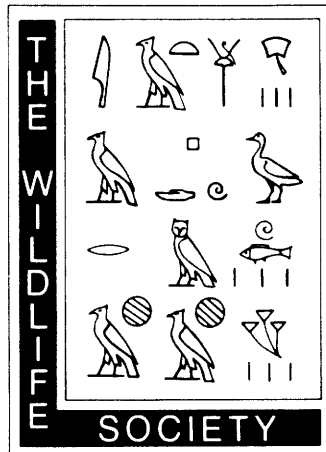


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INTERRELATIONSHIPS OF WOLVES, PREY, AND MAN IN INTERIOR ALASKA

by

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FRONTISPIECE. Wolf in interior Alaska. (Photo by R. O. Stephenson)

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Abstract: The interrelationships among wolves (*Canis lupus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and man were studied in a 17,060 km² area in interior Alaska during the 1970's, and historical data from the 1950's and 1960's were reviewed and re-evaluated. Objectives of this study were to define factors limiting a moose and caribou population; to review moose-wolf relationships in ecosystems where wolf populations are, to a large extent, naturally regulated; to demonstrate the effects of man's harvest of prey species on the wolf-prey relationship; and to identify problems of managing prey populations for hunting and nonconsumptive human use where wolf populations are naturally regulated. Moose and caribou populations increased following a wolf reduction program in the 1950's and reached peak abundance in the 1960's. Deep snow and heavy browsing caused an initial crash of moose in 1965-66. Moose continued to decline until 1976, primarily due to periodic deep snow, harvest by man, and predation by wolves. These factors were interactive, each altering the impact of the others. The long-term effect of moose mortality from deep snow was to increase the impact of predation by lowering moose/wolf ratios. Hunting and wolf predation were the principal causes of moose mortality from 1971-75. Harvests removed from 6-19% of the moose population annually; mean harvest rate equaled mean yearling recruitment. After 1974, harvest removed 2% of the moose. Predation by wolves removed an estimated 13-34% of the moose during winters 1973-74 and 1974-75 and a high proportion of calves during summer. Mortality from predation during winter exceeded recruitment of calf moose, and together hunting and wolf predation caused a rapid decline in moose.

Hunting by man and predation by wolves were also the primary proximate mortality causes in the decline of caribou. However, calf recruitment was so low from 1971-75 that a significant decline would have occurred without hunting. After 1973 when hunting was stopped, predation limited the population. Following a 61% reduction in wolves in 1976, survival of calf and yearling moose increased 2- to 4-fold, adult mortality declined, and the moose population increased. Survival of caribou calves also increased significantly, and the population grew rapidly. Dall sheep were a minor prey species in this predator-prey system. The impact of wolf predation on the sheep population was minor compared with impacts on moose and caribou populations.

Analysis of moose, caribou, and wolf management in our study area demonstrated that caution must be exercised in harvesting ungulates in ecosystems where wolves are essentially naturally regulated. Mortality from severe winters, hunting, and wolf predation were largely additive. In this and other studies, wolf predation sustained ungulate declines that were initiated by other factors, causing ungulates to occasionally reach low densities. From the standpoint of ungulate management, no sensitive, fast-acting feedback mechanism exists that naturally decreases numbers of wolves as prey density declines; therefore, predation can have an antiregulatory effect on ungulate populations. The escape of ungulates from control by wolves may be an infrequent event under natural conditions. If so, this poses a problem for wildlife managers seeking to maintain at least moderate ungulate densities. When wolf predation limits a depressed ungulate population, managers can either wait for a natural recovery, which could require decades, or reduce numbers of wolves. Prey/wolf ratios can assist in the initial interpretation of wolf-prey relationships. Where predators occur at near-natural levels, managers should not use survival of young ungulates as an indicator of the vegetation-ungulate relationship because predation on young animals obscures this relationship.

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INTRODUCTION

The influence of wolf predation on ungulate population growth remains poorly understood in spite of many comprehensive studies on wolf-ungulate relationships during the past 20 years (Mech 1966; Pimlott 1967; Pimlott et al. 1969; Keith 1974; Haber 1977; Mech and Karns 1977; Peterson 1977; Wolfe 1977; Carbyn 1980; Fuller and Keith 1980; Ballard et al.

1981a,b; Nelson and Mech 1981; Peterson and Page 1983). For this reason, the subject of wolf-prey relationships is highly controversial. In the mid-1970's, wolf removal in our study area became the focus of a national controversy over its ethics and efficacy in ungulate management. Findings presented in this monograph should add considerable information about the effectiveness of wolf removal.

Following predator reduction in the 1950's, moose and caribou increased in our study area to high densities by the early 1960's (Hemming 1971, Bishop and Rausch 1974). Many Alaskans noted the correlation between predator removal and the subsequent substantial increase in moose and caribou and assumed the relationship to be causal. Others argued that the correlation was coincidental, that documentation of predator removal was insufficient, and that the apparent increase in ungulates was either inadequately documented or related to environmental variables other than reduced predation.

Numbers of moose and caribou declined sharply in the study area during the early 1970's, as is shown in this monograph. The cause or causes of the declines were not well understood by the Alaska Department of Fish and Game (ADF&G). By 1974, mortality from deep snow, harvest by hunters, and predation by wolves were implicated by our preliminary assessments of the decline of moose; mortality from hunting, reproductive failure, and predation by wolves were implicated in the decline of caribou (Davis and Preston 1980).

In an attempt to stop the decline of ungulates, mortality from manageable factors (hunting and wolf predation) was reduced, and predator-prey research was intensified to identify causes of the decline. By reducing wolf numbers in winter 1975-76, we tested the hypothesis that wolf predation was preventing the increase in numbers of moose and caribou. The null hypothesis was that prey recruitment and numbers would remain unchanged regardless of wolf abundance. By intensifying research, we hoped to identify factors contributing to the declines and to better understand the relationships among these factors. If wolf removal was followed by increased numbers of moose and caribou, we hoped to determine if it was a causal relationship.

The objectives of this monograph, however, are broader than simply assessing the effects of wolf removal. We also attempt-

ed to define other factors limiting the moose and caribou populations, to review wolf-moose relationships in ecosystems where wolf populations are largely regulated naturally, to evaluate the influence of man's harvest of prey on the wolf-prey relationship, and to identify the problems of managing prey populations for hunting and nonconsumptive use where wolf populations are naturally regulated.

This monograph has a management focus and should help wildlife managers understand how man can interact with wolf-prey systems, yet ensure integrity of these systems. We believe that no ecosystem exists that is unaffected by man's actions. We use the term "natural" to describe systems where man is a minor influence on prey, wolves, and their habitat. Natural status may be a few years or longer duration. Man-caused perturbations often disrupt natural wolf-prey relationships, but if man's influence again becomes minor following the disturbance, the nature of this now-natural predator-prey response can be helpful in interpreting natural systems (Sinclair 1979, Caughley 1981). We confine our discussions to relatively simple wolf-prey systems in which wolves are the most important predators and coexist with 1 or 2 principal ungulate prey species.

Acknowledgments.—We are indebted to many people who contributed to the design and execution of the study. M. Buchholtz, D. Haggstrom, and L. Jennings surveyed moose, caribou, and wolves, were responsible for the removal of wolves, and willingly shared their data and ideas; P. Valkenburg assisted with caribou surveys; J. Coady contributed unpublished data on radio-collared moose from 1973-75; W. Heimer contributed unpublished data on the Dall sheep population; C. Nielsen and J. Ernest helped necropsy wolves; W. Ballard, J. Barnett, R. Bishop, J. Burns, J. Coady, A. Franzmann, S. Harbo, L. Jennings, D. Kelleyhouse, D. McKnight, S. Miller, R. Page, and V. Van Ballenberghe offered constructive criticism on earlier drafts. Finally, we thank A. T. Bergerud, L. D. Mech,

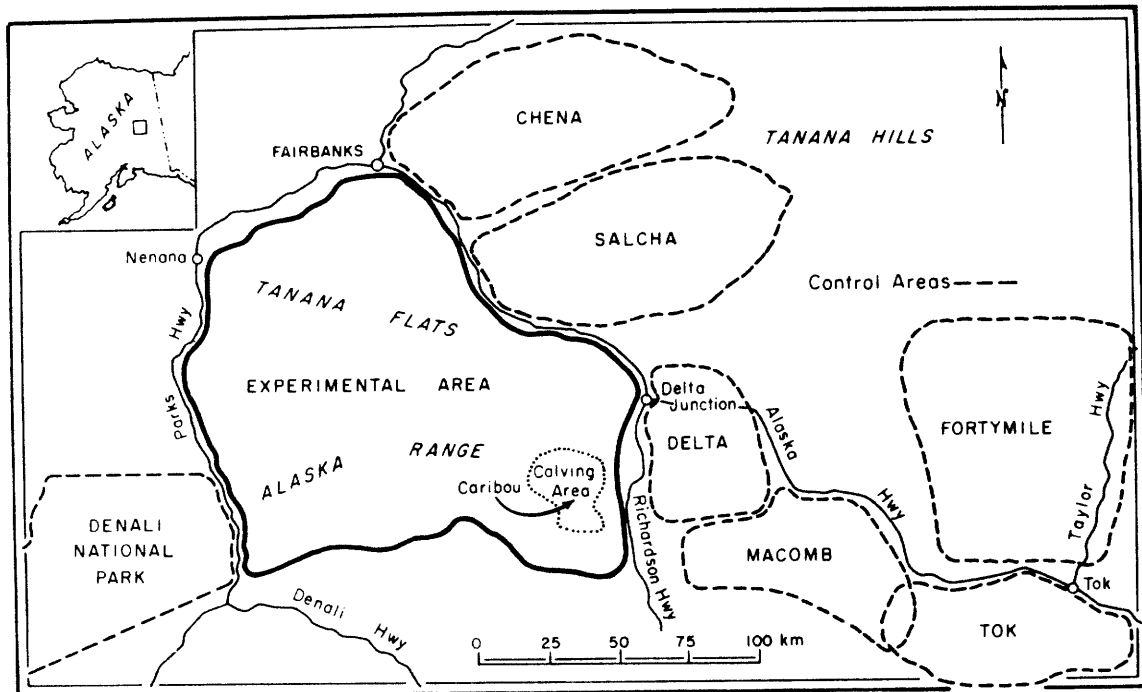


Fig. 1. Study area in interior Alaska. Experimental area (with wolf reduction) and control areas (without wolf reduction) are outlined in solid and dashed lines, respectively.

and R. L. Kirkpatrick whose comments and suggestions substantially improved this monograph.

STUDY AREA

The study area (Fig. 1) consisted of an experimental area where research and wolf removal were focused and 7 control areas (Denali National Park, Chena, Salcha, Delta, Macomb, Tok, and Fortymile) where wolf numbers were not reduced. Control areas were used in assessing results of the wolf reduction experiment.

The experimental area, located in east central Alaska south of Fairbanks (Fig. 1), was large (17,060 km²) and physiographically diverse. The southern portion (9,740 km²) consisted of the northern foothills and mountains of the Alaska Range. Elevations vary up to 4,000 m; however, ungulates and their predators seldom range above 2,000 m. The transition is abrupt from northern lowlands (Tanana Flats) to the foothills. The Tanana Flats include

7,320 km² at elevations from 13–300 m and, except for approximately 10 small, scattered hills, are without significant relief. The Flats are underlain by permafrost, and drainage is poor, resulting in numerous shallow ponds and extensive bogs, but there are many small, clear streams flowing into large glacier-fed rivers.

The physiography is diverse among the control areas. The Delta area is similar in terrain to the foothill-flats interface of the experimental area. The Chena, Salcha, and Fortymile areas are dominated by hills and low mountains. Denali National Park (formerly Mount McKinley National Park) and the Macomb and Tok areas are dominated by foothill-mountain terrain. Haber (1977) described physiography, climate, and wolf-ungulate relationships in Denali National Park.

In experimental and control areas, fire has been a dominant influence on lowland vegetation, resulting in a mosaic of shrub and young forest dominated seres, climax bogs, and mature black spruce (*Picea*

mariana) forest (LeResche et al. 1974). Vegetation in the hills, foothills, and mountain grades from taiga of white spruce (*P. glauca*), black spruce, paper birch (*Betula papyrifera*), and quaking aspen (*Populus tremuloides*) at low elevations into shrub communities of willow (*Salix* spp.) and dwarf birch (*B. glandulosa* and *B. nana*) with alpine tundra at high elevations (LeResche et al. 1974).

The climate in experimental and control areas is typical of interior Alaska. Temperatures frequently reach 25 C in summer and -10 to -40 C in winter (Oct-Apr). Snow depths are generally below 80 cm, and snow usually remains loosely packed except where windblown at high altitudes. Snow depths differ somewhat throughout the study area; however, a common pattern exists among control and experimental areas. Mild and severe winters in the experimental area were similar in control areas.

Large carnivores inhabiting the study area were wolves, black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*). Their prey include moose, caribou, Dall sheep (*Ovis dalli*), beavers (*Castor canadensis*), snowshoe hares (*Lepus americanus*), and ground squirrels (*Citellus parryi*).

METHODS

Wolf Population Status

Estimating Wolf Abundance.—The primary technique used to determine distribution and abundance of wolves was to count tracks in snow from the air during mid- to late winter (Stephenson 1978a). During the first several days following fresh snowfall, 1-3 experienced pilot-observer teams flew fixed-wing aircraft (usually PA-18 Super Cubs) in roughly predetermined patterns designed to maximize coverage of probable wolf travel routes. Fresh wolf tracks were followed and the direction of travel and number of wolves determined. If a pack was not located, the number of wolves was estimated from the

number of separate trails observed. Late winter population size was the sum of observed wolves and wolf tracks thought to represent different individuals. Fall population size, which was used for calculation of prey/wolf ratios and population trend, was equal to the late winter population plus the number of wolves harvested prior to surveys.

Aerial wolf surveys in the experimental area were conducted during late winter, from 1973-79 and used to estimate wolf abundance in the preceding falls. During 1973-75, 37, 8, and 54 hours, respectively, were spent surveying 30-67% of the 17,060 km² area. Additional information from local trappers and pilots was solicited in each of these years, particularly from nonsurveyed areas. In 1976, the entire experimental area was surveyed, and repeated reconnaissance flights were made in connection with efforts to remove wolves. Estimated wolf abundance was based on 324 hours of search. Wolf population estimates made during late winter 1977-79 were based on 325, 111, and 101 hours, respectively, of flying time (wolf surveys and removal operations combined). Wolf abundance prior to 1973 was estimated from general observations of biologists and others with long experience in the area who could compare abundance in earlier years with the number present in 1975-76.

Experimental Removal of Wolves.—Wolves were removed from the experimental area by ADF&G personnel shooting from a helicopter or fixed-wing aircraft during mid- to late winter 1976-79. Entire packs were removed when possible. A statewide mandatory reporting program for wolves provided reliable information on the number, sex, and location of wolves harvested by hunters and trappers in the study area beginning in 1972. The harvest of wolves by the public contributed significantly to the reduction of wolves.

Age Structure, Food Habits, and Reproductive Rate.—Laboratory examination of 162 wolves killed in the experi-

mental area from 1976–79 provided information on age, sex, food habits, and reproduction. Wolves less than 1 year old were identified by tooth development and wear and by the appearance of the epiphyseal suture at the distal end of the radius-ulna (Rausch 1967). Age of wolves >1 year was estimated from cementum layers in canine teeth (Stephenson and Sexton 1974; Goodwin and Ballard, unpubl. data), but tooth wear also aided in the age estimation. Food remains in the stomach and intestines were identified. Uteri of females were examined for placental scars and fetuses. Ovaries were examined grossly for signs of reproductive activity (developing or mature follicles), hardened in 10% formalin for at least 2 weeks, and then hand-sectioned at 1 mm intervals to count corpora lutea. Changing proportions of wolf fetuses resorbed and of reproductively active females were analyzed for significance using Chi-square tests.

Moose Population Status

Estimating Moose Abundance.—Stratified random sampling was used to estimate numbers of moose in the experimental area during November 1978 (Gasaway et al. 1979). Three strata in each of 3 subsections of the area were delineated during a superficial aerial survey. Randomly selected blocks from each stratum were searched at an intensity averaging about 1.5 min/km² from Super Cub, Citabria, or Helio Courier aircraft flying at 105–120 km/hour and 60–120 m above ground. Transects at 0.4–0.8 km intervals were flown over flat terrain; contour and circling flight paths were used in foothills and mountains. When moose were seen, the aircraft was diverted from the flight path and circled over the moose while searching for additional moose. Pilots assisted in counting moose. Snow depths generally ranged from 15–30 cm and tracks in snow were used as clues in locating moose. Fifty-five blocks averaging 40 km² were searched. Eighteen percent of the 12,650 km² of moose habitat was

sampled. The population estimate was the sum of strata estimates, i.e., density × area, and was corrected for moose missed. It was estimated that 17% of moose were missed under these survey conditions based on sightability of radio-collared moose in the experimental area (Gasaway et al. 1979). Early winter was chosen because sightability of moose is highest then (Gasaway et al. 1979).

Surveys to determine the population trend in the experimental area were conducted in late October–early December from 1960–77. Four physiographic areas were surveyed: Tanana Flats, foothills of the Alaska Range, central mountains, and southwestern mountains. These survey areas consisted of about 2,500, 1,040, 360, and 520 km², respectively. Survey aircraft, air speed, and altitude above ground were similar to those used in the above population estimate. Transects at 0.8–1.2 km intervals were flown over flats and contour flight paths were flown in foothills and mountains. A circling low pass was flown over each group while searching for additional moose. Tracks in snow aided pilots and observers in locating and counting moose; generally, snow cover was complete and depths ranged from 15–45 cm. All moose seen in the survey areas were tallied.

The population trend in the experimental area from 1960–77 was based on moose/hour in the 4 survey areas. Data were divided into 8 time periods because of variation in the frequency of surveys among the survey areas (Table 1). For each area and period, mean moose/hour was calculated if more than 1 survey was flown. This value was divided by the 1975 moose/hour value for each respective area, forming an index of abundance relative to 1975. The relative value for each of the 4 areas was then averaged (each with equal weight) for each period to produce the overall index of abundance. The index was 1.0 for 1975 and a multiple of the 1975 index for all other periods.

Actual numbers of moose from 1960–77 were approximated by linking the index of abundance to the 1978 population

Table 1. Frequency of aerial surveys in 4 areas within the experimental area that were used to calculate the index of moose abundance for time periods from 1960–77.

Time period (years)	Survey area			
	Tanana Flats	Foothills	Central mountains	South- western mountains
1960–65	4	3	1	
1966–67	2	1	1	1
1968–69	2	1		
1970–71	2	2	1	
1972–73	2	2	1	1
1974	1	1		
1975	1	1	1	1
1976				
1977	1	1		1

estimate, which serves as a reference point. No trend surveys were done in 1978 because all effort was put into the population estimate. However, we estimated a growth rate of approximately 7% in 1978 based on yearling recruitment data in 1978, adult mortality of radio-collared moose, and harvest by hunters. The 1978 population estimate was reduced by 7% to establish a 1977 population level. From this point, the approximate number of moose for 1960–77 was extrapolated back for each period using the index of abundance. A smoothed curve was fitted by hand to the population estimates from 1960–78.

During the mid- to late 1950's, the moose population rapidly increased in the experimental area (Bishop and Rausch 1974). Because neither rate of increase nor population size was known, we used a relative density estimate by P. Shepherd to establish an approximate starting point for the curve in 1956. This portion of the curve serves only to indicate a general trend. Shepherd observed roughly similar moose densities while working in the experimental area from 1956–58 and again in 1967–68. Using this approach, approximately a 10% growth rate was required for the population to reach its estimated peak numbers. This is a reasonable rate for a rapidly growing population with few predators (Peek et al. 1976, Bailey 1978).

The estimated number of moose was only an approximation of the true num-

ber; therefore, the limitations of these estimates must be recognized. No confidence intervals can be calculated except for 1978. In other studies, 95% confidence intervals were commonly wide, ranging from ± 20 –35% of the estimated population (Peterson 1977, Bailey 1978), and these confidence intervals may not have contained the true number because estimates were not corrected for missed moose. Prior to 1978, our population estimates probably have less precision than those above, and precision is lowest in the earliest years. Our estimates are best used to show general size and major trends and to provide the historical perspective leading up to the wolf removal experiment in the mid-1970's. Attempting to measure change over a 1-year period, for example, goes beyond the limits of these data. For convenience in writing, a single value of moose abundance is used for each year. This value is taken from the moose abundance curve described above. We do not intend to imply greater accuracy than these data warrant by using a single annual estimate of moose abundance. Despite the limitations, we believe these data provide a good historical perspective of moose abundance.

Estimating Birth Rate, Timing of Mortality, and Recruitment.—One hundred and seventy adult moose were immobilized and collared to provide data for estimating pregnancy rates, timing of birth, birth rate, frequency of twinning, calf survival rates, and adult mortality rates. Twenty-three and 18 adult moose were radio-collared (AVM Instrument Co., Champaign, Ill.) in the foothills of the Alaska Range during October through December 1973 and 1974, respectively. These moose were immobilized with succinylcholine chloride (Anectine by Burroughs Wellcome and Co., Inc., Research Triangle Park, N.C.) administered by a Cap-Chur dart rifle (Palmer Chemical and Equipment Co., Douglasville, Ga.) fired from a helicopter. Similarly, 58 cow moose were immobilized between 8 and 14 May 1975 on the Tanana Flats (Fig. 1). A vinyl-covered, canvas collar (Denver Tent

Co., Denver, Colo.) with 15-cm high numbers was placed on each moose. During August and October 1976, 36 moose were immobilized with M-99 (D-M Pharmaceuticals, Inc., Rockville, Md.) (Gasaway et al. 1978a) and radio-collared in the experimental area, and 8 were immobilized and radio-collared in the Chena and Salcha control areas. Similarly, 19 moose were radio-collared (Telonics, Mesa, Ariz.) in May 1978-79 on the Tanana Flats, and 8 moose were radio-collared in April 1981 in the southwestern mountains of the experimental area. Moose were generally located 1-4 times/month from an aircraft.

Pregnancy rates were determined by rectal palpation of 58 immobilized cows in May 1975 (Arthur 1964). Timing of birth, birth rate, and twinning frequency were determined through frequent aerial observations (1- to 3-day intervals) of radio-collared cows during May and June 1977 and 1978. Chronology of calf mortality throughout the first year of life was determined before (Oct 1973-Aug 1975) and after (Aug 1976-Oct 1978) wolf removal by monitoring the fates of calves produced by radio-collared moose. Percentage calf survival was calculated as the number of calves surviving divided by the number of calves observed during a period. When radio-collared cows died, their calves were dropped from the sample because the fates of their calves could not be determined.

Recruitment, in the form of calf/cow and yearling/cow ratios, was estimated from aerial surveys in experimental and control areas. Surveys during November in the experimental area were the same ones used to estimate the population trend from 1960-77. Because of snow melt in November 1976, ratios were based on incomplete surveys. Survey procedures in the control areas from 1973-78 were similar to those used in the experimental area 1960-77. All moose observed were classified as calf, yearling male, adult male, or adult female. In November 1978 in the experimental area, similar sex and age composition data were collected during the population estimation survey. In No-

vember 1979, the area surveyed was reduced to coincide with a long-term change in monitoring strategy; however, portions of the previous Tanana Flats (600 km²) and foothill (540 km²) surveys were counted and provide comparable age ratios. During May and prior to most cow-yearling separations, 3 blocks (totaling 1,100 km²) on the Tanana Flats in the experimental area were aerially surveyed in all but 3 years from 1960-80 to estimate yearling recruitment. In a few survey years only 1 or 2 of the 3 blocks were surveyed. Survey procedures were similar to those previously described for November on the Tanana Flats except snow was absent.

Calf/cow and yearling/cow ratios, used to evaluate recruitment of cohorts, were based on estimates of cows ≥ 30 and ≥ 36 months of age. This omitted 1 unproductive cohort from the cow base. The number of cows ≥ 30 months old in the November sample was estimated by subtracting the number of yearling males observed from total cows observed. Yearling males were assumed to equal yearling females in number. The number of cows ≥ 36 months old in May was estimated assuming that the proportion of 24-month-old cows was similar to the proportion of yearling cows present during the previous early winter survey.

Using the age classes ≥ 30 and ≥ 36 months for cows in November and May, respectively, maintained a constant number of cohorts in the cow base for each offspring/cow ratio. This allowed the best age-specific comparison of offspring survival from ratio data. Change in a ratio over time is generally assumed to equate to a change in abundance of the offspring; however, ratios contain 2 major pitfalls affecting accuracy of survival and recruitment estimates. Firstly, the number of cows (the ratio base) changes between periods because of mortality and recruitment, and this change varies in growing and declining populations. The result is an underestimation of offspring mortality (Connolly 1981). Secondly, differential sightability bias exists among cows with and without calves, which results in an

underestimate of the calf/cow ratio in November (Gasaway et al. 1981). Both problems mask real changes in offspring abundance. In addition, during May in our study area, migrant moose that only summered in the experimental area were present in large numbers; this most likely affected the May yearling/cow ratio after wolf removal because of differential mortality of moose residing year-round in the experimental area and those migrating out for winter. Therefore, changes in the ratio of a cohort over time should not be viewed as an absolute change in abundance of the offspring; rather, ratios should be used to identify major trends and approximate proportions. Statistically significant changes in observed ratios after wolf removal were evaluated using a Chi-square statistic based on Miller's (1966) method of comparing proportions. The same method was used for comparing changes in recruitment of caribou and sheep before and after wolf removal.

Estimating Adult Mortality.—Natural mortality (not caused by man) rates of adult moose were estimated from observations of radio-collared animals. Cause of death was determined by evidence obtained at the carcass. If the site was not investigated on the ground, the cause of death was recorded as unknown.

Minimum natural mortality rates for radio-collared adult moose were derived using the estimator

$$\text{minimum percent mortality} = \frac{a}{b} \times 100$$

where

- a = number of mortalities tallied among radio-collared animals during a specified period, and
 b = estimated number of collared animal-periods (This may be any specified period; we used 5-month moose-summings, 7-month moose-winters, or 12-month moose-years.).

The estimated number of collared animal periods is calculated as

$$b = \frac{c \times d}{e}$$

where

- c = mean number of months that collars were transmitting, excluding animals that died,
 d = total number of radio-collared animals, including animals that died, and
 e = time interval in months that corresponds to animal-period (e.g., 7-month moose-winter).

Animal-periods, rather than the actual number of individuals, must be used when estimating mortality for radio-collared moose because all moose are not observed for complete periods. Moose often were collared within a period rather than at the beginning (e.g., in Nov for a moose-winter beginning 1 Oct) or radio transmitters failed, leaving an incomplete record for some moose. The use of animal-periods eliminates these problems and provides data equivalent to complete records for individuals.

The above formula underestimates mortality rates when there is a seasonal peak in mortality near the end of the observation period accompanied by increased radio transmitter failures, as was the case for the 1973–75 data. In addition, mortality is underestimated if transmitter failure occurs between time of death and the next attempted radiolocation; however, this bias cannot be quantified. Despite these shortcomings, we know of no better (less biased) estimator of mortality rates of radio-collared animals.

The estimated annual kill of moose by hunters was the number of animals reported killed plus an arbitrary 15% correction factor for unreported animals and wounding losses. If the correction factor is in error, we suspect the true value is greater than our estimate.

Age of moose that were collared, killed by hunters, or found dead was estimated from cementum annuli in first incisors (Sergeant and Pimlott 1959, Gasaway et al. 1978b). Amount of femur marrow fat in moose that were found dead was used as an index of their physical condition (Neiland 1970).

Winter Severity.—Snow depth record-

ed by the National Weather Service at Fairbanks was used as an index of snow depth within the study area. Depth of snow on the ground on the first and fifteenth of each month was plotted, points were connected, and the area under the curve was measured with a compensating polar planimeter. The area under the curve was used to compare severity among winters.

Caribou Population Status

Estimating Abundance and Recruitment.—Population estimates of the Delta herd in the experimental area were made in 1973 and 1979 using an aerial photo-direct count-extrapolation method (Davis et al. 1979). The technique included precensus reconnaissance, aerial photography of postcalving aggregations and counting or estimating of peripheral animals, and sex-age classification of animals in the postcalving concentration. The number of adult females in the herd was estimated from these data. After estimating the percentage females in the herd during the rut, the total population was calculated as

total population

$$= \frac{(\text{No. females postcalving} \times 100)}{\text{Percent females during rut}}$$

Four major assumptions implicit in the technique are (1) all adult females in the herd are counted in the postcalving aggregations, (2) adult females are randomly distributed throughout the postcalving aggregations, (3) age and sex cohorts are randomly distributed throughout the herd during rut, and (4) no mortality of adult females occurs between postcalving in mid-June and the composition count in rut.

Approximate herd size in the 1970's was also estimated during surveys designed primarily to estimate initial production and recruitment. Number of calves born (estimated from distended udder counts), neonate survival, and approximate herd size were obtained from surveys of postcalving aggregations in mid-June 1973–79. Recruitment was estimated from com-

position surveys in October or November 1969–79. Distribution of the herd prior to classification was determined from fixed-wing aircraft, and caribou were classified mainly from the ground with aid of a spotting scope, although some small groups were classified from a helicopter in fall.

The effect of wolf predation on recruitment and population growth was evaluated by comparisons before and after wolf reduction in the experimental area. Additionally, data from the experimental area were compared to that from adjacent herds in the Macomb and Denali control areas (Fig. 1).

Estimating Harvest.—The estimated annual kill of caribou by hunters was the kill reported on a mail-in report card plus an arbitrary 20% correction factor for unreported animals and wounding losses. If the correction factor is in error, we suspect the true value is greater than our estimate.

Sheep Population Status

Estimating Abundance and Recruitment.—The population estimate was based on an aerial survey of all sheep habitat in the experimental area in 1970 (Heimer and Smith 1975). The number of sheep seen was multiplied by 1.3 to correct for sheep not seen. The sightability correction factor was based on sightings of 48 of 63 collared sheep during an aerial survey (W. Heimer, unpubl. data).

Changes in sheep population size from 1970–79 were extrapolated from the intensively studied Dry Creek subpopulation, which contained 30% of the sheep in the experimental area (Heimer 1981). In that subpopulation, the number of sheep declined at an average annual rate of about 7% from 1970–75, and then remained stable from 1976–79 (Heimer 1981).

Dall lamb and yearling survival (based on offspring/ewe ratios) was assessed from data collected at the Dry Creek mineral lick in the central portion of the experimental area during June and July 1969–79 (Heimer 1981). Sheep entering the lick

Table 2. Mean offspring/ewe ratios collected at 5 mineral licks in the experimental area in relation to ratios at the Dry Creek lick.^a

Year	Lamb/100 ewes			Yearlings/100 ewes		
	Experimental area		Dry Creek	Experimental area		Dry Creek
	\bar{x}	SE		\bar{x}	SE	
1974	30	5.4	28	32	7.7	25
1975	30	4.8	28	20	5.1	23
1976	29	3.8	36	16	3.5	16
1977	57	4.0	58	18	4.4	17

^a Unpublished data furnished by A. Smith, ADF&G.

were classified by sex and age by an observer with a spotting scope in a blind. Lamb/ewe and yearling/ewe ratios at this lick reflect ratios in the population (Table 2). Offspring/ewe ratios from Denali National Park were obtained in 1974–79 from the northeast corner of the Park, adjacent to the experimental area. Sheep were classified from the ground with the aid of a spotting scope.

Impact of wolf predation on lamb and yearling survival of Dall sheep was assessed by comparing data from the experimental area before and after wolf removal and by comparing the experimental area to the adjacent control area, Denali National Park (Fig. 1). Wolf removal in the experimental area did not reduce wolf numbers in the Park.

Estimating Harvest.—The annual kill of sheep by hunters was the number reported on mail-in report cards. No correction factor was used because harvest was

a minor factor influencing sheep abundance.

Hare Population Trend

Hare population trends were determined from an ADF&G questionnaire mailed to trappers and hunters in interior Alaska (J. Ernest, unpubl. data).

RESULTS

Wolf Population Status

Population Size and Trend.—Wolves were numerous in the experimental area during the early 1950's, and a federal predator removal program was initiated in 1954 (C. Gray and P. Shepherd, pers. observ.). P. Shepherd, who worked as a predator control officer in the experimental area between 1956–58, observed that wolves were scarce by 1958, with density similar to that in spring 1976 when he surveyed the experimental area for wolves following removal efforts (Table 3). After cessation of the wolf removal program in 1960, the wolf population increased through the 1960's (ADF&G biologists and P. Shepherd, pers. observ.) (Fig. 2). Peak abundance of wolves occurred during the late 1960's and early 1970's according to long-time wolf hunter and guide, A. Wright (pers. observ.). However, he observed that wolf abundance had declined

Table 3. Estimated wolf population size and number harvested in experimental area, 1972–79.

Winter period	Early winter wolf population	No. wolves killed			Percent pups in kill	Percent of early winter population killed	No. wolves remaining during late winter surveys
		ADF&G	Public	Total			
1972–73	192 ^a (265) ^b	0	42	42		22 (16) ^c	
1973–74	229 ^a (260) ^b	0	51	51		22 (20) ^c	
1974–75	179 ^a (250) ^b	0	59	59		33 (24) ^c	
1975–76	239	67	78	145	30	61	60–80
1976–77	125	27	26	53	31	42	70–80
1977–78	100	39	4	43	25	43	55–65
1978–79	80	18	12	30	33	38	45–55

^a Probably a low estimate (see text).

^b Best estimates (in parentheses) for early winters 1972–74 were taken from Fig. 2.

^c Based on best estimate.

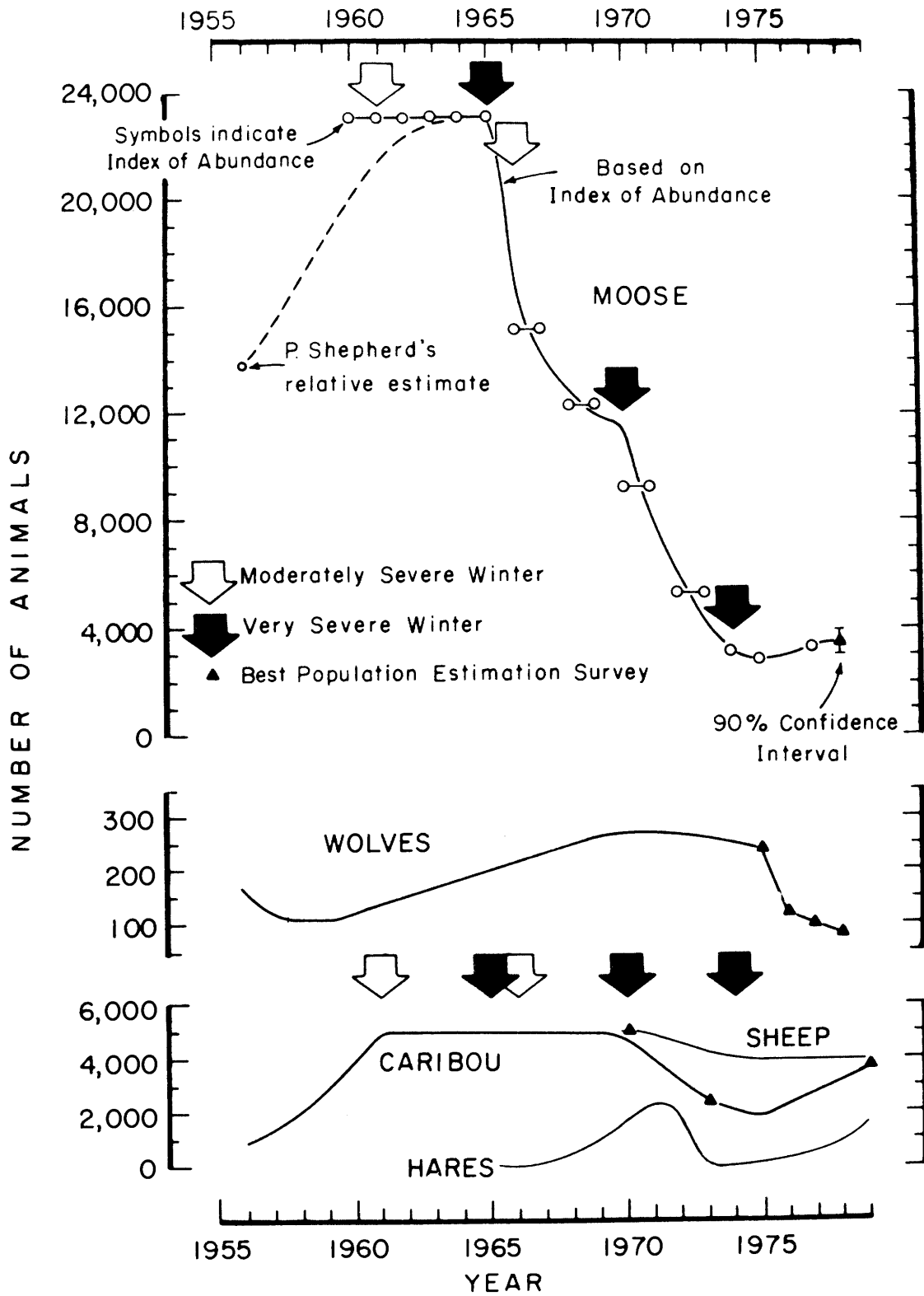


Fig. 2. Estimated number of moose, wolves, caribou, and sheep, and relative number of hares in experimental area in interior Alaska from 1956-79. Dotted line was not based on quantitative data and is used to indicate trend only.

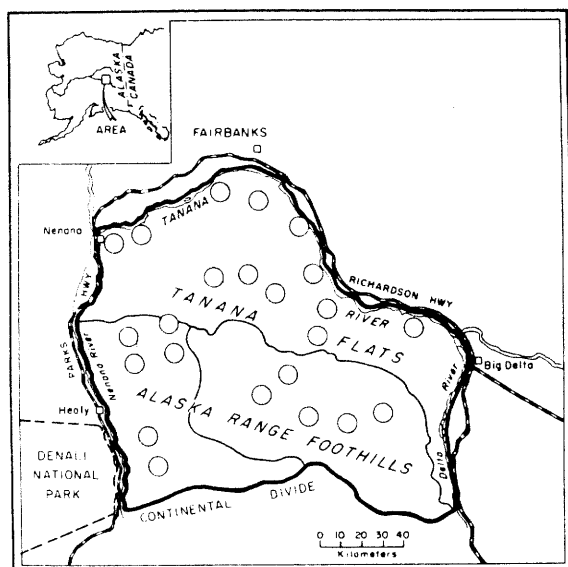


Fig. 3. General locations of 23 wolf packs observed during aerial surveys conducted Jan–Apr 1976. The 3 portions of experimental area used to evaluate moose calf survival with respect to varying levels of wolf reduction are shown.

by 1972 when we began wolf surveys with him as a pilot.

The early winter 1975 estimate of 239 wolves was based on 324 hours of aerial observation from January–March 1976 and was considered the most accurate estimate up to that time (Table 3). Estimates from 1972–74 probably underestimated the true population size because of incomplete coverage of the area (8–54 hours/survey). The early winter wolf population in the experimental area probably exceeded 239 from 1972–75; the best estimates used in Table 3 were taken from Fig. 2.

The wolf population in the experimental area was comprised of 23 packs during winter 1975–76 (Fig. 3). The average wolf pack territory size was calculated by dividing the wolf habitat (15,300 km²) by the number of packs. We assumed that all available habitat was occupied by exclusive territories (little or no overlap) and that lone wolves composed approximately 10% of the population as observed on Isle Royale (R. Peterson, unpubl. data) and in Minnesota (Mech 1973). The average pack territory was estimated to be about 665 km². Density in early winter 1975 was 1

Table 4. Approximate numbers of moose, caribou, and wolves in experimental area and corresponding prey/predator ratios. All population estimates are for early winter and originate from those in Fig. 2.

Date	No. of moose	No. of caribou	No. of wolves	Moose/wolf	Caribou/wolf
1963	22,600	5,000	170	129	29
1965	23,000	5,000	200	115	25
1967	14,500	5,000	230	61	22
1969	12,000	5,000	270	44	19
1971	8,000	4,000	270	30	15
1973	4,200	2,400	260	16	9
1974	3,100	2,100	250	12	8
1975	2,800	1,800	240	12	8
1976	3,000	2,300	125	24	18
1977	3,300	2,700	100	33	27
1978	3,500	3,100	80	44	39

wolf/64 km². The estimated average pack size was 9.3 wolves during early winter. The number of wolves was reduced by about 60% during winter 1975–76 and was maintained at a reduced level through 1979 (Table 3).

We wanted to retain a viable wolf population during the experiment by specifying a minimum number of 30–35 wolves that were to remain in the experimental area. This minimum number was 1 wolf/100 moose during early winter, but the ratios actually achieved were only 1 wolf/24–44 moose (Table 4).

Harvest of Wolves.—The wolf harvest rate doubled in the experimental area as a result of wolf removal beginning in 1975–76. In each of the 3 years before wolf removal, about 20% of the early winter wolf population was harvested, based on the best population estimate (Table 3). During the removal program, the early winter wolf population was harvested at rates of 38–61%, which caused an annual decline in the early winter population (Table 3).

Effectiveness of the wolf reduction program varied in different portions of the experimental area. Wolves were reduced most on the Tanana Flats and least in the western foothill-mountain area (Table 5). Low wolf density was desired on the Tanana Flats, the principal moose calving and summering area (Fig. 4); consequently, most reduction effort was exerted there.

Table 5. Number and density of wolves before (early winter 1975) and after (early winters 1976–78) wolf reduction in 3 portions of experimental area. Mean and standard error among years 1976–78 are given. The 3 areas are shown in Fig. 3.

	Number		Density	
	Wolves	SE	km ² of habitat/wolf	SE
Tanana Flats				
Before	120		61	
After	32	6	229	39
Eastern foothills and mountains				
Before	58		77	
After	31	5	144	26
Western foothills and mountains				
Before	61		58	
After	38	7	93	20

The number of wolves remaining in the foothills and mountains, especially in the western portion, was greater than intended throughout the removal period. Effective wolf removal in these areas was precluded by the absence of snow suitable for tracking wolves.

Productivity of Wolves.—Productivity declined between the mid-1960's and 1976 (Table 6). The average number of placental scars, corpora lutea, and fetuses/female ≥ 3 years of age were markedly lower in 1976 than in 1957–66 (Table 6, Rausch 1967). Rausch (1967) found only 2 resorbing fetuses in 40 pregnant females from interior Alaska whereas we found a greater proportion ($P < 0.05$) in 1976, with 2 resorbing fetuses in 5 pregnant females. The percentage of reproductively active females ≥ 2 years of age declined from 89% in Rausch's (1967) statewide sample to 71% (15 of 21) during 1976, although the difference was not significant ($P > 0.05$). Age structure of our wolf population also reflected a change in productivity; 39–60% ($\bar{x} = 43\%$) of the wolves killed during the 1960's in interior Alaska (Rausch 1967) were pups compared with 25–33% pups during winters 1975–76 through 1978–79 in the experimental area (Table 3). Age structure of the wolf population in winter 1975–76 indicated particularly low survival of the yearling co-

hort, which composed only 11% of the sample (Fig. 5).

Food Habits of Wolves.—Moose were the primary prey of wolves in the experimental area during winter, based on food remains in stomachs. Of 156 wolves trapped or shot in the experimental area from 1975–79, 55% of the stomachs contained moose, 12% caribou, 2% sheep, 3% snowshoe hares, 2% microtines and birds, and 26% were empty. Sheep were a minor prey species; sheep remains were found in only 5% of the 65 wolves that had food in their stomachs and were killed in or near sheep habitat.

Black and Grizzly Bear Population Status

There were no quantitative estimates of bear density or population size in the experimental area through the 1970's. Black bears were common during the 1970's on the Tanana Flats, where moose calve, and were rare in the mountainous portion of the area. Between May and August from 1975–79, approximately 5–20 sightings of black bears were made annually in 50 to over 100 hours of low flying on the Tanana Flats. Grizzly bears were rarely observed on the Tanana Flats but were frequently seen in the mountainous areas used by many moose during fall and winter. We have seen only 1 grizzly on the Flats in 10 years, whereas 8–12 grizzly observations were made per year during studies of moose and caribou in the foothills and mountains. A grizzly density of about 1 bear/65 km² was estimated for the eastern foothill-mountain portion of the experimental area in 1982 using a capture and mark method (H. Reynolds, unpubl. data). This density is moderate for interior and northern Alaska, where density ranges from 1 bear/40 km² to 1 bear/120 km² (Reynolds 1976, 1980; Miller and Ballard 1982).

Moose Population Status

Population Size and Trend.—Moose increased in the late 1950's (Bishop and

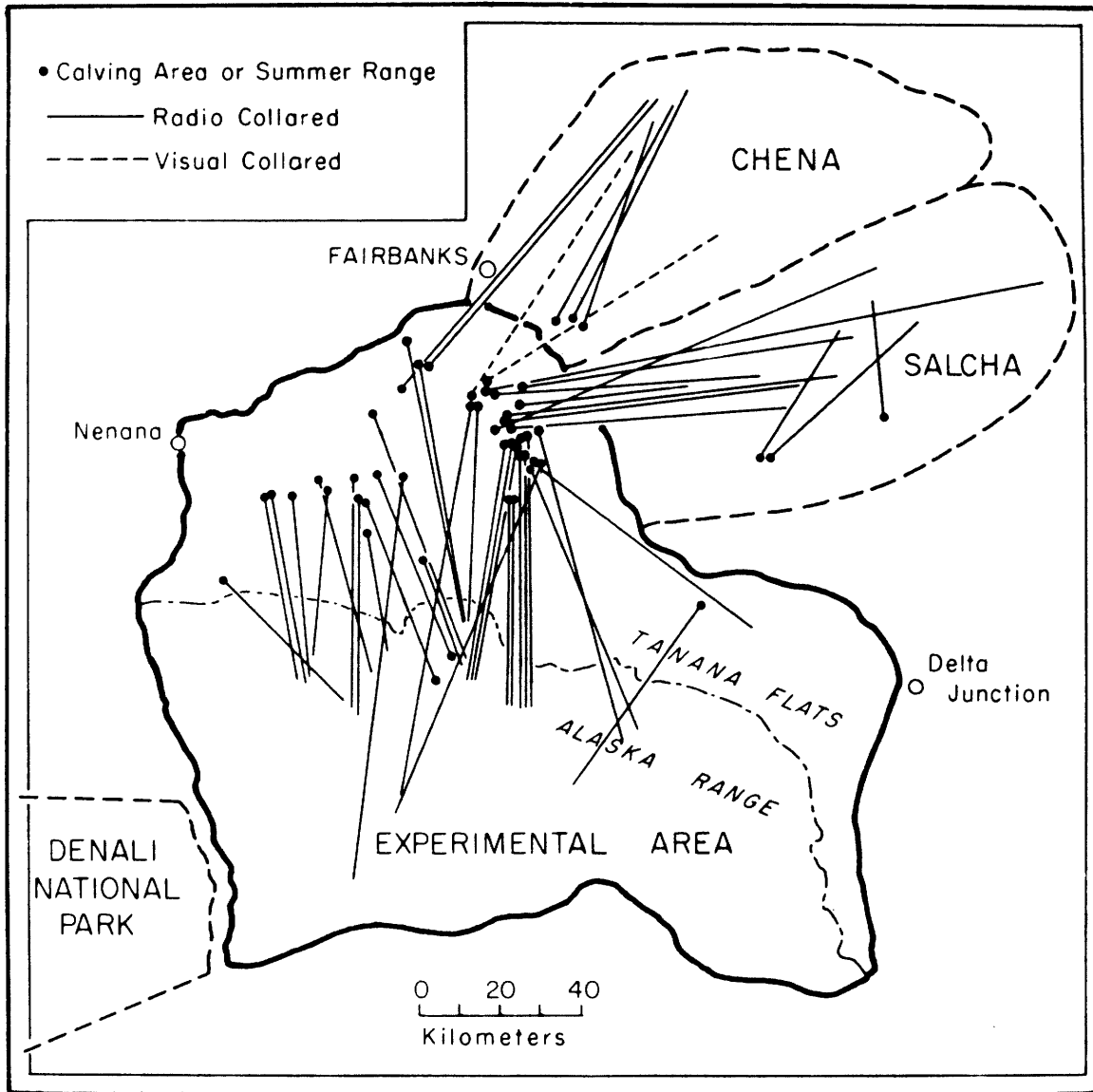


Fig. 4. General migratory patterns of male and female adult moose collared within experimental area and 2 control areas (Chena and Salcha). Each line represents the movements of individual moose during 1–4 years of monitoring. Wintering areas are near undotted ends of the lines.

Table 6. Indicators of productivity in female wolves ≥ 3 years old in interior Alaska.

Area and year	Placental scars			Corpora lutea			Fetuses		
	No. of wolves	\bar{x}	95% CI	No. of wolves	\bar{x}	95% CI	No. of wolves	\bar{x}	95% CI
Interior Alaska ^a									
1957–66	45	7.1		56	6.8		18	6.6	
Experimental area									
1976–79	7	4.3	± 0.9	9	5.4	± 0.8	5	4.6	± 0.7

^a Data from Rausch (1967). Rausch's interior Alaska study area included our entire study area plus additional land.

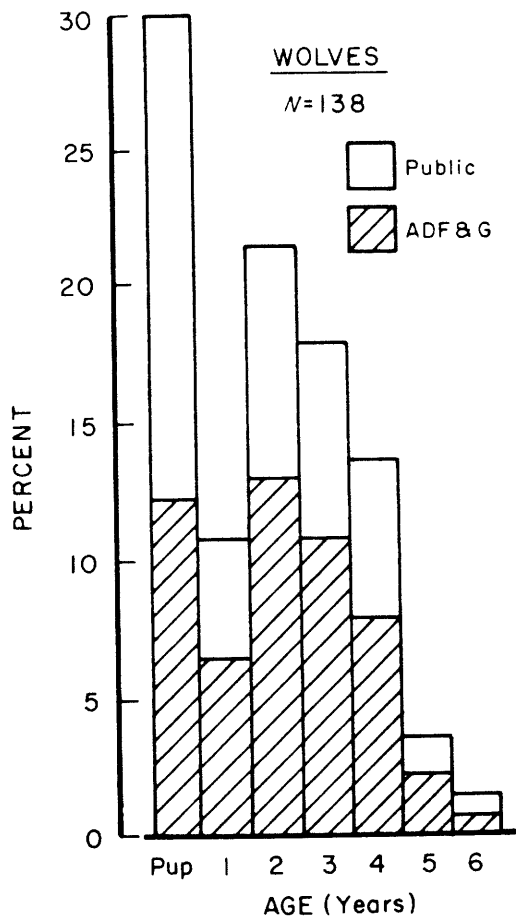


Fig. 5. Age distribution of wolves killed in experimental area during winter 1975-76.

Rausch 1974) and peaked in the early 1960's (Fig. 2). Little quantitative data were collected in the 1950's; therefore, the 1950's portion of the moose abundance curve (Fig. 2) indicates only trend. Personnel conducting surveys in the 1950's (S. Olson, P. Shepherd, and R. Tremblay, pers. commun.) agreed that moose were relatively abundant in the experimental area during the mid-and late 1950's. Further, a small portion of the experimental area (the Salchaket moose count area in the Tanana Flats) was surveyed for moose in 1957 and 1958 and 37 and 69 moose/hour were seen, respectively. These values are in the range of moose/hour observed during the 1960's (Appendix 1) and indicate that moose were abundant. The only

Table 7. Index of moose abundance from aerial surveys and extrapolated number of moose in experimental area.

Year	Index of moose abundance	Extrapolated no. of moose
1960-65	8.2	23,000
1966-67	5.4	15,100
1968-69	4.4	12,300
1970-71	3.3	9,200
1972-73	1.9	5,300
1974	1.1	3,100
1975	1.0	2,800
1977	1.2	3,300
1978	*	3,500 ^b

* Sampling procedures were not comparable to other years.

^b 90% confidence interval = ± 460 .

population estimation survey from the 1950's that included any of our experimental area resulted in a density estimate of 0.12 moose/km² (Olson 1956). However, it is erroneous to conclude that moose were relatively scarce in our experimental area based on that survey (S. Olson and R. Tremblay, pers. commun.). About one-half of the survey covered a portion of the Tanana Valley outside the experimental area that has historically contained a lower density of moose than the experimental area. The moose density estimate from the survey was an underestimate because the survey was superficial, was not corrected for moose missed, and had as a primary objective the estimation of relative abundance of large and small game species and map habitat (S. Olson and R. Tremblay, pers. commun.).

Projected moose numbers suggested a peak at approximately 23,000 (1.5/km²) in the early 1960's (Fig. 2) and a subsequent decline to approximately 2,800 (0.2/km²) in 1975 based on an index of abundance (Table 7) (see Methods for qualifications on precision). The index was based on moose seen per hour of survey (Appendix 1). The projected peak moose density was similar to peak densities in the Nelchina and Susitna basins in Alaska during the late 1950's (W. Ballard, unpubl. data) and on the Kenai Peninsula, Alaska in the early 1970's (Bailey 1978). Also, many other Alaskan moose populations apparently peaked at comparable high densities

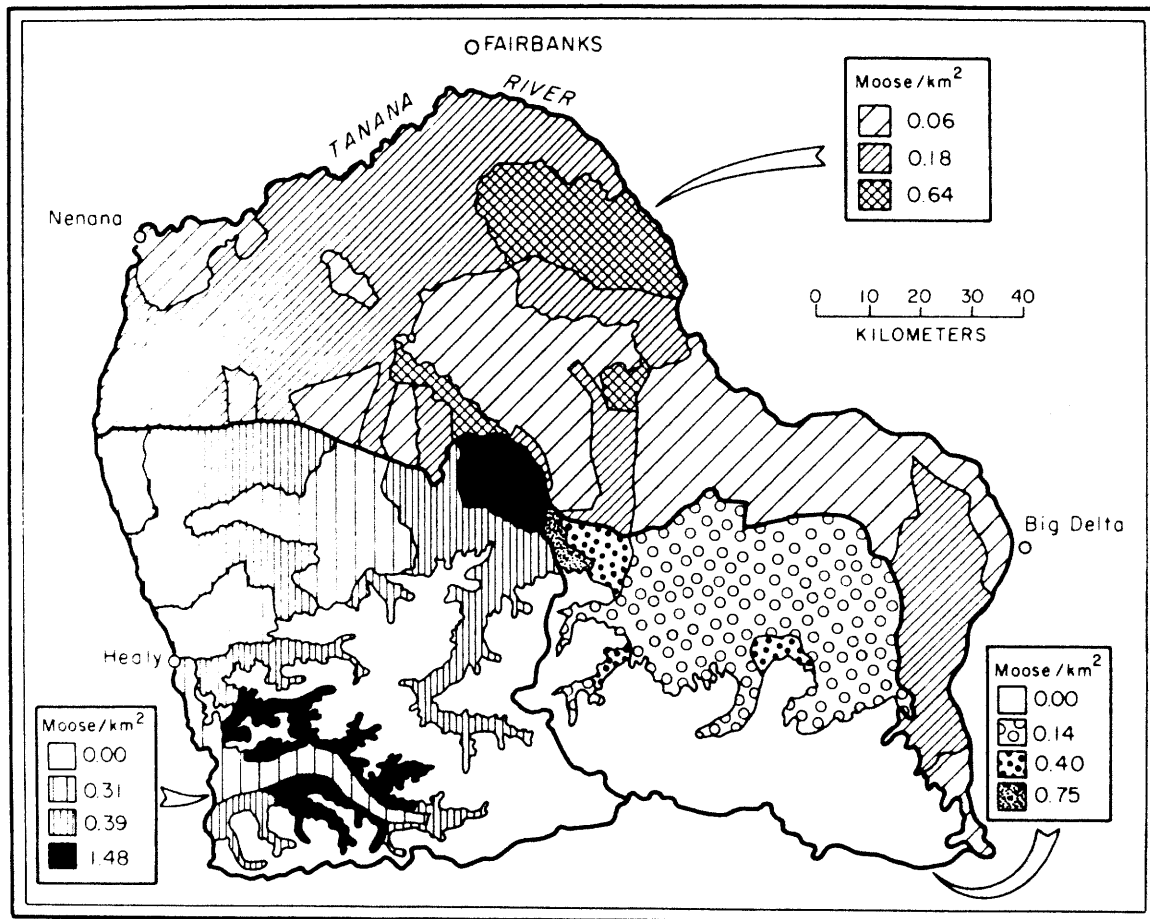


Fig. 6. Density of moose in 3 portions (delineated by heavy lines) of experimental area during the Nov 1978 population estimation survey.

in the 1960's and early 1970's; however, densities were not quantitatively estimated.

Numbers of moose began to increase in the experimental area during 1976. In 1978, $3,500 \pm 13\%$ (90% CI) moose were estimated; densities ranged from 0.06–1.48/km² among strata (Fig. 6). In November 1982, after completion of this study, moose abundance was estimated in the Tanana Flats portion of the experimental area (first population estimate since 1978). We include this estimate to show the sustained growth of the moose population in that area. Numbers of moose increased significantly (*t* test, $P < 0.01$) from $1,306 \pm 17\%$ in 1978 to $3,233 \pm 34\%$ (90% CI) in 1982, an exponential rate (*r*) of 0.23.

The survey method was similar to that used in 1978, except in 1982, sightability of moose was estimated during the survey (Gasaway et al. 1981) and the variance of the sightability estimate was included in the variance used to calculate the CI.

Movements of Moose.—Within the experimental area there were both migratory and nonmigratory moose. Migratory radio-collared bull and cow moose typically moved in February–April to the Tanana Flats where cows calved. They remained there during summer and returned during August–October to adjacent hills and mountains (Fig. 4). Many of these migrant radio-collared moose wintered outside the experimental area in adjacent Chena and Salcha control areas.

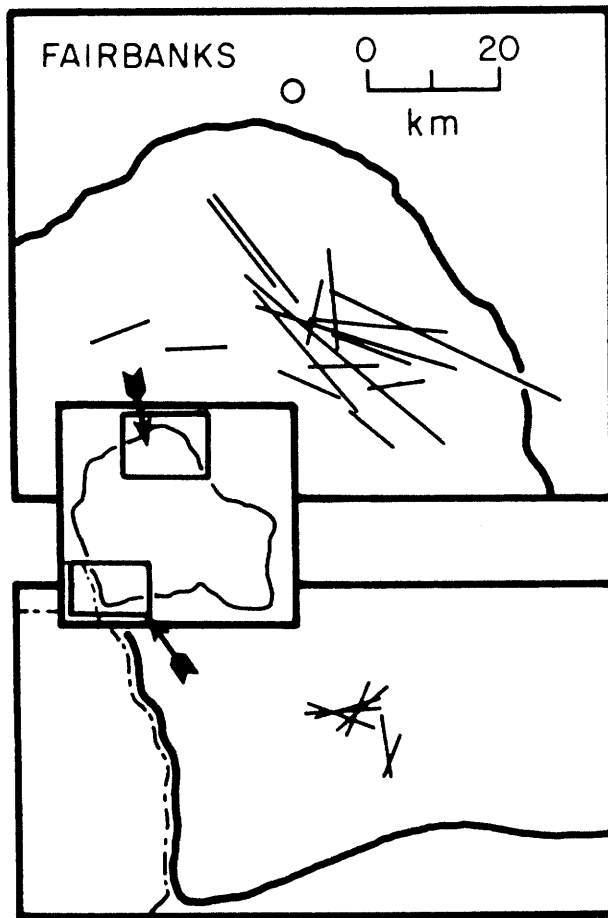


Fig. 7. Home range lengths and general locations of nonmigratory male and female adult moose radio-collared in experimental area. Each line represents the long axis of individual home ranges during 1-4 years of monitoring.

Nonmigratory moose (those making short seasonal movements within a physiographic area) were common on the Tanana Flats and southwestern mountains (Fig. 7); however, they occurred less commonly in other areas. During spring and summer, seasonal migrants probably increased the density on the Tanana Flats 2- to 4-fold over the density of residents. The resident density in 1978 is approximated by the early winter density (Fig. 6).

Production and Mortality of Calves.—

Ninety percent of the births occurred between 15 May and 1 June with a median calving date of 21 May (Fig. 8). Estimated birth rates were 111 and 116 calves/100 females ≥ 24 and 36 months of age at par-

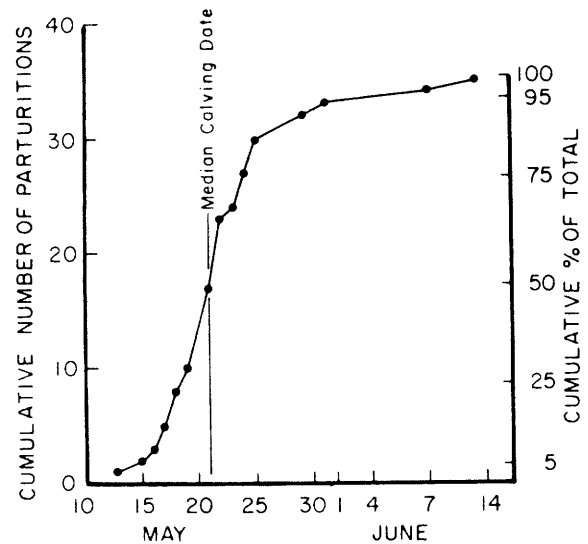


Fig. 8. Chronology of parturition for 35 radio-collared cow moose in experimental area, 1977 and 1978.

turition, respectively. Birth rates were calculated by multiplying 1.32 (32% of 35 parturient, radio-collared cows produced twins during 1977 and 1978) times the percentage of pregnant females in 1975 (Table 8).

Chronology of moose calf mortality is shown by survival curves of calves produced by radio-collared cows from 1973-78 (Fig. 9). Most deaths occurred during late May, June, and July. High calf mortality during summer was substantiated by the consistently lower calf/cow ratios obtained from early winter aerial surveys in the experimental area (Table 9) compared to the estimated birth rate for these cows (116 calves/100 cows ≥ 36 months of age).

All indices of calf and yearling moose survival abruptly increased in the experimental area beginning in 1976. This increased survival coincided with the re-

Table 8. Pregnancy rate of cow moose captured and collared 8-14 May 1975 in experimental area.

Age (months)	N	Percent pregnant
≥ 24	55	84
≥ 36	52	88
≥ 48	48	94

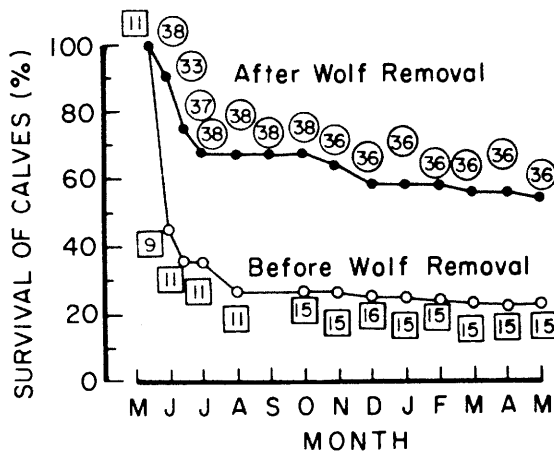


Fig. 9. Percent survival of calves associated with radio-collared cow moose in experimental area. Observations between Oct 1973–Aug 1975 were before wolf reduction, whereas those from Aug 1976–Oct 1978 were after the reduction. Total numbers of calves followed are in circles and squares.

duction of wolves. During summers 1976–78, survival of calves of radio-collared cows was more than twice that during summers of 1974–75 (Fig. 9). Improved calf survival during summer was substantiated by 2- to 3-fold increases ($P < 0.01$) in calf/cow ratios in early winter 1976–79 compared to the period 1973–75 prior to wolf reduction (Table 9). Improved calf survival resulted in an average of 500 more calves present during November 1976–78 than during November 1973–75 (Table 10). Twin abundance increased during early winter 1976 (Table 9) and was negatively correlated with wolf abundance (Fig. 10). Cohorts from 1976 and later survived well (at least up to 18 months of age) following the reduction of wolves, and yearling/cow ratios increased 2- to 4-fold ($P < 0.01$) over levels observed from 1973–75 (Table 9, Fig. 9).

However, calf survival did not increase uniformly throughout the experimental area from 1976–78 (Table 11). The greatest increase occurred on the Tanana Flats and the least in the western foothills and mountains. Calf and yearling recruitment in the 3 portions of the experimental area (Table 11) were negatively correlated with wolf density, $r = -0.896$ ($P < 0.02$) and $r = -0.768$ ($P < 0.1$). Calves produced in

this western area were subjected to greater year-round predation than were calves in other portions of the experimental area, in part because this area supported the highest densities of wolves (Table 11) and grizzly bears and because many moose remained in the area year-round rather than migrating to the Tanana Flats to calve (Fig. 7).

Among control areas, calf survival improved significantly ($P < 0.01$) in adjacent areas influenced by the wolf reduction in the experimental area (Fig. 11). A significant number of moose migrated seasonally to the Tanana Flats from adjacent (Chena, Salcha, and Delta) control areas. The migrants produced and reared calves on the Tanana Flats and returned with the calves to the control areas during fall (Fig. 4) where they were counted in November surveys (Fig. 11). Hence, the migrants' calves had a greater chance of surviving in summer after wolf reduction in the experimental area. No increase in calf/cow ratios was found in 3 control areas (Denali National Park, Fortymile, and Tok) that had no known seasonal interchange of moose with the experimental area (Fig. 11).

Snow depth profoundly influenced the survival of cohorts during their first year. Recruitment to 12 months of age declined as the snow index increased (Fig. 12). Winters 1965–66, 1970–71, and 1974–75 had the greatest snow depth, with record snowfall occurring during winter 1970–71 (Fig. 13). During winters 1965–66 and 1970–71, calf mortality was very high as demonstrated by the relative scarcity of 1965 and 1970 cohorts in the sample of hunter-killed cow moose (Fig. 14), by low yearling/100 female counts for that cohort (Table 9), and by Bishop and Rausch's (1974) and our observations of many dead moose. Winter 1974–75 had less influence on calves of the year than the other 2 severe winters, despite the low yearling/cow ratios for the 1974 cohort (Table 9); we observed no unusual level of mortality during field work in winters 1974–75, and the overwinter decline in calf/cow ratio was similar to that in the 2 preceding win-

Table 9. Offspring/cow ratios for 1956–79 cohorts from 6–18 months of age, as determined from aerial moose surveys in experimental area. *N* equals total number of moose classified.

Birth year for cohort	Age of cohort in months						
	6			12		18	
	<i>N</i>	Calves/100 cows ≥ 30 months old	Twins/100 cows with calves	<i>N</i>	Yearlings/100 cows ≥ 36 months old	<i>N</i>	Yearlings/100 cows ≥ 30 months old ^a
1956	221	58 ^b					
1957	74	39				194	54
1958	194	54	14			180	36
1959	180	58	26			1,250	44
1960	1,250	45	5	2,055	34 ^c		
1961† ^d				1,403	26 ^{c*}		
1962	1,066	48	6			1,244	28
1963	1,244	50	6				
1964				501	26 ^c	1,728	12
1965‡	1,728	26	1	1,754	9 ^c	2,971	4
1966‡	2,971	18	3	420	12	528	16
1967	528	27	1			897	22
1968	897	43	5	477	29	1,254	32
1969	1,254	49	4	516	41	888	16
1970‡	888	31	2	449	6	1,669	6
1971	1,669	28	4	711	18	1,133	18
1972	1,133	33	2	885	23	1,317	13
1973	1,317	24	4	586	13	629	5
1974	629	19	0	374	8	602	10
				After wolf reduction for yearlings			
1975	602	15	0	163	25 ^{§*}	362	32 ^{§*}
	After wolf reduction for calves						
1976	362	51 [†]	8	280	44	700	44
1977	700	49	9	351	37	403	50
1978	403	61	14	399	36	316	52
1979	316	57	11	280	53		

^a Yearling males are doubled to estimate total yearlings.

^b Data from 1956–59 from Bishop and Rausch (1974).

^c Pooled data from repetitive surveys were used.

^d Cohorts experiencing severe winter weather during their first year are indicated as follows: † deep snow unaccompanied by inconspicuous mortality, and ‡ deep snow accompanied by conspicuous mortality.

^e The proportion of 24-month-old females was based on early winter survey data from 2 years previous because of missing data from previous year.

[†] Ratios after wolf removals are significantly different ($P < 0.01$) from ratios 3 years before wolf removal.

[§] Wolf removal began when the 1975 cohort was about 8 months old.

ters with average snowfall (Table 9, Fig. 13). Additionally, only 1 of 6 calves accompanying radio-collared cows in October 1974 died during winter. Most mortality of the 1974 cohort probably occurred prior to winter as suggested in Fig. 9. Moderately severe winters occurred in 1961–62 and 1966–67; however, only the 1966 cohort was markedly affected (Fig. 12, 14). Snow depths experienced by cows while pregnant had no apparent effect on calf abundance the following fall ($r = -0.239$, $P > 0.1$).

Because snow depth affects calf surviv-

al, the possible effect of snow must be minimized to determine whether wolf removal and increased calf survival were correlated. Recruitment to 12 months for cohorts produced after wolf removal (1976–78) was well above recruitment for previous cohorts experiencing winters of similar severity (Fig. 12), thus strengthening the correlation between wolf removal and improved recruitment.

Mortality of Adult Moose.—Natural mortality rates (excluding man-caused mortality) of adult moose declined following the reduction in wolf density in 1976.

Table 10. Estimated production and survival of moose calves relative to wolf abundance in experimental area, 1963–78.

Year	Moose population (Nov) ^a	Cows ≥24 months old (May) ^b	Calves		Wolves (Nov) ^e	Calves produced/wolf	Calves surviving/wolf (Nov)	Percent calves surviving (Nov) ^d
			Produced (May) ^c	Surviving (Nov) ^d				
1963	22,600	9,000	10,000	4,500	170	59	26	45
1965	23,000	12,700	14,100	3,400	200	71	17	24
1967	14,500	7,400	8,200	2,000	230	36	9	24
1969	12,000	5,600	6,200	2,700	270	23	10	44
1971	8,000	4,700	5,200	1,300	270	19	5	26
1973	4,200	2,400	2,700	600	260	10	2	22
1974	3,100	2,000	2,200	400	250	9	2	18
1975	2,800	1,700	1,900	300	240	8	1	16
1976	3,000	1,300	1,400	700	125	11	6	50
1977	3,300	1,600	1,800	800	100	18	8	44
1978	3,500	1,800	2,000	1,100	80	25	14	55

^a Values are estimates in Fig. 2.

^b [Population estimate × (% cows in sample minus % yearling bulls in sample)].

^c [(No. cows ≥24 months old) × (1.11 calves/cows)].

^d [(Calves/100 cows ≥24 months old seen during aerial surveys) × (estimated no. cows ≥24 months old) ÷ 100].

^e Values are estimates in Fig. 2 and Table 3.

^f [(No. calves surviving ÷ no. calves produced) × 100].

The annual natural mortality rate for all radio-collared moose was 20% in the 3 years before wolf removal and 6% for the 3 years after wolf removal (Table 12). These values are the sum of natural mortalities from all sources. To more accurately assess the impact of wolf predation,

a comparison of age-specific mortality was required because age structure differed between periods. This analysis showed that death rates were lower for middle-aged and old moose after wolves were reduced in 1976 (Table 13).

Wolf predation was the primary natural cause of death for adult moose from 1973–75. All radio-collared moose dying of natural causes during this period were known or probable wolf-kills (Table 12). Sixteen of 18 additional moose found dead during these winters were known or probable wolf-kills. Fat in femur marrow from wolf-killed moose averaged 78% (SE = 6, range 39–98, $N = 12$), indicating none was near death from undernutrition, i.e., about 10% marrow fat (Franzmann and Arneson 1976).

High rates of natural mortality among middle-aged and old moose resulted in a rapid change in population age structure and a rapid decline in moose between 1972 and early 1976. During 1972–74, 41% of the cows were estimated to be ≥11 years of age (Table 14), and approximately 40% of these animals were dying annually (Table 13). A mean age of 11 years for 18 adults found dead during winters 1973–74 and 1974–75 also indicated high mortality among old moose. With the large

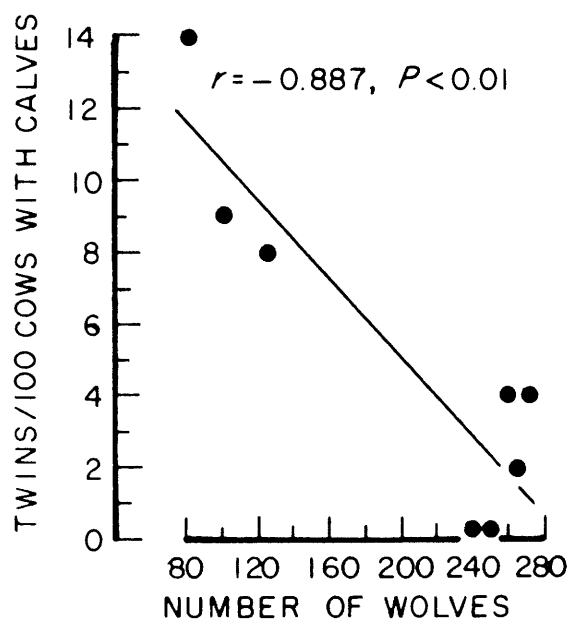


Fig. 10. Correlations between number of wolves and twin moose calves/100 cows with calves in experimental area (1971–78).

Table 11. Moose calf survival indices and wolf density within 3 portions of experimental area before (1975) and after (1976–78) wolf reduction. The 3 areas are shown in Fig. 3.

		Calves/100 cows ≥30 months old		Yearlings/100 cows ≥30 months old		Wolf density (km ² of habitat/wolf)	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
Tanana Flats	Before	25		17		61	
	After	65	4	59	5	229	39
Eastern foothills and mountains	Before	9		7		77	
	After	45	6	25	10	144	26
Western foothills and mountains	Before	0		7		58	
	After	18	7	11	2	93	20

cohorts produced in the early 1960's (Table 10, Fig. 14) rapidly disappearing (Table 13), the age structure became weighted toward young and middle-aged cows by 1976 (Table 14). Additional support that this rapid change did occur comes from a modeled population; similar changes in age structure were produced in 3 years using age structure, recruitment, and mortality estimates from our study (Fig. 14; Tables 9, 13).

Hunting had its greatest impact on the

moose population from 1970–74 (Table 15). Beginning in 1970, the number of moose and the percentage harvested by hunters rapidly escalated because of increased numbers of hunters, improved access, and increased use of snow machines and aircraft. Rapidly rising meat prices and a beef shortage also resulted in increased hunting effort, and we estimated that 19% of the moose population was harvested in 1973. In 1974 the hunting season was shortened from 100 to 52 days with a

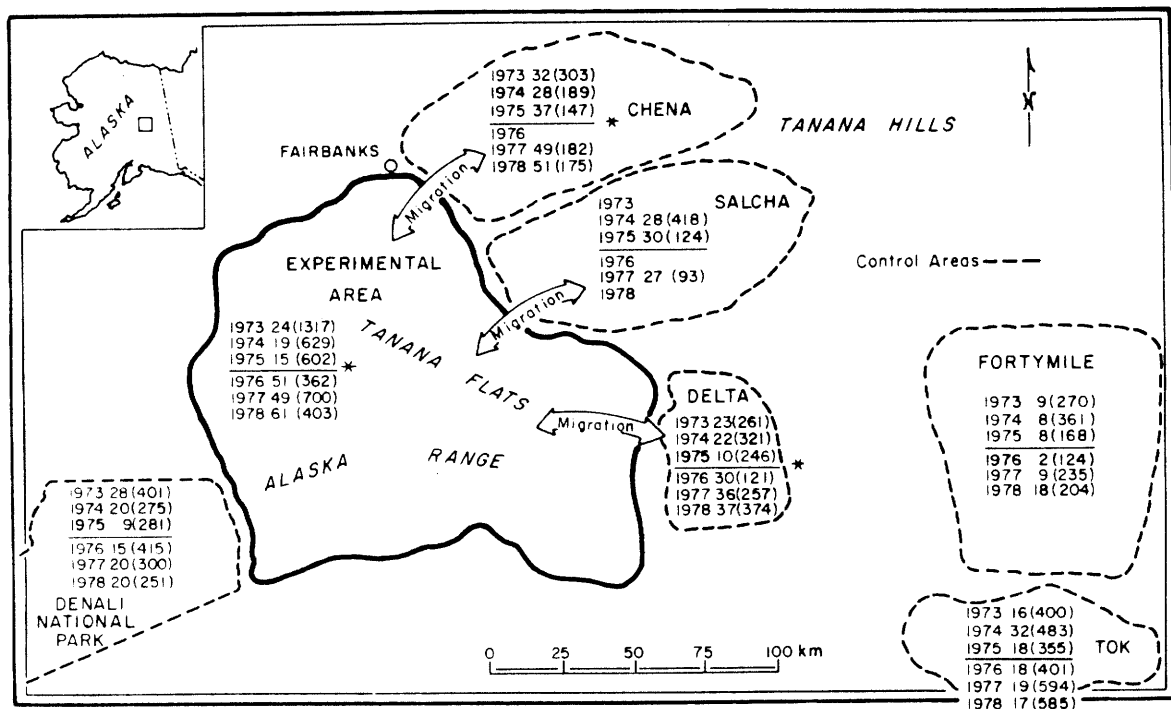


Fig. 11. Calves/100 cow moose ≥30 months of age in early winter in experimental area and 6 control areas. Ratios before (1973–75) and after (1976–78) wolf reduction are separated by a solid line, and significant differences ($P < 0.01$) between the before and after ratios are indicated by asterisks. Number of moose classified is in parentheses. Denali National Park data were from Haber (1977) for 1973 and W. Troyer's count areas 13–17 for 1974–78 (National Park Service files).

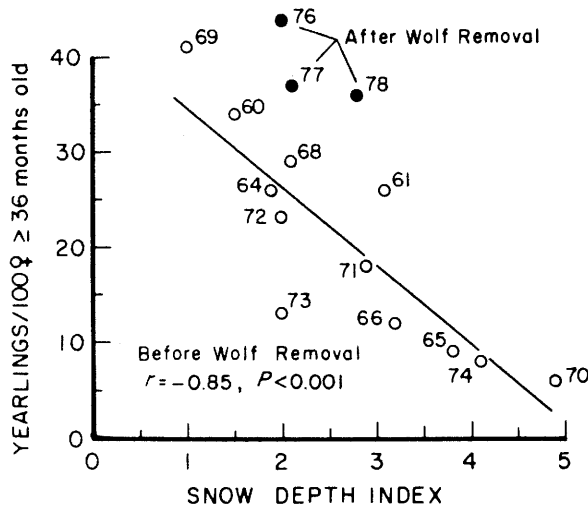


Fig. 12. Correlation between snow depth index and yearlings/100 cow moose ≥ 36 months old during May in experimental area for cohorts before and after wolf removal. Year is indicated next to points.

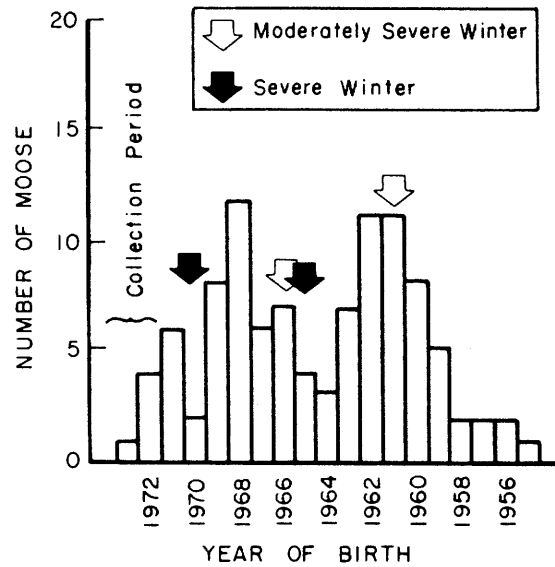


Fig. 14. Relative cohort size of cow moose in experimental area, based on 102 moose killed by hunters during 1972–74.

bag limit of 1 moose of either sex. After 1974, a 10-day, bulls-only season resulted in small annual harvests (Table 15).

Remains of adult moose dying from natural causes other than predation were conspicuous only during winters 1965–66 and 1970–71 (Bishop and Rausch 1974). However, there were no accurate data on adult mortality rates during either winter.

Moose Habitat Quality and Quantity.—At peak abundance during 1960–65, moose may have been near range carrying capacity. Heavy browsing reduced plant vigor and killed willows (*Salix* spp.) in areas where moose concentrated (P. Shepherd and O. Burris, pers. observ.). High moose density and reduced browse avail-

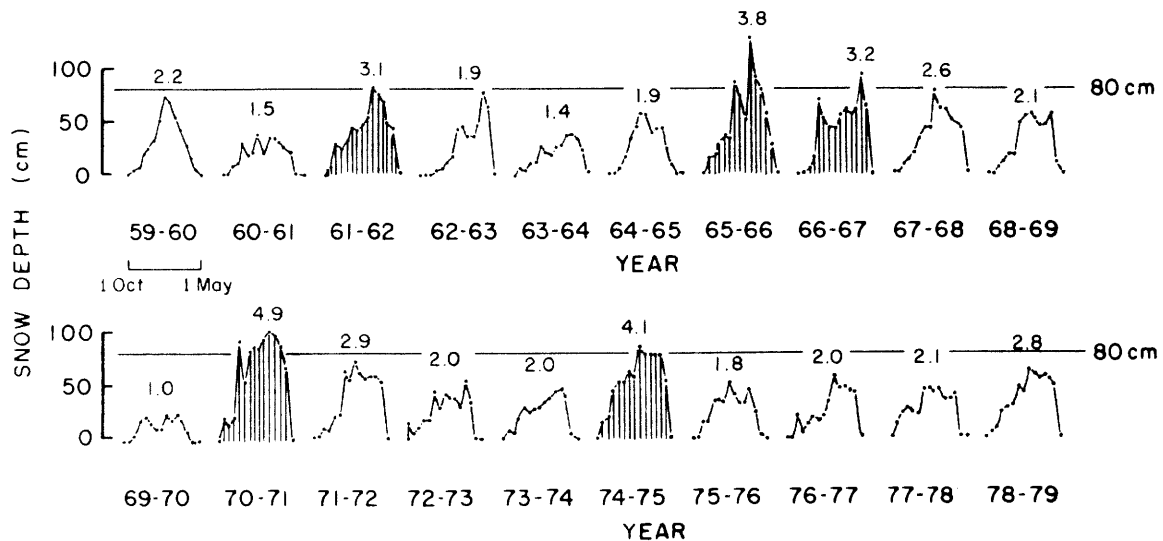


Fig. 13. Snow depth on the ground during winters 1959–60 through 1978–79 at Fairbanks, Alaska. Curves are constructed from snow depth measurements on the first and fifteenth of each month. Snow depth index (shown above each curve) was calculated by dividing the area under each curve by the area of winter of lowest snowfall, 1969–70. Snow depth of 80 cm, indicated by the solid line, is considered the critical depth for calf moose survival (Coady 1974a). Severe winters are shaded.

Table 12. Seasonal mortality rates of radio-collared adult moose in experimental area before (1973–75) and after wolf reduction (1976–78). Number of radio-collared moose dying are in parentheses.

	No. of individual moose	No. moose- summers or moose-winters ^a	Percent mortality			Total
			Shot	Wolf predation	Unknown natural	
May–Sep (summer)						
Before	22	12.8	0	0	0	0
After	29	44.8	0	0	2 (1)	2 (1)
Oct–Apr (winter)						
Before	33	34.7	6 (2)	20 (7)	0	26 (9)
After	29	54.2	0	2 (1)	2 (1)	4 (2)

^a One moose-summer or moose-winter is equal to observing 1 radio-collared moose for 1 entire seasonal period. Fractional time periods were caused by radio transmitters failing or moose being radio-collared for only a part of a seasonal period. METHODS section describes calculation of numbers of moose-periods.

ability probably contributed to the extensive die-off during the severe winter of 1965–66 (Bishop and Rausch 1974).

Limited data suggest that habitat did not limit the moose population following the precipitous decline from 1965–67. Browse quality and/or quantity were adequate for moose calves to survive well during 1968 and 1969 as indicated by calf/cow ratios and by yearling/cow ratios the following years (Table 9). Browse utilization studies on the Tanana Flats during the early 1970's indicated low to moderate browsing rates on the annual production of preferred willow and other woody moose food (Coady 1974b). After winter, Coady assigned plants to relative browse utilization classes 0 through 3, which corresponded to 0, 1–33, 34–66, and 67–100% browsing on twigs produced during the previous growing season. Five preferred *Salix* species had an average browse rank

of only 1.3 (SE = 0.1, range 1.0–1.6) while 5 other species of willow averaged 0.5 (SE = 0.2, range 0–1.0). Balsam poplar (*Populus balsamifera*), quaking aspen, and paper birch were also lightly browsed with mean ranks of 1.0, 0.4, and 0.4, respectively.

Caribou Population Status

Population Size and Trend.—Numbers of caribou in the experimental area fluctuated greatly during the past 30 years (Fig. 2). Although scarce during the late 1940's and early 1950's (Scott et al. 1950, Olson 1957), caribou rapidly increased during the late 1950's (Olson 1957, 1958) and through the mid-1960's (Skoog 1963, 1968). P. Shepherd observed approximately 1,500 and 3,000 caribou in 1957 and 1959, respectively, and between 1963 and the late 1960's approximately 5,000

Table 13. Natural age-specific minimum annual mortality rates of radio-collared moose in the experimental area before (1973–75) and after (1976–78) wolf reduction. Number of radio-collared moose dying are in parentheses.

Age (years)	Before wolf reduction			After wolf reduction		
	No. of moose ^a	Moose-years of observations ^b	Percent mortality	No. of moose ^a	Moose-years of observations	Percent mortality
1–5	6	5.6	0	14	12.2	0
6–10	7	6.0	33 (2)	33	28.5	7 (2)
≥11	9	7.4	41 (3)	5	4.7	21 (1)

^a Individuals were counted as a new moose when they increased in age by 1 year. Actual number of different moose was 19 before and 27 after wolf reduction.

^b One moose-year is equal to observing 1 radio-collared moose for 1 year. Fractional time periods were caused by moose being monitored for periods other than whole years.

Table 14. Percentage of cow moose ≥ 11 years of age in samples of cows from experimental area.

Year of sampling	Cows in sample	Percent ≥ 11 years old
1972-74	102 ^a	41
1975	55 ^b	25
1976	26 ^b	19

^a Killed by hunters.^b Immobilized during study.

caribou resided year-round in the southern half of the experimental area and the Macomb control area (Skoog 1968). The herd was thought to have begun a decline about 1970. A population estimate in 1973 indicated 2,400 caribou; in early 1976, the herd numbered approximately 1,500–2,000 based on less rigorous aerial surveys and extrapolations from recruitment rates. The population probably began to increase when recruitment increased during 1976. This change coincided with wolf removal and began 3 years after hunting ended. By 1979 the herd numbered 3,700–4,000.

In contrast, the Macomb and Denali herds in adjacent control areas were stable following wolf reduction in the experimental area from 1976–79. The Denali herd declined from about 8,000 in 1966 to 1,500 by 1972 (Haber 1977) and remained near that level (1,200–1,500) through 1979 (Davis 1980). The Macomb herd numbered 700–800 from 1976–79 (Davis 1980).

Mortality of Calves.—Declining caribou calf/cow ratios in the experimental area indicated that calf mortality during summer and fall progressively increased from 1970–74 (Fig. 15, complete data in Appendix 2). By 1974, virtually all calves died prior to winter. The possibility of reduced natality as opposed to increased mortality during this period was considered and rejected because adjusted data on the occurrence of distended udders indicated that birth rates were high from 1974–79 (Table 16) (Davis and Preston 1980). Distended udder counts during calving and mid-June of 1978 and 1979 allowed calculation of a correction factor

Table 15. Estimated number of moose harvested in relation to estimated population size within experimental area.

Year	No. of moose pre hunting ^a	No. harvested	Percent females in harvest	Percent population harvested
1963	22,900	302	31	1
1964	23,300	274	26	1
1965	23,300	335	22	1
1966	17,200	216	24	1
1967	14,300	299	40	2
1968	13,000	377	31	3
1969	12,400	376	29	3
1970	11,800	449	33	4
1971	8,500	483	30	6
1972	6,700	699	41	10
1973	5,200	964	51	19
1974	3,600	489	47	14
1975	2,900	63	0	2
1976	3,100	62	0	2
1977	3,400	50	0	1
1978	3,600	80	0	2

^a Estimated by adding number of moose harvested to early winter population estimate from Fig. 2 and rounded to nearest 100 moose.

for udders that had regressed by mid-June of 1974–79 when regular surveys were conducted (Table 16). Bergerud (1964) demonstrated the validity of distended udder counts as an index of natality.

Calf survival improved markedly ($P < 0.01$) in the experimental area beginning in 1976 after wolf reduction (Fig. 15). Calf recruitment to 6 months of age from 1972–78 was negatively correlated ($P < 0.01$) with the number of wolves (Fig. 16) and positively correlated with the caribou/wolf ratio in Table 4 ($r = 0.797$, $P < 0.05$, $N = 7$). Increases in calf survival in the 2 adjacent control areas during 1976 were small ($P > 0.1$), unlike the increase ($P < 0.01$) in the experimental area; however, during the 4 years after wolf reduction, calf survival did increase significantly ($P < 0.01$) in control areas, although not as dramatically as in the experimental area (Fig. 15). Therefore, wolf reduction appeared to increase calf survival.

Harvest by Hunters.—High exploitation was a major factor causing the precipitous decline of the herd during the early 1970's. Estimated harvest rates ranged from 7–19% of the postcalving population from 1970–73 (Table 17). The

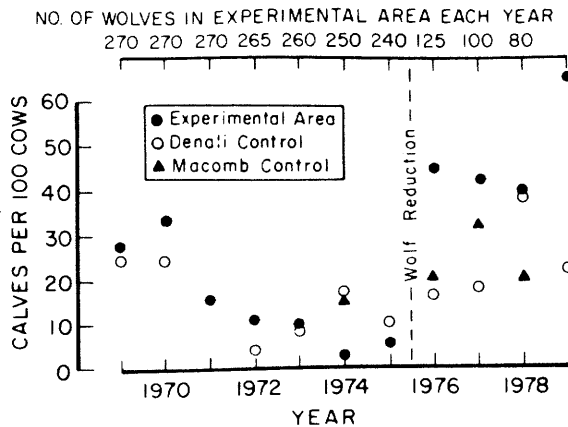


Fig. 15. Calves/100 cow caribou in experimental and 2 control areas in relation to wolf removal in experimental area.

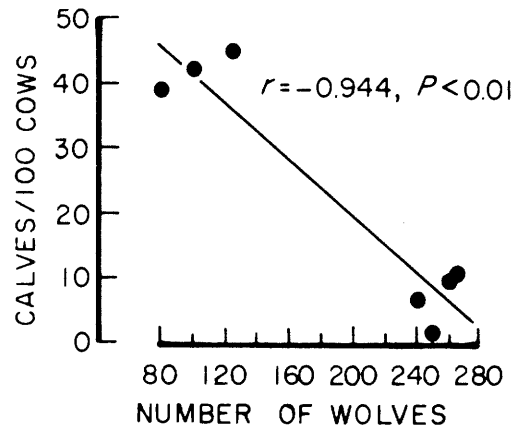


Fig. 16. Correlation between numbers of wolves and calves/100 cow caribou during early winter in experimental area (1972-78).

high harvests in 1971-73 exceeded the low recruitment and accelerated the population decline through 1973 when hunting was stopped. However, hunting contributed less to the decline than did low recruitment.

Sheep Population Status

Population Size and Trend.—Sheep population size in the experimental area apparently fluctuated relatively little from

1969-79. Although no quantitative data existed prior to 1970, hunting guides with long experience in this area believed that sheep were at least as abundant during the 1960's as in 1970, the year of the only complete aerial survey. During that survey, 4,142 sheep were counted (Heimer and Smith 1975). When multiplied by a sightability correction factor of 1.3, these data suggest that approximately 5,000 sheep were present. From 1970-75, the number of sheep slowly declined and remained stable from 1976-79 (Heimer 1981, Fig. 2).

Mortality of Lambs.—Lamb production and/or survival varied between 1969-79 in the experimental area. The decline in sheep from 1970-75 coincided with low

Table 16. Observed and adjusted percentages of cows with distended udders (DU) seen during ground counts of the Delta caribou herd in experimental area, 1973-79.

Date	No. cows in sample	Percent with distended udders		
		Observed at calving	Observed post-calving	Adjusted back to calving ^a
13-14 Jun 1974	942		24	58
11-12 Jun 1975	839		38	91
16-22 Jun 1976	699		62	149 ^c
16-19 Jun 1977	784		30	72
28 May 1978	343	71 ^b		
13-14 Jun 1978	661		28	67
24-28 May 1979	479	98		
23 Jun 1979	424		45	108 ^c

^a Adjusted values = % postcalving cows with distended udders \times 2.4. The correction factor (2.4) is calculated as follows:

$$\left(\frac{\% \text{ cows with DU at calving 1978}}{\% \text{ cows with DU postcalving 1978}} + \frac{\% \text{ cows with DU at calving 1979}}{\% \text{ cows with DU postcalving 1979}} \right) \div 2$$

^b Minimum value, based on calves/100 animals older than calves during fixed wing aerial survey.

^c Adjusted value exceeds 100%.

Table 17. Estimated number of caribou harvested by hunters in relation to estimated population size within experimental area.

Year	No. of caribou pre hunting	No. harvested	Percent population harvested
1968	5,000	175	4
1969	5,000	270	5
1970	4,500	330	7
1971	4,000	750	19
1972	3,200	620	19
1973	2,400	280	12
1974-79		0	0

^a Hunting season closed from 30 Sep 1973 to Aug 1980. In all other years, the season was 10 Aug to 31 Mar.

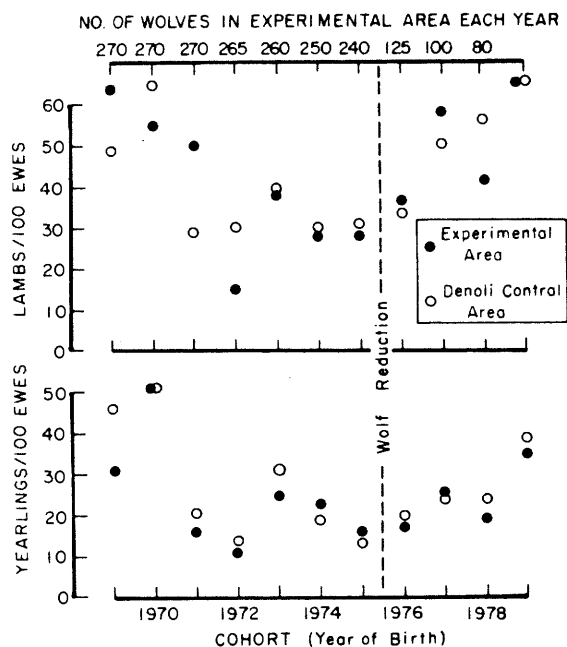


Fig. 17. Offspring/100 ewe Dall sheep in experimental and control areas in relation to wolf removal in experimental area.

lamb production and/or high early lamb mortality in the Dry Creek subpopulation (Fig. 17, complete data are in Appendix 3). Increased ($P < 0.05$) lamb/ewe ratios from 1976–79, compared to 1973–75, coincided with stabilization of population size (Fig. 2) and reduced wolf density; however, the higher lamb/ewe ratio after 1975, compared to 1973–75, did not result in a significant ($P < 0.01$) increase in the yearling/ewe ratio until 1979 (Fig. 17). In fact, a comparison of lamb/ewe and yearling/ewe ratios for each cohort indicates that percent survival to 1 year of age for lambs observed at the lick was significantly lower ($P < 0.01$) after wolf removal than in 1973–75 (Appendix 3).

Lamb/ewe and yearling/ewe ratios in the adjacent control area, Denali National Park, were correlated ($r = 0.728$, $r = 0.911$, $P < 0.02$) with those in the experimental area (Fig. 17). Therefore, the pattern of lamb survival in the experimental area was not correlated with the reduction of wolves in 1976–79. Other factors apparently overrode any effect of wolf reduction.

Harvest by Hunters.—The annual harvest of approximately 100–115 rams had little influence on the changes in population size during the 1970's. Hunters harvested only rams with horns greater than three-fourths curl (270°) except during 1979 when the minimum curl was seven-eighths (315°). Harvested rams were ≥ 5 years old.

Hare and Beaver Population Status

Hares underwent large, cyclic fluctuations in the study area (Fig. 2). Beavers were abundant in isolated pockets of favorable habitat on the Tanana Flats; however, their overall density was low. Despite a general drying trend during the 1970's, beavers increased locally in the early and mid-1970's as a result of decreased harvest by trapping (R. Long, pers. observ.).

DISCUSSION

Impact of Harvest on Wolf Demography

Increased productivity of wolves does not necessarily occur when populations are heavily exploited. Reviews by Pimlott et al. (1969) and Keith (1983) concluded that productivity, as measured by the percentage of pups, should increase when a population is exploited at a high rate. They cite examples of pups composing 70% of a population. R. Peterson (unpubl. data) also found that the percentage of pups in early winter increased as the harvest rate increased on the Kenai Peninsula, Alaska. However, the increase in the proportion of pups resulted primarily from decreased numbers of adults and yearlings in each pack rather than from a major change in the production of pups/pack (R. Peterson, unpubl. data). Peterson's observations show how a change in population composition can occur while productivity remains relatively stable. Changes in wolf population composition after high exploitation have commonly been attributed only to changes in productivity.

Contrary to the above observations, we observed no increase in percentage pups in our study area after wolf reduction in 1976. This may have resulted from killing a high proportion of pack members, which could have left many packs without breeding age animals of 1 or both sexes.

Additionally, low ungulate biomass in our experimental area during the mid-1970's probably was the factor causing relatively low productivity by individual wolves, just as it was in northern Minnesota in the mid-1970's (Mech 1977a) and other areas (Keith 1983). In 1975, ungulate biomass was approximately 90 kg/km², based on population estimates for moose, caribou, and sheep. This is low compared to our calculated values of ungulate prey biomass for other areas in North America. For example, on Isle Royale, estimated biomass/km² was 900 kg from 1968-70 (Peterson 1977) and 450 kg during the late 1970's (Peterson and Page 1983). Comparable values were 450 kg in Minnesota (Van Ballenberghe et al. 1975), 540 kg in Algonquin Park, Ontario (Pimlott et al. 1969), and 550-1,300 kg on the Kenai National Moose Range, Alaska between 1964-75 (Bailey 1978). These values are comparable to the estimated biomass in our study area during the early to mid-1960's (500 kg/km²) when Rausch (1967) documented higher productivity for individual wolves. It should be noted, however, that productivity of individual wolves in our experimental area declined only slightly compared to the large decline in prey biomass from the early 1960's to the mid-1970's.

Sustained annual harvests $\geq 20\%$ of early winter wolf populations have had significant effects on wolf numbers in North America where wolf productivity was low. Populations have not grown at harvest rates of about 25% (Pimlott et al. 1969; Van Ballenberghe et al. 1975; R. Peterson, unpubl. data). In our experimental area, an approximate harvest rate of 20% by trappers during 3 winters before wolf removal was significant in limiting wolf numbers. With pups composing 30% of our population during 1975-76, the pop-

ulation could not have been stable if natural mortality had exceeded 10%, and generally, natural mortality rates exceed 10% (Van Ballenberghe et al. 1975; Mech 1977a; Ballard et al. 1981b; R. Peterson, unpubl. data). Keith's (1983) review indicates harvest rates in excess of 30% generally have caused wolves to decline. In addition, on the Kenai Peninsula, Alaska, a 31% harvest rate caused a moderate population decline of wolves (R. Peterson, unpubl. data). In our experimental area, wolf harvest rates from 38-61% in winters 1975-76 through 1978-79 resulted in a rapid decline of wolves. The level of harvest that wolf populations can sustain varies considerably depending on food supplies and productivity (Keith 1983), but it appears that harvest rates greater than 30% are usually required for managers to reduce wolf numbers.

Factors Affecting Moose Abundance

Habitat quality, winter weather, harvest of moose, and predation had major effects on rates of growth and decline of the moose population. The importance of each factor varied during the study, and several factors generally acted in concert during rapid population changes, as was also found for moose on Isle Royale (Peterson 1977) and for deer (*Odocoileus virginianus*) in Minnesota (Mech and Karns 1977).

Habitat Quality and Weather.—Influence of browse availability on the moose population varied between the 1950's and 1979. Browse availability may have affected moose population growth but only at peak abundance in the early 1960's. No changes in habitat or browse use explain or coincide with the steady decline in calf survival from 1972-75 and the increased calf survival and survival of twins from 1976-79. In fact, from 1972-79, most prime seral habitat was the result of wildfires during the 1950's and early 1960's. Effective wildfire suppression since the 1950's caused slowly decreasing habitat quality through 1979. If habitat quality were involved, calf survival should have

continued downward in 1976 rather than increasing. A factor that may have contributed to improved nutrition, despite decreasing habitat quality, was the decline in intraspecific competition associated with declining moose density. However, reduced intraspecific competition could hardly be the primary cause of the 2- to 3-fold increase in calf survival in 1976, 11 years after the peak population.

Deep snow has had a marked effect on moose survival and abundance in the experimental area (Bishop and Rausch 1974) and elsewhere (Peterson and Allen 1974; Peterson 1976, 1977). The severity of winters 1965–66, 1966–67, and 1970–71 was particularly important in causing the decline of the moose population in the experimental area. There were no good estimates of mortality during these winters; however, recruitment and age structure data and observations suggest large numbers of moose, particularly calves, died (Bishop and Rausch 1974).

The 2 rapid and substantial moose declines resulting from deep snow had long-term significance. The crash between 1965 and 1967 may have produced a more favorable vegetation-moose relationship resulting in higher calf and yearling recruitment for the 1968 and 1969 cohorts (Table 9). However, an adverse effect of the crash was that prey/predator ratios rapidly decreased (Table 4) as in Minnesota (Mech and Karns 1977). These ratios decreased further during the severe winter of 1970–71, likely increasing the impact of wolf predation on moose. This change coupled with increased harvest of moose by man contributed significantly to the continuous decline of the moose population until 1976.

Changes in snow accumulation cannot explain the increased moose calf survival, the increased frequency of twins (Table 9), or the population growth that began in summer 1976. Snow accumulation was near or below average for all winters between 1972–79, except winter 1974–75 (Fig. 13); the greater snow depth that winter probably contributed to the scarcity of yearlings in November 1975. However, the calf/cow ratio in 1975 was still

in the expected range based on the trend in previous years (Table 9), and no correlation existed ($P > 0.1$) between winter severity (when cows were pregnant) and calf abundance the following fall.

Reproduction in Moose.—The pregnancy rate for moose in the experimental area was within the normal range for North American moose. In a review of pregnancy rates, Blood (1974) reported a range of 71–90% for cows >24 months of age. The pregnancy rate for similar-aged moose in south central Alaska was 95% (Rausch 1959, Atwell 1963). By comparison, 88% of the cows >24 months of age in the experimental area were pregnant during May 1975 (Table 8) when the population was near its lowest; yet few calves were seen during early winter (Table 9). Therefore, a low pregnancy rate did not cause the scarcity of calves, nor could pregnancy rates have increased sufficiently to cause the abundance of calves and increased twin frequency seen in 1976 after wolf reduction (Table 9).

Harvest of Moose.—The legal harvest of moose by hunters significantly influenced the moose population trend in the early 1970's. From 1970–74 the large kill contributed strongly to the rapid decline of moose. During this period the mean estimated annual percentage of standing stock harvested was 10% (range 4–19%, Table 15), which equaled the mean rate of yearling recruitment during May (cohorts 1969–73). Additional sources of adult mortality (predation, accidents, and poaching) made a decline in numbers inevitable and caused a rapid decline in the moose/wolf ratio. Thus, the kill by hunters, like that of severe winters, increased the potential effect of predation on moose.

Restriction in harvest levels would have reduced the rate of decline in moose during the early 1970's by increasing yearling and adult survival; however, summer calf survival, and hence recruitment, would have remained relatively low because of other factors. The major reduction in harvest of moose during 1975–78 did not cause increased recruitment (Table 9) or the decreased natural adult mortality (Ta-

ble 12), beginning in 1976, inasmuch as harvest had little effect on either of these parameters. However, the restricted harvest did aid in population growth.

Predation by Bears.—In light of studies of black bear predation on elk (*Cervus elaphus*) calves in Idaho (Schlegel 1976) and moose calves in Alaska (Franzmann et al. 1980), black bears must be considered a potentially major predator during about 4 weeks postcalving. On the Kenai Peninsula, 34% of 47 radio-collared calves were killed by black bears (Franzmann et al. 1980) where density was estimated to be 0.3 bears/km² (Schwartz and Franzmann 1981). The black bear density on the Kenai Peninsula appeared to be at least 5 times greater than that on the Tanana Flats according to J. Davis (pers. observ.); therefore, we assumed that black bears killed a much lower percentage of the calves in our study area and had a small effect on recruitment.

Grizzly bears commonly prey on calf and adult moose in Alaska. Grizzlies killed 43% of 120 radio-collared calves in the Nelchina basin, mostly during June and July (Ballard et al. 1981a). However, grizzly density in the Nelchina basin calving area was relatively high at 1 bear/41 km² (Miller and Ballard 1982). In most of our experimental area, grizzlies seemed to be minor predators on neonate moose because of spatial and temporal separation between the species. Only during fall, when calf and adult moose moved into grizzly habitat in large numbers, were grizzlies potentially important predators; however, at this time grizzlies kill few calves (Ballard et al. 1981a). Therefore, we conclude that black and grizzly bears had a minor effect on numbers of moose in our experimental area.

Predation by Wolves.—In the following sections, we will examine the relationship between moose population dynamics and wolf density that was altered by the removal of wolves. Further, we shall discuss changes in the moose-wolf relationship during our study and the probable influence of declining alternate prey populations.

Effects of Wolf Removal on Moose.—Increased survival of moose and population growth coincided with wolf removal during the mid-1950's and again in 1976. However, the impact of wolf removal in the 1950's cannot be quantitatively assessed because few data were collected and because bears also were killed by poisoned baits used in the removal efforts (P. Shepherd, pers. observ.). A clearer picture of the relationship between moose survival and wolf reduction was obtained in 1976–79 when calf and yearling survival rates increased 2- to 4-fold (Table 9, Fig. 9), and adult mortality rates sharply declined in the experimental area (Tables 12, 13). Survival of moose calves to 6, 12, and 18 months of age were negatively correlated ($P < 0.02$) with wolf abundance during 1972–78 (Fig. 18). Among control areas, calf survival improved only where moose migrated to the wolf removal area to calve and rear young but wintered in a control area where they were counted during surveys (Fig. 11). No significant ($P > 0.1$) change occurred in the 3 control areas having no interchange of moose with the experimental area.

We conclude that increased survival of calf, yearling, and adult moose in the experimental area, beginning in 1976, was primarily attributable to decreased predation by wolves. Other variables considered did not explain the dramatically improved survival of moose during the study. Two additional inferences are drawn. Firstly, average to low snow accumulation from 1976–79 and favorable range conditions maximized both moose survival and the effects of the specific level of wolf reduction applied. Secondly, bears had a minor effect on numbers of moose in our experimental area, compared to the Nelchina basin (Ballard et al. 1981a) and Kenai Peninsula (Franzmann et al. 1980), because a large reduction in wolf density resulted in calf and yearling survival that was near the highest recorded in Alaska.

Age structure of a moose population, in addition to the level of predation, is an important determinant of mean adult mortality rates. Because natural mortality

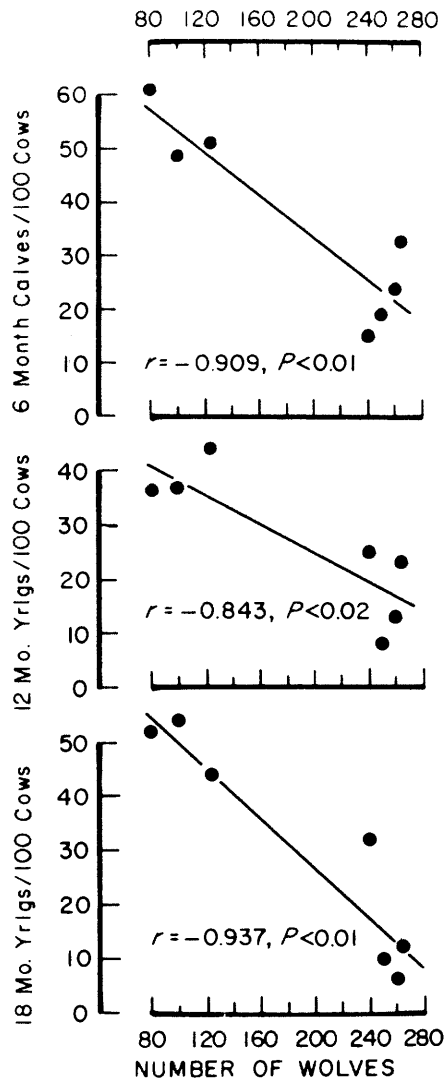


Fig. 18. Correlation between number of wolves and off-spring/100 cow moose ≥ 30 months of age in experimental area (1972–78).

rates of adult moose increase with age (Table 13), the mean mortality rate for a population increases with increasing mean age of adults. Moose populations with high percentages of old-aged moose should retain higher mortality rates and lower growth rates after predator reduction, compared to populations of predominately young and middle-aged moose. In our study, old moose rapidly disappeared because of high mortality rates during the 3 years preceding wolf reduction; this caused the mean age to decline. Had wolf

removal begun several years earlier when about 40% of the cow moose were ≥ 11 years old, the adult mortality rate after wolf reduction may have remained higher than our observed rate.

Variability of Moose-Wolf Relationships.—Moose/wolf ratios differed as much as 11-fold during the study (Table 4) indicating that the potential impact of wolf predation on the moose population was highly variable. Wolf predation had little effect on the population during the early 1960's when the ratio was over 100 moose/wolf, and no evidence suggests predation initially contributed to the rapid decline of the population during severe winters 1965–67. However, wolf predation became increasingly important among factors limiting the moose population. During the 1970–75 the rapid decline of moose and the relatively slow decline of wolves produced a precipitous drop in moose/wolf ratios to as few as 12 moose/wolf (Table 4). At low ratios, the impact of predation was great as demonstrated by the response of moose to wolf reduction and the percentage of the moose population killed by wolves during the winter.

Predation rates for wolf packs primarily consuming moose have been estimated elsewhere and indicate a likely range of kill rates for packs in our study. In south central Alaska, a pack of 10 wolves killed a moose or caribou every 1.2 days during a 45-day period in late winter (Burkholder 1959). Later, in the same area but with lower prey densities, an intensively studied pack of 6 killed 1 moose or caribou/6.2 days (Stephenson 1978b), and 5 intensively observed packs of 2–11 wolves killed 1 moose or caribou (75% moose) every 3.8 days (Ballard and Spraker 1979). In Denali National Park, Haber (1977) estimated wolf packs of 5–24 killed an average of 1 moose or Dall sheep/2.9 days throughout the year. On Isle Royale, a pack of 15 killed an average of 1 moose/3 days during late winter (Mech 1966); in subsequent studies on Isle Royale, Peterson (1977) found a similar kill rate (range of 1 kill/1.8–4.2 days) between 1971–74 for

2 packs ranging from 8–16 wolves. During late winter 1977–78 the predation rate among 4 packs on Isle Royale decreased to 1 moose/6.5 days (R. Peterson, unpubl. data); the lower rate was attributed to decreased availability of vulnerable moose. During 2 winters, a kill rate of 1 moose/4.7 days was observed for a pack of 8–13 in Alberta whose only ungulate prey was moose (Fuller and Keith 1980).

Moose killed by wolves in our experimental area were estimated using relatively high and low kill rates cited above. During winter 1975–76 there were at least 23 wolf packs inhabiting the area. At kill rates of 1 kill/3 or 6 days per pack, an average of 35 and 70 kills, respectively, would have been made per pack during the 7-month winter period for a total kill of 800 and 1,600, respectively, by all 23 packs. In stomachs of wolves shot in the experimental area, moose occurred in 75% of those containing food. Assuming that 75% of the kills were moose, then 600–1,200 moose may have been killed. If about 4,500 moose were present in October 1973 and 3,500 moose in 1974, then wolves killed about 13–27% of the standing crop of moose during winter 1973–74 and 17–34% during winter 1974–75.

The above percentages of moose killed and 20% kill rate of our radio-collared moose (Table 12) are comparable to values from other studies. On Isle Royale, when there were 20 moose/wolf, R. Peterson (unpubl. data) estimated that wolves killed 10–15% of the moose population during 4 winter months. Our extrapolation of these kill rates to include our 7-month winter period indicates that 17–26% of the moose population would have been killed. Fuller and Keith (1980) estimated that wolves in their study area annually killed 15% of the moose >12 months old; however, the percentage of the total moose population removed was substantially greater because calves composed 46% of kills during winter.

On the basis of either of our estimates of wolf-caused mortality to moose, wolf predation alone could have caused the moose population to decline between

1973–75 when there were 12–15 moose/wolf. During early winter 1973–75, calf recruitment to 6 months of age had been only 14, 12, and 9% (percent calves seen among moose on surveys), whereas the calculated kill of calves and adults during winter ranged from 13–34%. We suggest that the actual percentage of moose killed was on the low end of the estimated range inasmuch as moose were relatively scarce by the mid-1970's, and wolves probably could not maintain high kill rates.

Wolf predation on moose less than 6 months old was greater than on the population as a whole during winter. Wolves apparently killed an increasing percentage of the calf crop as the number of calves available declined from about 60 calves/wolf in the mid-1960's to about 8 calves/wolf by 1975 (Table 10). During the same time, the ratio of calves surviving/wolf declined even faster, reaching about 1:1 by 1975. Wolf removal, beginning in 1976, abruptly increased the ratio of calves surviving to values near those calculated for 1970. Apparently, wolves killed most calves produced during summers 1974 and 1975.

We do not know when wolves would have naturally declined enough to have allowed moose to increase to a level that would provide for both hunting and non-consumptive human use had wolf removal not been initiated. After wolf reduction in 1976, no natural changes occurred in our control areas that allowed moose to increase. We suspect that without wolf removal, predation would have continued to cause moose to decline for an extended period, even though wolves would have declined eventually from food shortage (Mech 1970, Mech and Karns 1977). On the average, only about 12 moose were available to each wolf during winter by 1975, while the equivalent of about 2.6–5.3 moose/wolf were killed. The number of readily available moose was even less than 12 because some individuals have a low probability of being killed by wolves.

Alternate Prey and Moose-Wolf Relationships.—When primary ungulate prey

decline significantly, wolf predation shifts, when possible, to high and/or increasing alternate prey populations (Peterson 1976, Voigt et al. 1976, Mech and Karns 1977, Theberge and Strickland 1978). This shift can allow wolf populations to persist, to maintain relatively high pup production and survival, and to continue to exert high predation pressure on their declining primary prey. In contrast, the synchronous decline in abundance and the localized distribution of most alternate prey in our experimental area between 1970–76 probably prevented wolves from making major shifts in food habits, despite the rapidly declining moose/wolf ratio.

Wolf Abundance and Survival of Caribou and Sheep

Twice since the mid-1950's caribou in the experimental area have rapidly increased, and both increases followed a reduction in wolf numbers. Mortality of calf caribou was also closely related to wolf abundance. Consequently, we conclude that wolves were an important factor limiting this caribou population. Wolf predation had a relatively small effect on the sheep population inasmuch as the sheep population showed little response to wolf removal. The scarcity of sheep remains in wolves killed in the experimental area also suggested that wolves did not rely heavily on sheep, at least in winter. Therefore, major ungulate prey species in this wolf-prey system during the mid-1970's were moose and caribou.

Predation Confounding Evaluation of Vegetation-Ungulate Relationships

Range condition as the determinant of ungulate population status has been emphasized by wildlife biologists for years. Caughley (1976:198) stated that ungulate populations will irrupt "... in the presence or absence of predators ... whenever an ungulate population is faced with a standing crop of vegetation in excess of that needed for maintenance and replace-

ment of animals ...". Caughley (1976) described the vegetation-ungulate relationship as a continuum between a vast surplus of food and a severe food shortage. He defined 2 useful points along the continuum as follows: ecological carrying capacity is the maximum density of animals that can be sustained indefinitely without inducing trends in vegetation, and economic carrying capacity is the density of stock at equilibrium with the range conditions providing maximum sustained yield. The latter point represents a lower ungulate density and greater standing crop of food than does the former.

In Caughley's (1976) model, a moose population exceeding ecological carrying capacity becomes nutritionally limited and declines as a result of lowered calf production and survival. Population age structure becomes increasingly weighted toward older cohorts. Conversely, near economic carrying capacity, high calf production and survival would be expected, moose would increase in the absence of a large harvest, and age structure would be weighted toward young adult moose. These generalizations usually hold for ungulates where there is little or no predation (Blood 1974, Staines 1978, McCullough 1979).

However, where wolves have attained near natural densities when ungulate prey were near or below economic carrying capacity, predation has sometimes been important in maintaining declines of deer, moose, and caribou or holding them at low densities (Mech and Karns 1977; Bergerud 1978, 1980; Olson 1979; present study). Despite favorable range conditions, the age structure and/or survival rates in these ungulate populations were similar to those expected in populations facing food shortages. The combined effects of wolf and grizzly bear predation on moose had similar effects in south central Alaska (Ballard and Taylor 1978). Therefore, we conclude that some indices used to assess the vegetation-moose relationship in Alaska during the 1960's and 1970's (i.e., calf and yearling abundance, change in population size, and population

age structure) were unreliable in the presence of moderate to high predator densities. Bergerud (1978) made the same observation for the vegetation-caribou relationship. There is growing recognition that these indices sometimes reflect the number of predators relative to prey rather than the vegetation-ungulate relationship.

Misjudging the vegetation-ungulate relationship in areas where wolves and/or bears are common has resulted in inappropriate management of ungulates and predators in Alaska (Bergerud 1978). Sub-optimal nutrition and the lingering effects of severe winter weather were thought to have caused low production and survival when, in fact, the birth rate was near maximum and predation was lowering survival in several caribou herds (Davis et al. 1978, 1980; Boertje 1981) and moose populations (Johnson 1971, Buchholtz 1974, Rausch et al. 1974). To improve nutrition, game managers allowed harvest levels that reduced ungulate densities. This reduction increased the effect of predation, further lowering survival. Much of the confusion caused by such situations has been resolved as a result of recent predator-prey studies (Bergerud 1974, 1978, 1980; Schlegel 1976; Mech and Karns 1977; Peterson 1977; Franzmann et al. 1980; Fuller and Keith 1980; Packard and Mech 1980; Ballard et al. 1981*a,b*). Many biologists now realize that management strategies appropriate where predators are largely absent, and upon which a good deal of their training was based, are not necessarily appropriate in situations where significant numbers of large predators exist.

Moose/Wolf Ratios for Evaluating the Importance of Predation

The general effects of predation on ungulate populations are difficult to assess without intensive studies. Despite the simplicity of prey/wolf ratios (e.g., they do not reflect changing prey vulnerability and predation rates, age structure of populations, or the vegetation-ungulate relationship), knowledge of these ratios can help

assess the effects of predation on relatively simple systems. Mech (1970) reviewed ungulate prey-wolf relationships for many North American prey species and concluded that when prey/wolf ratios were about 11,000 kg/wolf or less, predation was the major factor limiting prey numbers; this was the equivalent of about 30 moose/wolf (Mech 1966). Since Mech's review, additional data have become available on moose/wolf ratios relative to population control.

Three general categories of moose-wolf relationships can be described using empirical moose/wolf ratios obtained during winter in studies where moose were the primary prey. Firstly, at <20 moose/wolf, predation is usually sufficient to cause a decline in moose abundance and low survival of both calves and adults (Peterson and Page 1983, Table 4 this study).

Secondly, at 20–30 moose/wolf, predation can be the primary factor controlling numbers of moose; whether the moose population remains stable or declines is largely dependent on the combined effect of other factors influencing the dynamics of the moose population, including hunting, food supply, alternate prey, and winter severity (Peterson 1976, Fuller and Keith 1980, Peterson and Page 1983, Table 4 this study). Two cases exist where populations were reported to have increased at these ratios. During 1976 in our study, the overall ratio was about 24 moose/wolf; however, wolves were reduced to a low level in the primary calving area, which allowed very high recruitment. In the other case, at ratios of 17–26 moose/wolf, Haber (1977) observed recruitment (2–12% yearlings, $\bar{x} = 7\%$) that was too low to account for his estimated increase of moose in the Savage River area of Denali National Park. Haber attributed growth largely to ingress of cow moose from adjacent areas; however, no ingress was observed. Possibly, moose were not increasing.

Thirdly, at >30 moose/wolf, predation can be significant but not necessarily limit growth. Moose populations are likely to remain stable or increase if they are below

ecological carrying capacity and if other sources of mortality are not exceptionally great (Mech 1966, 1970; Peterson 1977; Allen 1979; W. Ballard, unpubl. data; R. Peterson, unpubl. data; Table 4 this study). However, regardless of how much above 30 moose/wolf a ratio is, high additive mortality (from hunting, predation, severe winters, or other factors) can cause a decline.

These preliminary guidelines should assist managers in making initial assessments of moose-wolf relationships using only population estimates for wolves and moose. The interpretation of the moose-wolf relationship will be clearest when observed ratios are near the extremes. Errors in estimating population sizes, variation in the prey-wolf relationship at a specific ratio, and environmental variables all affect the ratio and moose-wolf relationship estimated from the above guidelines. Keith (1983) described another useful method of assessing the significance of ungulate/wolf ratios; however, it requires determining the finite rate of increase for ungulate prey, a value often difficult to obtain in a short time.

Interactions Among Wolf, Moose, and Human Populations

We primarily have discussed how wolves, man, weather, alternate prey, and habitat affected the trend of a moose population. Now we examine the mechanisms exercising long-term control over moose and wolves. Of particular management interest is the nature of the wolf-moose-human relationship in ecosystems where moose and wolves are largely unregulated by man. In such areas, some animals are killed by man, but population trends are often controlled by other factors. Perturbations and resultant responses of wolf, moose, and caribou populations, as in our study, increase the understanding of the more naturally regulated situations, as well as ecosystems where man has a greater controlling influence. In the following 3 sections we discuss, in a management context, the compensatory nature of mortal-

ity sources affecting moose, how predation can sustain declines in ungulate populations, and potential mechanisms that can prevent extirpation of prey and predator and allow ungulates to temporarily escape the control of wolves.

Noncompensatory Mortality—Its Role in Moose Population Control.—Mortality is often referred to as either compensatory or noncompensatory (Errington 1967). Although this concept is intuitively appealing and is fundamental to understanding population control, there is generally little clear-cut evidence that mortality is either compensatory or noncompensatory. Our use of compensation follows Connolly (1978:377):

“... mortality can be regarded as either compensatory or noncompensatory ... depending on whether it supplants or is additive to other causes of loss. A coyote may kill a fawn that otherwise would have survived to maturity, or an adult deer which might have lived for several more years. In my view, such losses would be noncompensatory if the available deer habitat was understocked. But the killing of a sick or weak deer about to succumb from the rigors of winter is compensatory because the death of that animal was inevitable.”

Experimental removals of predators have provided perhaps the least ambiguous data on the nature of predator-caused mortality. Bergerud's (1971) study of lynx (*Felis lynx*) predation on calf caribou showed predation was largely noncompensatory. Caribou calf survival improved with lynx removal, and population growth among herds was inversely related to lynx density. In a Utah study, coyote (*Canis latrans*) removal did not reverse low mule deer (*Odocoileus hemionus*) fawn survival due to habitat deterioration (Robinette et al. 1977). In this case, mortality from predation was compensatory.

The experimental removal of wolves in our study assisted us in categorizing major mortality sources (predation, severe winter weather, and hunting) as predomi-

nantly compensatory or noncompensatory and helped define the interrelationships among these mortality sources when moose were below ecological carrying capacity. When moose are above ecological carrying capacity, mortality is less of a management problem; therefore, we did not discuss this situation. The 2 instances in which wolf removal was followed by moose population growth in our study area demonstrated that wolf predation under those circumstances was largely noncompensatory. Some mortality due to severe winters was compensatory because the greatest mortality occurred among moose with normally high mortality rates, i.e., calves and the least fit adults. However, most mortality during severe winters was noncompensatory inasmuch as nearly all calves in the population died. In comparison, during mild and average winters more than half survived (Table 9, Fig. 9).

The harvest of cow moose by hunters was also largely noncompensatory. Hunters were generally not selective and only by chance killed cows that were highly vulnerable to wolves or to other mortality sources. Killing these few vulnerable individuals was compensatory only if the number of cows killed by wolves decreased by the same amount. High predation rates on middle-aged cow moose (6–10 years old) indicated wolves were not restricted to killing old adults in our study area during the early 1970's. Also, under some circumstances, wolves kill considerable numbers of young and middle-aged moose (Peterson 1977; R. Peterson, unpubl. data) and deer (Mech and Karns 1977). Wolves also kill adult moose that are in a nutritional condition comparable to the general population rather than selecting clearly malnourished moose (Stephenson and Johnson 1973; Franzmann and Arneson 1976; Ballard et al. 1981*b*; R. Peterson, unpubl. data). Therefore, wolves may at times kill less vulnerable individuals in lieu of those highly vulnerable moose killed by hunters. Under these conditions, cow harvests may not markedly limit prey available to wolves or reduce

predation sufficiently to result in compensation. Thus, mortality from cow harvests was largely additive during the rapid decline of moose in the early 1970's.

The impact of hunting is generally greater on bull moose than on cows. In hunted populations, fewer bulls than cows reach the age when natural mortality rates and vulnerability to predation increase. Because only 1 bull/5–10 cow moose is needed for successful reproduction in certain populations (Bishop and Rausch 1974), it can be argued that a sustained heavy harvest of bulls substitutes for most other forms of mortality. Hence, mortality due to hunting bulls can be largely compensatory, even though some animals die up to 15 years prematurely. However, when predation on moose is great, the harvest of bulls by hunters becomes noncompensatory. Bulls that are surplus to reproductive needs provide prey for wolves, reducing predation on calves and cows. Thus, we view the harvest of bulls during our study as largely noncompensatory.

In most cases, mortality from predation, hunting, and severe winter weather has noncompensatory components. Therefore, managers must view mortality from these sources as largely additive when moose are well below ecological carrying capacity, just as Nelson and Mech (1981) concluded for deer in Minnesota.

Noncompensatory mortality implies some degree of "control" (as opposed to regulation) over the numbers and growth of populations (Keith 1974). Keith (1974) defined population control as the maintenance of a population through density-dependent and/or density-independent processes. In contrast, regulation of populations is the dampening of numerical fluctuations by only density-dependent processes (Keith 1974). Therefore, severe weather, hunting, and predation were, to various degrees, controlling moose population growth in our study area. Predation, and sometimes hunting, operated in an inverse density-dependent fashion, i.e., the impact of the mortality source increased as numbers of moose decreased.

Lidicker (1978) appropriately defined this special type of control as "antiregulatory" and indicated that predation generally takes this form.

Antiregulatory control by wolves sufficient to sustain declines in numbers of ungulates has been well documented in Minnesota, Isle Royale, and to a lesser extent in Alaska. In each case, the large mammal component of the ecosystem was relatively simple, i.e., 1 major predator coexisting with 1 or 2 major prey species.

In northeastern Minnesota (Mech and Karns 1977) and on Isle Royale (Peterson 1976, 1977; Peterson and Page 1983), declines in numbers of deer and moose, respectively, were precipitated by severe winters that occurred when deer were near or above ecological carrying capacity and moose were at a high density but below carrying capacity. Wolves did not appear to limit growth of these populations before the severe winters. However, wolves increasingly controlled prey numbers because the rapid numerical decline in ungulates coincided with stable or increasing numbers of wolves. Factors adversely affecting ungulate nutrition increased vulnerability to predation and resulted in a temporary increase in predation rate (Peterson and Allen 1974, Peterson 1976, Mech and Karns 1977), allowing wolves to thrive. Prey reached low densities once wolves exerted sufficient control over their prey populations to cause a sustained decline. Mech and Karns (1977) documented the extirpation of deer by wolves in an area of about 2,500 km². They concluded that in the absence of wolves the deer herd would not have disappeared, the decline would not have been so drastic in the surrounding area, and the deer population would have recovered sooner. Wolves eventually declined but only after deer had reached extremely low levels (Mech and Karns 1977), and deer have remained scarce through 1982 (P. Karns, pers. commun.). On Isle Royale, moose declined during 10 years and by 1980 reached about one-half of their peak numbers (Peterson and Page 1983; R. Peterson, un-

publ. data). However, a natural reduction in the wolf population did not occur until 1981, about 11 years after the moose decline began (Peterson and Page 1983).

Throughout the islands of southeastern Alaska, numbers of black-tailed deer (*Odocoileus hemionus sitkensis*) declined from high densities between 1964–69 primarily as a result of mortality caused by severe winter weather (Merriam 1970, cited in Olson 1979). On islands not inhabited by wolves, deer subsequently increased to high densities by 1978 (Olson 1979), whereas on islands with wolves present, deer remained at low densities or continued to decline (Olson 1979). By 1976 deer were nearly absent on some large islands, and the primary source of mortality appeared to be wolf predation (Olson 1979). Observations by ADF&G biologists suggest that deer began increasing about 1976 in some wolf-inhabited areas, but only after wolf density had markedly declined. Olson (1979) concluded that wolves can reduce numbers of deer and delay population recovery following heavy winter losses.

One of the most significant lessons to be learned from the patterns observed in Minnesota, Alaska, and on Isle Royale is that a combination of controlling factors can initiate a decline of ungulates, which may then continue to very low densities as wolf predation becomes an increasingly important controlling factor. In none of these situations was increased prey productivity and survival, caused by increased forage availability, sufficient to offset mortality from predation, at least during the decade following the initiation of the decline. These observations also suggest that wolf population size changes very slowly in response to declines in prey density. This brings our discussion to the factors regulating wolves during prey declines and the mechanisms allowing wolf-ungulate systems to be sustained over long periods.

Response of Wolves to Declining Moose Density.—Apparently no sensitive, fast-acting feedback mechanism reg-

ulates numbers of wolves relative to declining prey density. Feedback is a process where a change in prey density or vulnerability affects the size of the wolf population or its predation rate. The previous examples, in which wolves prolonged declines in deer, caribou, or moose populations until prey reached a low density or were locally extirpated, demonstrate the relative ineffectiveness and slow-acting nature of the feedback system. For the wildlife manager, only feedback mechanisms that rapidly reduce the impact of predation on declining ungulate populations are effective in a regulatory sense.

Recently, Packard and Mech (1980) reviewed population regulation of wolves. They concluded that during periods of declining prey availability, social behavior often seems to be the proximate cause of numerical change in wolves, whereas food is the ultimate controlling factor. Social factors that appear to be important in regulating numbers of wolves include territoriality, intraspecific strife, exclusive breeding, delayed maturity, dispersal, and disparate sex ratios. Packard and Mech indicated that social factors produce a lag in the response of a wolf population to a decline in primary ungulate prey resources. The effect of this loose regulation of wolf populations fosters wide oscillations in numbers of prey (Packard and Mech 1980) through the antiregulatory effects of predation (Lidicker 1978).

Examples of loose regulatory feedback in wolf populations are found in studies from Minnesota and Isle Royale and in our study in Alaska. In northeastern Minnesota, Mech (1977a) reported that wolves underwent a 6-year decline in numbers primarily due to malnutrition and intraspecific strife. However, wolf numbers had declined only 55% 7 years after their primary prey, white-tailed deer, began declining, but during that time deer were nearly extirpated. Although the decline in deer eventually resulted in a reduction of wolves (loose regulatory feedback), the effect of wolf predation remained antiregulatory for deer down to the point of extirpation in a portion of the study area.

On Isle Royale, wolves increased from 17 in 1969 (Peterson 1977) to 50 in 1980 (Peterson and Page 1983), and moose declined from a peak abundance of 1,200–1,600 in 1969 (Peterson 1977, Peterson and Page 1983) to about 650 in 1980 (Peterson and Page 1983; R. Peterson, unpubl. data). The lag in the numerical response of wolves was 11 years, although Peterson (unpubl. data) observed a decline in predation rate. The rapid decline of moose and alternate prey in our study area, compared with the slow change in numbers of wolves, was described above.

Ineffective regulatory feedback mechanisms also exist between some small mammals and their predators. Reviews by Keith (1974) and Lidicker (1978) concluded that predation on lagomorphs and microtines (1) acts in an antiregulatory way during prey population declines initiated by food shortages, (2) brings populations to very low densities and hence increases the amplitude of fluctuation and lengthens the period of low density, (3) maintains low prey densities after vegetation recovers, and (4) precludes escape of prey populations from control by predators until after predators have declined.

Therefore, slow numerical and functional responses to declines in primary prey are common to many species of mammalian predators, including wolves. Once a predator-maintained decline in a prey population begins, the only effective short-term management option is to reduce mortality from sources that can be influenced, including predation. This approach was supported by the results of modeling an ungulate-wolf system (Walters et al. 1981). The long-term consequence of procrastination by managers will likely be a scarcity of primary and alternate prey as well as predators for many years.

The large and small mammalian predators (wolves, foxes, lynx, weasels, hawks, owls, etc.) involved in the systems mentioned above are to a large extent obligate carnivores. In many areas, predation by omnivores (facultative carnivores) such as black and grizzly bears also plays an im-

portant role in prey-predator relationships (Schlegel 1976, Franzmann et al. 1980, Ballard et al. 1981a). Although bears can be efficient predators on moose, they can rely on a wide variety of other animals and plants for food. This should cause regulatory feedback to be even looser than that observed for obligate carnivores, i.e., the abundance of moose may have little influence on the number and productivity of bears. Coexistence of these 2 types of predators increases the complexity of wildlife management considerably.

The "balance-of-nature" concept is firmly entrenched in the public's mind, and it has underlain the teachings of some university courses in wildlife management and ecology for at least 2 decades. The balanced system envisioned is one that generally remains near an equilibrium through sensitive regulatory feedback mechanisms. A "prudent" predator is required in this system, i.e., one that will "consume its prey such as to maximize its own food supply while at the same time minimizing the possibility that the prey population will be unable to maintain itself and serve as food in the future" (Slobodkin 1961:138). Murray (1979) suggested that prudent predators should harvest individuals with low reproductive value and exercise restraint in numbers of prey killed. Murray points out that many predators kill prereproductive prey, and he finds no mechanisms other than group selection to ensure the evolution of prudent restraint on the part of individual predators, much less a population of predators. Therefore, prudent predation is probably limited to some members of the human species who can evaluate the consequences of their action (Murray 1979).

Reviews by Keith (1974), Lidicker (1978), and Packard and Mech (1980) and observations in Alaska demonstrate that in some simple northern ecosystems mammalian predators, including the wolf, are not prudent during prey declines, that increased amplitude in fluctuating numbers of prey can be caused by predation, and that wide oscillations in predator and prey abundance are common today. Therefore,

the balance-of-nature concept does not accurately describe some prey-predator systems where predator and prey are affected by man but the predator is not controlled by man, and probably in some systems where man has no influence, if such places exist. Acceptance of the dramatic natural changes that occasionally occur in predator and prey numbers would simplify the future management of some wildlife resources such as wolves and their prey.

Escape of Moose Populations from Control by Wolves.—Ungulates have coexisted with wolves for millenia with apparent infrequent extirpation over large areas and with occasional irruptions of ungulates in the presence of naturally regulated wolf populations. Therefore, natural mechanisms must exist that allow ungulate populations to eventually escape antiregulatory control by wolves (the antiregulatory process leads to extirpation if not checked). Mechanisms that stop ungulate declines and allow prey to increase and the time required for these events are important practical considerations for the wildlife manager charged with maintaining ungulate and wolf populations.

Several mechanisms, acting singly or in combination, reduce predation on individuals that in turn might allow ungulate populations to escape antiregulatory control of naturally regulated predator populations (natural systems as we define them include some harvest by man). The prerequisite for escape is an abundant food supply. One mechanism is the simple reduction in numbers of wolves. Such a reduction can occur through decreased production and survival of pups and increased mortality of adults due to disease and nutritional stress, although the rate of change can be very slow (Merriam 1968, Mech 1977a). Other factors, including dispersal, intraspecific strife, exclusive breeding, and disparate sex ratios, assist in lowering densities within wolf pack territories (Packard and Mech 1980, Keith 1983). However, lower wolf densities alone may be inadequate to allow ungulates to stabilize or increase.

Redistribution of wolf packs can create areas devoid of wolves or areas where ungulates are preyed on only seasonally. Such changes in the wolf's land tenure system can result from emigration of packs, the attrition of all pack members, or by adoption of migratory habits in response to availability of prey such as caribou (Stephenson and James 1982). Moose are behaviorally adapted to live at very low densities. Where moose are the sole ungulate prey, wolves may disappear over large areas, and low moose populations remain viable and ready for expansion, although this has not been documented. Redistribution of both wolves and moose may occur after very large wildfires, which may provide an advantage to some moose. If redistribution of wolves is to reduce predation, voids must not be entirely refilled. We suspect that areas void of wolves may persist for long periods if the wolf population is low and declining because of locally severe prey shortages.

A change in prey preference by wolves during a decline also may ease predation on a primary prey species. A total switch in prey selection is unlikely, but a change in emphasis can occur (Mech and Karns 1977, Stephenson 1978*b*, Theberge and Strickland 1978). Altered food habits could be perpetuated for a generation or longer because packs sometimes have distinct prey preferences (Holleman and Stephenson 1981) and hunting methods are to some extent learned by young wolves.

Reservoirs of security, where prey are slightly less vulnerable to predation, provide some relief from predation and an opportunity for prey populations to expand after predators decline. Boundaries of pack territories served as reservoirs for a declining deer population in northeastern Minnesota, maintaining the potential for deer to repopulate areas when wolves declined (Mech 1977*b*). A second type of prey reservoir can exist where terrain and vegetation impair the hunting efficiency of wolves. An obvious example would be the rocky cliffs that can protect mountain sheep and goats from predation. Such areas are less obvious in the case of moose, but

they exist. Tall sedge tussocks on the Tana Flats may favor moose during both summer and winter. Moose have defended themselves from wolves by backing up to cliffs (Peterson 1977) and by entering areas of dense, fallen timber where wolves cannot maneuver quickly (R. Peterson, unpubl. data). However, the surest escape is provided by lakes, rivers, and deep marshes (Mech 1966; R. Peterson, unpubl. data). These features can provide escape for moose that can become founders of an expanding population after wolves decline sufficiently.

Young adult deer and moose have a higher probability of surviving an encounter with wolves than do older adults (Mech 1966; Pimlott et al. 1969; Mech and Frenzel 1971; Haber 1977; Mech and Karns 1977; Peterson 1977; R. Peterson, unpubl. data; Table 13 this study), aiding some individuals in surviving as wolves decline. Mech (1977*b*) speculated that when wolves become scarce, young adult deer will disperse into unpopulated areas, and that their relatively low vulnerability to predation will aid population growth. However, Nelson and Mech (1981) found that at least during low density, young deer tend to colonize areas close to their does. Furthermore, observations of moose movements indicate the same tendency in subadult moose (Gasaway et al. 1980). Thus, it appears that moose and deer populations grow first in localized areas before slowly expanding into adjacent regions. Once a population is increasing and is comprised of mainly young adults, the average vulnerability of the adult population is low compared to an old-aged population. Even when a high number of moose/wolf exist in growing populations, surplus killing of adults and calves in winter occurred only when severe winter weather increased the vulnerability of moose (Peterson 1977). Thus, young growing moose populations apparently do not produce an abundance of vulnerable individuals that can be easily exploited by wolves (Peterson 1977).

A final escape mechanism to consider is the potential for wolf population growth

to lag, relative to a prey population (Packard and Mech 1980). Social factors reduce the growth rate of wolf populations considerably below their maximum potential. Packard and Mech (1980) suggested that wolf territoriality limits the number of breeding units, and exclusive breeding limits recruitment within each unit. In contrast, at low densities, ungulate prey are not significantly affected by intrinsic factors inhibiting population growth.

These differences in observed population growth rates between predator and prey (Peterson 1977) create the potential for ungulates to periodically increase or irrupt in the presence of naturally or near naturally regulated wolf populations. On Isle Royale, for example, moose increased from about 500 in 1948–49 (Krefting 1974) to 1,200–1,600 in 1969 (Wolfe and Jordan, unpubl. data cited in Peterson 1977; Peterson and Page 1983). Although little is known about wolf abundance prior to 1955, 25 wolves were known to be present in 1956 (Cole 1957, cited in Krefting 1974), but in 1969 only 17 wolves were present (Wolfe and Allen 1973). During these intervening years, the highest number of wolves present was 28 in 1965 (Jordan et al. 1967). These data suggest that wolf abundance changed very little during a period when numbers of moose may have increased as much as 300%. Results from Isle Royale should not be viewed as being strictly applicable to other areas; the island is small enough to be dominated by 1 wolf pack (as occurred prior to 1972), and the possibilities for ingress and egress are limited. However, these data demonstrate that factors other than prey abundance can regulate wolf population levels while prey numbers increase.

A lag in wolf population growth may allow moose to escape predation through rapid range extensions (dispersal) into areas with few or no wolves naturally present. For example, in recent history, on the Yukon-Lower Koyukuk drainages in west central Alaska, moose were first observed about 1930 and were well established and increasing by 1940 when wolves first appeared (S. Huntington and R.

Quimby, pers. commun.). Moose and wolves became increasingly abundant until the 1950's.

Coady (1980) described the establishment of a moose population in the Brooks Range and on the north slope of Alaska during the early 1900's when wolves were naturally regulated. A major factor contributing to the success of this immigrant moose population was the apparent preference by wolves for caribou, their traditional prey there (Coady 1980). Caribou remain the primary ungulate prey of wolves even though moose have been locally abundant for 40 years. Thus, under certain circumstances, learned hunting behavior and strong prey preferences can offer substantially long-term protection to potential prey species.

Wolf-ungulate relationships are diverse, and we stress that reductions in prey numbers do not inevitably lead to their being controlled and driven to very low densities by wolf predation. In Alaska, a variety of factors including severe winter weather, flooding of calving areas, high harvest by hunters, predation by bears, natural successional changes of seral habitat, and overuse of range have acted alone or in combination to reduce numbers of moose. Such reductions have not always been sufficient to preclude an increase in prey numbers after the short-term mortality source was no longer operative. Whether predation becomes a primary controlling factor following a decline depends on the density reached by both predator and prey, the existence of alternate prey, and the combined effects of mortality factors acting on the prey population.

Because little detailed information is available on the interrelationships between wolves and prey prior to the increase in modern man's influence on wildlife and habitat, the character of that relationship under pristine conditions remains to a large degree unknown. Bergerud (1967), Pimlott (1967), and Keith (1974) concluded that in pristine ecosystems in North America large predators generally controlled moose, deer, and car-

ibou numbers. Recent observations in Alaska lead us to agree with their conclusions. Therefore, the escape, and subsequent increase, of ungulate populations from control by predators was presumably a short-lived event occurring at widely separated intervals rather than a frequently recurring phenomenon. An alternate possibility is that wolves and prey were roughly cyclic, although not necessarily at regular intervals (Peterson and Page 1983).

Either conclusion poses serious problems to wildlife managers. In Alaska, there are no pristine ecosystems, but some areas have wolf and ungulate populations that are largely under natural control. These predator and prey populations are exploited to varying degrees, but harvest rates of predators are commonly insufficient to substantially affect predation on ungulates. When predation limits growth of ungulate populations, managers have 3 options: (1) wait for a more-or-less natural change of events, (2) reduce or eliminate harvest by man during critical periods for prey populations, or (3) hasten the increase in prey by reducing predators.

Considering the lengthy period (maybe decades) that may be required for natural events to produce a major increase in numbers of ungulates, option 1 is not viable. Option 2, decreasing or eliminating harvest, has been tried in Alaska. It can forestall wolves limiting moose but cannot permanently prevent it as demonstrated by wolves limiting moose in the absence of hunting on Isle Royale (Peterson and Page 1983). Additionally, reducing or eliminating harvest will have little effect once predators exert sufficient control to cause a prey decline or to maintain prey at low densities; therefore, control of harvest is best used in conjunction with other options rather than alone.

Artificial predator reduction in conjunction with reduction in harvest of prey is the most viable management option to increase moose populations over short time intervals. As the moose population grows, wolf removal can be reduced and harvest of prey by man increased. Increased pre-

dition and harvest will reduce the growth rate of the moose population, and eventually predation will again become a major limiting factor. Therefore, when hunting and moderate densities of moose are to be maintained, wolves must be managed. Wolf management, which includes the periodic reduction of wolf numbers, can ensure a sustained long-term sharing of the moose resource between man and wolves, while avoiding low prey densities that support few wolves, hunters, or wildlife observers.

Alaskan wolf and ungulate management programs began changing in the late 1970's as biologists recognized the degree of control wolves exerted over ungulates and the infrequency of natural ungulate escapes. Some programs were redesigned to artificially reduce wolves in order to increase numbers of ungulates and/or increase harvest of ungulates by man. The assumption was that wolf removal in these areas would increase calf and adult ungulate survival because predation was largely additive. But predator-ungulate relationships vary widely over time within an ecosystem and among ecosystems of varying complexity (Mech and Karns 1977, Ballard et al. 1981b, Keith 1983, Peterson and Page 1983, present study). Therefore, the managers reasoned that varying the numbers of wolves in an ecosystem at a specific time should produce a continuum of prey population responses with the limits determined by the dynamics of that prey population in the presence of high and low wolf densities. The greater the effect of wolf predation on ungulates at high wolf densities, the wider the continuum limits. Consequently, a simple formula for managing predators to achieve specific ungulate responses was unlikely.

Variability in the response of prey dynamics to wolf removal is illustrated by contrasting Alaska's only 2 removal studies with sufficient data to clearly evaluate prey responses, i.e., the present study and the study in the Susitna and Nelchina basins of south central Alaska (Ballard et al. 1981b; W. Ballard, unpubl. data) (Table 18). Experimental wolf removal in the

Table 18. Effects of wolf removal on moose population dynamics in 2 Alaskan predator-prey systems.

	Present study area	Susitna-Nelchina River basins ^a
Moose/wolf		
Before wolf removal	12	50
After wolf removal	24-44	100-200
Moose/grizzly bear	Unknown but greater than Susitna-Nelchina	10-20
Major predator on moose	Wolf	Grizzly bear
Effects of wolf reduction on		
Moose calf survival	Large increase	Small increase
Adult moose survival	Large increase	Small increase
Population change	From decline to moderate increase	From decline to slow increase

^a Unpublished data from W. B. Ballard.

Susitna-Nelchina area had a small effect on moose population dynamics compared with wolf removal in the present study for 2 major reasons. Firstly, normal hunting and trapping plus illegal hunting in the Susitna-Nelchina area maintained wolves at a much lower than natural density prior to and during the removal experiment, and wolf density in control areas declined simultaneously with density in the experimental removal area. Consequently, moose/wolf ratios throughout the area exceeded 50/1, suggesting the effect of wolf predation on the moose population would be small. Secondly, grizzly bears were about 4 times more abundant than wolves and were the greatest predator on calf and adult moose. High predation rates on calves by grizzlies would have maintained low moose recruitment regardless of wolf density. Had wolves been at higher (near natural) densities prior to removal, the effect of wolf predation on moose presumably would have been greater, causing a continued decline in moose abundance in areas without removal. Effects of wolf removal in these studies depended on the control wolves exerted over moose and on the presence of other predators.

As expected, other recent Alaskan management programs involving wolf removal have produced variable results, in part because predator-prey relationships span even greater diversity than the 2 studies

compared above. Wolf removal was correlated with increased ungulate survival in some areas and not in others (Table 19). However, the lack of correlation does not necessitate conclusion of no effect because these were management programs initiated where and when it appeared that desired management objectives could be facilitated without regard to rigorous testing of hypothesis or rigorous documentation of effects. Also confounding interpretation of results is the short duration of most programs (≤ 3 years), and often too few wolves were removed to substantially alter ungulate/wolf ratios in subsequent years. Therefore, the effects of many of these programs cannot be clearly evaluated. However, when managers do effect a large reduction in wolf numbers with little or no detectable response from the primary prey, a clear signal is sent to investigate other potential limiting factors. Used in this manner, short-term wolf removal can be a powerful investigative tool.

CONCLUSIONS

1. Predation by wolves can exert substantial control over ungulate prey populations, as demonstrated by wolf removal experiments.

2. If under natural conditions the escape from predation and increase of un-

Table 19. Status of Alaskan wolf management programs involving wolf removal, 1976-82.

Area and game management unit	Objective	Winter period of wolf removal	Primary prey	Other predators	Annual percentage of fall wolf population killed ^a (range)	Prey response to wolf removal and comments
Northwest Alaska 23, 24, 26	Increase caribou numbers and subsistence harvest	1976-77	Caribou, moose, and Dall sheep	Grizzly bears locally abundant	15	Caribou numbers rapidly increased because of reduced harvest of caribou and reduced predation. Increased conventional hunting and trapping of wolves coincided with wolf removal in 1976-77; the percentage kill was high in portions of caribou winter range. Documentations of overall reduction in wolf population was poor, but indices suggest a major reduction between 1976-81, primarily from natural causes.
Aniak drainage 19A & B	Maintain moose numbers while increasing subsistence moose harvest	1978-79	Moose	Black and grizzly bears	70	No increase in already high calf/cow ratio. Survey design would not detect small population changes; therefore, could not quantify effect of wolf removal.
Innoko drainage 21A & E	Increase moose numbers and subsistence moose harvest	1978-79 to 1980-81	Moose	Black and grizzly bears	40-60	Calf survival increased with wolf removal. Wolf removal suspended in 1981 because of high moose recruitment.
Nowitna drainage 21A & B	Increase moose numbers and moose harvest	1978-79 to 1980-81	Moose	Black bears abundant	10-30	No increase in calf/cow ratio. Survey design would not detect small population changes. Wolf removal suspended in 1981 because census revealed more moose than previously estimated and wolf removal was prohibited by U.S. Fish and Wildlife Serv. in most important moose hunting areas. Too few wolves killed to expect change in moose.

Table 19. Continued.

Area and game management unit	Objective	Winter period of wolf removal	Primary prey	Other predators	Annual percentage of fall wolf population killed* (range)	Prey response to wolf removal and comments
Chena, Salcha, & Chatamika drainages 20B & C	Hasten increase of moose and moose harvest	1980-81 to 1981-82	Moose	Black and grizzly bears	20-30	No increase in already moderate to high calf/cow ratios, and increasing population trend continues. Too few wolves killed to expect major change in moose. Population increase coincided with wolf removal in our adjacent experimental area.
Tanana & Goodpaster drainages 20D	Increase moose and caribou numbers and harvest	1980-81 to 1981-82	Moose and caribou	Black and grizzly bears abundant	10-40	Moose: no increase in calf/cow ratio in eastern portion where bears are abundant. Calf/cow ratio increased in western portion, and moose are increasing. Caribou: calf/cow ratio increased. Many wolves were killed in the calving area of Macomb herd, a control herd in the present study.
Fortymile drainage 20E	Increase moose numbers and moose harvest	1981-82	Moose and caribou	Grizzly bears abundant	80	No increase in calf/cow ratio. Grizzlies were very abundant relative to moose, probably <10 moose/grizzly. Grizzlies could be the major predator on calves, as in the Susitna-Nelchina basins (Ballard et al. 1981a; W. Ballard, unpubl. data). Effects of wolf removal could not be evaluated after 1 year.

* Harvest of wolves from all sources (normal hunting and trapping and ADF&G wolf removal program). Harvest levels of <30% may change the ungulate/wolf ratio very little during the following year.

gulate populations is either infrequent and short-lived or cyclic, it will be difficult for managers to maintain high ungulate density for extended periods without at times artificially reducing predation.

3. When wolf predation is the primary factor limiting an ungulate population, a manager has 2 choices. These are either wait for a natural recovery of prey while reducing or eliminating harvest or reduce the numbers of wolves while controlling harvest of prey. Periodic artificial removal of wolves is the most practical option because natural escapes by ungulates occur too infrequently to satisfy wildlife users.

4. To prevent extremes in ungulate density and ensure sustained use of wildlife, managers must correctly identify and alleviate factors that trigger and/or sustain ungulate declines. This is especially difficult where wolves remain abundant. Knowledge of prey/wolf ratios can assist in the initial interpretation of prey-wolf relationships. Predation can confound interpretation of vegetation-ungulate relationships because low survival of young can be viewed as an indication of food limitations when actually the population is limited by predation.

5. In retrospect, errors were made in managing the moose, caribou, and wolf populations in our study area during the early 1970's. Moose population size was not estimated accurately enough, and its rate of decline was initially underestimated. Consequently, appropriate hunting regulations were implemented belatedly. Also, biologists underestimated the combined impact of wolf predation and hunting on moose and caribou during the early 1970's and did not adequately manage wolves. During this period of intense hunting, biologists patiently awaited a compensatory rebound in yearling recruitment from improved range that would offset harvest. However, it was a futile vigil—calf moose and caribou became increasingly scarce through 1975. Mortality from severe winters, hunting, and wolf predation were largely additive. Underestimating the direct impact of man's harvest on moose and caribou pop-

ulations and its compounding effect on predation led to a grave management situation. Therefore, great caution must be exercised in harvesting ungulates in ecosystems where wolves are harvested lightly or are essentially naturally regulated.

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APPENDIXES

Appendix 1. Moose seen per hour of survey in 4 areas within the experimental area that were used to calculate the index of moose abundance for time periods from 1960-77.

Time period (years)	Survey areas			
	Tanana Flats	Foothills	Central mountains	South-western mountains
1960-65	58	127	169	
1966-67	35	143	103	137
1968-69	46	84		
1970-71	31	55	57	
1972-73	25	35	30	61
1974	11	22		
1975	11	18	14	48
1977	22	19		30

Appendix 2. Early winter calf/cow ratios among caribou from experimental area (Delta herd) and the Macomb central area (Macomb herd), and postcalving calf/cow ratios (Jun–Jul) in Denali National Park (McKinley herd).

Year	Control areas					
	Experimental area		Macomb		Denali	
	No. cows classified	Calves/100 cows	No. cows classified	Calves/100 cows	No. cows classified	Calves/100 cows
1969	410	28			1,878	25 ^a
1970	383	34			1,030	25
1971	738	16				
1972	795	11			861	4 ^b
1973	735	10			586	9
1974	868	2	269	15	1,723	17
1975	839	<13 ^c			301	10
After wolf reduction						
1976	572	45 ^{de}	159	20 ^{df}	666	16 ^{df}
1977	756	42	167	32	471	18
1978	324	39	234	20 ^g	618	38
1979	177	65			751	22

^a 1969–70 and 1973 data from Haber (1977). Sample size for 1969–70 is total number of caribou classified.

^b Unpublished National Park Service data, 1972, 1974–79.

^c No early winter survey in 1975. However, few calves could have been present because only 13 calves/100 cows were observed on 11–12 Jun. 1975 among 976 animals in postcalving aggregations.

^d Ratios after wolf removal are significantly different ($P < 0.01$) from ratios 3 years before wolf removal.

^e Ratio in 1976, after wolf removal, is significantly different ($P < 0.01$) from ratios 3 years before wolf removal.

^f Ratio in 1976 is not significantly different ($P > 0.1$) from ratios 3 years before wolf removal.

^g Calf/cow ratio was not recorded; however, calves were 12% of sample. This was equivalent to 20 calves/100 cows in 1976 and is assumed equivalent to that in 1978.

Appendix 3. Lamb/ewe and yearling/ewe ratios (Jun–Jul) for Dall sheep at Dry Creek mineral lick in experimental area and adjacent control area, Denali National Park. *N* equals total number sheep classified during survey in cohort's year of birth.

Cohort (year of birth)	Experimental area				Denali National Park			
	<i>N</i>	Lambs/100 ewes	Yearlings/100 ewes	Percent lambs surviving for 1 year	<i>N</i>	Lambs/100 ewes	Yearlings/100 ewes	Percent lambs surviving for 1 year
1969		64	31	48	307	49 ^a	46	94
1970		55	51	93	363	65	51	78
1971		50	16	32	310	9	21	72
1972	5,222 ^b	15	11	73	1,081	30	14	47
1973	3,223	38	25	66	843	39 ^c	32	82
1974	624	28	23	82	137	30	19	63
1975	882	28	16	57	114	31	13	42
After wolf reduction								
1976	727	36 ^{de}	17 ^{de}	47 ^f	339	33 ^{de}	20 ^{de}	61
1977	554	58	25	43	323	50	24	48
1978	977	41	19	46	212	56	24	43
1979	918	65	36	55	246	65	39	60

^a 1969–72 from Haber (1977).

^b Sample size is not available for 1969–71; however, they were in the range of samples for 1972–79.

^c From Whitten (1975).

^d Ratios after wolf removal are significantly different ($P < 0.05$) from ratios 3 years before wolf removal.

^e Ratio in 1976, after wolf removal, is not significantly different ($P > 0.1$) from ratios 3 years before wolf removal.

^f Percentage surviving after wolf removal was significantly lower ($P < 0.01$) than during the 3 years before wolf removal.