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FACTORS LIMITING MOOSE POPULATION GROWTH IN GAME MANAGEMENT UNIT 20E

By

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SUMMARY

Preliminary data have been presented to test 2 hypotheses: (1) food limits moose (Alces alces) population growth, and (2) predation limits moose population growth in Subunit 20E. Data presented earlier (Boertje et al. 1985) support rejection of the food-limiting hypothesis. A definitive test of the predation-limiting hypothesis has not yet been possible because (1) the program to reduce wolf (Canis lupus) predation has been discontinued, and (2) programs to reduce grizzly bear (Ursus arctos) predation adequate to conclusively test the hypothesis have not yet been effective. Data collected to date, however, strongly support acceptance of the hypothesis that predation by grizzly bears and wolves is limiting moose population growth in Subunit 20E.

Moose densities in Subunit 20E have declined drastically during the last 2 decades to 0.08 moose/km^2 (0.2 moose/mi^2) in 1981--the lowest density recorded using the stratified, random sampling technique. No increase in this low-density moose population is predicted given the current management regime.

During the early 1980's, wolves in Subunit 20E occurred at low densities both before and after wolf removal. Relatively high wolf densities existed in the experimental area during the 1970's, as well as in Subunit 20A during the early and mid-1970's (Gasaway et al. 1983), and on the Kenai Peninsula during the years 1976-81 (Peterson et al. 1984). However, wolves in the experimental area in the 1980's were, and still are, abundant relative to the number of moose present (10-15 moose:wolf).

Grizzly bears are abundant in the experimental area. We tentatively estimate grizzly bear density in the experimental area

at 1 grizzly bear/50 km^2 (1 grizzly/19 mi^2), based on observed numbers of bears and results of other grizzly bear studies. Grizzly bears may be 3-4 times more abundant than wolves. Data suggest a ratio of 4 moose:grizzly bear in Subunit 20E. Although harvest of grizzlies has increased substantially since 1980, harvest rates averaging approximately 5% (range = 2%-7%) in the experimental area during the years 1981-85 are probably inadequate to measurably reduce numbers of grizzly bears.

Predation has been 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 by 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. If wolf numbers had not been reduced, wolves might have killed more than 15% of the calves.

Natural mortality of radio-collared adult moose averaged 11% annually after the fall wolf population had been reduced by 30-40%; of the 5 radio-collared moose that died, 2 were killed by grizzly bears, 1 by wolves, and 2 from unknown causes. The latter 2 were scavenged by grizzly bears and may have been killed by them. Radio-collared grizzly bears killed adult moose at a mean rate of 1 moose:106 bear-days during fall (18 Sep-18 Oct) 1985. At this kill rate, grizzly bears would have a large impact on the low-density moose population. Currently, 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 are likely both beneficial and detrimental to moose depending on when and how long caribou are present in the predators' home ranges. When both caribou and moose are present in a wolf pack's territory, wolves often kill caribou rather than adult moose; therefore, the moose population benefits. However, a short-term abundance of caribou may allow wolves and possibly grizzly bears to maintain higher densities than if only moose occurred. When caribou leave the predators' home ranges, the higher predator population preys primarily on moose, and predators are abundant relative to the number of moose in the experimental area (3 moose:wolf and grizzly bear during fall 1984). Based on this study and on the effects predators had on other moose populations where the number of moose per predator was low, we conclude predation is the major force suppressing growth of the moose population in Subunit 20E when caribou are absent.

If the wolf population is to increase in Subunit 20E, prey populations must increase. Although 78 necropsied wolves had consumed about equal proportions of moose and caribou biomass, moose are the only widely distributed resident prey in Subunit 20E, and therefore the only dependable food source when caribou leave the wolf pack territories. However, the low-density moose population cannot support many wolves. Radio-collared wolves did not abandon their territories to maintain contact with migrating caribou.

A moderate increase in the number of moose in Subunit 20E will require lessening of grizzly bear and wolf predation. The wolf reduction experiment in 1982 demonstrated that reducing only wolf predation will not increase calf survival enough to allow numbers of moose to increase at a moderate rate. Simultaneous reductions in the wolf and grizzly bear populations would likely allow the moose population to increase.

Currently, the moose population has no surplus for man to harvest or for population growth. Since 1976, most moose production in Subunit 20E has been utilized by grizzlies and wolves, not by man, and current regulations and policies make changes in this situation unlikely.

Key words: Alaska, calf mortality, grizzly bears, moose, 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 decline or remain at low densities throughout much of interior Alaska. 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, effective management of these ungulates and carnivores is important to Alaskans statewide for sustained aesthetic appeal, hunting, trapping, and sustained revenues from tourists and out-of-state hunters. Indeed, this complex of ungulates and carnivores is synonymous with the concept of Alaskan wilderness. The lack of effective management has far-reaching detrimental impacts on the livelihoods of many Alaskans.

To effectively manage moose, caribou, and the carnivores dependent on them for food, factors limiting ungulate and carnivore population growth must occasionally be altered. Such changes provide 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 and to what extent populations are limited. Knowledge gained from intensive 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.

Subunit 20E in eastcentral Alaska is one of the areas in interior Alaska where moose, caribou, and large carnivores declined to low densities during the 1970's. We report here on causes of the declines in numbers of moose and wolves. We also attempt to test hypotheses of factors currently limiting moose. Moose in Subunit 20E prospered during and shortly after a predator poisoning program during the years 1947-59 (Davis et al. 1978*a*). Poisoning was aimed at reducing wolf predation; however, both black (*Ursus americanus*) and grizzly bears (*Ursus arctos*) were also killed by the poison. Moose had declined to a low density by 1981. The early part of this decline in moose numbers in the mid-1960's corresponded to a period of high wolf density (Davis et al. 1978*a*), but wolf abundance declined during 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 630 ± 140 (90% confidence interval) moose occupied 7,500 km^2 (2,900 mi^2) of moose habitat in the southwest quarter of Subunit 20E during fall 1981. The mean moose density was 0.08 moose/km^2 (0.2 moose/mi^2), which is the lowest of 11 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 (GMU 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).

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 along the highway. Antlerless moose seasons were discontinued after 1974, and moose hunting seasons were closed from 1977 through 1981. Yet, the moose population continued to decline in all portions of the subunit, including previously unhunted areas. Harvests during the years 1970-76 ranged from approximately 70-100 moose (probably 1%-2% of the population), and reported bull harvests since 1981 (10-day seasons) were 17 in 1982, 31 in 1983, 29 in 1984, and 47 in 1985 (less than 3% of the population).

Several winters of deep snowfall have adversely affected moose in portions of Interior Alaska (Bishop and Rausch, 1974, Gasaway et al. 1983), but we have no evidence that snow depth alone adversely affected moose survival and abundance in Subunit 20E. March snow depths were only 53-71 cm (21-28 in) in the experimental area during the relatively deep snowfall winters of 1965-66, 1966-67, 1970-71, and 1978-79 (U.S. Dep. Agric., Soil Conserv. Serv., Anchorage). These snow depths do not exceed 80 cm (31 in), the snow depth considered critical for calf moose survival in Interior Alaska (Coady, 1974). If snow depths had adversely affected calf survival, we would expect to see declines in yearling recruitment, as observed by Bishop and Rausch (1974) following deep snowfalls. However, yearling recruitment was low throughout the period 1965-85, even in years of low snowfall. Therefore, we conclude that snow depth alone was probably not a major factor precipitating the decline in moose numbers in Subunit 20E.

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 the Board of Game has not authorized regulations that would significantly reduce 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 of factors limiting moose population growth are outlined below. Some aspects of these tests were reported in a previous progress report (Boertje et al. 1985).

H_1: PREDATION LIMITS MOOSE POPULATION GROWTH.

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

1. Assess effects of the wolf removal programs (1980-84) 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. Accept 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 1986-89.

a. Accept H_1 if moose survival increases and population grows.

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

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

a. Accept H_1 if moose survival increases and population grows.

b. Reject 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. Accept H_2 if there is very high browse utilization.

b. Reject 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. Reject 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. Accept H_2 if moose are in poor condition during a winter of normal weather.

b. Reject 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 (<80% pregnancy rate for females >2 years old and <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 (<15%) for adult moose.

   b. Supports rejection of H_2 if average fat content is >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 rapidly grow; 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 (9,800 km^2, [3,800 mi^2]) where research and predator removal are focused and 3 control areas (upper North Fork of the Ladue River, upper Sixtymile 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 vegetation consists primarily of dwarf birch (B. nana) and willow, interspersed with willow-lined drainages, and is used extensively by moose from September through November. Most of the upper Sixtymile River control area and a portion of the North Fork Ladue control area are in subalpine habitat. 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 Mount Fairplay, and in the North Fork Ladue and Washington Creek control areas. All 3 areas are now prime moose habitat with willow and birch dominating regrowth.

Elevations in most of the experimental area range from 600 m (2,000 ft) in valley bottoms to treeline at the crest of many of the rolling hills (1,000 m [3,300 ft]). Elevations of 6 mountain peaks in the experimental area range from 1,500-1,750 m (5,000-5,800 ft). The upper Sixtymile and North Fork Ladue control areas have elevations ranging from 600-1,650 m (2,000-5,400 ft), and the Washington Creek control area ranges in elevation from 300-650 m (1,000-2,100 ft) with nearby mountain peaks of 1,600-1,700 m (5,200-5,600 ft).

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 50 cm (20 in), and snow usually remains loosely packed except where windblown at high altitudes. Average total snow depth in March during 1970-85 in an open black spruce forest near Mount Fairplay (Fig. 1) was 44 cm (17 in) (U.S. Dep. Agric., Soil Conserv. Serv., Anchorage).

Large carnivores inhabiting the study area include wolves, black bears, and grizzly bears. Their prey include moose, caribou, beaver (Castor canadensis), and snowshoe hare (Lepus americanus). Dall sheep (Ovis dalli) (approximately 100-150) are restricted to the northwest border of the experimental area. Some Fortymile Herd caribou (numbering approximately 14,000 animals in summer 1984) spend a portion of most years (usually June, fall, and winter) in the experimental and control areas (Davis et al. 1978b; Shryer 1983; Valkenburg and Davis 1985; Valkenburg and Davis, in press). Seasonal distribution of caribou fluctuates greatly among years, but in most years caribou spend more time in the experimental area than in control areas. 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 wolves estimated from tracks thought to represent different individuals. In addition, we added 10% 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.

Aerial wolf surveys in the experimental area were conducted during winters 1981-82 through 1984-85; approximately 80, 70, 170, and 30 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 flight hours for wolf removal, moose surveys, and radio-tracking moose and grizzly bears were included. Information was also obtained from local trappers and pilots each winter.

Removal of Wolves:

During winters 1980-81 through 1982-83 and November 1983, ADF&G removed wolves from the experimental area. ADF&G wolf removal during winter 1980-81 was restricted to Subunit 20D and involved removing wolves from 2 packs (Mansfield Creek and Divide 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:

Wolf food habits in the experimental area were based on observations of the carcasses of large prey during monitoring of radio-marked and unmarked packs, on the stomach and intestinal contents of 78 wolves killed, and on radiocesium (C^{137}) levels (Holleman and Stephenson 1981) of the 78 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, we radio-collared 3 wolves in 2 separate packs to estimate predation rates and to locate carcasses of prey. 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.

Age Structure, Productivity, and Nutritional Condition:

Examination of 78 wolves killed in the experimental area during winters 1980-81 through 1984-85 provided data on wolf age, sex, reproduction, and nutritional condition. 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. Reproduction was assessed by counting placental scars and fetuses in uteri, and counting corpora lutea in sectioned ovaries. 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 and near rivers; especially while radio-collaring other bears and checking bait stations, and (3) searching for uncollared mates while radio-tracking collared bears.

We used both visual and radio-snare bait stations baited with train-killed moose carcasses and/or assorted scrap meat. Visual bait stations were made by dropping 100-150 kg (220-330 lb) 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 (55-220 lb) 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 (9-12 ft) in length, 1 m (3 ft) in width, and at least 1.3 m (4 ft) 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 (6 ft) 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 (6-8 in) from the ground. Inside dimensions of corral opening(s) were 0.6-0.7 m (24-28 in). The radio snare was attached to a tree at the corral opening with 23 kg-test (50 lb-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, 1.2 in x 2.4 in) (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 radiolocate 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 different grizzly bears were immobilized and radio-collared during 1985 in the experimental area, 18 were collared between 4 May-18 June and 2 between 9-18 October. One radio-collared bear died soon after collaring, probably because of hyperthermia.

We darted all bears from a Hughes 500 helicopter and used Cap-Chur darting equipment. Ideally, females and small males were immobilized with 1 5-cc dart containing 4 mg M99 and 5 mg Acepromazine; during spring large males were immobilized with 1 7-cc dart containing either 7 mg M99 or 6 mg M99 and 5 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 7.5 mg Acepromazine. The antagonist, M50-50, was administered in equal volume to M99, and, when Carfentanil was the immobilizing drug, 500 mg Naloxone (10 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 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.

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. Three types of collars were used: (1) break-away configuration 5A grizzly bear collars with 30 months of operational life for bears estimated to be <6 years old, (2) configuration 6B grizzly bear collars with 36 months of operational life for bears estimated to be ≥6 years old, and (3) configuration 5B wolf collars with 24 months of operational life for bears ≥6 years old. Wolf collars were constructed of 1 layer of black fiberglass impregnated with urethane over a dacron layer impregnated with butyl. Pulse rate on the grizzly bear collars changed from approximately 60-65 beats/min to 40-45 beats/min when movement ceased for 6 hours.

Estimating Predation Rate:

Fall predation rates (number of kills/number of bear-days) were documented by radio-tracking 11-13 grizzly bears 28 of 31 days between 18 September and 18 October. Days that bears spent in or near established dens (i.e., ≤200 m from dens) were excluded from the calculation of predation rates. To help verify cause of death, we skinned all carcasses, usually within 24 hours of death.

Between 18 September and 7 October, we used data from 13 different grizzly bears (3 males and 10 females) to calculate predation rates. On 8 October, 1 male shed its collar, and on 10 October 1 female's radio apparently failed; therefore, sample size declined to 11 bears. Data from 6 of the 19 radio-collared bears were not used to calculate predation rates for the following reasons: (1) 2 young males moved out of the study area prior to 18 September and could not be located, (2) 1 female was shot on 15 September, (3) 1 adult male ripped its collar off prior to 18 September, and (4) 2 males were initially radio-collared between 9-18 October and their fall behavior may have been affected by immobilization.

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 through 21 March 1984 to provide data on physical status, population age structure, pregnancy rates, birth rates, frequency of twinning, movements, and adult mortality. Pulse rate of radio collars doubled (150 beats/min) when movement ceased for 4 hours. 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.

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 rate 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 between 15 and 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 the months of June 1984-November 1985 to provide data on movements and adult 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 collared between 16 and 24 May 1984 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. The capture crew also fired gunshots in a few instances to scare the cow. We wore sterilized latex gloves and held calves away from our clothing (Ballard et al. 1979). Disturbance to the cow and calf commonly 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 surviving radio-collared calves remained bonded with cows and were used to estimate causes 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 hrs (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 sewn with cotton thread were used exclusively. Transmitters were rinsed in alcohol to remove scent before they were installed 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 Timing and Causes of Calf Moose Mortality:

To determine timing of calf mortality, we visually located radio-collared calves daily (on all but 3 days), from the 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, 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, death sites, and signs of predators were recorded (Ballard et al. 1979). We necropsied calves that were sufficiently intact.

Estimating Moose Population Composition and Trend:

Trend count and contour count surveys were flown to determine composition of the moose population. The 2 counts differ in that trend counts have specific boundaries and a prescribed search intensity (4-6 min/mi^2 of moose habitat). Contour counts are flown in roughly similar areas from year to year and with less intensive search patterns than trend counts.

Trend counts were flown in 4 areas beginning in 1982; 3 count areas were in control areas (the 1969 Washington Creek burn, the upper Sixtymile River, and the 1969 North Ladue River burn) and 1 was immediately north of Mount Fairplay (the 1966 Chicken burn) within the experimental area (Fig. 1). Only a portion of the Washington Creek trend count area was flown in 1983 because of a scarcity of snow in Subunit 20E. Sizes of trend count areas are 108-161 km^2 (42-62 mi^2).

Contour counts have been flown annually since 1966 in the experimental area. Primary contour count areas have included Mount Veta, Mosquito Flats, Sixtymile Butte, and Mount Fairplay. Some areas were flown for several years and then abandoned (e.g., Taylor Mountain 1969-76) or expanded (e.g., Mount Fairplay) because of a scarcity of moose. New contour surveys (e.g., upper Mosquito Fork and Prindle Volcano) were also developed during recent years in attempts to observe moose over a wider area for comparisons of calf survival among areas.

RESULTS AND DISCUSSION

Testing the Predator-limiting Hypothesis

Wolf Population Status:

Population Size and Pack Territories: Distribution of packs in the experimental area is shown in Figs. 2-5. Vacant areas between pack territories are largely the result of limited observations, which caused the underestimation of territory sizes. Radio-collared wolves (Table 1) were not observed to abandon territories to maintain contact with migrating caribou.

The number of wolves present during fall has not increased significantly since the wolf reduction program began, despite a declining percentage of wolves harvested (Table 1). Failure of the wolf population to rapidly increase after cessation of wolf control resulted from continued harvest and low productivity, which was likely a function of low prey availability (Keith 1983; see Section "Age Structure, Productivity, and Nutritional Condition" in Results and Discussion).

Winter Food Habits: The average diet of wolves in the experimental area during winter (Nov-Apr) comprised approximately equal proportions of moose and caribou biomass. Of 78 wolves trapped or shot between 1981 and 1985, 25 of the stomachs contained caribou, 24 contained moose, 2 contained snowshoe hares, 24 were empty, and 3 were scavenged or not examined. Radiocesium levels of the necropsied wolves (Table 2) indicate that 4 packs (Mansfield Creek, Billy Creek, Mitchels Ranch, and Divide) of 11 studied relied more heavily on moose than caribou during winter; 3 packs (Ketchumstuk, Mount Fairplay, Dennison Fork) consumed about equal proportions of moose and caribou; and 4 packs (Middle Fork, Joseph, Portage, West Fork) relied more heavily on caribou than moose.

Both moose and caribou were common among confirmed or suspected wolf kills made during winter (Nov-Apr). Of the 169 carcasses located during the years 1981-85, 56% were moose and 44% 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.

Age Structure, Productivity, and Nutritional Condition: The percentage of pups in the wolf population in Subunit 20E also indicates low productivity that likely results from a scarcity of prey. Pups composed 36% of the harvest of 78 wolves in the experimental area during the years 1981-85 (Table 2), compared with 43% pups during 1959-66 in interior Alaska when prey were abundant (Rausch 1967). Pup percentages of 60%-73% have been reported in exploited wolf populations where prey were abundant (Rausch 1967, 1969; Kelsall 1968; Stephenson and Sexton 1974). Keith (1983) compared percentages of pups in 8 exploited populations and concluded that the percentage of pups is directly correlated to food supplies ($\underline{P} < 0.01$), yet percentage of pups gave little indication of population trend.

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 from the experimental area will be compared in subsequent reports with wolf condition data from areas of high prey densities.

Grizzly Bear Population Status:

Population Size and Home Ranges: The observed grizzly bear density during spring 1985 was 1 bear/118 km^2 (1 bear/45 mi^2). However, this is an underestimate because only a portion of the bears were observed. This density estimate was based on 33 bears known to have been present in a 3,900 km^2 (1,500 mi^2) portion of the experimental area. The 33 grizzlies comprised 20 marked bears, 11 unmarked bears that were observed during 1985 collaring and radio-tracking operations, and 2 bears harvested during the spring prior to collaring operations.

The density of bears in the experimental area was likely over twice the observed density estimate. At this time, we tentatively suggest the density may be roughly 1 grizzly bear/50 km^2 (1 grizzly/19 mi^2). This density is less than 1 grizzly/35-45 km^2 (1 grizzly/14-17 mi^2) estimated elsewhere in Alaska, e.g., the northcentral Alaska Range (Reynolds and Hechtel 1985), the western Brooks Range (Reynolds and Hechtel 1984), and in GMU 13 (Miller and Ballard 1984). It is difficult to observe a high percentage of the grizzly bears present; therefore, density estimates based on observed numbers will be low. For example, Reynolds and Hechtel (1985) believed they accounted for only 67% to 83% of the grizzly bears in their study area after 4 years of attempting to collar all grizzlies. Reynolds and Hechtel (1985) would be expected to have observed a relatively high proportion of the bears in their study area compared with our area because their study area was largely above treeline and bears were therefore more visible.

Annual home ranges and distribution of radio-collared grizzly bears will be discussed in the next progress report.

Harvest: Harvest of grizzly bears has increased in Subunit 20E since 1980. From 1961 through 1980, annual reported grizzly harvests were 0-4 bears, with the exception of 1979, when 6 were harvested. Less restrictive harvest regulations, which began in 1981, resulted in harvests of 10 grizzly bears in 1981, 23 in 1982, 24 in 1983, 22 in 1984 (plus 1 capture mortality), and 12 in 1985 (plus 1 capture mortality). If we assume a density of 1 grizzly/50 km^2 (1 grizzly/19 mi^2) in Subunit 20E, with approximately 26,000 km^2 (10,000 mi^2) of grizzly habitat, the harvest rate averaged 4% (range = 2%-5%) during the years 1981-85. Harvest rates within the 9,800-km^2 (3,800 mi^2) experimental area averaged 5% (range = 2%-7%) during the same period, assuming the same grizzly bear density. Average annual harvest rates of 4%-5% would likely not cause a decline in the grizzly bear population.

Fall Predation Rate and Importance as Scavengers: Radio-collared grizzly bears killed at a minimum mean rate of 1 kill:53 bear-days between 18 September and 18 October 1985. Collared grizzlies made 6 kills in the 318 days they were away from their dens; bears spent 65 additional days at or near dens. Adult moose were killed at a mean rate of 1:106 bear-days. Radio-collared grizzly bears killed 3 adult moose (2 cows, 1 bull), 2 caribou (1 male yearling and 1 male 2-year-old), and 1 black bear. Predation rates by sex and age class of grizzly bears will be calculated in the next progress report when additional data are available. No other studies have examined fall predation rates by grizzly bears; therefore, comparative data are lacking.

The estimated predation rate is a minimal rate because we could not be certain all kills were observed. However, several factors indicate we observed all ungulate kills. For instance,

(1) bears tended to be on or immediately adjacent to, and protective of, carcasses; (2) we visually sighted nondenned bears on 98% of attempts; (3) in all cases, we sighted carcasses within 30 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, except when a single nondenned sow was hidden by fog on 2 consecutive days.

During fall, grizzly bears killed slightly more large animal biomass than they scavenged. During the 318 bear-days, grizzlies killed approximately 1,800 kg (4,000 lb) of prey compared with approximately 1,400 kg (3,000 lb) available from scavenging. Scavenged carcasses included 2 adult bull moose that died from antler wounds and 1 whole hunter-killed adult male caribou. Also, 2 caribou gut piles were scavenged. Animals killed or scavenged were not necessarily completely consumed by the bears.

Grizzly bears and wolves scavenged each others' kills, which influenced the kill 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 more wolves were displaced from each kill. During fall 1985, the reverse scavenging pattern was seen; wolves scavenged all 4 adult moose and 1 of 2 caribou that were killed by grizzly bears. Seasonal scavenging patterns, if they exist, may become apparent when spring and summer observation periods are completed.

Age Structure and Productivity: More complete data on these topics will be presented in next year's report. Ages of 12 radio-collared bears were estimated from sectioned premolars: 2 bears were 4 years old; 2 were 5 years; 4 were 8 years; and 1 each were 10, 11, 13, and 14 years old. Only 2 of 12 radio-collared females were observed with offspring during 1985; 1 with 2 yearlings and 1 with 1 yearling. However, our capture procedures were biased toward capturing breeding females and highly mobile females attracted to bait stations.

Calf Moose Production and Mortality:

Calf production by cow moose in the experimental area was high. 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, and the observed frequency of twin calves (Boertje et al. 1985).

Calf mortality was high between 1966 and 1981 in the experimental area. Calves:100 cows ≥2 years old observed during aerial surveys averaged 16 (SD = 8.1, range = 2-28) for the years 1966-81 (Table 4). If we assume 130 calves:100 cows ≥2 years old were produced annually, calf mortality averaged 88%

(range = 78%-98%) at 6 months of age in 1966-81. Even the lowest mortality estimate (78%) is high when compared with many other Alaskan moose populations (Bishop and Rausch 1974).

A reduction in numbers of wolves 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 5). This survey area was centrally located in an approximately 10,400 km^2 (4,000 mi^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 prereduction ratios (Table 5). Additionally, calf ratios among moose observed in the entire experimental area did not increase compared with either prereduction ratios in the entire experimental area (Table 4) or with ratios in the control areas (Table 6). High calf mortality remained widespread in Subunit 20E after 1981 (Tables 4, 6).

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 change in a constant relationship.

The reduction in wolf abundance, beginning in 1982 (Table 1), may have slightly increased the number of calves surviving, despite no increase in calf:cow ratios (Tables 4, 5, 6). The reduction in wolf abundance should have increased adult cow moose survival and slowed the rate of population decline. This relative increase in the number of cows would result in an absolute increase in the number of calves produced and surviving.

The survival curve for radio-collared calves indicates most mortality occurred shortly after birth (Fig. 6). 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 failed during May 1985. The general shape of the survival curve (Fig. 6) is characteristic of curves or mortality rates reported for other moose populations where predators were abundant (Franzmann et al. 1980, Ballard et al. 1981a, Gasaway et al. 1983).

Predation by grizzly bears was the primary cause of calf mortality after the spring wolf population had been reduced to approximately 40% of the estimated spring prereduction density in the calf study area. Estimated 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, assuming a calf orphaned during September was killed during winter) to wolves, 12% (4 calves) to drowning, and 3% (1 calf) to black bears.

The proportion of radio-collared calves dying from wolf predation during 1984-85 would likely have been greater if wolves had been at their prereduction 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 probable 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 reducing wolf predation without a simultaneous reduction of grizzly bear predation on calves will not result in calf survival that is adequate to replace the dying adults and allow the population to grow at a moderate rate.

Adult Moose Mortality:

An 11% annual natural mortality rate was estimated (Gasaway et al. 1983) for 30 radio-collared cow moose during the 1st 19 months of collar life. However, the estimator may overestimate the actual rate because all mortality of radio-collared adult moose occurred during the months of May through October and the 19-month observation interval included 2 such periods. Bias can be eliminated by using 1 or more year-long observation periods.

Predation was the primary cause of death for adult moose. Of 27 dead moose that we investigated from the ground, 20 were killed by predators, 4 were possibly killed by predators, 2 died from antler wounds, and 1 drowned (Table 7). Of 6 dead moose that were seen only from the air in 1984-85, all were partially eaten by wolves or grizzly bears (Appendix A).

Both grizzly bears and wolves were major predators on adult moose from 1 May through 31 October, whereas wolves were the only predator the remainder of the year (Table 7). 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 used for locating dead moose. We used a variety of methods to locate the moose carcasses listed in Table 7. Methods included 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 7) 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 moose are observed for complete years (12, 24, or 36 mos.). In this progress report, the estimator was biased because 19 months of data were used. The proportion of moose killed by wolves may increase when the 2nd year's data are complete, because only wolves will have preyed on moose during the remaining period (Nov through Apr).

For the purposes of this report we recognize the bias in the estimator and present a preliminary analysis of causes of adult moose mortality. Five of 30 radio-collared cow moose died during 19 months; 2 were killed by grizzly bears, 1 was killed by wolves, and 2 died from unknown causes. The latter 2 were scavenged by grizzly bears and could have been killed by them, but we could not confirm cause of death. Condition of 1 of these cows could not be assessed because fly larvae had completely consumed the marrow contents (Kie 1978). Body condition of the other cow was probably good because the marrow contained 92% fat.

As in other studies of differential vulnerability among adult moose (Gasaway et al. 1983, Peterson et al. 1984), predators selectively killed primarily old-aged moose (Fig. 7). The mean ages of all predator-killed adults $\geq$2 years old (13 years, SD 3.1, n = 19) and predator-killed cows (13 years, SD 3.8, n = 12) were significantly greater (P < 0.001, Student's t-test) than the mean age of a sample of adult cows radio-collared from the living population (8 years, SD 3.5, n = 27; Boertje et al. 1985). These data reaffirm that young and middle-aged adult moose (2-8 years old) have a lower vulnerability to 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 predators, e.g., vulnerable moose, varies with the age structure of the moose population. The population of moose in the experimental area has a proportionately high number of vulnerable adult moose because of its old age structure (Fig. 7); however, on an absolute basis, the moose population provides little food because of its low density.

Few moose died in a severely malnourished state, as indicated by the percentage fat in bone marrow (Table 7). 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 2 of 21 moose found dead had <20% fat in marrow, of which 1 was <10% (Appendix A). Ages of these 2 bull moose were 12 and 13 years. Because few bulls live longer than 13 years (W. Gasaway, P. Karns, and K. Morris, unpubl. data), it can be argued that these 2 moose may have been near the end of their physiological life and hence were having difficulty obtaining adequate forage even though sufficient browse is present on the range. However, we propose an alternative that may apply to these moose.

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. The reasons for malnutrition are what is important 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 a week 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 content 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. On 27 March 1984, R. Boertje radio-collared a cow moose that had recently been attacked by wolves; sufficient flesh had been removed to expose a dorsal portion of the pelvis. The moose recovered and lived at least 2 years. 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 which were not highly vulnerable. Initially, the wolves were only able to wound these moose, but later these same moose became highly vulnerable.

Wounds from predators can cause prey to decline in condition and to increase in vulnerability to future predator attacks. Biologists should recognize that moose in poor condition may be victims of nonlethal predator attacks. Previous wounds are difficult to detect because biologists rarely investigate intact moose carcasses and fresh wounds may obscure prior wounds.

Adult bull and cow moose died in approximate proportion to their occurrence in the population. The sex ratio among 22 moose dying from all causes (100 males:100 females) (Table 7) was not significantly different ($\underline{P} < 0.1$, Student's $\underline{t}$-test) from the mean of ratios (82 males:100 females) among moose surveyed during 1981-85 (Table 4). Also, the sex ratio among moose killed by predators (70 males:100 females, $\underline{n} = 17$) and among the combined confirmed and possible predator kills (73 males:100 females, $\underline{n} = 19$) (Table 7) did not differ significantly ($\underline{P} > 0.1$) from the sex ratio in the living population (82 males:100 females). The selection by predators of both bulls and cows is different from that found by Peterson et al. (1984) and is likely a result of the high proportion of old, and thus vulnerable, bulls and cows. Heavily hunted moose populations characteristically have proportionately few bulls in the highly vulnerable old age classes, and consequently, predation focuses on cows.

Bull moose were a major food source for predators in our study area, and, unless wolf or grizzly bear predation is reduced, the moose population will continue to have no surplus moose for man to harvest. With the moose population at a low density and its growth apparently limited by predation, hunters and predators compete for bulls. If man removes many bulls, predators will prey increasingly on the few remaining cows and calves.

The result will be even lower recruitment, increased adult mortality, and an accelerated decline in numbers of moose.

Predator-Prey Relationships:

Predators are abundant relative to the number of moose in the experimental area (Tables 8, 9). When caribou migrate out of the experimental area, predation rates on moose are predicted to be high. This prediction is based on the effects predators have 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). However, when the caribou herd was in the experimental area, prey were abundant for most wolf packs and grizzly bears (Table 9). The high number of alternate prey (caribou) per predator should have temporarily reduced predation rates on moose.

Numbers of prey relative to wolves increased between 1981 and 1984. Growth of the caribou herd (Valkenburg and Davis 1985) and wolf removal contributed about equally to this increase. Future changes in the number of prey per wolf will largely depend upon which population grows at the fastest rate, wolves or caribou.

Calf and adult moose in the experimental area sustained high rates of natural mortality, 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 moose population at its low density. In next year's report, we will 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. At present, we are collecting data for use in making an unbiased estimate of the adult mortality rate.

Maintenance of wolf pack territories (Figs. 2-5) 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 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. In 1981-85, the number of caribou in the experimental area at 1 time probably ranged from 200 to almost the entire herd (approximately 14,000; Valkenburg and Davis 1985). However, it is likely that each year all packs had some caribou pass through their territory, and wolves killed caribou when available.

Food was scarce for wolves when caribou were not present. The food shortage was reflected in the low reproductive rate and the lack of population growth through fall 1984, despite declining annual harvest rates. The wolf population probably has little potential to increase before becoming food-limited.

Wolves are currently not abundant in the experimental area and will not become abundant until their prey base increases. The density of wolves during fall of 1981 and 1984 were 8 and 5 wolves/1,000 km^2 (21 and 13 wolves/1,000 mi^2), respectively (Table 1), compared with 16/1,000 km^2 (41/1,000 mi^2) in Subunit 20A during 1975 (Gasaway et al. 1983) and 11-19/1,000 km^2 (28-49/1,000 mi^2) on the northwestern Kenai Peninsula from 1976 through 1982 (Peterson et al. 1984). The apparently predator-limited moose population in the experimental area is not likely to 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.

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, (5) moderate to high condition indices for adult moose, and (6) high percentage of marrow fat in wolf-killed adult moose.

Additional data on marrow fat content in 11 dead moose found in 1984-85 continue to support rejection of the food-limiting hypothesis. None of these moose had <20% marrow fat (Appendix A), which confirms that few moose in the population were in a severely malnourished state (Franzmann and Arneson 1976, Peterson et al. 1984). Nine of the 11 moose were killed by predators and the other 2 may have been killed by predators. Bears and wolves should have led us to moose in poor condition, if present, because bears and wolves scavenged moose carcasses and it is likely they can kill animals in poor condition more easily than 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. Reducing the effect of a potential limiting factor and measuring the change in moose abundance is the only unequivocal test. However, evidence indicates grizzly bear and wolf predation is the cause of low moose survival, and the data set is strong enough to tentatively accept the hypothesis that predation limits moose population growth.

3. After fall wolf numbers were reduced by 30-40%, grizzly bear predation had a greater effect on moose population dynamics than wolf predation. Data were unavailable to determine which predator had greater impact prior to reducing wolf numbers.

4. A moderate increase in moose numbers in Subunit 20E cannot be accomplished without simultaneously reducing grizzly bear and wolf predation. Reducing grizzly bear predation will improve summer calf and adult survival. Reducing wolf predation will improve year-round moose survival but will have its greatest effects on winter calf survival and year-round survival of adult moose. Attempting to increase numbers of moose by reducing either wolf <u>or</u> grizzly predation will require a high impact on that predator population, much higher than if both predators are reduced simultaneously. Also, it is questionable whether detectable short-term increases in the moose population would occur if only 1 predator were reduced to moderate numbers, particularly if the predator were the wolf.

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 to be both beneficial and detrimental to moose, depending on when and how long caribou are present in the predators' home ranges. 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 predators' home ranges, the greater predator population preys primarily on moose, much to the 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. Estimate spring and summer predation rates by grizzly bears on adult moose to evaluate overall predation rates on moose.

2. Continue monitoring radio-collared adult moose to achieve an unbiased estimator of annual mortality rate.

3. Estimate rates of winter predation by wolves on adult moose where caribou are scarce and where they are abundant. Wolf predation rates on an extremely low-density moose population have not been measured.

4. Propose regulations that will encourage increased grizzly bear and wolf mortality to allow growth of the moose population. Increasing the now meager food base for predators and scavengers will ultimately result in an increase in numbers of predators and scavengers.

5. Summarize knowledge of interrelationships of grizzly bears, wolves, man, moose, and caribou in Subunit 20E to ensure that people understand that: (1) moose are currently being allocated almost entirely to grizzly bears and wolves, and (2) no increase in this low-density moose population is predicted given the current allocation regulations.

6. If allocation of moose among man and predators is changed, measure the effects of these changes to assess how much control must be exerted to allow this low-density moose population to increase. Apply findings elsewhere as appropriate.

7. Discontinue field aspects of this study by May 1987 unless the predation-limiting hypothesis can be tested by reducing predation on the moose population.

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LITERATURE CITED

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

Ballard, W. B., and D. G. Larsen. In press. Implications of predator-prey relationships to moose management. Viltrevy. 1986.

__________, S. D. Miller, and T. H. Spraker. 1980. Moose calf mortality study. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-9, W-17-10, W-17-11, and W-21-1. Juneau. 123pp.

__________, T. H. Spraker, and K. P. Taylor. 1981a. Causes of neonatal moose calf mortality in southcentral Alaska. J. Wildl. Manage. 45(2):335-342.

__________, R. O. Stephenson, and T. H. Spraker. 1981b. Nelchina Basin wolf studies. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-8, W-17-9, W-17-10, and W-17-11. Juneau. 201pp.

__________, A. W. Franzmann, K. P. Taylor, T. H. Spraker, C. C. Schwartz, and R. O. Peterson. 1979. Comparison of techniques utilized to determine moose calf mortality in Alaska. Proc. North Am. Moose Conf. Workshop 15:362-387.

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

__________. 1978. The status and management of caribou in British Columbia. Fish and Wildlife Branch Report, Victoria, B.C. 150pp.

Bishop, R. H., and R. A. Rausch. 1974. Moose population fluctuations in Alaska, 1950-1972. Nat. Can. (Que.) 101:559-593.

Boertje, R. D., W. C. Gasaway, S. D. DuBois, D. G. Kelleyhouse, D. V. Grangaard, D. J. Preston, and R. O. Stephenson. 1985. Factors limiting moose population growth in Game Management Unit 20E. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-22-3 and W-22-4. Juneau. 51pp.

Coady, J. W. 1974. Influence of snow on behavior of moose. Nat. Can. (Que.) 101:417-436.

Davis, J. L., R. E. LeResche, and R. T. Shideler. 1978a. Size, composition, and productivity of the Fortymile caribou herd. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-6 and W-17-7. Juneau. 69pp.

__________, R. T. Shideler, and R. E. LeResche. 1978b. Movements and distribution of the Fortymile caribou herd. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-6 and W-17-7. Juneau. 69pp.

Fong, D. W. 1981. Seasonal variation of marrow fat content from Newfoundland moose. J. Wildl. Manage. 45:545-548.

Franzmann, A. W., and P. D. Arneson. 1976. Marrow fat in Alaskan moose femurs in relation to mortality factors. J. Wildl. Manage. 40:336-339.

__________, and R. E. LeResche. 1978. Alaskan moose blood studies with emphasis on condition evaluation. J. Wildl. Manage. 42:334-351.

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

__________, __________, and R. O. Peterson. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. J. Wildl. Manage. 44(3):764-768.

__________, R. E. LeResche, P. D. Arneson, and J. L. Davis. 1976. Moose productivity and physiology. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-17-R. Juneau. 87pp.

Gasaway, W. C., A. W. Franzmann, and J. B. Faro. 1978a. Immobilizing moose with a mixture of etorphine and xylazine hydrochloride. J. Wildl. Manage. 42(3):686-690.

__________, D. B. Harkness, and R. A. Rausch. 1978b. Accuracy of moose age determinations from incisor cementum layers. J. Wildl. Manage. 42:558-563.

__________, S. D. DuBois, D. J. Reed, and S. J. Harbo. In press. Estimating moose population parameters from aerial surveys. Biol. Pap., Univ. of Alaska, Fairbanks. 1986.

__________, R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84. 50pp.

Glenn, L. P. 1972. Report on 1971 brown bear studies. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-17-3 and W-17-4. Juneau. 109pp.

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

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

Kelsall, J. P. 1968. The migratory barren-ground caribou of Canada. Can. Wildl. Serv. Monogr. No. 3, Ottawa. 340pp.

Kie, J. G. 1978. Femur marrow fat in white-tailed deer carcasses. J. Wildl. Manage. 42:661-663.

Mech, L. D. 1966. The wolves of Isle Royale. U.S. Natl. Park Serv. Fauna Ser. 7. U.S. Gov. Printing Off., Washington, D.C. 210pp.

__________. 1973. Wolf numbers in the Superior National Forest of Minnesota. U.S. Dep. Agric. For. Serv., Res. Pap. NC-97, North Cent. For. Exp. Sta., St. Paul, Minn. 10pp.

__________, and G. D. Del Giudice. 1985. Limitations of the marrow-fat technique as an indicator of body condition. Wildl. Soc. Bull. 13:204-206.

Miller, S., and W. B. Ballard. 1984. Density and biomass estimates for an interior Alaskan brown bear population. Can. Field-Nat. 96(4):448-454.

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

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

__________, and J. Scheidler. 1978. Ecological studies of wolves on Isle Royale. Mich. Tech. Univ., Houghton. 14pp. Mimeo.

__________, J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildl. Monogr. 88. 52pp.

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

__________. 1969. A summary of wolf studies in southcentral Alaska, 1957-1968. Trans. Am. Wildl. and Nat. Resour. Conf. 34:117-131.

Reynolds, H. V. 1974. North Slope grizzly bear studies. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-17-6. Juneau. 27pp.

__________, and J. L. Hechtel. 1984. Structure, status, reproductive biology, movement, distribution, and habitat utilization of a grizzly bear population. Alaska Dep. Fish and Game. Fed. Aid. in Wildl. Rest. Final Rep. Proj. W-21-1, W-21-2, W-22-1, and W-22-2. Juneau. 29pp.

__________, and __________. 1985. Population structure, reproductive biology, and movement patterns of grizzly bears in the northcentral Alaska Range. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-22-2. Juneau. 29pp.

Schwartz, C. C., A. W. Franzmann, and D. C. Johnson. 1983. Black bear predation on moose (bear ecology studies). Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-10, W-17-11, W-21-1, W-21-2, and W-22-1. Juneau. 135pp.

Sergeant, D. E., and D. H. Pimlott. 1959. Age determination in moose from sectioned incisor teeth. J. Wildl. Manage. 23:315-321.

Shryer, J. 1983. 1982 movements and distribution of the Fortymile caribou herd within the Fortymile Resource Area. Bureau of Land Management files. Fairbanks District Office. 13pp.

Stephenson, R. O. 1978. Characteristics of exploited wolf populations. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Final Rep. Proj. W-17-3 through W-17-8. Juneau. 21pp.

__________, and J. Sexton. 1974. Wolf report. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog Rep. Proj. W-17-5. Juneau. 28pp.

Valkenburg, P., and J. L. Davis. 1985. Population status of the Fortymile caribou herd. Alaska Dep. Fish and Game. Fed. Aid in Wildl. Rest. Prog. Rep. Proj. W-22-3. Juneau. 22pp.

__________, and __________. In press. Calving distribution of Alaska's Steese-Fortymile herd: a case of infidelity? Proc. 4th Intl. Reindeer/Caribou Symposium, Whitehorse. Rangifer.

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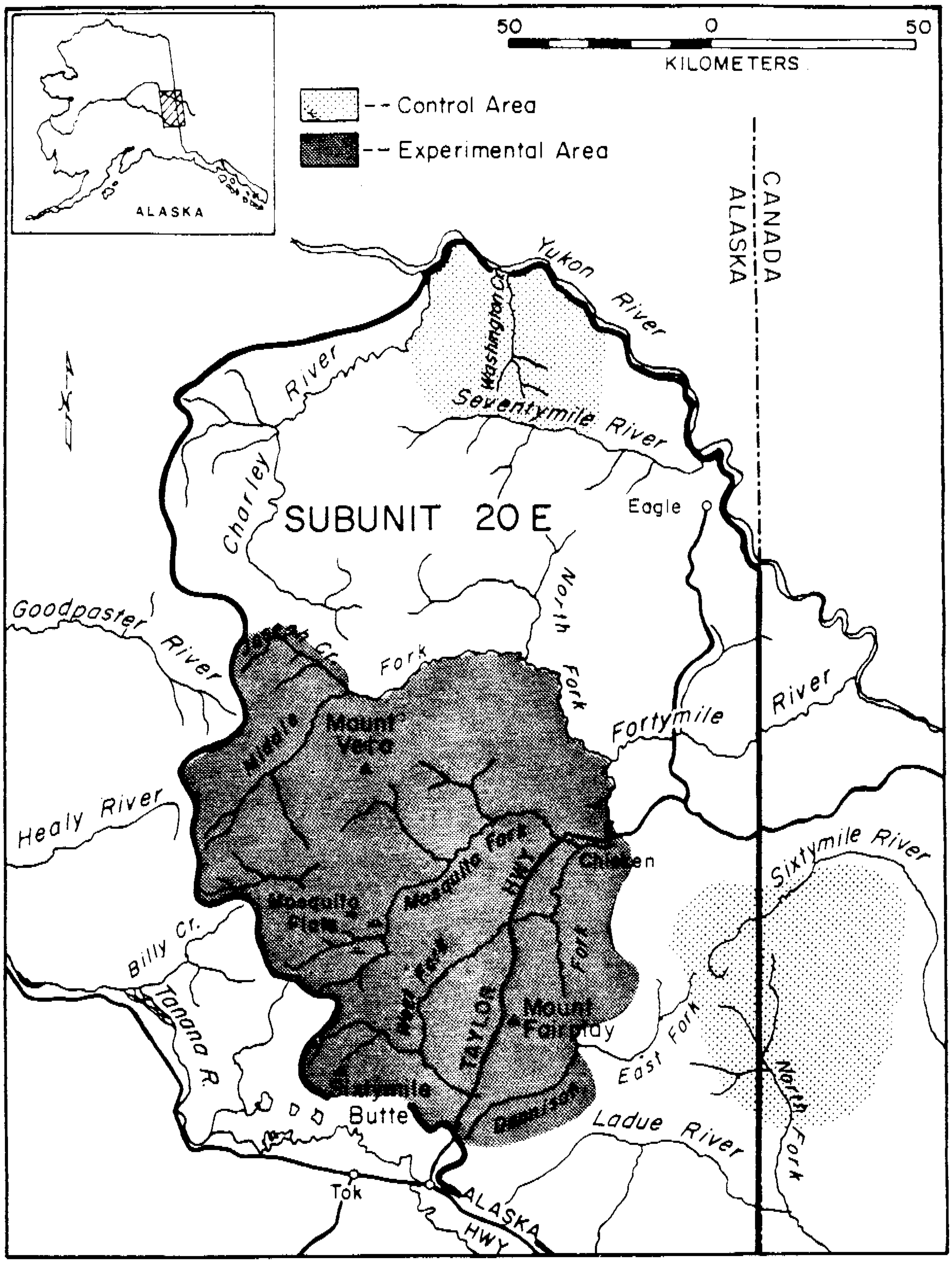

Fig. 1. Experimental area (with wolf removal) and control areas (without wolf removal) in Subunit 20E, Alaska, and adjacent Yukon Territory, Canada.

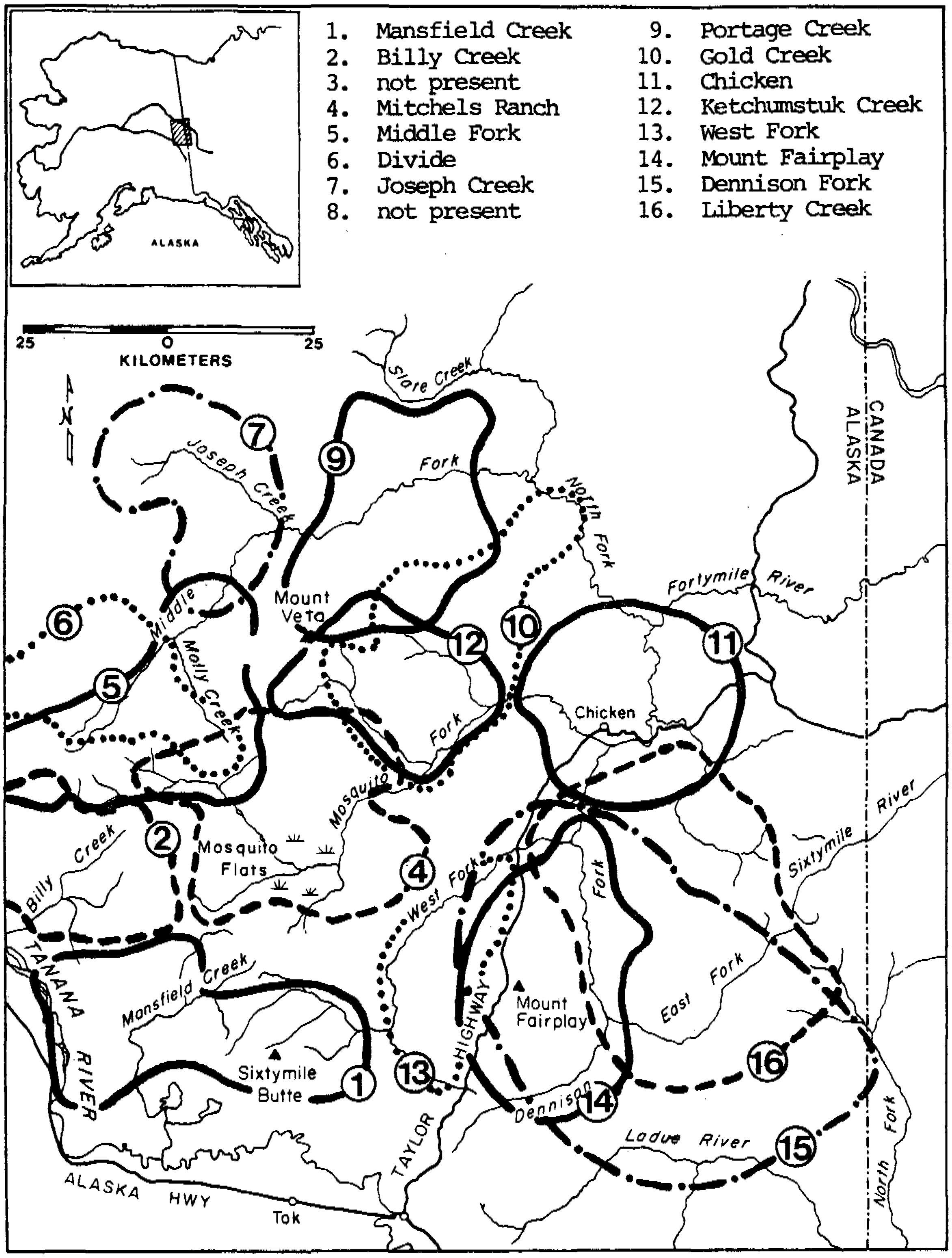

Fig. 2. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1980-82.

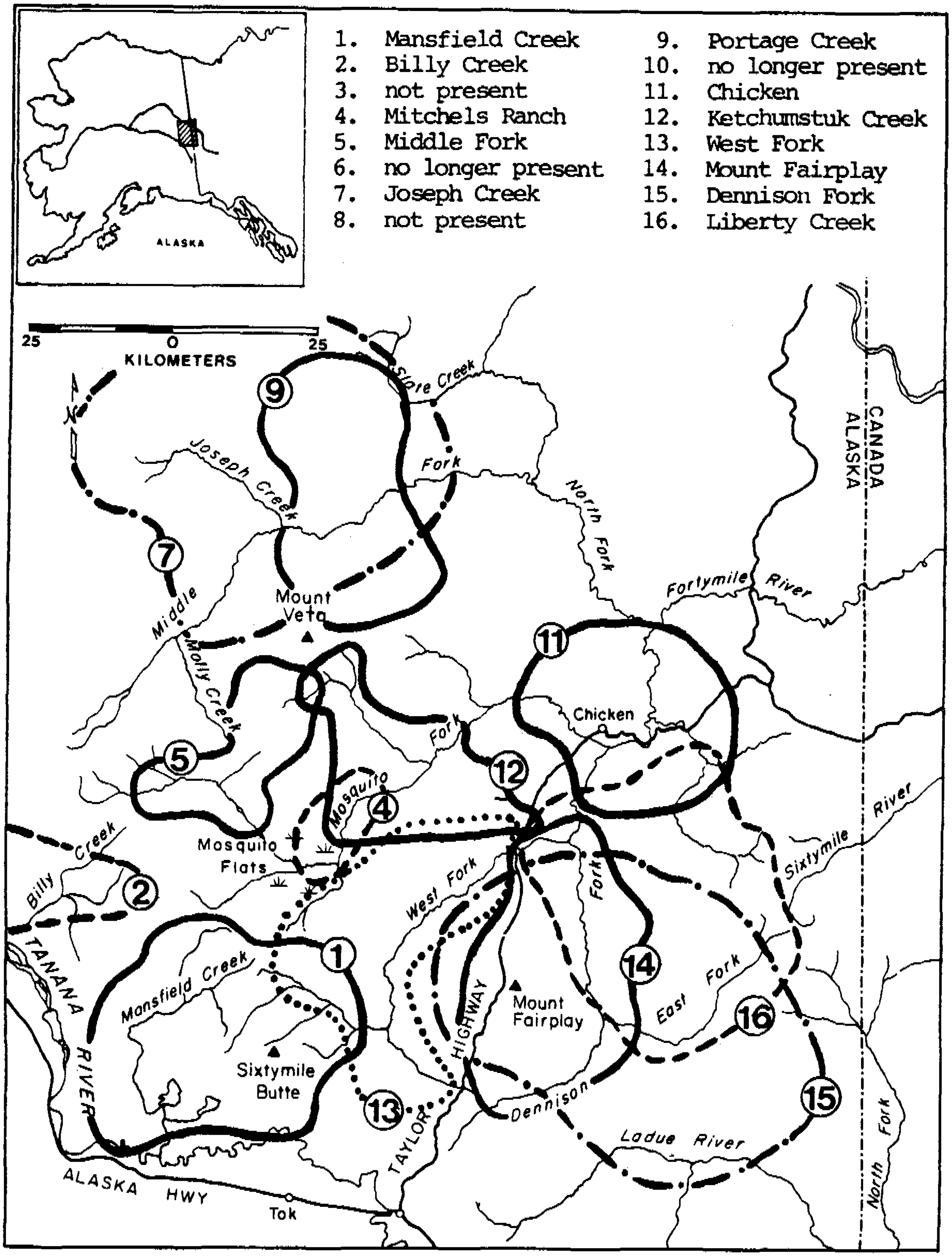

Fig. 3. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1982-83.

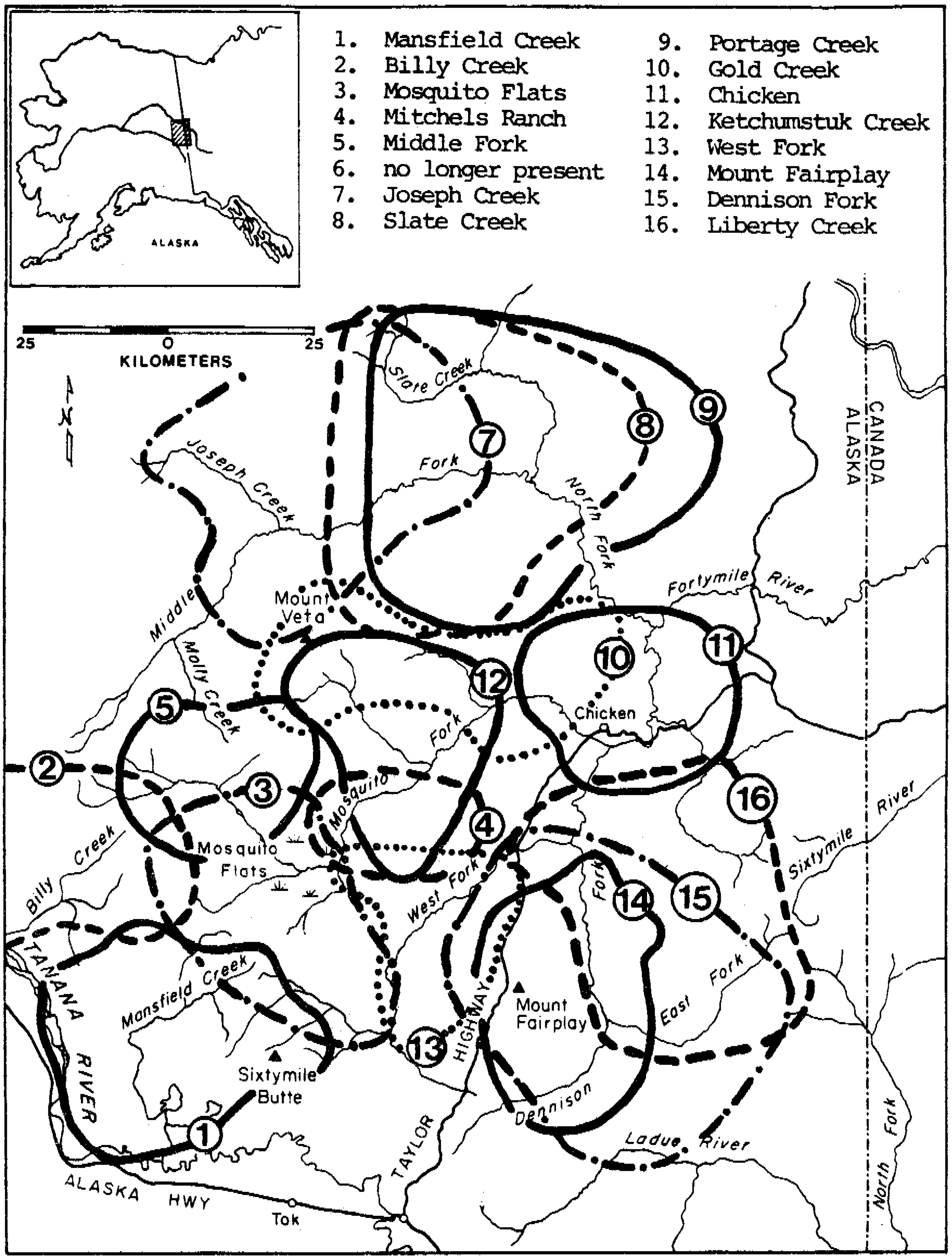

Fig. 4. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1983-84.

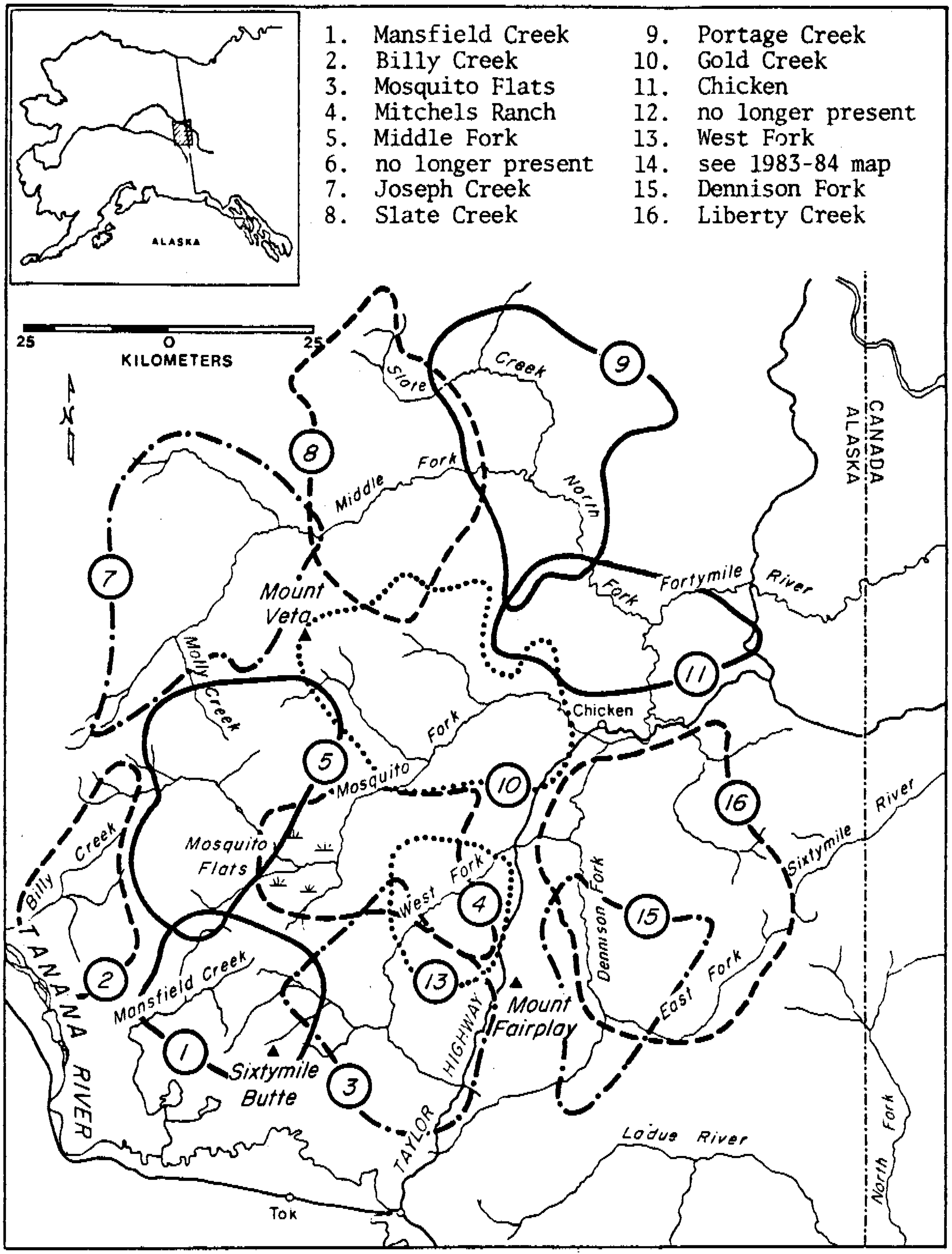

Fig. 5. Location and minimum size of wolf pack territories in and overlapping into the experimental area of Subunit 20E, Alaska, 1984-85.

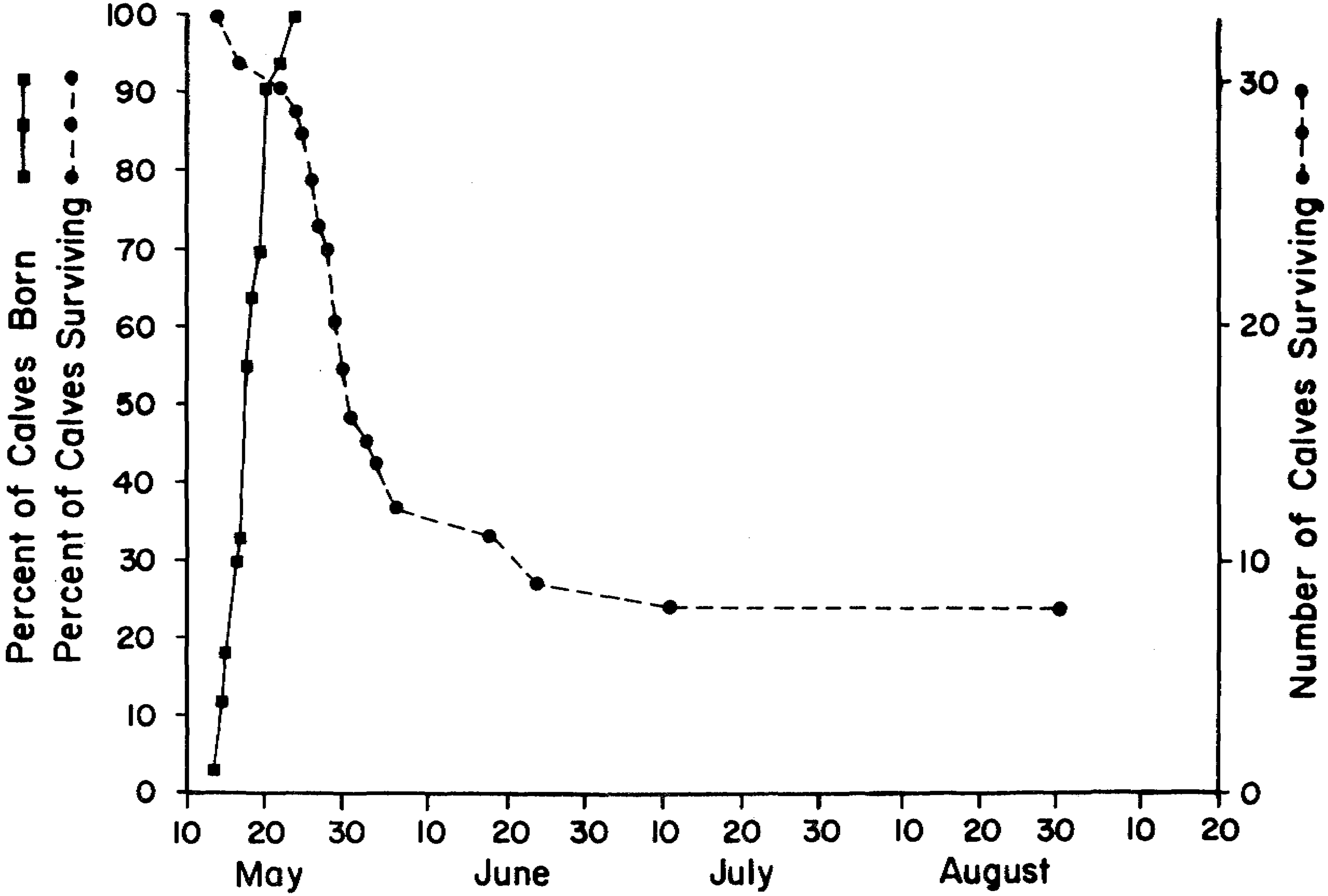

Fig. 6. Timing of birth and death of 33 moose calves radio-collared during May 1984 in and near the Mosquito Flats, Alaska.

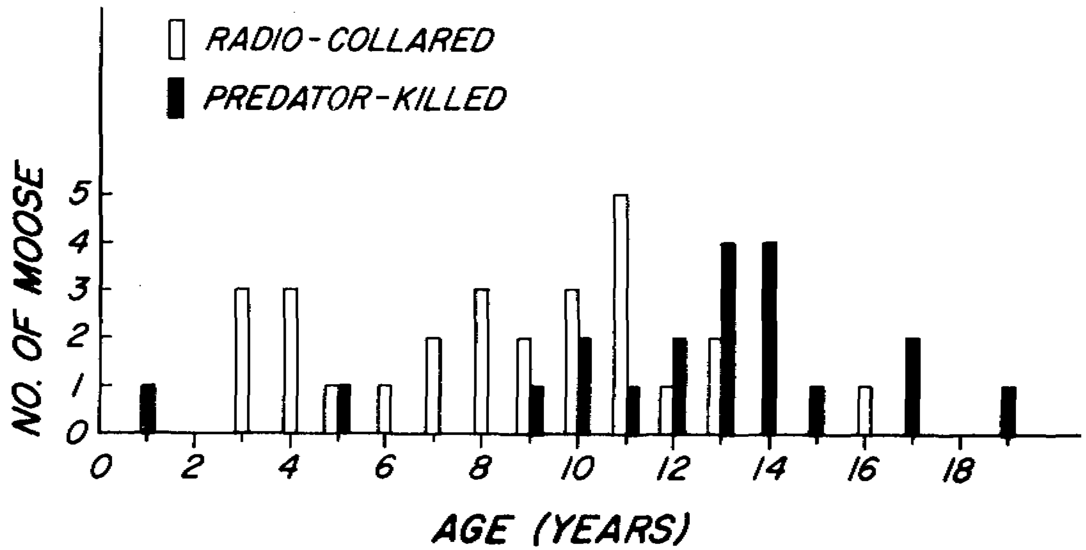

Fig. 7. Age distribution of 27 radio-collared cow moose and 20 bull and cow moose killed by predators in the experimental area and adjacent portion of Subunit 20D, Alaska, 1981-85.

Table 1. Estimated numbers of wolves and respective wolf pack names in and adjacent to the experimental area of Subunit 20E, Alaska, fall 1981–fall 1985. Numbers added to pack sizes are singles or pairs of wolves observed in the pack's territory but not associated with the pack.

Pack No.	Pack name	Before wolf removal fall 1981	After wolf removal[a] 1982 spring		1983 spring		1984 spring		1985 spring	
			1982 spring	1982 fall	1983 spring	1983 fall	1984 spring	1984 fall	1985 spring	1985 fall
1	Mansfield Creek	7[b] + 2	0 + 2	8 + 2[c]	1	5	3	4	3	6
2	Billy Creek	8[d] + 1[c]	2[c]	2[c]	1	8	8[d]	8[d]	2	8
3	Mosquito Flats	0	0	0	0	8	4	5	5	7
4	Mitchels Ranch	15[d]	2	2	2	4	2[c]	5	5[c]	7[c]
5	Middle Fork	11[e]	2	3	3	5[c]	2	3 + 2	3 + 1	5-6
6	Divide	8[f]	0	0	0	0	0	0	0	0
7	Joseph Creek	6	2	2	2	6	3[c]	3[c]	2	2
8	Slate Creek	0	0	0	0	6	6	6	4	8
9	Portage Creek	12[c]	4[c]	4[c]	0	9	8[c]	9[c]	9	12
10	Gold Creek	5[c]	0	0	0	3	3	8	8[c]	11[c]
11	Chicken	7	3	5	4	8	4	5	5	--
12	Ketchumstuk	3	3	5[c]	2	1 + 1	1[c] + 1[c]	0	0	2
13	West Fork	7 + 3	2	10 + 4	10 + 2	3 + 1	2 + 1	2 + 1	2 + 1	2
14	Mount Fairplay	2	2	2 + 1	2	2	2	2	0	--
15	Dennison Fork	9	9	9 + 2	1	1 + 1	1	3	3	--
16	Liberty Creek	8	8	8	8	10	6[c]	6[c]	6	--
	Unidentifed lone wolves	11	11	8	8	5	5	6	4	--
	Total wolf numbers	125	52	77	46	87	62	78	63	--
	Percentage change		-58%	+48%	-40%	+89%	-29%	+26%	-19%	--
	Density (wolves/1,000 km²)	8	3	5	3	6	4	5	4	--
	(wolves/1,000 mi²)	21	9	13	8	14	10	13	10	--

Table 1. Continued.

[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] The Mansfield Creek pack was removed from Subunit 20D in winter 1980-81.

[c] One wolf had a functioning radio collar.

[d] Two wolves had functioning radio collars.

[e] Three wolves had functioning radio collars.

[f] Two wolves in this pack were removed from Subunit 20D in winter 1980-81; the remainder were removed from Subunit 20E in winter 1981-82.

Table 2. Necropsy data from 78 wolves killed in and adjacent to the experimental area of Subunit 20E, Alaska, during winters 1980-85.

Pack name	Date	Age (yr)	Sex	Weight (kg)	Xiphoid fat(g)	Kidney fat(g)	Subcu. fat(mm)	Body length (cm)	Radio-cesium[a]
Mansfield Creek	3/16/81	3	F	40	--	87	16	132	639
Mansfield Creek	3/16/81	3	M	43	--	112	33	130	546
Mansfield Creek	2/2/83	5	F	41	145	--	28	129	--
Mansfield Creek	2/19/83	4	M	45	--	--	--	131	--
Mansfield Creek	10/26/83	2-3	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	7	F	36	--	46	6	--	1,691
Billy Creek	3/19/83	3	M	50	137	--	30	134	12,325
Billy Creek	2/85	4-5	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	3	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	3-4	F	40	136	104	18	125	661
Mitchels Ranch	3/28/82	3	F	43	173	81	26	125	718
Mitchels Ranch	3/29/82	2	F	32	135	88	33	--	675
Mitchels Ranch	3/29/82	3	M	50	267	91	42	129	571
Mitchels Ranch	2/16/84	4	F	36	165	--	22	122	4,202

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]
Middle Fork	4/22/81	Pup	F	36	--	50	12	136	1,984
Middle Fork	4/22/81	2	M	42	--	79	24	142	2,139
Middle Fork	12/15/81	2	M	48	232	69	48	--	5,993
Middle Fork	1/4/82	4	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	3	M	39	100	40	18	118	10,364
Middle Fork	3/5/82	8	F	39	130	102	29	123	20,338
Middle Fork	3/7/82	3	M	50	177	108	27	128	15,718
Middle Fork	3/9/82	2	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	3	M	45	140	--	37	130	9,885
Middle Fork	10/30/83	3	F	48	115	--	15	130	13,410
Middle Fork	12/3/83	3	F	43	160	--	36	124	10,060
Middle Fork	12/3/83	5	M	44	168	--	27	118	10,920
Middle Fork	1/10/84	4	M	34	40	--	3	127	14,435
Middle Fork	1/85	Ad	F	39	185	--	40	--	1,890
Divide	12/3/81	4-5	M	50	265	132	58	130	1,003
Divide	12/81	Pup	Unk	34	--	--	--	--	1,591
Joseph Creek	2/19/82	Ad	M	52	70	73	39	--	10,860
Joseph Creek	2/28/82	3	M	52	--	--	27	130	7,136
Portage Creek	1/4/82	4	F	36	219	110	27	128	11,246
Portage Creek	3/5/82	3	M	39	100	43	18	118	10,364
Portage Creek	3/5/82	8	F	36	130	102	29	123	20,338
Portage Creek	3/7/82	3	M	50	177	108	27	128	15,718
Portage Creek	3/9/82	2	Unk	34	108	118	28	122	15,532
Portage Creek	3/11/82	Pup	F	34	--	48	21	--	12,377

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	3/12/82	Pup	M	29	--	37	18	--	17,380
Portage Creek	3/20/82	Pup	F	29	44	53	21	--	13,356
Ketchumstuk	3/7/82	5	F	43	95	80	12	128	5,080
Ketchumstuk	3/31/82	4	M	50	186	99	26	129	4,672
Ketchumstuk	3/31/82	5	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
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	6-10	M	38	117	49	5	132	17,248
West Fork	4/9/82	4	M	41	130	60	22	131	10,047
West Fork	4/9/82	2-3	F	37	98	54	10	124	15,588
West Fork	11/5/83	4	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	2	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
Dennison Fork	1/83	Pup	F	--	0	--	0	--	8,500
Dennison Fork	1/83	--	Unk	--	0	--	0	109	7,205
Dennison Fork	1/83	Pup	M	--	0	--	0	117	--
Dennison Fork	3/6/83	3	F	40	272	--	65	119	--
Dennison Fork	3/7/83	Pup	F	32	110	--	23	120	--
Dennison Fork	11/83	5	M	48	110	--	10	131	10,665
Dennison Fork	11/83	5	M	50	80	--	12	132	8,502

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]
Liberty Creek	3/18/83	2	M	53	175	--	32	135	--
Liberty Creek	3/18/83	2	M	48	210	--	30	137	--

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

Table 3. Indicators of productivity in female wolves $\geq$3 years old in interior Alaska, 1957-85.

Area and year	Placental scars			Corpora lutea			Fetuses		
	No. of wolves	$\bar{x}$	95% CI	No. of wolves	$\bar{x}$	95% CI	No. of wolves	$\bar{x}$	95% CI
Interior Alaska 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. Moose sex and age ratios in the experimental area of Subunit 20E, Alaska, October-November 1966-85.

Date	Total bulls: 100 cows	Yrlg bulls: 100 cows	Yrlg bull % in herd	Calves: 100 cows	Calves: 100 cows >2 yr old	Incidence of twins: 100 cows with calf	Calf % in herd	Total moose surveyed
Before wolf removal:								
1966[a]	59	14	8	21	24	0	12	509
1967[a]	47	12	8	7	8	0	5	498
1968	64	4	2	13	13	0	7	389
1969	55	11	6	25	28	11	14	365
1970	46	9	5	24	26	0	14	368
1971[a]	39	7	4	18	20	0	10	251
1972	37	4	2	16	17	0	11	363
1973	40	7	5	8	8	0	5	269
1974	39	3	2	8	8	11	6	361
1975	42	2	1	8	8	0	5	168
1976	40	3	2	2	2	0	2	124
1977	51	11	7	8	9	0	5	235
1978	56	13	7	13	14	10	7	175
1979[a]	21	4	3	19	23	25	14	73
1980	92	12	6	20	22	13	9	108
1981	88	14	7	20	24	10	10	184
After wolf removal:								
1982	82	15	8	15	17	0	7	255
1983[b]	--	--	--	--	--	0	7	215
1984	74	11	6	22	24	11	11	444[c]
1985	85	15	8	15	18	5	8	545[c]

[a] Winters of relatively deep snow were 1965-66, 1966-67, 1970-71, and 1978-79.
[b] Surveys delayed until January 1984 because of shallow snow. Antler shedding had begun.
[c] New survey areas were added within the experimental area to increase sample size.

Table 5. Offspring:cow ratios and percentage calves in sample for 1978-85 cohorts 6 and 18 months of age, as determined by aerial moose surveys in the Mount Veta-Mosquito Flats contour count area in Subunit 20E, Alaska, before (1978-81) and after (1982-85) wolf removal. n = total number of moose classified.

	Age of cohort in months					
	6				18	
Cohort	n[a]	Number of cows ≥2 yr old	Calves: 100 cows ≥2 yr old	% calves	n[a]	Yearlings: 100 cows ≥2 yr old[b]
1978	112	58	14	7	67	9
1979	67	46	17	12	59	33
1980	59	24	21	8		33
					Yearlings: after wolf removal	
1981[c]		72	26	12	119	18
		Calves: after wolf removal				
1982	119	55	16	8	70	
1983	70[d]			9	119	20
1984	119	61	13	7	160	10
1985	160	78	21	10		

[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.

Table 6. Moose sex and age ratios in trend count areas in the control areas of Subunit 20E, Alaska, and adjacent Yukon Territory, 1982-85.

Date	Total bulls: 100 cows	Yrlg bulls: 100 cows	Yrlg bull % in herd	Calves: 100 cows	Calves: 100 cows $\geq$2 yr old	Incidence of twins: 100 cows w/calf	Calf % in herd	Density (moose: km^2)	Total moose surveyed
1982	71	14	7	33	39	0	16	0.10	43
1983[a]	65	13	7	17	20	0	10	0.43	42
1984	119	0	0	12	12	0	5	0.09	37
1985	88	9	4	11	12	17	10	0.17	69

[a] Only a portion of 1 of the 3 control areas was flown during 1983 because of shallow snow.

Table 7. Cause of death, age, sex, and percentage fat in marrow of adult moose found dead during 1981-October 1985 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	4	10	6	4	1-14	64	32	3	28-89[b]	1:2
	Grizzly bears	6	12	5	6	5-19	74	15	6	50-94[c]	2:3
	Probably grizzly bear or wolf	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
Nov-Apr	Wolves	10	14	2	10	11-17	67	34	10	7-93	4:5
	Drowned	1	2		1						1:0
Year-round	Predators	20	12	4	20	1-19	69	28	19	7-94	7:10
	Probably predators	4	12	5	4	6-18	91	2	2	89-92	1:1
	All causes	27	12	4	26	1-19	71	27	21	7-94	11:11

[a] Four dead radio-collared cow moose were omitted from the sample to eliminate bias from having only cows radio-collared.

[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 8. Moose, caribou, wolf, and grizzly bear density in the experimental area (9,800 km^2, 3,800 mi^2) before (1981) and after (1984) wolf removal, Subunit 20E, Alaska.

	Density of animals/1,000 km^2				
		Caribou[b]			
Period	Moose[a]	Min	Max	Wolf[c]	Grizzly bear[d]
Before wolf removal, fall 1981	77	20	770	8	20
After wolf removal, fall 1984	77	20	1,330	5	20

[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 and 13,000 were present during fall 1981 and 1984, respectively (Valkenburg and Davis 1985).

[c] Wolf density was calculated for the total area (15,500 km^2) (6,000 mi^2) occupied by wolf packs in Fig. 2.

[d] Approximate density of grizzly bears was estimated from numbers observed in the study area and estimated densities in other Alaskan study areas. See section titled "Grizzly Bear Population Status."

Table 9. Estimated ratio of prey per predator in the experimental area before (1981) and after (1984) wolf removal, Subunit 20E, Alaska. Ratios were calculated from density estimates in Table 8.

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	10	4	3	12	110	3	30
After wolf removal, fall 1984	15	4	3	19	280	4	56

Appendix A. 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, 1981-85.

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[a]	Probably wolf	--	Joseph
2 May 1985	G	F	10[a]	Probably wolf or grizzly bear	--	Telegraph Creek

Appendix A. Continued.

Date of death	Investigated from ground (G) or air (A)	Sex	Age (yrs)	Cause of death	Percentage fat in marrow	Location
30 May 1985	A	--	Yrlg/ad	Probably grizzly bear	--	Ketchumstuk Creek
10 Jun 1985	G	F	13	Wolf	89	Mosquito Flats
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

[a] Age estimated by wear.