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FACTORS LIMITING MOOSE POPULATION GROWTH IN SUBUNIT 20E

by
Rodney D. Boertje
William C. Gasaway
Daniel V. Grangaard
David G. Kelleyhouse
Robert O. Stephenson
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Job 1.37R
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PROGRESS REPORT (RESEARCH)

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Cooperators: Daniel V. Grangaard, David G. Kelleyhouse, and Robert O. Stephenson, Alaska Department of Fish and Game

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SUMMARY

Data have been presented to test 2 hypotheses: (1) food limits moose (*Alces alces*) population growth, and (2) predation limits moose population growth in Game Management Subunit 20E. Data presented by Boertje et al. (1985) support rejection of the food-limiting hypothesis. Data in this report strongly support acceptance of the hypothesis that predation by grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) is limiting moose population growth in Subunit 20E. Definitive tests of the predation-limiting hypothesis are not possible unless programs to reduce grizzly bear and wolf predation are effective.

Moose population density in Subunit 20E declined drastically during the 1960's and through the mid-1970's and has since remained low. In 1981, the moose density was 86 moose/1,000 km^2 ± 23 moose (90% CI)--the lowest density recorded in Alaska using the stratified random sampling technique. No significant increase in this low-density moose population is predicted during the next 5 years given the current management regime.

During the 1980's, wolf densities have been low in the experimental area (4-8 wolves/1,000 km^2 in fall), yet wolves have been abundant relative to moose (1 wolf:11-17 moose) even immediately after ADF&G wolf control. Consumption of about 50% caribou, in effect, doubles the number of moose in the wolf:moose ratio, resulting in 1 wolf:22-34 moose. We would expect the moose population to remain stable or increase at these ratios if grizzly bears were not important predators. Wolf densities will remain low until their prey base increases

substantially. When prey was abundant during the late 1960's and early 1970's, much higher wolf densities existed in the experimental area.

Grizzly bears are abundant in the experimental area (approx. 16 bears/1,000 km^2 during spring 1986), and are extremely abundant relative to moose (1 grizzly bear:5 moose). Grizzly bears are about 3 times more abundant than wolves.

Harvest of grizzlies has increased substantially since 1980. Annual harvest rates during the years 1982 through 1986 have averaged approximately 8% in the 4,000-km^2 grizzly bear study area and approximately 4% in Subunit 20E. No significant short-term declines in the grizzly bear population are expected from average harvest rates of 4% or 8%, but we have inadequate data to assess the precise effects of these harvest rates.

Predation was the largest source of mortality for calf and adult moose. Predators killed most of the annual calf crop in 1984. Of 33 radio-collared moose calves, grizzly bears killed 52%, wolves killed 15%, and black bears (Ursus americanus) 3%, for a total of 70% predator-caused mortality. These data were collected after the spring wolf population in the calf study area had been reduced approximately 60%, and the wolf pack in the center of the calf study area was reduced from 15 wolves during fall 1981 to 2 during spring 1984.

Preliminary data suggest natural mortality of radio-collared adult moose averaged 7% annually after the fall wolf population had been reduced by 20-40%; of the 6 radio-collared moose that died, 3 were killed by grizzly bears, 1 by wolves, and 2 died from unknown causes. The latter 2 were eaten by grizzly bears and may have been killed by them. The sampling design currently used to estimate adult moose mortality rates contains 2 biases; 1 bias overestimates and 1 underestimates the mortality rate.

During fall 1985 through summer 1986, adult radio-collared male grizzly bears and females without cub(s) of the year killed adult moose at mean rates of 3.7 and 0.7 moose/year, respectively. At these kill rates, grizzly bears would have a large impact on the low-density moose population, killing 6-9% of the early winter moose population in the grizzly bear study area annually. It appears grizzly bear predation has a larger effect on moose population dynamics than does wolf predation.

The effects of a slowly increasing migratory caribou (Rangifer tarandus) herd on short-term moose-predator relationships can be both beneficial and detrimental to moose depending on when and how long caribou are present in the predator's home range.

However, the net effect of caribou on moose survival in the experimental area during the mid-1980's has been more beneficial than detrimental.

If we wish to stimulate a moderate rate of increase in moose numbers in Subunit 20E, reduction of the major sources of moose mortality (i.e., grizzly bear and wolf predation) will be required. Simultaneous reductions in the wolf and grizzly bear populations will likely allow the moose population to increase without drastically reducing either predator population. The wolf reduction experiment in 1982 demonstrated that reducing only wolf predation will not increase moose calf survival enough to allow numbers of moose to increase at a significant rate; however, reducing wolf predation may increase the rate of growth of the caribou herd, which may continue to benefit moose. Reducing grizzly bear predation will currently have the most significant direct effect on increasing moose numbers.

Currently, the moose population has few surplus moose for man to harvest and probably little or no surplus moose for population growth. Since 1976, essentially all moose production in Subunit 20E has been utilized by grizzly bears and wolves. Unless hunters and trappers can increase their harvest of grizzly bears and wolves, current regulations and policies make changes in this situation unlikely.

Key Words: Alaska, calf mortality, grizzly bears, moose, moose mortality, predation, predator-prey relationships, wolves.

CONTENTS

BACKGROUND

Moose (Alces alces), caribou (Rangifer tarandus), and the predators and scavengers that depend on them, e.g., wolves (Canis lupus) and wolverines (Gulo gulo), continue to remain at low densities throughout much of Interior Alaska. In the short term, low densities of wildlife deprive the state of a potentially valuable renewable resource. More importantly in the long term, public expectations and demands for effective management decline, and ignorance of the value of enhanced wildlife populations increases. Many past management actions, such as shortening or eliminating hunting seasons, have been ineffective at increasing numbers of moose and caribou, the primary or secondary food base for many carnivores. Yet, increased abundance of these ungulates and carnivores is vital to many Alaskans to increase hunting, aesthetic, and trapping opportunities, and to increase revenues from tourists and nonlocal and out-of-state hunters. Indeed, moose, caribou, wolves, grizzly bears (Ursus arctos), and wolverines are synonymous with the concept of Alaskan wilderness, and deserve enhancement. The lack of management actions that would increase ungulate populations has far-reaching detrimental impacts on the livelihoods and quality of life of many Alaskans.

To increase populations of moose, caribou, and the carnivores dependent on them for food, factors limiting ungulate and carnivore population growth must occasionally be altered. This provides long-term benefits to ungulates, carnivores, and man.

Intensive studies of ungulate-browse-predator interrelationships provide an understanding of how and what limits growth of ungulate and predator populations. Knowledge gained from these studies in particular areas allows more accurate predictions of effective management actions in similar ecosystems where information is less complete. Additionally, intensive studies provide insights on how to increase low-density animal populations and, most important, how to prevent populations from declining to low densities. Increasing low-density animal populations can be costly because extreme or long-term management actions may be required. Only by preventing populations from reaching low densities can man enjoy sustained benefits from wildlife.

Game Management Subunit 20E in eastcentral Alaska is one of the areas in Interior Alaska where moose, caribou, wolverines, and wolves declined to low densities during the 1970's. Moose and caribou in Subunit 20E prospered during and shortly after a predator poisoning program during the years 1948 through 1959 (Davis et al. 1978a). Poisoning was aimed at reducing wolf predation; however, both black (Ursus americanus) and grizzly bears were killed. Moose and caribou had declined to a low density by 1976. The early part of this decline in moose and caribou numbers in the mid-1960's corresponded to a period of high wolf density (Davis et al. 1978a), but wolf abundance declined from the late 1960's to the mid-1970's as prey became scarce (D. Grangaard, pers. observ.).

Moose-predator relationships in Subunit 20E contrast sharply with moose-predator relationships studied elsewhere in Alaska, particularly in regard to the relatively low moose density and moose:predator ratios in Subunit 20E. We estimated that 646 moose ± 27% (90% CI) occupied 7,500 km^2 of moose habitat in the southwest quarter of Subunit 20E during fall 1981. The mean moose density was 86 moose/1,000 km^2, which is the lowest of 12 densities recorded in Alaska using a stratified random sampling technique (Gasaway et al., in press). This low density and continued poor recruitment stimulated the Alaska Board of Game to authorize wolf removal during November 1981. In other areas of Alaska where predators were removed to increase moose numbers (Game Management Unit 13 and Subunit 20A), moose densities were initially 10 and 3 times greater, respectively, than in Subunit 20E, but recruitment was similarly poor (Ballard et al. 1981b, Gasaway et al. 1983).

We proposed to test hypotheses about factors currently limiting moose population growth in Subunit 20E through actions that would lead directly to their acceptance or rejection. Predator removal (Bergerud 1971, Ballard et al. 1980, Gasaway et al. 1983) has allowed a more rapid and accurate assessment of factors limiting ungulates than strictly using the "collar-and-watch" approach; therefore, we planned to rely heavily on predator removal to provide definitive tests of hypotheses. However, the Alaska Board of Game withdrew authorization to reduce wolf abundance soon after this research began, and to date liberalized hunting regulations for grizzly bears have not caused a significant reduction in grizzly bear predation. Therefore, tests involving reductions in wolf predation are incomplete and reductions in grizzly predation have not begun.

The proposed tests of the 2 hypotheses concerning factors limiting moose population growth are outlined below. Some aspects of these tests were reported in previous progress reports (Boertje et al. 1985, Gasaway et al. 1986).

H_1: PREDATION LIMITS MOOSE POPULATION GROWTH.

Actions taken, and to be taken, and tests of the hypothesis:

1. Assess effects of ADF&G wolf removal programs (Nov 1981-Oct 1983) in and adjacent to the experimental area. Control areas (without wolf removal) are in the nearby Ladue River, Sixtymile River, and Washington Creek drainages.

    a. Supports acceptance of H_1 if calf survival and numbers of moose increase in response to wolf removal by fall 1985.

    b. Rejection of H_1 not possible if no positive population response. Assess bear predation.

2. Radio-collar 30 calf moose in experimental area during 1984 to assess bear predation and remaining wolf predation.

    a. Supports acceptance of H_1 if predation was a large mortality source.

    b. Supports rejection of H_1 if little predation occurred.

3. Radio-collar 15 grizzly bears to determine predation rates on adult moose in 1985-86.

    a. Supports acceptance of H_1 if grizzly bears regularly kill adult moose.

    b. Supports rejection of H_1 if grizzly bears kill few moose.

4. If grizzly bears are implicated, reduce grizzly bear predation in experimental area during the years 1987 through 1989.

    a. Supports acceptance of H_1 if moose survival increases and population grows.

b. Supports rejection of H_1 if no change in numbers of moose occurs and if black bears are not implicated as major predators on calves.

5. If black bears are a major predator on calves and there is little response by moose to wolf and grizzly reductions, reduce black bear abundance.

a. Supports acceptance of H_1 if moose survival increases and population grows.

b. Supports rejection of H_1 if no change in moose survival.

H_2: WINTER FOOD LIMITS MOOSE POPULATION GROWTH.

Actions taken, and to be taken, and tests of the hypothesis:

1. Estimate browse availability and utilization in the experimental area.

a. Supports acceptance of H_2 if there is very high browse utilization.

b. Supports rejection of H_2 if there is adequate browse and low rates of use.

2. Measure moose population trend and calf survival in experimental and control areas after adequately reducing predation.

a. Supports acceptance of H_2 if no positive moose population response.

b. Supports rejection of H_2 if population increases in experimental area with no improvement in vegetation.

3. Assess condition of live cow moose by blood chemistry, physical status, and morphometric measurement.

a. Supports acceptance of H_2 if moose are in poor condition during a winter of normal weather.

b. Supports rejection of H_2 if moose are in good condition as determined by standards set by Franzmann and LeResche (1978) and Franzmann and Schwartz (1983).

4. Estimate pregnancy and twinning rates in 1984.

   a. Supports acceptance of H_2 if rates are low ($\leq$80% pregnancy rate for females $\geq$2 years old and $\leq$20% twinning rate).

   b. Supports rejection of H_2 if rates are average or above average.

5. Estimate marrow fat content of adult moose found dead.

   a. Supports acceptance of H_2 if fat content is consistently low ($\leq$20%) for adult moose.

   b. Supports rejection of H_2 if average fat content is $\geq$50%.

Tests of these hypotheses were originally proposed during 1981. Tests involving reductions in wolf predation were necessarily altered as the study progressed because the Board of Game discontinued the program to reduce the wolf population.

OBJECTIVES

To determine if either predation or food limits the low-density moose population in Subunit 20E; if predation is limiting, determine how much control managers need to exert over wolf and bear populations to allow a low-density moose population to recover; to correlate moose:predator ratios and moose population dynamics; and to apply findings to the management of other moose and predator populations in Interior Alaska as appropriate.

STUDY AREA

The study area (Fig. 1) consists of an experimental area (9,700 km^2) where research and predator removal are focused, and 2 control areas (North Ladue River and Washington Creek) where predator numbers will not be reduced.

The experimental area, located in eastcentral Alaska north of Tok (Fig. 1), consists of rolling hills covered with mature black spruce (*Picea mariana*) interspersed with subalpine and alpine areas, poorly drained lowlands, shrub-dominated burned areas, and drainages bordered by willow (*Salix* spp.), shrub birch (*Betula* spp.), alder (*Alnus* spp.), and white spruce (*P. glauca*). Subalpine shrub vegetation consists primarily of dwarf birch (B. nana) and willow, interspersed with willow-lined drainages. Subalpine areas are used extensively by moose during September through November. Most of the upper Sixtymile River survey area and a portion of the North Ladue survey area are in subalpine habitat; both survey areas are in the North Ladue control area. Poorly drained lowlands occur most notably in the Mosquito Fork drainage (Mosquito Flats) and upper Middle Fork, and are dominated by shrub birch, willows, and sedge (Carex and Eriophorum spp.) meadows. The Mosquito Flats is an important moose wintering area. Extensive burns occurred during the mid- to late 1960's in the experimental area north and northeast of Mt. Fairplay, and in the North Ladue and Washington Creek survey areas. All 3 areas are prime moose habitat with willows and birch dominating regrowth.

Elevation in most of the experimental area ranges from 600 m in valley bottoms to treeline at the crest of many of the rolling hills (1,000 m). Elevations of 6 mountain peaks in the experimental area range from 1,500 to 1,750 m. The Sixtymile and North Ladue survey areas have elevations ranging from 600 to 1,650 m, and the Washington Creek survey area ranges in elevation from 300 to 650 m with nearby mountain peaks of 1,600 to 1,700 m.

The climate in the experimental and control areas is typically more continental (colder in winter and drier year-round) than more westerly portions of Interior Alaska. Temperatures frequently reach 20 to 25 C in summer and -20 to -45 C during winter (Nov-Apr). Snow depths are usually below 60 cm, and snow usually remains loosely packed except where windblown at high altitudes.

Large carnivores inhabiting the study area include wolves, black bears, and grizzly bears. Their prey include moose, caribou, beaver (Castor canadensis), snowshoe hare (Lepus americanus), and hoary marmots (Marmota caligata). Arctic ground squirrels (Citellus parryi) are absent from the study area. Dall sheep (Ovis dalli) (approx. 100-150) are restricted to the northwest border of the experimental area. Seasonal distribution of the Fortymile Caribou Herd (numbering approx. 15,000 animals in summer 1986) fluctuates among years, but in most years caribou spend more time in the experimental area (usually portions of June, fall, and winter) than in control areas (portions of fall and winter). Also, in most years caribou use the North Ladue control area more than the Washington Creek control area (Davis et al. 1978b, Shryer 1983, Valkenburg and Davis 1987). Snowshoe hares have not been abundant in the study area since the early 1970's.

METHODS

Wolf Population Status

Estimating Wolf Abundance:

The primary technique used to determine distribution and abundance of wolves was to count wolves or wolf tracks in snow from the air from February through April (Stephenson 1978, Gasaway et al. 1983). To assist in estimating wolf abundance and distribution during winters 1980-84, 1 to 3 wolves in several packs were captured in leghold traps or locking snares, immobilized with 12.5 mg Sernylan (50 mg phencyclidine hydrochloride/ml; Bio-Ceutic Laboratories, St. Joseph, Mo.) using a jab-stick, and radio-collared (configuration 5B collars, Telonics, Mesa, Ariz.). Spring population size was the sum of observed wolves in packs plus wolf numbers estimated from tracks thought to represent different individuals. In addition, we added 10% of the fall population to account for single wolves not associated with packs (Mech 1973). Some single wolves were observed; the remainder were assumed to be present. Fall population size, which was used to calculate prey:wolf ratios and population trend, was estimated using fall counts, when available, or spring counts plus the number of wolves harvested prior to spring surveys. Fall population size also included 10% for single wolves not associated with packs. Fall population size was underestimated in some cases because wolves dying from natural causes prior to spring surveys could not be included unless they were counted during fall. Wolf density estimates are based on wolf numbers in a 15,500-km^2 area, which encompasses all the wolf pack territories in, or partially in, the experimental area.

Aerial wolf surveys in the experimental area were conducted during winters 1981-82 through 1985-86; approximately 80, 70, 170, 30, and 40 flight hours, respectively, were spent surveying, radio-collaring, and radio-tracking wolves. Total flight hours during which wolf population and movement data were gathered numbered 2-4 times the above figures when including flight hours for wolf removal, moose surveys, and radio-tracking moose and grizzly bears. Information was also obtained from local trappers and pilots each winter.

Removal of Wolves:

During winters 1980-81 through 1982-83 and during October 1983, ADF&G removed wolves that ranged fully or in part in the experimental area. ADF&G wolf removal during winter 1980-81 was limited to Subunit 20D and involved removing wolves from 3 packs (Mansfield Creek, Billy Creek, and Middle Fork packs) that had territories extending into the experimental area.

Wolves were killed primarily by shooting them from a helicopter or fixed-wing aircraft, although some were trapped or snared. Trappers and hunters assisted with wolf removal. Reliable information on the number, sex, and location of wolves harvested by hunters and trappers was obtained from a statewide mandatory reporting program.

Identifying Food Habits:

Identification of wolf food habits in the experimental area was based on observations of the carcasses of large prey during monitoring of radio-marked and unmarked packs, and also on assessment of the stomach and intestinal contents of 83 wolf carcasses, and levels of radiocesium (C^{137}) (Holleman and Stephenson 1981) found in 79 wolf carcasses. Radiocesium levels in skeletal muscles of wolves indicated the relative proportion of caribou and moose in the wolves' winter diets during the 30 days prior to death.

During spring 1985 and 1986, we radio-collared 2 wolves in each of 2 packs to aid in locating carcasses of prey for estimation of predation rates. We darted the wolves from a Hughes 500 helicopter and used Cap-Chur darting equipment (Palmer Co., Douglasville, Ga.) and 3-cc darts containing 2.5 mg M99 (1 mg etorphine hydrochloride/ml, D-M Pharmaceuticals, Rockville, Md.) and 5 mg Acepromazine (10 mg acepromazine maleate/ml, Ayerst Labs, New York, N.Y.). The antagonist, M50-50 (2 mg diprenorphine hydrochloride/ml, D-M Pharmaceuticals, Rockville, Md.), was administered in equal volume to M99.

Assessing Productivity, Age Structure, and Nutritional Condition:

Examination of 87 wolves killed in the experimental area during winters 1980-81 through 1985-86 provided data on wolf sex, reproduction, age, and nutritional condition. Reproduction was assessed by counting placental scars and fetuses in uteri, and counting corpora lutea in sectioned ovaries. Wolves less than 1 year old were identified by tooth development and wear and by the uncalcified epiphysis at the distal end of the radius-ulna (Rausch 1967). Ages of wolves greater than 1 year old were estimated from tooth development and wear. Nutritional condition was assessed by body weight; weight of the xiphoid fat deposit; weight of fat around each kidney; total depth of subcutaneous fat over the sternum, flank, and rump; and body length.

Grizzly Bear Population Status

Locating, Capturing, and Radio-collaring Grizzly Bears:

Three techniques were used to locate grizzly bears: (1) radio-snaring bears at bait stations; (2) searching from fixed-wing aircraft and from a Hughes 500 helicopter for bears on ridges, near rivers, and on old kills, especially while radio-collaring other bears and checking bait stations; and (3) searching for uncollared bears (particularly mates during the breeding season) while radio-tracking collared bears.

We used both visual and radio-snare bait stations baited with train-killed moose and/or assorted scrap meat. Visual bait stations were made by dropping 100-150 kg of bait marked with orange flagging from DeHavilland Beaver aircraft or a Bell 205 helicopter. No snares were set and sites were not visited on the ground except to later pick up litter. Radio-snare bait stations usually contained 25-100 kg of bait dropped from Hughes 500 or Bell 205 helicopters. Radio-snare bait stations functioned best when the bait was placed on the ground in the center of a sturdy corral with inside dimensions of approximately 3-4 m in length, 1 m in width, and at least 1.3 m in height. Corrals were constructed from small trees cut near the bait site. These trees were wired to or woven between standing trees. Radio snares were made from aircraft cable and were approximately 2 m in circumference. Radio snares were hung in opening(s) at the end(s) of the corral; the lowest point of the snare was approximately 15-20 cm from the ground. Corral opening(s) were 0.6-0.7 m wide. The radio snare was attached to a tree at the corral opening with 23 kg-test monofilament line to ensure the snare would cinch snugly on the bear, yet allow the bear to move freely away from the bait station. A small radio transmitter (3 cm x 6 cm, configuration S2B5, Telonics, Mesa, Ariz.) was securely attached to each snare with filament tape and then covered by electrical tape. These small transmitters, formerly used in collars placed on newborn moose (Boertje et al. 1985), allowed us to radio-locate bears that had visited radio-snare bait stations. Once radio-snared bears were located, they were captured and radio snares were replaced with radio collars.

Twenty-four different grizzly bears were immobilized during 1985-86 in Subunit 20E, and 5 were recaptured to replace lost collars or to remove radio snares. Of these 29 immobilizations, 1 grizzly died, apparently of hyperthermia; 1 drowned; and 1 suffocated by pushing against a tussock.

We darted all bears from a Hughes 500 helicopter and used Cap-Chur darting equipment. During spring 1985, females and small males were immobilized with 1 5-cc dart containing 4 mg M99 and 10 mg Acepromazine, and large males were immobilized with 1 7-cc dart containing either 7 mg M99 or 6 mg M99 and 10 mg Acepromazine. During fall, 2 large males were immobilized, 1 with 24 mg M99 and 10 mg Acepromazine and another with 6 mg Carfentanil (3 mg carfentanil citrate/ml, Wildlife Laboratories, Fort Collins, Colo.), 1.5 ml propylene glycol, and 12.5 mg Acepromazine. During spring 1986, females and small males were immobilized with 3.6 mg Carfentanil and 18 mg Acepromazine and large males with 6 mg Carfentanil and 10 mg Acepromazine. The antagonist M50-50 was administered in equal volume to M99, and, when Carfentanil was the immobilizing drug, 500-600 mg Naloxone (10 mg or 50 mg naloxone hydrochloride/ml of sterile saline, Sigma Chemicals, St. Louis, Mo.) was administered as an antagonist.

When possible, immobilized bears were measured, weighed, and ear-tagged, and a 1st premolar tooth and blood were extracted, following procedures described by Reynolds (1974). Only bears estimated to be older than 3 years were radio-collared. Techniques used to section, stain, and mount teeth for age determination have been described by Glenn (1972). Whole blood was collected from femoral arteries and centrifuged. Sera were collected and frozen for disease studies.

In 1985, all grizzly bear radio collars (Telonics, Mesa, Ariz.) were constructed of dacron machine belting impregnated with butyl, to which was attached a hermetically sealed metal box containing the transmitter and batteries. However, adult male bears ripped off some of these collars in 1985, so in 1986 all grizzly bear collars were constructed of materials used in wolf collars, i.e., 1 layer of black fiberglass impregnated with urethane over a dacron layer impregnated with butyl. None of these black fiberglass collars were lost. Three types of transmitters were used: (1) break-away configuration 5A grizzly bear transmitters with 30 months of operational life for bears estimated to be <6 years old, (2) configuration 6B grizzly bear transmitters with 36 months of operational life for bears estimated to be ≥ 6 years old, and (3) configuration 5B wolf transmitters with 24 months of operational life for bears ≥ 6 years old. Pulse rate on the grizzly bear transmitters changed from approximately 60-65 beats/min to 40-45 beats/min when movement ceased for 6 hours.

Estimating Population Density:

To estimate the minimum population density for 1 May 1986, the direct count method (Pearson 1975, Reynolds and Hechtel 1984) was used in conjunction with harvest data and intensive radio-collaring and radio-tracking of bears in 1985 and 1986. Observations of grizzly bears were recorded during 170 flight days between 21 May 1984 and 10 August 1986. The direct count method demands careful listing of descriptions, including locations and dates, of each unmarked bear observed in or near the study area. After careful consideration of all data, individual unmarked bears are distinguished on the basis of coloration, size, location, accompanying bears, and date observed (Reynolds and Hechtel 1984). The direct count method assumes bears (except cubs) that were distinguishable and not harvested in or near the study area in 1984 or 1985 were alive and present 1 May 1986. Bears that lost collars or whose collars malfunctioned were similarly treated. We assumed emigration equaled immigration.

To derive the minimum population density, home ranges are delineated for each bear and the proportion of each home range that lies outside the study area is subtracted from the total number of bears observed in or near the study area. We relied in part on knowledge of home range size and distribution of radio-collared bears to distinguish unmarked bears and to delineate approximate home ranges for unmarked bears. Home ranges of unmarked bears were delineated with respect to bear age and sex when possible.

The minimum population density for 1 November 1986 was derived from the 1 May minimum estimate by subtracting the known natural mortality, collaring mortalities, and reported harvest that occurred after 1 May.

Probable grizzly bear numbers on 1 May and 1 November 1986 were estimated by adding to the minimum observed number our best guess of the number of additional bears in the study area. This best guess is based on available habitat, the fact that vegetative cover can allow bears to escape detection for several years (Reynolds and Hechtel 1986), and that bears observed were not all individually distinguishable.

Estimating Predation Rates on Moose and Caribou Older Than 1 Year:

Spring, summer, and fall predation rates (number of bear-days/ number of kills) were calculated from daily (except 5 days) radio-tracking flights between 30 April and 10 June 1986 (42 days), 9 July and 10 August 1986 (33 days), and 18 September and 18 October (31 days), respectively. Of the 5 days not flown, no 2 days were consecutive; therefore, based on observations of the length of time bears spent on yearling and adult kills, we included these 5 days when totaling the number of bear-days. Data were also included from the few instances when individual bears were radio-located but obscured by fog or dense vegetation; however, the obscured bear was always sighted the following day to confirm whether a kill had been made; i.e., no bear was obscured for 2 or more consecutive days. Bear-days excluded from the calculation of predation rates included the 1st 5 days following immobilization and days that bears spent in or near established dens (i.e., <200 m from dens). The two-tailed Student's *t*-test was used to test for differences in seasonal predation rates. On all flights, a Piper Super Cub was piloted by R. Warbelow, accompanied by 1 observer. Bears were usually sighted on the 1st pass or 1st circle. If bears were traveling when first observed, we searched the expected preceding travel path for kills and then relocated the bear before we departed.

We visited all moose and caribou carcasses, using a Hughes 500 helicopter or Piper Super Cub, to distinguish predation from scavenging. Carcasses were usually necropsied within 36 hours of being sighted. Femurs and lower incisors were collected from each carcass when possible, and the site was examined for evidence of a struggle.

To derive annual grizzly predation rates, we extrapolated predation rates from the 3 seasonal observation periods to 44 spring days (1 May-13 Jun), 68 summer days (14 Jun-20 Aug), and 56 fall days (21 Aug-15 Oct), unless otherwise stated. Advancing "spring" to 20 June made virtually no change in the extrapolated total number of adult moose killed per year. These dates are based on phenology, bear breeding behavior, chronology of breeding (J. Hechtel, unpubl. data), and mean den exit and entrance dates in the study area (R. Boertje, unpubl. data). Data on den exit and entrance dates were only from bears for which predation rates were calculated, i.e., adult male bears ≥8 years old and females (≥4 years old) without cub(s) of the year. The term "females without cub(s) of the year" includes lone females, females with yearlings, and females with 2-year-olds.

Estimating Minimum Predation Rates on Calves:

Minimum bear predation rates on calves were determined by recording all observations of radio-collared bears feeding on calf carcasses. Observations were made during the same daily flights used to estimate predation rates on moose and caribou older than 1 year. Since calves were not observed regularly until 22 May in 1986, minimum spring predation rates were calculated only for 22 May through 10 June. The two-tailed Student's *t*-test was used to test for differences in seasonal minimum predation rates between male bears, females without cub(s) of the year, and females with cub(s) of the year.

Although necropsies were not performed on a majority of these calves, we assumed all calves attended by radio-collared bears were killed by the bears, except in 1 case where aerial observations indicated a calf may have drowned. Our assumption that virtually all the calves attended by grizzly bears were killed by the bears was based on data from necropsied calves attended by bears in 1984 and 1986 and from direct aerial observations in 1984 through 1986, of bears killing and subsequently feeding on calves.

Moose Population Status

Estimating Parameters of Adult Moose:

Thirty adult female moose were immobilized and radio-collared (configuration 6B collars, Telonics, Mesa, Ariz.) in the Mosquito Flats from 19-21 March 1984 to provide data on physical status, population age structure, pregnancy rates, birth rates, frequency of twinning, movements, and adult mortality. Immobilization followed procedures described by Gasaway et al. (1978a) using 8 mg M99, 200 mg Rompun (100 mg xylazine hydrochloride/ml, Haver-Lockhart, Shawnee, Kans.), and 600 NF units lyophilized Wydase (hyaluronidase, Wyeth Laboratories, Philadelphia, Pa.) per dart. In addition, 6 bull and 4 cow moose were radio-collared in the West Fork of the Dennison River drainage between 21 and 22 March 1986 to provide additional data on adult mortality. These moose were immobilized with 5 or 6 mg Carfentanil and 10 mg Acepromazine and given 500 or 600 mg Naloxone as an antagonist. Pulse rate of radio collars doubled (150 beats/min) when movement ceased for 4 hours.

Data obtained from immobilized moose included: body condition (Franzmann et al. 1976), blood chemistry as an index of condition (Franzmann and LeResche 1978), morphometric measurements (Franzmann and Schwartz 1983), age from cementum annuli in 1st incisors (Sergeant and Pimlott 1959, Gasaway et al. 1978b), and pregnancy through rectal palpation (Arthur 1964). The percentage fat in marrow of long bones of dead moose (Neiland 1970) was used as an index of severe or terminal malnutrition. All radio-collared cows were visually located daily from 15-24 May 1984 and at 3- to 7-day intervals thereafter until 15 June to estimate birth rate and frequency of twinning. Also, radio-collared cows were located visually or audibly at least once a month during June 1984 through November 1986 to provide data on movements and mortality rates (Gasaway et al. 1983). A fixed-wing aircraft (Bellanca Scout or Piper Super Cub) equipped with telemetry gear (Telonics, Mesa, Ariz.) was used to locate moose.

Locating, Capturing, and Radio-collaring Calf Moose:

Calves were collared from 16-24 May 1984. Calves were located from fixed-wing aircraft (Bellanca Scout and Piper Super Cub) or a Hughes 500 helicopter. The helicopter hovered over the calf or calves, forcing the cow away while we caught and radio-collared the calf or calves. Where trees prevented the helicopter from landing or hovering near the ground, the capture crew descended on a rope lowered from the helicopter. Subsequent to collaring the calf, the capture crew was slung from the scene on the end of the rope. The capture crew fired gunshots in a few instances to frighten the cow away from the calf. We wore sterilized latex gloves and held calves away from our clothing (Ballard et al. 1979). Disturbance to the cow and calf was reduced to only 2-4 min in an effort to minimize cow-calf separation (Ballard et al. 1979).

Thirty-five calves were radio-collared to provide data on natural mortality. Four calves were collared on 16 May, 2 on 17 May, 7 on 18 May, 4 on 20 May, 10 on 21 May, 6 on 22 May, and 2 on 24 May. Two calves were killed by their dams and classified as capture-related mortalities. The 33 radio-collared calves that remained bonded with a cow were used to assess cause and rate of mortality.

Radio collars used on the calves were similar to those used by Schwartz et al. (1983). We attached mortality-mode radio transmitters (configuration S2B5, Telonics, Mesa, Ariz.) which pulsed at approximately 75 beats/min (normal mode). Pulse rate doubled when motion ceased for 1-2 hours (mortality mode). Transmitters were sewn into an 8-cm x 10-cm (3-in x 4-in) pocket made in 4 layers of a 183-cm x 10-cm (72-in x 4-in) Ace brand bandage (Schwartz et al. 1983). The remaining bandage material served as the collar (2 layers of material), which was approximately 35 cm (14 in) in circumference. Single-layer zig-zag stitches of cotton thread were used to secure the bandage. Transmitters were rinsed in alcohol to remove scent before installation in the washed and well-rinsed collars. Antennas protruded from opposite ends of the collar. We wrote identifying numbers on each collar and handled collars only with sterilized gloves. Each collar was stored in a plastic bag.

Estimating Chronology and Assessing Causes of Calf Moose Mortality:

To estimate chronology of calf mortality in 1984, we visually located radio-collared calves daily (except 3 days) from date of collaring to 4 July using fixed-wing aircraft. After 4 July, we located calves on 11 July, 20 July, and on a monthly basis until collars failed.

To assess causes of calf mortality in 1984, we examined all carcasses or remains of carcasses from the ground. Death sites were reached by helicopter or fixed-wing aircraft. Descriptions of carcass remains, locality, and signs of predators were recorded (Ballard et al. 1979). We necropsied calves that were sufficiently intact.

Estimating Moose Abundance and Population Trend:

Stratified random sampling (Gasaway et al., in press) was used to estimate numbers of moose in a 7,500-km^2 portion of the experimental area during October 1981. Two strata were delineated during a superficial aerial survey (stratification flight). Randomly selected sample units from each stratum were searched at an intensity averaging 1.7 min/km^2 from a Super Cub or Citabria aircraft flying at 105-120 km/hr and 60-120 m above ground. Transects at 0.4-km intervals were flown over flat terrain; contour flights at 0.4-km intervals and circling flight paths were used in mountains. When moose were seen, the aircraft diverted from the flight path and circled over the moose while we searched for additional moose. Pilots assisted in counting moose. Snow depths ranged from 10 to 30 cm and tracks in snow were used as clues in locating moose. A sightability correction factor that accounts for under-counting bias was applied to the estimate of observable moose to estimate the total number of moose present. This sightability correction factor was obtained from a survey in the lower Nowitna drainage in Interior Alaska and was applied to the present survey data as described by Gasaway et al. (in press). Survey conditions in the Nowitna drainage during 1980 were nearly comparable to those in our experimental area during the 1981 survey. We attempted to estimate sightability during the 1981 population estimation survey; however, it was not economically feasible because of the low moose density (Gasaway et al., in press).

Relative abundance of moose in the experimental area from 1949 to 1986 was reconstructed from aerial surveys and from observations of people living in the study area (Gasaway et al. 1983). Surveys to determine the population trend were conducted during mid-October through late November 1956 through 1986. Five areas were surveyed: Ketchumstuk Creek, Taylor Mountain, Mt. Fairplay, upper West Fork of the Dennison, and Sixtymile Butte. Survey aircraft airspeed and altitude above ground were similar to those used in the above population estimation survey; however, the search intensity was lower. Transects were flown over flats, and contours near timberline were flown in the mountains. A circling low pass was flown over each group while searching for additional moose. Snow cover was generally complete and depths ranged from 10 to 30 cm. Tracks in snow aided pilots and observers in locating moose.

The population trend and relative abundance of moose in the experimental area from 1966 to 1986 was estimated from the number of moose seen per hour in the 5 survey areas. Moose per hour rather than number of moose seen was used as the trend indicator because the area searched varied among years.

Trend in each area was identified by smoothing curves with a moving 3-point median polish.

A composite of the 5 trend areas was used to reflect overall changes in moose abundance in the experimental area. The composite curve was produced by plotting the median value among the 5 surveys for each year. When an annual value for a survey area was missing (i.e., if no survey flown or snow conditions not comparable), the value was estimated by extrapolating between the former and latter year's surveys. Two of the 5 areas (upper West Fork and Sixtymile Butte) were not surveyed until after 1966 and Taylor Mountain and the Upper West Fork were discontinued after 1976 and 1980, respectively, because few moose could be found (Appendix A). Trend curve trajectories were extended to provide estimates for these missing years (Appendix A).

The moose population rapidly increased from about 1950 through the early 1960's based on observations of people in the area (D. Euers and J. Terwilliger, pers. commun.) and on high recruitment of yearlings to the population. However, we have no aerial survey data for the 1950's and early 1960's that were comparable to data used to estimate population trend after 1965. Therefore, we used a relative density estimate for 1949 as a reference point (D. Euers, pers. commun.). D. Euers observed wildlife in the experimental area from 1948 to 1986; he indicated moose may have been approximately twice as dense in 1949 as during the early 1980's. We assumed moose stopped increasing when calf survival decreased to a low level in the mid-1960's.

In addition to the above trend areas, 6 other areas were used to evaluate short-term population trends during the more intensive portion of the study, 1981-86. Three survey areas (Mosquito Flats, Telegraph Creek, and North Fairplay) were in the experimental area, 1 was in the Washington Creek control area, and 2 (North Ladue and Sixtymile River) were in the North Ladue control areas. Numbers of moose seen were used to evaluate trend in these areas. Trend was estimated by correlation and linear regression. The 3 control survey areas and the North Fairplay survey area were begun in 1982 and were flown using intensive search methods ($\geq$1.5 min/km^2) similar to those of population estimation surveys (Gasaway et al., in press). The Mosquito Flats and Telegraph areas were begun in 1977 and 1979, respectively, and were flown less intensively, similar to the surveys used to estimate the long-term trend, 1966-86.

Estimating Recruitment:

Recruitment, in the form of calf:cow and yearling:cow ratios, was estimated from aerial surveys in the experimental and control areas. These aerial surveys included surveys used to estimate population trend and abundance during the years 1966 through 1986 and occasional additional surveys for population composition during the years 1956 through 1965. The methods used for the later surveys were similar to surveys used to estimate long-term trend during the years 1966 through 1986. All moose observed were classified as calf, yearling male, adult male, or cow.

Calf:cow and yearling:cow ratios, used to evaluate recruitment of cohorts, were based on estimates of cows ≥ 2 years old (Gasaway et al. 1983). This omitted 1 unproductive cohort from the cow base. The number of cows ≥ 2 years old in the sample was estimated by subtracting the number of yearling males observed from total cows observed. Number of yearling males was assumed to equal the number of yearling females in the sample.

Changes in an offspring:cow ratio over time are assumed to reflect changes in the abundance of a cohort; however, ratios usually provide biased estimates of offspring survival (Connolly 1981, Gasaway et al. 1983). The bias of greatest concern in this study was the underestimation of the calf:cow ratio from aerial survey data collected during early winter trend surveys (Gasaway et al. 1981). Therefore, as concluded by Gasaway et al. (1983), changes in offspring:cow ratios over time should not be viewed as absolute changes in abundance of the offspring; rather, ratios should be used to identify major trends and approximate proportions of offspring.

RESULTS AND DISCUSSION

Testing the Predator-limiting Hypothesis

Wolf Population Status:

Historical Wolf Abundance, 1940-81: Wolf abundance varied widely in the experimental area between the early 1940's and 1981 in response to predator control as well as changes in prey abundance (Fig. 2). Wolves increased to a high level by the mid-1940's (Murie 1944). Predator control/poisoning by the United States Fish and Wildlife Service, Branch of Predator and Rodent Control (BPRC), was begun during 1948 in the experimental area and wolves rapidly declined to a low density (Kelly 1950*a*, 1953; D. Euers, pers. commun.). Wolves were maintained at a low density through 1960, except for a brief period during the mid-1950's when predator control was suspended (Kelly 1953, 1957; Olson 1959, cited *in* Davis et al. 1978*a*). No quantitative abundance data are available for the 1940's and 1950's, but wolves and wolf sign were scarce during the period indicated by "low" on Fig. 2 (Kelly 1953). Methods used to kill wolves were poisoning with cyanide guns (coyote getters) and strychnine-laced baits, shooting from aircraft, and year-round trapping and snaring (Kelly 1953, 1958). Additionally, members of the public could legally take wolves by the above methods except for the use of poisons. A bounty was paid as an incentive for the public to kill wolves. For a more comprehensive review of historical wolf abundance see Davis et al. (1978a).

Following the suspension of the BPRC efforts during 1960, wolves increased to a high density in the presence of large numbers of moose and caribou (D. Euers and J. Terwilliger, pers. commun.; Fig. 2). Wolf numbers declined naturally from about 1969 through 1976 and then remained low until 1981 (D. Grangaard and J. Terwilliger, pers. observ.), probably because of prey shortages (Fig. 2).

Population Size and Harvest, 1981-86: Wolves with territories in or partially in the experimental area numbered 125 in fall 1981 before wolf removal and declined during intensive ADF&G wolf removal to 64 in fall 1982 and 87 in fall 1983 (Table 1). Subsequent to cessation of ADF&G wolf removal in October 1983, fall wolf numbers increased 24%, from 78 in 1984 to 97 in 1985, despite low prey abundance. This increase is comparable to the average annual increase of 29% calculated by Keith (1983) from 7 increasing wolf populations in North America, where prey were moderately to highly abundant relative to wolves (>30 moose/wolf). Three of these 7 populations were trapped or hunted, but their increases were comparable to the 4 unexploited populations. Wolf surveys scheduled for spring 1987 in the experimental area will clarify whether wolf numbers can continue to increase given the low prey abundance.

Immigration of wolves presumably played a major role in the 156% increase in wolves from May through September 1983. Pup production in the experimental area was insufficient to account for the increase. During winter 1983-84, none of the 10 wolves collected were pups or yearlings (Table 2), indicating low pup production and/or survival and suggesting that immigration was largely wolves ≥ 2 years old. Also, based on an average estimate of 42% pups in the 1981-85 populations (Table 2), 72% growth was calculated (42% pups/58% adults x 100), which was less than half the observed increase from May through September 1983. In contrast, 60-73% pups have been reported in exploited wolf populations where prey were abundant (Rausch 1967, 1969; Kelsall 1968; Stephenson and Sexton 1974); the 150-270% spring-to-fall population increases estimated from these pup percentages were much greater than we observed.

Additional data are required to clarify what harvest levels/ strategies the wolf population can sustain without decreasing in number (Table 1). Excluding the apparent effect of immigration during summer 1983, and possibly summer 1982 when vacant territories existed, the study population has declined 10% following a 28% harvest in winter 1983-84 and has increased 24% following a 17% harvest in winter 1984-85 (Table 1). Defining harvest levels/strategies that the study population can sustain without decreasing requires further study as do the mechanisms, affected by harvest, that result in a stationary population. Some important factors that affect how a wolf population reacts to a particular harvest level include sex and age structure of the harvest, number of prey per predator, the effect of harvest on natural mortality rates, and whether vacant territories are created by harvest and subsequently filled by immigrating wolves. These combined factors have not been adequately addressed in the literature. However, Keith (1983) summarized data that implied wolf populations can sustain harvests of about 30% of fall populations, assuming at least moderate prey abundance relative to wolves. In contrast, Gasaway et al. (1983) reported that harvest rates of 20% were significant in limiting wolf populations in Subunit 20A when wolf productivity was low.

Immigration and recolonization of wolf pack territories commonly follow intensive wolf removal programs. A high rate of immigration occurred in the experimental area during 1983 following 2 winters of wolf removal. Ballard and Stephenson (1982) and Bergerud and Elliot (1986) also reported moderate and high rates of immigration following intensive wolf removal in Alaska and British Columbia, respectively. Immigration is probably greatest when wolves are relatively common, productive, and harvested at low levels (<20%) in the surrounding area. High rates of immigration indicate that several consecutive years of wolf removal and large wolf removal areas are required if the effect of wolf predation on prey populations is to be maintained at a low level.

Distribution: Wolf packs in several instances shifted or enlarged winter territories from year to year (Figs. 3-7). In at least 1 instance, a shift was made to maintain contact with wintering caribou. However, in no instance did we observe radio-collared wolves associated with packs (Table 1) abandon their home range to maintain contact with the spring, summer, or fall caribou migrations, as observed in other areas where migratory caribou are the primary prey available (Parker 1973, Stephenson and James 1982).

Observations of wolves trespassing on neighboring territories were well documented in numerous instances (Figs. 3-7) and were more common than observations of vacant areas between pack territories. Vacant areas (Figs. 3-7) are probably largely the result of limited observations, which caused underestimation of territory sizes. The large amount of overlap in the wolf pack territories (Figs. 3-7) reflect the generally low abundance of resident prey (Mech 1977) and reliance, in part, on migrating caribou. Caribou distribution varies annually and seasonally and is unpredictable.

Winter Food Habits: The average winter (Nov-Apr) diet of wolves in the experimental area during the years 1981 through 1986 comprised approximately equal proportions of moose and caribou biomass, although diets of packs changed between and within winters depending on the availability of caribou. For example, radiocesium levels of the necropsied wolves (Table 2) indicated annual variations between and within packs in relative amounts of caribou consumed. Of the 11 packs from which carcasses were examined, only the Mansfield pack probably consumed no caribou, and only the Divide pack consumed low proportions of caribou. Caribou are usually absent from these wolf pack territories during winter except in late March or April. The Billy Creek pack during February and March 1985 and Mitchels Ranch pack during February 1982 also consumed virtually no caribou. However, in samples from other years, the Mitchels Ranch and Billy Creek packs consumed moderate to high proportions of caribou, comparable to the remaining packs--except the Portage Creek pack, which consumed virtually all caribou.

Both moose and caribou were common among confirmed or suspected wolf kills made during winter (Nov-Apr). Of the 187 carcasses located during the years 1981 through 1986, 53% were moose and 45% were caribou. However, caribou remains were more difficult to see and identify than remains of moose. Therefore, the proportion of caribou killed by wolves was probably underestimated. The size of the bias is unknown. Of 83 wolf stomachs examined from 1981 through spring 1986, 26 contained caribou, 24 contained moose, 2 contained snowshoe hares, and 31 were empty.

Estimation of wolf predation rates in Subunit 20E requires further study. The only reliable data available to date are from daily observations of the Gold Creek pack from 30 April-10 June (42 days) 1986 during which 5 wolves ≥ 1 year old, which were rearing 5 pups, killed 2 adult caribou and 2 adult moose and scavenged 1 adult caribou. These data suggest a kill/scavenging rate of 14 days/moose kill/pack, assuming 3 adult caribou are equivalent to 1 adult moose (Keith 1983). However, a few moose calves or beavers may also have been killed during this period. Winter wolf kill rates in the literature range from 3.1 to 5.5 days/moose kill/pack (Keith (1983); however, the abundance of moose in these studies was several times greater than moose densities in Subunit 20E and caribou were not present in 3 of the 5 studies cited. No estimates of winter wolf predation rates are available for a situation similar to that in the experimental area, i.e., an area with low moose density and in which caribou were being used as a major alternate prey.

Productivity, Age Structure, and Nutritional Condition: Productivity of female wolves ≥3 years old in the experimental area between 1981 and 1985 was comparable to values in Subunit 20A when prey was scarce (1976-79), and markedly lower than found in Interior Alaska between 1957 and 1966 when prey was abundant (Table 3). Similarly, the percentage of reproductively active females ≥2 years old was only 75% (15 of 20 wolves) in the experimental area of Subunit 20E and 71% (15 of 21 wolves) in Subunit 20A in 1976 (Gasaway et al. 1983), compared with 89% in Rausch's (1967) statewide sample.

Data on nutritional condition of necropsied wolves (e.g., body weight and length and weight of fat deposits) (Table 2), from the experimental area will be compared in subsequent reports with wolf condition data from areas of high prey densities. Body length of pups may be the best relative indicator of general nutritional condition, because total weight and fat deposits can change rapidly if a temporary food shortage occurs, e.g., if animals are trapped.

Grizzly Bear Population Status

Historical Abundance of Grizzly Bears, 1950-84:

Density of grizzly bears was probably low during the 1950's and increased to a relatively high level by the mid-1970's (Fig. 2). Several factors contributed to the low density during the 1950's. First, miners were common in the experimental areas during the 1940's and 1950's, and they regularly shot bears to minimize conflicts around their camps (D. Euers, pers. commun.). Second, bears were killed by snares legally set to catch wolves on a year-round basis for the bounty (O. Burris and A. Lowhigh, pers. commun.). Finally, the BPRC's predator control program from 1948 to 1960 killed some grizzly and black bears incidental to killing wolves, the target species in the Fortymile drainage (D. Euers, pers. commun.). Cyanide coyote getters were set year-round and strychnine baits, while used largely during winter (Kelly 1950b), were available to bears during spring. The number of bears killed could not be determined for the same reasons that the number of wolves killed remained unknown. Coyote getters did not kill large carnivores quickly. Therefore, bears as well as wolves often could not be found after they triggered a coyote getter and received a dose of cyanide (Kelly 1950b, 1953); however, Kelly assumed there was a dead animal for each coyote getter that was triggered. Additionally, P. Shepherd (pers. commun.), a predator control officer in Interior Alaska, said that he and others had killed bears using the poison sets. C. McMahon (pers. commun.) indicated grizzly bears and wolves sharply declined during the 1950's when poisons were used to control wolves in an area beginning about 80 km southeast of the experimental area; Mr. McMahon has been a wolf hunter, trapper, and pilot in the area since 1941. Grizzly bears increased to a high density in this area from 1960 to the mid-1970's (Miller and Ballard 1982; C. McMahon, pers. commun.). A similar situation likely occurred in the experimental area. Bears were common in the experimental area by the mid-1970's, although no estimate of density was made until 1984-86.

Population Density, 1984-86: Estimated minimum grizzly bear density in the 4,000-km² grizzly bear study area (Fig. 1) was 14 bears/1,000 km² on 1 May 1986 and 10 bears/1,000 km² on 1 November 1986. These estimates were calculated from 75 grizzly bears: 31 bears radio-collared or young associated with radio-collared individuals, and 44 unmarked, individually distinguishable bears. Delineation and distribution of approximate home ranges of the 75 bears allowed subtraction of fractions of home ranges outside the 4,000-km² area which left a minimum population estimate of 55 bears in 4,000 km² on 1 May. Eight of the 75 bears died from natural causes, 9 were harvested, and 2 died during collaring, leaving at least 56 bears in or near the study area on 1 November. Deletion of fractions of home ranges outside the 4,000-km² area left 39 bears in 4,000 km² on 1 November.

Probable grizzly bear numbers in the 4,000-km² grizzly bear study area were 65 (16 bears/1,000 km²) on 1 May 1986 and 49 (12 bears/1,000 km²) on 1 November 1986. These estimates assume there were 10 bears in the 4,000-km² area that were not observed or not distinguishable from observed bears.

Probable spring grizzly bear densities estimated elsewhere in Alaska are greater than found in Subunit 20E. For example, probable density estimates range from 24 bears/1,000 km² in southcentral Alaska (Miller and Ballard 1982) and the western Brooks Range (Reynolds and Hechtel 1984) to 20-23 bears/1,000 km² in the northcentral Alaska Range (Reynolds and Hechtel 1986). Habitat differences and lower prey abundance may possibly account for the lower grizzly bear density in Subunit 20E: the subunit is largely forested and contains no ground squirrels as well as low numbers of moose and caribou.

Sex and Age Structure: Of the 65 grizzly bears in the 4,000-km² grizzly bear study area on 1 May 1986, we estimated there were 10 males ≥ 6 years old, 12 females ≥ 4 years old without young, 3 females with 5 yearlings or 2-3 year olds, 6 females with 14 cubs of the year, and 15 subadults. These estimates are based on the same population of 75 marked bears mentioned previously. Also, the 10 bears added to the minimum population estimate were assumed to be mostly females with cub(s) of the year, because these bears are the most difficult to observe (Miller and Ballard 1982). Sex and age structure of captured bears (Fig. 8) was biased toward adults because we did not attempt to capture bears less than 4 years old except to remove radio snares. Capture was also biased toward males. Males frequently lost their collars; therefore, we attempted to capture all adult males seen. Sex and age structure of grizzly bears harvested in Subunit 20E during the years 1981 through 1985 (Fig. 9) is also biased toward males because males move greater distances than females and because the taking of females accompanied by cub(s) or yearling(s) is prohibited.

Because predation rates on moose were significantly different ($P < 0.1$, two-tailed Student's *t*-test) between male and female grizzly bears, sex and age structure of the grizzly population has important predator-prey implications. We assumed that only adult males ≥ 6 years old and females ≥ 4 years old without cub(s) of the year killed moose or caribou older than 1 year. During 1986, harvest of these sex and age classes in and near the study area were minimal and natural mortality was 0. Therefore, we estimated that 8 adult males and 14 females were potentially important predators on moose and caribou older than 1 year in the 4,000-km^2 area during 1986.

Natural Mortality and Harvest: Predation by adult male grizzly bears on sows and cubs was thought to be the major cause of observed natural mortality. Observed natural mortality rates for cubs of the year in 1986 was 60% (6 of 10). We also observed 2 cases in which adult females with cubs of the year were killed and consumed by adult males. Reported cases of cannibalism of adult females are rare (Reynolds and Hechtel 1986) compared with cannibalism of cubs of the year by adult male bears (Reynolds and Hechtel 1984). In 3 of 4 cases of a missing cub or cubs, collared adult male bears were observed in the immediate vicinity of the missing cub(s). In the remaining case, the female and 1 remaining cub remained on a mountain peak for 2 days subsequent to probable cub predation. One set of triplets was reduced to a single on 29 May. A 2nd set of triplets was reduced to twins on 15 July. These twins survived an attack on 23 August during which their mother was killed by an adult male. One set of twins was reduced to a single on 6 June, and another set of twins and their mother were killed on 22 May by a collared adult male.

Harvest of grizzly bears has increased substantially in Subunit 20E since 1980 due to greatly increased numbers of hunters in the subunit resulting from less restrictive moose, caribou, and grizzly bear hunting regulations. From 1961 through 1980, annual reported grizzly harvests were 0-4 bears, with the exception of 1979 when 6 were harvested. Less restrictive hunting regulations, which began in 1981 for grizzly bears and 1982 for caribou and moose, resulted in harvests of 10 grizzly bears in 1981, 23 in 1982, 24 in 1983, 22 in 1984, 12 in 1985, and 21 in 1986.

If we assume spring grizzly bear densities in the 4,000-km^2 grizzly bear study area (16 bear/1,000 km^2) are comparable to densities in the entire Subunit 20E (28,500 km^2), then the subunit harvest rate averaged 4% (range = 3-5%) during the years 1982 through 1986. An average annual harvest rate of about 8% (range = 5-9%, or 20-29% of the harvest in the subunit) occurred in the 4,000-km^2 grizzly bear study area during the years 1982 through 1986. No significant short-term declines in the grizzly population are expected from average harvest rates of 4% or 8%, but we have inadequate data to assess the precise effects of these harvest rates. Population trend and sex-age composition estimates are required to assess the effects of hunting on population dynamics. The data collected during 1985-86 in the grizzly bear study area indicated the population could have been limited by an 8% harvest rate. For example, in 1986 only about 6 cubs survived the summer and at least 10 adults and subadults died (6 harvested, 2 capture mortalities, and 2 natural mortalities). Bears shot within about 10 km of either side of the study area's border counted as 0.5 bears in totaling harvest; this helped exclude bears that were shot while along the border but which did not reside year-round in the study area. However, immigration from the lightly hunted adjacent area could have replaced some of the 10 bears killed in this 4,000-km^2 area. Hence, the effect of hunting on the population remains unknown.

Predation Rates on Moose and Caribou Older Than Calves: The extrapolated annual predation rate for adult male grizzly bears was 3.5 moose/year/bear. Seven adult male grizzly bears killed 9 adult moose during 375 bear-days (1 kill/42 bear-days; Table 4). Estimated predation rates by male bears were highest during spring (1 kill/26 bear-days), lowest during summer (1 kill/132 bear-days), and intermediate during fall (1 kill/43 bear-days). Estimated predation rates had large standard errors (Table 4); therefore, despite large differences among mean rates, they were not significantly different ($P > 0.1$). A study of brown bear (*Ursus arctos arctos*) predation on elk (*Cervus elaphus*) and livestock in the Soviet Union (Novikov et al. 1969) also reported that predation was greatest during spring and fall.

The extrapolated annual predation rates for female grizzly bears ≥4 years old without cub(s) of the year was 0.7 moose/year/bear and 1.0 caribou/year/bear. Eleven female grizzly bears without cub(s) of the year killed 3 moose and 3 caribou during 561 bear-days (Table 4). Estimated predation rates were not significantly different among seasons ($P > 0.2$). However, the seasonal pattern in estimated predation rates was similar to those for adult male grizzlies; i.e., rates were highest during spring, lowest during summer, and intermediate during fall.

Adult male bears ≥8 years old killed adult moose at significantly greater rates ($P < 0.1$) than female bears ≥4 years old without cub(s) of the year, when data were combined for all 3 observation periods (Table 4). However, only adult females without cub(s) of the year killed adult caribou. When predation data on moose and caribou older than calves were combined, no differences ($0.1 < P < 0.2$) were found between male and female grizzly predation rates. Data on adult female bears with cub(s) of the year were treated separately because these bears killed no adult moose or caribou during 169 bear-days in spring and summer, probably due in part to restricted movements and low prey densities. Data on female bears with yearling(s) (0 kills during 22 bear-days in fall) were combined with data on lone females (4 kills during 467 bear-days) and females with 2-year-old(s) (2 kills during 72 bear-days in spring and summer), based on data from Spraker et al. (1981) and Miller (1985, 1986) that indicates the predatory behavior of females with yearling(s) resembles the behavior of females alone or with 2-year-old(s) more closely than the behavior of females with cub(s) of the year.

A majority of the collared adult male grizzlies killed adult moose; however, some males killed more frequently than others. Of the 7 radio-collared male bears, 2 males killed 3 moose each ($n = 65$ and 72 bear-days), 1 male killed 2 moose ($n = 69$ bear-days), 1 male killed 1 moose ($n = 49$ bear-days), and 3 males killed 0 moose ($n = 15$, 31, and 74 bear-days). Circumstantial evidence from the Soviet Union (Novikov et al. 1969) also suggests that large numbers of brown bears are predators, but that certain brown bears are particularly predatory.

Certain females without cub(s) of the year also killed more than others, but, due to low numbers of bear-days in several instances and low frequency of kills, data are inadequate to assess whether a majority of adult females killed adult ungulates. Two females each killed 1 moose and 1 caribou ($n = 94$ and 106 bear-days), 1 female killed 1 moose ($n = 63$ bear-days), 1 female killed 1 caribou ($n = 27$ bear-days), and 7 females killed no moose or caribou older than 1 year ($n = 5$, 17, 22, 24, 47, 73, and 83 bear-days).

The observed predation rate was not necessarily a minimal rate. Several factors indicate we observed all moose and caribou older than calves (Table 4) killed by the collared grizzlies during the daily observation periods. For instance, (1) we visually sighted nondenned bears on 99% of our attempts; (2) bears were on or immediately adjacent to (<10 m), and protective of, carcasses (except in 1 case, and, in some cases, after our necropsy of the carcass); (3) in all cases, we sighted carcasses within 36 hours of when bears made the kills (as evidenced by daily map locations of bears); and (4) nondenned bears were sighted at least once every 2 consecutive days. The low density of understory and overstory vegetation, excellent weather, and pilot skill contributed to the high sightability. Previous studies of collared grizzlies in southcentral Alaska (Miller 1985) have had relatively low sightability (82%), and Miller could not locate bears daily due to inclement weather.

Adult grizzly bears can apparently consume an adult moose in about 7-14 days. Accurate grizzly bear consumption rates of adult moose carcasses were obtained in 4 instances where bears remained on or immediately adjacent to carcasses (<100 m) during consecutive daily observations and bears completely consumed the carcasses before departing. These consumption rates were as follows: an 11-year-old male grizzly spent 14 days on an adult bull in October, an 11-year-old male spent 8 days on an adult cow in September, an adult female and 1 2-year-old spent 7 days on an adult cow in June, and an adult female and 2 2-year-olds spent 7 days on an adult bull in June. Other consumption rates were as follows: a small lone bear spent 2 days and, subsequently, an adult male spent 5 days on an adult bull in July. Two adult males completely consumed an adult cow within 6 days of the date of kill during revisitations of the carcass in May, and 4 different lone bears consumed an adult cow within 14 days of the date of kill in June, but bears were known to have visited the carcass on only 7 of these days. Our necropsy investigations sometimes resulted in bears revisiting rather than remaining on carcasses. Revisitations were noted by subsequent locations of bears and monitoring disturbance of the carcass. Daily monitoring of carcasses was incomplete in 4 cases due to termination of flights 1 to 4 days after kills were made. Also, wolves scavenged 3 carcasses, which compromised data on bear consumption rates.

Grizzly bears consumed caribou older than calves in 2 to 3 days. An adult female bear completely consumed a 1.3-year-old caribou in 2 days, a female and 2 2-year-olds consumed an adult female caribou in 3 days, and 2 lone grizzlies consumed a 2.3-year-old male caribou in 3 days (1 day by an adult female followed by 2 days by an adult male).

Grizzly bear consumption rates of adult moose (7-14 days) and adult or yearling caribou (2-3 days) have important implications when documenting predation rates. For example, intervals of >2 days between observations may underestimate grizzly predation rates on adult caribou. Also, data based on observation days or visual sightings of bears can substantially overestimate predation rates on adult moose, because the probability of observing a grizzly bear on the remains of an adult moose carcass is much greater (up to 7 to 14 times greater) than observing the bear the day on which the kill was made. For example, bears seen on the remains of an adult moose carcass the 1st day of an observation period may account for up to 7 to 14 bear-days; thus, 1 kill per 7 to 14 bear-days rather than the inflated 1 kill per 1 observation day. Ballard et al. (1981) reported an estimate of grizzly predation rates on adult moose as 1 adult moose "kill" per 16 observation days (n = 28 "kills"); this rate likely strongly overestimates actual predation rates (Fuller and Keith 1980).

Predation Rates on Calves: Minimum total predation rates on calves (Table 5) were not significantly different ($P > 0.2$) among male bears (1 kill/18 days), females without cub(s) of the year (1 kill/5 days), and females with cub(s) of the year (1 kill/7 days). Additionally, within a season, predation rates did not vary significantly ($P > 0.1$) among males, females without cub(s) of the year, and females with cub(s) of the year. However, total minimum spring predation rates were significantly greater ($P < 0.02$) than summer rates. Within a class of bear, only females without cub(s) of the year killed significantly fewer calves ($P < 0.02$) during summer than spring. However, daily spring observations may have disproportionately underestimated calf kills by males compared with females, because larger-bodied males may have consumed spring calves more rapidly than females.

A spring vs. summer comparison of predation rates (Table 5) requires qualification for 2 reasons. First, summer predation rates are largely dependent on spring predation rates, because availability of calves declines rapidly during spring due largely to predation (see Calf Moose Productivity and Mortality). Second, spring versus summer data are not directly comparable because flights were probably too infrequent (20-36 hours between flights) to accurately estimate predation rates on newborn calves. In spring, bears attended 17 (81%) of 21 single calf carcasses during only 1 flight, 2 single carcasses were attended a minimum of 20 and 24 hours each, and a set of twins was attended a minimum of 36 hours. Bears remained on calf carcasses longer in summer, probably due to increased body size of calves, which presumably resulted in more accurate summer versus spring predation rates. Ten (83%) of 12 single calves killed in summer were attended by single bears or bears with cub(s) of the year during at least 2 daily flights ($\bar{x}$ minumum = 36 hrs, SD = 20, range = 20-72). No calves were killed after 31 July, presumably due in part to the relatively few calves remaining by 18 September and to the enhanced ability of calves to avoid predation by August.

Thirteen (87%) of 15 grizzly bears radio-tracked in spring and/or summer 1986 killed calf moose; however, a few individuals killed a majority of the calves. One bear killed 8 calves (n = 23 bear-days), 3 killed 5 calves each (n = 23, 44, and 55 bear-days), 2 killed 4 calves each (n = 44 and 55 bear-days), 3 killed 3 calves each (n = 56 bear-days each), 3 killed 2 calves each (n = 19, 36, and 55 bear-days), 1 killed 1 calf (n = 44 bear-days), and 3 killed 0 calves (n = 4, 22, and 32 bear-days).

Only 1 calf caribou was killed by grizzly bears during this study; an adult male grizzly killed a calf caribou on 10 August. However, calf caribou were extremely scarce or absent in the grizzly bear study area during May through July and large numbers of caribou (>5,000) were within home ranges of only 2 collared bears during 1 through 10 August. Caribou were more uniformly distributed and probably available to most collared grizzly bears during September and early October observations.

Relative Importance of Scavenging Compared With Predation: Collared grizzly bears were primarily predators, not scavengers. The amount of animal biomass available for scavenging by collared grizzly bears during daily spring, summer, and fall flights was only 12, 25, and 120 kg/bear-month, compared with 330, 180, and 170 kg available/bear-month of prey killed, respectively. Scavenged carcasses during spring included 1 adult caribou that died from antler wounds and 1 drowned calf moose. A portion of 1 adult female moose killed by wolves was scavenged during summer; 2 adult bull moose that died from antler wounds, 1 hunter-killed adult caribou, and 2 caribou gut piles were scavenged during fall. Prey killed during spring included 33 moose calves, 7 adult female moose, 1 adult male moose, 1 black bear, 1 adult female grizzly bear, and 4 grizzly cubs. Prey killed during summer included 14 moose calves, 1 caribou calf, 1 adult male moose, and 1 adult female caribou. Prey killed during fall included 1 adult male moose, 2 adult female moose, 1 2-year-old male caribou, 1 yearling male caribou, and 1 black bear. Animals killed or scavenged were not necessarily completely consumed by the bears.

Grizzly bears and wolves scavenged each others' kills, which influenced the predation rate of each predator. During May and June 1984, grizzly bears scavenged all 3 wolf-killed moose ≥1 year old within 2-5 days of the moose's death. One or 2 wolves were displaced from each kill. However, during May and June 1986, grizzly bears failed to scavenge either of 2 wolf-killed moose or 2 wolf-killed caribou within 5-6 days of the prey's death. During July 1986, a grizzly scavenged a wolf-killed moose 1 day after the moose's death, displacing 3 wolves greater than 1 year old and 4 pups. During fall 1985, the reverse scavenging pattern was seen; wolves scavenged 3 of 4 adult moose and 1 of 2 caribou that were killed by grizzly bears, all within 1 to 5 days of the prey's death.

Moose Population Status:

Population Trend and Size: Moose increased during the early 1950's, reaching peak density during the mid-1960's (Fig. 2). No relative abundance data were collected during the 1950's and early 1960's that were comparable to survey data after 1965; therefore, the pre-1966 portion of the curve was based on personal observations of people in the area (see Methods) and evidence of high recruitment of yearling moose (Table 6). For these reasons, the pre-1966 portion of the curve (Fig. 2) indicates only the general trend and a crude index of relative abundance.

The moose population declined from the mid-1960's through 1976 and remained low through 1986 (Fig. 2). The decline of moose occurred relatively synchronously throughout the experimental area, based on declines in 5 widely spaced survey areas (Fig. 10). Trend data, based on moose per hour (Fig. 10), indicate the population remained at a relatively low density from 1976 to 1986. Only in the Mt. Fairplay and Ketchumstuk areas was there a suggestion of an increase since 1984. Additional trend survey areas were used to assess change during the intensive period of the study, 1981-86. The Mosquito Flats trend area indicates no significant change in moose abundance occurred after 1977 (Fig. 11). The number of moose seen in the North Fairplay trend area, begun in 1982, was quite variable and no trend could be inferred (Fig. 11). The only trend area that indicated a significant change in abundance was Telegraph Creek; the correlation coefficient was significant at $P < 0.1$ (Fig. 11). We conclude from the trend data (Figs. 10 and 11) that the number of moose from 1982 to 1986 was more likely stationary to slightly increasing than decreasing.

During October 1981, 646 moose ± 27% (90% CI) were estimated in 7,500 km^2 of moose habitat west of the Taylor Highway in the experimental area. The estimated moose density was 86 moose/1,000 km^2 ± 23 moose (90% CI). We assumed that the sustained low density from 1976 to 1986 was close to the 1981 density (Fig. 2).

The decline in numbers of moose in the experimental area from the mid-1960's to 1976 (Fig. 2) was not precipitated by high mortality resulting from deep snow, as occurred elsewhere in much of Alaska, particularly Subunit 20A (Bishop and Rausch 1974). Snow depths on the ground on 1 March and 1 April were less than 80 cm during the period 1963 through 1970 at the 3 sites in or adjacent to the experimental area (Tok, Chicken, and Boundary; Figs. 12 and 13). Eighty centimeters has been considered the critical snow depth for calf moose in Interior Alaska (Coady 1974); below this depth high mortality is not expected for calf or adult moose. The first moderately deep snow winter during the decline was 1966-67; by this winter, calf and yearling survival had already begun to decline (Fig. 13). Additionally, survival of the 1966 cohort to 18 months of age (indicated by yearlings:100 cows $\geq$2 years old) was greater than for the next 4 cohorts that lived through winters of shallower snow (Fig. 13). Thus, winter 1966-67 was not severe enough to cause high calf or adult mortality.

Moose mortality caused by deep snow did not maintain the decline from the mid-1960's through 1976 or prevent the population from growing after 1976. This conclusion is based on the fact that calf survival was not correlated with snow depths in or adjacent to the experimental area (see Calf Moose Production and Mortality). Also, no unusually high mortality of moose in the experimental area was observed by D. Grangaard while trapping during winters 1969-70 through 1985-86.

Man's harvest of moose has not been a major factor limiting moose population growth in Subunit 20E. Harvest of moose has been relatively low since the 1960's and hunting access was limited primarily to the Taylor Highway until the 1980's. If hunting was once a limiting factor, its effects would have been localized. Antlerless moose seasons were discontinued after 1974, and moose hunting seasons were closed during the years 1977 through 1981. Yet, the moose population continued to decline in all portions of the subunit, including previously unhunted areas. Harvests during the years 1970 through 1976 ranged only from approximately 70-100 moose (probably 1-2% of the population), and reported bull harvests since 1981 (10-day seasons) were 17 during 1982, 31 during 1983, 29 during 1984, 38 during 1985, and 35 during 1986 (less than 3% of the population).

No significant ($\underline{P} > 0.1$, linear regression) trend in numbers of moose was observed in 3 survey areas within the 2 control areas from 1982 to 1986 (Fig. 14). However, from inspection of the trend data (Fig. 14), we conclude that the number of moose in the survey areas was more likely stationary to slightly increasing than declining.

Calf Moose Production and Mortality:

Calf production by cow moose in the experimental area was high in 1984. We estimated that 100 cows ≥2 years old gave birth to approximately 130 calves. This estimate is based on estimates of age structure of cows from aerial survey data, percentage of radio-collared moose that were pregnant in March 1984, and the observed frequency of twin calves during the calf mortality study in 1984 (Boertje et al. 1985).

Calf mortality was high between 1966 and 1981 in the experimental area. Calves:100 cows ≥2 years old observed during early winter aerial surveys averaged 16 (SD = 8.1, range = 2-28) for the years 1966-81 (Table 6). If we assume 130 calves:100 cows ≥2 years old were produced annually, then the estimated calf mortality averaged 88% (range = 78-98%) at 6 months of age during the years 1966 through 1981. These estimates of mortality to 6 months of age overestimate mortality because the proportion of calves present at 6 months of age is underestimated from aerial surveys (Gasaway et al. 1981). However, the lowest estimated mortality rate (78%) is high relative to comparable rates for other Alaskan moose populations (Bishop and Rausch 1974).

Snow depth had a minor influence on trends in calf and yearling:cow ratios observed in the experimental area (Fig. 13). Snow depth experienced by cows while pregnant was not correlated ($P > 0.1$) with calf abundance the following early winter from 1956 through 1985; hence, snow depth had no detectable effect on calf production and/or survival to 6 months of age. Calf survival to 18 months of age, as indicated by yearlings:100 cows ≥2 years old, was not correlated ($P > 0.1$) with snow depth during the calf's 1st winter. In contrast to this finding, snow depths and survival to yearling age were correlated ($P < 0.001$) in Subunit 20A (Gasaway et al. 1983), suggesting snow had a greater impact on Subunit 20A moose. Yearling abundance, relative to calves of the same cohort in early winter, appears unexpectedly low only following winter 1978-79 (Fig. 13). Snow depth may have been a major influence during that winter, but no evidence for high winter mortality was observed by D. Grangaard while trapping in the experimental area during that winter or any other winter from 1969 through 1986. Even if a high percentage of the calves had died during winter 1978-79, the effect on the population would have been small since most calves had died prior to winter (Fig. 13). Therefore, we conclude that factors other than snow depth have been the primary determinants of recruitment to the population in the experimental area.

The survival curve for radio-collared calves indicates most mortality occurred shortly after birth (Fig. 15). Twenty-five (76%) of the 33 calves, collared as neonates in 1984, died within 8 weeks of birth. Subsequently, 1 calf died about 26 December. Another calf probably died by winter's end, but the calf's death could not be verified. This calf shed its collar during August and was orphaned during September when its radio-collared dam was killed by a grizzly bear. The 6 remaining calves survived at least until their transmitters failed; 1 failed during March and 5 during May 1985. The general shape of the survival curve (Fig. 15) is characteristic of curves of mortality rates reported for other moose populations where predators were abundant (Franzmann et al. 1980, Ballard et al. 1981a, Gasaway et al. 1983).

ADF&G reduction in numbers of wolves beginning in winter 1981-82 did not cause an increase in the calf:cow ratio. The best test of the effect of reducing wolves on calf:cow ratios occurred during fall 1982 in the Mt. Veta-Mosquito Flats moose survey area (Table 7). This survey area was centrally located in an approximately 10,400 km^2 area where wolves were reduced from 85 during fall 1981 to 19 during April 1982. If a major reduction in numbers of wolves could cause a marked increase in the calf:cow ratio, it would have been detected in the Mt. Veta-Mosquito Flats area. However, calf ratios did not increase following wolf reductions compared with pre-reduction ratios (Table 7). Additionally, calf ratios among moose observed in the entire experimental area during the years 1982 through 1986 did not increase compared with either pre-reduction ratios (1978-81) in the entire experimental area (Table 6) or with ratios in the control areas (Table 8). High calf mortality up to 6 months of age remained widespread in Subunit 20E after 1981 (Tables 6, 8).

When attempting to detect a change in survival, it should be remembered that calf:cow ratios reflect relative numbers of calves and cows in the population, not changes in actual numbers of animals. Therefore, ratios can remain unchanged while the numbers of calves and cows increase or decrease in a constant relationship.

ADF&G reduction in wolf abundance, beginning in winter 1981-82, may have slightly increased the number of calves surviving (Figs. 10 and 11), despite no increase in calf:cow ratios (Tables 6, 7, 8). The reduction in wolf abundance should have increased adult cow moose survival, which would result in an absolute increase in the number of calves produced and surviving, despite no increase in calf:cow ratios. Mt. Fairplay, Ketchumstuk, and Telegraph Creek aerial surveys (Figs. 10 and 11) suggested a slight moose population increase since winter 1981-82, which implies that calf and cow numbers increased slightly following wolf removal.

Predation by grizzly bears was the primary cause of calf mortality (1984 cohort); however, the spring wolf population in the calf study area was reduced during the years 1981 through 1983 by approximately 60% of the estimated spring pre-reduction density. Mortality of radio-collared calves born during 1984 was 82% (27 of 33 calves); 52% (17 calves) of the mortality was attributed to grizzly bears, 15% (5 calves, if we assume a calf orphaned during September was killed during winter) to wolves, 12% (4 calves) to drowning, and 3% (1 calf) to black bears. During winter, wolves apparently kill few of the calves that survive to November. Radio-collared cows attended 9 and 10 calves during early winter 1984-85 and 1985-86, respectively; yet only 3 (16%) of the 19 calves died during winter (Nov-Apr).

The proportion of radio-collared calves dying from wolf predation during 1984 and 1985 would likely have been greater if wolves had been at their pre-reduction density. Changes in size of the Mitchels Ranch pack, located in the center of the calf mortality study area (Boertje et al. 1985), exemplifies the effect that wolf removal may have had on calf mortality. This pack had 15 members during fall 1981, but it was reduced to a breeding pair during spring 1984 (Table 1). It seems reasonable that the pack of 15 would have killed more calves than the pair of wolves.

Black bears were not an important predator on calf moose in the experimental area, nor did we attribute any deaths of adult moose to black bear predation. Therefore, testing the predator-limiting hypothesis by reducing numbers of black bears is unnecessary.

A moderate rate of growth of the moose population cannot occur until calf survival markedly increases. Our data indicate predation is the major cause of low calf survival. The lack of increase in early winter calf:cow ratios following wolf removal during 1982 indicates that either grizzly bears were the most significant predator on calves prior to wolf removal, or an increase in grizzly bear predation on calves compensated for reduced wolf predation. In either case, it is clear that reduction of wolf predation without a simultaneous reduction of grizzly bear predation on calves will not result in calf survival that is well in excess of the number of dying adults. Reduction of both wolf and bear predation is essential if the moose population is to increase at a moderate rate.

Adult Moose Mortality:

A 7% mean annual natural (not man-caused) mortality rate was estimated (Gasaway et al. 1983) for 39 moose radio-collared during the period 21 March 1984 to 1 November 1986. The 7%

mortality rate is probably an underestimate of the actual moose mortality rate in the experimental area, because a large proportion of the radio-collared moose were collared in a high-density 130-km² moose wintering area (the Mosquito Flats), where moose apparently have had, and presumably still have, a lower mortality rate than moose in much of the remainder of the experimental area. The higher survival rate may be related to greater numbers of prey/predator and habitat relationships that affect hunting strategies of predators and the predictability of finding moose. On the other hand, the 7% mortality rate may be an overestimate of the mortality rate of moose in this high-density wintering area because all mortality of radio-collared adult moose occurred during May through October and the observation interval included 3 such periods but only 2 winter periods (Nov-Apr). This latter bias will be eliminated in the final report by using 3 year-round observation periods.

Predation was the primary cause of death for adult moose. Cause of death was determined for 38 moose, 34 (89%) were killed by predators, 2 (5%) died from antler wounds, 1 (3%) drowned, and 1 (3%) was shot (Table 9). Predators probably killed 5 additional moose that we investigated from the ground, but cause of death could not be confirmed because too much time had elapsed between death of the moose and discovery of the carcass; i.e., evidence of cause of death had been obscured by predators/scavengers. Of 9 dead moose (4 were of unknown age) that were seen only from the air during 1985-86, all were partially eaten by wolves or grizzly bears (Appendix B). When we applied the data discussed above, it appeared likely that predators killed most of these 9 moose.

Both grizzly bears and wolves were major predators on adult moose from 1 May to 31 October, whereas wolves were the only predator the remainder of the year (Table 9). However, it is difficult to estimate the relative proportion of adult moose dying from grizzly bear and wolf predation because the proportions in a sample vary with season and the methods of locating dead moose. We used a variety of methods to locate moose carcasses, including locating radio-collared wolves, grizzly bears, and moose; tracking wolves in snow during aerial surveys; and incidental sightings during field work. Because of sampling biases, the observed proportion of kills made by bears and wolves (Table 9) does not estimate the actual proportion.

The least biased method of estimating the proportion of moose dying from grizzly bear and wolf predation uses mortalities of radio-collared moose, where observation periods are in multiples of years. In this progress report, the estimator was biased because the observation period lacked the 1986-87 winter months. The proportion of moose killed by wolves may increase when the last year's data are complete because only wolves will prey on moose during the remaining period (Nov 1986-Mar 1987).

We recognize the bias in the estimator and present a preliminary analysis of causes of adult moose mortality. Eight of 39 radio-collared adult moose died since March 1984; 3 were killed by grizzly bears, 1 was killed by wolves, 2 died from unknown natural causes, and 2 were shot. The 2 that died from unknown causes were eaten by grizzly bears and could have been killed by them, but we could not confirm cause of death. Nutritional condition of 1 of these could not be assessed because fly larvae had completely consumed the marrow contents (Kie 1978). Condition of the other was probably good, as indicated by 92% marrow fat.

Wolves selectively killed primarily old-aged moose in the experimental area, as in other Alaskan studies of differential vulnerability among adult moose (Gasaway et al. 1983, Peterson et al. 1984). The mean age of nonradio-collared wolf-killed cows ≥ 2 years old (13.2 years, SD = 4.0, $n = 12$) was significantly greater ($P < 0.01$, two-tailed Student's t-test) than the mean age of adult radio-collared cows ≥ 2 years old sampled from the living population (8.6 years, SD = 3.5, $n = 32$). These data reaffirm that young and middle-aged adult moose have a lower vulnerability to wolf predation than old moose (≥ 11 years old; Mech 1966, Gasaway et al. 1983, Peterson et al. 1984), even in our experimental area where moose were scarce. Peterson et al. (1984) show that the potential food available to wolves, i.e., vulnerable moose, varies with the age structure of the moose population. The population of moose in the experimental area has a high proportion of vulnerable adult cow moose (34% of 32 cows were ≥ 11 years old); however, on an absolute basis, the moose population provides little food because of its low density.

In contrast to wolves, grizzly bears did not selectively kill old-age adult moose. The mean age of grizzly-killed nonradio-collared cows ≥ 2 years old (9.8 yrs, SD = 5.0, $n = 9$) was not significantly greater ($P > 0.5$, two-tailed Student's t-test) than the mean age of adult radio-collared cows ≥ 2 years old sampled from the living population. Apparently, most cow moose were vulnerable to predation by grizzly bears. The grizzly bear is a larger, more powerful predator than the wolf and its strength and quick-killing techniques allow it to kill younger cow moose that are presumably in better physical condition than moose killed by wolves. A contrast of hunting and killing techniques by wolves and grizzly bears will be presented in later reports.

Compared with grizzly bears, wolves killed older cow moose, but not necessarily older male moose. The mean age of all wolf-killed cows (13.2 yrs, SD = 3.8, $n = 13$) was significantly greater ($P < 0.1$, two-tailed Student's t-test) than the mean for bear-killed cows (9.6 yrs, SD = 4.8, $n = 11$). The sample size of kills of male moose was small, but preliminary data suggest the mean age of all male moose ≥1 year old that were killed by wolves (10.8 yrs, SD = 5.5, $n = 5$) and grizzly bears (12.3 yrs, SD = 3.6, $n = 4$) did not differ significantly ($P > 0.2$).

Few moose died in a severely malnourished state, as indicated by the percentage fat in bone marrow (Table 9). Franzmann and Arneson (1976) used a value of ≤10% marrow fat as an indicator of severe malnutrition, and Peterson et al. (1984) used a value of ≤20%. Only 4 of 38 moose found dead had <20% fat in marrow, of which 3 were ≤10% (Appendix B). These 4 moose were old; ages were 12 and 13 years for 2 bulls and 17 years each for 2 cows. Because few bulls live longer than 13 years (W. Gasaway, P. Karns, and K. Morris, unpubl. data) and few cows live beyond 17 (Peterson et al. 1984; Gasaway, unpubl. data), it can be argued that these 4 moose may have been near the end of their physiological life and hence in poor condition. However, we propose an alternative hypothesis that may apply to moose that die with a low percentage of marrow fat.

Reasons for malnutrition observed in prey are rarely determined. Commonly, a severely malnourished state is attributed to a diverse collection of possible causes, including inadequate forage, disabilities associated with age, or the secondary effects of disease or injury. Conventional wisdom assumes that predators select malnourished prey because of the prey's increased vulnerability. We concur. But identifying that a prey animal was malnourished at the time of death is in many cases little more than an interesting fact. Identifying the reason for malnutrition is the important point if we are to understand the basis for differential prey vulnerability.

We propose that an overlooked cause of malnutrition among ungulates is wounding by predators. The following case history helps support the point. We observed a wound on a 13-year-old radio-collared moose on 28 September 1985. The wound was on the spine between the shoulders. This cow was killed by a radio-collared grizzly bear on 11 October 1985. At that time, the cow had only 50% fat in marrow, no subcutaneous fat, and visceral fat was limited to a small quantity on the heart. This lean condition is not typical of cows during October. We suspect she survived an attack by a grizzly bear and then lost weight and became more vulnerable before being killed. Had she been killed as little as 2 weeks later, her marrow fat could have been very low (Mech and Del Giudice 1985). If this scenario is correct, other moose found dead with low marrow fat may have declined in condition as a result of prior wounds by predators.

Following are additional observations of moose escaping from predators after being wounded. R. Boertje radio-collared a cow moose on 27 March 1984 that had recently been attacked by wolves and had sufficient flesh removed to expose a dorsal portion of the pelvis. The moose recovered, living at least 1 year; however, its fat reserve may have temporarily declined following the attack. In Alaska, R. Nowlin observed a radio-collared calf moose during December that had been attacked and wounded by wolves. The moose could not walk and remained near the attack site until death about 3 weeks later. In another incident, Nowlin found a dead radio-collared bull moose, that had not been fed upon by scavengers, with signs indicating it had been attacked by wolves. This attack apparently resulted in a massive infection near the anus and internally to the kidneys, but just 3 weeks earlier the moose was observed to be in good condition. Had either of the moose that Nowlin observed been killed by a predator several days or more after the initial attack, the condition index, as indicated by the percentage marrow fat, may have been low. On Isle Royale during winter 1977-78, Peterson and Scheidler (1978) observed 5 cases of moose escaping after being wounded by wolves; 4 of these moose either died from wounds or were later killed by wolves. Peterson and Scheidler (1978) speculated that as moose declined on Isle Royale and prey became scarce, wolves attempted to kill moose that were not highly vulnerable. Initially, the wolves were only able to wound these moose, but later the moose became highly vulnerable.

Depending on the severity, wounds from predators can certainly cause prey to decline in condition and can increase vulnerability to future predator attacks. Biologists must recognize that moose in poor condition may have been victims of non-lethal predator attacks. Previous wounds on moose are difficult to detect because biologists rarely investigate: (1) live moose close enough to detect wounds, or (2) intact moose carcasses where prior wounds are not obscured by more recent wounds or consumption of flesh. The fact that large ungulates frequently survive attacks by large carnivores was graphically displayed on zebra (Equus burchelli) in Etosha National Park, Namibia. Fifteen percent of adult zebra that were observed at close range (<70 m) carried scars from lion attacks (W. Gasaway, unpubl. data). Scars can be identified easily on zebra compared with moose because of the zebra's short hair, mismatched stripes at scars, and because observations were at close range.

Adult bull and cow moose died in approximate proportion to their occurrence in the population. The sex ratio among 35 moose dying from all causes (59 bulls:100 cows; Table 9) was not significantly different ($\underline{P} > 0.1$, two-tailed Student's $\underline{t}$-test) from the mean of ratios (83 bulls:100 cows, $\underline{n} = 1,306$) among moose surveyed in the experimental area during the years 1981 through 1985. Also, the sex ratio among moose killed by wolves ($\underline{n} = 17$) or by bears ($\underline{n} = 13$) did not differ significantly ($\underline{P} > 0.1$) from the sex ratio in the living population (Table 9). However, when moose killed by wolves and grizzly bears were combined (43 bulls:100 cows, $\underline{n} = 30$) the sex ratio was significantly different ($\underline{P} < 0.1$) from that in the living population. The larger sample size made the difference statistically significant and suggests that predators in the experimental area may select for cows.

Bull moose were a major food source for predators in our study area (regardless of whether predators select cow moose), and, unless wolf or grizzly bear predation is reduced, the moose population will continue to have no, or few, surplus bull moose for man to harvest. With the moose population at a low density and its growth limited by predation, hunters and predators compete for the few available bulls. If man removes many bulls, predators will prey increasingly on the few remaining cows and calves (Peterson et al. 1984). The result will be even lower recruitment, increased adult mortality, and possibly a decline in numbers of moose.

Predator-Prey Relationships:

Predators are abundant relative to the number of moose in the experimental area (Tables 10, 11); however, moose-predator relationships change seasonally as caribou move in and out of the area. The range of the caribou herd is large relative to the experimental area (Fig. 16). When most caribou migrate out of the experimental area, predation rates on moose are predicted to be high, based on the effects predators had on other moose populations where the number of moose per predator was low (Gasaway et al. 1983; Peterson and Page 1983; Ballard and Larsen, in press; Van Ballenberghe, in press). However, when most of the caribou herd is in the experimental area, prey is abundant for most wolf packs and grizzly bears (Table 11). The high number of alternate prey (caribou) per predator temporarily reduces predation rates on moose. When caribou are available to wolves, even in low numbers, wolves hunted and killed them. Preliminary food habits data indicate the average wolf diet consists of approximately 50% caribou during winter. In effect, this consumption of caribou doubles the number of moose in the moose:wolf ratio (Table 11), resulting in 28 moose:1 wolf during fall 1985 as opposed to 14:1. We would expect the moose population to remain stationary or increase at a ratio of 28 moose:1 wolf if grizzly bears were not important predators.

Numbers of prey relative to wolves increased between 1981 and 1984. Growth of the caribou herd (Valkenburg and Davis 1987) and wolf removal (Table 1) contributed about equally to this increase. Future changes in the number of prey per wolf will largely depend upon whether the wolf or caribou population grows fastest, whether the moose population increases, and how caribou are distributed in the experimental area. A shift in distribution of caribou within or out of their present range will rapidly alter predator-prey relationships in the experimental area.

Maintenance of territorial wolf packs (Figs. 3-7) in the experimental area is dependent on moose. Moose are the only year-round resident ungulates in most pack territories and therefore serve as the only dependable food source. Although caribou are a major alternate prey source, their abundance varies seasonally, annually, and geographically, and radio-collared wolves in packs were not observed to abandon their territories to maintain contact with migrating caribou. Therefore, few resident wolf packs could survive if moose were not present. During the years 1981 through 1986, the number of caribou in the experimental area probably ranged from about 200 to almost the entire herd (approx. 15,000; Valkenburg and Davis 1987). However, it is likely that each year all packs had some caribou travel through their territory, and that wolves killed caribou when available.

Wolves have not been abundant in the experimental area since the mid-1970's and will not become abundant until their prey base increases substantially (Fig. 2). The density of wolves during falls 1981, 1984, and 1985 were 8, 5, and 6 wolves/1,000 km^2, respectively (Table 10), compared with 16/1,000 km^2 in Subunit 20A during 1975 (Gasaway et al. 1983) and 11-19/1,000 km^2 on the northwestern Kenai Peninsula during the years 1976 through 1982 (Peterson et al. 1984). Food shortage for Subunit 20E wolves was reflected by a low reproductive rate (Table 3), no major recovery after declining to a low density in 1976 (Fig. 2), and the slow population growth after wolves were reduced further during winters 1981-82, 1982-83, and early winter 1983 (Table 1). The predator-limited moose population in the experimental area is not likely to substantially increase in the near future. Therefore, if wolves are to increase, the caribou herd must continue to grow and must redistribute itself spatially and temporally into the wolf pack territories to become a more dependable food source. However, wolf predation may currently prevent the caribou herd from rapidly increasing (Valkenburg and Davis 1987).

Compared with wolves, grizzly bears currently kill many more moose calves, and less, or approximately equivalent numbers of moose ≥ 1 year old. Grizzly bears are about 3 times more abundant than wolves and killed 52% of 33 radio-collared calves in 1984 compared to 15% calves killed by wolves; however, wolf numbers had been reduced substantially in the calf study area. During fall 1985 through summer 1986, adult radio-collared male grizzly bears and females without cub(s) of the year killed adult moose at mean rates of 3.5 and 0.7 moose/year, respectively, as previously discussed. At these kill rates, grizzly bears would annually kill approximately 38 moose older than 1 year or 5-9% of the early winter moose in the grizzly bear study area, where the number of moose was 450 ± 250 (90% CI) in 1981. Actual numbers of moose were probably in the higher half of the CI based on later trend surveys. Wolves may also be killing approximately 6-9% of the early winter moose population, based on kill rates of the Gold Creek pack and assuming moose compose only about 50% of the wolves' diet. However, based on mortality rates of radio-collared adult moose, wolves are killing <6% of the early winter moose population.

Calf and adult moose in the experimental area sustained high and moderate rates of natural mortality, respectively, and, as previously discussed, predation was the major cause of that mortality. We believe the mortality data presented make a strong case for predation limiting this low-density moose population. In next year's report, we will attempt to present a population model that integrates production, recruitment, and mortality. This model will show the relative importance of predation by wolves and grizzly bears on moose population dynamics.

Testing the Food-limiting Hypothesis

Data presented by Boertje et al. (1985) supported rejection of the hypothesis that food limits moose population growth in the experimental area. These data were: (1) low use (<5%) of annual browse production, (2) high pregnancy rate (100%) among 27 adult female moose examined, (3) high twinning frequency (52%) among cows giving birth, (4) large morphometric measurements for adult female moose (Table 12), (5) moderate to high condition indices for adult moose ($\bar{x}$ = 7.0, SD = 1.1, n = 39), moderate condition-related blood parameters (Table 13), and (6) high percentage of marrow fat in wolf-killed adult moose (Appendix B). Only 4 (10%) of 39 moose found dead during the period 1981 through 1986 had ≤20% marrow fat (Appendix B), which confirms that few moose in the population were in a severely malnourished state (Franzmann and Arneson 1976, Peterson et al. 1984). Bears and wolves should have led us to more moose in poor condition, if present, because bears and wolves scavenged moose carcasses. In addition, these predators should be able to kill moose in poor condition more easily than they can kill moose in good condition.

CONCLUSIONS

1. We reject the hypothesis that food was limiting moose population growth in Subunit 20E based on measurements of browse availability and use, and on moose reproductive and nutritional status.

2. To date, we have no unequivocal test of the predation-limiting hypothesis because we have not been authorized to adequately manipulate wolf and grizzly bear populations in the experimental area. Only by reducing the effect of a potential limiting factor and measuring the change in moose abundance will we be able to make an unequivocal test. However, mortality data presented make a strong case for predation limiting this moose population at its low density.

3. After wolf numbers were reduced by 20-40%, grizzly bear predation had a greater effect on moose population dynamics than wolf predation. Data were unavailable to determine which predator had a greater impact on moose prior to reducing wolf numbers.

4. Stimulation of a moderate rate of increase (10% annually) in moose numbers in Subunit 20E would probably be best accomplished by simultaneously reducing grizzly bear and wolf predation. Reducing grizzly bear predation will improve summer calf and adult survival. Reducing wolf predation will directly improve year-round moose survival and probably indirectly improve moose survival by increasing the rate of growth of the caribou herd. If we wish to increase numbers of moose by reducing either wolf or grizzly predation, it will require a high impact on that predator population, much higher than if both predators were reduced simultaneously. Also, it is questionable whether detectable short-term increases in the moose population would occur if, for example, only the wolf population were reduced to moderate numbers.

5. Currently, the moose population has no surplus moose for man to harvest and no surplus moose for population growth.

6. The effects of a slowly increasing migratory caribou herd on short-term moose-predator relationships are likely both beneficial and detrimental to moose, depending on when and how long caribou are present in the predator's home range. When both caribou and moose are present in a wolf pack's territory, wolves often kill caribou rather than adult moose (Gasaway and Boertje, unpubl. data); therefore, the moose population benefits. However, a short-term abundance of caribou may allow wolves and possibly grizzly bears to maintain greater densities than if only moose occurred. When caribou leave the predator's home range, the increased predator population preys

primarily on moose--to the added detriment of the moose population.

Alternatively, moose, as a widely distributed resident prey base, sustain predators throughout all seasonal caribou ranges of the Fortymile Herd, thus causing higher rates of predation on caribou than if no moose were present (Bergerud 1978). Moose, therefore, have primarily detrimental effects on caribou population dynamics.

RECOMMENDATIONS

1. The Board of Game, ADF&G, and local advisory committees support general goals of increasing numbers of moose, caribou, and wolves in Subunit 20E. Debate continues on how best to accomplish these goals, and no specific goals or implementation plans are approved by the Board of Game or local advisory committees. We recommend specific goals be adopted with accompanying management actions necessary to implement the goals.

Based on findings of this study, we recommend the following management actions for achieving increased numbers of moose in Subunit 20E:

(1) Simultaneously reduce grizzly bear and wolf predation to improve moose survival. If we attempt to increase moose numbers by reducing just wolf or grizzly predation, the reduction will require a high impact on that predator population--much higher than if both predators are reduced simultaneously. A reduction in predation can be accomplished directly by the Board of Game through the regulatory process. Advisory committees, the public, ADF&G, conservation groups, and the Board of Game can promote recreational hunting of bears and wolves, thereby involving hunters directly in the wildlife management process. Predation on moose may also be reduced by ensuring continued growth of the Fortymile Caribou Herd to provide alternate prey for predators.

(2) Maintain low harvest rates of male moose and caribou to ensure that hunting does not prevent growth of these populations.

(3) If effective steps are taken now to increase moose survival, habitat may begin to limit the moose population in 2 or 3 decades (based on 10% annual growth of the moose population). Some of the most favorable moose habitat in Subunit 20E has been produced in about 2 decades following fire, so a responsible management plan

requires burning now to ensure adequate food for a growing moose population 2 or 3 decades in the future.

The goal of increasing wolf numbers will be met if the above management actions are effectively implemented. Low prey densities have limited production and survival of wolves in Subunit 20E for much of the past decade, except possibly during intensive control. Higher prey densities will support higher wolf densities and the wolves will be more productive.

2. Summarize knowledge of interrelationships of grizzly bears, wolves, man, moose, and caribou in Subunit 20E to ensure that it is understood that little or no increase in the low-density moose population is predicted given the current allocation regulations, except possibly if caribou numbers increase. Current moose production is being utilized almost entirely by grizzly bears and wolves.

3. If the Board of Game changes the allocation of moose among man and predators through predator reduction, then we should measure the effects of these reductions.

4. Discontinue most field aspects of this study by May 1987 unless the predation-limiting hypothesis can be tested by reducing predation on the moose population. Prepare manuscripts for publication and proposals for new research.

5. Long-term monitoring of moose, caribou, wolves, and grizzly bears should continue in Subunit 20E so that changing predator-prey relationships can be evaluated. Specifically, ADF&G should continue to monitor: (1) moose and caribou population trend and composition; (2) wolf population size and the effect of harvest on wolf population growth rate; (3) wolf food habits, productivity, and condition; and (4) grizzly bear harvest and its potential effect on grizzly bear abundance and moose population growth.

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PREPARED BY:

Rodney D. Boertje
Game Biologist II

William C. Gasaway
Game Biologist III

SUBMITTED BY:

Wayne L. Regelin
Regional Research Coordinator

APPROVED BY:

W. Lewis Pamplin Jr./bt
Director, Division of Game

S R Peterson
Research Chief, Division of Game

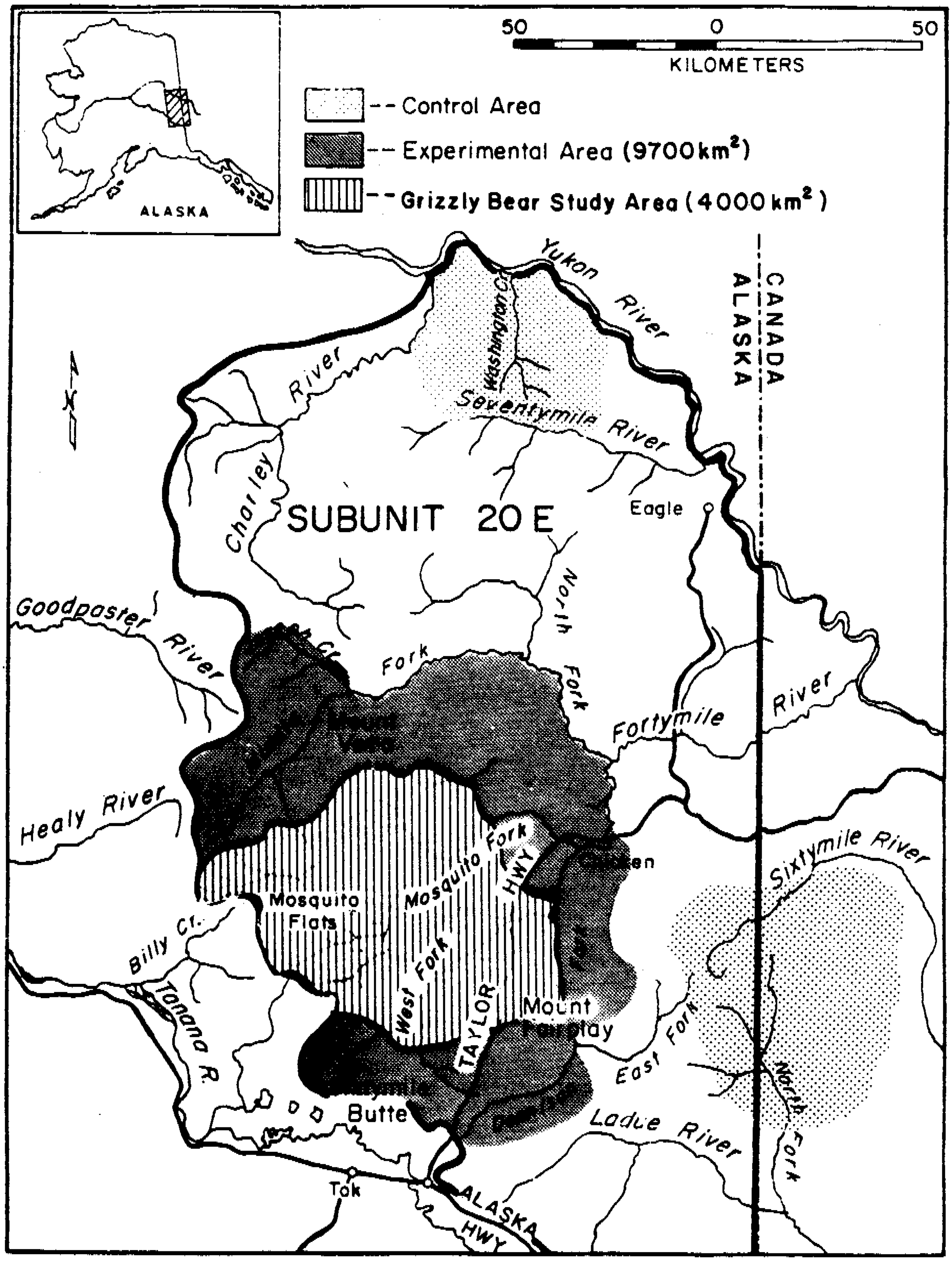

Fig. 1. Experimental area (with wolf removal), control areas (without wolf removal), and grizzly bear study area in Subunit 20E, Alaska, and adjacent Yukon Territory, Canada.

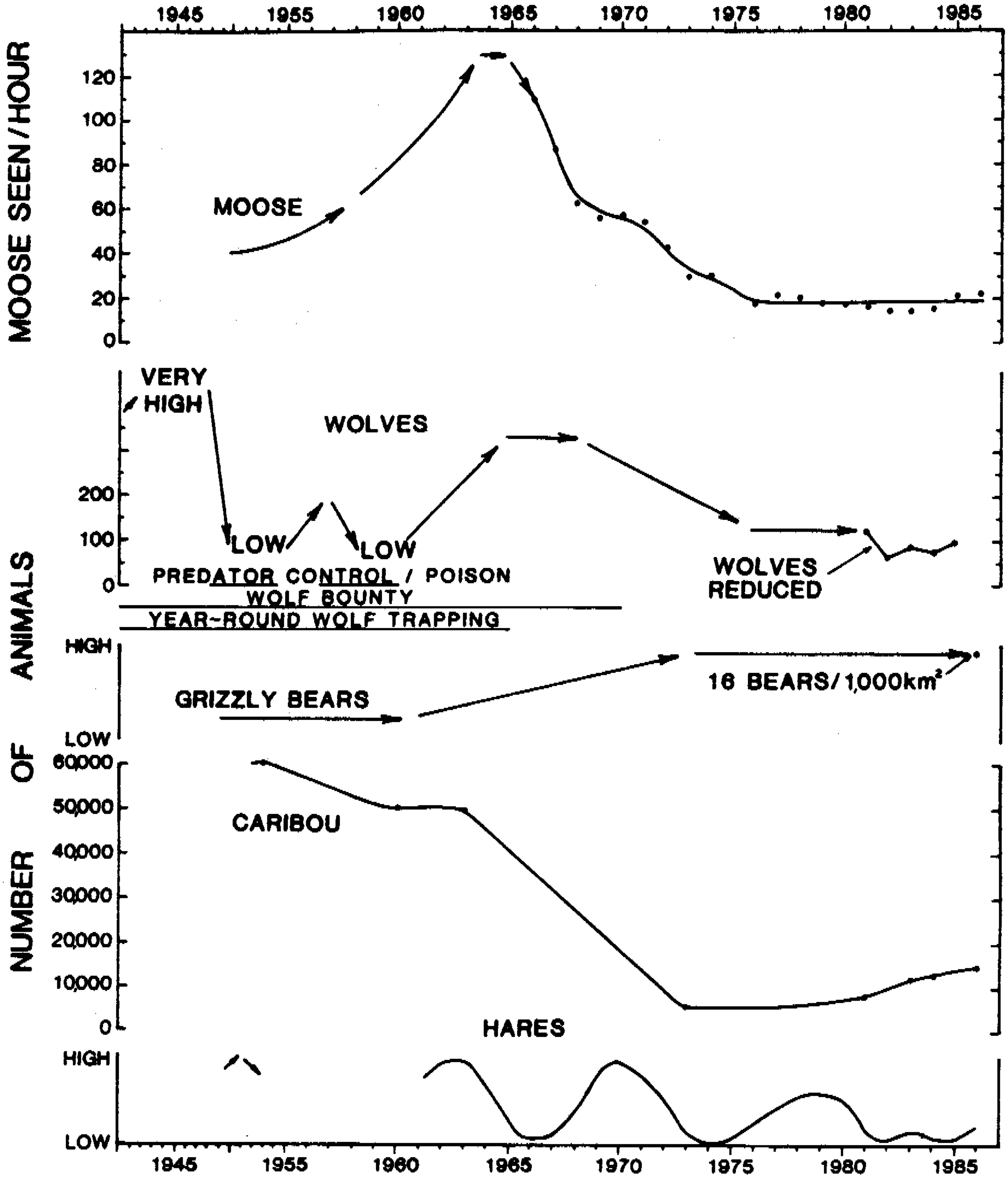

Fig. 2. Estimated and relative numbers of moose, wolves, grizzly bears, caribou, and hares in the experimental area of Subunit 20E, Alaska, 1940-86. Dots indicate estimated values; arrows indicate trends and approximate relative abundance based on qualitative observations.

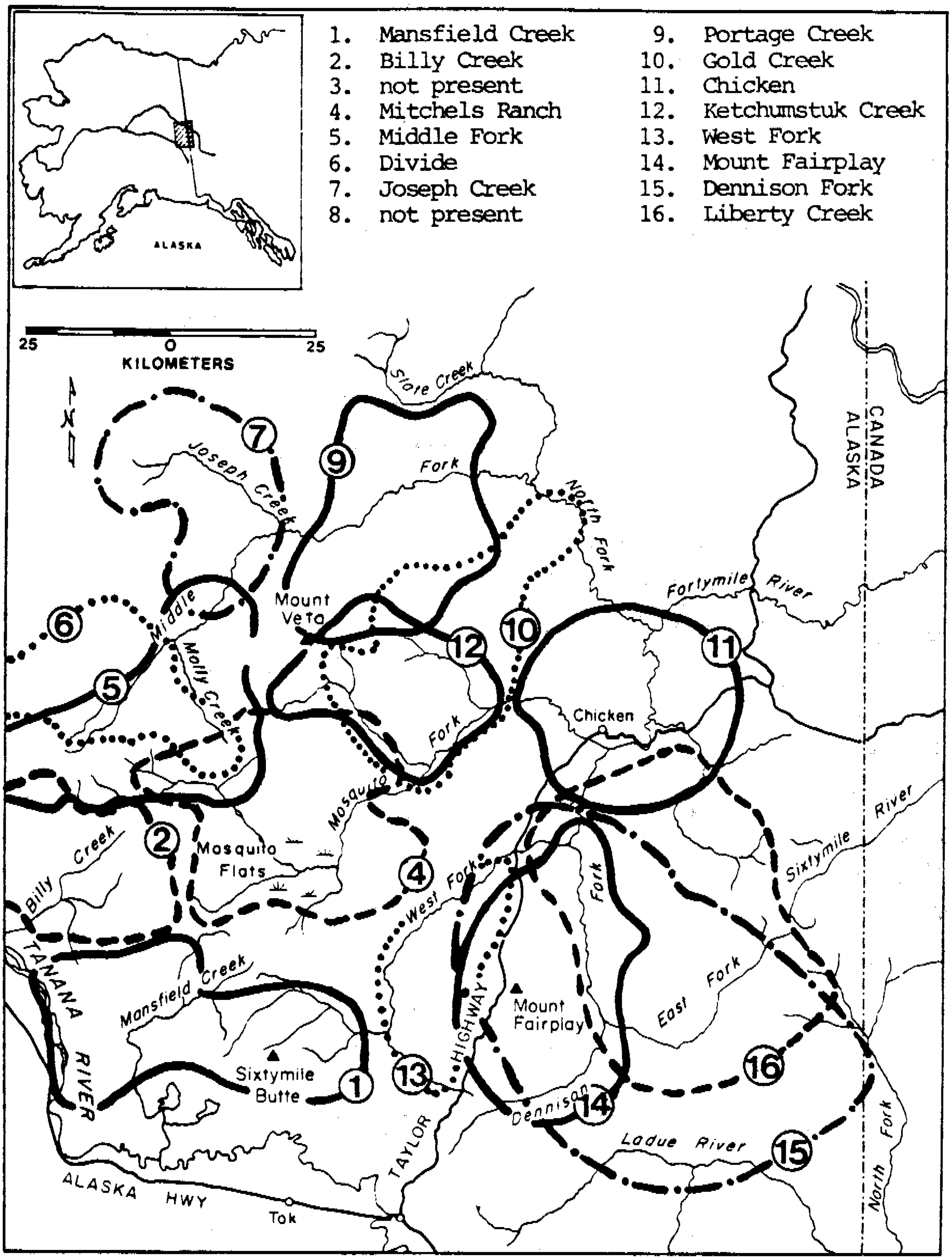

Fig. 3. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1980-82.

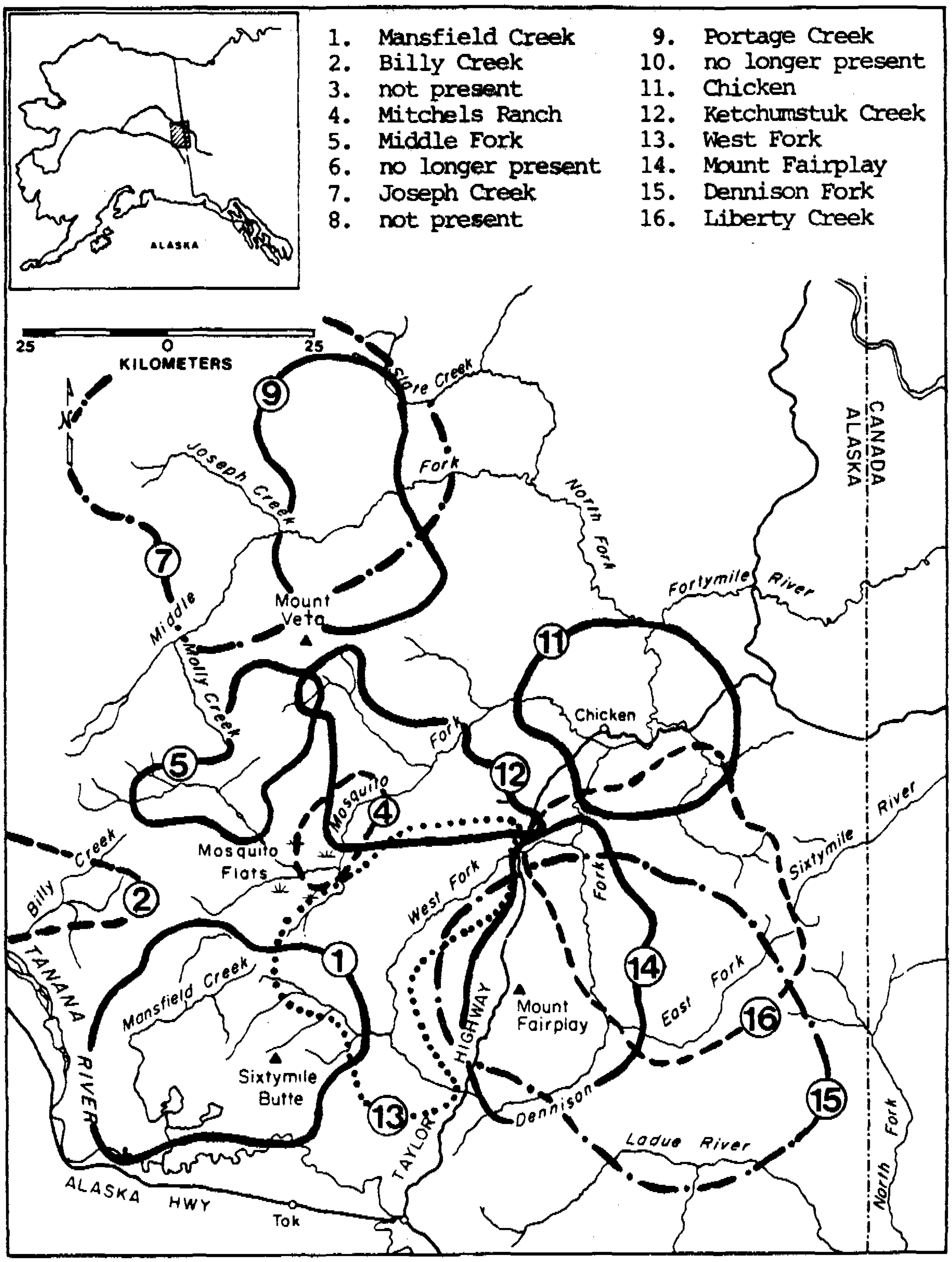

Fig. 4. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1982-83.

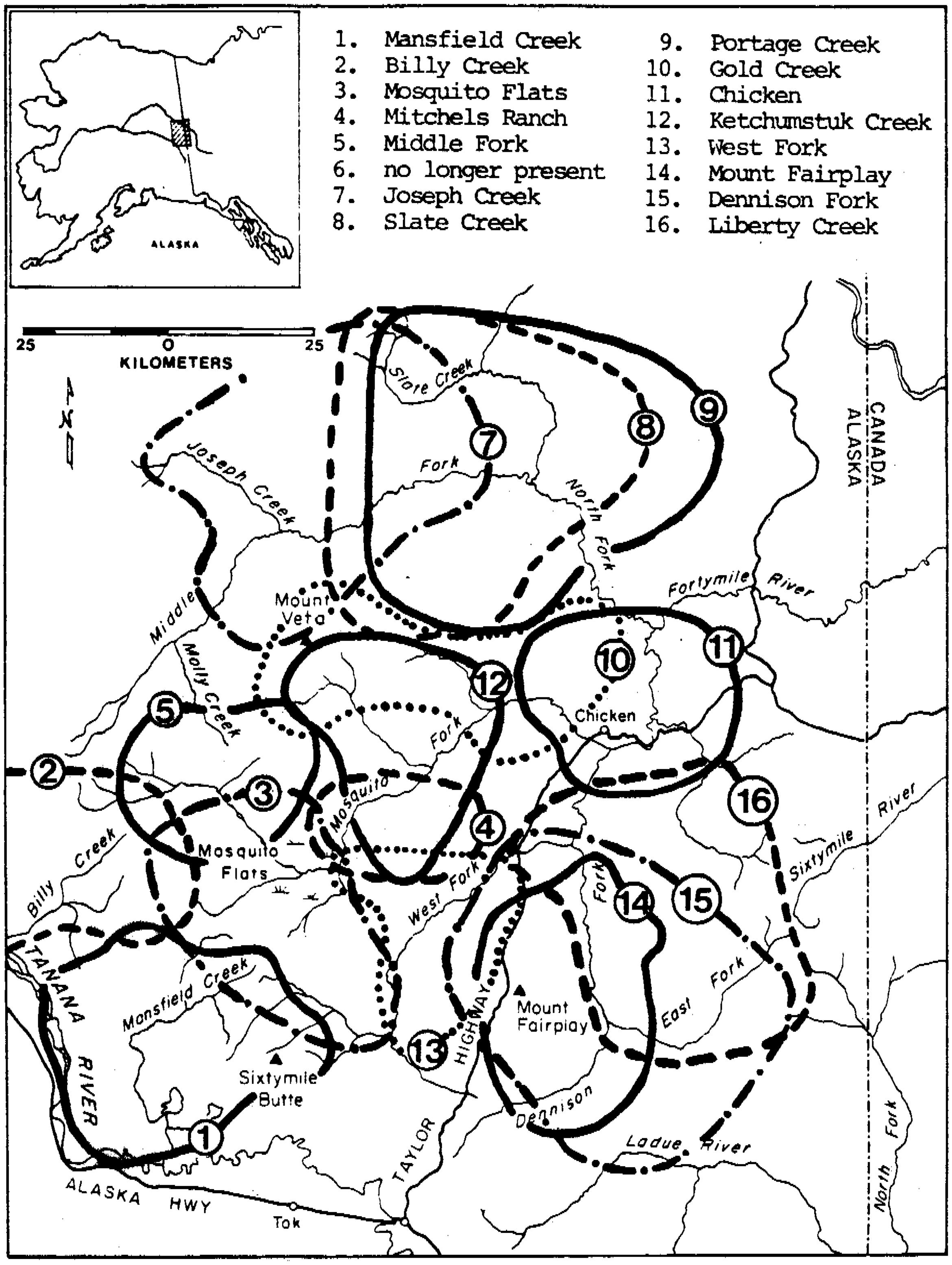

Fig. 5. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1983-84.

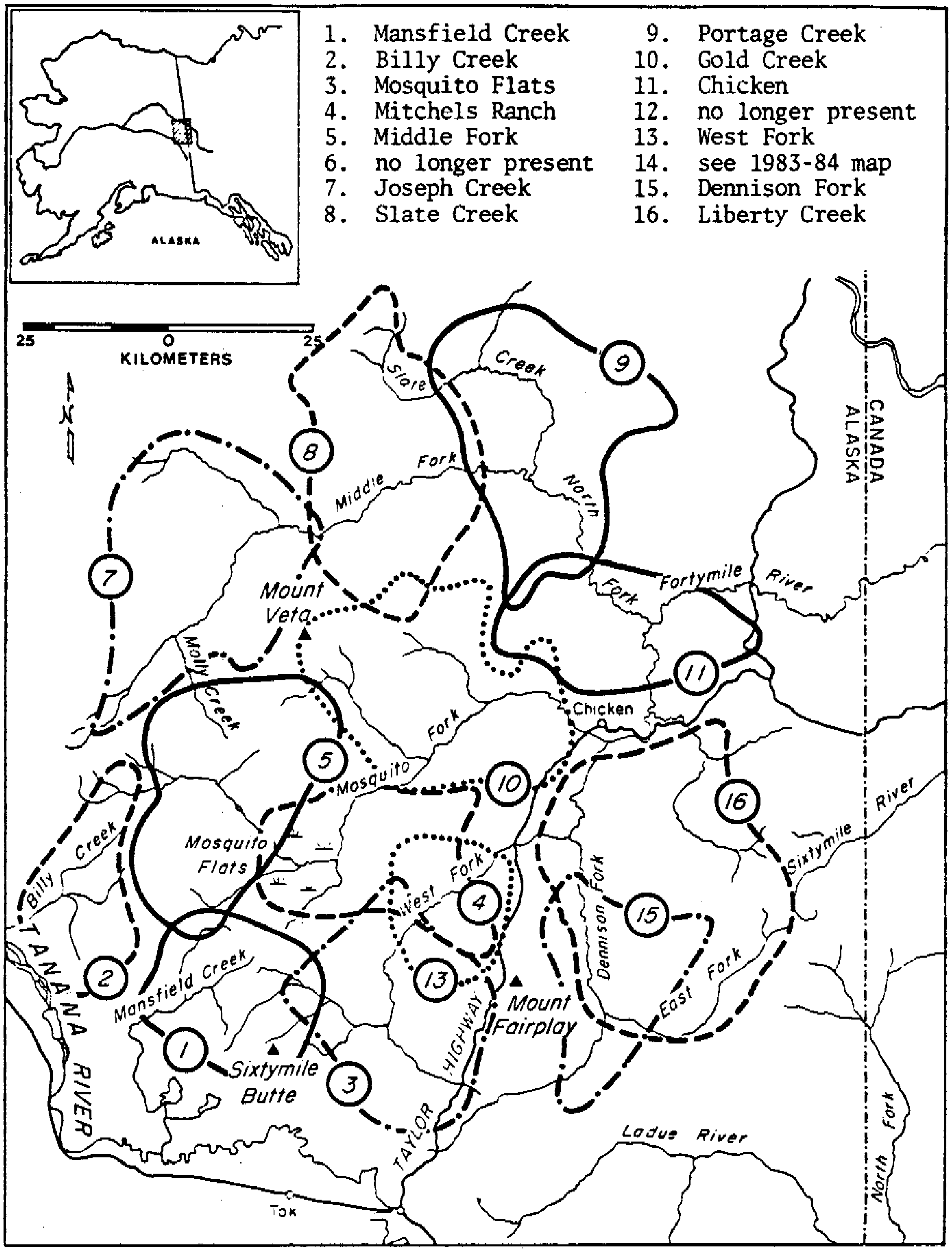

Fig. 6. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1984-85.

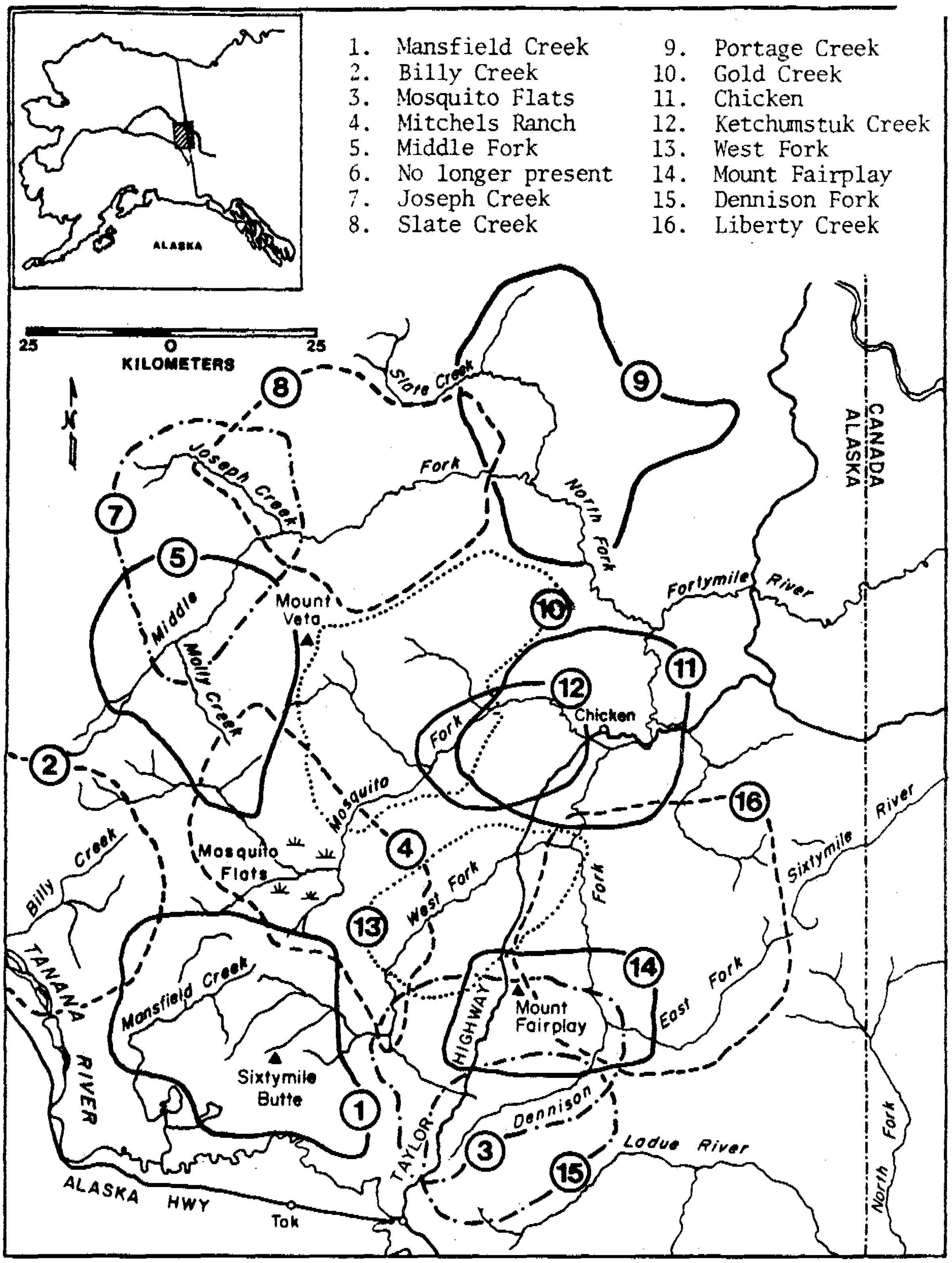

Fig. 7. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1985-86.

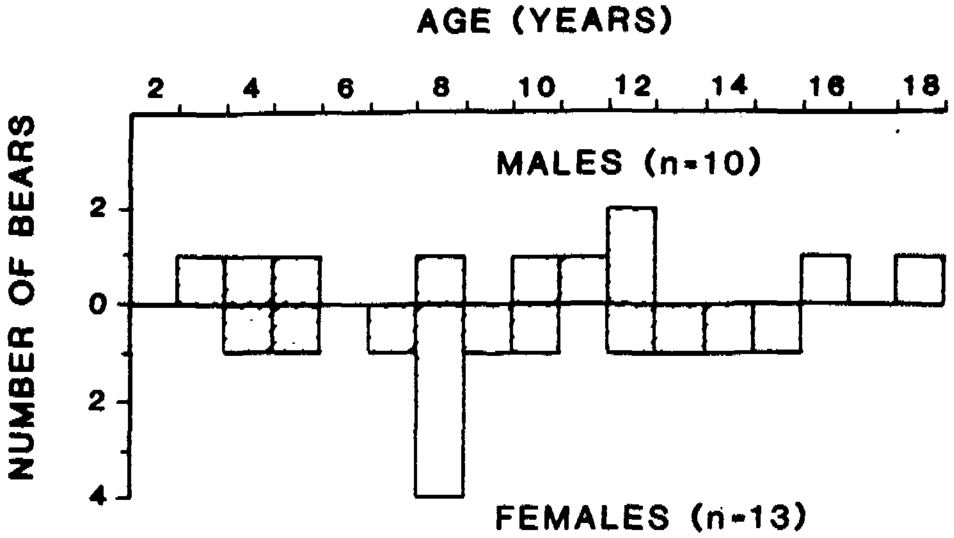

Fig. 8. Sex and age structure of 23 grizzly bears captured in Subunit 20E, Alaska, 1985-86.

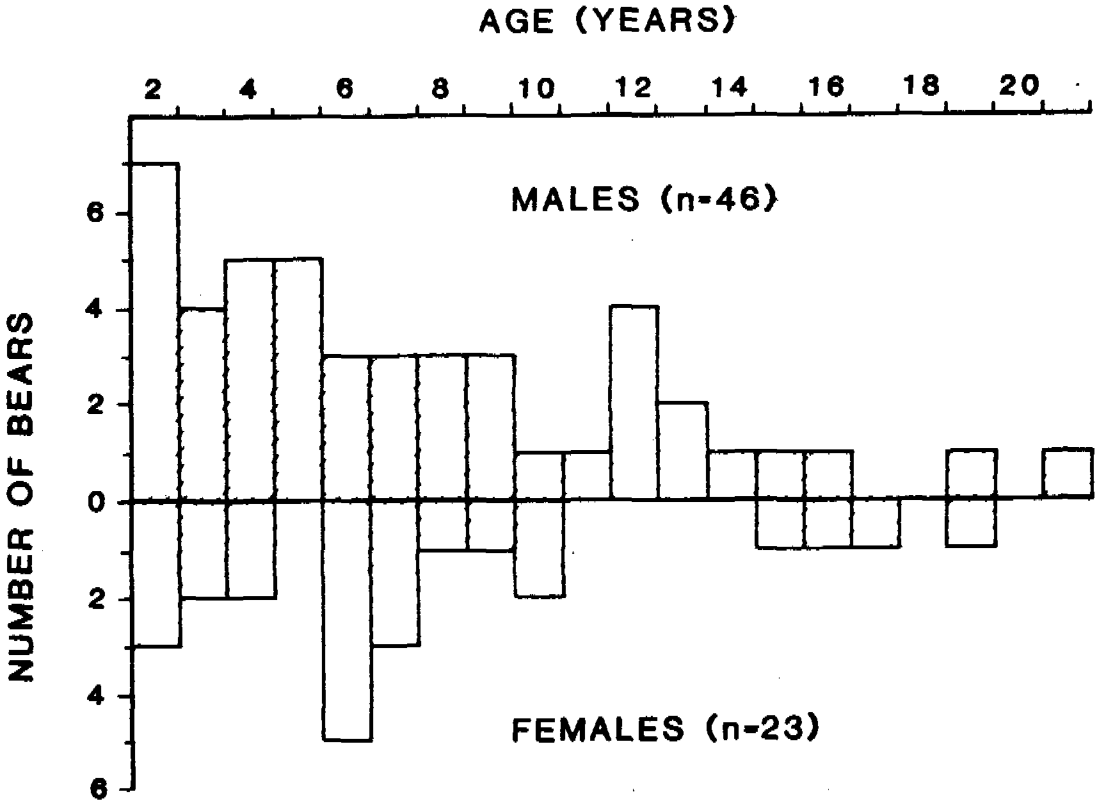

Fig. 9. Sex and age structure of pooled data from 69 grizzly bears harvested from Subunit 20E, Alaska, 1981-85.

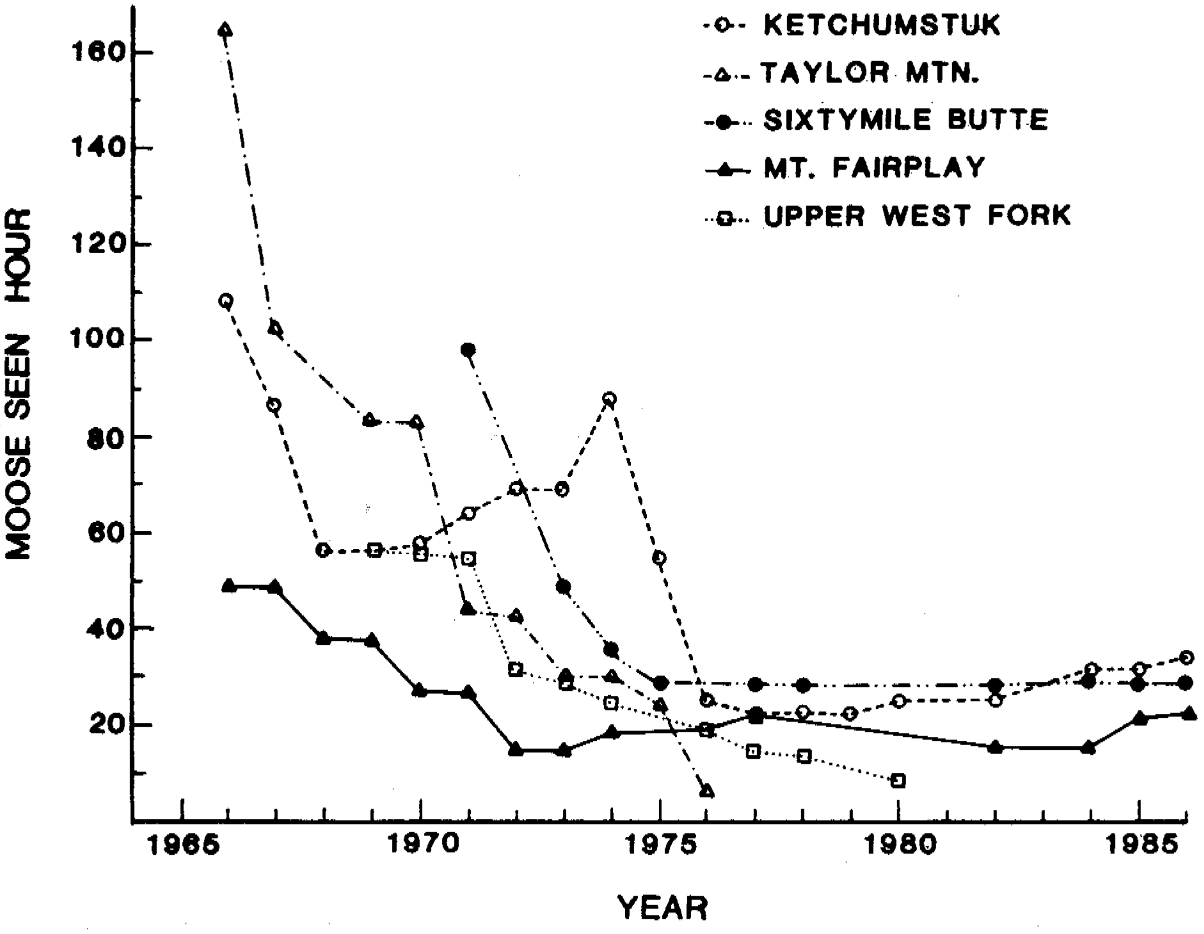

Fig. 10. Trends in number of moose seen per hour in 5 aerial survey areas in the experimental area of Subunit 20E, Alaska, 1966-86.

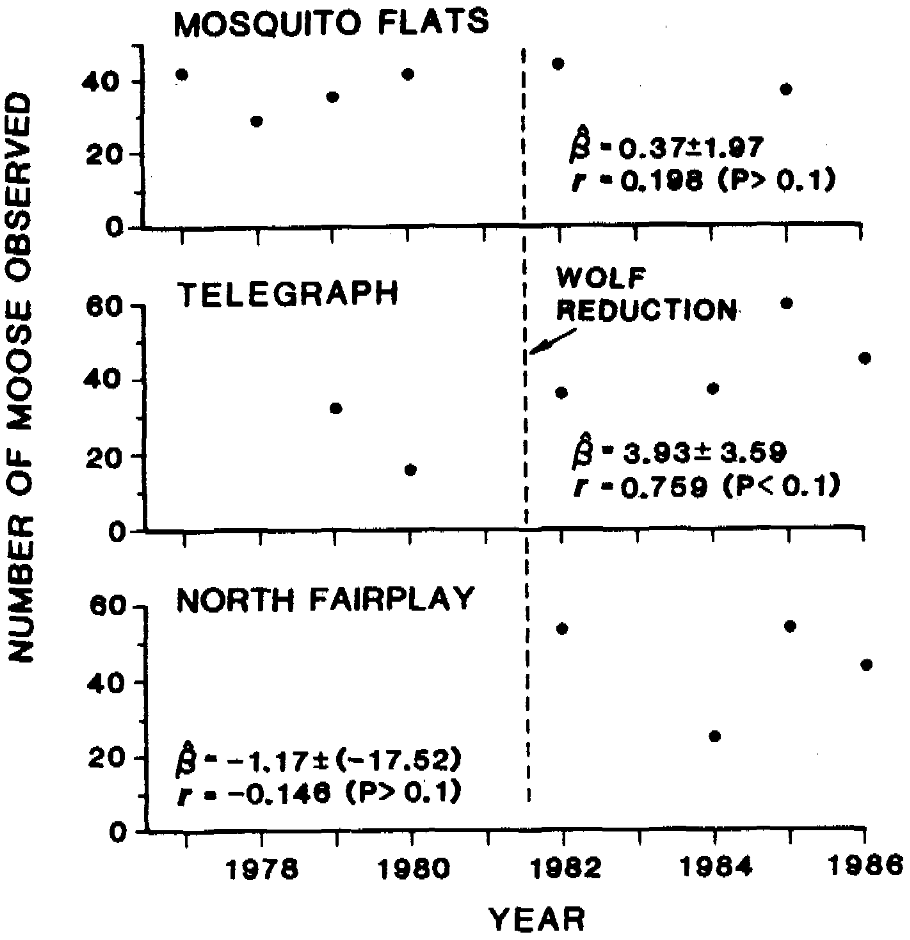

Fig. 11. Trends in number of moose observed in 3 aerial survey areas in the experimental area of Subunit 20E, Alaska, 1977-86. + 90% CI equals the estimated slope of the linear regression line, and r equals the correlation coefficient.

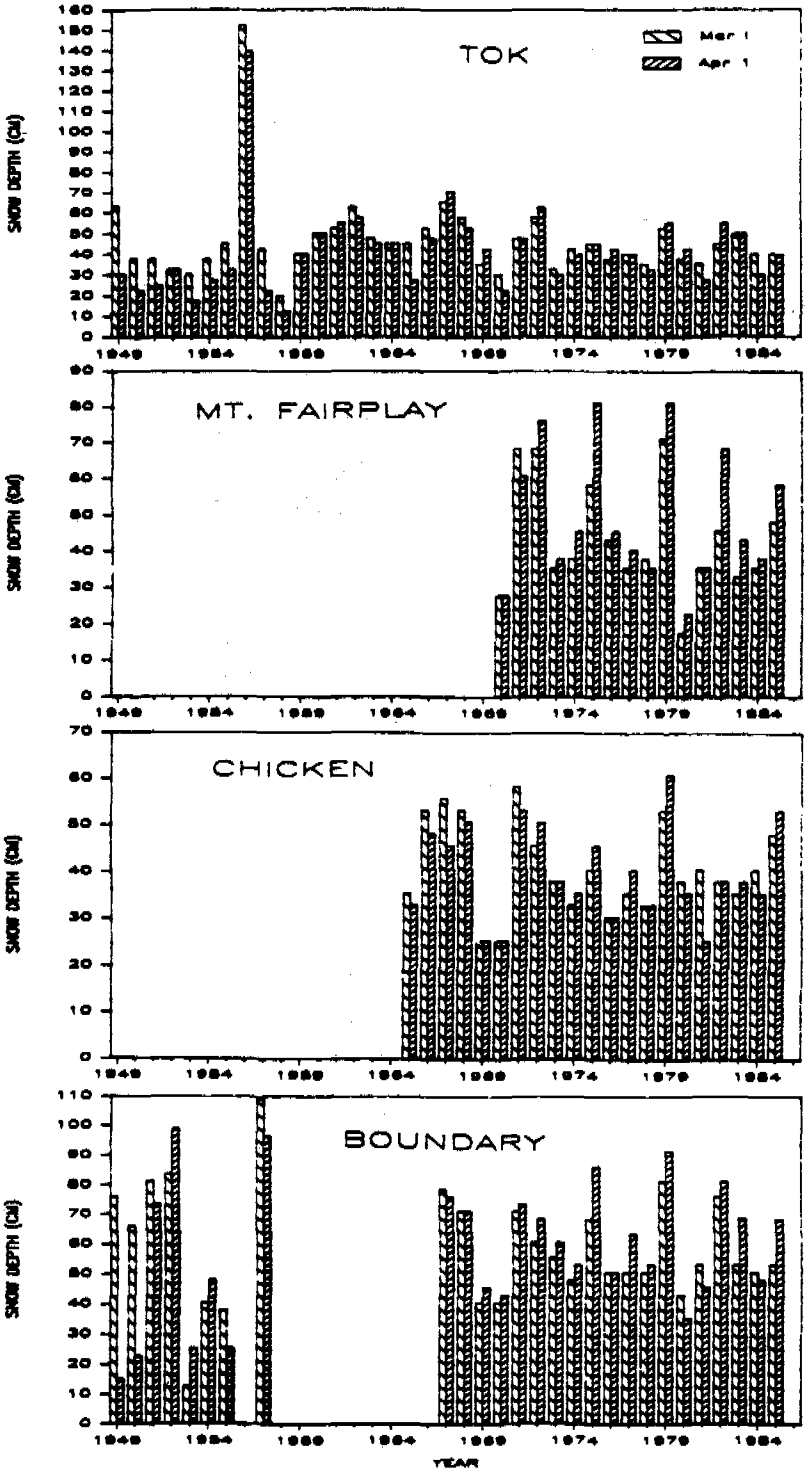

Fig. 12. Snow depth on 1 March and 1 April at 2 sites in the experimental area (Mt. Fairplay and Chicken), 1 site 30 km east of the experimental area (Boundary), and 1 site adjacent to the experimental area (Tok) of Subunit 20E, Alaska, 1949-85.

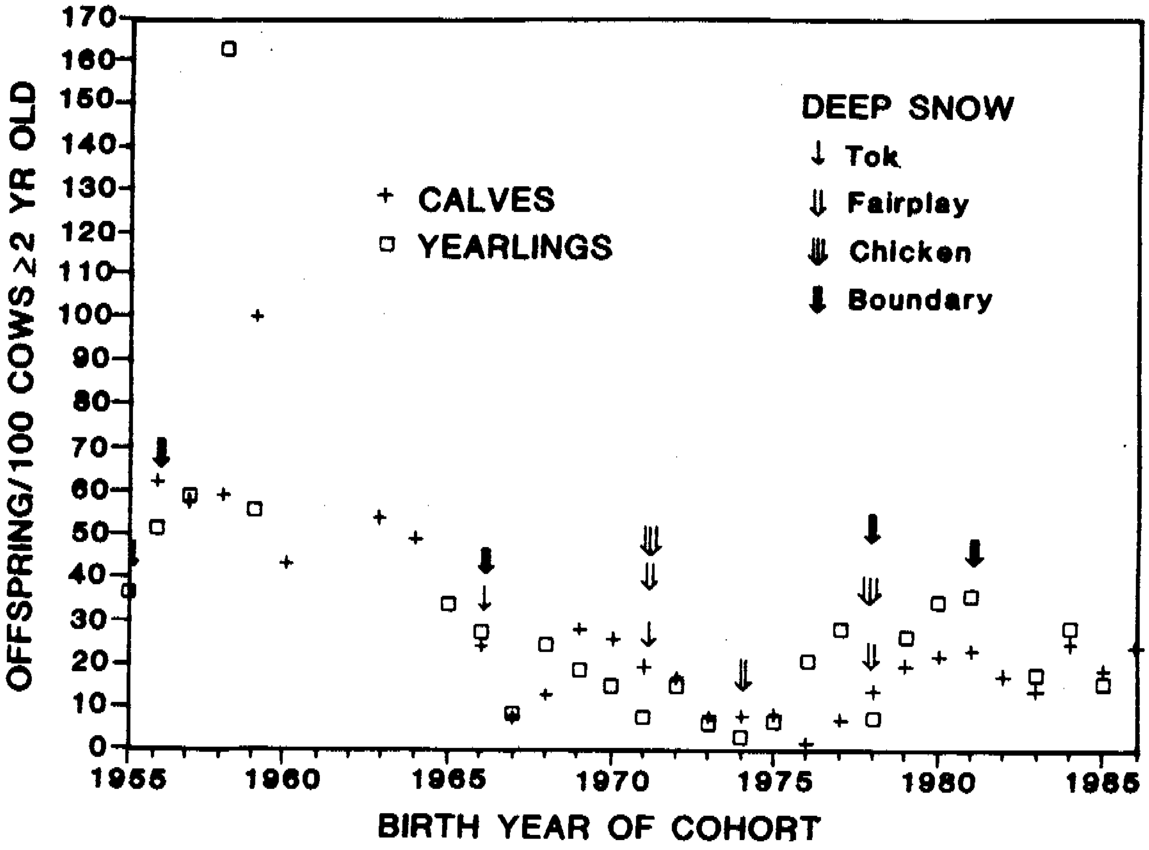

Fig. 13. The relative abundance of cohorts at 6 and 18 months of age in relationship to winters of deep snow at 4 snow measurement stations in or adjacent to the experimental area of Subunit 20E, Alaska, 1955-86. Arrows indicate winters of deep snow during the calf's 1st year of life.

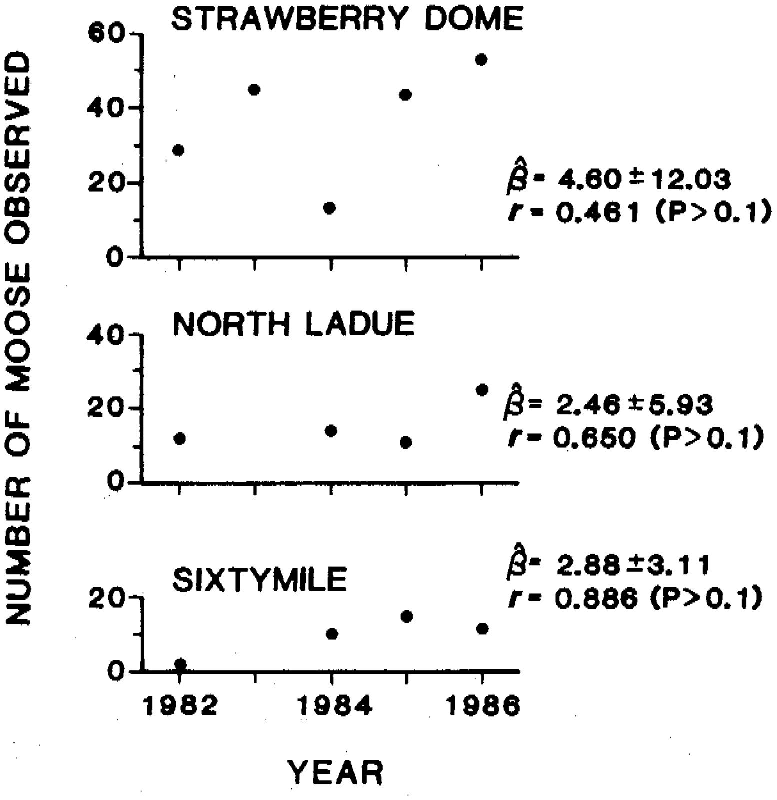

Fig. 14. Trends in number of moose observed in 3 aerial survey areas in the 2 control areas of Subunit 20E, Alaska, and adjacent Yukon Territory, Canada, 1982-86. + 90% CI equals the estimated slope of the linear regression line, and r equals the correlation coefficient.

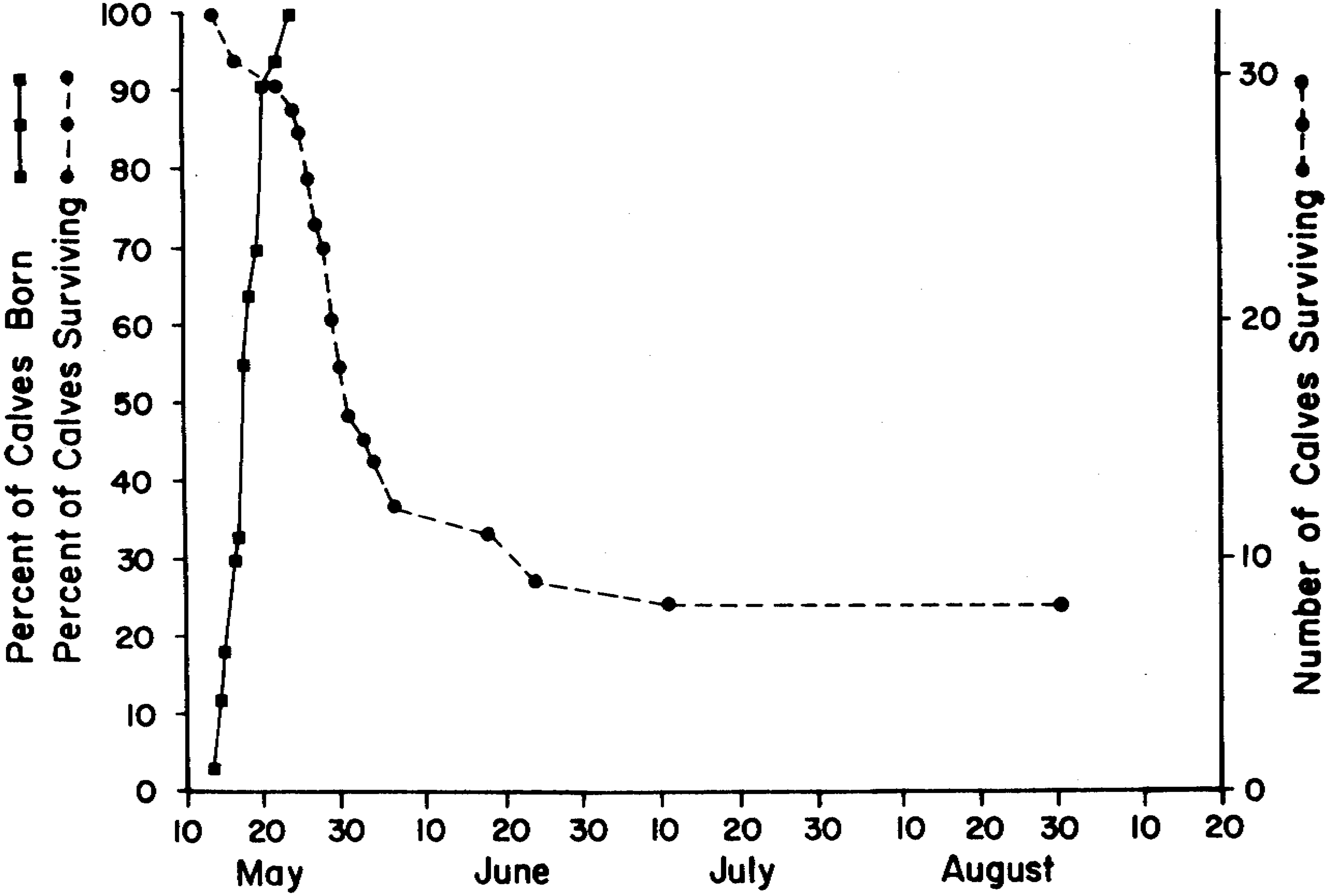

Fig. 15. Timing of birth and death of 33 moose calves radio-collared during May 1984 in and near the Mosquito Flats, Alaska.

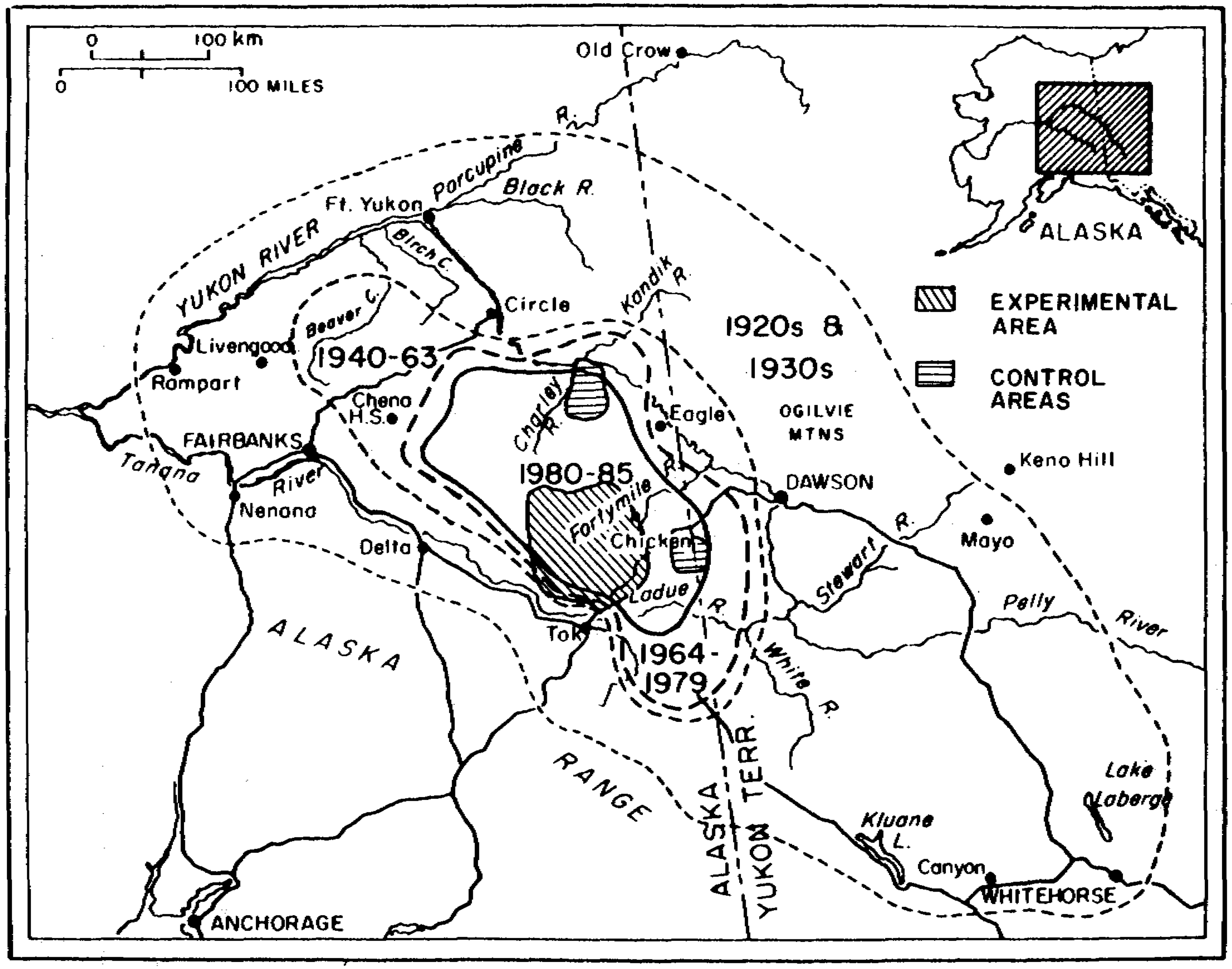

Fig. 16. Range of the Fortymile Caribou Herd, 1920-85, in relation to the experimental and control areas of Subunit 20E, Alaska. Caribou distribution map is from Valkenburg and Davis (1987).

Table 1. Estimated numbers of wolves and respective wolf pack names in a 15,500-km^2 area including the experimental area and adjacent areas of Subunit 20E, Alaska, fall 1981-fall 1986.

Pack No.	Pack name	Before wolf removal	After wolf removal[a]									
			1982		1983		1984		1985		1986	
		fall 1981	spring	fall	spring	fall	spring	fall	spring	fall	spring	fall
1	Mansfield Creek	9	2	10[b]	1	5	3	4	3	6	6	10+
2	Billy Creek	9[d]	2[b]	2[b]	1	8	8[c]	8[c]	2	8	4	13+
3	Mosquito Flats	0	0	0	0	8	4	5	5	7	7	7
4	Mitchels Ranch	15[c]	2	2	2	4	2[b]	5	5[b]	7[b]	6[c]	7[b]
5	Middle Fork	11[d]	2	3	3	5[b]	2	5	4	6	4	5
6	Divide	8	0	0	0	0	0	0	0	0	0	--
7	Joseph Creek	6	2	2	2	6	3[b]	3[b]	2	2	2	4-6
8	Slate Creek	0	0	0	0	6	6	6	4	8	8	--
9	Portage Creek	12[b]	4[b]	4[b]	0	9	8[b]	9[b]	9	12	10	--
10	Gold Creek	5[b]	0	0	0	3	3	8	8[b]	11[c]	8[c]	10[c]
11	Chicken	7	3	5	4	8	4	5	5	4	3	7
12	Ketchumstuk	3	3	5[b]	2	1	1[b]	0	0	2	1	1
13	West Fork	10	2	4	2	3	2	2	2	2	2	--
14	Mount Fairplay	2	2	2	2	2	2	2	0	3	2	2
15	Dennison Fork	9	9	11	1	1	1	3	3	3	1	--
16	Liberty Creek	8	8	8	8	10	6[b]	6[b]	6	7	5	--
	Lone wolves	11	11	6	6	8	8	7	7	9	9	--
	Total wolf numbers	125	52	64	34	87	63	78	65	97	78	--
	Percentage change		-58%	+23%	-47%	+156%	-28%	+24%	-17%	+49%	-20%	
	Density (wolves/1,000 km^2)	8	3	4	2	6	4	5	4	6	5	

Table 1. Continued.

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[a] Department wolf take was 9 during winter 1980-81, 56 during 1981-82, 15 during 1982-83, and 7 during October 1983. The remaining wolf mortality includes some natural mortality and harvest by private trappers and hunters.

[b] One wolf had a functioning radio collar.

[c] Two wolves had functioning radio collars.

[d] Three wolves had functioning radio collars.

Table 2. Necropsy data from 87 wolves killed in and adjacent to the experimental area of Subunit 20E, Alaska, during winters 1980-86.

Pack name	Date	Age (yr)	Sex	Total weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Mansfield Creek	3/16/81	2	F	40	--	87	16	132	639
Mansfield Creek	3/16/81	2	M	43	--	112	33	130	546
Mansfield Creek	2/2/83	4	F	41	145	--	28	129	--
Mansfield Creek	2/19/83	3	M	45	--	--	--	131	--
Mansfield Creek	10/26/83	2	M	40	80	--	28	129	818
Billy Creek	2/10/81	Pup	M	39	--	81	31	128	5,701
Billy Creek	3/25/81	Pup	F	34	--	75	30	130	7,475
Billy Creek	2/28/82	6	F	36	--	46	6	--	1,691
Billy Creek	3/19/83	2	M	50	137	--	30	134	12,325
Billy Creek	2/85	3	M	36	158	--	19	129	157
Billy Creek	3/85	Pup	M	41	188	--	35	133	178
Billy Creek	3/85	Pup	M	43	173	--	35	133	191
Billy Creek	3/85	Pup	F	34	115	--	32	121	129
Billy Creek	3/18/85	2	F	36	125	--	40	127	126
Billy Creek	3/18/85	Pup	F	30	80	--	22	121	545
Mitchels Ranch	3/24/81	Pup	F	37	--	83	33	124	3,203
Mitchels Ranch	3/3/82	Pup	M	39	235	55	43	135	362
Mitchels Ranch	3/28/82	Pup	M	44	167	69	23	127	462
Mitchels Ranch	3/28/82	2	F	40	136	104	18	125	661
Mitchels Ranch	3/28/82	2	F	43	173	81	26	125	718
Mitchels Ranch	3/29/82	1	F	32	135	88	33	--	675
Mitchels Ranch	3/29/82	2	M	50	267	91	42	129	571
Mitchels Ranch	2/16/84	3	F	36	165	--	22	122	4,202
Mitchels Ranch	1/15/86	Pup	F	17	0	--	0	114	7,040

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Total weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Middle Fork	4/22/81	Pup	F	36	--	50	12	136	1,984
Middle Fork	4/22/81	1	M	42	--	79	24	142	2,139
Middle Fork	12/15/81	1	M	48	232	69	48	--	5,993
Middle Fork	1/4/82	3	F	36	219	105	27	128	11,246
Middle Fork	3/4/82	Pup	F	34	44	48	21	112	12,377
Middle Fork	3/4/82	Pup	F	30	44	53	21	113	13,356
Middle Fork	3/5/82	2	M	39	100	40	18	118	10,364
Middle Fork	3/5/82	7	F	39	130	102	29	123	20,338
Middle Fork	3/7/82	2	M	50	177	108	27	128	15,718
Middle Fork	3/9/82	1	Unk	34	108	118	26	122	15,532
Middle Fork	3/12/82	Pup	M	29	71	37	18	119	17,380
Middle Fork	10/26/83	2	M	45	140	--	37	130	9,885
Middle Fork	10/30/83	2	F	48	115	--	15	130	13,410
Middle Fork	12/3/83	2	F	43	160	--	36	124	10,060
Middle Fork	12/3/83	4	M	44	168	--	27	118	10,920
Middle Fork	1/10/84	3	M	34	40	--	3	127	14,435
Middle Fork	1/85	Ad	F	39	185	--	40	--	1,890
Divide	12/3/81	4	M	50	265	132	58	130	1,003
Divide	12/81	Pup	--	34	--	--	--	--	1,591
Joseph Creek	2/19/82	Ad	M	52	70	73	39	--	10,860
Joseph Creek	2/28/82	2	M	52	--	--	27	130	7,136
Portage Creek	1/4/82	3	F	36	219	110	27	128	11,246
Portage Creek	3/5/82	2	M	39	100	43	18	118	10,364
Portage Creek	3/5/82	7	F	36	130	102	29	123	20,338
Portage Creek	3/7/82	2	M	50	177	108	27	128	15,718
Portage Creek	3/9/82	1	Unk	34	108	118	28	122	15,532

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Portage Creek	3/11/82	Pup	F	34	--	48	21	--	12,377
Portage Creek	3/12/82	Pup	M	29	--	37	18	--	17,380
Portage Creek	3/20/82	Pup	F	29	44	53	21	--	13,356
Gold Creek	1/15/86	Pup	M	23	42	--	8	117	5,440
Gold Creek	1/15/86	Pup	F	24	95	--	26	115	3,290
Gold Creek	1/15/86	Pup	F	30	150	--	35	114	3,250
Ketchumstuk	3/7/82	4	F	43	95	80	12	128	5,080
Ketchumstuk	3/31/82	3	M	50	186	99	26	129	4,672
Ketchumstuk	3/31/82	4	F	45	125	140	23	128	5,256
Ketchumstuk	4/1/82	Pup	M	29	0	0	0	120	13,092
Ketchumstuk	4/1/82	Pup	M	37	118	139	25	120	5,339
Ketchumstuk	11/17/85	Ad	M	42	--	--	--	--	6,740
West Fork	2/7/82	Pup	F	39	--	--	21	109	5,193
West Fork	2/7/82	Pup	F	29	43	40	13	108	4,996
West Fork	3/31/82	5-9	M	38	117	49	5	132	17,248
West Fork	4/9/82	3	M	41	130	60	22	131	10,047
West Fork	4/9/82	2	F	37	98	54	10	124	15,588
West Fork	11/5/83	3	M	48	130	--	40	126	6,804
Mount Fairplay	11/20/82	Ad	F	39	--	--	22	--	8,231
Dennison Fork	10/18/82	Pup	M	23	10	13	2	111	457
Dennison Fork	10/29/82	Pup	M	25	41	--	11	113	--
Dennison Fork	11/5/82	1	F	39	51	--	3	124	7,860
Dennison Fork	12/14/82	Pup	F	23	53	--	13	108	5,527
Dennison Fork	12/14/82	Pup	F	26	60	--	24	115	5,315

Table 2. Continued.

Pack name	Date	Age (yr)	Sex	Total weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Dennison Fork	1/83	Pup	F	--	0	--	0	--	8,500
Dennison Fork	1/83	--	--	--	0	--	0	109	7,205
Dennison Fork	1/83	Pup	M	--	0	--	0	117	--
Dennison Fork	3/6/83	2	F	40	272	--	65	119	--
Dennison Fork	3/7/83	Pup	F	32	110	--	23	120	--
Dennison Fork	11/83	4	M	48	110	--	10	131	10,665
Dennison Fork	11/83	4	M	50	80	--	12	132	8,502
Dennison Fork	1/86	Pup	M	19	0	--	0	98	5,010
Dennison Fork	1/86	Pup	F	21	25	--	0	99	4,550
Liberty Creek	3/18/83	1	M	53	175	--	32	135	--
Liberty Creek	3/18/83	1	M	48	210	--	30	137	--
Liberty Creek	12/85	Pup	M	23	12	--	2	106	5,330
Liberty Creek	12/85	Ad	M	39	27	--	1	126	6,620

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[a] Cs-137 concentration in pCi/kg wet muscle.

Table 3. Indicators of productivity in female wolves ≥ 3 years old in Interior Alaska, 1957-85.

	Placental scars			Corpora lutea			Fetuses		
Area and year	No. of wolves	$\bar{x}$	95% CI	No. of wolves	$\bar{x}$	95% CI	No. of wolves	$\bar{x}$	95% CI
Interior Alaska 1957-66 (Rausch 1967)	45	7.1		56	6.8		18	6.6	
Subunit 20A 1976-79 (Gasaway et al. 1983)	7	4.3	±0.9	9	5.4	±0.8	5	4.6	±0.7
Subunit 20E experimental area 1981-85	9	5.0	±1.1	5	4.6	±2.1	2	4.5	±2.2

Table 4. Numbers of radio-collared grizzly bears, bear-days, and adult moose and caribou kills used to calculate grizzly bear predation rates (SE), Subunit 20E, Alaska, September 1985-August 1986.

Observation period	Spring 30 Apr- 10 Jun (42 days)	Summer 9 Jul- 10 Aug (33 days)	Fall 18 Sep- 18 Oct (31 days)	Total
Male bears ≥8 yrs old				
No. bears radio-tracked	6	4	4	7
No. bear-days	157	132	86	375
No. moose ≥1 yr old killed	6	1	2	9
No. caribou ≥1 yr old killed	0	0	0	0
No. bear-days per moose kill	26 (11)	132 (128)	43 (39)	42[a] (14)
Female bears ≥4 yrs old without cub(s) of the year				
No. bears radio-tracked	6	4	10	11
No. bear-days	204	120	237	561
No. moose ≥1 yr old killed	2	0	1	3
No. caribou ≥1 yr old killed	0	1	2	3
No. bear-days per moose kill	102 (59)	--	237 (231)	187[a] (76)
No. bear-days per caribou kill	--	120 (117)	118 (76)	187 (86)
No. bear-days per kill	102 (59)	120 (117)	79 (37)	94 (33)
Totals				
No. bears radio-tracked	12	8	14	18
No. bear-days	361	252	323	936
No. moose ≥1 yr old killed	8	1	3	12
No. ungulates ≥1 yr old killed	8	2	5	15
No. bear-days per moose kill	45 (16)	252 (251)	108 (75)	78 (25)
No. bear-days per ungulate kill	45 (16)	126 (81)	65 (28)	62 (16)

[a] Mean total kill rates were significantly greater ($P < 0.1$, two-tailed Student's *t*-test) for males than females. No other means differed significantly ($P > 0.1$) when tested between sexes or among seasons or totals.

Table 6. Offspring:cow ratios for 1955-86 cohorts at 6 and 18 months of age, as determined from aerial surveys in the experimental area of Subunit 20E, Alaska.

		Age of cohort in months					
		6			18		
Birth year for cohort	No. moose classified	No. cows ≥2 yrs old	Calves: 100 cows ≥2 yrs old	Calves as % of adults ≥2 yrs old	No. cows ≥2 yrs old	Yrlg: 100 cows ≥2 yrs old	Yrlgs as % of adults ≥2 yrs old
1955	--	--	--	--	50	36[a]	23
1956	129	50	62	39	47	51	27
1957	140	47	57	30	48	58	38
1958	129	48	58	38	53	162	76
1959	253	53	100	47	123	55	26
1960	390	123	43	20	--	--	--
1961	--	--	--	--	--	--	--
1962	--	--	--	--	--	--	--
1963[b]	151	--	54[c]	--	--	--	--
1964[b]	271	--	49[c]	--	--	--	--
1965	--	--	--	--	242	34	22
1966	509	242	24	16	284	27[a]	20
1967	498	284	8	6	209	9	5
1968	389	209	13	8	177	25	17
1969	365	177	28	19	191	19	13
1970	386	191	26	19	132	15	11
1971	238	132	20	15	228	8[a]	6
1972	363	228	17	13	169	15	11
1973	269	169	8	6	238	7	5
1974	361	238	8	6	110	4[a]	3
1975	168	110	8	6	84	7	5
1976	124	84	2	2	124	21	15
1977	235	124	7	5	84	29	17
1978	175	84	14	9	50	8[a]	7
1979	73	50	20	17	45	27	14
1980	108	45	22	12	75	35	19
1981	184	75	24	13	110	36[a]	20
1982	255[d]	110	17	10	--	--	--
1983[b]	215[d]	--	13[c]	--	122	18	10
1984	271[d]	122	25	14	145	29	15
1985	342[d]	145	19	10	187	16	9
1986	396[d]	187	25	14	--	--	--

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[a] Relatively deep snow occurred during cohort's 1st winter.

[b] Surveys delayed until January-February; therefore, sex identification was not possible.

[c] Estimated from regression of percentage calves vs. calves:100 cows ≥2 years old in the experimental area.

[d] New survey areas were added within the experimental area to increase sample size for composition.

Table 7. Offspring:cow ratios and percentage calves for 1978-86 cohorts at 6 and 18 months of age, as determined by aerial moose surveys in the Mount Veta-Mosquito Flats moose survey area in Subunit 20E, Alaska, before (1978-81) and after (1982-86) wolf removal. *n* = total number of moose classified.

Birth year for cohort	Age of cohort in months					
	6				18	
	n[a]	No. of cows ≥2 yrs old	Calves: 100 cows ≥2 yrs old	% Calves in total sample	No. of cows ≥2 yrs old	Yearlings: 100 cows ≥2 yrs old[b]
1978	112	58	14	7	46	9
1979	67	46	17	12	24	33
1980	59	24	21	8	72	33
					Yearlings: after wolf removal	
1981[c]		72	26	12	55	18
		Calves: after wolf removal				
1982	119	55	16	8	--	--
1983	70[d]	--	--	9	61	20
1984	119	61	13	7	78	10
1985	160	78	21	10	91	26
1986	203	91	26	12		

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

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

[c] Data from 1981 moose population estimate in experimental area west of the Taylor Highway (Fig. 1).

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

Table 8. Offspring:cow ratios for 1981-86 cohorts at 6 and 18 months of age, as determined from aerial surveys in 3 control areas in Subunit 20E, Alaska, and the adjacent Yukon Territory. *n* equals the number of moose classified.

			Age of cohort in months					
			6			18		
Birth year for cohort	*n*	Density (moose/km^2)	No. of cows ≥2 yrs old	Calves: 100 cows ≥2 yrs old	Calves as % of adults ≥2 yrs old	No. of cows ≥2 yrs old	Yearlings: 100 cows ≥2 yrs old[b]	Yearlings as % of adults ≥2 yrs old
1981	--	--	--	--	--	18	33	22
1982	43	0.10	18	39	26	20[a]	30	19
1983	42[a]	--	20[a]	20	12	16	0	0
1984	37	0.09	16	12	6	30	20	11
1985	69	0.17	30	23	12	32	50	25
1986	90	0.22	32	31	16	--	--	--

[a] Only a portion of 1 of 3 control areas was surveyed because of shallow snow.

[b] Numbers of yearling males are doubled to estimate total yearlings.

Table 9. Cause of death, age, percentage fat in marrow, and sex ratio of yearling and adult moose found dead during 1981 through October 1986 in the experimental area and in the adjacent portion of Subunit 20D, Alaska. All carcasses were investigated from the ground.

			Age (yrs)				Percentage fat in marrow				Sex ratio[a]
Period	Cause of death	n	$\bar{x}$	SD	n	Range	$\bar{x}$	SD	n	Range	n bulls:n cows
May-Oct	Wolves	7	12	6	7	1-17	47	36	6	8-89[b]	1:5
	Grizzly bear	15	10	5	15	3-19	66	20	16	22-94[c]	4:9
	Probably grizzly bear or wolves	2	8	--	2	6-10	89	--	1	--	1:1
	Probably grizzly bear	2	15	--	2	12-18	92	--	1	--	--
	Antler wounds during rut	2	12	--	2	11-12	--	--	--	--	2:0
	Shot	1	15	--	1	--	78	--	1	--	--
Nov-Apr	Wolves	12	13	4	12	3-17	68	31	12	7-93	4:7
	Probably wolves	1	--	--	--	--	67	--	1	--	--
	Drowned	1	2	--	1	--	--	--	--	--	1:0
Year-round	Predation	34	--	--	--	--	--	--	--	--	9:21
	Probably predators	5	--	--	--	--	--	--	--	--	1:1
	All causes	43	--	--	--	--	--	--	--	--	13:22

[a] Five dead radio-collared cow moose and 1 radio-collared bull moose were omitted from the sample to eliminate bias from having a sex ratio among radio-collared animals different from that of the moose population.

[b] Yearling had 28% fat, which is in the expected range for June (Fong 1981).

[c] Radio-collared cow with 50% fat in marrow had a wound on her back ≥2 weeks before her death. The wound likely resulted from an attack by a grizzly bear.

Table 10. Moose, caribou, wolf, and grizzly bear density in the experimental area (9,700 km^2) before (1981) and after (1984-85) wolf removal, Subunit 20E, Alaska.

	Density in animals/1,000 km^2				
		Caribou[b]			
Period	Moose[a]	Min	Max	Wolf[c]	Grizzly bear[d]
Before wolf removal, fall 1981	86	20	770	8	16
After wolf removal, fall 1984	86	20	1,330	5	16
Fall 1985	86	20	1,440	6	16

[a] Moose density was determined in the experimental area west of the Taylor Highway during fall 1981 and assumed stable.

[b] Caribou density was estimated by assuming a minimum of 200 animals were present at all times and a maximum of 7,500, 13,000, and 14,000 were present during fall 1981, 1984, and 1985, respectively (Valkenburg and Davis 1987).

[c] Wolf density was calculated for the total area (15,500 km^2) occupied by wolf packs in Fig. 3.

[d] Approximate density of grizzly bears was estimated from numbers observed in the grizzly bear study area.

Table 11. Estimated ratio of prey per predator in the experimental area before (1981) and after (1984-85) wolf removal, Subunit 20E, Alaska. Ratios were calculated from density estimates in Table 10.

Period	Moose: wolf	Moose: grizzly bear	Moose:wolf + grizzly bear	Moose + min. caribou:wolf	Moose + max. caribou:wolf	Moose + min. caribou:wolf + grizzly bear	Moose + max. caribou:wolf + grizzly bear
Before wolf removal, fall 1981	11	5	4	13	110	4	36
After wolf removal, fall 1984	17	5	4	21	280	5	67
Fall 1985	14	5	4	18	250	5	69

Table 12. Morphometric measurements from adult female Alaskan moose populations[a] during late winter/early spring season, 1969-86.

Population	Total length (cm)		
	x̄	SD	n
GMU[b] 15, 1977	272	26	13
GMU 1, 1978	276	14	4
GMU 20, 1971	276	15	8
GMU 15 (inside MRC[c])	283	21	40
GMU 15, 1970	285	20	55
GMU 15 (outside MRC)	286	11	51
GMU 15, 1975	286	11	23
GMU 1, 1982	286	17	16
GMU 5, 1978	288	11	32
GMU 13, 1981	289	15	8
GMU 13, 1979	290	13	12
GMU 22, 1981	290	19	27
GMU 13, 1977	292	16	25
GMU 15, 1971	292	13	45
GMU 13, 1975	296	10	53
GMU 6, 1974	302	9	25
GMU 9, 1977	302	7	54
GMU 20A, 1975-79	309	9	45
GMU 20E, 1984-86	314	14	34
GMU 13, 1980	315	16	26
Mean of means	291	--	20

[a] All data taken from Franzmann and Schwartz (1983), except GMU 20A, 1975-79 (W. Gasaway, unpubl. data); GMU 1, 1982 (Boertje and Young 1982); and GMU 20E, 1984-86 (this study).

[b] Game Management Unit.

[c] Moose Research Center.

Table 13. A physiological condition indicator from blood (packed cell volume, PCV) for Alaskan moose populations[a] during late winter/early spring season, 1969-86.

	% PCV in blood		
Population[a]	$\bar{x}$	SD	n
GMU[b] 14, 1974	35.8	10.2	21
GMU 15, 1977	36.5	4.4	12
GMU 1, 1978	36.6	6.1	14
GMU 20A, 1979	37.2	4.8	18
GMU 9, 1977	39.0	5.4	56
GMU 5, 1978	40.4	3.4	36
GMU 1, 1982	40.8	5.9	16
GMU 13, 1979	40.9	3.6	10
GMU 15 (inside MRC[c])	41.0	5.0	37
GMU 20E, 1984-86	41.1	4.9	36
GMU 15 (outside MRC)	41.8	5.2	38
GMU 22, 1981	42.6	4.0	25
GMU 13, 1980	43.0	5.2	23
GMU 13, 1981	43.8	4.3	9
GMU 15, 1975	46.4	3.0	25
GMU 13, 1975	49.2	3.8	55
GMU 6, 1974	53.5	3.8	32
Mean of means	41.7	--	17

[a] All population parameters are from Franzmann and Schwartz (1983), except GMU 20A, 1975-79 (W. Gasaway, unpubl. data); GMU 1, 1982 (Boertje and Young 1982); and GMU 20E, 1984-86 (this study).

[b] Game Management Unit.

[c] Moose Research Center.

Appendix A. Moose per hour seen during aerial surveys in 5 portions of the experimental area. Values for each area have been smoothed using moving-3 point median polish. These values were used to estimate moose population trend from 1966 through 1986. Underlined values are extrapolations within trend areas where data were missing. Composite trend index is the median of the 5 annual values.

Year	Ketchumstuk	Taylor Mountain	Sixtymile Butte	Mt. Fairplay	Upper West Fork	Composite trend index
1966	109	165	150	49	75	109
1967	87	102	140	49	69	87
1968	57	93	130	38	63	63
1969	57	83	120	38	57	57
1970	58	83	110	27	57	58
1971	63	44	98	27	55	55
1972	69	43	74	15	31	43
1973	69	30	49	15	29	30
1974	88	30	36	19	25	30
1975	55	24	28	19	21	24
1976	25	6	28	19	19	19
1977	22	6	28	22	14	22
1978	22	6	28	21	13	21
1979	22	6	28	19	10	19
1980	25	6	28	18	8	18
1981	--	--	--	--	--	--
1982	25	6	28	15	8	15
1983	--	--	--	--	--	--
1984	31	6	29	15	8	15
1985	31	6	29	21	8	21
1986	34	6	29	22	8	22

Appendix B. Sex, age, cause of death, and percentage fat in long bone marrow of moose found dead in the experimental area and in the adjacent portion of Subunit 20D, Alaska, 1981-86.

Date of death	Investigated from ground (G) or air (A)	Sex	Age (yrs)	Cause of death	Percentage fat in marrow	Location
19 Feb 1981	G	M	12	Wolf	7	Mansfield Creek, 20D
20 Feb 1981	G	M	13[a]	Wolf	16	Fortymile River
Mar 1981	G	M	14	Wolf	35	Billy Creek, 20D
8 Mar 1981	G	F	12	Wolf	86	Mosquito Flats
10 Mar 1981	G	M	14	Wolf	93	Mosquito Flats
13 Mar 1981	G	F	17	Wolf	90	Mosquito Flats
16 Feb 1983	G	--	15	Wolf	87	Mosquito Flats
16 Feb 1983	G	F	17	Wolf	82	Mosquito Flats
10 Mar 1983	G	F	14	Wolf	85	Billy Creek, 20D
24 Mar 1983	G	F	11	Wolf	93	Billy Creek, 20D
Mar-Apr 1984	G	M	2	Drowned	--	Mosquito Flats
15 May 1984	G	M	6	Probably wolf or grizzly bear	89	West Fork
25 May 1984	G	F	10[a]	Wolves wounded/ grizzly bear killed	82	Mosquito Fork
21 May 1984	G	F	5	Grizzly bear	69	Mosquito Flats
28 May 1984	G	F	10[a]	Wolf	--	Mosquito Flats
16 Jun 1984	G	M	1	Wolf	28	Mosquito Flats
17 Jun 1984	G	F	14	Wolf	74	Mosquito Flats
Oct 1984	G	F	12	Probably grizzly bear	92	Ketchumstuk Creek
13 Mar 1985	A	--	Ad	Probably wolf	--	Ketchumstuk Creek
13 Mar 1985	A	--	Ad	Probably wolf	--	Ketchumstuk Creek
13 Mar 1985	A	--	Ad	Probably wolf	--	Sixtymile Butte
15 Mar 1985	A	--	--	Probably wolf	--	Mosquito Fork
29 Mar 1985	A	M	2-3[b]	Probably wolf	--	Joseph
2 May 1985	G	F	10[a]	Probably wolf or grizzly bear	--	Telegraph Creek
30 May 1985	A	--	Yrlg/ad	Probably grizzly bear	--	Ketchumstuk Creek
10 Jun 1985	G	F	13	Wolf	89	Mosquito Flats

Appendix B. Continued.

Date of death	Investigated from ground (G) or air (A)	Sex	Age (yrs)	Cause of death	Percentage fat in marrow	Location
10 Jun 1985	G	F	18	Probably grizzly bear	--	Mosquito Flats
18 Sep 1985	G	F	19	Grizzly bear	73	Mosquito Flats
1 Oct 1985	G	M	12	Fight with bull moose	--	Fish Creek
3 Oct 1985	G	M	9	Grizzly bear	94	Mosquito Flats
10 Oct 1985	G	M	11	Fight with bull moose	--	Dennison Fork
11 Oct 1985	G	M	13	Grizzly bear	76	Mosquito Flats
11 Oct 1985	G	F	13	Grizzly bear	50	Mosquito Flats
14 Jan 1986	G	--	Yrlg/ad	Probably wolf	67	Ketchumstuk Creek
17 Jan 1986	A	--	Ad	Wolf	--	West Fork
17 Jan 1986	A	--	--	Unknown, eaten by wolf	--	West Fork
22 Jan 1986	A	--	--	Wolf	--	Copper Creek
4 Mar 1986	G	F	10	Wolf	59	Gold Creek
16 Mar 1986	G	F	4	Wolf	78	Ketchumstuk Creek
9 May 1986	G	F	13	Grizzly bear	89	West Fork
9 May 1986	G	F	17	Wolf	10	Copper Creek
19 May 1986	G	F	9	Grizzly bear	72	Mosquito Flats
23 May 1986	G	F	17	Wolf	8	Cedar Creek
29 May 1986	G	F	3	Grizzly bear	69	West Fork
1 Jun 1986	G	M	10	Grizzly bear	63	Mosquito Fork
4 Jun 1986	G	F	14	Grizzly bear	22	Joseph Creek
5 Jun 1986	G	F	4	Grizzly bear	44	Little Whiteman Creek
9 Jun 1986	G	F	9	Grizzly bear	63	Telegraph Creek
10 Jun 1986	G	F	Ad	Grizzly bear	34	Ketchumstuk Creek
26 Jul 1986	G	M	17	Grizzly bear	91	Gold Creek
27 Jul 1986	G	F	15	Wolf	75	Mosquito Flats
8 Oct 1986	G	M	7	Grizzly bear	69	Mosquito Fork
9 Oct 1986	G	F	15	Shot	78	Mosquito Flats

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[a] Age estimated by wear.

[b] Age estimated by antler size.