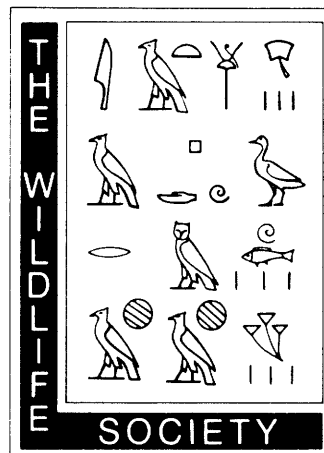


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THE ROLE OF PREDATION IN LIMITING MOOSE AT LOW DENSITIES IN ALASKA AND YUKON AND IMPLICATIONS FOR CONSERVATION

by

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FRONTISPIECE. Authors Rodney D. Boertje (left) and Daniel V. Grangaard (right) measure and radio collar an immobilized 19-year-old male grizzly bear to investigate grizzly bear density and predation in east-central Alaska (photo by R. M. Warbelow).

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

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Abstract: We address 3 major questions facing wildlife managers and wildlife users of northern ecosystems: (1) Why do moose (*Alces alces*) often remain at low densities relative to K carrying capacity (KCC) in lightly harvested systems? (2) What is the range of potential moose harvest yields from these northern systems? and (3) What are some steps that can reduce the controversy over management of moose, wolves (*Canis lupus*), and bears (*Ursus arctos* and *U. americanus*)? We assessed the roles that nutrition, snow, harvest, disease, and predation played in limiting moose densities in a 9,700-km² area in east-central Alaska during 1948–88. Our intensive study occurred during 1981–88, and we reviewed and reanalyzed historical data. We also present published and unpublished moose, wolf, and bear inventory data and moose harvest data from 35 other areas.

We identified predation by wolves and bears as the major factor limiting moose at low densities in the experimental area during 1976–88. Moose irrupted simultaneously with a predator reduction program (1948–60) that included poisoning. The subsequent decline of moose ended about 1976, at which time wolves declined and survival of moose increased. During the mid-1980's and after the recent wolf reduction (1981–83), we estimated that predators annually killed 31% of the postcalving moose population, compared with 6% killed by factors other than predation and 1.5% by humans. We concluded that mortality due to predation had a substantial additive component during the low-density phase.

Data from throughout Alaska and Yukon indicate that where wolves and bears were near KCC and moose were a primary prey, moose populations were within a low-density dynamic equilibrium (LDDE) (\bar{x} = 148, range = 45–417 moose/1,000 km² of moose habitat). Moose usually attained elevated densities (\bar{x} = 663, range = 169–1,447 moose/1,000 km²) where humans held wolves and/or bears below KCC. These elevated moose populations yielded approximate sustainable harvests of 20–130 moose/1,000 km² compared with 0–18/1,000 km² in systems with predators near KCC.

We describe several options and recommendations aimed at reducing the controversy over managing predation to elevate moose harvest. One management option, after moose reach elevated levels, is to maintain wolves at densities found in systems without predation management. Greater public participation in the development of wildlife management plans is recommended if conservationists are to unite in addressing the most serious long-term threat to moose–wolf–bear systems, i.e. the loss of habitat.

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INTRODUCTION

Predation is now well recognized as a major factor affecting the dynamics of moose (*Alces alces*) populations. During the 1980's, ecologists demonstrated that predation could strongly depress rates of moose population growth and accelerate declines to low densities through inversely density-dependent processes (Gasaway et al. 1983, Keith 1983, Messier and Crete 1985, Ballard and Larsen 1987, Crete 1987, Van Ballenberghe 1987, Bergerud and Snider 1988, Page 1989). In addition, growing evidence indicates that combined predation by wolves (*Canis lupus*) and bears (grizzly bears, *Ursus arctos*, and/or

black bears, *U. americanus*) can maintain moose populations within a low-density dynamic equilibrium (LDDE) for extended periods in unexploited and lightly harvested systems (Messier and Crete 1985; Ballard and Larsen 1987; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988; Larsen et al. 1989a,b). The LDDE is well below the level that could be supported by food, i.e., below K carrying capacity (KCC). KCC is conceptually the number of animals that can be supported at equilibrium in a steady environment and in the absence of time lags, harvest, and predation (McCullough 1979: 85); nutrition is the primary limiting factor at KCC.

The purpose of this monograph is to (1)

describe the relative effects of factors limiting moose at low densities in our intensive study area in Alaska, (2) use evidence from Alaska and Yukon Territory (Yukon) to provide support for the concept that combined wolf and bear predation can limit moose at densities below KCC where wolves and bears are lightly harvested and near their KCC, (3) describe how predation can affect moose harvest yields for humans, and (4) recommend conservation objectives to help reduce the controversy over managing predation.

To accomplish the above objectives, we (1) report results of our field studies in east-central Alaska, (2) present published and unpublished data on moose, wolf, and bear densities and moose harvest from 35 other areas in Alaska and Yukon with lightly harvested or harvest-limited predator populations, and (3) review published literature from North America. Our field studies were in an area that (1) was typical of wilderness in central and eastern Alaska and Yukon and which had predator species similar to most of Alaska and Yukon, (2) had a low moose density temporarily interrupted by an irruption (Caughley 1970) that coincided with an intense wolf and bear reduction program, and (3) had low harvest rates of moose and predators. We evaluate the role nutrition, snow, harvest, disease, and predation played in limiting moose at low densities in the experimental area. Data on moose, predators, and moose harvest rates in areas where predator populations were harvest-limited versus lightly harvested are presented and reanalyzed to extend our conclusions outside the experimental area. We used man-caused perturbations to help interpret the role of specific processes, as suggested by Sinclair (1979) and Caughley (1981).

We use the term "harvest-limited" to describe wolf and/or bear populations where intensive harvests maintained populations below food-limited densities, i.e., well below KCC. Thus, harvests were significant in shaping moose-predator relationships. We considered predator populations to be below KCC if significant population growth could be expected fol-

lowing cessation of harvest. Annual harvest rates of harvest-limited wolf populations generally exceeded 28% and reached 60% (e.g., Gasaway et al. 1983, Peterson et al. 1984, Ballard et al. 1987). Harvest rates of >25% were needed to lower wolf densities (Keith 1983, Fuller 1989, this study). Some harvest-limited wolf populations were temporarily harvested at rates <25% but remained below KCC because of time lags from prior intensive harvests and increased moose densities, e.g., on the Kenai Peninsula, Alaska (Peterson et al. 1984). Few harvest rates for bear populations were available, but long-term harvests of >7% can cause declines in grizzly bear densities (Reynolds 1990).

In contrast, we use the term "lightly harvested" to describe wolf and/or bear populations or moose-wolf-bear systems where harvests caused no or slight reductions in predators or density relative to their respective KCC. Thus, harvests were minor factors affecting relationships between moose and predators. An important point is that harvest-limited wolf populations are not necessarily at lower densities than lightly harvested wolf populations. For example, on the Kenai Peninsula during the 1970's, the harvest-limited wolf population exceeded densities found in lightly harvested wolf populations in central and east-central Alaska, in part because of the higher prey base on the Kenai (Peterson et al. 1984). Humans today influence all ecosystems containing moose, wolves, and bears; therefore, our focus was on understanding effects of minor (lightly harvested) versus major (harvest-limited) human intervention.

Although most moose, wolf, and bear populations in systems classed as lightly harvested have had low harvest rates during the past 15–30 years, humans had strong impacts on some of these populations previously. Market hunting of ungulates and use of poisons on predators occurred early in the 1900's, and government programs during the late 1940's and 1950's in Alaska reduced wolves and bears (Harbo and Dean 1983). We recognize that current systems described herein could in

part be products of past actions (Van Ballenberghe 1987).

The management focus of this monograph is intended to help wildlife managers and wildlife users resolve the controversy over predator conservation and management in moose-wolf-bear systems. We make recommendations that promote coexistence between humans and large predators. Our approach contrasts with management that largely extirpated wolves and grizzly bears in the continental United States and southern Canada. We believe understanding the biological realities can lead to management that accommodates diverse sets of values.

We define here our usage of several terms that have ambiguous connotations. "Conservation" is the protection, planned management, and wise use of natural resources. A "conservationist" is a person who advocates conservation. "Limiting factors" retard the rate of increase in population size or density and occur through density-dependent (stabilizing) and/or density-independent (potentially destabilizing) processes. "Regulating factors" affect population growth rate only in a density-dependent manner (Watson and Moss 1970; Messier 1991). We generally describe the effects of factors on moose population growth or density in the context of limitation rather than regulation and describe populations as being "limited" or "maintained" at low densities. "Maintained" adds a time component to the use of "limited."

Acknowledgments.—We are indebted to many people who contributed to this study. S. D. DuBois and D. J. Preston assisted with the calf mortality study, browse-use assessment, and the adult moose movement and mortality study; J. L. Hechtel and E. B. Crain assisted with daily radio-tracking of grizzly bears to estimate predation rates; and P. Valkenburg assisted in locating, capturing, and radio collaring grizzly bears. R. M. Warbelow piloted a helicopter and fixed-wing airplanes throughout the study. The U.S. Army 172nd Infantry Brigade (Alaska) provided helicopter support during spring 1985, and

the Alaska Railroad Corporation provided moose carcasses for attracting bears. R. T. Bowyer, M. Crete, F. Messier, S. D. Miller, J. W. Schoen, and V. Van Ballenberghe provided valuable comments on previous drafts.

STUDY AREA

We conducted the study in an experimental area (9,700 km²) where predator numbers were reduced and in 2 control areas (Washington Creek, 1,200 km²; North Ladue, 1,150 km²) where predator numbers were not reduced (Fig. 1). The study area (experimental and control areas) was in Game Management Unit (GMU) 20E in east-central Alaska and adjacent Yukon. The study area was centered around 64°N latitude and 142°E longitude.

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

Excellent moose habitat dominated the 2 control areas. Wildfires burned much of the control areas during 1969, and willow and birch predominated during the study.

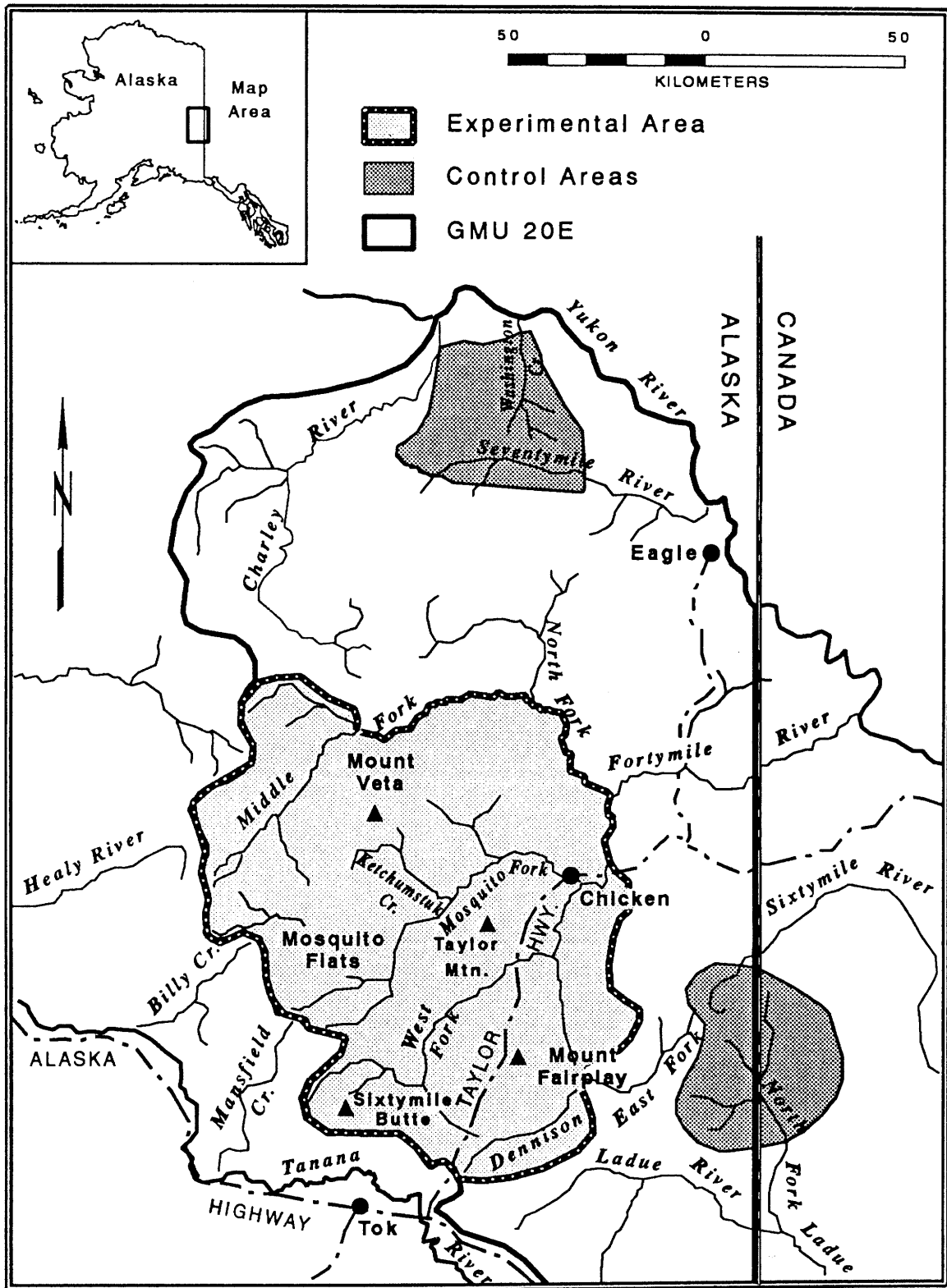


Fig. 1. Experimental area (with wolf removal) and 2 control areas (without wolf removal) in Game Management Unit (GMU) 20E, Alaska, and adjacent Yukon.

The unburned uplands supported predominantly willow, birch, and scattered black spruce; unburned lowlands supported predominantly black spruce interspersed with birch and willow. Elevations are 600–1,650 m in the North Ladue control area and 250–1,100 m in the Washington Creek control area.

The climate is subarctic and continental. "Winter" includes the months of October–April. Leaves emerged on most shrubs during 1–7 June 1983–86, and leaf senescence occurred during the last 2 weeks of August. The total annual precipitation averaged 24 cm at Tok (National Oceanic and Atmospheric Administration 1986) (Fig. 1). Snow depths were usually <60 cm, and snow usually remained loosely packed except where windblown at high elevations.

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

METHODS

Moose Population Status

Estimating Moose Abundance and Population Trend.—Moose population size was estimated in a 7,700-km² portion of moose habitat in the experimental area during October 1981 and 1988 using stratified random sampling (Gasaway et al. 1986). Moose habitat included all the area, exclusive of large lakes, below the upper

limits of vegetation characteristically used by moose. Randomly selected sample units from each stratum were searched at an intensity averaging 1.7 minutes/km² from a Super Cub or Citabria airplane flying at 105–120 km/hr and 60–120 m above ground. When moose were seen by the pilot or observer, the airplane was diverted from the flight path to circle the moose while observers searched for additional moose. Snow depths ranged from 10 to 40 cm, and tracks in snow were used as clues in locating moose. During 1988, a sightability correction factor (SCF) for undercounting bias was estimated by resurveying sample units at a higher search intensity (Gasaway et al. 1986); this SCF was applied to the 1981 and 1988 density estimates. During 1981, procedures to estimate a SCF had not been developed for low-density populations.

Relative abundance of moose and population trend in the experimental area during 1956–88 were reconstructed from several sources. For the period 1956–64, we estimated λ (finite rate of population change) using recruitment data from aerial winter composition surveys and an estimate of adult mortality from Gasaway et al. (1983) (*see* formulas in footnotes of table on page 17). We deemed these aerial composition surveys unsuitable for estimating trends in number of moose because of variation in timing and areas flown. For the period 1966–88, we used aerial surveys from 5 areas to estimate trend. Number of moose observed per hour during surveys, rather than number of moose observed, was used as the trend indicator during this period because the size of the area searched varied among years and boundaries were not defined. Trend in each of the 5 areas was estimated by plotting the median of each group of 3 consecutive points (Tukey and Tukey 1977). Overall population trend was subsequently illustrated by plotting the median value of the 5 survey areas for each year during 1966–88. Surveys in individual areas spanned 23, 23, 18, 13, and 12 years. Survey conditions did not allow data collection in 1 of 8 years, and no trend surveys were attempted during 1981. Miss-

ing annual values were estimated by interpolation before constructing the composite curve.

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

Three areas were surveyed annually in the control areas during 1982–87 to evaluate moose population trends. One survey area was in the Washington Creek control area, and two were in the North Ladue control area. Numbers of moose observed in each survey area were regressed against year; trends were considered significant if the 90% CI for the slope of the regression line did not include zero. The 3 survey areas had definite boundaries and ranged in size from 119 to 162 km². Survey methods were the same as those used to estimate population size, except stratification was unnecessary (Gasaway et al. 1986). No other data were collected in the control areas.

Estimating Recruitment, Adult Mortality, and Harvest of Moose.—Sex and age of moose observed in the experimental area during early winter aerial surveys from 1956 to 1988 were used to estimate calves or yearlings per 100 adult cows and the proportion of recruits (yearlings) among yearlings and adults. Moose observed were classified as calf, yearling bull, adult bull, or cow. Number of total yearlings in the sample was assumed equal to twice the number of yearling bulls. We estimated the number of adult cows (≥ 24 months old) in a sample by subtracting the number of yearling bulls observed from the total cows observed; i.e., we assumed numbers of yearling bulls and yearling cows were equal (Gasaway et al. 1983).

Methods for estimating adult mortality are cited in tables and text, except for the period 1984–87. Nonhunting adult mortality was estimated during 1984–87 using data from 33 cow and 5 bull radio-collared moose and the computer program “SURVIVE” (White 1983). Radio-collared moose were located visually or by telem-

etry at least once a month during March 1984 through March 1987 to estimate mortality rates. Radio collars contained a mortality sensor that doubled the pulse rate if the collar remained motionless for 4 hours.

We estimated the annual moose harvest rate in the experimental area during 1965–76 as follows:

1. The 1976 posthunt population was estimated to equal the number of moose estimated during 1981 because the number of moose observed per hour of survey varied little during 1976–81.
2. Posthunt moose numbers were extrapolated from 1976 to 1965 using the mean estimated finite rate of change in moose observed per hour of survey as an annual index of abundance (Gasaway et al. 1983).
3. Prehunt population size was estimated by adding annual reported harvest $\times 1.177$ (to adjust for unreported harvest; Gasaway et al. 1983) to the annual posthunt population projection.
4. We estimated that the percentage of the GMU 20E harvest from the experimental area during 1965–76 was similar to the percentage during 1983–88 (62%) because we observed similar moose and hunter distributions during the 2 periods.

Hunting mortality rate during the 1980's was based on the reported harvest $\times 1.177$ and estimates of population size.

Estimating Moose Physical Status, Population Age Structure, Pregnancy Rates, and Twinning Frequency.—Four characteristics were determined from 40 immobilized moose (≥ 22 months old) in the experimental area: (1) body form and composition based on a subjective 0 to 10 class ranking (Franzmann 1977) (Table 1), (2) total length of moose measured along the dorsal body contour from the center of the small hairless patch on the nose to the tip of the tail bone (Franzmann and Schwartz 1983), (3) age from cementum annuli in an extracted central incisor (Gasaway et al. 1978), and (4) pregnancy by rectal palpation (Arthur 1964). Immobilization procedures were described by

Table 1. Classes and criteria used to evaluate the physical condition of moose immobilized during 1984–87 in the experimental area, east-central Alaska (from Franzmann 1977).

Class	Criteria
10	A prime fat moose with thick, firm rump fat by sight; well fleshed over back and loin; shoulders round and full.
9	A choice fat moose with evidence of rump fat by feel; fleshed over back and loin; shoulders round and full.
8	A good fat moose with slight evidence of rump fat by feel; bony structures of back and loin not prominent; well-fleshed shoulders.
7	An "average" moose with no evidence of rump fat but well fleshed; bony structures of back and loin evident by feel; shoulders with some angularity.
6	A moderately fleshed moose beginning to demonstrate one of the following conditions: definition of neck from shoulders, upper foreleg (humerus and musculature) distinct from chest, or rib cage prominent.
5	A condition in which 2 characteristics listed in Class 6 are evident.
4	A condition in which all 3 characteristics listed in Class 6 are evident.
3	A condition in which the hide fits loosely about neck and shoulders; head is carried at a lower profile; walking and running postures appear normal.
2	Signs of malnutrition are obvious; outline of scapula is evident; head and neck are low and extended; moose walks normally, but trots and paces with difficulty and cannot canter.
1	A point of no return. A generalized appearance of weakness. The moose walks with difficulty and can no longer trot, pace, or canter.
0	A dead moose from malnutrition and/or accompanying circumstances.

Boertje et al. (1987). Percent fat in marrow of long bones of dead moose (Neiland 1970) was used as an index of severe malnutrition. Twinning frequency was estimated by observing all radio-collared cows daily during 15–24 May 1984 and at 3–7-day intervals thereafter until 15 June 1984. Moose were located from an airplane (Bellanca Scout or Piper Super Cub) equipped with radiotelemetry equipment (Telonics, Inc., Mesa, Ariz.).

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

Radio transmitters and expansion collars made of elastic bandages were described by Boertje et al. (1987). Radio collars contained a mortality sensor that doubled the pulse rate if the collar remained motionless for 1–2 hours. Transmitters were rinsed in alcohol to remove scent before being sewn into the washed and well-rinsed collars. Subsequently, we handled collars with sterilized gloves and stored them in a plastic bag.

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

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

Estimating Browse Use.—During May and June 1982 and 1984, we estimated browse use in the experimental area at 100

points systematically selected along each of 29 500-step transects (Boertje et al. 1985). We subjectively chose sites that received relatively heavy use by moose during winter. Sixteen transects were in the Mosquito Flats, an area of relatively high winter moose density; four were in high-concentration rutting areas near the Mosquito Flats; four were in an 18-year-old burn with excellent moose habitat; and five were in moose habitat along the Taylor Highway. Use of current growth of the nearest available browse plant was categorized as none (0%), low (1–25%), moderate (26–75%), and high (76–100%). Mean percentage of twigs browsed was estimated by multiplying the number of plants in each browse category by 0, 13, 50, or 88%, depending on the use category, and dividing by the total number of plants in all categories.

Wolf Population Status

Estimating Wolf Abundance.—Wolf distribution and abundance in the experimental area was primarily estimated by counting wolves or wolf tracks in snow from the air during October–April (Gasaway et al. 1983). To assist in these estimates during winters 1980–81 through 1988–89, 1–3 wolves in 9 of the 12–16 annual study packs were immobilized with darts or captured in leg-hold traps or locking snares and then radio collared. Radio-collared wolves were present annually in 1–6 of the 12–16 packs. We administered 12.5 mg Sernylan (50 mg phencyclidine hydrochloride/ml; Bio-Ceutic Laboratories, St. Joseph, Mo.) using a jabstick or 2.5 mg M-99 (etorphine hydrochloride; D-M Pharmaceuticals, Inc., Rockfield, Md.) via darts.

Wolf densities are based on our best estimate of wolf numbers in a 15,500-km² area, which encompassed all the wolf pack territories in, or partially in, the experimental area. Population size during late winter was the sum of observed wolves in packs, additional wolves enumerated based on tracks, plus 10% of the early winter population to account for single wolves not

associated with packs (Mech 1973). Early winter population size, which was used to calculate prey : wolf ratios and population trend, was estimated using early winter counts, when available, or late winter counts plus the number of wolves harvested before late winter surveys. Early winter population size occasionally was underestimated because wolves dying from natural causes before late winter surveys could not be included unless they were counted during early winter.

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

Harvest and Removal of Wolves.—The numbers and locations of wolves harvested by trappers and hunters in the experimental area were obtained from a mandatory reporting program during 1972–89. In addition, Alaska Department of Fish and Game (ADF&G) staff killed some wolves that ranged fully or in part in the experimental area; a large majority of these was killed during winters 1981–82 and 1982–83. Most wolves killed by ADF&G were shot from a helicopter or airplane; the remainder were trapped or snared.

Determining Wolf Food Habits.—Wolf food habits in and adjacent to the experimental area were determined from (1) examination of wolf stomach contents, (2) radiocesium (Cs-137) levels in 1 kg of wet muscle from wolves and caribou (Holleman and Stephenson 1981), (3) scat analysis (Floyd et al. 1978), and (4) observations of the carcasses of large prey during the monitoring of a radio-marked pack. Hunters and trappers contributed wolf carcasses.

The percent caribou in each wolf pack's

winter diet (\bar{x}) during the month prior to the wolves' deaths (Holleman and Stephenson 1981) was calculated using a stochastic, propagation-of-error model. A bootstrap procedure (Efron 1982) was integrated in the model to produce estimates of standard error. This model chose variables at random for each wolf using the following formula and ran 1,000 replications for each of 16 wolf packs:

$$\bar{x} = 100[(A - B) \cdot (C)^{-1}] \cdot [(D) \cdot (E)^{-1} (1.16)] [(F)^{-1}]$$

where

- A = Cs-137 concentration in 1 kg of muscle from wolves in and adjacent to the experimental area (n for individual packs = 2, 2, 2, 3, 4, 5, 6, 6, 8, 8, 11, 12, 12, 14, 18, 22),
- B = Cs-137 in wolves from an area of central Alaska devoid of caribou ($n = 59$),
- C = Cs-137 in caribou from the experimental area ($n = 42$),
- D = ingesta-free wolf body weight from central Alaska ($n = 390$),
- E = an *in vivo* kinetic factor described by a 2-compartment model, which reflects the retention and elimination of Cs-137 in wolves ($n = 5$; Holleman et al. 1971, Holleman and Luick 1976), and
- F = kg food available/39 kg wolf/day from 22 North American estimates where moose and caribou were the primary prey and prey were not highly vulnerable.

The constant (1.16) is the additional percent muscle in a wolf compared with a caribou in terms of body weight (Holleman 1974, Adamczewski et al. 1987). The average percent caribou in all the wolves' diets was calculated by weighting percent caribou in the diets of each wolf pack by the sum of each respective pack's early winter numbers during 1981–88.

All Cs-137 samples were corrected to a single date based on (1) the half-life of Cs-137 in caribou from the Nelchina Herd during 1969–90 ($n = 37$, R. D. Boertje, unpubl. data) and (2) the additional Cs-

137 introduced to caribou ($n = 9$) in the experimental area from the Chernobyl nuclear plant (U.S.S.R.) explosion, calculated from Cs-137 to Cs-134 ratios. Variation in these factors was integrated into the model described above.

Assessing Wolf Productivity.—Examination of female wolves ≥ 1 year old killed in the experimental area during March or April 1980–88 provided data on wolf productivity. Wolves < 1 year old were identified by tooth development and wear and by the uncalcified epiphysis at the distal end of the radius-ulna (Rausch 1967). Ovaries were hardened in 10% formalin for at least 2 weeks and then hand-sectioned at 1-mm intervals to count corpora lutea.

Sources of Data

Synthesis of data on prey and predator densities, sex and age composition of moose populations, and moose harvests from broad expanses of Alaska and the Yukon required that we cite numerous unpublished agency inventory reports. Methods used in these unpublished reports were similar to those in published reports.

PREY AND PREDATOR POPULATIONS IN THE EXPERIMENTAL AREA

Moose Population Status

Population Trend and Density.—The moose population irrupted from about 1950 through the early 1960's and then rapidly declined (Fig. 2). Although no systematic trend surveys occurred during the irruption, a marked increase in the moose population was observed from the early 1950's through 1964–65 (D. V. Euers, who initiated predator reduction efforts by the U.S. Fish and Wildlife Service [USF&WS] in the experimental area during 1949; R. H. Bishop, biologist, ADF&G; S. D. Jones, predator removal officer, USF&WS; pers. commun.). Also, (1) the high yearling recruitment observed during composition surveys (1956–60, Table 2) was typical of irrupting populations (Pimlott 1959, Gas-

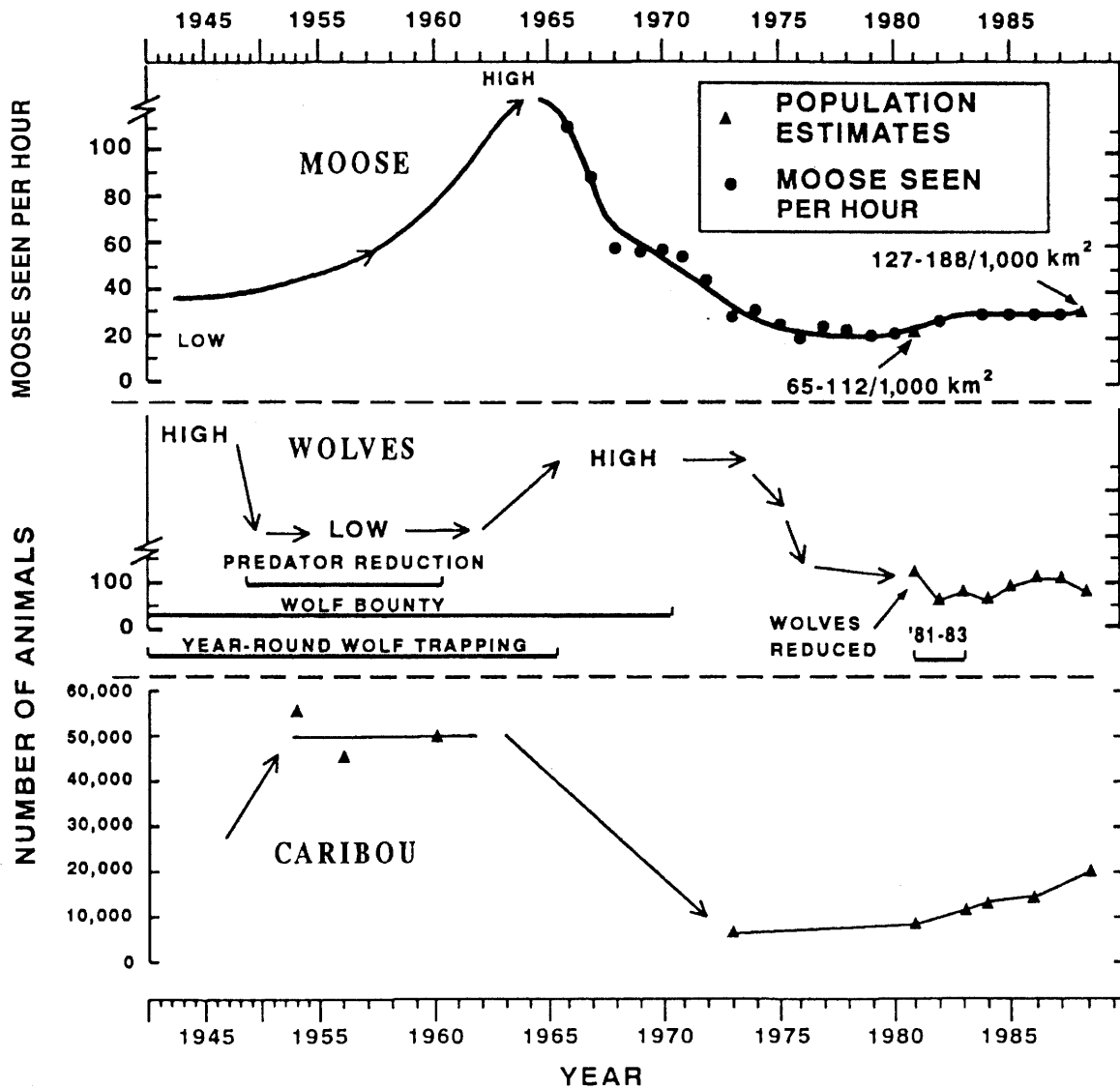


Fig. 2. Estimated and relative numbers of moose, wolves, and caribou in the experimental area, east-central Alaska, 1940–88. Arrows indicate trends and approximate relative abundance based on qualitative observations. The 90% CI's for moose densities are shown for 1981 and 1988.

away et al. 1983), and (2) the preponderance of young year classes during 1965–66 suggests this lightly hunted population had recently grown rapidly (59 bulls : 100 cows during 1966, $n = 509$ moose; Fig. 3). During the irruption, we estimated λ at 1.18 using recruitment and mortality estimates (Table 3). The moose population throughout the area rapidly declined ($\lambda = 0.85$, Table 3) from the mid-1960's through 1976 (Fig. 2), based on surveys in 5 widely distributed areas (Fig. 4).

Following the irruption and decline, a

low-density population again prevailed (Fig. 2). Numbers of moose observed per hour remained largely unchanged during 1976–81. During 1981, density in the 7,700 km² of moose habitat west of the Taylor Highway was estimated at 88 moose/1,000 km² (probable 90% CI = 65–112/1,000 km²). Moose density in this area significantly increased to 157 moose/1,000 km² (90% CI = 127–188) between 1981 and 1988 ($P < 0.001$, 2-tailed Student's t test on densities uncorrected for sightability). Estimates of annual finite rates of increase

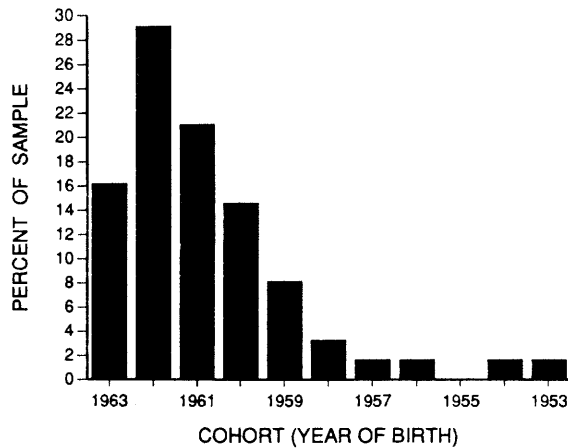


Fig. 3. The year classes of 62 bull moose harvested during 1965 and 1966 in Game Management Unit 20E, east-central Alaska (data from Buchholtz and Jennings 1974). We included only those cohorts that were older than 18 months during 2 hunting seasons, i.e., 1964–66 cohorts were excluded.

in the early winter population during 1981–88 are (1) 1.09 (90% CI = 1.05–1.13) using 1981 and 1988 moose population estimates and (2) 1.04 and 1.05 based on a population model and estimates of mortality and recruitment (*see Causes and Extent of Calf and Adult Moose Mortality*; Table 3).

Moose Production and Mortality.—Calf production by adult cows during May 1984 in the experimental area was high (138 calves/100 cows ≥ 24 months old) compared with many other North American moose populations (Pimlott 1959; Simkin 1965, 1974; Blood 1974). Our estimate is based on (1) 11.5% (13 of 113) 24-month-old cows among cows older than 12 months (estimated from the \bar{x} of female yearlings per 100 adult cows during 1981–87, Appendix A), (2) pregnancy rates of 100% for cows ≥ 36 months old ($n = 27$ radio-

lared cows during 1984) and 30% for 24-month-old cows (a moderate value from Blood [1974] and Simkin [1974]), and (3) twinning frequencies of 52% for cows ≥ 36 months old ($n = 27$ cows with calves during 1984) and 0% for cows 24 months old (Pimlott 1959, Blood 1974).

Increased calf mortality, reflected in significantly fewer calves per 100 cows after 1965 ($P < 0.001$, 2-tailed Mann-Whitney test), coincided with the population decline and subsequent low-density phase (Table 2). Estimated calf mortality (calculated as $1 - [(\bar{x} \text{ calves per 100 adult cows} \div 138 \text{ calves produced by these cows}) \times (\text{adult survival rate in Table 3 prorated to 5 months})] \times 100$) averaged 55% by 5 months of age during the 1956–60 portion of the irruptive increase, compared with 89% mortality during the 1966–75 portion of the decline and 87% during the recent low-density phase (1976–88). Most calf mortality occurred shortly after birth, based on the mortality of radio-collared calves during 1984; 76% of these 33 calves died within 8 weeks of birth and 76–79% within 5 months (Fig. 5).

Estimated mortality rates of adult moose were highest during periods of population decline and lowest during periods of population growth (Table 3). Total estimated adult mortality rates averaged 22% annually during the precipitous decline (1966–76) of which approximately 19% was from nonhunting causes (*see Harvest as a Limiting Factor*). In contrast, annual total and nonhunting mortality rates during 1981–88 were estimated as 8.7% (95% CI = 2.9–14.5%) and 6.8% (1.6–12.0%), respectively, based on monitoring 38 radio-

Table 2. Moose calves per cow, yearlings per cow, and proportions of recruits (R) for cohorts born in the experimental area during 4 periods, east-central Alaska, 1955–88. Adult cows were ≥ 29 months old. Data are from aerial surveys during early winter. Data for individual years are in Appendix A.

Population phase	Birth year of cohort	Total moose classified (range among years)	Calves per 100 adult cows			Yearlings per 100 adult cows			Yearlings per yearlings + adults (R)		
			\bar{x}	SD	No. yrs	\bar{x}	SD	No. yrs	\bar{x}	SD	No. yrs
Irruption	1955–60	129–390	64	21.3	5	72	51.0	5	0.26	0.10	5
Decline	1966–75	124–509	16	8.1	10	14	8.0	10	0.09	0.04	10
Low density	1976–80	73–235	13	8.5	5	24	10.2	5	0.12	0.04	5
Low density	1981–88	255–585	22	5.0	8	26	9.2	6	0.13	0.04	6

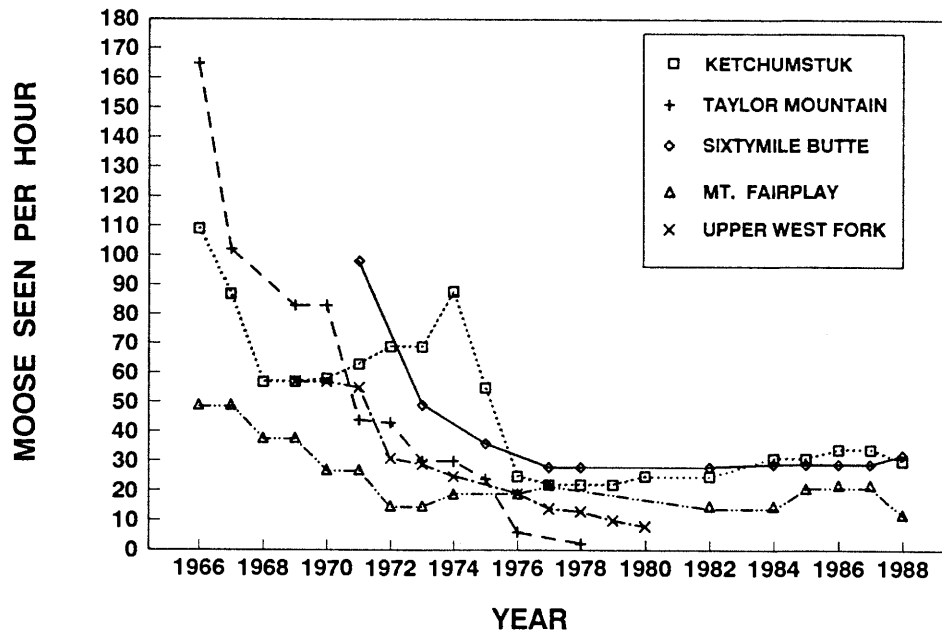


Fig. 4. Trends in number of moose seen per hour in 5 aerial survey areas in the experimental area, east-central Alaska, 1966–88.

collared adult moose during March 1984 through March 1987. Cow moose in this sample had a mean age of 8.5 years (SD = 3.4, $n = 31$). The contrasting rates for nonhunting mortality, 19 and 6.8%, above

were similar to estimates for radio-collared adult moose during a precipitous decline (20%) and subsequent irruption (6%) in another interior Alaska population (Gasaway et al. 1983).

Table 3. Mean estimated adult mortality rates, proportion of recruits, and finite rates of change for the moose population in the experimental area during 4 periods (Fig. 2), east-central Alaska. The range of observed or calculated annual values is in parentheses.

Phase of moose population	Mean estimated annual adult mortality rate (\bar{M})	Mean estimated proportion of recruits (\bar{R}) ^a	Mean estimated finite rate of population change (λ)	Data sources and assumptions
Irruption (1950–early 1960's)	0.08	0.22 (0.18–0.28)	1.18 ^b (1.15–1.28)	\bar{M} from Gasaway et al. (1983), where moose increasing and wolves scarce (Fig. 2); \bar{R} for 1955–57 and 1959 cohorts (Appendix A).
Rapid decline (1966–76)	0.22 ^c (0.17–0.28)	0.09 (0.03–0.16)	0.85	\bar{R} for 1966–75 cohorts (Table 2); λ from regressing the log e of moose observed per hour of survey against year, 1966–76 (Fig. 2).
Low-density (1976–81)	0.15 ^c (0.06–0.16)	0.12 (0.06–0.16)	1.00	\bar{R} for 1976–80 cohorts (Table 2); λ from stationary trend (Fig. 2).
Low-density (1981–88)	0.09 ^d (0.03–0.14) ^e	0.13 (0.09–0.17)	1.05 ^b (1.00–1.10)	$\bar{M}_n = 0.068\%$ from radio-collared moose 1984–87, and $\bar{M}_h = 0.026\%$ from harvest reports 1982–88; \bar{R} for 1981–87 cohorts (Table 2).

^a \bar{R} = yearlings ÷ yearlings and adults, in the annual sample of moose seen during aerial surveys.
^b $\lambda = (1 - \bar{M}) / (1 - \bar{R})$, where λ was estimated annually using constant \bar{M} and the annually observed \bar{R} (Bergerud and Elliot 1986).
^c $\bar{M} = 1 - \lambda(1 - \bar{R})$, where \bar{M} (the number dying during a year ÷ number starting the year) was estimated annually using constant λ and annually observed \bar{R} (Bergerud and Elliot 1986).
^d $\bar{M} = 1 - (1 - \bar{M}_h)(1 - \bar{M}_n)$, where \bar{M}_h = mean mortality from hunting and \bar{M}_n = mean nonhunting mortality (Bergerud and Elliot 1986).
^e 90% CI from total mortality of radio-collared moose.

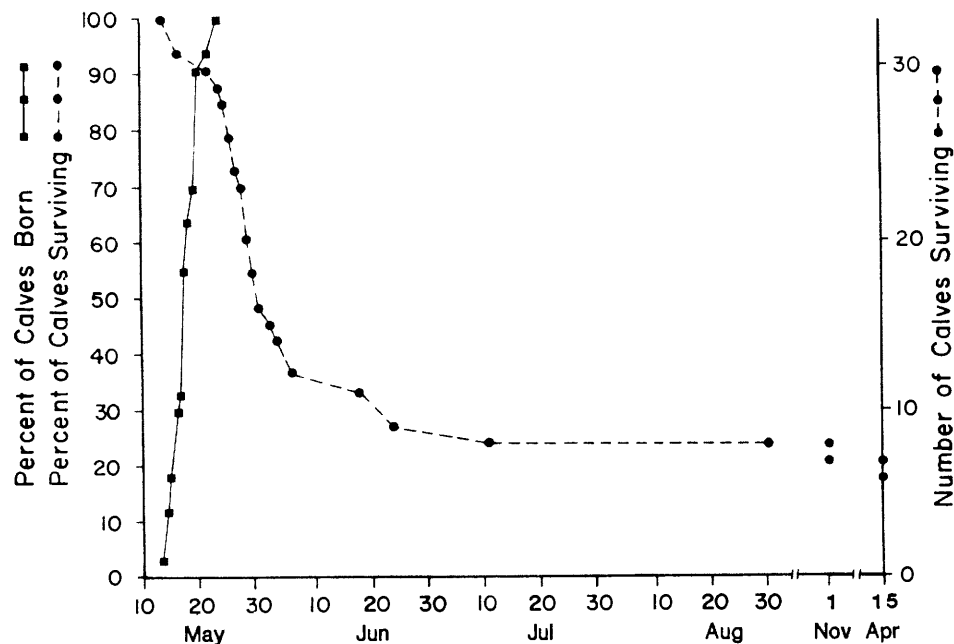


Fig. 5. Chronology of birth and death of 33 moose calves radio-collared during May 1984 in and near the Mosquito Flats in the experimental area, east-central Alaska. The ranges of values during November and April result from the unknown fate of 1 calf.

Caribou Population Status

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

Wolf Population Status

Historical Wolf Abundance and Harvest, 1940–81.—The high density of wolves in the region (Murie 1944) was rapidly reduced by a federal predator reduction program during 1948–60 (Kelly 1950a, 1957; Olson 1959a cited in Davis et al. 1978) (Fig. 2). Wolves were killed by strychnine-laced baits dropped from air-

planes, cyanide guns (coyote-getters), shooting from airplanes, year-round trapping, and snaring (Kelly 1950b, 1953, 1958). Bounties encouraged public harvest using the above methods, except that poisons were restricted to government use.

After predator removal ceased in 1960, our observations indicated wolves again became abundant and subsequently declined during the mid-1970's after prey became scarce (D. V. Grangaard, pers. obs.) (Fig. 2). The decline in wolf numbers was reflected by the number of wolves annually trapped in the experimental area by D. V. Grangaard between 1971 and 1980 on the same line and with similar effort among years. He trapped an average of 32 wolves (SD = 12) during winters 1971–72 through 1975–76, 15 wolves during winter 1976–77, and an average of 6 (SD = 4) during 1977–78 through spring 1980. During early winter 1981, ADF&G began accurately estimating wolf abundance and began a wolf reduction program (Table 4).

The wolf population was lightly harvested (\bar{x} = 11% annual harvest rate of

Table 4. Estimated wolf population size and number harvested in a 15,500-km² area, which contains all 16 packs (Appendix B) that ranged entirely or partially in the experimental area, east-central Alaska.

Winter period	Best estimate of early winter wolf population	Number of wolves killed				Percentage of early winter population killed	No. of wolves remaining during late winter surveys
		ADF&G	Public	Observed natural	Total		
1972-73			67		67		
1973-74			56		56		
1974-75			26		26		
1975-76			35		35		
1976-77			20		20		
1977-78			27		27		
1978-79			9		9		
1979-80			11		11		
1980-81		9 ^a	13		22		
1981-82	125 ^b	56	17		73	58	52
1982-83	64	15	15		30	47	34
1983-84	87	7	17		24	28	63
1984-85	79		13	1	14	18	65
1985-86	97		19		19	20	78
1986-87	114	6 ^c	24	1	31	27	83
1987-88	111		35		35	32	76
1988-89	87		7		7	8	80

^a These 9 wolves were removed from packs partially in the experimental area (Appendix B).

^b Estimated number of wolves pre-ADF&G wolf removal in the 15,500-km² area.

^c These wolves were collected to obtain radioecesium and reproductive data.

1981 population) and stable in and adjacent to the experimental area for at least 3 years before the 1981-83 wolf removal (D. V. Grangaard, pers. obs.) (Table 4). This harvest rate is below sustained harvest rates ($\geq 25\%$) that have precluded wolf population growth in the experimental area and elsewhere (Keith 1983, Ballard et al. 1987, Fuller 1989, present study).

Wolf Population Size, Harvest, Productivity, and Land Tenure System, 1981-88.—ADF&G wolf removal and public harvest during 1981-83 reduced the wolf population. Subsequent harvest by public hunters and trappers maintained the population below preremoval size (Table 4). From 1983 to 1988, annual kill rates of 28, 18, 20, 27, and 32%, respectively, resulted in no net change in wolf numbers (Table 4). These data indicate the reduced wolf population can sustain harvests of about 25% of the early winter population, given low to moderate prey abundance relative to wolves (16-39 moose equivalents/wolf).

Significantly lower wolf productivity ($P < 0.1$, 2-tailed Student's *t* test) occurred in the experimental area before wolf removal compared with after wolf removal.

This indicates wolves were nutritionally limited by the initial low moose and caribou densities (Fig. 2), i.e., wolves were near KCC before wolf removal. The average number of corpora lutea per female > 1 year old before wolf removal was only 3.2 ± 2.7 (95% CI, $n = 6$) compared with 5.4 ± 1.1 ($n = 14$) after wolf removal.

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

Grizzly Bear Population Status

During 1986, grizzly bear density in a 4,000-km² portion of the experimental area was estimated to be 16 bears of all ages/1,000 km² on 1 May and 12 bears/1,000 km² on 1 November (Boertje et al. 1987). Approximately 65% of the spring bear population was ≥ 2 years old.

The grizzly bear population was intensively exploited during the 1950's. Poisons and snares used during the wolf reduction

program (1948–60) killed grizzly and black bears incidental to killing wolves (P. E. K. Shepherd and S. D. Jones, predator removal officers, USF&WS, pers. commun.). Also, miners shot bears to minimize conflicts, and bears were killed in snares that were set year-round to catch wolves for bounty (O. E. Burris, biologist, ADF&G, pers. commun.).

The grizzly bear population was lightly exploited in the experimental area during 1961–81 and moderately exploited during 1982–88. During 1961–81, annual harvests of 0–6 grizzly bears ($\bar{x} = 2$, $n = 21$, $SE = 0.3$) were reported through the mandatory reporting system (ADF&G, unpubl. data). Hunting regulations were liberalized for grizzly bears during 1981. During 1982–88, harvests increased to 6–14 grizzly bears ($\bar{x} = 12$, $n = 7$, $SE = 1.1$), yielding an 8% mean annual harvest rate, assuming spring grizzly bear densities were comparable with densities in the 4,000-km² grizzly bear study area (16 bears/1,000 km²). An 8% harvest rate appears sufficient to cause the population to decline slowly. For example, Reynolds (1990) reported an 8–9% annual harvest rate resulted in a 2% annual decline in a central Alaska grizzly bear population during an 8-year study.

Black Bear Population Status

Black bears were scarce in the experimental area during the 1980's. We observed only 12 different black bears while capturing and monitoring grizzly bears in a 4,000-km² portion of the experimental area during 150 days during 1985–86 (Boertje et al. 1988).

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

FACTORS LIMITING MOOSE DENSITY IN THE EXPERIMENTAL AREA

In this section, we assess the roles that nutrition, snow, harvest, disease, and pre-

ation played in limiting moose at low densities in the experimental area. As defined previously, "limiting factors" retard the rate of increase in population size by density-dependent or density-independent processes. We used inductive and hypothetico-deductive methods to build arguments about the importance of each factor, and we acknowledge the limitation of inductive method to identify the causes of an event. Inductive methods provide post facto knowledge on correlations between facts. In contrast, hypothetico-deductive methods help to generate facts by testing predictions from prior hypotheses (Romesburg 1981).

Nutrition as a Limiting Factor

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

Decline Phase.—Nutrition could have been one of the major factors limiting moose at peak density and during the early decline. Reduced recruitment and adult survival early in the decline were suggestive of density-dependent processes nutritionally limiting the population (McCullough 1979) (Tables 2, 3). Reduced recruitment and adult survival, however, are equivocal indicators of nutritional stress. Deep snow, when moose are at high densities (Rolley and Keith 1980, Gasaway et al. 1983), and predation (Gasaway et al. 1983; Larsen et al. 1989a,b) can similarly reduce recruitment and adult survival.

Based on relative size of Alaskan moose, nutrition was likely not a major factor limiting moose population growth during the latter half of the decline (1970–76). For example, cow moose ≥ 45 months old born

during the decline were the largest (\bar{x} = 318 cm, n = 22, SE = 2.8) of 20 populations measured in Alaska; by comparison, the mean lengths of cows from 7 increasing Alaskan populations ranged between 289 and 315 cm (\bar{x} = 298) (Franzmann and Schwartz 1983, Boertje et al. 1987). The large size of moose in the experimental area indicated nutritional status during the period of skeletal growth (up to 36 months old for cows) was excellent (Palsson and Verges 1952, Franzmann et al. 1978).

Low-density Phase, 1976–88.—The size, condition, and reproductive rate of moose in the experimental area during the low-density phase, 1976–88, were inconsistent with predicted values for a nutrition-limited population as shown by the following:

1. The mean total length of cow moose ≥ 45 months old and born after 1975 in the experimental area (\bar{x} = 306 cm, n = 12, SE = 3.5) was (1) large relative to mean lengths from 6 Alaskan populations that were at high densities and stationary or declining in numbers (\bar{x} of \bar{x} 's = 288 cm, range of means = 272–302) and (2) among the largest means from 7 Alaskan populations that were increasing in numbers (\bar{x} of \bar{x} 's = 298 cm, range of means = 289–315) (Franzmann and Schwartz 1983, Boertje et al. 1987).
2. A physical body condition index (Franzmann 1977) estimated during late winter indicated captured moose were in average condition for that season (\bar{x} = 7.0, n = 39, SE = 0.2).
3. Only 4 of 42 adult moose dying from predation and other nonhuman causes during 1981–87 had <20% marrow fat, a fat level indicating severe malnourishment (Peterson et al. 1984). These 4 moose may have been in poor condition because they were old—12 and 13 years for 2 bulls and 17 years each for 2 cows. Few bulls live past 13 years (W. C. Gasaway, unpubl. data) and few cows live past 17 (Peterson et al. 1984).
4. We observed no starvation of moose during 1975–88, despite at least 1 winter (1978–79) with relatively deep snow (Figs. 6, 7).
5. The 52% twinning and 100% pregnancy rates observed in the experimental area were well above the values reported from populations near or above KCC (Table 5).

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

Snow as a Limiting Factor

We found no evidence that deep snow and the accompanying nutritional stress precipitated the decline of moose during the mid-1960's, or played a significant role in maintaining the decline and subsequent low densities. When moose were near peak densities, snow depths in the experimental area did not exceed 90 cm (Fig. 6), a depth above which substantial mortality has been observed in interior Alaska when moose densities were moderate to high (Bishop and Rausch 1974, Coady 1974b, Gasaway et al. 1983). Additionally, declines in relative cohort strength and calves or year-

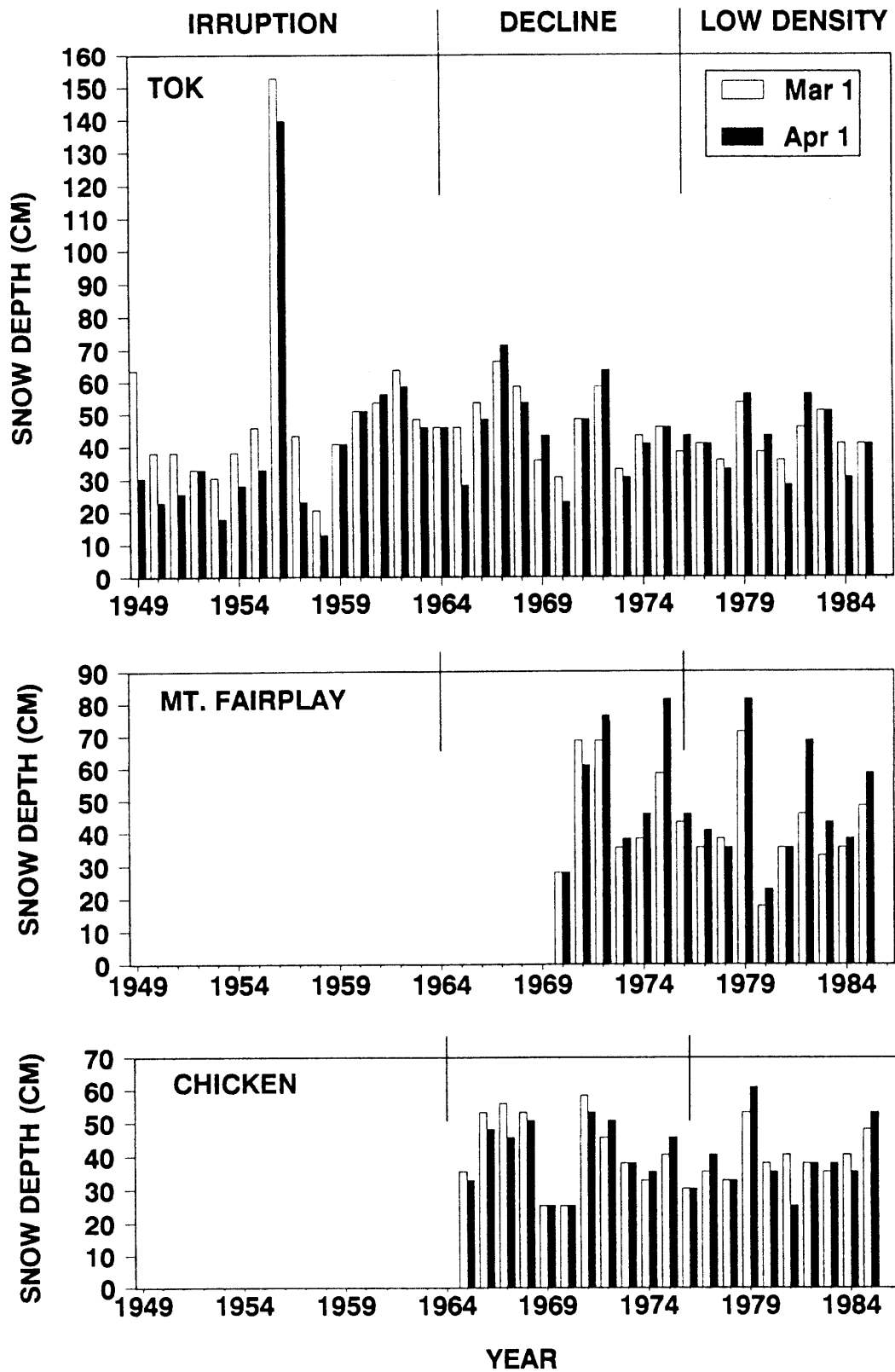


Fig. 6. Snow depth on 1 March and 1 April at 2 sites in the experimental area (Mt. Fairplay and Chicken) and 1 site 15 km south of the experimental area (Tok) in east-central Alaska, 1949-85.

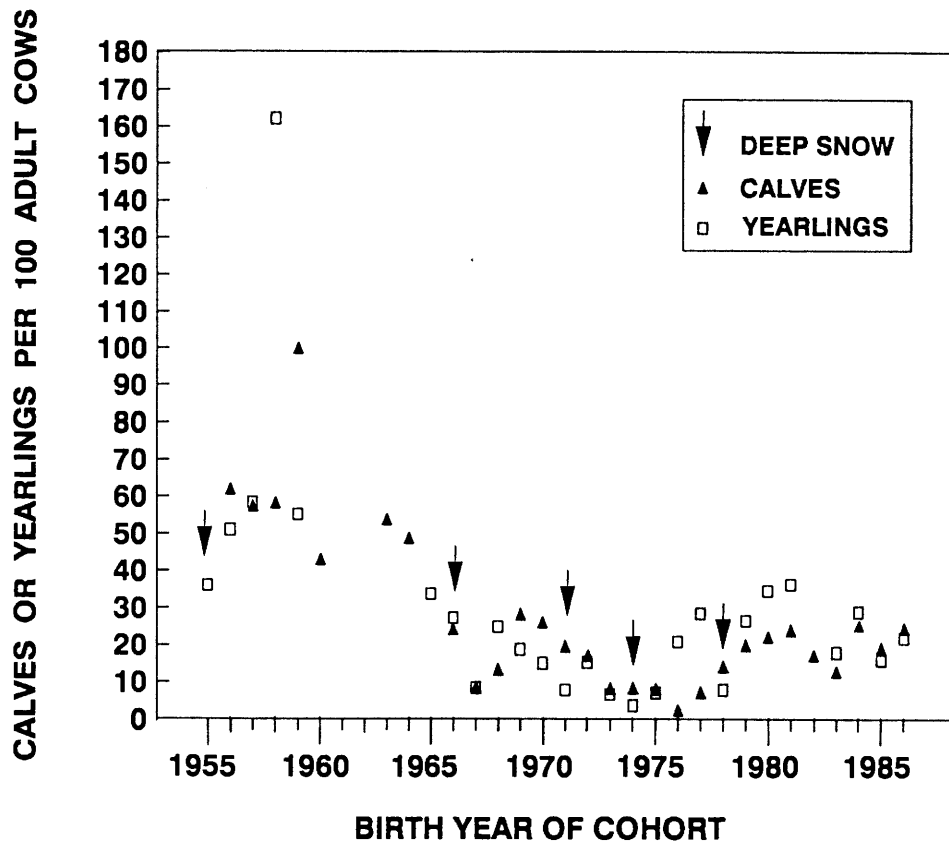


Fig. 7. Abundance of yearlings compared with calves of the same cohort (Appendix A) to illustrate effects of deep snow during the calf's first winter, 1955–86. Arrows indicate deep snow relative to other winters at 1 or more of 3 sites in or adjacent to the experimental area (Fig. 6).

lings:cow ratios preceded the first relatively deep snowfall (Tok 1966–67; Figs. 6, 7, 8), and the 1966–67 snowfall had little apparent effect on calf survival. For example, the yearling:cow ratio for the 1966 cohort was greater than for the next 4 cohorts (Fig. 7), which lived through winters of shallower snow (Fig. 6). During the decline and low-density phases, measured snow depths exceeded 70 cm 4 times (Fig. 6), a depth that impedes movements of moose, but snow did not reach the critical 90 cm depths (Coady 1974b). Only 3–4 calf deaths due to causes other than predation were observed during 1 winter (1970–71), and yearling abundance (relative to calves of the same cohort) in early

winter appeared unexpectedly low only following winter 1978–79 (Fig. 7). Also, snow depth experienced by pregnant cows from 1956 to 1985 was not correlated ($r = <0.14$, $P > 0.1$ for 3 correlations) with calves per 100 adult cows the following early winter. Additionally, no correlations ($r = <0.15$, $P > 0.1$ for 3 correlations) were found between yearlings per 100 adult cows and snow depth during the calf's first winter. Snow data were the sum of March and April snow depths at the 3 snow stations (Fig. 6).

Two factors may have reduced the effect of snow depth in our study area compared with areas where snow depth has clearly affected moose population dynam-

Table 5. Productivity of moose in relation to K carrying capacity (KCC) for populations from North America. Ranking in relation to KCC was based on the original authors' comments in papers or on personal communications cited below.

Population	Year	Age of cows (months)	% births that were twins ^a	n	% pregnant	n	Relation to KCC	Reference
Present study	1984	>29	52	27	100	28	??	Present study
Innoko River, Alas.	1988	>29	90	10	100	17	Below	J. S. Whitman, ADF&G, unpubl. data
Rochester, Alta.	1975-78	>29	88	8			Below	Mytton and Keith 1981
Alaska Peninsula	1977	>29	80	15	84	57	Below	Faro and Franzmann 1978
Kenai Peninsula, Alas.	1982-83	>19	71	102			Below	Franzmann and Schwartz 1985
West-central Alas.	1988-89	>19	56	61			Below	A. J. Loranger, USF&WS, and T. O. Osborne, ADF&G, unpubl. data
Pukaskwa Park, Ont.	1975-79	>29	54	37	97	37	Below	Bergerud and Snider 1988
Elk Island, Alta.	1960-64	>29	50	28	82	34	Below	Blood 1974
South-central Alas.	1977-80	>29	41	64	88	59	Below	Ballard and Taylor 1980; Ballard et al. 1982
East Newfoundland	1953-56	>29	41	29	87	38	Below	Pimlott 1959; W. E. Mercer, Newfoundland Wildl. Div., pers. commun.
Central Alas.	1975-78	>29	32	35	88	52	Below	Gasaway et al. 1983
South-central Alas.	1950's	>29	28	87	94	93	Below	Rausch 1959
Southern Yukon	1983-85	>29	28	58	84	43	Below	Larsen et al. 1989a
New Brunswick	1980-86	>29	23	52	79	33	Below	Boer 1987; A. H. Boer, New Brunswick Fish and Wildl. Branch, pers. commun.
British Columbia	1952-56	>29	25	80	76	80	Near	Edwards and Ritcey 1958; R. W. Ritcey, British Columbia Wildl. Branch, pers. commun.
Kenai Peninsula, Alas.	1977-78	>19	22	49			Near	Franzmann and Schwartz 1985
Elk Island, Alta.	1959-73	>29	12	216	84	258	Near	Blood 1974
South Newfoundland	1973-75	>19	2	88			Near	W. R. Skinner, unpubl. data cited in Albright and Keith 1987; W. E. Mercer, pers. commun.
South Newfoundland	1982-84	>19	1	107			Near	Albright and Keith 1987; W. E. Mercer, pers. commun.
Sandy-M-Town, Newf.	1953-56	>19	3	87	74	116	Above	Pimlott 1959; W. E. Mercer, pers. commun.
Moose Research Center, Alas.	1973-75	>29	0	22	60	37	Above	Franzmann et al. 1976; A. W. Franzmann, ADF&G, pers. commun.

^a Estimated *in utero* or at birth.

ics. First, maximum snow depth was lower in our study area than in areas of Alaska where snow depth affected calf survival (Bishop and Rausch 1974, Gasaway et al. 1983, Ballard et al. 1991). Second, the effect of snow on calves may have been masked by predation that, at least during the 1980's, killed most of the calves before winter (*see* Predation as a Limiting Factor).

Harvest as a Limiting Factor

Harvest increased early in the irruption phase compared with preirruption harvests and, therefore, was not an important factor limiting moose just before the irruption. Increased harvest resulted from construction of the Taylor Highway (1946–56), which provided access and brought increased numbers of hunters to this wilderness. Most of the moose harvest occurred along the highway from 1946 until 1972, when the scarcity of bull moose encouraged hunting in offroad areas (i.e., areas > 13 km from the road; Olson 1959b).

Most harvest apparently was a minor factor limiting growth of the moose population in the experimental area at peak numbers and during the decline. Few cows were harvested annually in all of GMU 20E (\bar{x} = 7.5, SD = 5.7, range = 0–19, in 28,500 km², Appendix C), and total harvest

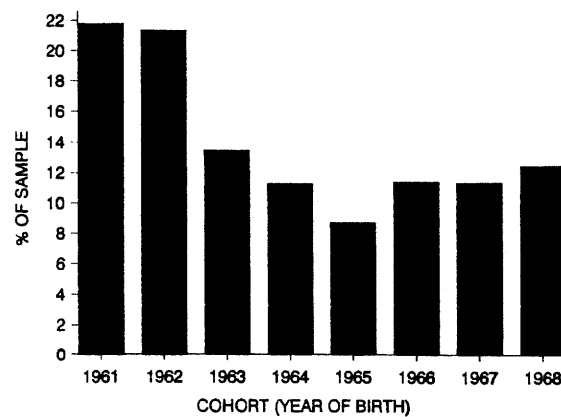


Fig. 8. Relative strength of male moose cohorts declined prior to the first winter of deep snow (1966–67 at Tok, Fig. 6). Data are from moose harvested ($n = 255$) during 1965–72 in Game Management Unit 20E, east-central Alaska (Buchholtz and Jennings 1974).

rates for moose in the experimental area were approximately 2% at peak numbers (about 5,500) in 1965 and 2–5% annually (\bar{x} = 3%, n = 12 years, 5,500 down to 880 moose) through 1976. Given that several assumptions affect estimated harvest rates (*see* Methods), we suggest these rates be viewed as conservative. By contrast, moose populations sustain harvest rates of 23–37% where moose are below KCC and predators are absent or substantially reduced in number (Messier and Crete 1984, Crete 1987, Nygren 1987). Thus, the 2–5% harvest rate on our study population had a

Table 6. Food species available to moose and the browsing rates on twigs during winters 1981–82 and 1983–84 in 29 transects in the experimental area, east-central Alaska. Browse categories are based on the percentage of browsed twigs on individual plants.

Species	Occurrence		% of plants in browse category				± % twigs browsed
	No. of plants	% of total sample	0	1–25	26–75	76–100	
<i>Salix alaxensis</i>	72	2.6	46	29	13	13	21
<i>S. planifolia</i>	1,399	49.6	82	12	4	2	5
<i>S. arbusculoides</i>	181	6.4	76	20	4	1	5
Subtotal	1,652	58.6	80	13	4	3	6
<i>S. bebbiana</i>	71	2.5	99	1	0	0	0
<i>S. glauca</i>	69	2.4	90	9	1	0	2
<i>S. scouleriana</i>	35	1.2	100	0	0	0	0
<i>S. spp.</i>	26	0.9	100	0	0	0	0
<i>Betula glandulosa</i>	959	34.0	99	1	0	0	0
<i>Alnus spp.</i>	5	0.2	100	0	0	0	0
<i>Populus tremuloides</i>	3	0.1	100	0	0	0	0
Total or mean	2,820	100.0	87	9	3	2	4

small influence on growth rate relative to other potential limiting factors. Harvests of primarily bulls, however, did significantly lower numbers of bulls per 100 cows ($\bar{x} = 31$, $n = 11$ years, $SE = 4$) in the 2 survey areas <13 km from the Taylor Highway during the 1966–76 decline compared with bulls per 100 cows in the 3 offroad survey areas >13 km during the same period ($\bar{x} = 51$, $n = 11$ years, $SE = 3$; $P < 0.05$, 1-tailed paired Wilcoxon test) and offroad areas during the irruption (1956–60; $\bar{x} = 88$, $n = 5$ years, $SE = 10$; $P < 0.0005$, 1-tailed Mann-Whitney test). Lowered numbers of bulls per 100 cows likely did not impair breeding because pregnancy rates of about 90% have occurred in portions of Alaska with only 4–20 bulls per 100 cows (Bishop and Rausch 1974).

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

Harvest had little influence on the low-density moose population during 1976–88. Moose hunting was prohibited during 1977–81 and bulls per 100 cows recovered to a mean of 82 in near and offroad areas during 1982–87, yet moose remained at low densities (Fig. 2). The average annual harvest of 31 ($SD = 8.1$, range = 25–45) bull moose in the experimental area during 1983–88 (Appendix C) was a 2.6% harvest rate, assuming a population of 1,200 moose (the average of the 1981 and 1988 early winter densities extrapolated to the 9,700 km² experimental area). High numbers of bulls per 100 cows during 1982–87 indicated resumption of bull-only harvests had a negligible impact on the population. Additionally, in our modeled moose population (*see* Predation as a Limiting Factor), hunting accounted for only 1.5% of the total annual mortality during the mid-1980's compared with 37% mortality from other causes. Thus, eliminating the con-

servative harvests would have a negligible effect on increasing the moose population.

Disease as a Limiting Factor

We found no evidence indicating disease was a limiting factor for moose in the experimental area. Several studies have concluded that Alaska moose are largely free of infectious diseases and parasites that seriously affect survival (Kocan et al. 1986, Lankester 1987, Zarnke 1988). The moose tick (*Dermacentor albipictus*) and the parasite causing neurological disease in moose, *Parelaphostrongylus tenuis*, are absent in Alaska moose (Franzmann 1978). Antibody tests of 35 sera samples from moose immobilized in the experimental area during 1984 and 1986 provided no evidence of exposure to brucellosis, Q fever, leptospirosis, contagious ecthyma, infectious bovine rhinotracheitis, bovine viral diarrhea, epizootic hemorrhagic disease, blue-tongue, parainfluenza III, or respiratory syncytial virus (Zarnke 1988).

Predation as a Limiting Factor

The irruption of moose that followed the intense wolf and bear removal program in the experimental area (1948–60) supports the hypothesis that predation limits moose at low densities. Irruptions of moose also followed similar programs in central and south-central Alaska during the 1950's (Bishop and Rausch 1974, Gasaway et al. 1983, Ballard et al. 1991). Likewise, during the 1970's intense wolf and bear removal in south-central Alaska and intense wolf removal in central Alaska again contributed to the growth of moose populations (Gasaway et al. 1983, Ballard et al. 1991). Because these intense predator removal programs consistently resulted in moose population increases, predation was likely a significant limiting factor. The following sections present evidence that predation was the primary factor limiting moose at low densities during the 1980's in the experimental area.

Predator Food Habits and Ratio of Prey to Predators.—Moose were the primary

Table 7. Moose, caribou, wolf, and grizzly bear density in the experimental area (9,700 km²) before (1981) and after (1984 and 1988) wolf removal, east-central Alaska.

Period	Density in animals/1,000 km ²				
	Moose ^a	Caribou ^b		Wolf ^c	Grizzly bear ^d
		Min.	Max.		
Before wolf removal, early winter 1981	88	20	770	8	16
After wolf removal, early winter 1984	102	20	1,060	5	16
Early winter 1988	157	20	1,550	6	16

^a Moose density was estimated in the experimental area west of the Taylor Highway during early winter 1981 and 1988, and moose density was assumed to increase at 5% annually between 1981 and 1984 (Table 3).

^b Caribou density was calculated using a minimum of 200 animals and a maximum of 95, 75, and 75% of the estimated number in the herd during 1981, 1984, and 1988, respectively. These approximate percentages were based on observations of P. Valkenburg (ADF&G, pers. commun.) during caribou surveys and radio-tracking flights. Estimated herd sizes were 7,900, 13,700, and 20,000 during 1981, 1984, and 1988, respectively (Valkenburg and Davis 1989).

^c Wolf density was from the total area (15,500 km²) occupied by wolf packs in Appendix B.

^d Density of grizzly bears was extrapolated from spring density in the grizzly bear study area (4,000 km²) and assumed stationary.

ungulate prey of wolves and grizzly bears in the experimental area during the 1980's, based on 4 types of data.

1. Radiocesium analyses (Holleman and Stephenson 1981) indicated caribou composed 33% (SE = 3%) of the wolves' winter diet (Nov–Apr) during winters 1981–82 through 1989–90. The majority of the winter diet was presumably composed mainly of moose, the only other ungulate.
2. Stomach contents of wolves indicated moose were a major component of the winter diet; of 143 stomachs examined from spring 1981 through spring 1988, 30% contained caribou, 29% contained moose, 4% contained small mammals or birds, and 37% were empty.
3. Analysis of 91 wolf scats collected at a den indicated adult and calf moose composed about 74% of the prey biomass consumed during spring and summer 1981; the remainder of the diet was 3% caribou, 16% snowshoe hares, and 7% rodents and birds.
4. Daily observations of radio-collared predators in the experimental area indicated moose composed about 75% of the observed biomass consumed by 1 wolf pack from 30 April to 10 June 1986, and moose composed 92% of prey biomass killed by grizzlies during 1985–86 (Boertje et al. 1988).

The low number of moose and caribou

per predator in the experimental area indicates predation could have strongly influenced the moose population during 1981 (Tables 7, 8) and the late 1970's given similar predator and prey populations (Fig. 2). We summarized prey numbers per predator from North American moose populations where predation had been shown to be or was highly suspected of being a major limiting factor (Table 9). The numbers of prey per predator in the experimental area in 1981 are among the lowest reported in North America. Furthermore, assuming wolves were consuming 33% caribou during winter, the adjusted number of moose per wolf (16 in 1981, Table 8) remained within the range where wolf predation can strongly affect moose population growth (Gasaway et al. 1983).

Causes and Extent of Calf and Adult Moose Mortality.—Predation was the primary cause of high moose calf mortality. Mortality of 33 radio-collared calves born during 1984 was 79–82% by 11 months of age; 52% of the calves were killed by grizzly bears, 12–15% by wolves, 3% by black bears, and 12% drowned. Thus, predators killed 67–70% of calves. The relative importance of wolf and grizzly bear predation, however, may have differed when wolves were more abundant. The 1984 calf mortality study occurred in the Mosquito Flats portion of the experimental area (Fig. 1) where the spring wolf population was

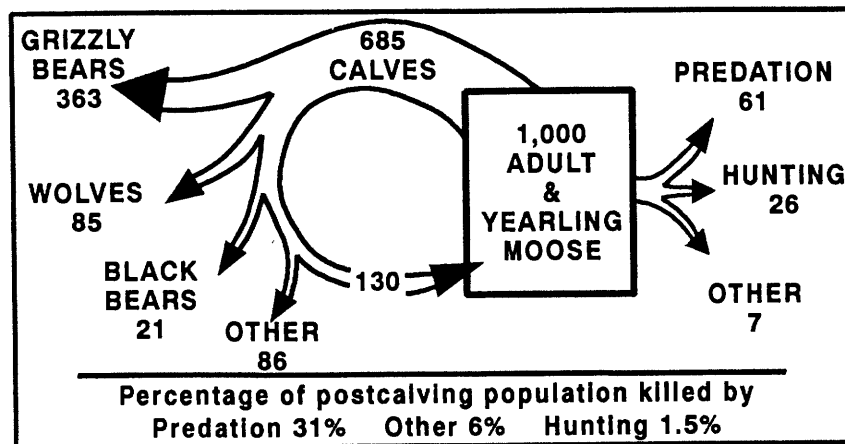


Fig. 9. The approximate number and percentage of moose dying from specific causes in the experimental area after wolf reduction, given a hypothetical precalving moose population of 1,000 moose in east-central Alaska, 1981–88. This model is derived from data in Appendix D and results in a λ of 1.04.

reduced to approximately 40% of the early winter 1981 density.

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

A model using natality and mortality data indicates predation was the major factor influencing moose population dynamics in the experimental area during 1981–88 (Fig. 9, based on Appendix D). Predators killed approximately 31% of the hypothetical population that included 1,685 neonate and older moose, whereas hunting and other factors accounted for only 1.5% and 6% of the population, respectively. This simulated adult and yearling population increases at 4% annually.

Additive and Compensatory Nature of Mortality When Moose Are Well Below KCC.—Because predation was the only significant source of mortality when moose were at low densities relative to KCC, predation was likely the primary limiting factor. Evidence that a substantial amount of the predation was additive to other sources of mortality would strengthen support for predation being the major limiting factor. We considered mortality from predation additive when predators killed moose that likely would have lived to reproduce. We considered predation compensatory when predators killed moose that likely would have died from other causes before reproducing.

McCullough (1979, 1984) presented a model that indicates mortality is mostly additive when white-tailed deer (*Odocoileus virginianus*) are near or below maximum

Table 8. Estimated numbers of prey per predator in the experimental area before (1981) and after (1984 and 1988) wolf removal, east-central Alaska. Numbers were calculated from density estimates in Table 7. Numbers in parentheses are approximations of the number of moose per wolf, adjusted for caribou in the wolf's winter diet, i.e., (the no. of moose available) \div (0.67 \times the estimated no. of wolves), because approximately 33% of the wolf's winter diet was caribou (see Predator Food Habits and Ratio of Prey to Predators).

Period	Moose per wolf	Moose per grizzly bear	Moose per wolf + grizzly bear	Moose + min. caribou per wolf	Moose + max. caribou per wolf	Moose + min. caribou per wolf + grizzly bear	Moose + max. caribou per wolf + grizzly bear
Before wolf removal, early winter 1981	11 (16)	6	4	14	107	5	36
After wolf removal, early winter 1984	20 (30)	6	5	24	232	6	55
Early winter 1988	26 (39)	10	7	30	285	8	78

Table 9. Estimated numbers of prey per predator in areas of North America where moose populations were stationary or declining and predation was either the major or suspected major factor limiting moose population growth.

Area	Moose per wolf	Moose per grizzly bear	Moose per wolf + grizzly bear	Moose + min. caribou per wolf + grizzly bear	Moose + max. caribou per wolf + grizzly bear	Moose + max. caribou + sheep per wolf + grizzly bear	Black bear	Reference
East-central Alaska, 1981	11	6	4	5	36	36	Scarce	Present study
Southwest Yukon, 1981*	12	9	5	6	29	29	Common	Larsen et al. 1989a; D. G. Larsen, Yuk. Wildl. Branch, unpubl. data
Central Alaska, GMU 20A, 1975	12	13	6	10	19	19	Common	Gasaway et al. 1983; Reynolds et al. 1987
Isle Royale, 1971-80	20						None	Peterson and Page 1983
Pukaskwa National Park, Ont.	24			25			Common	Bergerud et al. 1983
Ft. McMurray, Alta., 1975-78	28			28			Common	Fuller and Keith 1980; Hauge and Keith 1981
Southwest Quebec	28						Common	Messier and Crete 1985
Northeastern Denali National Park, Alas., 1986-87	48	9	8	8	34	34	Scarce	Haber 1977; Dalle-Molle 1987; Dean 1987; Mech 1987; Meier 1987; J. L. Davis, ADF&G, pers. commun.
South-central Alas., GMU 13E, 1975	64	20	15	33			Scarce	Ballard and Larsen 1987; Pitcher 1987

* Ratios were calculated from animal densities based on 1,000 km² of total land area; 68.5% of the total land area was moose habitat (D. G. Larsen, unpubl. data).

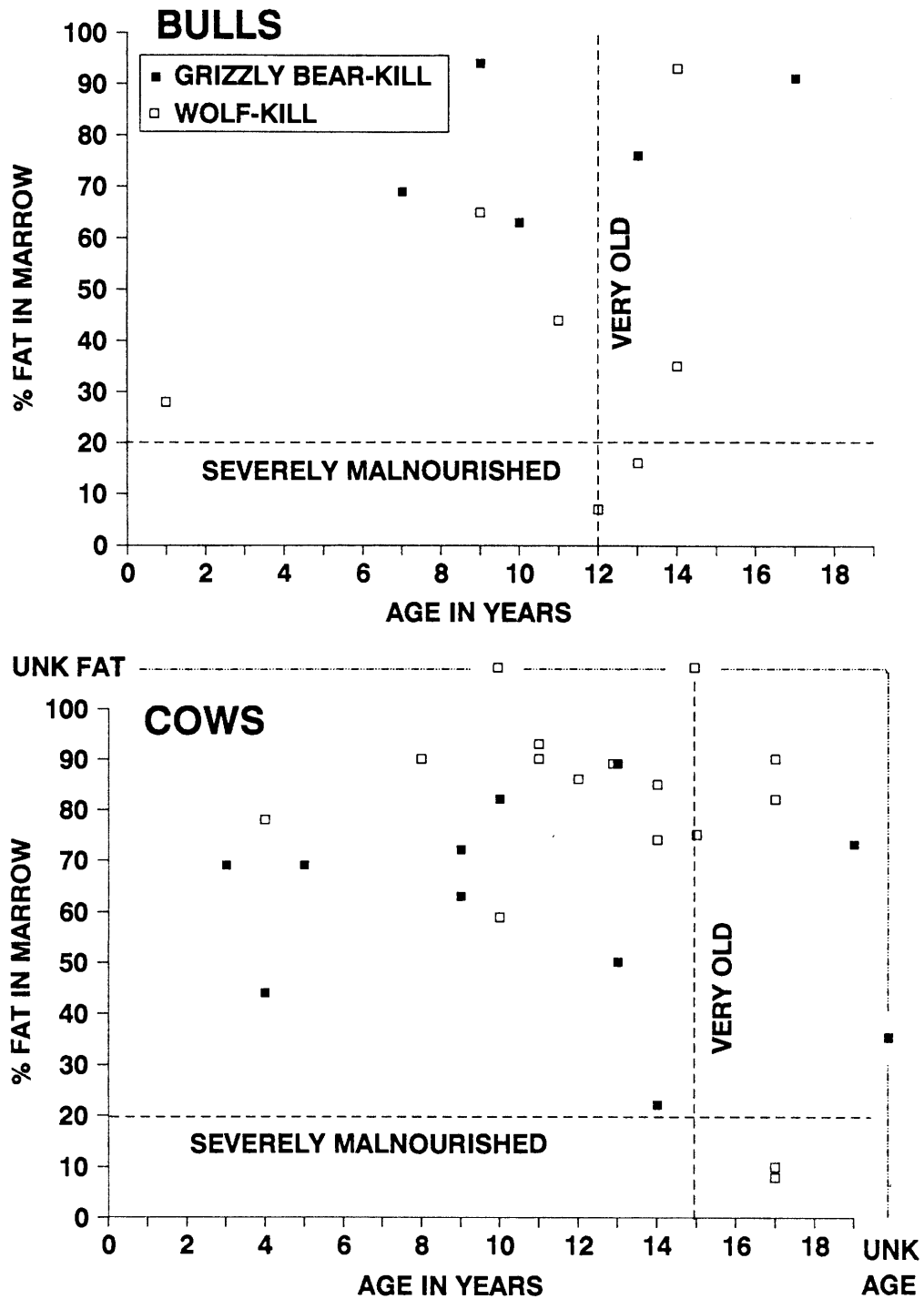


Fig. 10. Percent marrow fat and age of bull moose and cow moose killed by grizzly bears and wolves in the experimental area in east-central Alaska, 1981-87. UNK fat = unknown marrow fat levels.

sustained yield levels and increasingly compensatory as populations approach KCC. Assuming McCullough's model applies to moose, we predicted that mortality from

predation would have been largely additive when the moose population was at low densities and showed no signs of strong nutritional stress. We assess this prediction below.

Age and nutritional status of predator-killed adult moose indicated predation on adults was largely additive. We classed mortality as follows: (1) largely additive if moose were neither severely malnourished ($\geq 20\%$ fat in marrow, Peterson et al. 1984) nor old (bulls < 12 and cows < 15 years old), (2) largely compensatory if moose were old, and (3) compensatory if moose were severely malnourished or severely malnourished and very old. Most (24 of 37) predator-killed moose were in the largely additive class (Fig. 10); only 4 of 37 were classed wholly compensatory.

Assuming other mortality sources remain constant, a direct test for additive mortality involves substantially reducing predation and subsequently determining whether moose survival and population size increase (Bergerud 1971, Gasaway et al. 1983). We suggest that the high calf survival and population irruption following the start of wolf and bear removal during 1948 indicates predation was strongly additive during that period (Fig. 2; Tables 2, 3).

During the 1980's predation was not adequately reduced to fully evaluate the additive nature of predation. Planned sequential wolf and bear removal experiments were prematurely terminated during 1983. Nevertheless, the limited findings provide some insights. Three factors probably contributed to a small reduction in total predation in the experimental area: (1) moderate wolf reduction (Tables 4, 8) (2) a possible reduction in grizzly bear numbers from increased harvest (1982–88), and (3) increased caribou as alternate prey (Fig. 2). Of these factors, only the increase in caribou influenced predation in control areas. Moose numbers increased ($P < 0.001$, 2-tailed Student's t test) in the experimental area between 1981 and 1988 but at a low rate ($\lambda = 1.04$ – 1.09) based on a population model (Fig. 9, Appendix D), estimates of population size (Fig. 2), and estimates of mortality and recruitment (Table 3). Although no significant trends occurred in control areas (slopes of regression lines not different from zero, $P > 0.1$; Fig. 11), positive slopes on regression

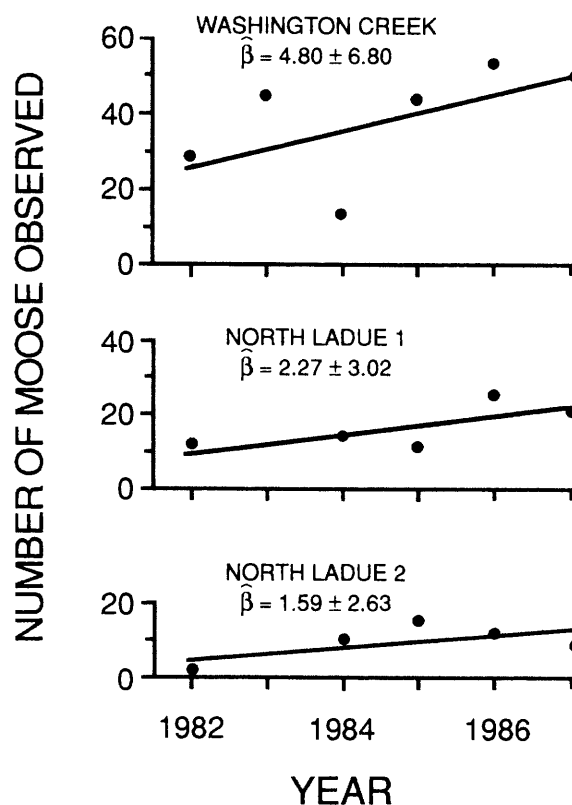


Fig. 11. Trends in number of moose observed in 2 control areas in east-central Alaska and the adjacent Yukon, 1982–87. β ($\pm 90\%$ CI) estimates the slope of the linear regression line.

lines lead us to speculate that moose in the control areas also may have increased. Because these data are equivocal, we draw no conclusions on the effects of the small reduction in predation on population growth. Connolly (1978) and Crete and Jolicoeur (1987) discuss the problems of interpreting results from insufficient reductions in predation.

The 1981–83 wolf removal in a portion of the experimental area allowed us to conclude that wolf predation on calves was not a detectable source of additive mortality when grizzly bears were abundant. Reducing wolf numbers from 85 during early winter 1981 to 19 during April 1982 in and around the Mount Veta–Mosquito Flats survey area produced no treatment effect on calves per cow or yearlings per cow for the 1982–86 cohorts (Table 10). Failure of calves per cow to increase during the 1980's wolf removal indicates ei-

Table 10. Calves per cows, percent calves, and yearlings per cows for 1978–86 cohorts as determined by aerial moose surveys in the Mount Veta–Mosquito Flats moose survey area in the experimental area, east-central Alaska, before (1978–81) and after (1982–86) wolf removal. n = total number of moose classified. Adult cows were ≥ 29 months old.

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

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

^b Yearling males were doubled to estimate total yearlings.

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

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

ther grizzlies were the predominant predator on young calves before and after wolf numbers were reduced, or increased grizzly bear predation compensated for reduced wolf predation. Lowered wolf predation likely was not compensated for by factors other than grizzly bear predation, e.g., drowning.

By severely reducing numbers of the predominant predator, other experiments demonstrated that predation on moose calves is largely additive when moose are well below KCC (Gasaway et al. 1983, Stewart et al. 1985, Ballard and Larsen 1987, Van Ballenberghe 1987, Ballard and Miller 1990). We speculate that if grizzly bears, the predominant predators on calves during 1984, had been severely reduced along with wolves, we would have observed increased calf survival. In lieu of a combined bear and wolf reduction program, we altered the food habits of predators by air-dropping 12–15 tons of train-killed moose and scrap meat during May and June 1985 in and around the Mosquito Flats calving area (Fig. 1). We observed grizzly bears, black bears, and wolves consume much of this meat. The 1985 early winter calves per cows in the Mosquito Flats increased to 53/100 cows ($n = 17$ cows) compared with a range of 11–15/100 ($n = 26–39$, $P = < 0.005$, Chi Square

Test of Independence) during the preceding 3 years and 26–36/100 ($n = 25–27$, $P < 0.10$) during the following 2 years. The 1985 response was not observed in 2 partially treated adjacent areas (11–12/100, $n = 17–65$, $P < 0.005$) or 3 untreated areas in the experimental area (10–19/100, $n = 25–70$, $P < 0.005$). Thus, because treated areas had higher calf survival, some predation was additive.

We conclude that data, aside from results of the inadequate predator removal experiment during the 1980's, indicate predation was largely additive to other sources of mortality, as predicted for deer populations that are well below KCC (McCullough 1979).

Conclusions on Factors Limiting Moose Density in the Experimental Area

Predation by bear and wolf populations was the primary factor limiting and maintaining moose at low densities relative to the available food resource during 1976–88. Nutrition, snow, and harvest were minor limiting factors when moose were at low densities. Disease was not identified as a limiting factor.

In the following section, we document that predation limits moose at low densities

elsewhere in North America. We use data from several study areas to support that, given certain conditions, low moose densities often occur.

THE ROLE OF WOLF AND BEAR PREDATION IN LIMITING MOOSE AT CHRONIC LOW DENSITIES IN NORTH AMERICA

Increasing evidence suggests predation by wolves and 1 or 2 species of bears is the primary factor limiting moose at densities well below KCC where moose are primary prey and predators and moose are lightly harvested. Examples exist in Quebec, Ontario, Yukon, and Alaska (Bergerud et al. 1983; Messier and Crete 1985; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988). The common conceptual model for moose population regulation in these multipredator systems is a single LDDE (K4 of model 4, Fig. 12) where moose densities fluctuate over time, but in a range well below KCC (Messier and Crete 1985; Crete 1987, 1989; Van Ballenberghe 1987; Bergerud and Snider 1988). Messier and Crete (1985) and Bergerud and Snider (1988) indicate this fluctuating equilibrium is maintained within limits by density-dependent (regulating) processes. We add that density-independent processes play a major role in determining the range of densities over which populations fluctuate. For example, black and grizzly bear predation on low- to high-density moose populations may be density-independent (Franzmann and Schwartz 1986, Boertje et al. 1988), and bear predation can be a major source of mortality to a population (Ballard and Larsen 1987, Crete and Jolicoeur 1987, Boertje et al. 1988, Larsen et al. 1989a, Schwartz and Franzmann 1989). Reducing bear predation could allow the moose populations to stabilize at higher densities, possibly through density-dependent processes.

We provide further support for this predator-limited, LDDE model using case histories in a large area with lightly harvested predator populations in Alaska and

Yukon (Fig. 13). The following conditions were common to most of this area: (1) predators included wolves, grizzly bears, and black bears (Table 11), (2) moose were a primary prey, (3) moose occurred at densities well below KCC, and (4) most moose populations were lightly harvested and moose harvest removed primarily bulls (Table 11). Moose harvest rates averaged 5% of the prehunt population ($n = 18$, range 0–13%, $SD = 4\%$) and about 3% of the derived postcalving population. The mean of 20 moose density estimates in this area was 148/1,000 km² (range = 45–417/1,000 km², $SD = 81$). The mean density was similar ($\bar{x} = 142/1,000$ km², $SD = 96$) when only the 13 sites with harvests of $\leq 7\%$ ($\bar{x} = 3\%$) of the prehunt population were included. Furthermore, moose density was only 190/1,000 km² in Denali National Park where moose hunting was prohibited and moose were below KCC (Risenhoover 1987) (Table 11).

Intensive studies within this area support the hypothesis that predation is the primary factor limiting moose density (sites designated by densities of 88, 190, and 249 moose/1,000 km² on Fig. 13) (Van Ballenberghe 1987; Larsen et al. 1989a,b; present study). One study in Denali National Park (site [density] 190, Fig. 13) presented an opposing view (Haber 1977), although subsequent studies in Denali supported the LDDE model (Risenhoover 1987, Van Ballenberghe 1987).

Additional support for the predator-limited LDDE model comes from a large area (Fig. 13) where harvest chronically or periodically held predators below KCC (i.e., below food-limited densities) (Figs. 14, 15). Moose densities within this area were higher ($\bar{x} = 663/1,000$ km², $n = 16$, range = 169–1,447, $SD = 389$) than densities in the area with lightly harvested predators ($P < 0.02$, Mann-Whitney test; Fig. 13). However, wolf densities were not significantly ($P > 0.1$, Mann-Whitney test) different in areas with lightly harvested (low prey biomass per wolf) and harvest-limited wolf populations (high prey biomass per wolf) (Figs. 14, 15), implying that the harvest-limited wolf populations were held below

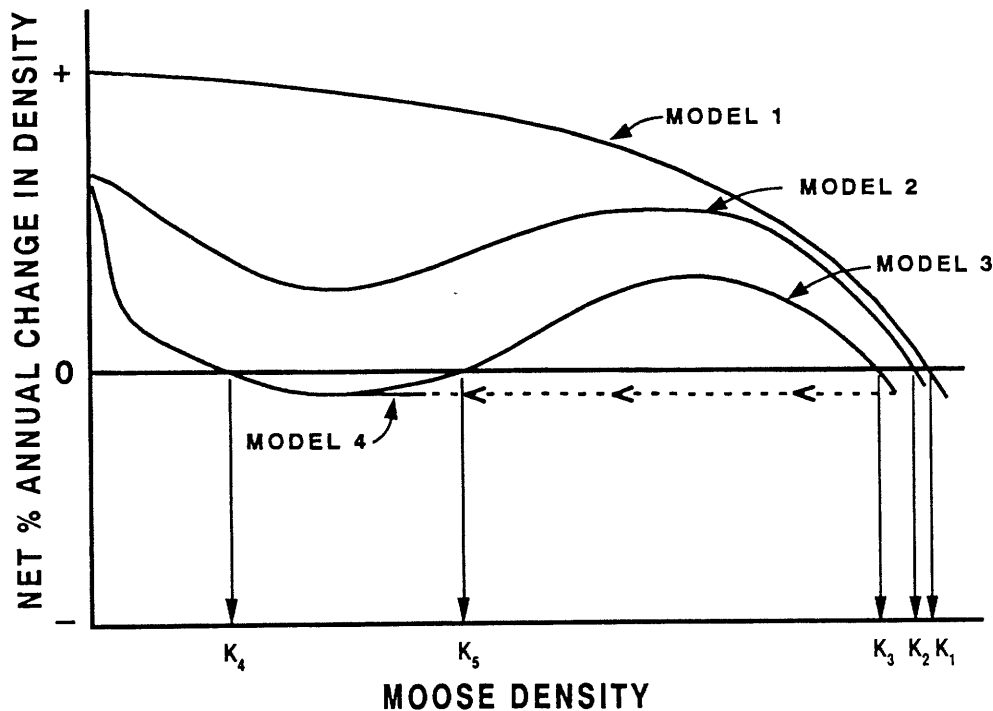


Fig. 12. Four proposed conceptual models of predator-moose-nutrition dynamics (after Messier and Crete 1985). Model 1—where predators are absent, moose densities fluctuate near K carrying capacity (KCC) (K_1). In the following models, predator populations are assumed to be unharvested or lightly harvested and moose are primary prey of predators. Model 2—where a single predator species occurs or both black and grizzly bears occur, moose densities fluctuate near KCC (K_2). Model 3—where bears and wolves occur, 2 or more relatively stable equilibria are possible; the high-density, nutrition-induced equilibrium (K_3) fluctuates near KCC and the low-density dynamic equilibrium (LDDE) (K_4) is maintained by predation. Additionally, 1 or more unstable equilibria are possible (K_5). Model 4—where bears and wolves occur, moose densities fluctuate near a single LDDE (K_4). We speculate that if rare natural events allow moose to increase above the LDDE, then moose may follow model 3 to a high density but will return to the LDDE via a series of years with negative net changes in density (dashed line). These negative net changes would likely result from periodic severe winters and predation.

KCC. The extent to which wolves were held below KCC is indicated by the difference between the predicted and observed wolf density. Reviews by Keith (1983) and Fuller (1989) regress wolf density on prey biomass (Fig. 14) and conclude that wolf density predictably increases with prey biomass, unless harvest prevents wolves from increasing. In our area of light harvest, wolf density was correlated ($r = 0.75$, $P < 0.01$) with moose density, similar to Keith's and Fuller's predictions. In contrast, wolf densities did not increase significantly with moose density ($r = 0.3$, $P > 0.1$) in our area of harvest-limited wolf populations; observed wolf densities were well below Keith's and Fuller's predictions (Fig. 14). Case histories of high harvest rates of wolf populations exist for sites designated by densities of 751, 776, 1,220, and

816–1,447 moose/1,000 km² on Fig. 13 (Gasaway et al. 1983, Peterson et al. 1984, Ballard et al. 1987, Schwartz and Franzmann 1989), and case histories of high harvest of grizzly bears exist for sites designated by 751 and 776 moose/1,000 km² (Reynolds and Hechtel 1988, Miller 1990).

Habitat studies and circumstantial evidence from predator removal and predation studies indicate that the LDDE is not primarily a function of habitat. Habitat studies in Denali National Park (Risenhoover 1987; site designated by 190 moose/1,000 km² on Fig. 13) and in our experimental area (site 88) concluded moose were below KCC. Also, responses to predator removal in 3 sites demonstrated that habitat in central and east-central Alaska can support elevated moose densities. For example, during and after intense wolf re-

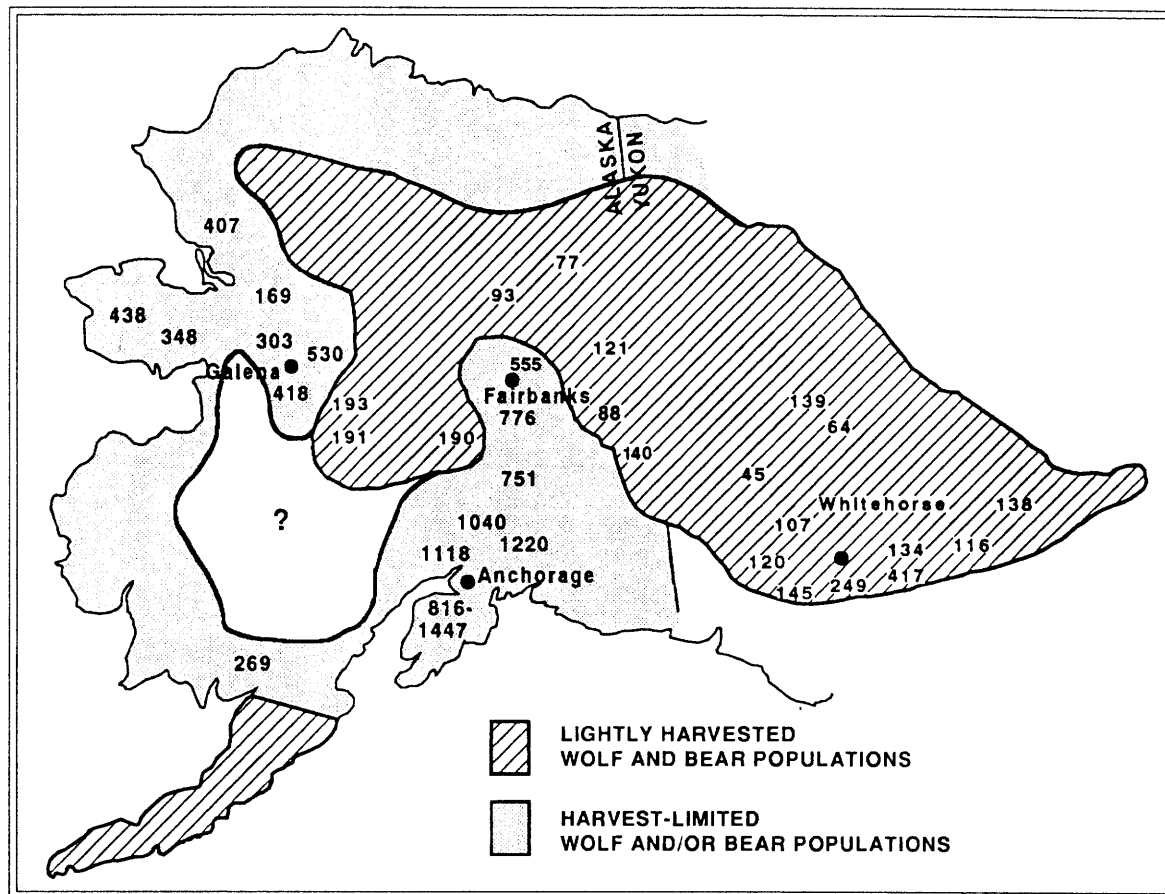


Fig. 13. Moose densities (moose/1,000 km²) within regions with lightly harvested wolf and bear populations versus areas where predators are or were recently harvest-limited. Moose surveys were conducted using stratified random sampling from 1965 to 1990. Data are from Tables 11 and 12. In most northern and western coastal areas, rabies and lack of prey also can limit wolf numbers, and in several areas caribou were also a primary prey.

removal programs in the late 1970's and early 1980's, moose increased from low levels (200/1,000 km² in site 776 and 222/1,000 km² in site 555, Fig. 13, Table 12; McNay 1990a). Current high densities of moose in these areas are substantiated by recent stratified random sampling (Table 12). Also, moose in central and east-central Alaska irrupted to high moose densities following multispecies predator reductions during the 1950's (site 776, Gasaway et al. 1983; site 88, present study).

The partial overlap in moose densities from the areas of lightly harvested versus harvest-limited predator populations (Fig. 13) can be accounted for, in part, by variation in habitat differences or moose harvest rates. For example, moose densities in northwest and southwest Alaska (sites with

densities of 169, 269, 348, 407, and 438) are underestimated compared with other sites, because in these cases "moose habitat" includes a high proportion of tundra, which is poor moose habitat. In contrast, the highest moose density observed in sites with lightly harvested predators (site 417) occurred in uniformly good moose habitat (a large 26-year-old burn). We attempted to increase the comparability of study sites by disregarding sites <2,000 km², where moose can be highly concentrated during surveys and habitat influences can be large. Finally, high but unknown local harvests reduced moose density in 2 of the sites with harvest-limited predator densities (sites 169 and 269; Larsen [1987] and Taylor [1983, 1984], respectively).

In contrast to the LDDE model above,

Table 11. Moose and predator densities and moose harvests per 1,000 km² and moose calves per cow in the sites on Fig. 13 where lightly harvested wolf and bear populations occur in Alaska and the Yukon, 1980-90. Study sites composed of <2,000 km² of moose habitat were excluded to enhance comparability among sites; small sites exhibit high variability in prey and predator densities and habitat quality.

Site and year of moose density estimate	Post-hunt moose density ^a	Area of moose habitat (km ²)	Wolf density ^a	Grizzly bear density ^a	Black bear density ^a	Alternate prey species and density ^a	Moose harvest ^b	Moose population trend ^c	Early winter moose calves/100 cows ^d	Source
Teslin burn, Yuk., 1984	417	2,515	18, high	Moderate	Moderate	Caribou, low	18	Stable	28	Hayes and Baer 1986; Larsen et al. 1989b
Rose Lake, Yuk., 1983	249	2,613	12, moderate	16, moderate	Moderate	Sheep, high	34	Decline	24	Hayes et al. 1985; Larsen et al. 1989a, b; Larsen and Markel 1989
Whitehorse North, Yuk., 1982	194	2,742	Moderate	10-15, moderate	10-15, moderate	Caribou and sheep, low	4	Decline	6	Markel and Larsen 1983
Lower Nowitna, GMU 21B, Alas., 1986	193	4,030	14-16, moderate-high	Low	High	None	20	Decline	30	Osborne 1987, 1988; T. O. Osborne, ADF&G, unpubl. data
Upper Nowitna, GMU 21A, Alas., 1980	191	9,832	8, moderate	Low	High	Caribou, low	2	Unknown	27	Haggstrom and Osborne 1981; R. O. Stephenson and S. D. DuBois, ADF&G, unpubl. data
Northern Denali National Park, GMU 20C, Alas., 1986-87	190	10,026	6, moderate	32, high	Low	Caribou, low; sheep, moderate	0	Stable	22	Meier 1987; Dean 1987; Mech 1987; Dalle-Molle 1987; Singer and Dalle-Molle 1985
Haines Junction, Yuk., 1983	145	2,332	13, moderate	16, moderate	Moderate	Sheep, low	22	Decline	18	Hayes and Baer 1986; Larsen et al. 1989b
Tetlin Flats and adjacent foothills, GMU 12, Alas., 1990	140	9,583	9, moderate	Moderate	Moderate	Caribou, moderate; sheep, high	7	Increase	38	Kelleyhouse 1990a, b, D. G. Kelleyhouse, ADF&G, unpubl. data; D. A. Haggstrom, ADF&G, unpubl. data
Mayo, Yuk., 1988	139	4,853	10, moderate	Present	Present	Caribou and sheep, low	Unknown	Unknown	54	Larsen et al. 1989c; R. D. Hayes and A. M. Baer, Yuk. Wildl. Branch, unpubl. data

Table 11. Continued.

Site and year of moose density estimate	Post-hunt moose density ^a	Area of moose habitat (km ²)	Wolf density ^a	Grizzly bear density ^a	Black bear density ^a	Alternate prey species and density ^a	Moose harvest ^b	Moose population trend ^c	Early winter moose calves/100 cows ^d	Source
Liard East, Yuk., 1986	138	2,210	Present	Present	Present	Caribou and sheep, low	Unknown	Unknown	42	Jingfors and Markel 1987
Nisutlin, Yuk., 1986	134	4,210	9-11, moderate	Present	Present	Caribou, low-moderate	12	Unknown	41	Hayes and Baer 1987a; Jingfors and Markel 1987
Upper Yukon, GMU 25B and 20E, Alas., 1987	121	9,210	3-6, low	Moderate	Moderate	Caribou, low	2	Unknown	10	Nowlin 1989; R. A. Nowlin, ADF&G, unpubl. data; S. R. Ulvi, Natl. Park. Serv., unpubl. data
Kluane Lake, Yuk., 1981	120	3,671	Low-moderate	10-15, moderate	10-15, moderate	Caribou and sheep, high	14	Decline	15	Larsen 1982
Liard West, Yuk., 1983	116	7,236	Present	Present	Present	Caribou and sheep, low	7	Unknown	16	Johnston and McEwen 1984
Aishihik, Yuk., 1981	107	3,519	3, low	10-15, moderate	10-15, moderate	Caribou and sheep, moderate	8	Decline	20	Larsen 1982; Hayes and Baer 1987b
Yukon Flats, GMU 25D West, Alas., 1986	93	16,107	3, low	Low	High	None	1	Increase	40	Nowlin 1985, 1988, 1989
Present study, 1981	88	7,700	8, moderate	16, moderate	Low	Caribou, moderate	0	Stable	20	Present study
Yukon Flats, GMU 25D East, Alas., 1984	77	27,584	Low	Low	High	None	1	Unknown	47	Nowlin 1984, 1986, 1988; R. A. Nowlin, ADF&G, pers. commun.

Table 11. Continued.

Site and year of moose density estimate	Post-hunt moose density ^a	Area of moose habitat (km ²)	Wolf density ^a	Grizzly bear density ^a	Black bear density ^a	Alternate prey species and density ^a	Moose harvest ^b	Moose population trend ^c	Early winter moose calves/100 cows ^d	Source
Dromedary Mountain, Yuk., 1982	64	3,548	10, moderate	Present	Present	Caribou and sheep, low	3	Unknown	15	Johnston and McLeod 1983; Hayes et al. 1991
Carmacks, Yuk., 1987	45	3,055	2, very low	Moderate	Low	Caribou and sheep, low	2	Unknown	15	Markel and Larsen 1988; Hayes et al. 1991

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

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

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

^d Numbers of calves per 100 cows is a 3-year mean (yr. of density estimate and 2 preceding yrs., when available).

which is a single equilibria model, Haber (1977) proposed a multiple-density equilibria model (model 3, Fig. 12). This model was based mainly on studies in eastern Denali National Park (1,100 km² of moose habitat). Van Ballenberghe (1980, 1987) and Crete (1987) challenged the model based largely on qualitative flaws, and Van Ballenberghe (1987) questioned whether the multiple-density equilibria concept is appropriate for natural moose-predator systems.

To help resolve debate over the appropriateness of the LDDE model versus the multiple-density equilibria model in moose-wolf-bear systems, Messier and Crete (1985), Crete (1987), and Van Ballenberghe (1987) suggested the following test: reduce predation on a moose population held at a low density by wolf and bear predation and allow moose to increase to near KCC, i.e., 0.6-0.7 KCC. The multiple-density equilibria model is supported if the lightly harvested moose population ($\leq 6\%$ harvest) maintains an equilibrium near KCC after cessation of predator removal. Alternatively, the LDDE model is supported if the lightly harvested moose population returns to a density well below KCC. Moose and predator population dynamics in our experimental area support the single LDDE model. The lightly harvested moose population increased to a high density following 12 years of reduced wolf and bear numbers and declined within 15 years to low, predator-maintained densities while annual moose harvests were $< 6\%$. However, annual harvests of the major current prey, caribou, did exceed 6% during the decline in moose numbers. More tests are needed to test the appropriateness of a multiple-density equilibrium model for prey.

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

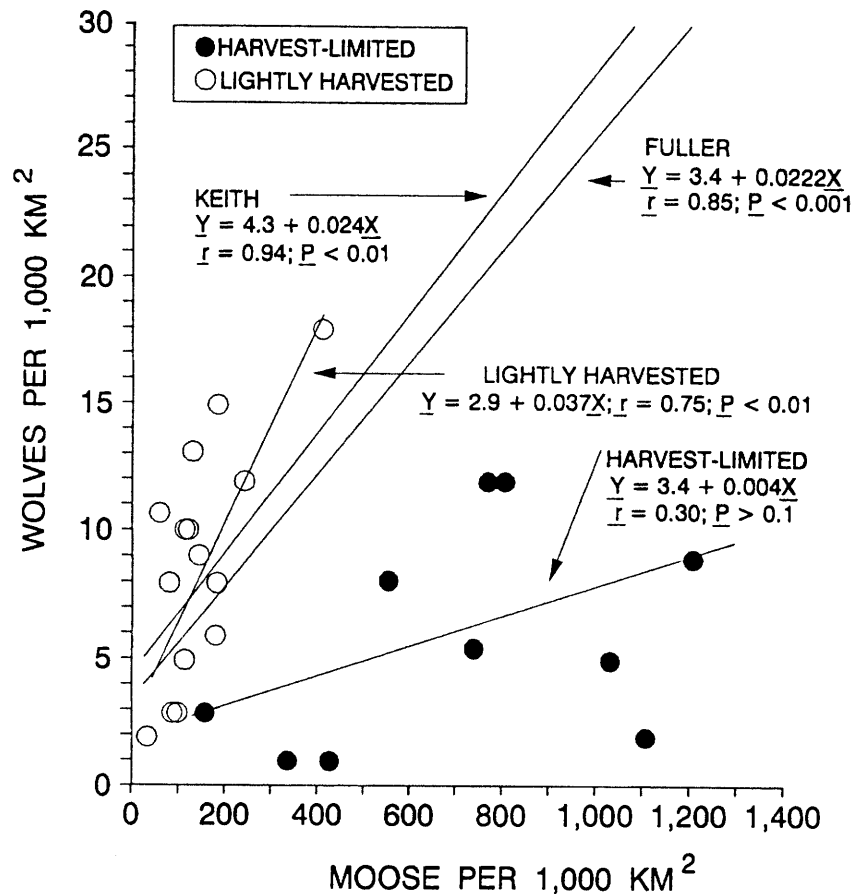


Fig. 14. Wolf density in relation to moose density in regions with lightly harvested and harvest-limited predator populations in Alaska and Yukon. Data points are from Tables 11 and 12. Keith's (1983) and Fuller's (1989) regressions of wolf density on prey biomass are used to predict the approximate K carrying capacity for wolves based on moose equivalents; these predictions are conservative because other prey occur in most Alaska and Yukon areas (Tables 11, 12) and Fuller's regression includes some heavily harvested wolf populations.

1. Moose remain abundant in areas where only a single predator species exists (Messier and Crete 1985; Crete 1987, 1989; Bergerud and Snider 1988; Messier 1989). To our knowledge, single predator systems, except Isle Royale, exist because of regional extirpation of the wolf. For example, in black bear-moose systems, moose density is about 2,000/1,000 km² in Quebec (Crete 1989) and commonly 1,100–2,400/1,000 km² on good range when moose are lightly harvested in Newfoundland (Bergerud and Manuel 1969, Mercer and Manuel 1974, Fryxell et al. 1988). Crete (1987, 1989) suggested a single high-density equilibrium model (model 2, Fig. 12) for black bear-moose systems, which

also may apply to grizzly bear-moose systems. Grizzly bears are the only major predator of moose on the Seward Peninsula, Alaska; despite moderate harvest rates, moose increased to 438 moose/1,000 km² by 1987 after first appearing during the 1950's (Fig. 13; Table 12). The only wolf-moose system of which we are aware is on Isle Royale. There, moose have fluctuated widely (1,000–3,000 moose/1,000 km²) during 20 years (Peterson 1988), but the lowest density on Isle Royale was more than double the highest moose density in lightly harvested moose-wolf-bear systems (Crete 1987, Bergerud and Snider 1988) (Fig. 13).

2. Moose populations can sustain high

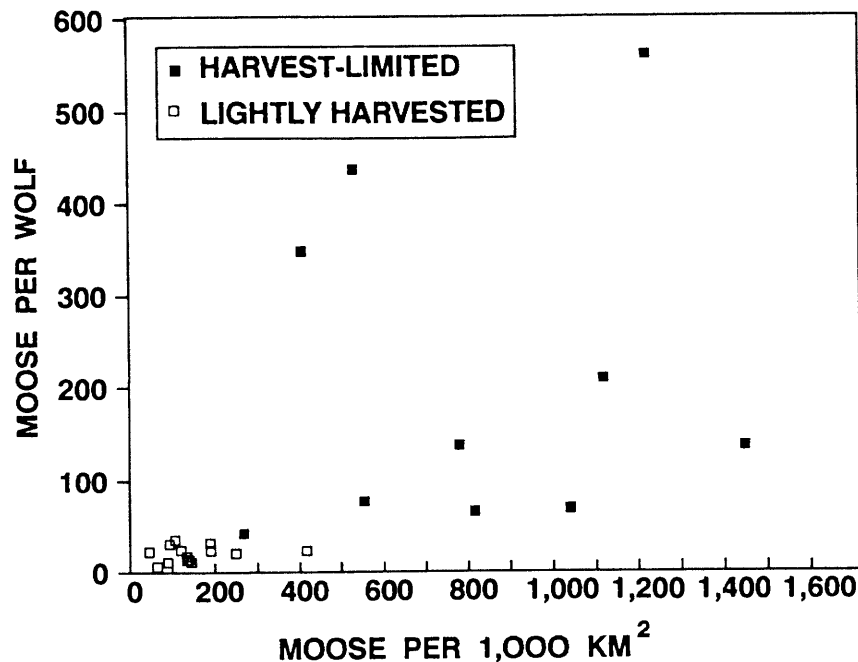


Fig. 15. Moose: wolf ratios in relation to moose density in regions with lightly harvested and harvest-limited wolf populations in Alaska and Yukon. Ratios were calculated by dividing moose density by wolf density for each area listed in Tables 11 and 12.

densities (K2 of model 2, Fig. 12) where black and grizzly bears exist (wolves extirpated), with or without alternate ungulate prey. Examples are found in Jackson Hole, Wyoming (Houston 1968) and the Kenai Peninsula, Alaska (Bailey 1978). Kenai studies show that moose can fluctuate near KCC for long periods and occasionally attain high densities (1,570/1,000 km²) when wolves are absent (early 1900's-1960's) and predation is restricted to that by black and brown bears (Bailey 1978, Peterson et al. 1984, Schwartz and Franzmann 1989).

- Where moose are minor prey in wolf-bear-multiprey systems, moose can become at least moderately abundant (Crete 1987, Bergerud and Snider 1988). This occurs primarily in the southern portion of moose range and possibly in mountainous western Canada where other ungulate species are more important to wolves. Examples are Algonquin Provincial Park, Ontario (400-700

moose/1,000 km², Wilton 1987) and Riding Mountain National Park, Manitoba (800 moose/1,000 km², Carbyn 1983). The role that high caribou densities play in northern moose-wolf-bear systems requires further study, but moose apparently are major prey when caribou are at low densities (Ballard et al. 1987, present study).

Acceptance of the single LDDE model for moose-wolf-bear systems suggests that (1) moose densities must have been low in these systems throughout much of pristine northern North America as suggested by Bergerud (1967), Pimlott (1967), and Keith (1974) and (2) attaining moose densities above the LDDE in these systems will require predator management, although exceptions may occur. In many cases, predator management may be necessary to elevate moose densities because moose, wolves, grizzly bears, and/or black bears are sympatric in most moose range (Burt and Grossenheider 1976) and moose are

commonly the primary prey of these predators and of humans (Ballard and Larsen 1987, Van Ballenberghe 1987, Boertje et al. 1988).

HARVEST RATES OF MOOSE IN AREAS WITH LIGHTLY HARVESTED AND HARVEST-LIMITED PREDATOR POPULATIONS, ALASKA AND YUKON

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

Harvest rates of moose increased rapidly with moose density and were, in part, a function of the level of predator management. Disregarding sustainability, harvests were low ($\bar{x} = 9$ moose/1,000 km², $n = 18$, SE = 2; Fig. 16) in Alaska and Yukon where moose populations were preyed on by lightly harvested predator populations. In contrast, harvests were significantly greater ($\bar{x} = 56$ moose/1,000 km², $n = 13$, SE = 15; $P < 0.02$ Mann-Whitney test) where moderate to heavy harvest of predators kept predators below KCC, although not always at low absolute densities (Figs. 13, 14, 16).

Moderate to heavy harvest of predators apparently increased the approximate sustainable yield of moose (largely bulls) in Alaska and Yukon study sites from 0–18 moose/1,000 km² for the LDDE to 20–130 moose/1,000 km² (Fig. 17). These 2 approximate sustainable yield curves were derived from empirical data from 23 populations (Tables 11, 12) at varying densities rather than from a single population varied over a range of densities (e.g., McCullough 1979). In reality, each population has a unique KCC and sustainable yield curve. Differences in sustainable yields are greatest at high densities; therefore, we place less faith in the yields predicted for high densities. Despite these limitations, we believe the 2 empirical yield

curves in Fig. 17 are useful first approximations of sustainable yields from low- and moderate-density moose populations in Alaska and Yukon (e.g., moose densities of 45–800 moose/1,000 km²).

The shape of the composite sustainable yield curve for Alaska and Yukon study sites differs from the sustainable yield curve for ungulates in predator-free areas (Caughley 1976, Crete 1987) (Fig. 18). Differences in these yield curves can be attributed to mortality from predation reducing the sustainable yield to humans (McCullough 1979) and the degree to which humans reduced predation and harvested the potential yield. Sustainable yield was low and limited to primarily bulls at the left side of the Alaska–Yukon curve (Fig. 18) when predators were lightly harvested (Fig. 17). Where moose densities were above the LDDE, reduced predation from human exploitation of predators was apparently responsible. The impact of predation diminished with increased moose density, as exemplified by the corresponding increase in moose : wolf ratios (Fig. 15). Empirically, as density increased to near food-limited levels, sustainable harvest accelerated, in part because cows were harvested at moderate and high densities. Just prior to attaining food-limited densities, a sharp decline in sustainable yield would likely occur (Fig. 18).

For moose populations at a LDDE, we give 2 examples where predators killed most of the potential sustainable yield that could be shared between hunters and predators. After the 1980's wolf removal in our experimental area, wolves and bears killed an estimated 54 moose/1,000 km² (31% of the postcalving population). This predation restricted potential sustainable yield by humans to about 6 moose/1,000 km² (the sum of postcalving harvest rate, 1.5%, and predicted postcalving population growth rate, 2%; Fig. 9). In a comparable Yukon study area, predators killed 120 moose/1,000 km² and humans killed at least 12 moose/1,000 km²; however, the predicted sustainable yield for humans was zero because the population was declining from predation alone (Larsen et al. 1989a).

Table 12. Moose and predator densities and moose harvests per 1,000 km² and moose calves per cow in the sites on Fig. 13 where wolf and/or bear populations are held below K carrying capacity by harvest in Alaska, 1965-90. Study sites composed of <2,000 km² of moose habitat were excluded to enhance comparability among sites; small sites exhibit high variability in prey and predator densities and habitat quality.

Site and year of moose density estimate	Posthunt moose density ^a	Area of moose habitat (km ²)	Wolf density ^a	Grizzly bear density ^a	Black bear density ^a	Alternate prey species and density ^a	Moose harvest ^b	Moose population trend ^c	Early winter moose calves/100 cows ^d	Source
Kenai Peninsula, GMU 15A, Alas., 1965-71	1,447	5,048	Very low	Low	High	Caribou, low	125	Stable	36	LeRoux 1973; Bailey 1978; Peterson et al. 1984
South-central, GMU 13A, Alas., 1987	1,220	4,861	8-10, moderate	18, moderate	Low	Caribou, high	24	Increase	29	W. P. Taylor and R. W. Tobey, ADF&G, unpubl. data
Matanuska, GMU 14A, Alas., 1988	1,118	4,116	1-3, very low	Low	Moderate	Caribou, very low; sheep, high	165	Increase	47	Grauvogel 1989; C. A. Grauvogel and W. P. Taylor, ADF&G, unpubl. data
Lower Susitna, GMU 14B, Alas., 1987	1,040	2,776	4-6, low	Moderate	Moderate-high	Caribou, low; sheep, moderate	114	Stable	30	Grauvogel 1989; C. A. Grauvogel and W. P. Taylor, ADF&G, unpubl. data
Kenai Peninsula, GMU 15A, Alas., 1987	816	3,310	12, moderate	Low	200-260, high	Caribou, low	108	Decline	31	Spraker 1985, 1986, 1987, 1988; T. H. Spraker, ADF&G, unpubl. data; Schwartz and Franzmann 1989
Tanana Flats and adjacent foothills, GMU 20A, Alas., 1988	776	12,650	12, moderate	15, moderate	Moderate	Caribou and sheep, high	33	Increase	37	McNay 1990a; M. E. McNay, ADF&G, unpubl. data; Reynolds and Hechtel 1988
South-central, GMU 13, Alas., 1983	751	3,737	5-6, low	25, high	Low	Caribou, low	55	Increase	32	Ballard et al. 1987, 1990; R. W. Tobey and W. P. Taylor, ADF&G, unpubl. data
Central, GMU 20B East, Alas., 1990	555	5,144	8, moderate	Low	Moderate	Caribou, very low	32	Increase	39	McNay 1990a,b; M. E. McNay, ADF&G, unpubl. data
Galena, GMU 21D, Alas., 1987	530	8,563	Low-moderate	Low-moderate	High	Caribou, low	19	Increase	34	Osborne 1989; T. O. Osborne, ADF&G, unpubl. data

Table 12. Continued.

Site and year of moose density estimate	Posthunt moose density ^a	Area of moose habitat (km ²)	Wolf density ^a	Grizzly bear density ^a	Black bear density ^a	Alternate prey species and density ^a	Moose harvest ^b	Moose population trend ^c	Early winter moose calves/100 cows ^d	Source
Seward Peninsula, GMU 22D, Alas., 1988	438	6,472	<1, very low	Moderate	None	Reindeer, moderate	25	Stable	29	Nelson 1989; R. R. Nelson, ADF&G, unpubl. data; T. E. Smith, ADF&G, unpubl. data
Kaiyuh Flats, GMU 21D, Alas., 1987	418	4,079	Low-moderate	Low-moderate	High	None	Unknown	Unknown	35	Osborne 1989
Noatak River, GMU 23, Alas., 1985	407	5,478	Low-moderate	20, high	Very low	Caribou, moderate	6	Increase	31	James 1984, 1986; Ballard et al. 1988; Quimby and James 1985; D. N. Larsen and J. R. Dau, ADF&G, unpubl. data
Seward Peninsula, GMU 22B, Alas., 1987	348	6,472	1, very low	Moderate-high	Very low	Reindeer, low	25	Unknown	20	Nelson 1988; R. R. Nelson, ADF&G, unpubl. data
Huslia River, GMU 24, Alas., 1988	303	6,262	Moderate	Moderate	Moderate-high	Caribou, moderate	2	Increase	42	T. O. Osborne, ADF&G, unpubl. data
Nushagak River, GMU 17C, Alas., 1983	269	4,750	Low	High	Low	Caribou, low	Unknown ^e	Increase	39	Taylor 1983, 1984; W. P. Taylor, ADF&G, unpubl. data; S. D. DuBois, ADF&G, unpubl. data
Selawik Refuge, GMU 23, Alas., 1985	169	11,292	4, low	Low	High	Caribou, high	Unknown ^e	Increase	30	Larsen 1987; D. N. Larsen, ADF&G, unpubl. data; Quimby and James 1985; Ballard et al. 1990; S. D. DuBois, ADF&G, unpubl. data

^a Numerical values are estimated densities; relative densities are presented so readers can form an impression of the complexity of these ecosystems. Relative densities represent our ranking based on our observations and those of biologists working at the sites.
^b Harvest is a 3-year mean (yr. of the moose density estimate and 2 preceding yrs.). Reported harvest was multiplied by 1.177 to adjust for unreported harvest (Gasaway et al. 1983).
^c Trend is based on the 9-5-year period prior to the moose density estimate.
^d Numbers of calves per 100 cows is a 3-year mean (yr. of density estimate and 2 preceding yrs., when available).
^e Native harvest was unknown but was high relative to the moose population and kept the moose at a low density.

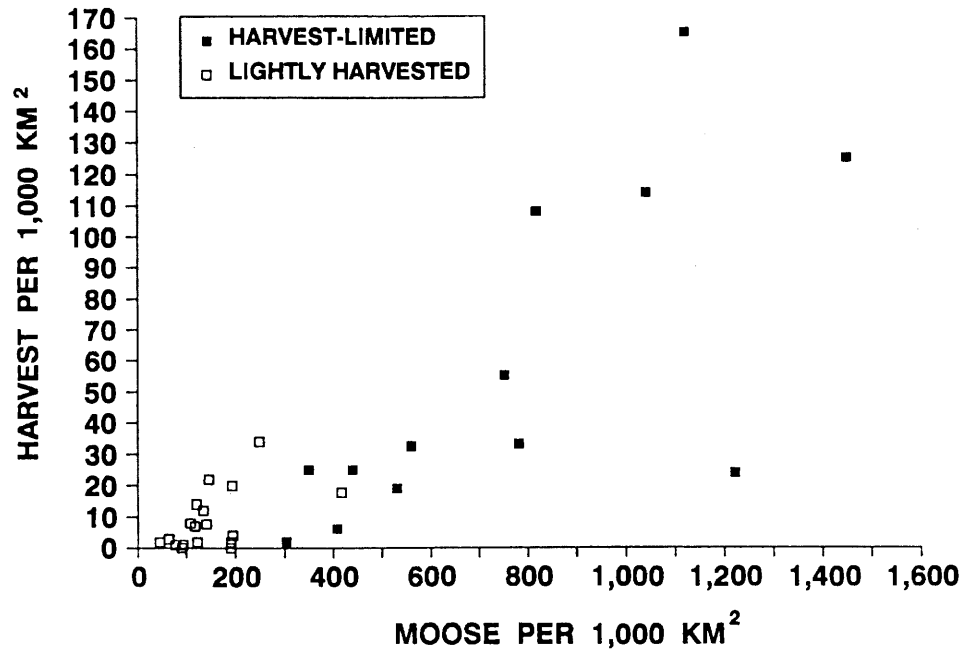


Fig. 16. Harvest rates of moose in relation to moose density in regions with lightly harvested and harvest-limited predator populations in Alaska and Yukon. Data are from Tables 11 and 12.

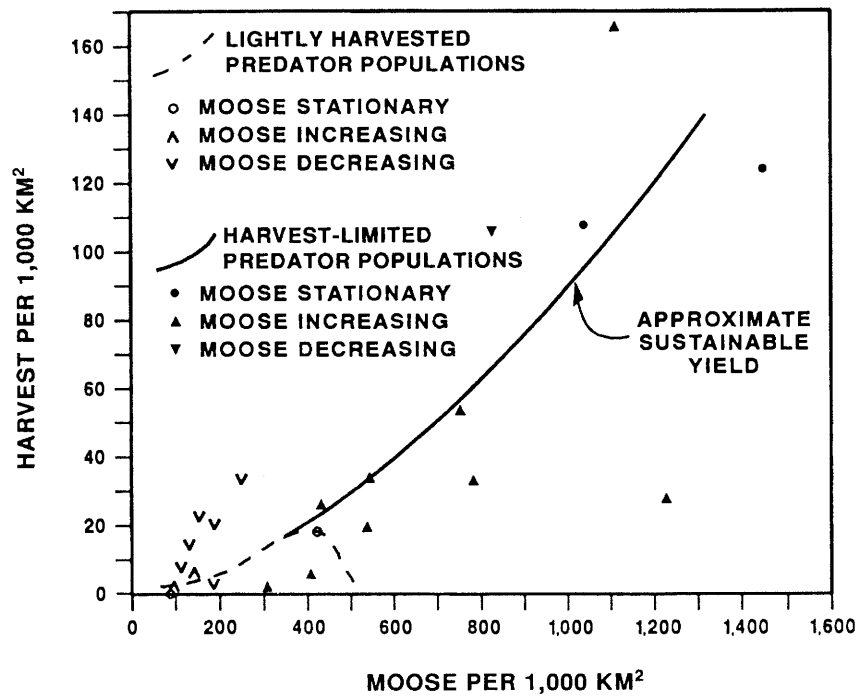


Fig. 17. Approximate sustainable yield of moose at varying moose densities in Alaska and Yukon. The lines were fit by hand assuming harvest rates were sustainable if population size was stationary, were above sustainable when moose numbers were declining, and were below sustainable when numbers were increasing. We omitted populations with unknown trends. Data are from Tables 11 and 12.

Messier and Crete's (1984) and Crete's (1987) yield model for low-density, predator-limited moose populations in Quebec differed from that which we observed in Alaska and Yukon (Fig. 18). In Quebec, the LDDE is about 370 moose/1,000 km² in systems with wolves and black bears. Messier and Crete imply that by simply lowering moose densities to 200–300 moose/1,000 km² through intensive harvesting, their sustained yield increased from 13 moose/1,000 km² to about 54 moose/1,000 km², compared with <18 moose/1,000 km² in Alaska and Yukon systems with lightly harvested predators. At these reduced moose densities in Quebec, wolf numbers and predation rates declined, and recruitment and harvest of moose increased (Messier and Crete 1984). However, increased harvest of black bears by moose hunters also may have contributed to the increased recruitment of moose (M. Crete, Ministère du Loisir, Quebec, pers. commun.). Messier (1985) speculated that wolf populations in Quebec may be unable to survive when moose densities are <200/1,000 km² and alternate prey are rare.

In contrast, moose densities as low as 45/1,000 km² in Alaska and Yukon were not consistently associated with increased moose recruitment (calves/100 cows during early winter, Fig. 19, Table 11). Black bears, wolves, and especially grizzly bears remained effective predators on calves at very low moose densities in these northern areas (e.g., Boertje et al. 1988; Larsen et al. 1989a,b; present study). Also, wolf populations in Alaska and Yukon persisted at densities of <100 moose/1,000 km² where alternate prey were absent or scarce (Fig. 14, Table 11).

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

In the 2 preceding sections, we conclude that moose densities and harvests by humans likely will remain low for long periods in Alaska and Yukon where moose

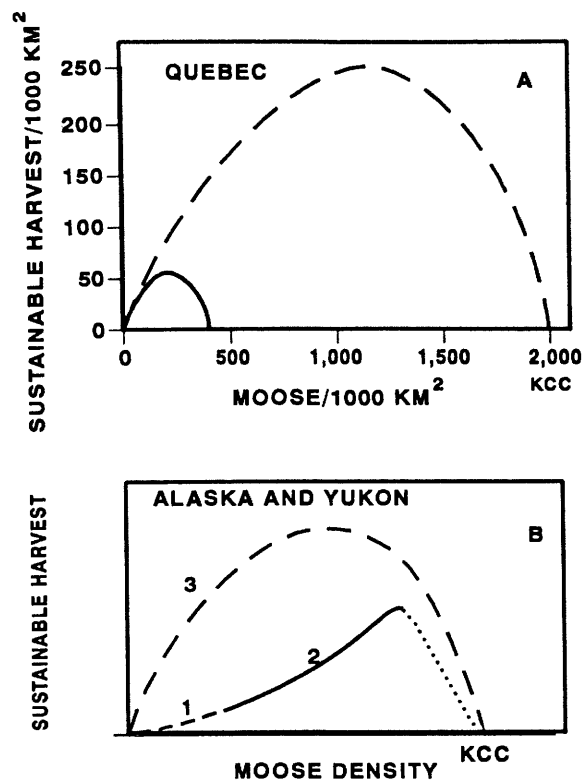


Fig. 18. Preliminary conceptual models for sustainable yields in relationship to moose density. A = yields in Quebec where wolves and black bears were present (solid) and absent (dashes) (after Crete 1987). B = yields in Alaska and Yukon where (1) wolves, grizzly bears, and black bears were present and lightly harvested (short dashed line from Fig. 17), (2) predators present but harvest-limited (solid line from Fig. 17, dots signify theoretical relationships), and (3) a hypothetical yield curve when predators are absent (long dashes).

are the primary prey of both wolves and bears and these predators are lightly harvested. Realization of this situation has caused a divisive controversy among conservationists across North America. On 1 side are advocates for managing predation to increase prey densities and harvests; on the other side are advocates for maintaining more natural, lightly harvested and protected systems at a LDDE. Substantial common ground exists among these conservationists. All are concerned about the perpetuation of wildlife resources. The most divisive issue is whether wildlife management should be directed toward enhancing wildlife densities and harvests. Controversy focuses on which, if any, lands should be intensively managed for enhanced densities, the appropriate share or

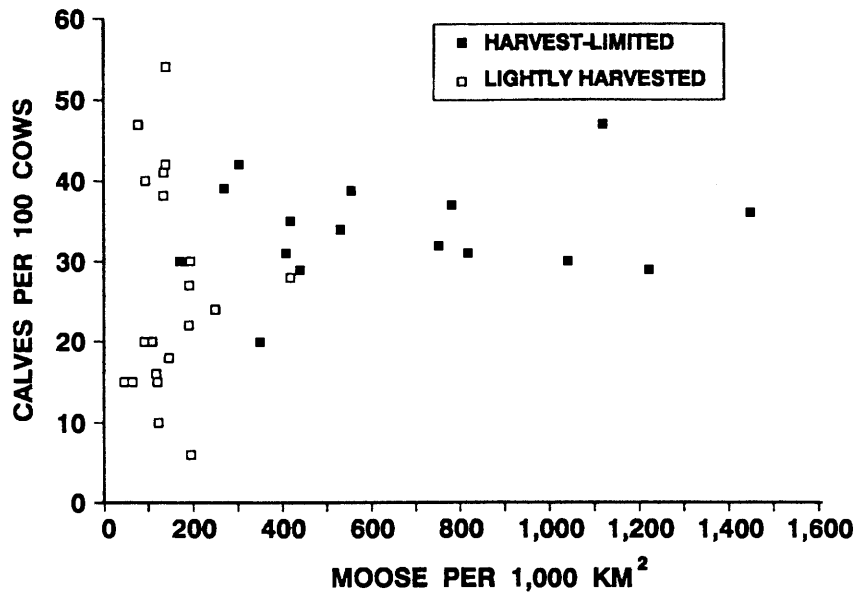


Fig. 19. Calves per 100 cow moose in relation to moose density in regions with lightly harvested and harvest-limited predator populations in Alaska and Yukon. Data are from Tables 11 and 12.

allocation of moose for humans and predators, and how those shares can be maintained given society's concerns for the treatment and welfare of the remaining large predator populations in North America. Reducing this controversy appears essential if conservationists are to unite in addressing the most serious threat to moose-wolf-bear systems, i.e., loss of habitat. In an effort to reduce the divisiveness, we offer a management approach that accommodates some of the major values and desires of conservationists with divergent objectives. The following 4 sections describe the approach.

Conservation Plans

Following the lead of citizens in British Columbia (Archibald 1989), we recommend that public and wildlife conservation agencies construct mutually-agreed-on conservation plans that outline where wolves and bears and their ungulate prey will be managed for specific uses. Options could range from protection to high harvest rates of wildlife. Society is demanding that administrative, decision-making processes involve the public and, where possible, satisfy a variety of public interests

(Tipple and Wellman 1988). We suggest that formalized conservation plans define by specific area (1) the priority uses of wildlife, (2) a commitment to the long-term welfare of large predators, and (3) types of predator management that are acceptable, if management of predation is to be used to elevate prey density and harvest. Without formal goals and accountability for specific areas, many people will remain convinced that the extirpation of large carnivores observed in much of North America will continue.

A Conceptual Conservation Plan for Areas Where Predation Management Is Sanctioned

We list here several biological components of a conceptual conservation plan for areas where predator management is sanctioned. Overall, this plan seeks to (1) maintain moose densities at moderate to high densities and (2) maintain long-term wolf densities similar to the average density in systems where predation is not reduced.

First, areas selected for this management should have a relatively high KCC for moose. A high KCC will simplify maintaining a moderate moose harvest while

maintaining long-term wolf densities near mean values in lightly harvested populations.

Second, if areas chosen for management are within the LDDE, predation must initially undergo a large reduction to increase moose density. We discuss methods of predator management below. Both field experiments and simulation models indicate that large reductions in predation and low moose harvest rates are required if low-density, predator-limited moose populations are to increase to high densities at annual rates that exceed 10% ($\lambda = 1.1$, i.e., a 7-year doubling time) (Gasaway et al. 1983; Crete and Jolicoeur 1987; Larsen et al. 1989a,b; present study). The intensity of predation reduction programs can be determined after the public and wildlife managers decide if the initial growth phase of low-density moose populations is to be short and swift or long and slow. At a 5% ($\lambda = 1.05$) growth rate, a moose population will double in about 14 years; at 20% ($\lambda = 1.2$), it will double in 4 years. Commonly, low-density moose populations will require 2 to 4 doubling periods to reach desired densities.

Third, 1 option for managing for elevated prey densities is to maintain moose densities above those at the peak of the total yield curve (Fig. 20), but well below KCC. This will reduce the risk of rapid population declines resulting from short-term increased predation or harvest (McCullough 1979, 1984; Van Ballenberghe and Dart 1982). Predation and harvest likely are largely additive mortality factors at densities below those at the peak of the yield curve, whereas they likely become increasingly compensatory as density approaches KCC (McCullough 1979). By maintaining density well below KCC (Fig. 20), managers can potentially avoid the low moose reproductive rates (Table 5), high mortality from deep snow (Gasaway et al. 1983), and low sustainable harvest rates (McCullough 1979) (Fig. 20) associated with densities near KCC. These elevated densities of moose should satisfy many consumptive and nonconsumptive needs of humans for moose, while ensuring

enough moose to support long-term densities of wolves similar to the average in lightly harvested systems (about 9/1,000 km²) (Fig. 14). Defining appropriate long-term bear densities in these managed systems is difficult because bear densities in LDDE systems vary greatly (Table 11). Also, affordable bear-census techniques are not available for large areas.

Fourth, 1 option for managing for elevated prey densities is to maintain the predator's share of the moose yield at the same level as found in the upper portion of the LDDE range (Fig. 20). This will likely require some form of predation management, which we discuss below. Our summary suggests that where moose are the primary prey of wolves and bears, moose densities can be sustained above the LDDE for long periods only where predators are harvest-limited. However, exceptions may occur.

Implementing this conservation plan should (1) maintain sufficient wildlife use and value to compete more effectively with alternative land uses destructive of moose-wolf-bear systems, e.g., reindeer herding, other domestic animal production, or agriculture; (2) assure the long-term security of wolves and bears in most managed areas; and (3) provide sufficient wildlife to satisfy many nonconsumptive and consumptive users of moose, wolves, and bears. We envision that management following this plan will help fulfill wildlife desires of people living in adjacent areas that are lightly harvested or protected from harvest. The plan we have offered is one of many variations on the theme of sharing an elevated moose population among hunters, bears, and wolves.

Options for Managing Predation

We recommend testing alternatives to intense, lethal, government-sponsored predator removal for elevating or maintaining elevated prey populations. Recent history indicates intense, government-sponsored predator removal is most effective, but is increasingly socially unacceptable as a widespread, routine management

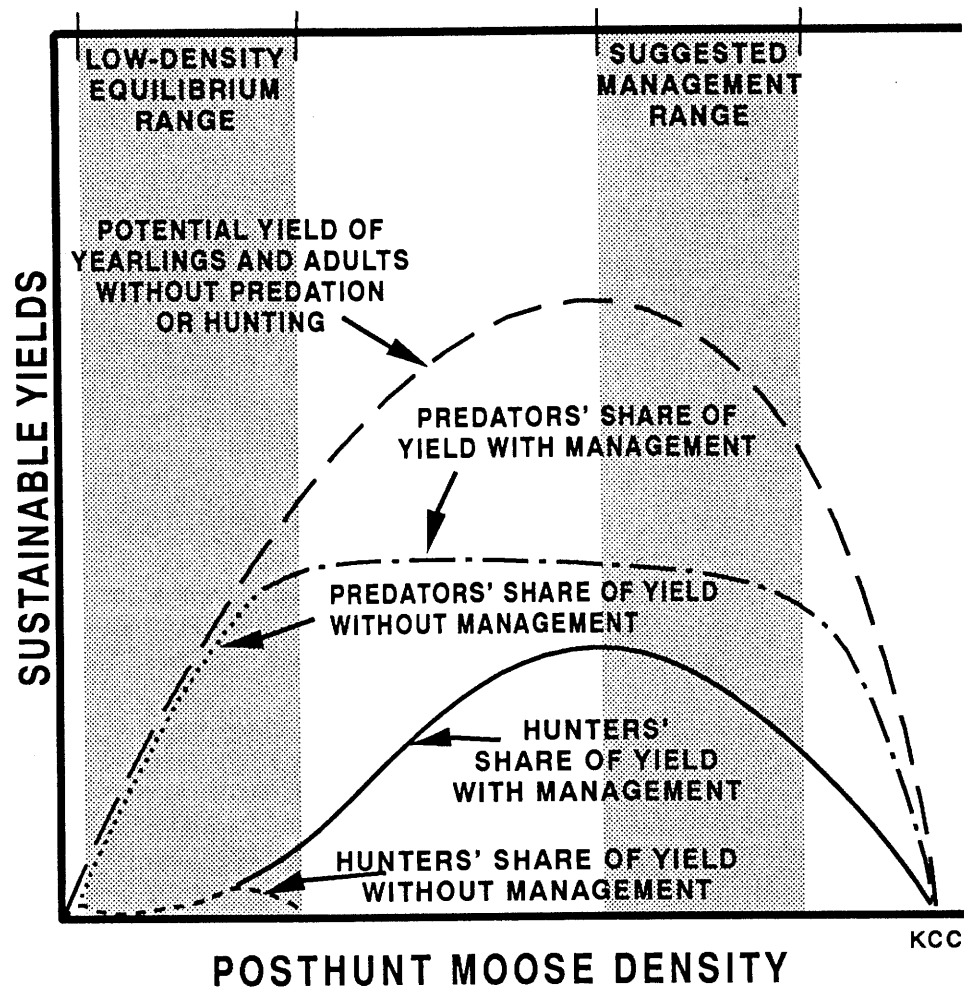


Fig. 20. A conceptual model of how predators and hunters can share the potential sustained yield from a moose population with and without predator management as moose density changes. This model applies to moose-wolf-bear systems in Alaska and Yukon where moose are the primary prey. In this model, (1) predator management maintains the predator's share to yield at the highest yields possible in systems at a low-density dynamic equilibrium, and (2) harvest available to hunters is the difference between the proportion of sustained yield killed by predators and the potential yield.

technique. Evaluating some alternatives may help reduce the controversy over predator-prey management (Kellert 1985).

To begin the search for a more socially acceptable management system, we list 6 potential alternatives (5 nonlethal and 1 lethal). First, diversionary feeding of predators on or near moose and caribou calving areas for 4-5 weeks may reduce predation on neonates. Our preliminary test indicates moose calf survival can increase during years that feeding occurs. Also, diversionary feeding has reduced damage by black bears to forest plantations in Washington (Flowers 1987). Second, increased alternate prey (e.g., caribou) may reduce predation on moose populations (Bergerud

and Elliot 1986, Crete 1987, Wilton 1987). Third, habitat enhancement (e.g., through fire management) may increase moose numbers through immigration of moose (causing increased moose : predator ratios) (Peek 1974, Gasaway et al. 1989) or improved moose physical condition and reproductive rate (Franzmann and Schwartz 1985). Fourth, chemically, surgically, immunologically, or hormonally reducing birth rates in predators can reduce growth rates of predator populations (Stellflug and Gates 1987, Orford et al. 1988). Fifth, the relocation of grizzly bears just before calving can improve moose calf survival in small areas (Ballard and Miller 1990).

Finally, conventional public hunting and

trapping of predators effectively limits some Alaska wolf and bear populations (Peterson et al. 1984, Reynolds and Hechtel 1988, Schwartz and Frazmann 1989, Miller 1990). Trapper and hunter education programs and liberalized seasons, bag limits, and methods of harvest are integral to increasing the effectiveness of this method. The potential effects of public hunting and trapping of wolf and bear populations in Yukon and portions of Alaska are less significant because of low human populations and reduced access. In some of these areas, the public may choose more controversial methods such as baiting of bears or use of airplanes to hunt wolves, an effective means of temporarily manipulating wolf densities in some parts of Alaska and Yukon (Ballard et al. 1987).

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

Plans for manipulating predation should consider altering wolf and bear predation simultaneously rather than intense management of 1 predator species. Nonlethal means, e.g., diversionary feeding and habitat management, may reduce predation by both wolves and bears simultaneously. However, lethal methods usually have been used only to reduce wolf numbers (e.g., Gasaway et al. 1983, Larsen et al. 1989b). If lethal means are used to reduce bear predation, conventional harvests are recommended. Reducing predation of only 1 species may result in compensatory predation by another species, hence diminishing the effects of intense single-species management (Schlegel 1976; M. Schlegel, unpubl. data cited in Ballard and Larsen

1987). Additionally, attempting to increase moose numbers by a short-term reduction in numbers of only 1 predator species may require large and potentially unacceptable levels of reduction (Ballard and Larsen 1987; Larsen et al. 1989a,b; present study). Managing predation by reducing only black or grizzly bear populations is not desirable because (1) bear populations have low recovery rates because of low reproductive and immigration rates (Bunnell and Tait 1981, Reynolds and Hechtel 1988), (2) bears often are managed for their economic value, and (3) the greater difficulty in censusing bears makes measuring the effects of management actions on bear populations more costly than in the case of wolves (Miller 1990).

Benefits for People and Wildlife

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

By making some concessions, conservationists on both sides of the controversy have much to gain in Alaska and Yukon. First, the long-term security of large predator populations can be assured in most managed areas—a departure from trends in predator conservation worldwide. Second, diverse human uses of wildlife can be provided. Third, in those areas where elevated moose abundance is sanctioned, opportunities will increase for (1) consumptive uses of moose and associated predators and scavengers and (2) nonconsumptive uses of moose, scavengers of moose, and occasionally wolves. Increased wildlife use will result in significant economic advantages from tourism and hunting. Fourth, on lands not already protected by Park or Refuge status, elevated moose densities accompanied by increased use of wildlife may strengthen the case for protecting

wildlife habitat from competing land uses. Finally, by moving past the predator-prey management controversy, a united conservation effort can work to retain the wilderness ecosystems that are necessary for maintaining moose-wolf-bear systems.

CONCLUSIONS

1. Low wolf reproductive rates and low harvest of wolves suggested the wolf population was near KCC in our experimental area before the 1981-83 wolf reduction program. Harvests of grizzly and black bears also were low.
2. The recent increase in the early winter moose population in our experimental area (4-9% annually during 1981-88) may have resulted, in part, from the combined effects of a wolf reduction program, elevated public harvest of grizzly bears and wolves, and an increase in alternate prey (caribou). However, the possibility exists of concurrent increases in the 2 control moose populations. Thus, the small reduction in predators possibly had little effect on the experimental moose population.
3. Despite the recent increase in the early winter moose population, moose density remained low (127-188 moose/1,000 km²) during 1988. Predation by wolf and bear populations was the primary factor maintaining moose populations at low densities for extended periods in our experimental area. By comparison, nutrition, snow, and harvest were minor limiting factors, and disease appeared inconsequential.
4. Predation by lightly harvested wolf and grizzly or black bear populations appears to limit lightly harvested moose populations at a LDDE for extended periods in much of Alaska and Yukon. In these systems, densities averaged 148 moose/1,000 km², 9 wolves/1,000 km², and bears were common. We suggest these lightly harvested systems typify conditions people can expect in the absence of programs that strongly limit predation. Average moose and wolf densities in lightly harvested systems were similar to densities in Denali National Park.
5. High-density moose populations in Alaska appear to be products of predator management, although exceptions may occur. Of 24 Alaska sites >2,000 km² examined, moose attained elevated densities (\bar{x} = 663 moose/1,000 km²) only where humans had previously reduced predators below KCC. Also, habitat studies and circumstantial evidence from predator reduction programs and predation studies indicate that moose populations at low densities are not limited by food in most of Alaska and Yukon.
6. Recent data from this and other studies indicate predator management is needed in most cases to attain elevated moose abundance where moose, wolves, and bears are sympatric and moose are the primary prey. In general, high densities of moose occur naturally only in areas where moose are (1) preyed on by only 1 predator species, (2) preyed on by black and grizzly bears (wolves absent), or (3) minor prey of wolves and bears in multiprey systems. Extirpation of predators by humans, however, has created circumstances for numbers (1) and (2) above, except for Isle Royale.
7. In Alaska and Yukon, elevating the sustainable moose harvest above levels common to populations at a LDDE required manipulating predation to increase moose density. This management has caused a divisive controversy among wildlife conservationists. We believe this controversy and the accompanying environmental, social, and economic costs can be reduced. Cooperation and compromise among conservationists can produce conservation plans in Alaska and Yukon that benefit both people and wildlife. For example, long-term wolf densities in areas managed for elevated moose harvests can be maintained near levels found in lightly harvested systems. Also, predator management techniques with wider social acceptability can be tested. Reducing the predator management con-

troversty will allow conservationists to unite in addressing a more serious threat to the existence of moose-wolf-bear systems in the North, i.e., the loss of wilderness ecosystems.

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APPENDIXES

Appendix A. Calves per cows, yearlings per cows, and proportions of recruits (*R*) for 1955 through 1988 cohorts, as determined from aerial surveys in the experimental area, east-central Alaska. Adult cows were ≥ 29 months old.

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

^a Total number of moose classified.

^b Surveys conducted during late winter after moose antler drop. Calves per 100 adult cows estimated from regression of calves per 100 adult cows versus percent calves in the samples of moose observed during early winter surveys in the study area.

Appendix B. Best estimates of numbers of wolves and respective wolf pack names in a 15,500-km² area, which contains all 16 packs that ranged entirely or partially in the experimental area, east-central Alaska. Data are summarized in Table 4.

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

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

^b Radio collar(s) were used to locate the pack.

Appendix C. Moose harvest and duration of hunting seasons for bulls and cows in Game Management Unit (GMU) 20E (28,500 km²), east-central Alaska (ADF&G files). Parentheses enclose harvests from the portion of the GMU in the experimental area.

Year	No. of moose harvested ^a	% cows in harvest	Duration of hunting seasons (days)	
			Bulls	Cows
1954	88 ^b	0	Unknown	0
1955	65 ^b	0	Unknown	0
1960	92 ^b	0	72	0
1961	142 ^b	0	73	0
1962	118 ^b	0	72	0
1963	124	5	72	1
1964	118	13	72	7
1965	124	5	72	2
1966	106	11	70	5
1967	130	6	72	7
1968	126	7	72	7
1969	124	5	72	7
1970	79	Unknown	72	7
1971	102	Unknown	72	7
1972	85	Unknown	72	7
1973	115	19	72	7
1974	95	11	72	7
1975	40	0	40	0
1976	40	0	40	0
1977	0	0	0	0
1978	0	0	0	0
1979	0	0	0	0
1980	0	0	0	0
1981	0	0	0	0
1982	22	0	10	0
1983	37 (25)	0	10	0
1984	34 (22)	0	10	0
1985	55 (28)	0	10	0
1986	51 (34)	0	10	0
1987	64 (32)	0	10	0
1988	67 (45)	0	10	0

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

^b Reported harvest is from check stations along the Taylor highway; during other years reported harvest is from harvest tickets or harvest tickets and check stations.

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

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