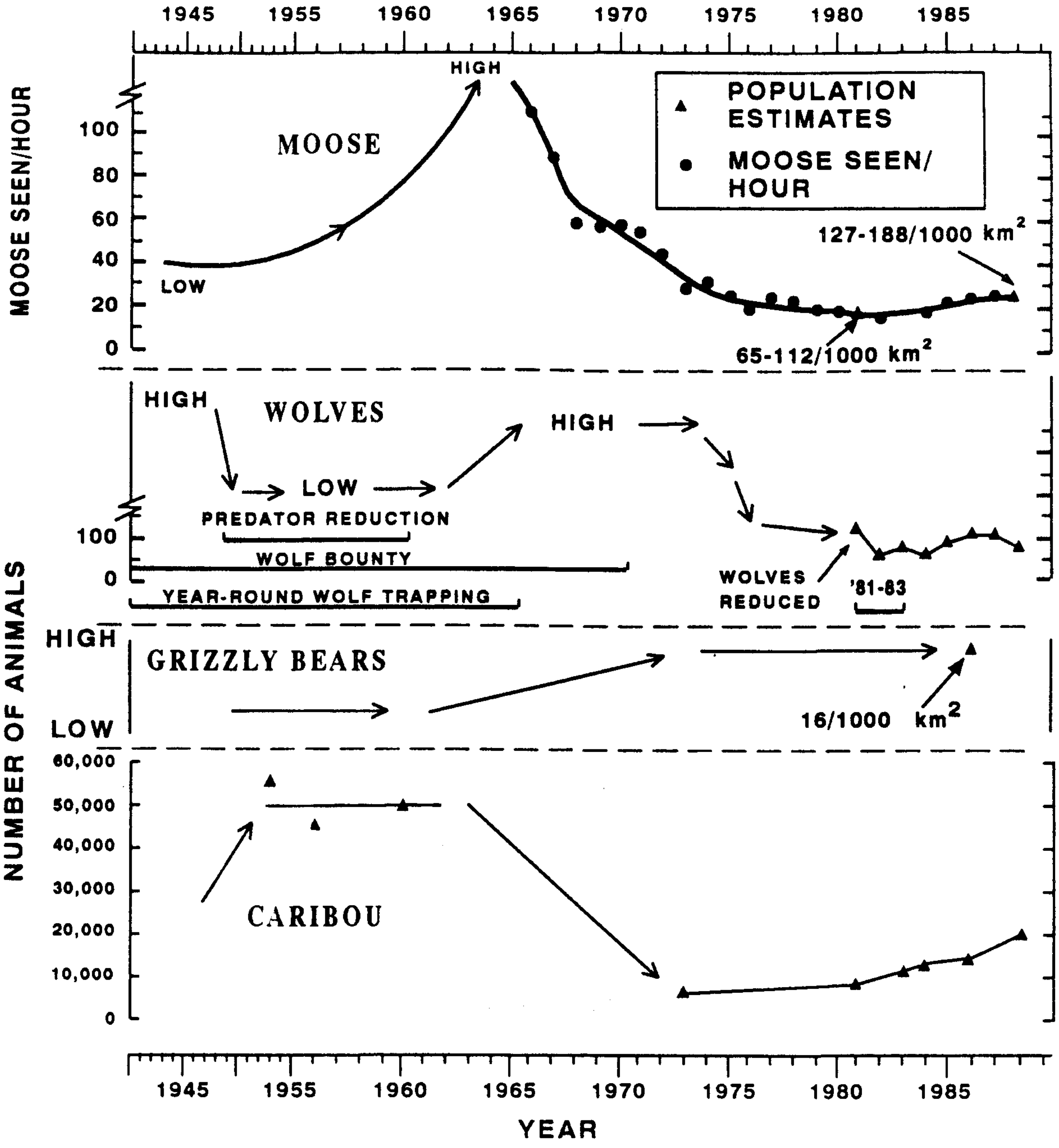


Fig. 2. Estimated and relative numbers of moose, wolves, grizzly bears, and caribou in the experimental area, east-central Alaska, 1940-88. Arrows indicate trends and approximate relative abundance based on qualitative observations. The 90% CI's for moose densities are shown for 1981 and 1988.

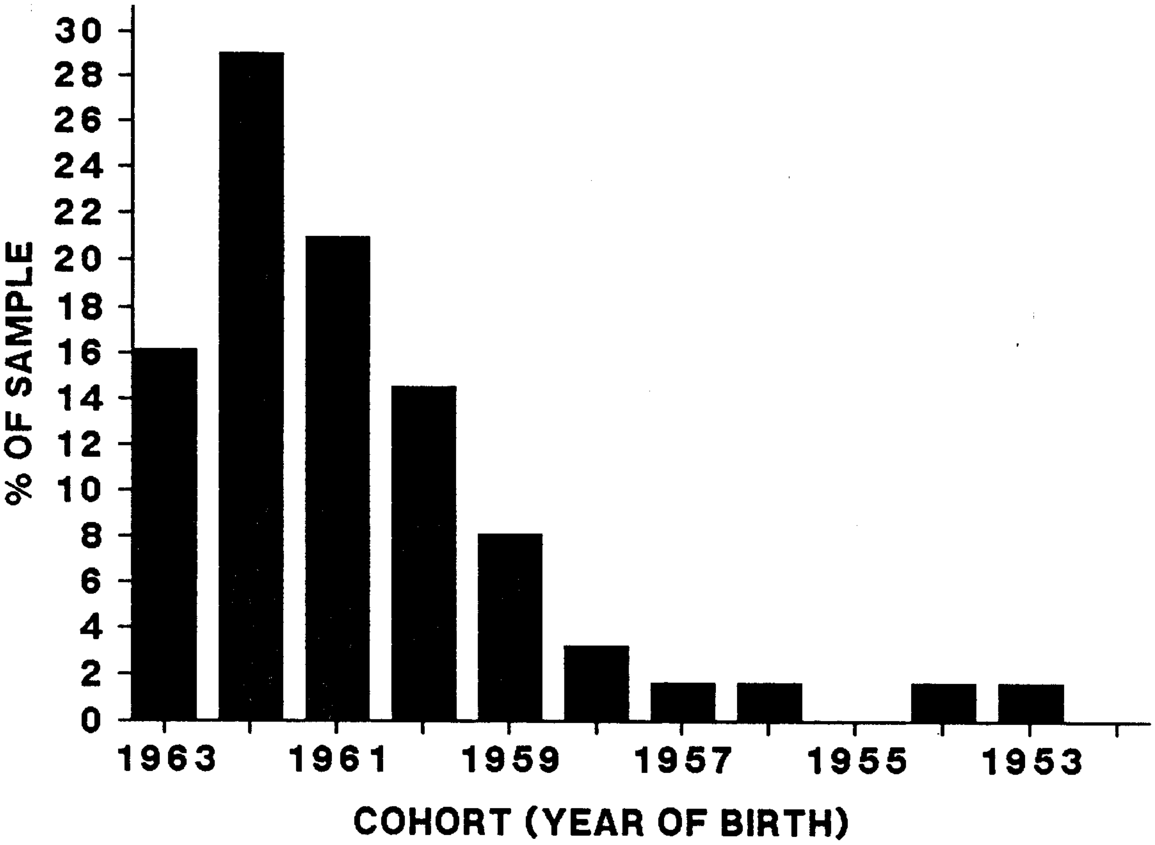


Fig. 3. The age structure of 62 bull moose harvested during 1965 and 1966 in Game Management Unit 20E, east-central Alaska (data from Buchholtz and Jennings 1974). We included only those cohorts that were older than 18 months during 2 hunting seasons, i.e., 1964-66 cohorts were excluded.

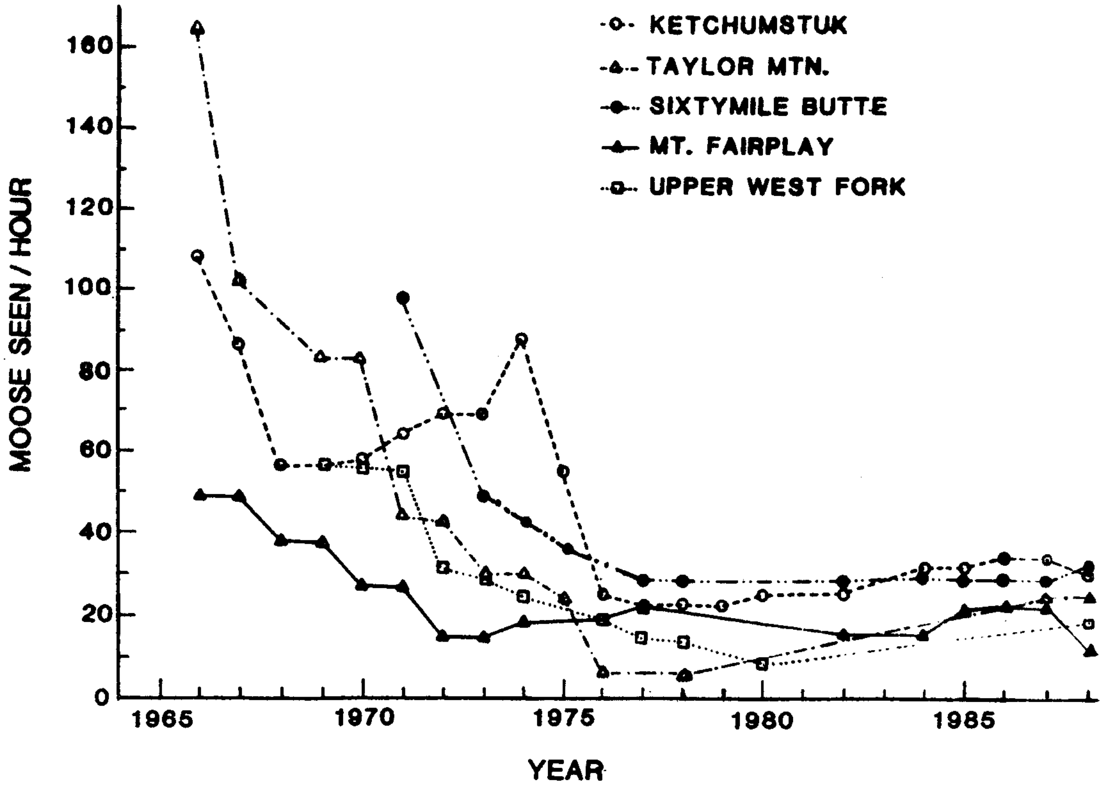


Fig. 4. Trends in number of moose seen/hour in 5 aerial survey areas in the experimental area, east-central Alaska, 1966-88.

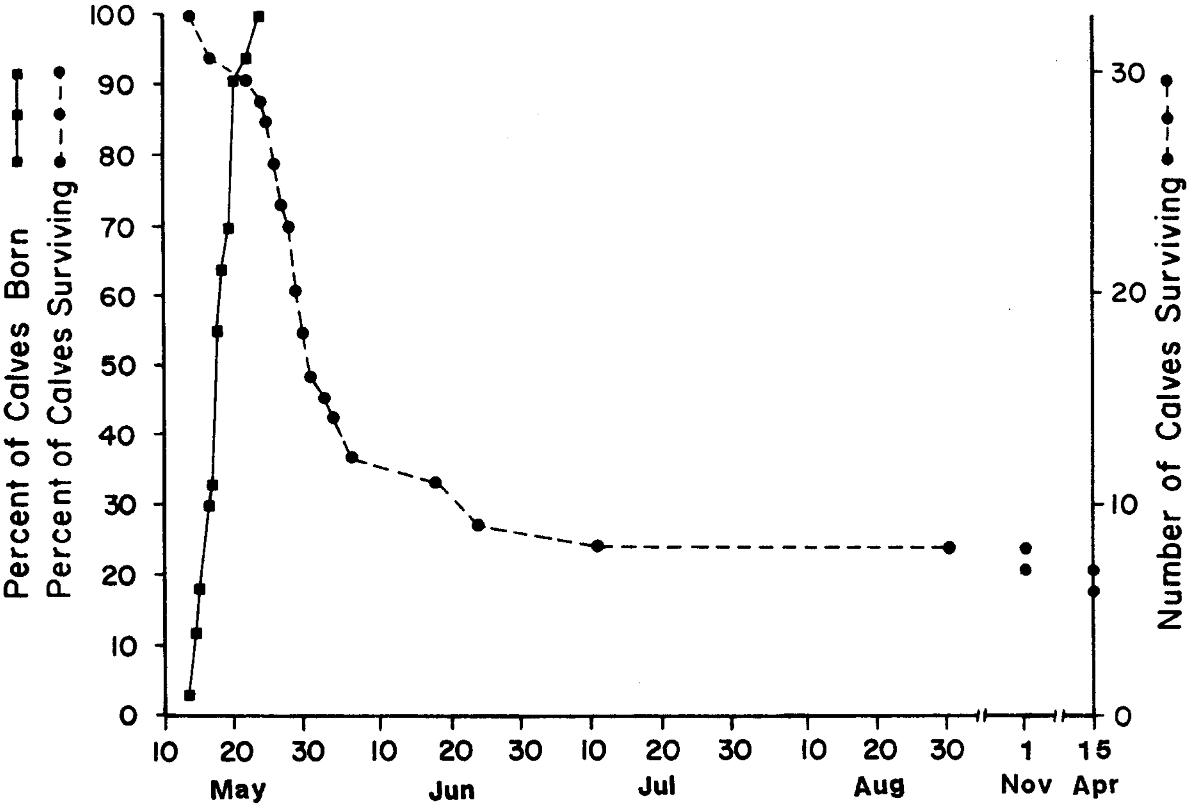


Fig. 5. Chronology of birth and death of 33 moose calves radio-collared during May 1984 in and near the Mosquito Flats in the experimental area, east-central Alaska. The range of values during November and April result from the unknown fate of 1 calf.

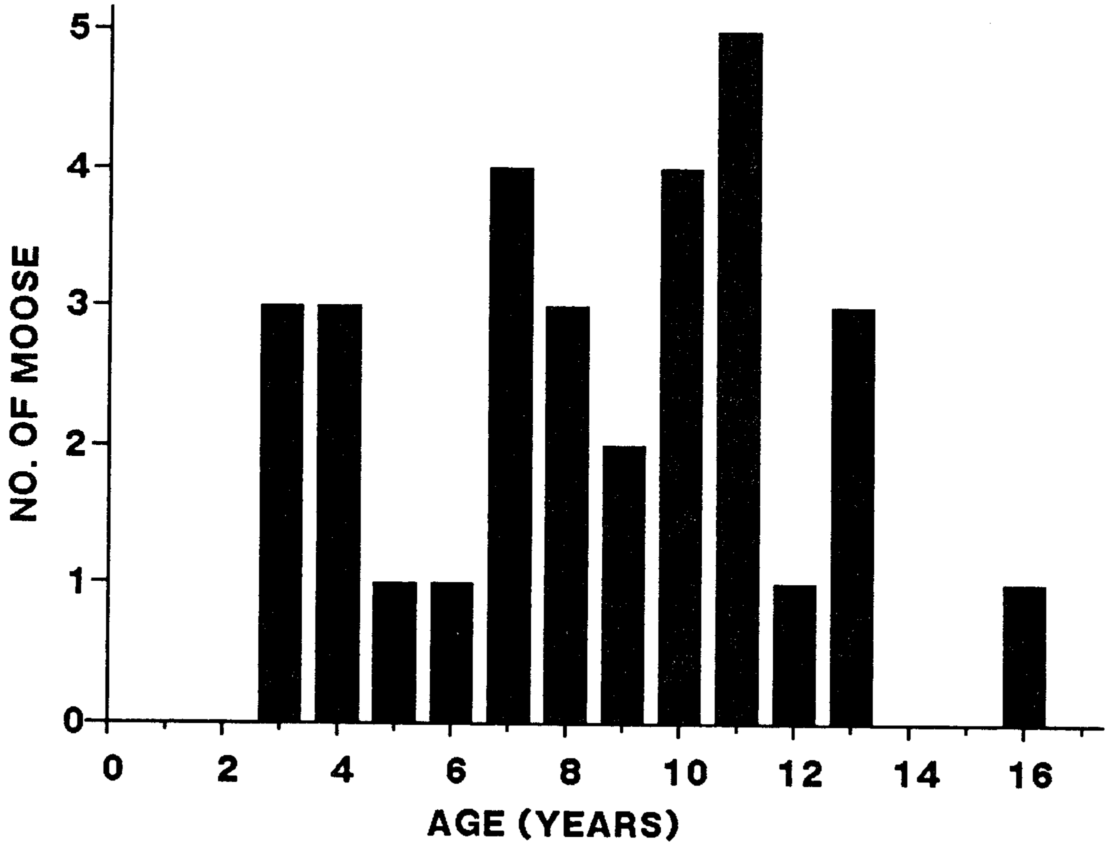


Fig. 6. Age distribution of 31 radio-collared cow moose captured during March 1984 and March 1986 in the experimental area, east-central Alaska.

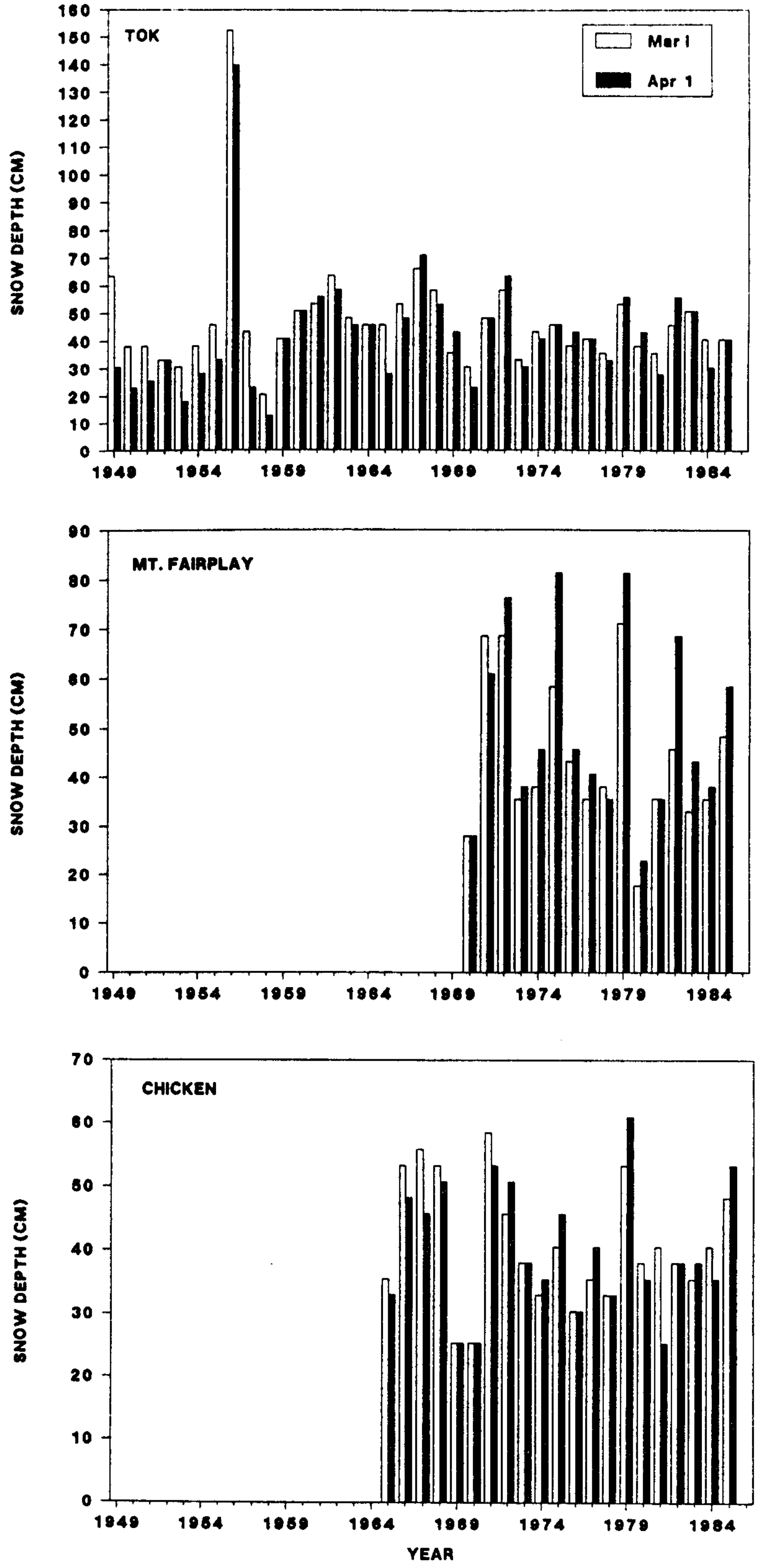


Fig. 7. Snow depth on 1 March and 1 April at 2 sites in the experimental area (Mt. Fairplay and Chicken) and 1 site 15 km south of the experimental area (Tok) in east-central Alaska, 1949-85.

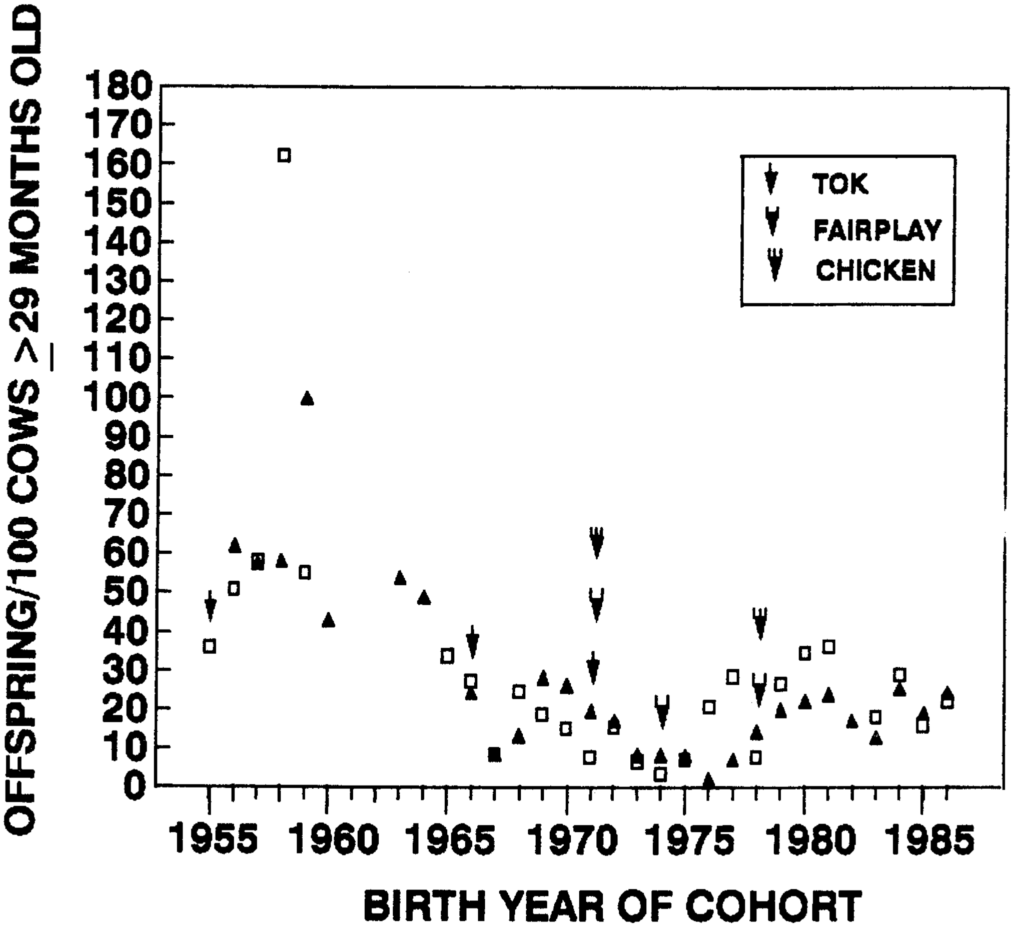


Fig. 8. The relative abundance of cohorts at 5-6 months (triangle) and 17-18 months of age (squares) in relationship to winters of relatively deep snow at 3 measurement stations in or adjacent to the experimental area in east-central Alaska, 1955-86. Arrows indicate that during the calf's first winter, snow was deep relative to other winters at that site (Fig. 7).

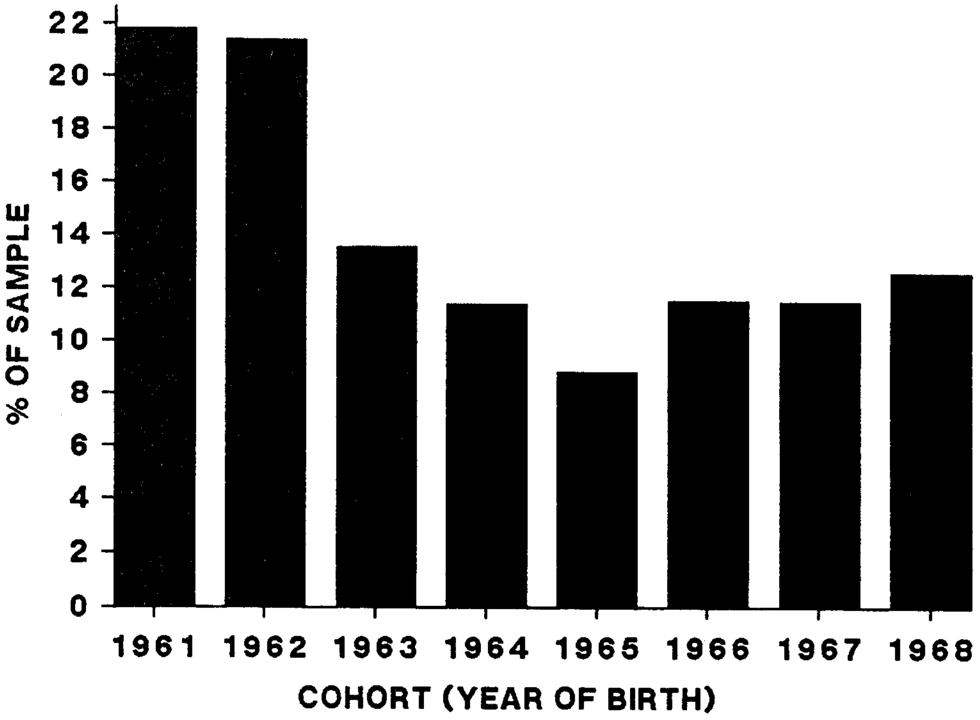


Fig. 9. Relative strength of the 1961-68 cohorts of male moose harvested ($\underline{n}$ = 255) from 1965 through 1972 in Game Management Unit 20E, east-central Alaska (data from Buchholtz and Jennings 1974).

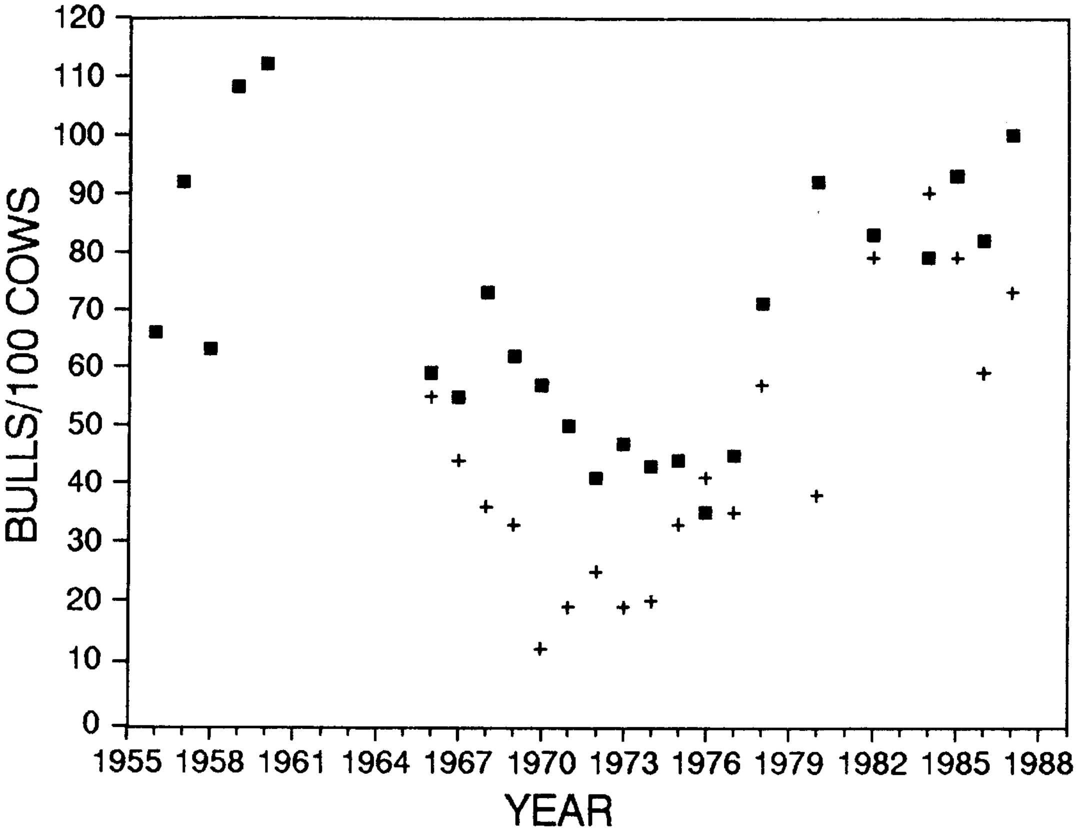


Fig. 10. Bulls/100 cows observed in areas <13 km from the Taylor Highway (square) and in areas >13 km from the Highway (plus) during early winter moose surveys in the experimental area in east-central Alaska, 1956-87.

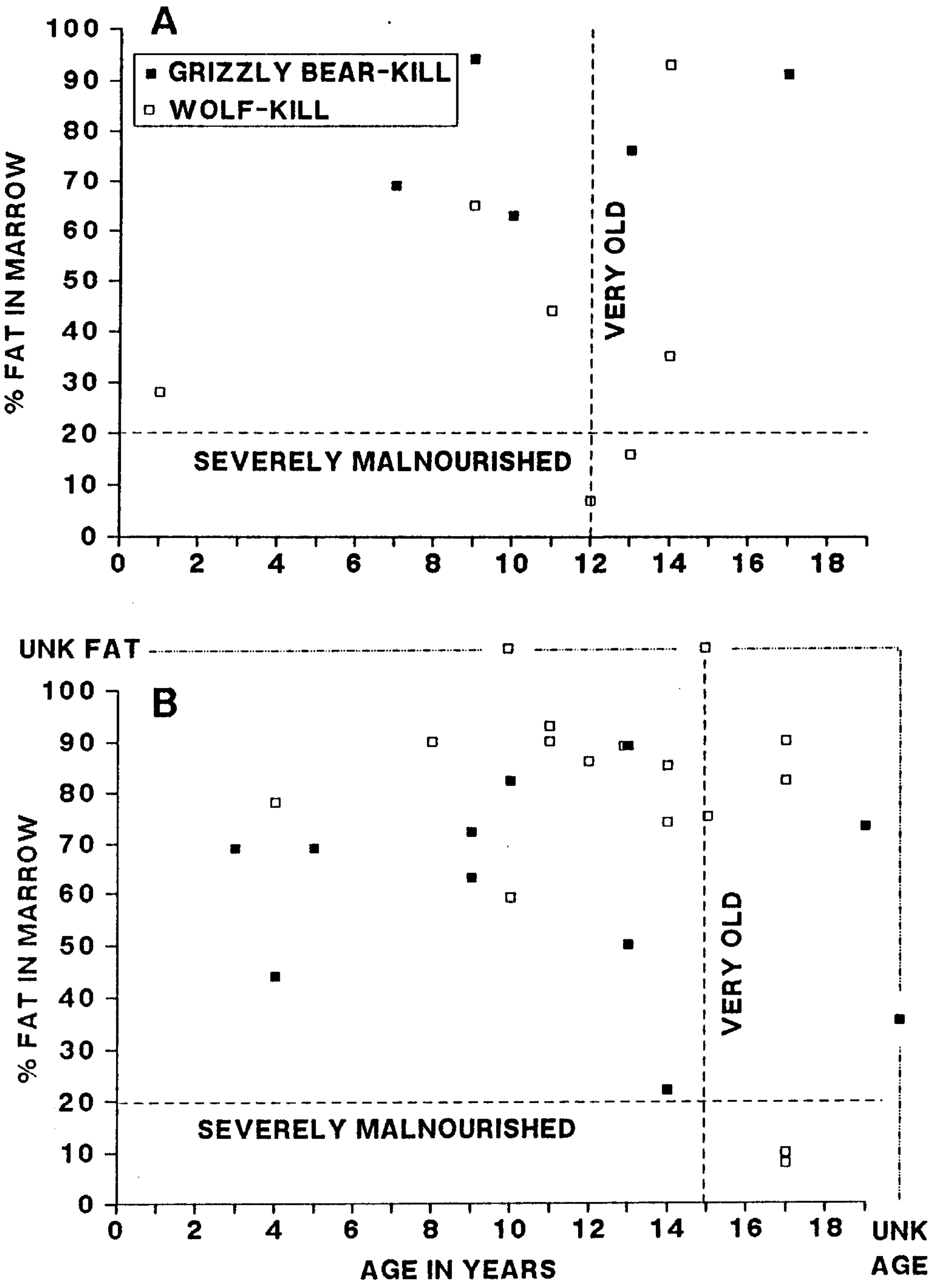


Fig. 11. Percent marrow fat and age of bull moose (A) and cow moose (B) killed by grizzly bears and wolves in the experimental area in east-central Alaska, 1981-87.

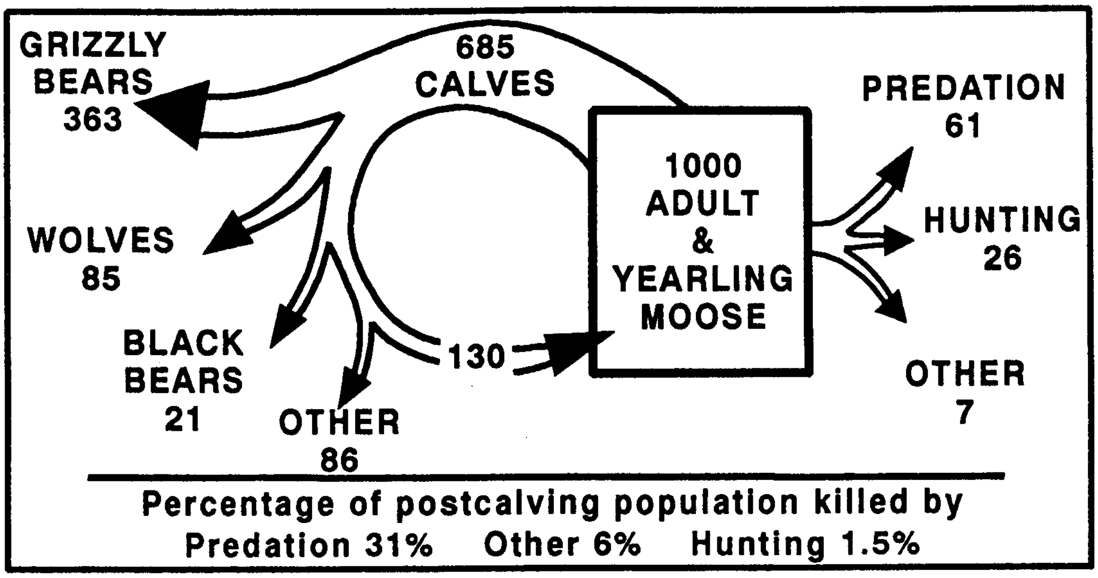


Fig. 12. The approximate number and percentage of moose dying from specific causes in the experimental area given a hypothetical precalving moose population of 1,000 moose in east-central Alaska, 1981-88. The model is derived from data in Appendix 3.

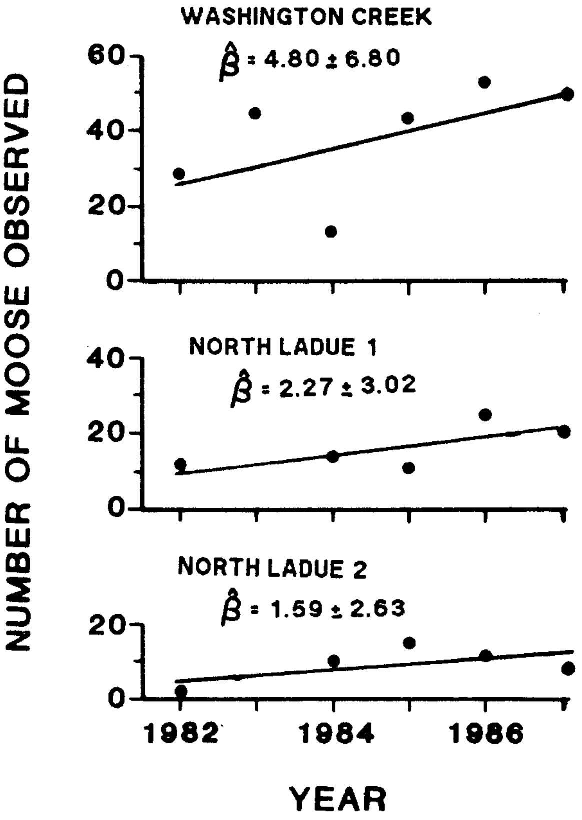


Fig. 13. Trends in number of moose observed in 2 control areas in east-central Alaska and the adjacent Yukon, Canada, 1982-87. $\hat{\beta}$ ±90% CI estimates the slope of the linear regression line.

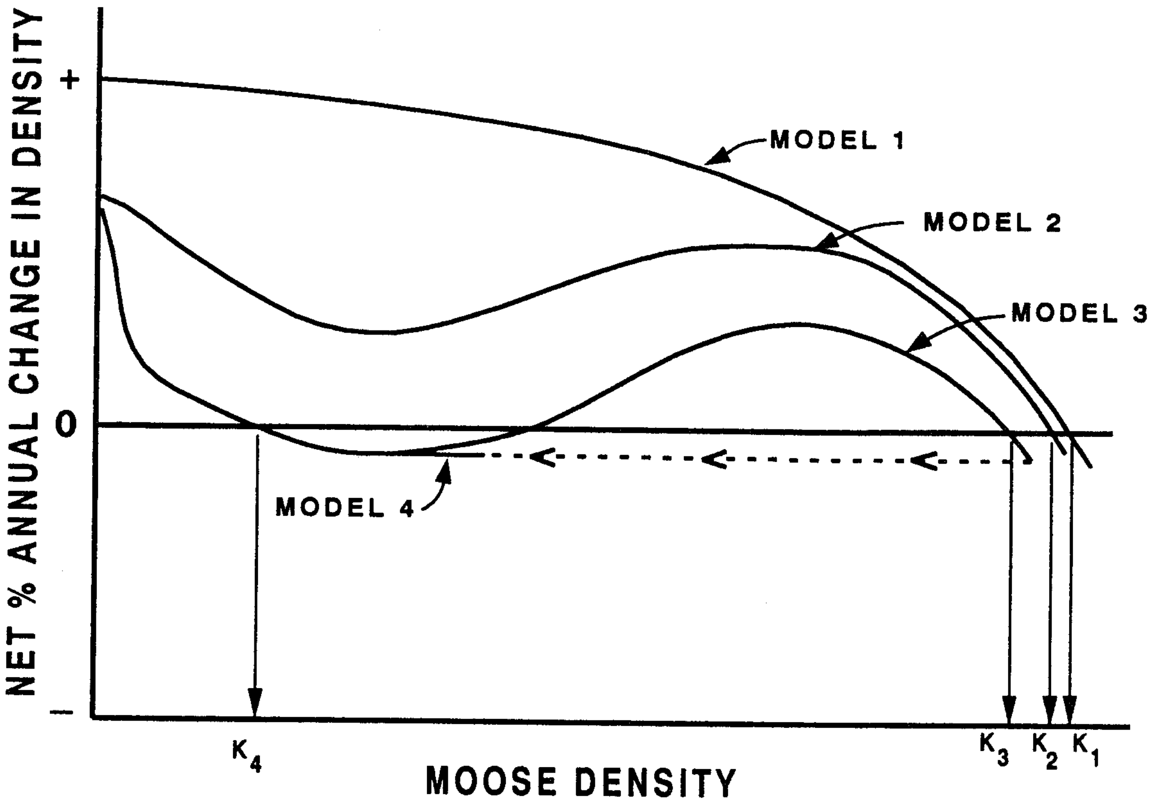


Fig. 14. Four proposed conceptual models of predator-moose-nutrition dynamics (after Messier and Crete 1985). Model 1: Where predators are absent, moose densities fluctuate near K carrying capacity (KCC) (K_1). In the following models, predator populations are assumed to be unexploited or lightly exploited and moose are primary prey of predators. Model 2: Where a single predator species occurs or both black and grizzly bears occur, moose densities fluctuate near KCC (K_2). Model 3: Where bears and wolves occur, 2 or more relatively stable equilibria are possible; the high-density, nutrition-induced equilibrium (K_3) fluctuates near KCC and the low-density equilibrium (LDE) (K_4) is maintained by predation. Model 4: Where bears and wolves occur, moose densities fluctuate near a single LDE (K_4). We speculate that if rare natural events allow moose to break out of the LDE, moose may follow model 3 to a high density and rapidly return to the LDE via a series of years with negative net changes in density (dashed line).

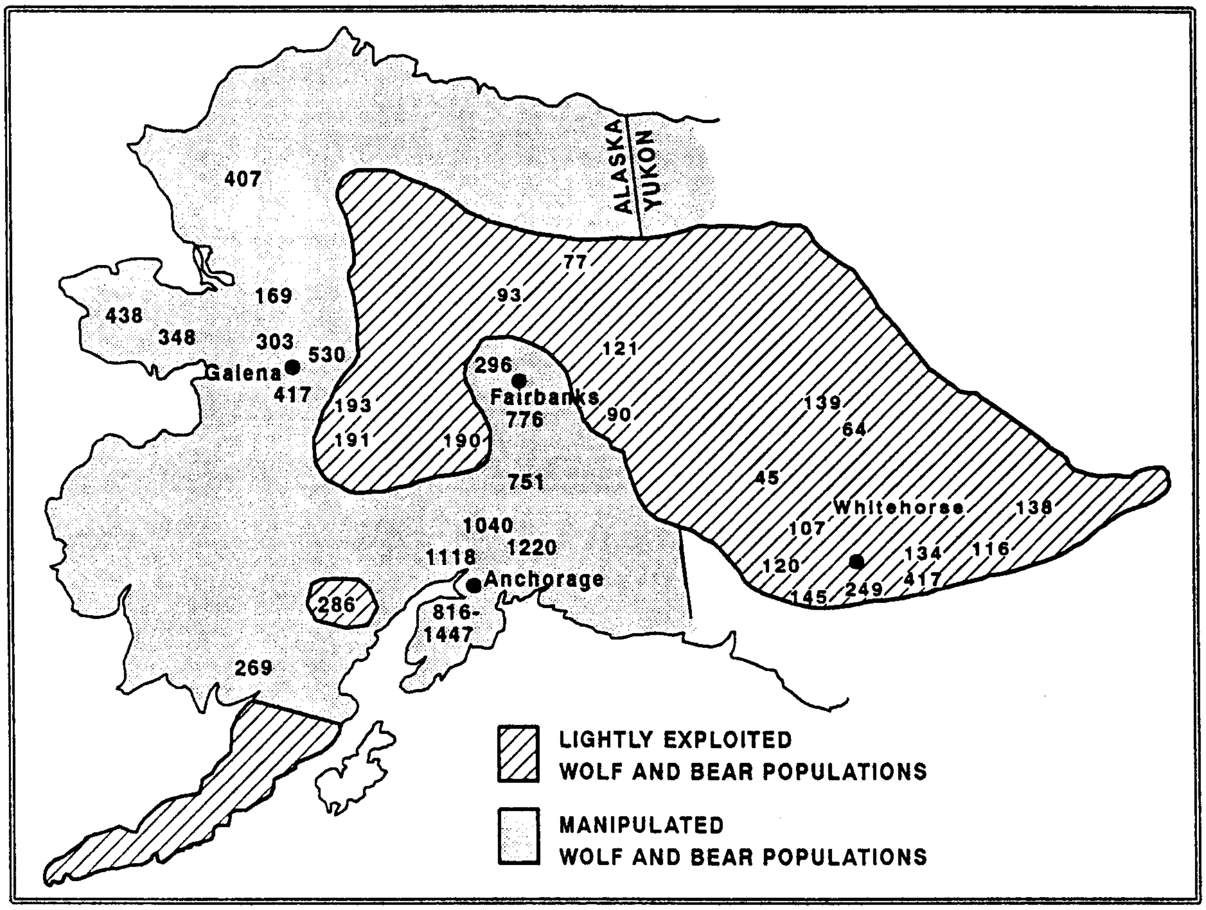


Fig. 15. Moose densities (moose/1,000 km^2) within regions with lightly exploited wolf and bear populations and regions where heavier exploitation manipulates predator populations. Moose surveys were conducted from 1965-88. Data are from Tables 14 and 15.

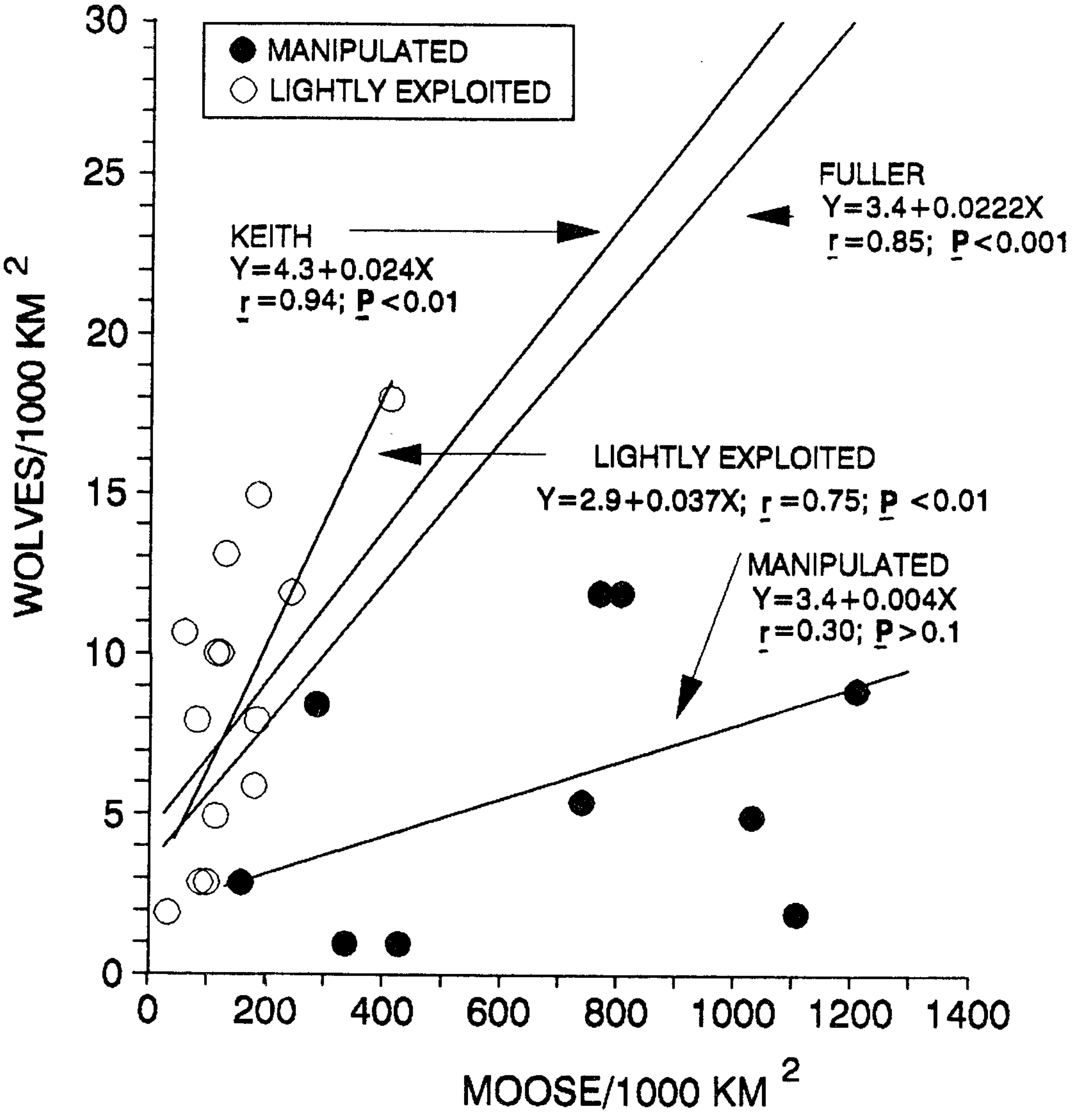


Fig. 16. Wolf density in relation to moose density in regions with lightly exploited and manipulated predator populations in Alaska and Yukon. Data points are from Tables 14 and 15. Keith's (1983) and Fuller's (1989) regressions of wolf density on prey biomass is used to predict the approximate K carrying capacity for wolves based on moose density alone; these predictions are conservative because other prey occur in most Alaska and Yukon areas (Tables 14, 15) and Fuller's regression includes some heavily exploited wolf populations.

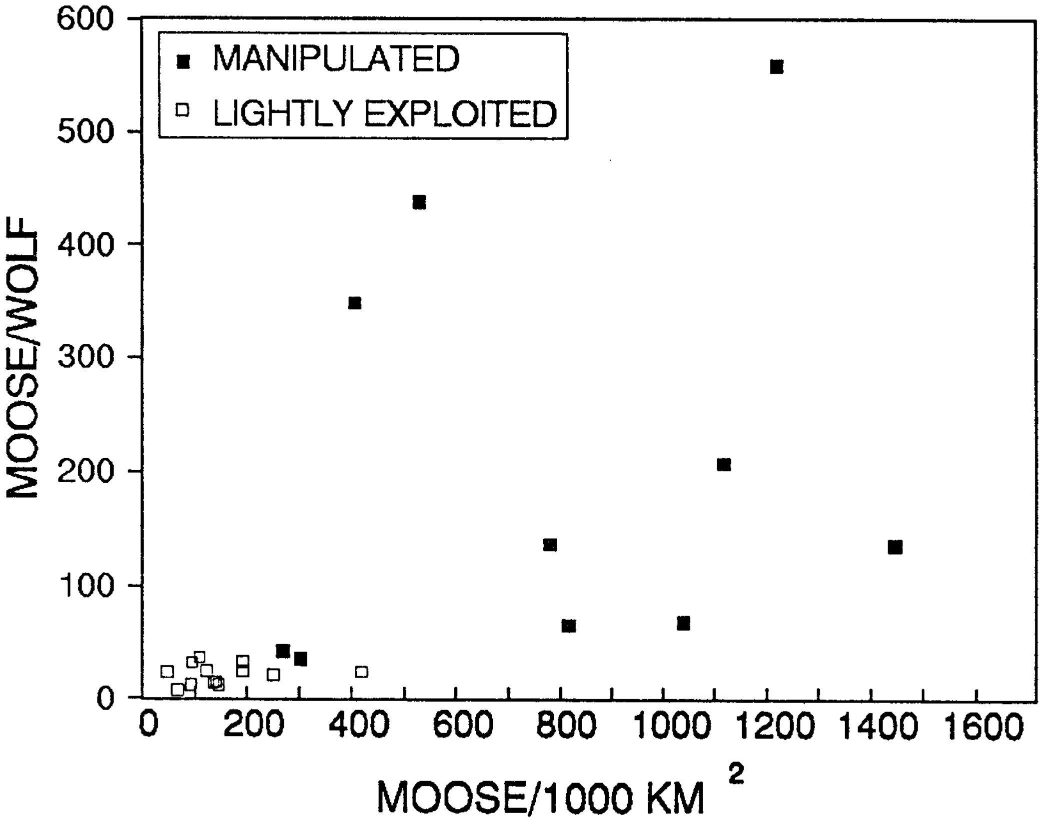


Fig. 17. Moose/wolf ratios in relation to moose density in regions with lightly exploited and manipulated wolf populations in Alaska and Yukon. Ratios were calculated by dividing moose density by wolf density for each area listed in Tables 14 and 15.

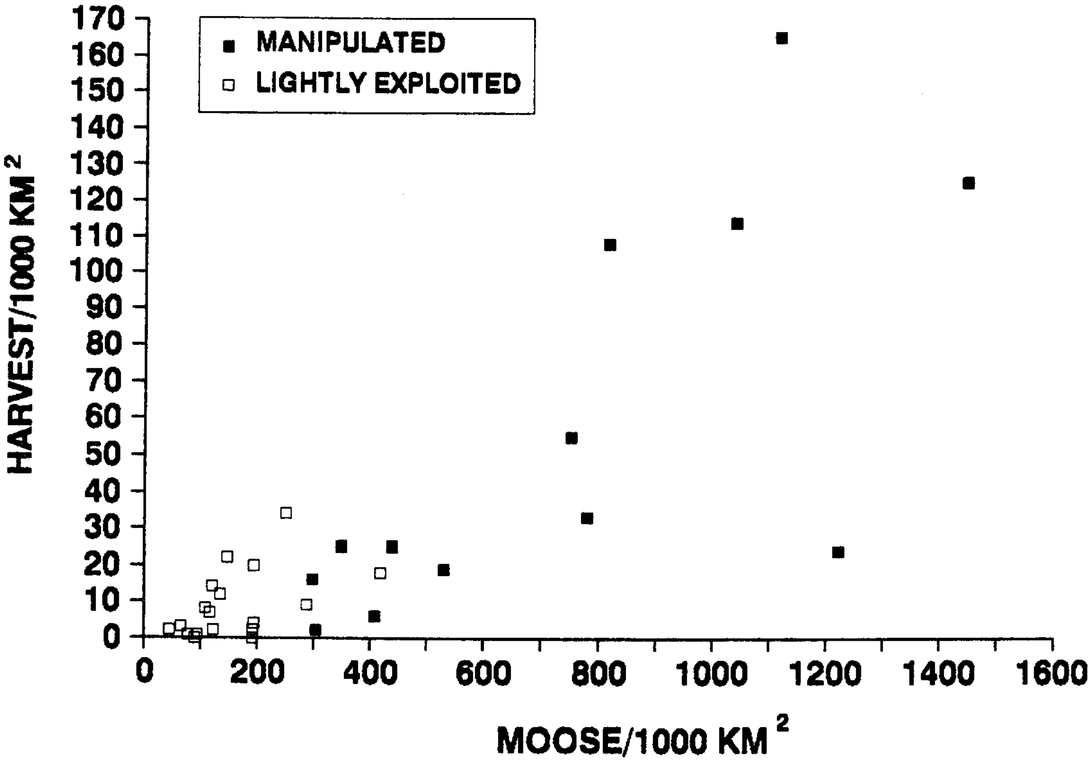


Fig. 18. Harvest rates of moose in relation to moose density in regions with lightly exploited and manipulated predator populations in Alaska and Yukon. Data are from Tables 14 and 15.

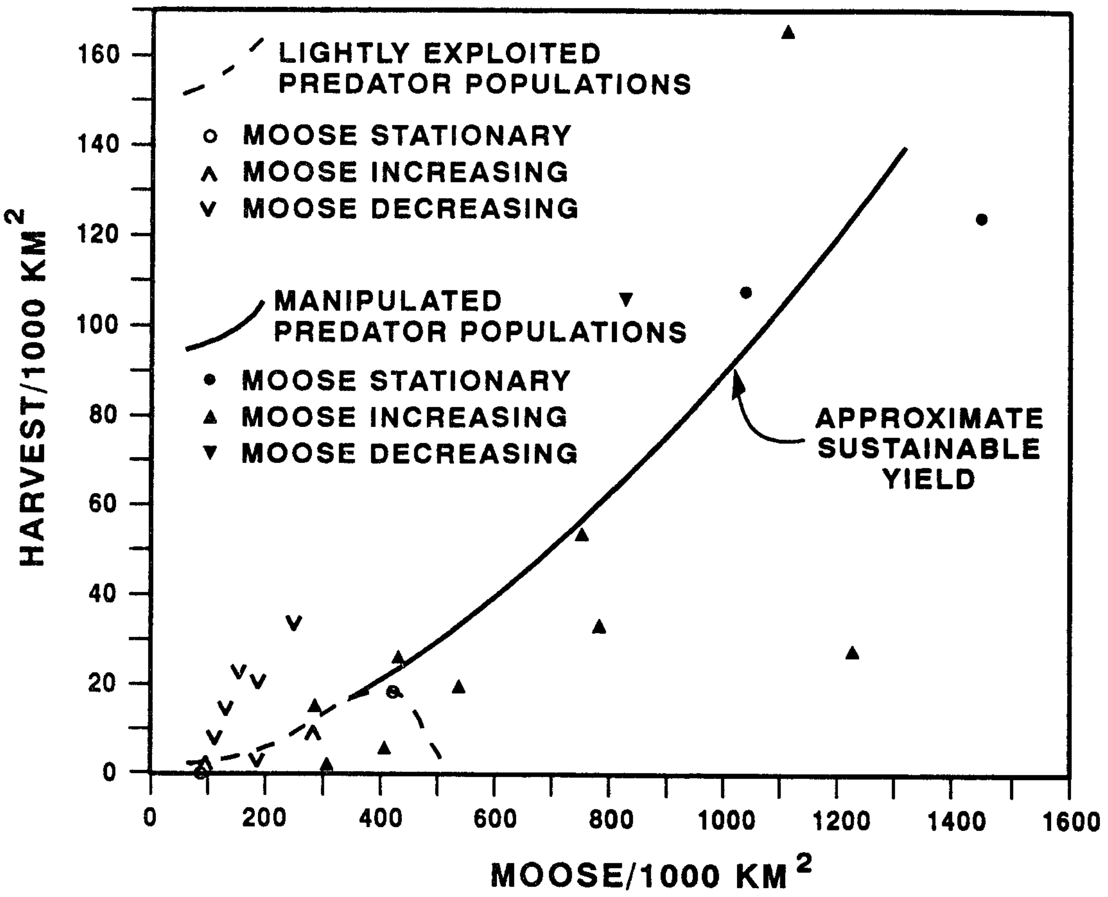


Fig. 19. Approximate sustainable yield of moose at varying moose densities in Alaska and Yukon. The line was fit by hand assuming harvest rates were sustainable if population size was stable, above sustainable when moose numbers were declining, and below sustainable when numbers were increasing. We omitted populations with unknown trends. Data are from Tables 14 and 15.

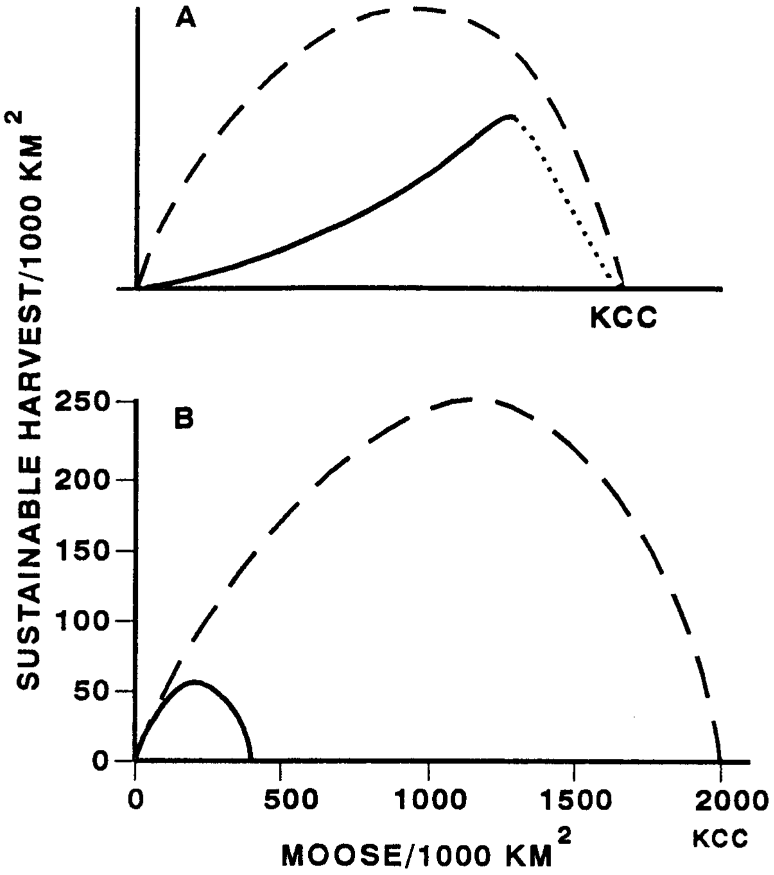


Fig. 20. Preliminary conceptual models for sustainable moose harvest rates in relationship to moose density. A) Yields in Alaska and Yukon where: (1) wolves, grizzly bears, and black bears were present (solid line signifies empirical data from Fig. 19 and dots theoretical relationships), and (2) a hypothetical yield curve when predators are absent (dashes). B) Yields in Quebec where wolves and black bears were present (solid) and absent (dashes) (after Crete 1987).

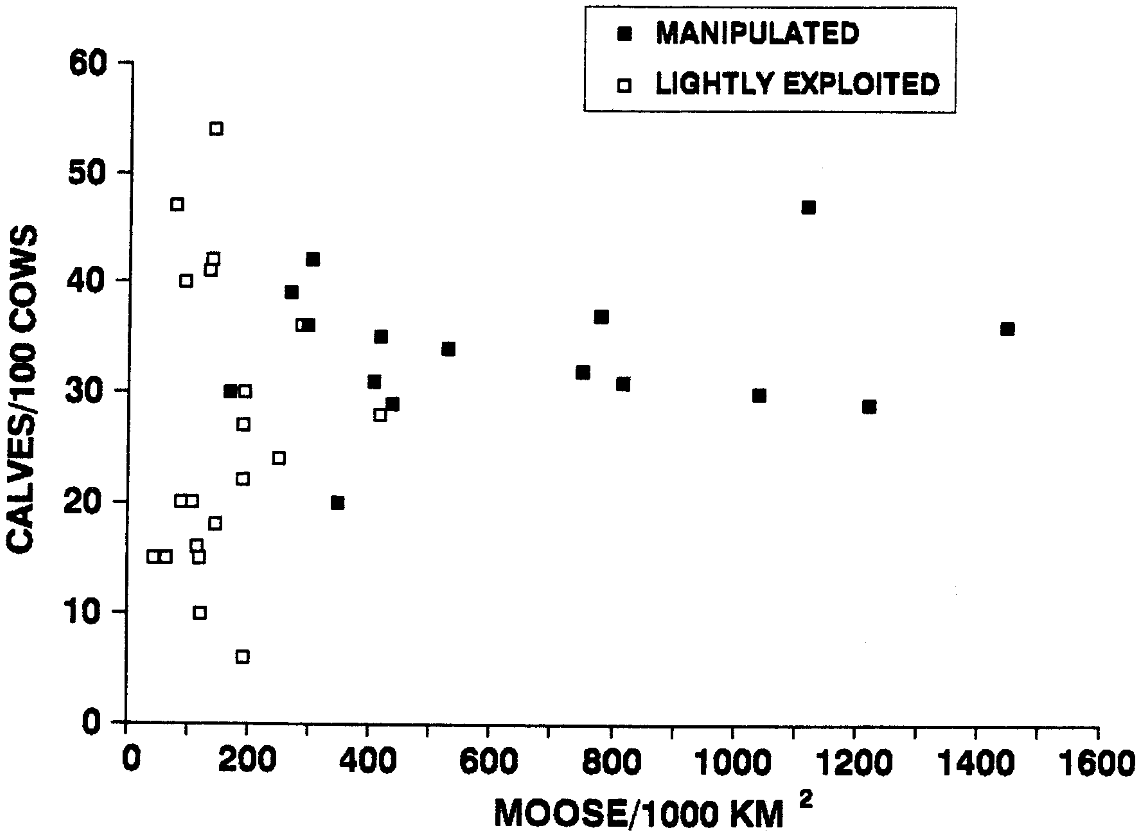


Fig. 21. Calves/100 cow moose in relation to moose density in regions with lightly exploited and manipulated predator populations in Alaska and Yukon. Data are from Tables 14 and 15.

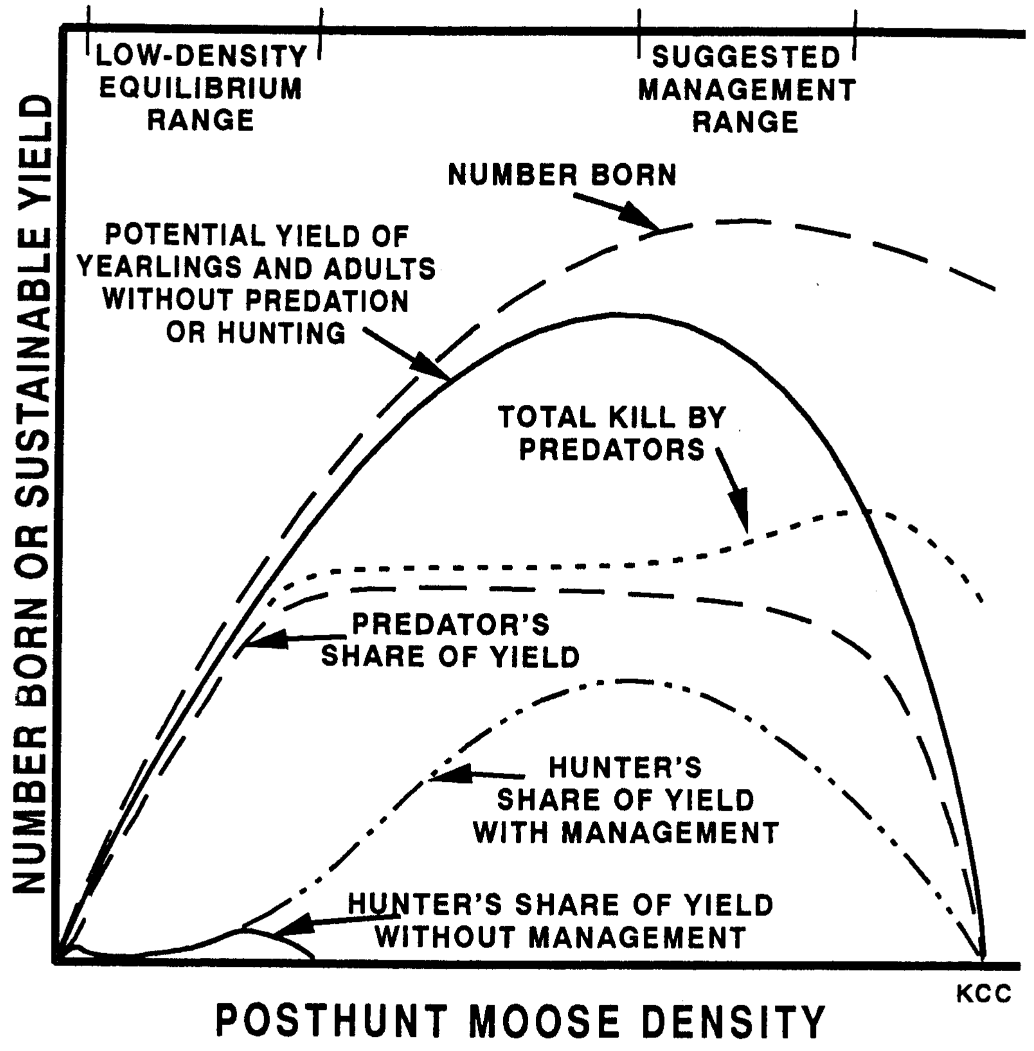


Fig. 22. A conceptual model of how predators and hunters can share the potential sustained yield from a moose population at differing relationships to K carrying capacity (KCC). This model applies to moose-wolf-bear systems in Alaska and Yukon where moose are the primary prey. We assumed that (1) management of predation maintains the total kill by predators equal to that in lightly exploited systems at a low-density equilibrium, (2) harvest available to hunters is the difference between the proportion of sustained yield killed by predators and the potential yield, (3) the total kill by predators includes one-half of the moose dying before being recruited as yearlings into the potential yield category, i.e., compensatory mortality.

Table 1. Early winter calf and yearling/cow ratios and proportions of recruits (R) for 1955 through 1988 cohorts, as determined from aerial surveys in the experimental area, east-central Alaska.

	Age of cohort in months				
	5 - 6		17 - 18		
Birth year for cohort	No. cows ≥29 month old	Calves/ 100 cows ≥29 month old	Total moose classified	Yrlgs/ 100 cows ≥29 month old	Yrlgs/yrlgs and adults (R)
1955			129	36	0.18
1956	50	62	140	51	0.21
1957	47	57	129	58	0.28
1958	48	58	253	162	0.43
1959	53	100	390	55	0.20
1960	123	43			
1961					
1962					
1963	151[a]	54[b]			
1964	271[a]	49[b]			
1965			509	34	0.18
1966	242	24	498	27	0.16
1967	284	8	389	9	0.05
1968	209	13	365	25	0.14
1969	177	28	386	19	0.12
1970	191	26	238	15	0.10
1971	132	20	363	8	0.06
1972	228	17	269	15	0.10
1973	169	8	361	7	0.05
1974	238	8	168	4	0.03
1975	110	8	124	7	0.05
1976	84	2	235	21	0.13
1977	124	7	175	29	0.15
1978	84	14	73	8	0.06
1979	50	20	108	27	0.12
1980	45	22	184	35	0.16
1981	75	24	255	36	0.17
1982	110	17			
1983	215[a]	13[b]	271	18	0.09
1984	122	25	342	29	0.13
1985	145	19	396	16	0.09
1986	187	25	480	22	0.11
1987	209	23	585	38	0.17
1988	239	28			

[a] Total number of moose classified.

[b] Surveys conducted during late winter after moose antler drop. Calves/100 cows ≥29 months old estimated from regression of calves/100cows ≥29 months old versus percent calves in the samples of moose observed during early winter surveys in the study area.

Table 2. Mean estimated adult mortality rates, proportion of recruits, and finite rates of change for the moose population in the experimental area during 4 phases of moose population growth (Fig. 2), east-central Alaska. The range of observed or calculated annual values is in parentheses.

Phase of moose population	Mean estimated annual adult mortality rate (M)	Mean estimated proportion of recruits (R)	Mean estimated finite rate of population change (λ)	Data sources/ assumptions
Irruption (1950-early 1960's)	0.08	0.22 (0.18-0.28)	1.18[a] (1.15-1.28)	M from Gasaway et al. 1983, where moose increasing and wolves scarce (Fig. 2); R for 1955-57 and 1959 cohorts (Table 1)
Rapid decline (1966-76)	0.22[b] (0.17-0.28)	0.09 (0.03-0.16)	0.85	R for 1966-75 cohorts (Table 1): mean λ from decline in overall moose/hour counts, 1966-76 (Fig. 2)
Nearly stationary (1976-81)	0.15[b] (0.08-0.18)	0.12 (0.06-0.16)	0.97	R for 1976-80 cohorts (Table 1), mean λ from moose/hour counts for 1976-80 (Fig. 2)
Slow increase (1981-88)	0.09[c] (0.03-0.14)[d]	0.13 (0.09-0.17)	1.05[a] (1.00-1.10)	M_n = 0.068% from radio-collared moose 1984-87, and M_h = 0.026% from harvest reports 1982-88; R for 1981-87 cohorts (Table 1)

[a] $\lambda = \frac{1 - M}{1 - R}$, where λ was estimated annually using constant M and observed R.

[b] $M = 1 - \lambda (1 - R)$, where M was estimated annually using constant λ and observed R.

[c] $M = 1 - (1 - M_h)(1 - M_n)$, where M_h = mortality from hunting and M_n = nonhunting mortality.

[d] 90% CI from total mortality of radio-collared moose.

Table 3. Productivity of moose in relation to K carrying capacity (KCC) for populations from North America. Ranking in relation to KCC was based on the original authors' comments in papers or on personal communications cited below.

Population	Year	Age of cows (months)	Percent births that were twins[a]	n	Percent pregnant	n	Relation to KCC	Reference
Present study	1984	>29	52	27	100	28	??	Present study
Innoko River, Ak.	1988	>29	90	10	100	17	Below	Jack Whitman, unpubl. data
Rochester, Alb.	1975-78	>29	88	8			Below	Mytton and Keith 1981
Alaska Peninsula	1977	>29	80	15	84	57	Below	Faro and Franzmann 1978
Kenai Peninsula, Ak.	1982-83	>19	71	102			Below	Franzmann and Schwartz 1985
West-central Ak.	1988-89	>19	56	61			Below	A. Loranger and T. Osborne, unpubl. data
Pukaskwa Park, Ont.	1975-19	>29	54	37	97	37	Below	Bergerud and Snider 1988
Elk Island, Alb.	1960-64	>29	50	28	82	34	Below	Blood 1974
South-central Ak.	1977-80	>29	41	64	88	59	Below	Ballard and Taylor 1980; Ballard, Gardner, Westlund, and Dau 1982

Table 3. Continued.

Population	Year	Age of cows (months)	Percent births that were twins[a]	n	Percent pregnant	n	Relation to KCC	Reference
East Newfoundland	1953-56	>29	41	29	87	38	Below	Pimlott 1959; E. Mercer, pers. commun.
Central Ak.	1975-78	>29	32	35	88	52	Below	Gasaway et al. 1983
South-central Ak.	1950's	>29	28	87	94	93	Below	Rausch 1959
Southern Yukon	1983-85	>29	28	58	84	43	Below	Larsen et al. 1989a
New Brunswick	1980-86	>29	23	52	79	33	Below	Boer 1987; A. Boer, pers. commun.
British Columbia	1952-56	>29	25	80	76	80	Near	Edwards and Ritcey 1958; R. Ritcey, pers. commun.
Kenai Peninsula, Ak.	1977-78	>19	22	49			Near	Franzmann and Schwartz 1985
Elk Island, Alb.	1959-73	>29	12	216	84	258	Near	Blood 1974
South Newfoundland	1973-75	>19	2	88			Near	Skinner, unpubl. data cited in Albright and Keith 1987; E. Mercer, pers. commun.
South Newfoundland	1982-84	>19	1	107			Near	Albright and Keith 1987; E. Mercer, pers. commun.

Table 3. Continued.

Population	Year	Age of cows (months)	Percent births that were twins[a]	n	Percent pregnant	n	Relation to KCC	Reference
Sandy-M-Town, Newfoundland	1953-56	>19	3	87	74	116	Above	Pimlott 1959; E. Mercer, pers. commun.
Moose Research Center, Ak.	1973-75	>29	0	22	60	37	Above	Franzmann et al. 1976; A. Franzmann, pers. commun.

---

[a] Estimated *in utero* or at birth.

Table 4. Estimated wolf population size and number harvested in a 15,500-km^2 area, which contains all 16 packs (Appendix 2) that ranged entirely or partially in the experimental area, east-central Alaska.

Winter period	Best estimate of early winter wolf population	Number of wolves killed				Percentage of early winter population killed	Number of wolves remaining during late winter surveys
		ADF&G	Public	Observed natural	Total		
1972-73			67		67		
1973-74			56		56		
1974-75			26		26		
1975-76			35		35		
1976-77			20		20		
1977-78			27		27		
1978-79			9		9		
1979-80			11		11		
1980-81		9[a]	13		22		
1981-82	125[b]	56	17		73	58	52
1982-83	64	15	15		30	47	34
1983-84	87	7	17		24	28	63
1984-85	79		13	1	14	18	65
1985-86	97		19		19	20	78
1986-87	114	6[c]	24	1	31	27	83
1987-88	111		35		35	32	76
1988-89	87		7		7	8	80

[a] These 9 wolves were removed from packs partially in the experimental area (Appendix 2).

[b] Estimated number of wolves pre-ADF&G wolf removal in the 15,500 km^2 area.

[c] These wolves were collected to obtain radiocesium and reproductive data.

Table 5. Indicators of productivity in female wolves older than pups during March or April and prey biomass in moose equivalents/wolf in central and east-central Alaska. Data for central Alaska are from Gasaway et al. (1983) and ADF&G files; moose equivalents were calculated assuming 1 moose equaled 3 caribou and 6 sheep. In east-central Alaska, moose equivalents/wolf were from Table 11. Wolf data pre-1965 were from Rausch (1967) and ADF&G files. Mean corpora lutea were calculated by including wolves with 0 corpora lutea.

Wolf population status	Study area and period	Corpora lutea			No. blastocysts or fetuses/females producing litters			Percent females older than pups in estrous or pregnant		Moose equivalents/ wolf
		n	$\bar{x}$	95% CI	n	$\bar{x}$	95% CI	n	Percent	
Pre-ADF&G wolf removal	Central Alaska, winter 1975-76	21	3.0	±1.3	5	4.6	±0.8	21	62	Low (17)
Pre-ADF&G wolf removal	East-central Alaska experimental area, winter 1981-82	6	3.2	±2.7				8	75	Low (15-19)
During and post-ADF&G wolf removal	East-central Alaska experimental area, winters 1982-83 through 1987-88	14	5.4	±1.1				14	93	Moderate (28-39)

Table 5. Continued.

Wolf population status	Study area and period	Corpora lutea			No. blastocysts or fetuses/females producing litters			Percent females older than pups in estrous or pregnant		Moose equivalents/ wolf
		n	$\bar{x}$	95% CI	n	$\bar{x}$	95% CI	n	Percent	
During ADF&G wolf removal	Central Alaska, winters 1976-77 through 1978-79	22	5.7	±0.7	10	5.5	±1.6	23	100	Moderate (37-65)
During and immediately after federal wolf removal by poisoning	Central and east-central Alaska, 1957-64	39	6.6	±0.6	12	7.2	±1.1	89	96	Abundant (e.g., >124-137 in central Alaska)

Table 6. Mean total length of adult female moose (≥45 months old) from Alaskan populations during late winter/early spring season, 1969-86. All data are from Franzmann and Schwartz (1983), except for Game Management Unit (GMU) 20A, 1975-79 (W. Gasaway, unpubl. data); GMU 1, 1982 (Boertje and Young 1982); and GMU 20E, 1984-86 (this study).

	Total length (cm)		
Location and period	$\bar{x}$	n	SE
GMU 15, 1977	272	13	7.2
GMU 15 (in MRC[a]), 1969-81	283	40	3.3
GMU 15, 1970	285	55	2.7
GMU 15 (out of MRC), 1969-81	286	51	1.5
GMU 15, 1975	286	23	2.3
GMU 1, 1982	286	16	4.2
GMU 5, 1978	288	32	1.9
GMU 13, 1981	289	8	5.3
GMU 20, 1971	289	8	5.3
GMU 13, 1979	290	12	3.8
GMU 22, 1981	290	27	3.7
GMU 13, 1977	292	25	3.2
GMU 15, 1971	292	45	1.9
GMU 13, 1975	296	53	1.4
GMU 6, 1974	302	25	1.8
GMU 9, 1977	302	54	1.0
Present study, 1984-86 (1976-82 cohorts)	306	12	3.5
GMU 20A, 1975-79	309	45	1.3
GMU 13, 1980	315	26	3.1
Present study, 1984-86 (1967-75 cohorts)	318	22	2.8

[a] Moose Research Center.

Table 7. A physiological condition indicator from blood (packed cell volume, PCV) for Alaskan moose populations during March or April 1969-89. All data are from Franzmann and Schwartz (1983), except Game Management Unit (GMU) 1, 1982 (Boertje and Young 1982); GMU 20A, 1989 (W. Gasaway and R. Boertje, unpubl. data); GMU 12, 1988 (D. Kelleyhouse, unpubl. data); and the present study.

	% PCV in blood		
Location and period	$\bar{x}$	n	SE
GMU 14, 1974	35.8	21	2.2
GMU 15, 1977	36.5	12	1.3
GMU 1, 1978	36.6	14	1.6
GMU 9, 1977	39.0	56	0.7
GMU 5, 1978	40.4	36	0.6
GMU 1, 1982	40.8	16	1.5
GMU 13, 1979	40.9	10	1.1
GMU 15 (in MRC[a]), 1969-81	41.0	37	0.8
Present study, 1984-86	41.1	36	0.8
GMU 15 (out of MRC), 1969-81	41.8	38	0.8
GMU 22, 1981	42.6	25	0.8
GMU 13, 1980	43.0	23	1.1
GMU 13, 1981	43.8	9	1.4
GMU 15, 1975	46.4	25	0.6
GMU 20A, 1989	47.3	38	0.4
GMU 13, 1975	49.2	55	0.5
GMU 12, 1988	50.0	39	1.5
GMU 6, 1974	53.5	32	0.7

[a] Moose Research Center.

Table 8. Food species available to moose and the browsing rates on twigs during winters 1981-82 and 1983-84 in 29 transects in the experimental area, east-central Alaska. Browse categories are based on the percentage of browsed twigs on individual plants.

	Occurrence						
			Percent of plants in browse category				
Species	Number of plants	Percent of total sample	0	1-25	26-75	76-100	Mean percent twigs browsed
Salix alaxensis	72	2.6	46	29	13	13	21
S. planifolia	1,399	49.6	82	12	4	2	5
S. arbusculoides	181	6.4	76	20	4	1	5
Subtotal	1,652	58.6	80	13	4	3	6
S. bebbiana	71	2.5	99	1	0	0	0
S. glauca	69	2.4	90	9	1	0	2
S. scouleriana	35	1.2	100	0	0	0	0
S. spp.	26	0.9	100	0	0	0	0
Betula glandulosa	959	34.0	99	1	0	0	0
Alnus spp.	5	0.2	100	0	0	0	0
Populus tremuloides	3	0.1	100	0	0	0	0
Total or mean	2,820	100.0	87	9	3	2	4

Table 9. Moose harvest and duration of hunting seasons for bulls and cows in Game Management Unit (GMU) 20E (28,500 km^2), east-central Alaska (ADF&G files). Parentheses enclose harvests from the portion of the GMU in the experimental area.

Year	Number of moose harvested[a]	Percent cows in harvest	Duration of hunting seasons (days)	
			Bulls	Cows
1954	88[b]	0	Unk	0
1955	65[b]	0	Unk	0
1960	92[b]	0	72	0
1961	142[b]	0	73	0
1962	118[b]	0	72	0
1963	124	5	72	1
1964	118	13	72	7
1965	124	5	72	2
1966	106	11	70	5
1967	130	6	72	7
1968	126	7	72	7
1969	124	5	72	7
1970	79	Unk	72	7
1971	102	Unk	72	7
1972	85	Unk	72	7
1973	115	19	72	7
1974	95	11	72	7
1975	40	0	40	0
1976	40	0	40	0
1977	0	0	0	0
1978	0	0	0	0
1979	0	0	0	0
1980	0	0	0	0
1981	0	0	0	0
1982	22	0	10	0
1983	37 (25)	0	10	0
1984	34 (22)	0	10	0
1985	55 (28)	0	10	0
1986	51 (34)	0	10	0
1987	64 (32)	0	10	0
1988	67 (45)	0	10	0

[a] Reported harvest was multiplied by 1.177 to adjust for unreported harvest (Gasaway et al. 1983).

[b] Reported harvest is from check stations along the Taylor Highway; during other years reported harvest is from harvest tickets or harvest tickets and check stations.

Table 10. Moose, caribou, wolf, and grizzly bear density in the experimental area (9,700 km^2) before (1981) and after (1984 and 1988) wolf removal, east-central Alaska.

	Density in animals/1,000 km^2				
		Caribou[b]			
Period	Moose[a]	Min.	Max.	Wolf[c]	Grizzly bear[d]
Before wolf removal, early winter 1981	88-112	20	770	8	16
After wolf removal, early winter 1984	101-128	20	1,070	5	16
Early winter 1988	127-157	20	1,550	6	16

[a] Moose density was estimated in the experimental area west of the Taylor Highway during early winter 1981 and 1988 and moose density was assumed to increase at 7% annually between 1981 and 1984. We used the upper half of the probable density range during 1981 and the lower half of the 90% CI for 1988 (<u>see</u> Population Trend and Density).

[b] Caribou density was estimated by assuming a minimum of 200 animals were present at all times and a maximum of 7,500, 10,400, and 15,000 were present during early winter 1981, 1984, and 1988, respectively (Valkenburg and Davis 1989; P. Valkenburg, pers. commun.).

[c] Wolf density was from the total area (15,500 km^2) occupied by wolf packs in Appendix 2.

[d] Density of grizzly bears was extrapolated from spring density in the grizzly bear study area (4,000 km^2) and assumed stationary.

Table 11. Estimated numbers of prey/predator in the experimental area before (1981) and after (1984 and 1988) wolf removal, east-central Alaska. Numbers were calculated from density estimates in Table 10. Numbers in parentheses are approximations of the number of moose/wolf, adjusted for caribou in the wolf's winter diet, e.g., (the number of moose available) / (0.72 x the estimated number of wolves), because approximately 28% of the wolf's winter diet was caribou.

Period	Moose/ wolf	Moose/ grizzly bear	Moose/wolf + grizzly bear	Moose + min. caribou/wolf	Moose + max. caribou/wolf	Moose + min. caribou/wolf + grizzly bear	Moose + max. caribou/wolf + grizzly bear
Before wolf removal, early winter 1981	11-14 (15-19)	6-7	4-5	14-17	107-110	5-6	36-37
After wolf removal, early winter 1984	20-26 (28-35)	6-8	5-6	24-30	234-240	6-7	56-57
Early winter 1988	21-26 (31-39)	8-10	6-7	25-30	280-285	7-8	76-78

Table 12. Estimated numbers of prey/predator in areas of North America where moose populations are stationary or declining and predation was either the major or suspected major factor limiting moose population growth.

Area	Moose/ wolf	Moose/ grizzly bear	Moose/ wolf + grizzly bear	Moose + min. caribou/ wolf + grizzly bear	Moose + max. caribou/ wolf + grizzly bear	Moose + max. caribou + sheep/wolf + grizzly bear	Black bear	Reference
East-central Alaska, 1981	12	6	4	5	37	37	Scarce	Present study
South-west Yukon, 1981[a]	12	9	5		6	29	Common	Larsen et al. 1989a; D. Larsen, unpubl. data
Central Alaska GMU 20A, 1975	12	13	6		10	19	Common	Gasaway et al. 1983, Reynolds et al. 1987
Isle Royale, 1971-80	20						None	Peterson and Page 1983
Pukaskwa National Park, Ontario	24				25		Common	Bergerud et al. 1983
Ft. McMurray, Alberta, 1975-78	28				28		Common	Fuller and Keith 1980, Hauge and Keith 1981

Table 12. Continued.

Area	Moose/ wolf	Moose/ grizzly bear	Moose/ wolf + grizzly bear	Moose + min. caribou/ wolf + grizzly bear	Moose + max. caribou/ wolf + grizzly bear	Moose + max. caribou + sheep/wolf + grizzly bear	Black bear	Reference
South-west Quebec	28						Common	Messier and Crete 1985
North-eastern Denali National Park, Alaska 1986-87	48	9	8	8	16	34	Scarce	Haber 1977; Dalle-Molle 1987; Dean 1987; Mech 1987; Meier 1987; J. Davis, pers. commun.
South-central Alaska, GMU 13E, 1975	64	20	15		33		Scarce	Ballard and Larsen 1987; Pitcher 1987

---

[a] Ratios were calculated from animal densities based on 1,000 km^2 of total land area; 68.5% of the total land area was moose habitat (D. Larsen, unpubl. data).

Table 13. Offspring/cow ratios and percent calves for 1978-86 cohorts as determined by aerial moose surveys in the Mount Veta-Mosquito Flats moose survey area in the experimental area, east-central Alaska, before (1978-81) and after (1982-86) wolf removal. n = total number of moose classified.

		Age of cohort in months				
		5-6			17-18	
Birth year for cohort	n[a]	No. of cows ≥29 month old	Calves/ 100 cows ≥29 month old	% Calves in total sample	No. of cows ≥29 month old	Yearlings/ 100 cows ≥29 month old[b]
1978	112	58	14	7	46	9
1979	67	46	17	12	24	33
1980	59	24	21	8	67	24
					Yearlings: after wolf removal	
1981[c]	142	67	17	6	55	18
		Calves: after wolf removal				
1982	119	55	16	8	--	--
1983	70[d]	--	--	9	61	20
1984	119	61	13	7	78	10
1985	160	78	21	10	91	26
1986	203	91	26	12		

[a] Numbers of moose observed cannot be used to estimate population trend because size of survey area varied among years.

[b] Yearling males were doubled to estimate total yearlings.

[c] Data from portion of 1981 moose population estimate in Middle Fork and Mosquito Fork drainages, excluding Joseph Creek.

[d] Survey flown during January 1984 after initiation of antler drop; therefore, sex and yearling age data were not collected.

Table 14. Moose and predator densities and moose harvest rates per 1,000 km^2 and moose calf/cow ratios in the sites on Fig. 15 where lightly exploited wolf and bear populations occur in Alaska and the Yukon, 1980-88. Study sites composed of <2,000 km^2 of moose habitat were excluded to enhance comparability among sites; small sites exhibit high variability in prey and predator densities.

Site and year of moose density estimate	Post hunt moose density[a]	Area of moose habitat (km^2)	Wolf density[a]	Grizzly bear density[a]	Black bear density[a]	Alternate prey species/ density[a]	Moose harvest[b]	Moose pop. trend[c]	Early winter moose calves/ 100 cows[d]	Source
Teslin burn, Yuk, 1984	417	2,515	18, high	Mod	Mod	Caribou/low	18	Stable	28	Hayes and Baer 1986; Larsen et al. 1989c
Mulchatna River, GMU 17B, Ak, 1987	286	4,183	Mod	Mod	Low	Caribou/mod	9	Increase	36	Taylor 1987, 1988, unpubl. data, pers. commun.
Rose Lake, Yuk, 1983	249	2,613	12, mod	16, mod	Mod	Sheep/high	34	Decline	24	Hayes et al. 1985; Larsen et al. 1989a,c; Larsen and Markel 1989
Whitehorse North, Yuk, 1982	194	2,742	Mod	10-15, mod	10-15, mod	Caribou and sheep/low	4	Decline	6	Markel and Larsen 1983
Lower Nowitna, GMU 21B, Ak, 1986	193	4,030	14-16, mod-high	Low	High	None	20	Decline	30	Osborne 1987, 1988, unpubl. data
Upper Nowitna, GMU 21A, Ak, 1980	191	9,832	8, mod	Low	High	Caribou/low	2	Unknown	27	Haggstrom and Osborne 1981; R. Stephenson and S. Dubois, unpubl. data

Table 14. Continued.

Site and year of moose density estimate	Post hunt moose density[a]	Area of moose habitat (km^2)	Wolf density[a]	Grizzly bear density[a]	Black bear density[a]	Alternate prey species/ density[a]	Moose harvest[b]	Moose pop. trend[c]	Early winter moose calves/ 100 cows[d]	Source
Northern Denali National Park, GMU 20C, Ak, 1986-87	190	10,026	6, mod	32, high	Low	Caribou/low, sheep/mod	0	Stable	22	Meier 1987; Dean 1987; Mech 1987; Dalle-Molle 1987; Singer and Dalle-Molle 1985
Haines Junction, Yuk, 1983	145	2,332	13, mod	16, mod	Mod	Sheep/low	22	Decline	18	Hayes and Baer 1986; Larsen et al. 1989c
Mayo, Yuk, 1988	139	4,853	10, mod	Present	Present	Caribou and sheep/low	Unknown	Unknown	54	Larsen et al. 1989b; Hayes and Baer, unpubl. data
Liard East, Yuk, 1986	138	2,210	Present	Present	Present	Caribou and sheep/low	Unknown	Unknown	42	Jingfors and Markel 1987
Nisutlin, Yuk, 1986	134	4,210	9-11, mod	Present	Present	Caribou/low-mod	12	Unknown	41	Hayes and Baer 1987a; Jingfors and Markel 1987
Upper Yukon, GMU 25B and 20E, Ak, 1987	121	9,210	3-6, low	Mod	Mod	Caribou/low	2	Unknown	10	Nowlin 1989, unpubl. data; S. Ulvi, unpubl. data

Table 14. Continued.

Site and year of moose density estimate	Post hunt moose density[a]	Area of moose habitat (km^2)	Wolf density[a]	Grizzly bear density[a]	Black bear density[a]	Alternate prey species/ density[a]	Moose harvest[b]	Moose pop. trend[c]	Early winter moose calves/ 100 cows[d]	Source
Kluane Lake, Yuk, 1981	120	3,671	Low-mod	10-15, mod	10-15, mod	Caribou and sheep/high	14	Decline	15	Larsen 1982
Liard West, Yuk, 1983	116	7,236	Present	Present	Present	Caribou and sheep/low	7	Unknown	16	Johnston and McEwen 1984
Aishihik, Yuk, 1981	107	3,519	3, low	10-15, mod	10-15, Mod	Caribou and sheep/mod	8	Decline	20	Larsen 1982; Hayes and Baer 1987b
Yukon Flats, GMU 25D West, Ak, 1986	93	16,107	3, low	Low	High	None	1	Increase	40	Nowlin 1985, 1988, 1989
Present study, 1981	88	7,700	8, mod	16, mod	Low	Caribou/mod	0	Stable	20	Present study
Yukon Flats, GMU 25D East, Ak, 1984	77	27,584	Low	Low	High	None	1	Unknown	47	Nowlin 1984, 1986, 1988, pers. commun.
Dromedary Mountain, Yuk, 1982	64	3,548	10, mod	Present	Present	Caribou and sheep/low	3	Unknown	15	Johnston and McLeod 1983; Hayes and Baer, in prep.
Carmacks, Yuk, 1987	45	3,055	2, very low	Mod	Low	Caribou and sheep/low	2	Unknown	15	Markel and Larsen 1988; Hayes and Baer, in prep.

Table 14. Continued.

---

[a] Numerical values are estimated densities; relative densities are presented so readers can form an impression of the complexity of these ecosystems. Relative densities represent our ranking based on our observations and those of biologists working at the sites.

[b] Harvest is a 3-year mean (year of the moose density estimate and 2 preceding years). In Alaska, reported harvest was multiplied by 1.177 to adjust for unreported harvest (Gasaway et al. 1983). In the Yukon, total harvest was estimated using the 3-year mean of mandatory reported harvest for nonnative hunters plus the 1988 harvest by natives, which was based on a personal interview survey.

[c] Trend is for the 3- to 5-year period prior to the moose density estimate.

[d] Numbers of calves/100 cows is a 3-year mean (year of density estimate and 2 preceding years, when available).

Table 15. Moose and predator densities and moose harvest rates per 1,000 km^2 and moose calf/cow ratios in the sites on Fig. 15 where wolf and/or bear populations are held below K carrying capacity by exploitation in Alaska, 1965-88. Study sites composed of <2,000 km^2 of moose habitat were excluded to enhance comparability among sites; small sites exhibit high variability in prey and predator densities.

Site and year of moose density estimate	Post hunt moose density[a]	Area of moose habitat (km^2)	Wolf density[a]	Grizzly bear density[a]	Black bear density[a]	Alternate prey species/ density[a]	Moose harvest[b]	Moose pop. trend[c]	Early winter moose calves/ 100 cows[d]	Source
Kenai Peninsula, GMU 15A, Ak, 1965-71	1,447	5,048	Very low	Low	High	Caribou/low	125	Stable	36	LeRoux 1973; Bailey 1978; Peterson et al. 1984
South-central, Ak, GMU 13A, 1987	1,220	4,861	8-10, mod	18, mod	Low	Caribou/high	24	Increase	29	W. Taylor and R. Tobey, unpubl. data
Matanuska, GMU 14A, Ak, 1988	1,118	4,116	1-3, very low	Low	Mod	Caribou/very low, sheep/high	165	Increase	47	C. Grauvogel and W. Taylor, unpubl. data; Grauvogel 1989
Lower Susitna, GMU 14B, Ak, 1987	1,040	2,776	4-6, low	Mod	Mod-high	Caribou/low, sheep/mod	114	Stable	30	C. Grauvogel and W. Taylor, unpubl. data; Grauvogel 1989
Kenai Peninsula, GMU 15A, Ak, 1987	816	3,310	12, mod	Low	200-260, high	Caribou/low	108	Decline	31	Spraker 1985, 1986, 1987, 1988, unpubl. data; Schwartz and Franzmann 1989
Tanana Flats and adjacent foothills, GMU 20A, Ak, 1988	776	12,650	12, mod	15, mod	Mod	Caribou and sheep/high	33	Increase	37	M. NcNay 1990, unpubl. data; Reynolds and Hechtel 1988

Table 15. Continued.

Site and year of moose density estimate	Post hunt moose density[a]	Area of moose habitat (km²)	Wolf density[a]	Grizzly bear density[a]	Black bear density[a]	Alternate prey species/ density[a]	Moose harvest[b]	Moose pop. trend[c]	Early winter moose calves/ 100 cows[d]	Source
South-central, GMU 13, Ak, 1983	751	3,737	5-6, low	25, high	Low	Caribou/low	55	Increase	32	Ballard et al. 1987, 1990; R. Tobey and W. Taylor, unpubl. data
Galena, GMU 21D, Ak, 1987	530	8,563	Low-mod	Low-mod	High	Caribou/low	19	Increase	34	Osborne 1989, unpubl. data
Seward Peninsula, GMU 22D, Ak, 1988	438	6,472	<1, very low	Mod	None	Reindeer/mod	25	Stable	29	Nelson 1989, unpubl. data; T. Smith, unpubl. data
Kaiyuh Flats, GMU 21D, Ak, 1987	417	4,079	Low-mod	Low-mod	High	None	Unk	Unknown	35	Osborne 1989
Noatak River, GMU 23, Ak, 1985	407	5,478	Low-mod	20, high	Very low	Caribou/mod	6	Increase	31	James 1984, 1986; Ballard et al. 1988; Quimby and James 1985; D. Larsen and J. Dau, unpubl. data
Seward Peninsula, GMU 22B, Ak, 1987	348	6,472	1, very low	Mod-high	Very low	Reindeer/low	25	Unknown	20	Nelson 1988, unpubl. data

Table 15. Continued.

Site and year of moose density estimate	Post hunt moose density[a]	Area of moose habitat (km^2)	Wolf density[a]	Grizzly bear density[a]	Black bear density[a]	Alternate prey species/density[a]	Moose harvest[b]	Moose pop. trend[c]	Early winter moose calves/100 cows[d]	Source
Huslia River, GMU 24, Ak, 1988	303	6,262	Mod	Mod	Mod-high	Caribou/mod	2	Increase	42	T. Osborne, unpubl. data
Central Ak, GMU 20B, 1985	296	22,390	8-9, mod	Mod	Mod	Caribou and sheep/very low	16	Increase	36	Crain and Haggstrom 1985, 1986, 1987; D. Haggstrom, unpubl. data
Nushagak River, GMU 17C, Ak, 1983	269	4,750	Low	High	Low	Caribou/low	Unk[e]	Increase	39	Taylor 1983, 1984, unpubl. data; S. DuBois, unpubl. data
Selawik Refuge, GMU 23, Ak, 1985	169	11,292	4, low	Low	High	Caribou/high	Unk	Increase	30	Larsen 1987, unpubl. data; S. Dubois, unpubl. data; Quimby and James 1985; Ballard et al. 1990

[a] Numerical values are estimated densities; relative densities are presented so readers can form an impression of the complexity of these ecosystems. Relative densities represent our ranking based on our observations and those of biologists working at the sites.

[b] Harvest is a 3-year mean (year of the moose density estimate and 2 preceding years). Reported harvest was multiplied by 1.177 to adjust for unreported harvest (Gasaway et al. 1983).

[c] Trend is based on the 3- to 5-year period prior to the moose density estimate.

[d] Numbers of calves/100 cows is a 3-year mean (year of density estimate and 2 preceding years, when available).

[e] Native harvest was unknown but was high relative to the moose population and kept the moose at a low density.

Appendix 1. Historical observations of moose.

Low to moderate densities of moose occurred in the experimental area from the late 1800's through the 1940's. Prospectors hunted moose successfully in the late 1800's through the 1940's in the experimental area (Wilson 1951; B. Roberts, long-term resident, pers. commun.), and moose were encountered regularly in portions of the experimental area during 1902 (Mitchell 1982). However, V. Cowden, a market hunter supplying the Chicken area, recorded in his journal that moose were scarce in the experimental area in the early 1900's except in the Mosquito Flats (W. L. Pamplin, ADF&G, pers. commun.), an area that Mitchell (1982) traveled in.

The moose population irrupted from about 1950 through the early 1960's, based on observations of long-term residents. First, observations of D. Euers (pers. commun.), who initiated efforts by the U.S. Branch of Predator and Rodent Control in the experimental area along the Taylor Highway during 1949, indicated recruitment increased markedly by 1951 and the population peaked at a high density about 1965. R. Bishop, ADF&G biologist; D. Jones, predator removal officer and wildlife observer since the mid-1950's; and J. Terwilliger, local hunter and trapper since the mid-1950's (pers. commun.), confirmed peak moose densities occurred in the experimental area during about 1964-65.

Appendix 2. Estimated numbers of wolves and respective wolf pack names in a 15,500-km^2 area, which contains all 16 packs that ranged entirely or partially in the experimental area, east-central Alaska. Data are summarized in Table 4.

			During wolf removal				After wolf removal											
		Before wolf	1982		1983		1984		1985		1986		1987		1988		1989
Pack No.	Pack name	removal early winter 1981	late winter	early winter	late winter	early winter	late winter	early winter	late winter	early winter	late winter	early winter	late winter	early winter	late winter	early winter	late winter
1	Mansfield Creek	9[a]	2	10[b]	1	5	3	4	3	6	6	12	8	8	5[b]	6[b]	6[b]
2	Billy Creek	9[a,b]	2[b]	2[b]	1	8	8[b]	8[b]	2	8	4	10	3	8	4	2	2
3	Mosquito Flats	0	0	0	0	8	4	5	5	7	7	5	2	8	7	8	8
4	Mitchels Ranch	15[b]	2	2	2	4	2[b]	6	5[b]	7[b]	6[b]	8[b]	5	6	4	3	3
5	Middle Fork	11[b]	2	3	3	5[b]	2	5	4	6	4	5	4	3	3	3	3
6	Divide	8	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2
7	Joseph Creek	6	2	2	2	6	3[b]	3[b]	2	2	2	5	5	7	6	3	3
8	Slate Creek	0	0	0	0	6	6	6	4	8	8	14	13	11	3	5	5
9	Portage Creek	12[b]	4[b]	4[b]	0	9	8[b]	9[b]	9	12[b]	10	13	10	13	8	14	13
10	Gold Creek	5[b]	0	0	0	3	3	8	8[b]	11[b]	8[b]	10[b]	7[b]	5[b]	3[b]	6[b]	3[b]
11	Chicken	7	3	5	4	8	4	5	5	4	3	7	3	4	3	4	3
12	Kechumstuk	3	3	5[b]	2	1	1[b]	0	0	2	1	0	0	8	6	9	9
13	West Fork	10	2	4	2	3	2	2	2	2	2	2	2	2	2	2	2
14	Mount Fairplay	2	2	2	2	2	2	2	0	3	2	2	0	2	2	2	2
15	Dennison Fork	9	9	11	1	1	1	3	3	3	1	3	3	7	2	3	3
16	Liberty Creek	8	8	8	8	10	6[b]	6[b]	6	7	5	6	6	7	7	7	5
	Lone wolves	11	11	6	6	8	8	7	7	9	9	10	10	10	9	8	8
Total wolf numbers		125	52	64	34	87	63	79	65	97	78	114	83	111	76	87	80
Percentage change			-58%	+23%	-47%	+156%	-28%	+24%	-18%	+49%	-20%	+46%	-27%	+35%	-32%	+16%	-8%
Density (wolves/1,000 km^2)		8	3	4	2	6	4	5	4	6	5	7	5	7	5	6	5

[a] Nine total wolves were removed from these 2 packs during winter 1980-81; pre-removal values are presented.

[b] Radiocollar(s) were used to locate the pack.

Appendix 3. Values and calculations used to model moose population dynamics in the experimental area, east-central Alaska, 1981-88.

Parameters, data, and calculations	Observed or calculated values
Hypothetical adult and yearling precalving population, 15 May	1,000
Proportion of females among moose ≥17 months old during early winter, mean 1982-88	0.56
Number of females ≥12 months old, 15 May (0.56 x 1,000)	560
Proportion of yearling females among females ≥17 months old, mean of 1981-87 cohorts, early winter	0.12
Number of females ≥24 months old (560 x 0.88)	493
Calves produced (493 x 138 calves/100 females ≥24 months old)	685
Calf mortality rate to 12 months old, 1981-87 cohorts (1 - [(26 yearlings/100 females ≥29 months old in early winter)/138 calves/100 females])	0.81
Number calves dying by 12 months old (0.81 x 685)	555
Proportion and cause of radio-collared calf mortality, 1984-85:	
Grizzly bears (17/26)	0.654
Wolf (4/26)	0.154
Black bear (1/26)	0.038
Drowning (4/26)	0.154
Adult and yearling moose dying of nonhunting causes (0.068 for radio-collared moose x 1,000)	68
Proportions and causes of nonhunting adult and yearling mortality:	
Predation (41/46 carcasses)	0.89
Nonpredation (5/46)	0.11
Annual harvest of adult and yearlings (0.026 x 1,000)	26
λ for adult and yearling population	1.04
λ for postcalving population	1.02

Federal Aid Project
funded by your purchase of
hunting equipment