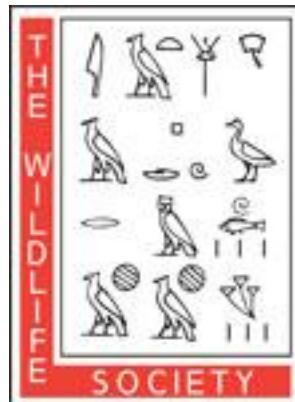


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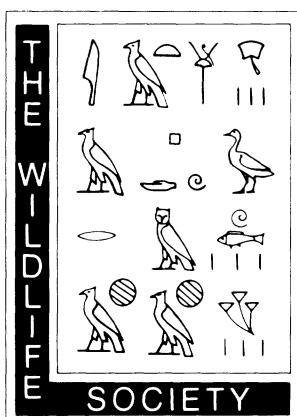
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WOLVES OF THE KENAI PENINSULA, ALASKA

by

ROLF O. PETERSON, JAMES D. WOOLINGTON,
AND THEODORE N. BAILEY

APRIL 1984

NO. 88



FRONTISPIECE. Swanson River Pack, Kenai Peninsula, 1978. (Photo by R. O. Peterson)

WOLVES OF THE KENAI PENINSULA, ALASKA

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Abstract: Wolves (*Canis lupus*) recolonized Alaska's Kenai Peninsula in the 1960's following a 50-year absence. During 1976-81 wolf ecology and population dynamics were studied in 3-7 contiguous wolf packs on the Kenai National Wildlife Refuge. Sixty-four wolves were captured and radio-collared 87 times; they were located 3,600 times from aircraft. Wolf density ranged from 11 to 20 wolves/1,000 km². Wolves fed primarily on moose (density 0.8/km²), and predation rate in winter averaged 1 moose/pack/4.7 days. Food consumption in winter was 0.12 kg/kg wolf/day, but intake apparently declined in summer. Calves composed 20% of the moose population but 47% of 206 wolf-killed moose examined; proportionately more calves were killed during a winter with deep snow. Average age for adult moose killed by wolves was 10.9 years, with wolf predation selectively removing the oldest moose in the population. All but 3 of 72 wolf-killed adult moose of which sex could be ascertained were females, reflecting the low proportion of bulls (12 bulls : 100 cows) brought about by moose harvest. Skeletal pathology was found in 35% of wolf-killed adult moose, and half of the wolf-killed calves taken after 1 January were severely malnourished.

Typically 1 litter of wolf pups was born annually to the dominant female in each pack. Pups born to a socially subordinate female were growth-retarded and apparently died. One-third of the radio-collared wolves dispersed from their original packs. Extraterritorial movements were most commonly undertaken by subordinate adult wolves during the February breeding season. Survival of dispersing wolves was only half that of nondispersers; most dispersers were killed before they could reproduce successfully. Dispersing individuals comprised 27% of wolves taken by hunters and trappers on the study area after open seasons were reinstated in 1974. Mortality was largely human-caused, averaging 33% annually. Harvest increased rapidly, reducing pack size and causing declines in pack territory size. Additional packs developed in vacated areas, and total wolf density was maintained until annual kill exceeded 30-40% of the early winter population. At the close of the study, wolf density on the study area appeared regulated by harvest.

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INTRODUCTION

Wolves (*Canis lupus*) were re-established on Alaska's Kenai Peninsula by natural immigration in the 1960's, after being absent for most of this century. The species had disappeared little more than a decade after a gold rush in 1895–96 brought thousands of prospectors to the region. Unregulated killing, market hunting, and man-caused fires caused substantial changes in the status of important wildlife species by the early 1900's. Caribou (*Rangifer tarandus*) were eliminated, probably as a result of overharvest (Davis and Franzmann 1979). Populations of Dall sheep (*Ovis dalli*) and moose (*Alces alces*) were locally reduced, although moose ultimately increased in vast areas of burned-over habitat (Spencer and Hakala 1964). Poison was widely used to take furbearers and to control large carnivores and may account for the elimination of wolves from the Kenai by about 1915 (Peterson and Woolington 1982). In south central Alaska, a period of intensive trapping followed the institution of bounties for wolves in 1915 and for coyotes in 1929 (McKnight 1970). A decade of federal wolf control began in 1948 that further reduced wolf populations on the south central mainland (Rausch

and Hinman 1977). The combination of sparse prey and intensive control operations on the mainland to the north, plus the existence of only a narrow peninsula access route, probably were responsible for wolf absence from the Kenai until the late 1950's.

Federal wolf control began to decline before Alaskan statehood in 1959, and under subsequent state management wolf populations in south central Alaska rapidly recovered (Rausch 1969). Isolated wolves were reported on the Kenai Peninsula in the early 1960's, with frequency of sightings and size of packs increasing through the latter part of the decade. In the early 1970's wolves were present throughout the western half of the peninsula. Following complete protection from 1961 to 1974, wolf hunting and trapping seasons were initiated on the Kenai in 1974 and 1975, respectively.

During this century the Kenai Peninsula became famous as a big game range. In the 1950's and 1960's moose were plentiful on the Kenai National Moose Range, now the Kenai National Wildlife Refuge (KNWR). A 1,200-km² fire in 1947 produced excellent habitat that supported high moose numbers on the northern half of the KNWR for about 25 years. Light

hunting pressure, lack of wolves, and a series of mild winters in the late 1960's contributed to high moose densities that could not be maintained by the available forage (Oldemeyer et al. 1977).

After 1971 the density of moose declined from 1.6/km² to approximately 0.8/km² (Bailey 1978, Bangs and Bailey 1980). Deteriorating habitat in the 1947 burn in conjunction with severe winter weather was considered the underlying cause (Oldemeyer et al. 1977). In addition, when cow moose were legally hunted during 1970–72, the 1971 kill exceeded 1,100 moose (ca. 14% of the population). Other human impacts included road kills and poaching. By the early 1970's moose were again subjected to wolf predation, and the numerous black bears (*Ursus americanus*) were preying on calves (Franzmann et al. 1980).

Uncertainties were involved in relationships of the moose decline to increased hunting pressure, severe winter weather, declining habitat quality, and loss to predators. This led to a cooperative predator-prey study by the Alaska Department of Fish and Game (ADF&G) and the U.S. Fish and Wildlife Service (USFWS). Aspects of the work on moose calf mortality were reported by Franzmann et al. (1980).

The primary objective of the present investigation was to appraise those factors influencing wolf density on the Kenai Peninsula, especially on the KNWR. Associated objectives were to determine the pattern of loss to wolf predation in a hunted moose population and to assess density and population trend in a wolf population exposed for the first time to harvest by hunters and trappers. Hunting regulations covering both wolves and moose on the KNWR, set by the Alaska Board of Game, conformed to those existing in much of Alaska. Intensive research extended from 1976 to 1980 with follow-up surveys concluding late in 1981.

Acknowledgments.—Help provided by individuals at many levels in the U.S. Fish and Wildlife Service and the valuable assistance of the staff of the Kenai National Wildlife Refuge are gratefully acknowl-

edged. The Alaska Department of Fish and Game aided in developing the project and provided materials and assistance throughout the study.

Refuge managers J. B. Monnie, J. F. Frates, and R. L. Delaney contributed much of the initiative and support required for the research. L. D. Mech (USFWS) was instrumental in designing the project, taught us techniques of handling and radio tracking wolves, and freely offered advice and assistance during the work. A. W. Franzmann (ADF&G) made valuable contributions. Assistant refuge manager V. D. Berns frequently aided in wolf capture efforts and flew most radio tracking flights, together with assistant refuge manager R. Richey and pilots of Kenai Air Alaska. V. Lofstedt and C. Lofstedt provided excellent helicopter support during wolf capture efforts. A. Johnson, J. Lewandoski, J. Gross, and J. Barthelow, all of the USFWS, and S. Stephens at Michigan Technological University assisted in the analysis of results with computer programs, hardware, and coding and editing data. Biological technicians E. E. Bangs and A. V. Marrs frequently volunteered their time in the field. P. LeRoux, T. Spraker, and other ADF&G biologists contributed key observations and compiled most of the wolf harvest data. Valuable suggestions for improving this monograph were made by D. L. Allen, T. K. Fuller, C. M. Kirkpatrick, R. L. Kirkpatrick, and R. O. Stephenson.

STUDY AREA

The Kenai Peninsula is located between Prince William Sound and Cook Inlet in south central Alaska (lat. 60°N, long. 150°W), and lies just south of Anchorage (Fig. 1A). Although 26,000 km² in area, the peninsula is connected to mainland Alaska by a narrow neck of land and ice only 16 km wide. Two major landforms characterize the peninsula: the rugged Kenai mountains rising to 1,500 m (with major icefields) dominate the eastern half, and the Kenai lowlands, a rolling plateau ranging from sea level to about 500 m,

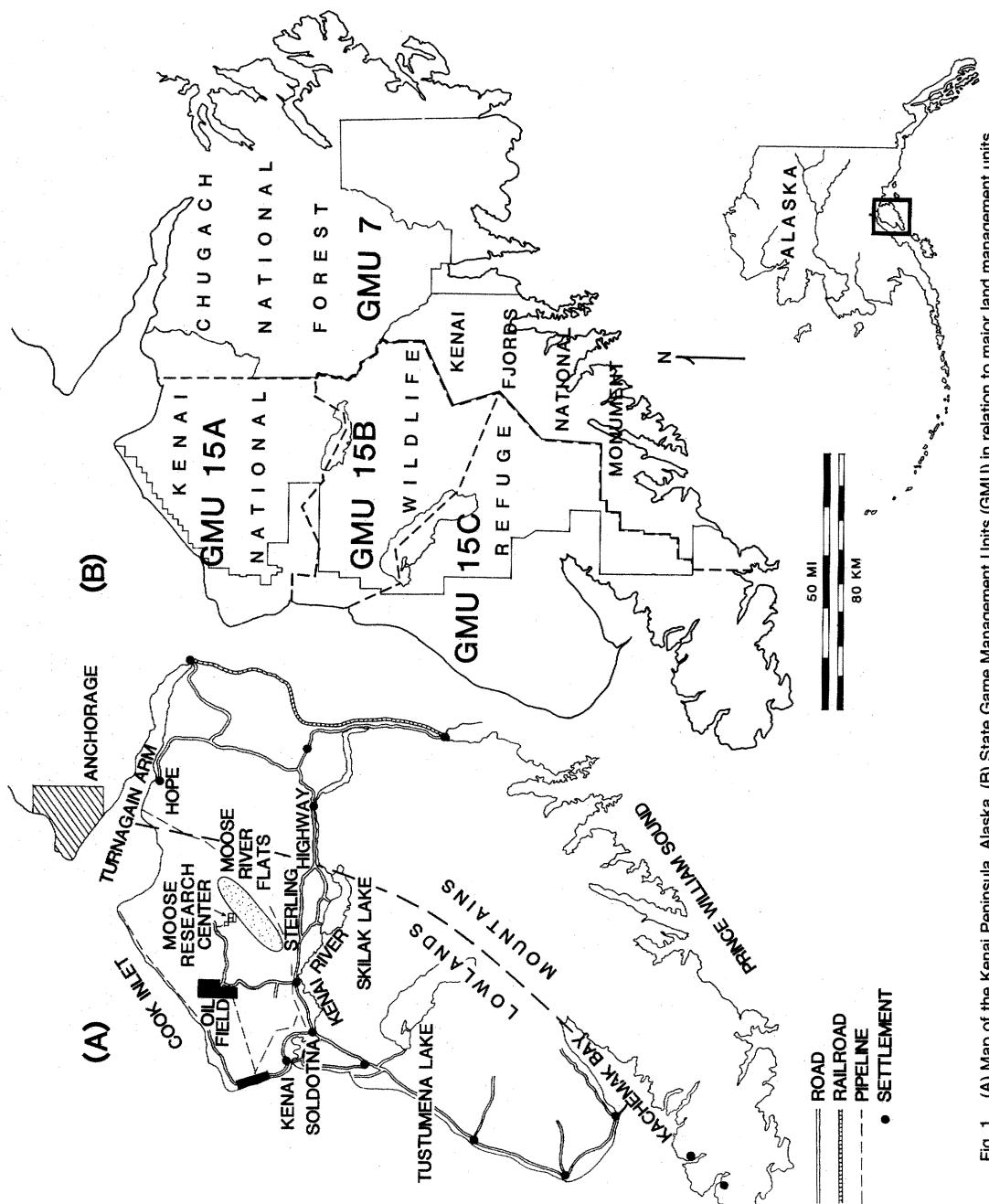


Fig. 1. (A) Map of the Kenai Peninsula, Alaska. (B) State Game Management Units (GMU) in relation to major land management units.

form the western half. Numerous bedrock fault-lines cross the landscape, the most notable separating the Kenai lowlands from the mountains. Patterns of uplift and subsidence are pronounced, with the lowlands generally rising and the mountains settling into the sea. During the 1964 earthquake the eastern shore dropped several feet, while the downward displacement of the western shore was almost negligible (Plafker 1969).

Forest vegetation includes white and black spruce (*Picea glauca* and *P. mariana*), white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and willow (*Salix* spp.), with black cottonwood (*Populus trichocarpa*) in stream bottoms and Sitka spruce (*Picea sitchensis*) in coastal areas. The altitudinal limit of trees in the mountains is approximately 500 m.

Of the 26,000 km² that make up the Kenai Peninsula, 14,600 km² are included in the following federal land units: Kenai National Wildlife Refuge (7,972 km²), Chugach National Forest (4,340 km²), and recently established Kenai Fjords National Monument (2,268 km²). The peninsula is divided into 2 ADF&G game management units, GMU 7 and 15. GMU 15 is further divided into 15A, 15B, and 15C (Fig. 1B). The study area encompassed the Kenai lowlands and adjacent mountains north of Tustumena Lake; most of this area was burned by wildfire during the last 100 years (Spencer and Hakala 1964, Davis and Franzmann 1979). Much of the 700-km² "benchland" between Skilak and Tustumena Lakes burned between 1885 and 1890, leading to abundant moose populations throughout this area by 1920 and contributing to the early reknown of the Kenai Peninsula among big game hunters. Large fires in 1947 and 1969 were accidentally started by humans. The northern lowlands supported few moose until the 1947 fire burned 1,250 km² in this area. The successional-stage vegetation that followed created optimum moose habitat, leading to exceptionally high densities of moose in the 1950's and 1960's. By the 1970's the 1947 burn had become marginal winter habitat, moose dying of

malnutrition were commonly observed, and the population declined (Oldemeyer et al. 1977). The 1969 fire covered an additional 352 km² of mature forest just northeast of the town of Kenai. Although this burn lacked the interspersion with unburned stands that characterized the 1947 burn, it produced substantial amounts of browse during this study and in early winter attracted large numbers of moose (Bangs and Bailey 1980).

Moose numbers on the KNWR north of Tustumena Lake were estimated at 3,800 (0.8/km²) in winter (Bailey 1978), remaining stable during the study. The population on the study area comprises several subpopulations, producing a complex pattern of seasonal mixing and segregation (LeResche 1972, Bailey et al. 1978). On the northern lowlands there are 2 primary groups, year-round residents and migratory moose, the latter segregated into 10–11 distinct breeding groups associated with specific mountain drainages or other areas. Mixing of the populations occurs in winter, when migratory moose over-winter with lowland residents.

Moose hunting during the study was restricted to a bull season during 1–20 September. Hunting pressure in GMU 15A was higher than in 15B, producing a highly skewed sex ratio in 15A. During early winter surveys during 1976–78, total males/100 females ranged from 11 to 14 in GMU 15A and 48 to 65 in GMU 15B. Calves numbered 25–40/100 females in GMU 15A and 7–28/100 females in GMU 15B (Spraker 1980). Our study was largely carried out in GMU 15A.

The hunting season for wolves was 10 August–30 April with a limit of 3, while the trapping season with no limit extended from 10 November–31 March. Trappers, as defined by ADF&G, could legally shoot wolves from the ground after locating them from aircraft, but hunters could not legally shoot game if airborne the same day.

Although moose are the primary prey of most of the Kenai wolf population, other ungulates with more restricted distributions may be locally important as prey

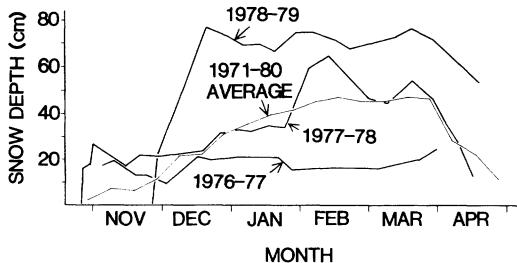


Fig. 2. Maximum recorded snow depth on study area on Kenai Peninsula lowlands during 3 winters of the study plus average for 1971-72 through 1979-80.

outside the study area. Caribou reintroduced in 1965-66 resulted in 2 populations totaling perhaps 300-400 animals. A population of 100 or less occupied the northern lowlands, and the remainder inhabited the Kenai mountains southwest of the town of Hope. Dall sheep and mountain goats (*Oreamnos americanus*) were present throughout much of the Kenai mountains. Beaver (*Castor canadensis*) were not abundant on the study area; our aerial surveys indicated fewer than 100 colonies for the entire refuge (<1.25 colonies/100 km²). Snowshoe hares (*Lepus americanus*) were sparse after reaching high levels in 1971-72 (J. Oldemeyer, pers. commun.).

Annual precipitation during 1944-77 averaged 48 cm and was evenly distributed throughout the year (Bangs and Bailey 1980). Complete snow cover usually was present from late November to early April, although snow depth rarely exceeded 50 cm. Winter severity was above average during 1971-75, a result of below normal temperatures and more persistent snow cover (Bangs and Bailey 1980). With the exception of 1978-79, winters during the study were relatively mild with frequent thaws and rain interspersed with wet snow. Even in midwinter, snow cover often was incomplete, and snow usually was dense and crusted. During the 1970's, an average maximum depth of 40-50 cm occurred in January-March, but in 1978-79 maximum snow depth was about 70 cm from mid-December through March (Fig. 2). Locally heavy accumulations were

noted southeast of Soldotna and east of the Swanson River oil field, whereas the area north of Skilak Lake typically had much less snow than elsewhere. High snow density and frequent crusts common on the Kenai tend to provide favorable hunting conditions for wolves (Peterson and Allen 1974).

METHODS

Wolf population density, the size and spatial distribution of packs, patterns of predation, and other aspects of wolf ecology were determined from radio-collared animals. Field work centered on year-round efforts to **radio-collar and subsequently locate wolves in as many packs as possible**. Approximately half the estimated wolf population on the peninsula was monitored at the height of the study.

We captured wolves in summer with leg-hold traps (33 captures in 6,800 trap-nights); in early winter we used helicopter darting (54 captures) to collar several additional wolves in each pack. Trapping was limited to the period May through October because the feet of trapped wolves commonly freeze in winter. Usually we darted during periods of complete snow-cover in early winter when packs were most cohesive.

Trapping was an effective way to catch adults and was the only means of examining wolves in seasons other than winter. The traps employed were Newhouse 4, 14, and 114 double long-spring, equipped with a 2-m chain and drag. Traps were set along roads, cutlines from seismic exploration, and a pipeline access road across the KNWR. We checked traps each morning and tranquilized (Seal et al. 1970) trapped wolves by an intramuscular injection of 1.0 mg/kg phencyclidine hydrochloride (Sernylan, Parke-Davis Co., St. Joseph, Mo.) and 0.5 mg/kg promazine hydrochloride (Sparine, Wyeth Laboratories, Philadelphia, Pa.).

Pups often were deliberately selected for darting because they were less elusive, remained in a pack for at least a year, and were seldom livetrapped in summer.

Drugs were delivered from a helicopter at close range with 3-cc projectile syringes fired from a Cap-Chur gun (Palmer Chemical and Equipment Co., Douglasville, Ga.). Effective drug dose was about 3 times that used for trapped wolves; we used fixed drug doses of either 100 mg Sernylan and 50 mg Sparine or 40 mg Sernylan and 220 mg Xylazine (Rompun, Chemagro, Kansas City, Mo.).

Although most trapped wolves suffered minor cuts and one was disabled, travel patterns and gait of trapped animals usually appeared normal within a few days. Darted wolves usually sustained only a minor dart wound, although 2 wolves died when darted. Additionally, 1 suffered a broken leg, and 1 was temporarily paralyzed after being hit in the spine.

Wolves were weighed and standard body measurements and teat characteristics were recorded. Whole blood samples in capillary tubes were spun in a microhematocrit centrifuge to provide packed-cell volume. Wolves were given intramuscular injections of 1,200,000 units of Bicillin (Wyeth Laboratories) and supplementary vitamin injections to reduce the likelihood of capture-related infections and to compensate for possible disruption of travel and feeding patterns. Wolves were classified as pup or adult by canine tooth appearance; pups captured in October still retained milk canines, whereas those caught in November or later showed various stages of permanent canine eruption. Lower incisor wear provided a relative indicator of adult age.

All wolves ($N = 64$) were fitted with radio-transmitter collars manufactured by either AVM Instrument Co. (Champaign, Ill.) or Telonics (Mesa, Ariz.) and ear-tagged with numbered yellow Rototags (Nasco, Fort Atkinson, Wis.). Sixteen wolves were captured twice, 2 were captured 3 times, and 1 was captured 4 times. We located wolves regularly from aircraft (PA-18 Supercub or Cessna 185) by the method of Mech (1974). Individual wolves were monitored for up to 3 years, but the average length of coverage was 10 months. Tracking was terminated because of

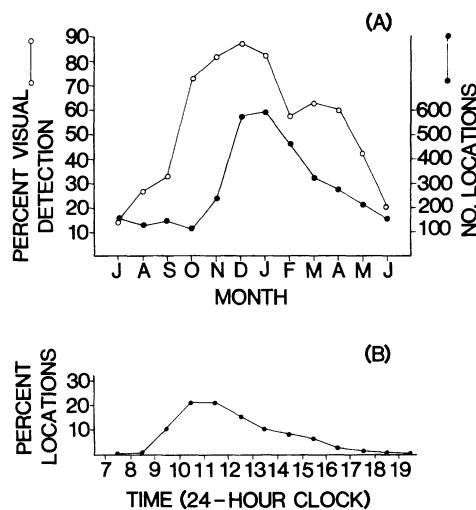


Fig. 3. Characteristics of wolf locations from aircraft ($N = 3,600$). (A) Visual detection of radio-collared wolves and the monthly distribution of all locations; (B) distribution of wolf locations according to time of day.

transmitter failure in about half of the cases, and the majority of the other wolves were killed. Maximum life of transmitters was 3 years.

Frequency of tracking flights ranged from 1 to 2/week in summer to almost daily in early winter. We visually observed wolves in 15% of the summer locations and in almost 90% of the winter locations (Fig. 3). Wolves were sighted during 60% of 3,600 locations obtained during 1976–81.

Each time a wolf was located by radio-fix we circled the area and attempted to observe the animal, count wolves in the pack, determine activity, and locate prey carcasses. When conditions permitted snow tracking, we backtracked wolves as far as possible to determine travel patterns and to find previous kills. Social status of some wolves was determined from individual histories or behavior (Peterson 1977). We conducted limited aerial searches for nonradioed packs adjacent to those being monitored regularly, but poor light and inadequate snow tracking conditions usually precluded effective use of this technique.

Aerial observations were used to assess

wolf food habits in winter. A direct determination of predation rate for most packs was prevented by poor visibility and tracking conditions, frequent pack splitting, or long intervals between flights caused by poor weather. However, Fuller and Keith (1980) developed an equation that was used to calculate a daily predation rate when packs were located at an average interval of up to 6 days. This was used to determine predation rate for packs that were located frequently during periods of uniformly good visibility. One pack (Swanson River) was monitored with sufficient intensity to provide a complete count of kills.

Records were kept of all dead moose located during 375 tracking flights from August 1976–May 1979. Moose carcasses were most readily located while circling over wolves at low altitude, and most were examined later on the ground. Teeth were collected for age estimation, sex was indicated by presence or absence of antler pedicels, a leg bone (usually femur) was taken for bone marrow fat determination, and any evidence of skeletal pathology (Peterson 1977) was described and collected. We estimated age by counting cementum annuli in molars using reflected light (Wolfe 1969) or in thin sections of incisors using transmitted light. Bone marrow fat content was assessed by the dry-weight method (Neiland 1970), with a correction applied for dehydration (Peterson et al. 1982a).

We classified dead moose as wolf kills if wolves had fed on the carcasses and there was positive evidence of attack, such as chase tracks, a large bloody area in the snow, blood-soaked hair on the lower rear legs, or vegetation that was blood-splattered or broken. Probable wolf kills were those exhibiting definite evidence of wolves' feeding, such as scats in the area and bones heavily chewed and scattered, and simultaneously no evidence of death from any other cause. Those classified as malnutrition deaths had low bone marrow fat (<10% for calves or <20% for adults) and typically exhibited the following characteristics: carcass on sternum in

heavy cover, no sign of struggle, multiple pellet groups nearby, and little or no evidence of feeding by predators. If evidence was conflicting or insufficient, the cause of death was considered unknown. The G test for heterogeneity of age structures and other statistical procedures followed Sokal and Rohlf (1969).

Observations of wolves in summer were not adequate to provide a complete profile of summer food habits, so we collected wolf scats on an opportunistic basis from May through October. Coyotes (*Canis latrans*) were present on the study area, and coyote and wolf scats often are indistinguishable (Weaver and Fritts 1979), so we collected only those scats that could be identified as wolf on the basis of tracks or from known dens and summer homesites.

Hunters and trappers were required to report harvested wolves to the ADF&G and, until 1977, turn in the radius leg bone. Through 1977 ADF&G personnel estimated wolf age (pup or adult) on the basis of radius epiphyseal closure (Rausch 1961). We determined whether or not the wolves taken were from study area packs on the basis of kill location, color, age and sex of the wolf, changes in observed pack size, and contacts with hunters and trappers.

Annual estimates of wolf density were based on (1) the study population in early winter, defined as the total maximum number of wolves in radioed packs or in adjacent, nonradioed packs for which reliable data existed and (2) the census area, defined as the total area (excluding dispersal) occupied by the study population. With few exceptions, radio-collared wolves were found in packs in early winter, the period of maximum pack cohesiveness. Estimated density was slightly conservative because nonradioed lone wolves that were never located with a pack were excluded. Considerations to be made when comparing our density estimates with others are how pack size was assessed, time of year, and inclusion of lone wolves.

Census areas for each year were defined primarily by the territories of radioed wolf packs. Pack territories were represented by convex polygons connect-

ing the outermost locations of each pack. Movements of dispersing wolves and occasional extraterritorial forays of packs were excluded (Appendix 1). Each winter, locations for each pack from 1 October through 30 April were used to determine the pack territory. In summer, with few exceptions, pack members continued to travel within their winter territory.

Wolf movements often were limited by human settlements or topographical features such as bodies of water or glaciers. Where appropriate, such features served to delineate the census area. When pack size and movements were consistent among years, all outer locations for a pack for those years were used to delineate a common census area boundary. If neither of the above conditions was met, boundaries were drawn along annual territory polygons. A detailed rationale for census area designations is presented in Appendix 2.

Although all packs were not included in the census area in all years, we have assumed that heterogeneity of wolf density in census areas was relatively constant among years. Packs along the census area margin were consistently included or excluded from annual density calculations, depending on the availability of data.

Radio-collared wolves were monitored on an intensive, regular basis from August 1976 through May 1980. However, monitoring was limited largely to early winter in 1980–81 and 1981–82. As the number of radio-collared packs declined, early winter searches for all other packs within the former census areas were intensified to determine pack sizes. Thus density estimates for 1980–81 and 1981–82 were comparable with earlier estimates; we believe pack territories did not change sufficiently to invalidate census area designations.

Our capture methods and the sport harvest were biased toward pups and adult wolves respectively and thus proved inadequate for estimating population age structure. We estimated pup : adult ratios for study packs from direct observations or by subtracting spring pack size from

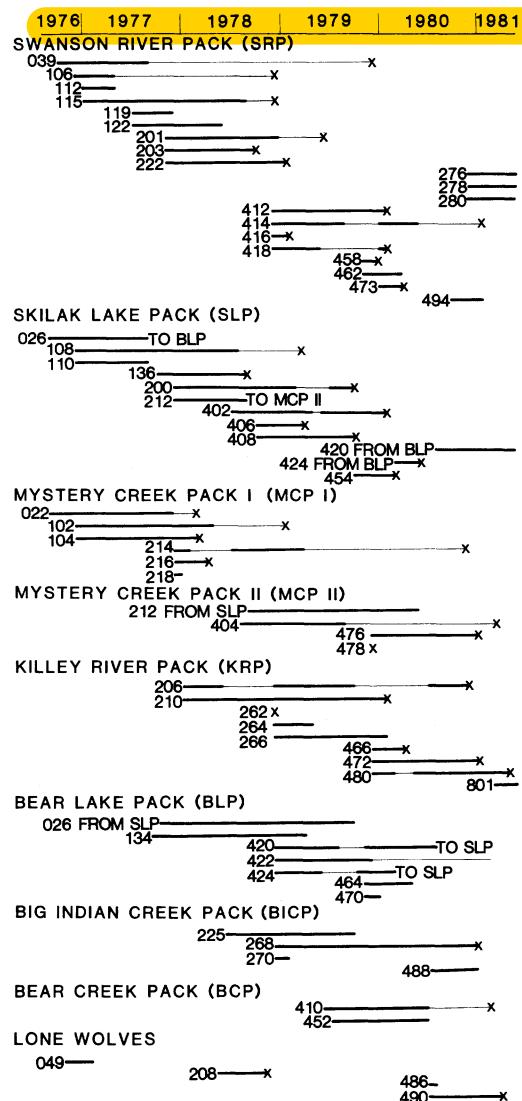


Fig. 4. Wolves radio-collared on the Kenai Peninsula. Broad line represents time with operating transmitter, narrow line the time known to be alive but transmitter inoperative, and X signifies mortality.

subsequent early winter pack size, assuming that loss of adults in the intervening period was offset by low estimates of pack size in spring.

Survival rate was determined monthly for wolves with functioning transmitters. Survival rates for longer periods of time were calculated by cumulative multiplication of monthly survival rates. Dispersal

Table 1. Body weights (kg) of Kenai Peninsula wolves.

	Male weight			Female weight			Difference between sexes (ANOVA)
	N	\bar{x}	SE	N	\bar{x}	SE	
Adults							
May-Aug	6	40.3	2.9	16	33.2	2.7	$P < 0.001$
Late Sep-Apr	15	45.3	3.6	17	35.2	2.4	$P < 0.001$
Total adults	21	43.9	4.0	33	34.2	2.7	$P < 0.10$
Pups							
Oct-Dec	22	32.4	5.3	10	28.7	4.6	$P < 0.001$

loss was calculated in a similar manner. The nature and extent of mortality factors were determined by monitoring radio-collared wolves and from data obtained by the ADF&G reporting program for harvested wolves.

PHYSICAL CHARACTERISTICS OF WOLVES

During the study 64 wolves were captured a total of 87 times, including 2 wolves that died during capture (Fig. 4, Appendix 3). When initially caught, 31 wolves were pups (10 females and 21 males) and 33 were adults (20 females and 13 males).

TAXONOMIC STATUS

The original Kenai Peninsula wolves were assigned to a unique species, *Canis occidentalis* (Richardson), by Osgood (1901) and to a unique subspecies, *Canis lupus alces*, by Goldman (1944). Pedersen (1982) reviewed the taxonomy of present wolf populations in Alaska and compared current Kenai wolf skulls to others from both the original Kenai population and the present mainland population. Preliminary findings are that the Kenai wolves are morphologically close enough to the Interior wolf (*C. l. pambasileus*) to be considered as an ecological race of this subspecies. The variables measured in Goldman's small sample of skulls, when analyzed by multivariate statistical methods, did not provide a clear separation between the original Kenai and Interior wolves.

Physical Condition

Most captured wolves appeared in good physical condition, but there were notable seasonal fluctuations (Table 1). Body weight was less in summer for both males ($P < 0.025$) and females ($P < 0.005$). Seasonal weight differences were not caused by lower weights of yearling wolves in summer; average weight of female yearlings was similar to that of older females in both summer ($P > 0.25$) and winter ($P > 0.75$); the sample of yearling males was insufficient for statistical comparison. With blood samples from both sexes pooled, blood packed cell volume (PCV) was less in summer (47.8) than winter (50.9) ($P < 0.005$). Only 1 adult wolf was captured in both summer and winter. This male (122) weighed 37.2 kg (PCV = 45.5) in July 1977 and 49.9 kg (PCV = 52.2) in November of the same year, conforming to the above pattern. These data suggest a lower food intake in summer (Seal and Mech 1983), but it is not clear whether food was less available or whether wolves voluntarily reduced intake.

Overall appearance of pups and adults was similar in early winter. The 2 pups caught in October had milk canines, but pups caught in November and December had permanent canine teeth in some stage of emergence. Although intact upper canines were longer than lower canines in adult wolves, uppers and lowers were about the same length while emerging in pups. Upper canines of pups averaged 22.3 mm (range 18–29). Unworn upper canines of virtually all adults exceeded 25 mm.

Table 2. Coat color proportions among Kenai Peninsula wolves.

Pack	Total number gray : black						Cumulative % gray
	1976-77	1977-78	1978-79	1979-80	1980-81	1981-82	
Swanson River	20:1	20:0	19:0	8:0	6:0	7:0	99
Killey River		7:6	7:7	9:4	6:2		60
Mystery Creek I & II	8:6	9:7	1:1	5:1			61
Big Indian Creek			7:5	8:6*			58
Bear Lake		1:1	4:4	5:5			50
Skilak Lake	3:8	3:6	4:10	3:2	2:0		37
Total							68

* Maximum observed numbers; entire pack not observed.

Color

Pelage color of Kenai wolves varied from light gray to completely black. Typical gray coloration included many dark markings and bands, especially along the back, whereas belly and flanks were more uniformly light gray or brown. Black wolves often had light coloration on the belly and lower sides and sometimes a white patch on the chest. "Black" pups that did not have a fully developed coat of black guard hairs sometimes appeared brown. No white wolves were observed during the study.

Approximately a third of wolves on the study area were black. The proportion of black wolves was nearly identical among study packs (32%), captured wolves (33%), and harvested wolves reported to ADF&G (30%) (Table 2).

The degree to which packs were genetically isolated from each other was indicated by the proportions of gray: black wolves observed in adjacent packs. Annual variation within packs was small. When proportions for each pack during all years were averaged, packs ranged from 1 to 63% black (Table 2). Litters born to gray parents ($N = 19$ pups) were 100% gray, whereas those born to gray females and black males were 40% black and 60% gray ($N = 25$ pups).

FEEDING ECOLOGY

Carcasses of 387 moose were located during the study, of which approximately

75% were near radio-collared wolves. We examined 301 carcasses or skeletal remains including 264 that were initially located from aircraft. Included were 206 moose killed or probably killed by wolves. We also located 25 moose, including 15 calves, that died of malnutrition from January through May.

Age and Sex of Wolf-killed Moose

Wolf-killed and probable wolf-killed moose did not differ in adult age distribution ($P > 0.50$), adult sex ratio ($P > 0.40$), or proportion of calves ($P > 0.50$). Consequently, these 2 groups were pooled for analysis as the "wolf-killed" sample. Of the 206 wolf-killed moose examined, 47% were calves. The proportion of calves among wolf kills was 36, 39, and 60% in 1976-77 ($N = 53$), 1977-78 ($N = 72$), and 1978-79 ($N = 60$), respectively, and was highest in the winter (Oct-Apr) with greatest snow accumulation (1978-79). Calf percentage in the population was 20% ($N = 606$), 19% ($N = 458$), and 21% ($N = 824$) in the same 3 years, respectively (Spraker 1980). The average proportion of moose calves among wolf kills in other studies has ranged from 13 to 56% and has often been correlated with snow depth.

Extensive gnawing on skulls usually precluded sex identification for calves, but among wolf-killed adult moose 69 were cows and only 3 were bulls. All bulls were yearlings. The low frequency of bulls among wolf-killed adults reflected the

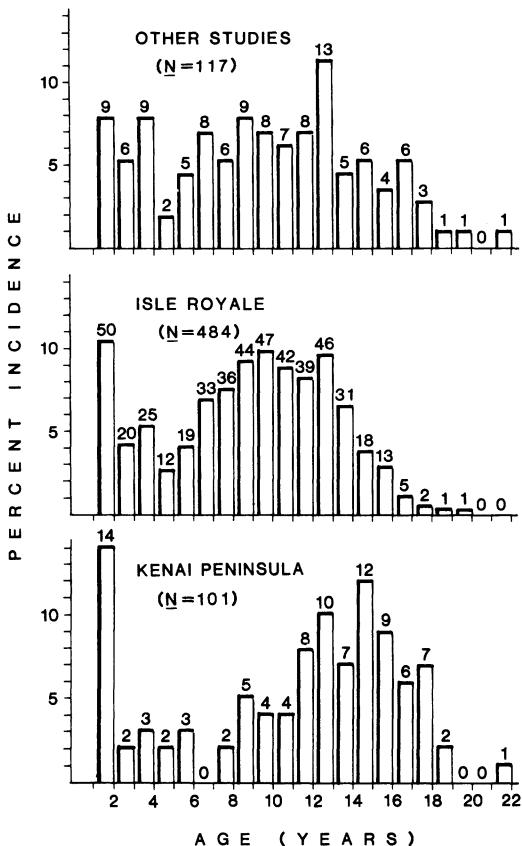


Fig. 5. Age distribution of wolf-killed adult moose in North America. Kenai Peninsula data are from this study. Isle Royale data are from Peterson (1977) and Scheidler (1979). Other studies in Canada and Alaska include Stephenson and Johnson (1972, 1973), Coady (1974, 1976), Stephenson (1975), Haber (1977), Ballard and Spraker (1979), Fuller and Keith (1980), and Hauge and Keith (1981).

scarcity of males on the study area resulting from intensive bull harvest. Bulls composed only 11% of the adults classified in the population in 1976–78, 42% of these being small-antlered (approximately the yearling cohort) (Spraker 1980).

The age distribution of wolf-killed adults was heavily skewed toward old moose, with half >12 years of age (Fig. 5). Many yearlings also were killed, but this age group was not proportionately as vulnerable as the old adults. Average age for adults was 10.9 years (12.5 years if yearlings are excluded).

The age distribution of wolf-killed moose was significantly different ($P < 0.005$) from that of 58 moose captured in 1980 (Table 3). We also compared ages of wolf kills to a series of living age distributions derived for 1977 using 368 hunter-killed moose taken in 1971. Three different natural mortality schedules were combined with 3 levels of recruitment to provide a range of possible age structures (Table 3). The age structure of moose captured in 1980, when corrected for year of collection, was similar ($P > 0.50$) to the "high" recruitment estimate in Table 3. None of the simulated age structures was similar (χ^2 test, $P < 0.005$) to the sample of wolf-killed moose. We conclude that wolf predation selectively removed older moose from the population.

Our simulated age structure masks substantial differences in sex and age structures between moose populations in GMU 15A and GMU 15B, as well as probable differences among local populations within each subunit. Also, the sample of wolf-killed moose came primarily from the 1947 burn within GMU 15A and may not be representative of wolf kills elsewhere on the peninsula. However, our simulated age structures bracket all reasonable age

Table 3. Age structure (%) of wolf-killed moose on the Kenai Peninsula compared with sample of live moose and other possible living age structures.

Age (years)	Wolf-killed moose (1976-79)	Live-captured ^a [1980]	Assumed relative recruitment rate, 1971-77, and simulated 1977 age structure				
			Low ^b	Low ^c	Low ^d	Medi-um ^e	High ^f
1-6	24	65	0	0	0	18	54
7-12	23	26	67	76	88	72	41
≥ 13	53	9	33	24	12	10	5

^a E. E. Bangs (pers. commun.).

^b Zero recruitment with mortality rate based on age distribution of 800 hunter-killed cow moose shot in 1971-73.

^c Zero recruitment with mortality rate derived from age distribution of wolf-killed moose in this study.

^d Zero recruitment with mortality rate derived for Isle Royale cow moose (Peterson 1977).

^e Average recruitment of 2.5 yearlings/100 females with mortality rate derived for Isle Royale cow moose (Peterson 1977).

^f Average recruitment of 10 yearlings/100 females with mortality rate derived from age distribution of wolf-killed moose in this study raised by 8% in each age group to produce youngest possible age structure.

structures for moose on the study area in the late 1970's.

The proportion of very old animals among wolf-killed moose on the Kenai was greater than reported elsewhere (Fig. 5), regardless of an apparent abundance of middle-aged cows (7–12 years old) that might be expected to sustain considerable predation loss. There were no differences ($P > 0.10$) between the age distributions of wolf-killed moose from Isle Royale, Michigan, and from studies in Canada and Alaska. Consequently, these data were pooled and compared to the age distribution of wolf-killed moose from the Kenai Peninsula. There were differences ($G_H = 65.91$, $P < 0.005$) among age distributions apparently caused by the unusually high proportion of old animals in the Kenai sample.

The most reasonable explanation for the large proportion of very old moose among wolf kills from the Kenai is that middle-aged moose may have been more resistant to wolf predation than in other study areas, perhaps because of the later onset of physical degeneration. There is some evidence that Kenai moose (at least females) may become vulnerable to wolves at a later age than Isle Royale moose (Peterson et al. 1982b); arthritis in the coxofemoral (hip) joint occurred much less frequently in cow moose from the Kenai than in those from Isle Royale, even with a higher frequency of extremely old moose (18+ years) in the Kenai sample.

Condition of Prey

The incidence of debilitating conditions among wolf-killed adult moose on the Kenai (35%) was similar to that on Isle Royale (38%, Peterson 1977). In 109 adult wolf kills, debilitating conditions included moderate or severe periodontitis (20 animals), arthritis evidenced by bony deformation (14), bone marrow fat content $\leq 20\%$ (4), broken leg (1), and a leg wedged between trees (1). Bone marrow was checked in only 37% of the wolf-killed adults, and only portions of skeletons were usually available.

Defining what is debilitating for moose confronted by wolves is subjective. Whereas mobility may be impaired when bony degeneration (arthritis) occurs, the influences of malnutrition and periodontitis are less obvious. It is evident, however, that wolves are sensitive to subtle behavior (e.g., flight response) that indicates moose condition. Any behavior or condition that increases the likelihood of wolf pursuit is important. Rau and Caron (1979) found that parasite load was directly correlated with mortality from human hunters. This finding suggests the presence of subtle behavioral responses to changes in physical condition that could be detected readily by wolves.

Bone marrow fat reserves were drawn upon in wolf-killed calves as early as December, whereas wolf-killed adults exhibited marrow fat depletion after February (Fig. 6). We concur with the findings of other biologists in Alaska that moose approaching death from malnutrition characteristically have a bone marrow fat level of $\leq 20\%$ in adults and $\leq 10\%$ in calves (Stephenson and Johnson 1972). In Newfoundland moose with ample food, Fong (1981) found that road-killed moose < 3 years of age commonly had used marrow fat reserves in late winter, but only 11% of 54 yearlings and 2-year olds exhibited marrow fat values $< 20\%$, and no moose older than 3 years had values $< 50\%$. Barrett (1982) found that fat content of femoral bone marrow in winter-killed pronghorn (*Antilocapra americana*) averaged 13, 18, and 20% for fawns, yearlings, and adults, respectively. In that study, femoral marrow fat exceeded 76% for all animals in good condition. Red deer (*Cervus elaphus*) with marrow fat values $< 35\%$ at winter's end were considered by Bubenik (1982) to be in inadequate condition, whereas those with $> 55\%$ fat were in good or excellent condition.

Moose calves were commonly malnourished, with 48% ($N = 31$) exhibiting bone marrow fat content of $\leq 10\%$ after 1 January. Although some calves had bone marrow fat in excess of 70% in early winter (Fig. 6), calves in winter generally have

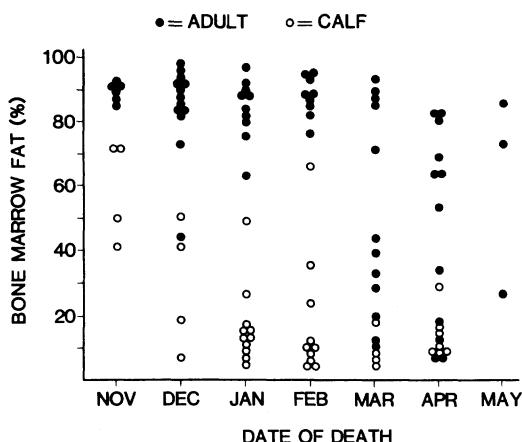


Fig. 6. Bone marrow fat content by month throughout winter for Kenai Peninsula moose dying of natural causes (mostly wolf predation).

less fat in reserve than adults because much of their energy intake in summer must be used for rapid body growth rather than for building fat reserves (A. W. Franzmann, pers. commun.).

Arthritis and periodontitis were generally age-related, first appearing around the age of 6 years (Fig. 7). Arthritis among moose on the Kenai Peninsula was observed only in females as no skeletons of old bulls were examined. Arthritis in females was largely limited to the vertebral column, primarily the sacrum, in contrast to the prevalence of arthritis in the coxo-femoral (hip) joint of moose on Isle Royale (Peterson 1977).

Six pairs of wolf-killed cows and calves were recorded during the study. Of 5 cows with calves examined, 1 had a freshly-broken metatarsus (possibly broken during the wolf encounter), and 2 exhibited moderate periodontitis. The only cow-calf kill recorded outside the winter season was in August 1978, with both animals dying 1 km from the nearest water (escape terrain).

Spatial Distribution of Kills

The spatial distribution of wolf-killed moose and that of the moose population appeared to be similar, underscoring the heavy winter use of the 1947 burn. Al-

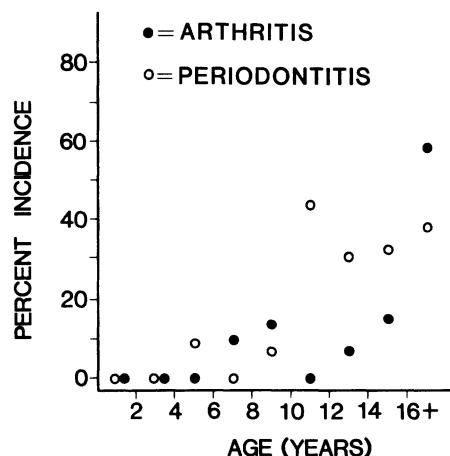


Fig. 7. Age-specific incidence of arthritis and periodontitis among Kenai Peninsula moose dying of natural causes (mostly wolf predation).

though radio-collared wolves were well-distributed throughout the study area, most kills were in the burn, often in the remaining small stands of mature timber.

A concentration of dead calves was obvious in the northern portion of the 1947 burn (Table 4). Kills of old adults were especially frequent north of Skilak Lake (Fig. 8), a known winter concentration area that attracts moose from the mountains to the east and benchland south of Skilak Lake (Bailey et al. 1978). LeResche (1972) reported 500–1,000 moose in a single township (93 km²) in this area in the early 1970's, and we observed >300 moose in this area in 1978.

Kills of 1–6-year-old moose in the 1969 burn were more than twice as frequent as in the 1947 burn (Table 4, Fig. 8). Young adults constituted 28% of dead moose in the 1969 burn vs. 11% elsewhere ($P < 0.01$). The 1969 burn became attractive to

Table 4. Age distribution (%) of dead moose in relation to recent burns on the Kenai Peninsula.

Age (years)	North half, 1947 burn (N = 73)	South half, 1947 burn (N = 94)	1969 burn (N = 40)	Unburned mature (N = 89)
Calf	60	38	32	34
1–6	7	10	28	16
≥ 7	33	52	40	50

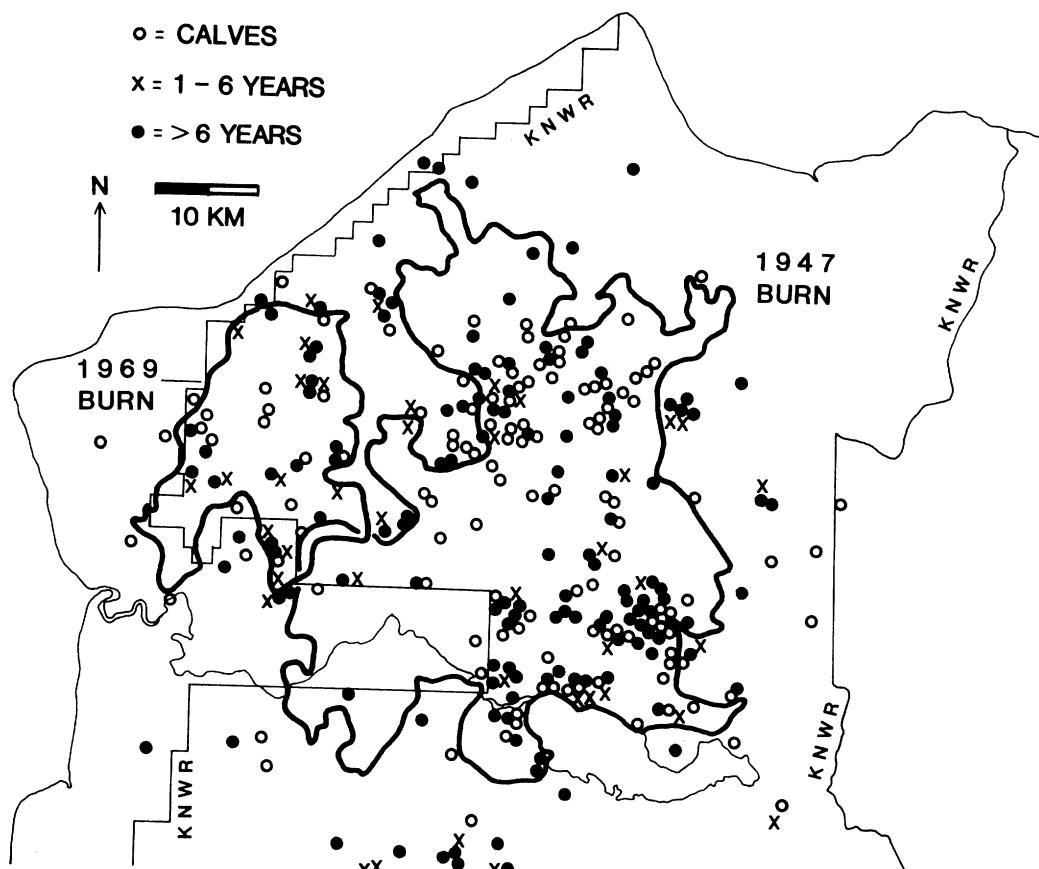


Fig. 8. Distribution of dead moose in relation to recent burns (bold outline) on the Kenai Peninsula lowlands.

moose in about 1975 (J. Oldemeyer, pers. commun.), and in 1979, 348 moose were observed there during an aerial survey covering 260 km², implying a minimum average density of 1.3 moose/km².

Winter Predation Rate and Consumption

Estimated kill rates of packs varied from 1 moose/3.1 days to 1 moose/21.4 days

Table 5. Predation rates for Kenai Peninsula wolf packs preying on moose in winter.

Pack	Dates	Locations (N)	Kills found (N)	Days in interval	Wolves per pack (\bar{x})	Days between kills
Bear Lake	1 Nov 1977–28 Apr 1978	66	12	179	2.0	21.4 ^a
Bear Lake	19 Dec 1978–8 Mar 1979	30	13	80	7.0	3.4 ^a
Skilak Lake	8 Nov 1977–30 Jan 1978	41	10	85	8.2	7.1 ^a
Swanson River	8 Nov 1977–4 Jan 1978	36	16	51	16.3	3.1 ^b
Swanson River	11 Dec 1978–5 Mar 1979	41	12	85	11.2	5.2 ^a

^a Calculated from formula developed by Fuller and Keith (1980).

^b Actual count of kills.

Table 6. Contents of 592 Kenai Peninsula wolf scats from May to October.^a

Season	No. Occurrences	Percent frequency of occurrence ^b									
		Moose				Snow-shoe hare	Beaver or muskrat	Small rodent	Bird	Other prey ^d	Vegetation
		Adult	Calf ^c	Unidentified	All						
Spring and early summer (early May and Jun)	287	28	21	14	63	16	5	5	1	1	8
Mid-summer (Jul to mid-Aug)	217	21	33	18	72	12	3	1	2		11
Late summer (mid-Aug to Oct)	157	15	31	23	69	6	6	4	1	1	14
Total	661				67	12	4	3	1	1	10

^a Collected from Skilak Lake den (1977-78), Mystery Creek den (1977), Bear Lake den (1978), Killey River den (1978), female 039's den (1977), rendezvous sites of Skilak Lake and Swanson River packs, and fresh scats from roads and trails.

^b Nonprey scat contents included wolf hair in 68 (11%) scats and moth larvae deposited on 77 (13%) scats. Bone pieces were found in 247 (42%) scats.

^c By mid-August moose calves acquired a darker coat of hair that more closely resembled adult pelage, thus complicating distinctions between calves and adults after that time.

^d Fish, insects, porcupine (*Erethizon dorsatum*), and a plastic bag.

(Table 5). The average interval between kills in winter for packs >2 wolves was 4.7 days, identical to the interval determined for 1 pack in 2 winters in Alberta (Fuller and Keith 1980) and essentially the same as the average interval of 5.0 days between kills made by Isle Royale packs from 1971 to 1982 (Peterson 1977 and unpubl. data). The Kenai data were gathered when snow depths were average or above-average (Fig. 2).

Applying weights used by Peterson (1977) for edible portions of a carcass and using sex and age of moose killed by the Swanson River Pack (obtained by actual count), we estimated prey consumption at 0.12 kg/kg wolf/day during the period of coverage. The range determined for other wolf packs preying on moose in winter was 0.09–0.19 kg/kg wolf/day (Peterson 1977 and unpubl. data; Fuller and Keith 1980). From this we infer an average level of prey vulnerability on the Kenai.

Like kill rates, the use of prey carcasses was moderate. Usually, lower leg bones were left unskinned and the skeleton remained articulated. Based on edible prey weights from Peterson (1977), adult cow moose provide an estimated 2.3 times as much edible mass as calves; therefore the frequency of adults among kills does not reflect the relative importance of this age-class to wolves. Although adult moose

comprised 53% of the kills, they provided 71% of the biomass available to Kenai wolves in winter. Nonetheless, because calves lack effective defense apart from that provided by their mother, wolves usually prey heaviest on this plentiful age group.

Summer Predation Patterns

Wolf scats from summer contained, in order of abundance, moose, snowshoe hare, beaver, and small rodents (Table 6). Moose accounted for 75% of the scat contents and comprised an estimated 97% of ingested prey biomass (Table 7). High reliance on moose in summer has also been noted in other areas when alternate prey are not abundant, but scat data from our study area suggested that in summer wolves relied more heavily on adult moose than reported in other studies (Table 7).

On the other hand, observations in summer indicated that wolves frequented old kills and probably scavenged extensively. Although there is no evidence that Kenai wolves obtained much food through scavenging, this activity could lead to a high incidence of adult moose hair in scats. We found 50 moose carcasses while locating wolves from June to September, mostly near radio-collared wolves. Most of the remains consisted of nothing more than a

Table 7. Comparative prey use by wolves during summer (May–Sep) in areas where moose constitute the principal prey as indicated by scat analyses.^a

Characteristic and study area	Adult moose	Calf moose	Beaver	Snowshoe hare
Percent prey occurrence in scats				
Kenai Peninsula, Alaska ^b	34	41	5	14
Nelchina Basin, Alaska ^c	9	44	13	14
Alberta, Canada ^d	30	14	34	13
Isle Royale, 1958–61 ^e	12	62	11	4
Isle Royale, 1973 ^f	7	42	51	0
Relative number of prey				
Kenai Peninsula, Alaska ^b	1.00	1.33	0.28	5.10
Nelchina Basin, Alaska ^c	1.00	5.40	2.76	19.20
Alberta, Canada ^d	1.00	0.91	3.56	6.27
Isle Royale, 1958–61 ^e	1.00	5.59	1.71	3.91
Isle Royale, 1973 ^f	1.00	6.45	13.60	0
Percent biomass of prey				
Kenai Peninsula, Alaska ^b	79.3	17.9	1.0	1.8
Nelchina Basin, Alaska ^c	47.1	43.0	5.9	4.0
Alberta, Canada ^d	74.3	15.0	9.0	1.6
Isle Royale, 1958–61 ^e	48.5	46.8	3.8	0.9
Isle Royale, 1973 ^f	36.3	40.8	22.9	0

^a Only moose, beaver, and snowshoe hare were considered; where some occurrence of moose was not classified as adult or calf, it was apportioned on the basis of the adult : calf ratio in the rest of the sample. Assumed whole prey weights (kg), based on Fuller and Keith (1980) and Franzmann et al. (1978), and prey weight (kg) represented by each occurrence in seat (calculated by the method of Floyd et al. 1978) were as follows: adult moose (350, 7.38), calf moose (50, 1.38), beaver (13.3, 0.64), snowshoe hare (1.33, 0.41). Consumable prey weight was estimated at 90% of whole weight for all prey except adult moose (75%) as in Fuller and Keith (1980). Moose, beaver, and snowshoe hare composed the following proportion of all prey occurrences: Kenai Peninsula (94%), Nelchina Basin (81%); Alberta (92%), Isle Royale, 1958–61 (88%); Isle Royale, 1973 (100%).

^b This study (Table 6).

^c All scats totaled (Ballard et al. 1981b).

^d Means for different packs (Fuller and Keith 1980).

^e All fresh scats totaled (Mech 1966).

^f All scats totaled; adult : calf ratio for moose derived from scats deposited before calf molt (Peterson 1977).

large mat of hair and bones. Only 21 were considered probable or definite wolf-kills (primarily from the previous winter), and only 8 (16%) were fresh wolf-kills dating from the summer period. This contrasts with the 80% incidence of fresh wolf-kills among 214 carcasses located from October to May (Fig. 9). Five of the 8 summer wolf-kills were adults, but the likelihood

of finding calf carcasses is small because little time is required for complete consumption.

Other studies suggest a low level of wolf predation on adult moose in summer, even where moose are the predominant ungulate prey. A composite sample of 16 radio-collared adult moose killed by wolves was provided by Coady (1974, 1976) and Hauge and Keith (1981). These moose were monitored on a year-round basis; 15 were killed from October to May, whereas only 1 was killed from June to September. From the stage of antler development observed for adult bull moose dying on Isle Royale, Peterson (1977) determined that only 6% died from May to August.

In the Nelchina Basin of south central Alaska, Ballard et al. (1981b) determined predation rates for radio-collared wolves by direct observation. Predation by abundant brown bears (*Ursus arctos*) caused high losses among moose calves by mid-summer, thereby reducing opportunities for wolves to rely on calves. The Nelchina data suggest that wolf packs killed all ages of moose at about the same rate in early summer (Jun–Jul) as in winter. This is in contrast to our data and the studies cited above and suggests variability in summer predation patterns.

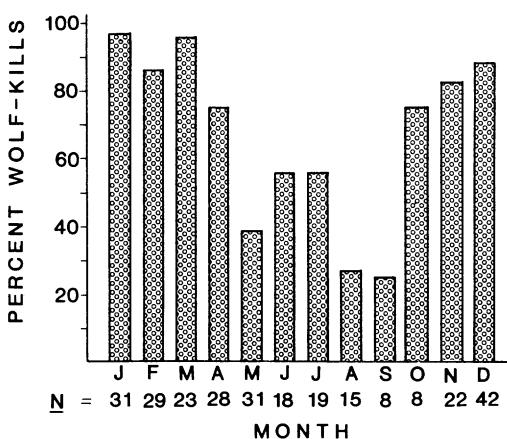


Fig. 9. Monthly distribution of the proportion of moose carcasses visited by wolves on the Kenai Peninsula that were considered fresh wolf-kills.

Table 8. ADF&G estimates of the Kenai Peninsula wolf population (LeRoux 1978 and pers. commun.).

Year	Estimated wolf population	
	Total peninsula	GMU 15A and GMU 15B
1968–69	10	
1969–70	10–15	
1970–71	17–27	
1971–72	27–39	
1972–73	40–71	30–35
1973–74	80–100	
1974–75	102–130	39–44
1975–76	116–160	
1976–77	116–142	36–42

Wolf-Moose Encounters

We observed 38 wolf-moose encounters in which wolves actively tested moose. The defensive behavior of Kenai moose when attacked or approached by wolves was identical to that reported by Mech (1966) and Peterson (1977). Six moose adopted an aggressive posture, and the wolves left immediately, whereas 14 others ran initially but then made a stand and rebuffed the wolves. Eight moose outran pursuing wolves. Significantly, wolves chased every moose that ran during the initial encounter. In the 38 encounters seen, wolves succeeded in killing the moose only twice.

During 6 wolf-moose encounters in April–November, moose escaped from wolves by entering water. In 1 case 5

wolves chased a moose for 0.5 km and then ceased pursuit when the cow swam out into a small lake. In no case did wolves pursue moose into water.

WOLF DYNAMICS

Growth of the Re-established Population

Peterson and Woolington (1982) assembled all reports of Kenai wolves prior to 1976 from ADF&G and KNWR files. Most early sightings were between Skilak and Tustumena lakes. By 1968 wolves also were reported north of Kenai River and south of Tustumena Lake indicating an expanding population, and by 1970 about a dozen reliable sightings were recorded. During 1970–75 an additional 102 wolf observations were recorded, primarily by ADF&G and USFWS biologists. Packs containing >10 wolves were reported from all major areas of the lowlands, with an average of 4.4 wolves seen per observation.

During 1971–77 ADF&G biologist Paul LeRoux conducted several aerial surveys of Kenai wolves based on snow tracking and direct observations by himself and others. Although such surveys have many inherent limitations, the resulting estimates of the total Kenai wolf population (Table 8) suggest a rapid increase in the early 1970's. This was a time of severe

Table 9. Estimated wolf density on the Kenai Peninsula study area.

	Year					
	1976–77	1977–78	1978–79	1979–80	1980–81	1981–82
Census area size (km^2) ^a	3,780	4,401	3,426	3,169	2,796	2,671 ^b
Total early winter wolf population ^{c,d}	43	60	54	44	31–35	48–52
Early winter wolf density (wolves/1,000 km^2)	11.4	13.6	15.8	13.9	11.1–12.5	18.0–19.5
Average early winter pack size (N packs) ^d	15.3 (3)	12.4 (5)	11.4 (5)	9.6 (5)	5.7–6.3 (7)	8.0–8.6 (7)
Average pack territory size (km^2) ^e	864	780	526	487	466	

^a Annual census areas outlined in Figure 8.

^b Census area based on previous year because territory polygons were not available.

^c Sum of maximum observed pack sizes in November and December.

^d Included when data were available were Swanson River, Skilak Lake, Mystery Creek I or II, Bear Lake, Killey River, and Elephant Lake packs (Appendix 6).

^e From Table 10, except in 1980–81, when study area size was divided by the number of contiguous packs on the area.

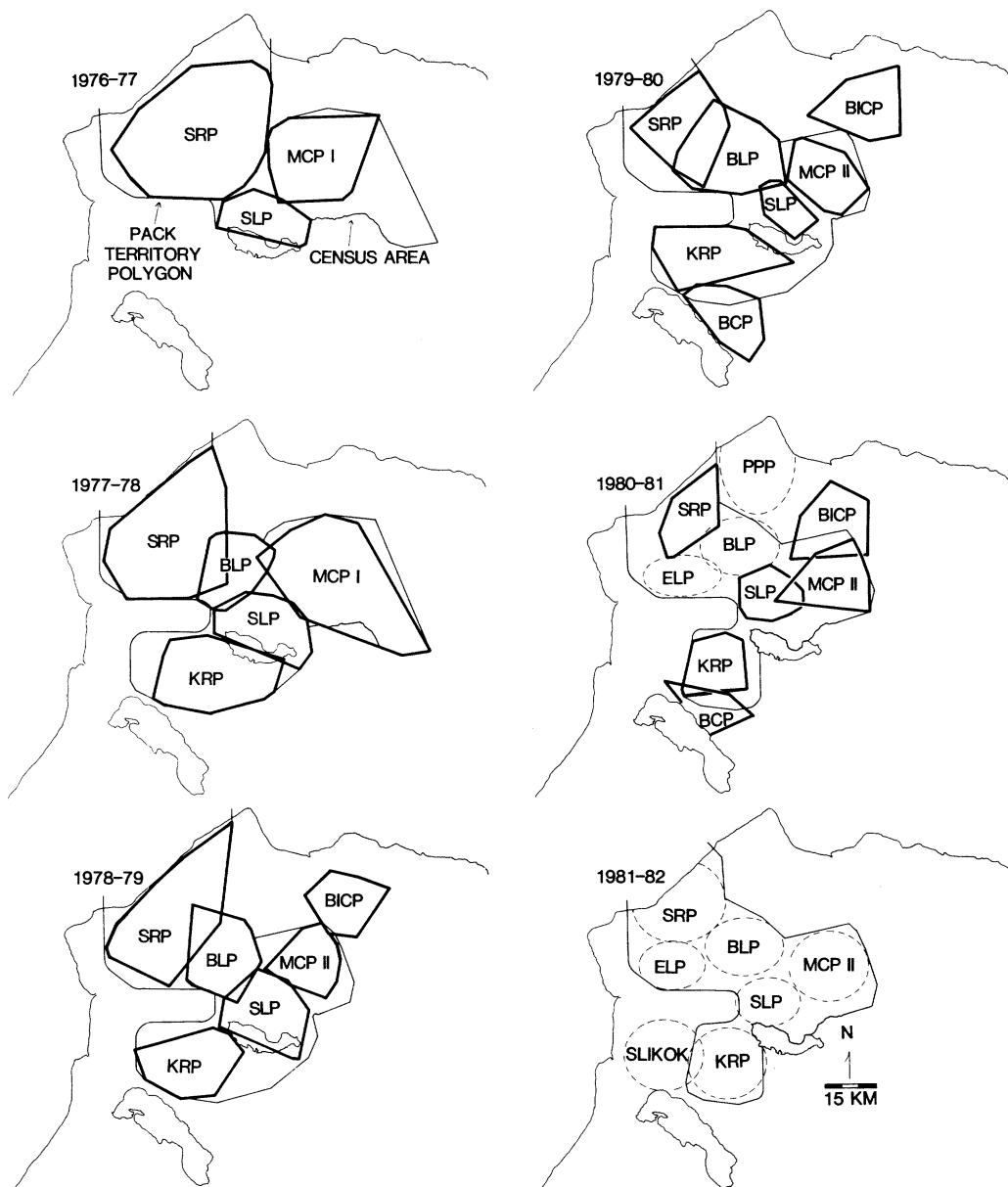


Fig. 10. Wolf pack territory polygons and census areas on the Kenai Peninsula, 1976–77 through 1981–82. Dashed ellipses in 1980–81 and 1981–82 represent approximate locations of packs based on observations and limited data on radio-collared wolves. (See Appendix 2.)

winters, substantial malnutrition loss among moose (Oldemeyer et al. 1977), and presumably ample prey for wolves.

Numbers

During the present investigation, wolf numbers in the study area underwent

marked changes. The density of 11 wolves/1,000 km² in winter 1976–77 increased to 16 in 1978–79, dropped back to 11–12 in 1980–81, and finally increased again to 18–19 in 1981–82 (Table 9). If wolf density is calculated on the basis of pack territory polygons rather than the census areas outlined in Figure 10, the re-

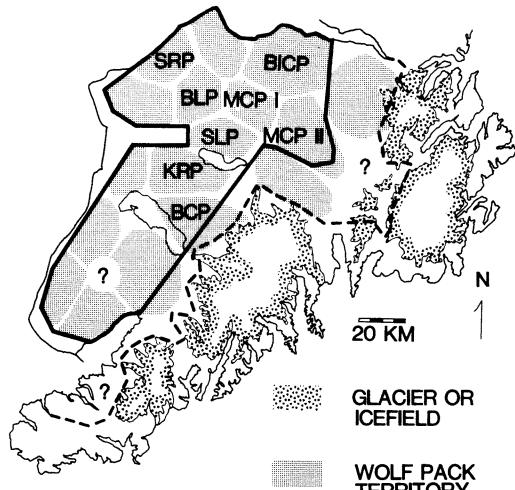


Fig. 11. Territories of radio-collared wolf packs (labeled) and speculative distribution of nonradioed packs (unlabeled) in 1981. Primary (solid line) and secondary (dashed line) wolf habitat is also indicated.

sulting estimates thus weighted for pack size for 4 winters from 1976–77 to 1979–80 are 15.4, 15.4, 20.5, and 18.1 wolves/1,000 km², respectively. These represent known maximum densities and, although exhibiting trends similar to census area densities ($r^2 = 0.61$), these estimates average 1.27 (SE = 0.10) times higher.

Packs were large when the study began (Table 9), and most available habitat on the study area appeared occupied. Trapping and hunting became legal in 1974 but relatively few wolves were killed before our study began (Appendix 4). The rapid phase of initial population growth had ceased by 1976, but 2 new packs (Bear Lake Pack and Mystery Creek Pack II) became established in vacancies that were evident in 1976 and 1977 (Fig. 10, Appendix 5). Therefore, even in 1976 there was some potential for further growth in the wolf population.

For management purposes, the Kenai Peninsula has advantages as a discrete geographical area, and an estimate of its total wolf population has major significance—with the reservation that all such populations are subject to rapid change. We divided the peninsula into primary

and secondary wolf habitat and nonwolf habitat (8,935 km², 5,343 km², and 11,796 km², respectively) on the basis of reported observations and kill records (Fig. 11). Nonwolf habitat included glaciers, ice-fields, heavily settled areas, and the precipitous southeast coast. Density estimates were then applied to the designated habitats. Wolf numbers in primary habitat were assumed to be 16 wolves/1,000 km² (average density for the study area where packs received relatively high hunting pressure was 14/1,000 km²), and a density of 8 wolves/1,000 km² was postulated for secondary habitat. The resulting estimate for the entire Kenai Peninsula was 186 wolves in early winter. Population estimates for GMU 15, GMU 7, and the KNWR were 133, 53, and 82 wolves, respectively.

Pack Size and Territory Characteristics

Average territory size for study area packs was 638 (SE = 367) km² (Table 10). Territory size for packs numbering >2 wolves was correlated ($r^2 = 0.79$, $P < 0.001$) exponentially with pack size (Fig. 12), under the condition of relatively constant prey base. Thus as the Swanson River and Skilak Lake packs both declined, so did their territories. Conversely, as the Bear Lake Pack grew, its territory increased.

If packs of 2 wolves are included in the regression analysis of territory size on pack size, the added data are responsible for a large increase in total residual mean square. Two pairs of wolves that became established in vacancies initially claimed disproportionately large territories. In terms of area per wolf, these animals (Mystery Creek Pack II in 1978–79 and Bear Lake Pack in 1977–78) had 3–4 times more area than members of larger packs. In the following year both pairs reproduced and the area per wolf declined to average levels. Mech (1977a) reported that when a pack declined from 7 wolves to the alpha pair, the pair still occupied most of the original pack territory.

We suggest that minimum territory size

Table 10. Wolf pack size, territory size, and density on the Kenai Peninsula, determined from early winter pack size and October–March territory.

Pack	Year	Territory size (km ²)	Early winter pack size	Wolves/1,000/km ²
Swanson River	1976–77	1,556	20	12.8
	1977–78	1,235	20	16.2
	1978–79	913	18	19.7
	1979–80	563	10	17.9
Skilak Lake	1976–77	325	9	27.7
	1977–78	459	9	19.6
	1978–79	473	12	25.6
	1979–80	177	5	28.6
Mystery Creek I and II	1976–77 ^a	711	14	19.6
	1977–78	1,092	16	14.7
	1978–79	308	2	6.5
	1979–80	378	6	15.9
Bear Lake	1977–78	400	2	5.0
	1978–79	463	8	17.2
	1979–80	684	10	14.7
Killey River	1977–78	713	13	18.2
	1978–79	475	14	29.4
	1979–80	631	13	20.4
Average (unweighted)		638	11.2	18.2

^a Excluded from most calculations because actual territory probably larger than our data indicate (see Appendix 6).

for a newly-formed pair of wolves is one that provides sufficient resources for 1–2 years of pack growth. Thereafter, given a constant food supply, further increases in pack size require a proportional enlargement of territory. Pack size appears to be food related (Zimen 1976); with abundant food, ultimate pack size is related to body size of prey (Peterson 1977).

Although packs were large initially, average pack size declined as wolf harvest increased during 1976–80 (Table 9). This reflected both a decline in maximum pack size and establishment of new packs on the study area. Major changes occurred in 3 different portions of the study area (Appendix 5). Geographical shifts in territory occurred for the Mystery Creek Pack I and the Swanson River Pack, whereas substantial declines in pack size were documented for Swanson River Pack and Skilak Lake Pack. We speculated that the Swanson River Pack shifted westward in

response to increased moose density near the 1969 burn. The shift of Mystery Creek Pack I into the mountains was unexplained. Decline of the Skilak Lake Pack was clearly caused by a high harvest, whereas the Swanson River Pack declined because of harvest, disease, and dispersal. In the latter case we observed a complex transition from 1 pack with 20 members in 1976–77 to 4 packs with 39–41 members in 1978–79; by 1980–81 all 4 packs remained, but wolf numbers had declined to 26–30.

Age and Sex Ratios

The estimated proportion of pups in early winter increased from 26% to 44% in the period 1977–80 (Table 11). We relied on both spring-to-fall increases in pack size and direct observations of pups in late summer for these figures. There are 2 biases inherent in an estimate based on the former method. First, adult mortality and dispersal from May to October (calculated from Table 12 and dispersal frequency data, see Methods) were each estimated to be 13%. This would lead to an underestimate of the number of pups produced. Second, however, lower visibility and less pack cohesion in spring likely resulted in low pack counts and consequently an overestimate of pup production. We have assumed that the first bias was offset by the second.

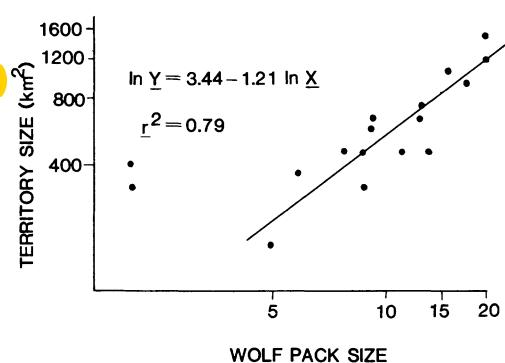


Fig. 12. Relationship between wolf pack size and territory size on the Kenai Peninsula study area, 1976–77 through 1979–80.

Table 11. Wolf pup : adult ratios in November–December in study packs on the Kenai Peninsula.

Pack	Year			
	1977	1978	1979	1980
Swanson River	7:13	4:15	5:5	4:2*
Skilak Lake	2:7	6:8	2:5*	0:2*
Mystery Creek	3:14		4:2*	
Bear Lake		6:2*	4:6	
Killey River		3:11	4:11	3:5*
Mean for all packs	4.0:11.8	4.8:9.0	3.8:5.8	3.5:3.0
Total N	46	55	48	14

* Number of pups determined by direct observations; in other cases spring-fall increase in pack size was used to estimate pup production (see text).

Although the significance of unbalanced sex ratios among wolves is not completely understood, Mech (1975) hypothesized that males predominate among offspring from saturated, high-density populations on a relatively low nutritional plane. We concluded that sex ratio for adult Kenai wolves was approximately equal, because the sex ratio of adults in the recorded harvest in 1974–80 was 95M : 100F. Sex ratio of hunter-killed pups was different from pups we captured. A significant excess of females (23M : 39F) was recorded for pups killed from November to April across the Peninsula ($\chi^2 = 4.1$, $P < 0.05$), but an excess of males (22M:10F) was evident in the pups we captured on the study area during October–December ($\chi^2 = 4.5$, $P < 0.05$). Inasmuch as 29 of the 31 pups were darted, bias due to capture technique seems unlikely.

Wolf harvest intensity may have been higher on the study area than for the entire Kenai wolf population. If wolf numbers there were reduced by hunting, as we suggested, Mech's (1975) hypothesis would predict that pup sex ratio would favor females, at least more so than the overall pup sex ratio on the peninsula; however, the available data suggest otherwise. The predominance of males among wolf pups in this study remains unexplained.

The sex ratio for live-trapped wolves from the study area points up the problem

of obtaining unbiased estimates of sex ratio, as well as suggesting unexplained sex differences in behavior. Fritts and Mech (1981) commented on the seemingly greater susceptibility of alpha females to capture in traps. The sexes of our live-trapped adults were weighted heavily toward females (7M : 19F) ($\chi^2 = 5.5$, $P < 0.025$), with alpha females frequently caught. In 1978 lactating females in 4 contiguous packs were trapped and radio-collared, with 3 of the 4 known to be alpha females. Again in 1979, all 4 individuals were trapped, and again all were lactating. Whereas live trapping in summer seemed selective for females, the sex ratio among adult wolves darted in winter (13M : 9F) was not significantly different from 50:50 ($\chi^2 = 0.45$, $P < 0.5$).

Reproduction

With a single exception, only 1 litter of pups was born annually in each pack. Pups were born to the dominant, or alpha, female in 6 of 7 cases in which we knew the social standing of the mother. Most pup births probably occurred in early May, when radio-collared wolves began frequenting dens. Judged from a highly distended uterus and fresh placental scars, female 424 had given birth to 6 pups just before dying in an illegal snare sometime during 6–13 May 1980.

Six dens of 5 packs were examined after being abandoned. Each den consisted of a single hole and chamber, often little larger than necessary to accommodate a single adult. Four of the dens were dug among the roots of large trees. Both the Skilak Lake Pack and the Killey River Pack used the same dens in 3 consecutive years. Pups were moved to summer homesites in late June or July, usually 2 km or less from the den site. Thereafter, pup activities centered around a succession of homesites, progressively farther from the den, as documented elsewhere (Joslin 1967, Carbyn 1975, Van Ballenberghe et al. 1975, Peterson 1977).

Litter size was estimated from uteri of 4 adult females with placental scars, in-

cluding 1 wolf with 7 wide scars and 5 less prominent scars (we considered this as indicating separate litters of consecutive years). The 5 litters thus indicated by placental scars ranged from 3 to 7 pups ($\bar{x} = 5$). An average of 4.0 pups/pack survived to early winter, based on spring-to-fall increases in pack size and direct observations (Table 11). Significantly, the number of surviving pups was unrelated ($r^2 = -0.08$, $P > 0.75$) to pack size the previous spring (Fig. 13); this takes on importance when considering the response of the population to harvest.

Although 10-month-old wolf pups have bred in rare cases in captivity (Medjo and Mech 1976), most females do not breed until they are at least 22 months old. We examined reproductive tracts from 5 known-age females at least 1 year old. Two yearlings (ca. 18 months old) had no placental scars, indicating that they had not bred as 10-month-old pups. Only 1 of the others (female 424) bred as a yearling; this wolf dispersed from the Bear Lake Pack and became the only breeding female in the Skilak Lake Pack.

Five of 15 captured females at least 2 years old showed no pigmentation or enlargement of teats and probably had never borne young (Appendix 7). Three mature nonparous females (wolves 039, 108, and 136) were known to be socially subordinate. Again, lack of teat development in yearlings suggested that none had bred as pups. However, the usefulness of teat development in assessing individual reproductive history has not been fully assessed. More information is needed on seasonal changes in teat characteristics for multiparous females, the relationship between the number of teats showing use and litter size, and the phenomenon of pseudopregnancy in wolves.

Social status obviously affects reproductive success for pack members. The record of female 039 from the Swanson River Pack suggests a possible fate of subordinate wolves that mate within their pack. This wolf was estimated to be 2–4 years old and a nonbreeder when captured in October 1976. She was clearly a subordi-

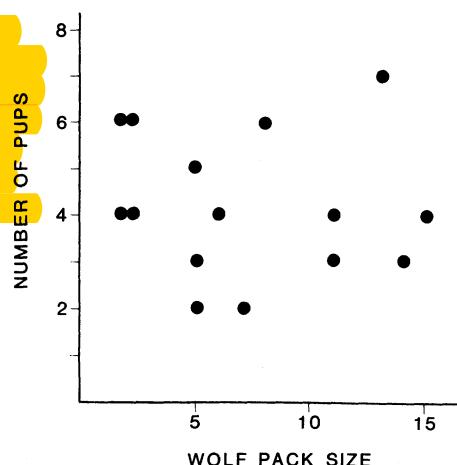


Fig. 13. Relationship between early winter wolf pup numbers (Table 11) and wolf pack size the previous spring on the Kenai Peninsula, 1977–80.

nate wolf, her peripheral status evidenced by the fact that she frequently lagged behind the pack. In 1977, both 039 and alpha female 119 bore young in dens 30 km apart. After establishing a den, 039 was never observed with any other adult wolves. From May 9 until almost mid-June we did not locate her away from the den in dense forest, but in late June, after moving 1 km to a site in more open habitat, we observed her with 7 pups. Thereafter, she was observed with no more than 2 pups that were seen for the last time on August 13. At that time the pups were obviously growth-retarded and about half as large as 119's pups.

At the den site of 039 we found no scats, a moose calf scapula, and no trails leading into the area. We suspect that 039 had attempted to raise her pups alone, inasmuch as we saw no other adults with her and movements of other radio-collared pack members showed almost no overlap with those of 039 (Fig. 14). We can only speculate that all her pups died. We do know that they did not subsequently join Swanson River Pack, because the 3 pups captured in this pack in November were large and no small pups were ever observed. Female 039's radio ceased to func-

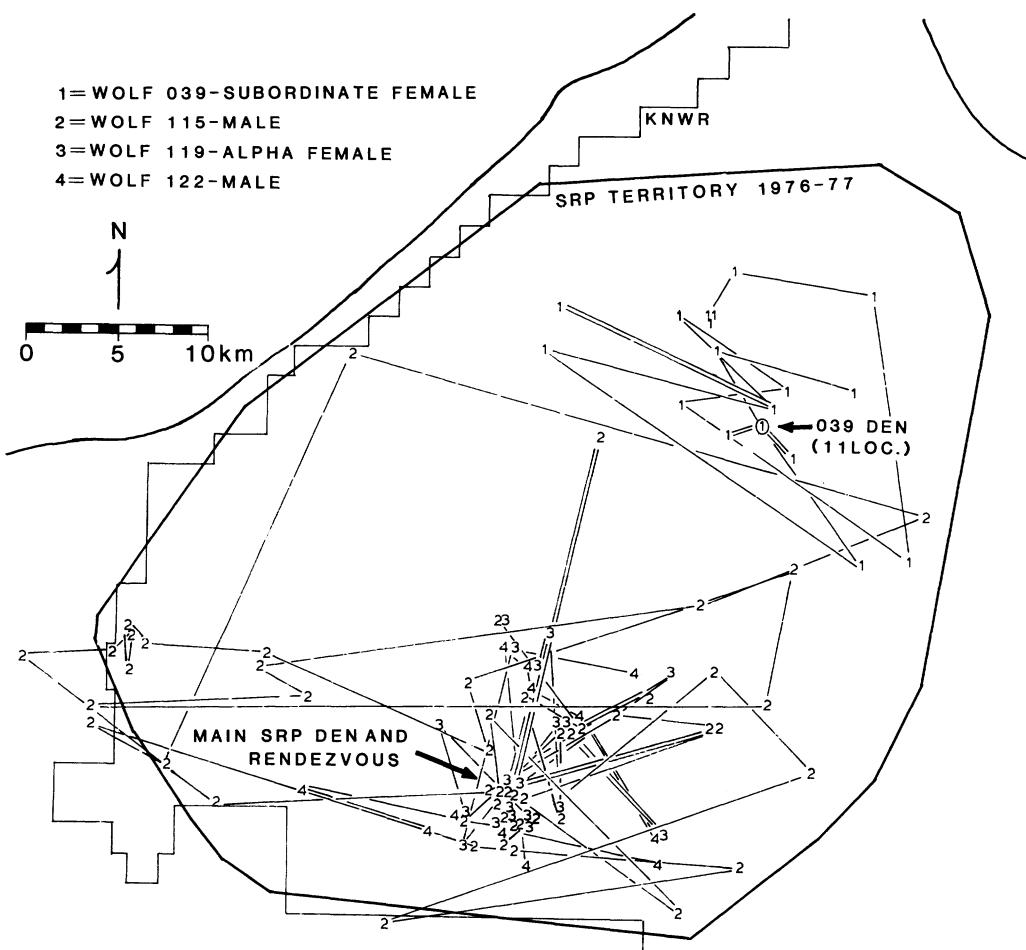


Fig. 14. Movements of Swanson River Pack subordinate female 039 and packmates 115, 119, and 122 during the summer of 1977, superimposed over the 1976-77 SRP territory.

tion in late August 1977, and we did not determine if she rejoined Swanson River Pack. In 1979 she was snared 15 km southeast of this pack's territory with no evidence of pack affiliation.

Inbreeding appears to be common among wolves, but its actual extent and significance remain unclear (Woolpy and Eckstrand 1979). Because of dispersal, adjacent packs may have genetic similarities and inbreeding may even occur when breeders are accepted from other packs. In 1980 the Skilak Lake alpha male paired with a dispersing 22-month-old female (424) from the adjacent Bear Lake Pack;

in 1981, following the death of female 424, the male paired with her sister (female 420). Both 420 and 424 were offspring of male 026, the Bear Lake Pack alpha male. Male 026 originated in the Skilak Lake Pack and very likely had been sired by the old Skilak Lake Pack alpha male. Circumstantial evidence thus indicates that females 420 and 424 bore young after mating with their "grandfather." The 6 pups born to female 424 presumably died when their mother was snared in early May, but 6 pups born to female 420 survived at least 6 months.

Reproduction in a large wolf pack rare-

Table 12. Annual (May–Apr) survival rates among wolves with operating transmitters.

	Wolf-months (N)	Deaths (N)	Annual survival rate ^a
Year			
1976–77 ^b	64	0	1.00
1977–78	122	1	0.92
1978–79	198	6	0.67
1979–80	178	10	0.52
1980–81	104	7	0.44
Class			
Resident adults	410	11	0.73
Dispersing adults	112	10	0.38
Pups	144	3	0.88 ^c
All wolves	666	24	0.67

^a Calculated from monthly survival rates (see Methods).

^b No wolves were monitored in May, June, and July.

^c Survival rate after 5 months of age.

ly reaches its potential level. In studies of captive wolves, Rabb et al. (1967) and Zimen (1976) found that mate preference and dominance relationships reduced the frequency of mating. Peterson (1979) observed a subordinate female chased from a pack after mating but did not determine the eventual fate of the animal. In this study we found that social relationships not only moderated mating frequency but also affected relative success in rearing pups.

Survival

Annual survival rate for radio-collared wolves declined during each year of the study, from 100% in 1976–77 to 44% in 1980–81 (Table 12). Wolves traveling outside of their pack's territory suffered high mortality. Virtually all such wolves observed were adults. The annual survival rate for dispersing adults was only 0.38, compared to 0.73 for resident adults. Dispersing adults accounted for 10 of the 21 deaths recorded among radio-collared adult wolves in this study.

No pups were monitored before October. The survival rate for pups from October to April (0.88) approximated that of resident adults for the same period (0.85).

Pup survival from May to October appeared to be 0.80 (litter size of 5.0 compared with 4.0 pups/pack in early winter). Estimated annual survival of pups was then 0.70 (0.80×0.88), approximately that of resident adults.

Average annual survival for all radio-collared wolves was 0.67. This was corroborated by an additional estimate based on the relative proportions of pups, resident adults, and dispersing adults in the population and the annual survival rates estimated for each group. Pup proportion was estimated at 36% (Table 11). The proportion of resident and dispersing adults was estimated at 54% and 10%, respectively, because 16% of the total monitoring time for adults was spent outside their pack's territory. The resulting estimate of annual survival rate for the composite group was 0.68.

The maximum annual increase measured for wolves appears to be 1.32, recorded for Isle Royale wolves (Peterson 1977). If this is the maximum rate of increase for a wolf population, then the average annual mortality rate of 0.33 ($1 - 0.67$) estimated for our study area wolves is high enough to prevent further increase. The extent of reduction would depend on actual pup recruitment. In our study, correlations between population fluctuations and wolf harvest support this view.

Table 13. Wolf harvest summary for the northern Kenai Peninsula lowlands.^a

Regulatory year	Wolves killed	Estimated early winter wolf population ^b	Estimated % harvested
1976–77	6	41	15
1977–78	8	48	17
1978–79	26	56	46
1979–80	21	50	42
1980–81	14	40–45	31–35
Average	15	47–48	30–31

^a GMU 15A and northern half of GMU 15B (3,566 km²); summary of ADF&G data (Appendix 4).

^b Derived by applying census area wolf density to the northern lowlands. Following are packs that were included in density calculations, if data were available: Swanson River, Skilak Lake, Mystery Creek I and II, Bear Lake, Killey River, and Elephant Lake.

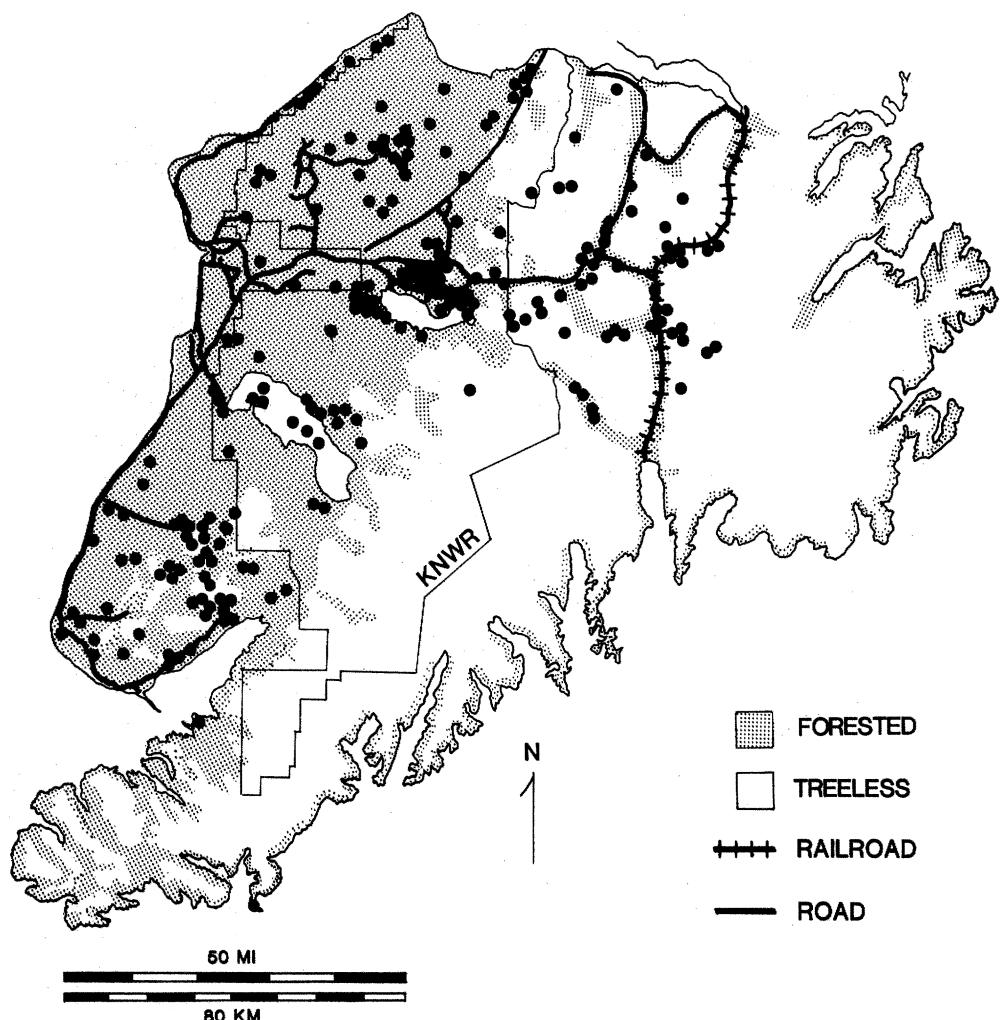


Fig. 15. Distribution of reported wolf harvest on the Kenai Peninsula from 1974–75 to 1979–80. Each dot represents one wolf killed and reported.

Mortality Factors

Harvest by hunters and trappers was the primary cause of mortality of our radio-collared wolves (all at least 5–6 months old). Of the 23 radio-collared wolves that died when transmitters were operating, 18 were killed by legal harvest, 3 died from natural causes, and 2 died from illegal or unknown causes.

The harvest of wolves by hunters and trappers on the study area and the entire Kenai Peninsula increased to a peak in

1978–79, then declined in 1979–80 and 1980–81 (Table 13). We estimated the early winter wolf population on the northern lowlands by applying wolf density determined for study packs to the 3,566 km² of wolf habitat contained in GMU 15A and the north half of GMU 15B. The legal kill in this area was obtained from ADF&G records. The magnitude of annual take was indicated by the proportion removed from the early winter population. This ranged from 15% in 1976–77 to 46% in 1978–79. The magnitude of recreational harvest on

the Kenai study area in 1978–79 and 1979–80 was comparable to that of a formal wolf control program accomplished by aerial shooting in interior Alaska (Gasaway et al. 1983).

Hunting and Trapping.—Wolf harvest was first allowed in 1974. In 1976–77, when our study began, regulations set by the state became identical to those in most of Alaska. Regulations required that every wolf taken be reported to ADF&G. Compliance with this regulation on the Kenai was good, but reported harvest must still be considered a minimum estimate of the actual kill. One radio-collared wolf (402) probably was killed but not reported, and 3 wolves, including 2 that were radio-collared (424 and 480), were found dead (and unreported) in abandoned snares.

Wolf harvest patterns were clearly linked to human access and visibility. Wolf harvest was highest in accessible portions of GMU 15A on the study area and in treeless areas in GMU 15C on the southern lowlands (Fig. 15). Snares and traps, taken together, were the principal means of taking wolves and were responsible for 56% of the reported total, whereas shooting was reported for 40% of the total harvest (Appendix 4).

Natural Mortality.—Deaths of 3 radio-collared wolves were attributed to natural causes. A malnourished pup from Killey River Pack died in March 1980. Two yearling wolves in the Swanson River Pack died, one in 1978 and one in 1980; both tested positive for canine distemper virus (CDV), and distemper was the presumed cause of death. This was the first recorded wolf mortality from CDV in Alaska, although similar cases have been reported from Manitoba (Carbyn 1982).

In light of known mortality from distemper among Swanson River Pack wolves, the decline of this pack in 1978–80 may be circumstantially linked to loss from disease as well as human harvest. One death followed closely an outbreak of distemper among dogs in the Kenai–Soldotna area, immediately adjacent to the Swanson River Pack territory.

Population Response to Harvest

Generalizing from the data of Rausch (1967) and others, Mech (1970:64) concluded that wolf populations could replace annual losses of about 50%. Unfortunately, the distinction between 50% loss and 50% harvest has been ignored, leading to the erroneous assumption that a 50% harvest would not lead to a decline in wolf density. This is a common assertion in the popular press and the basis for some wolf management programs (Rearden 1980).

In several recent studies, however, removal of 40% or less of the wolves present in early winter often led to a population decline the next year (Ballard et al. 1981b, Van Ballenberghe 1981, Gasaway et al. 1983). After reviewing several studies, Keith (1983) suggested that a kill exceeding 30% might be expected to reduce wolf numbers the next year.

Wolf density on the Kenai study area declined following 2 annual kills that exceeded 40%, but increased after 3 harvests of <35% (Fig. 16). These correlations, together with the fact that average annual mortality was comparable to the maximum observed rate of increase for wolves, strongly suggest that wolf density was regulated by the harvest, the dominant form of mortality. Whereas this study generally supports Keith (1983), resilience of different wolf populations will vary with changes in average litter size, pack size, and natural mortality rate. The effects of specific harvest levels will vary among populations and over time. Keith's 30% figure should be applied with an understanding of the above variables.

Our data indicate that a principal impact of hunting and trapping was the reduction of pack size (Fig. 16). Average pack size (Table 9) declined from 15 to about 6 wolves in 4 consecutive years as mortality increased (Table 12). However, pup numbers varied independently of pack size (Fig. 13), and 1 litter/pack predominated. Thus the proportion and total number of pups increased as additional packs developed on the study area and the

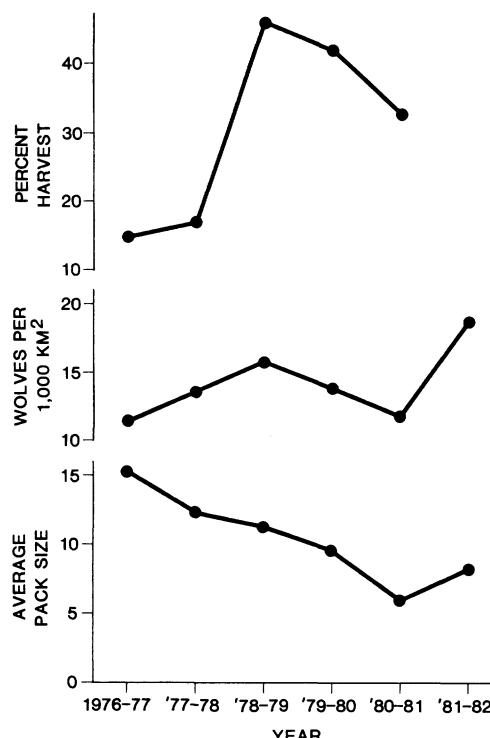


Fig. 16. Annual fluctuations in wolf density, pack size, and wolf harvest on Kenai Peninsula study area.

number of adults per pack declined (Table 11). We suggest that the increased proportions of pups and breeding females in exploited wolf populations (Rausch 1967) may result simply from constant litter size in smaller packs. Wolf density can be maintained in moderately cropped populations if additional packs (reproducing units) develop in vacancies created by reduced territory size of established packs. Measured territory size and pack size were directly correlated, at least for packs containing >2 wolves. As annual kill increased, the number of packs on the study area increased. The average space occupied by each pack (Table 9) was directly correlated with average pack size ($r^2 = 0.66$), and as average pack size declined and vacant territory appeared, additional packs developed.

It is unlikely that all of the new packs on the study area developed as a result of increased man-caused losses, inasmuch as

both Bear Lake Pack and Mystery Creek Pack II developed before hunting and trapping were significant. In response to the annual reductions and, probably to a lesser extent, final "filling in" of the wolf population after re-establishment, the number of packs per unit area increased. For example, in 1976-77 the Swanson River Pack containing 20 wolves occupied a large territory. By 1980, the pack's original territory contained 3 packs (Swanson River, Elephant Lake, and Point Possession) totaling 20 wolves, and a portion of the area originally occupied had been lost to the Bear Lake Pack.

BEHAVIOR

All but 4 of the 64 wolves radio-collared in this study were members of packs when captured. Relationships within and among these packs were dynamic, and we also evaluated the use of territory, pack cohesiveness, and relationships with bears.

Observed Activity

Changes in wolf activity patterns have been linked to nutritional status, which was indicated by increased sleeping and less travel during periods of poor hunting success (Mech 1977a). In our study, wolves in winter (Oct-Mar) were traveling in 50% of the observations ($N = 1,710$); wolves rested or slept during 24% and 15% of the winter sightings, respectively. Sleep, usually associated with recent feeding, was most common for wolves near kills in winter. The percentage of sightings during which wolves were traveling and sleeping in this study approximate those recorded by Mech for wolves at a high level of hunting success. There was little annual variation in activity.

Wolves were traveling during only 29% of the summer observations ($N = 512$). Although wolves slept little (6%) during daylight hours, they were most often resting (50%) in summer. Continuous monitoring of some wolves at dens (Peterson, unpubl. data) suggested that in summer most travel was at night.

Pack Cohesion and Interpack Associations

An index to pack cohesion was developed, based on packs in which >1 wolf was radio-collared. The index is the proportion of the time (no. locations) radioed wolves were together relative to the total number of times located. Thus, if 2 wolves were radio-collared in a pack and were together during 6 out of 10 locations, the cohesion index would be 0.60. Packs were most cohesive in November and December (Fig. 17); at this time pups were traveling with the adults, and peripheral adults were most likely to travel with packs. As the breeding season in February and early March approached, pack cohesion declined, reaching a winter low in March, which coincided with extraterritorial movements and dispersal. The return of some wolves to packs in April resulted in increased pack cohesion; it then dropped to a summertime low from June to September. Packs that consisted of only pairs or pairs and their pups exhibited higher pack cohesion than large packs at all times of the year and did not show as much decline in cohesiveness during the breeding season.

Apart from cases involving new pack formation, wolves from different packs rarely were found together. We recorded 7 instances of 1 or more wolves associating with other packs or individuals from other packs (Appendix 8). With the following exception, all such associations involved the Swanson River Pack (SRP) and Mystery Creek Pack (MCP). On 2 January 1979 male pup 414 from SRP was seen with 1 black and 2 gray wolves. At this time there were no black wolves in SRP. The 4 wolves were bedded on a lake, each separated by about 10 m from the others. Later the same day, 414 traveled single file with the other 3. They were located in the southern portion of SPR territory, where in the following year a discrete pack of 1 black and 2 gray wolves existed (the nonradioed Elephant Lake Pack).

Although most associations of wolves from different packs involved only a small

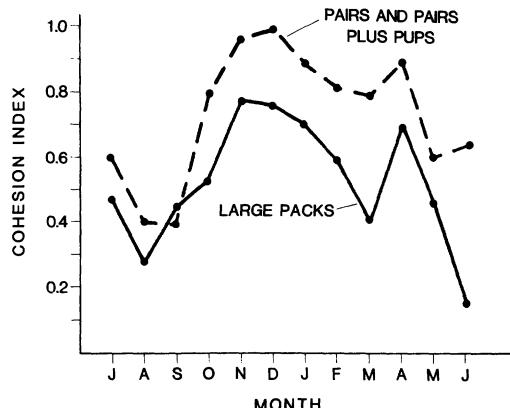


Fig. 17. Monthly distribution of wolf pack cohesion index for large (>2 adults) and small wolf packs on the Kenai Peninsula. The index is the number of locations radioed wolves were together divided by the total number of locations.

number of wolves, we twice observed 1–2 wolves from SRP with all or most of the MCP. After a MCP extraterritorial foray on 22 February 1977 brought them to the edge of SRP territory, SRP male 112 appeared to follow them back into MCP territory, associating first with MCP female 022 and then with the whole pack while on a kill on 3 March. At that time, we counted 6–7 wolves in the same area as female 022 and male 112 and concluded that 112 was with MCP. Two days later we found 11 wolves from MCP at the same site and male 112 traveling 3.4 km away, with a set of wolf tracks leading from the MCP to 112. About a year later, SRP males 112 and 201 associated with the MCP, together comprising a group of 15 wolves.

The relatively frequent association of SRP wolves with MCP suggests an unusual relationship between these 2 packs, perhaps former familial bonds. No such associations were recorded for wolves in any other packs, and this we regard as the more typical situation.

Seasonal Use of Territories and Dispersal

Spatial distribution of wolf activity was determined by a mean radius of activity calculation, representing the average dis-

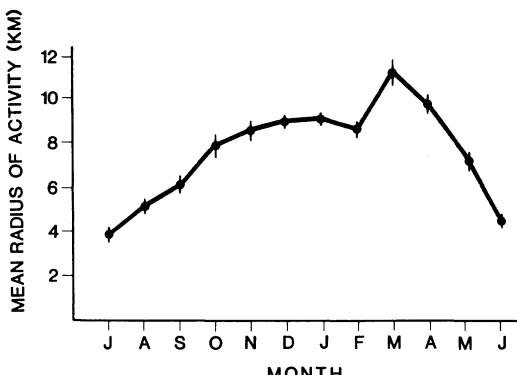


Fig. 18. Monthly mean radius of activity ($\text{km} \pm \text{SE}$) for radio-collared Kenai Peninsula wolves. Only lowland packs that exhibited no significant between-year shifts in territory location (i.e., Kiley River, Skilak Lake, and Bear Lake packs) were used in this analysis.

tance from all selected locations to the geometric center of these locations. Data from all years were pooled for packs on the lowlands that exhibited no annual shift in summer activity areas (dens and homesites). Packs inhabiting mountainous areas were not located frequently in summer. At other times the mountains often prevented us from locating wolves that were distant from known centers of activity; therefore, they were excluded from consideration.

Activity radii were shortest in June and July (Fig. 18) when adult activity was centered around relatively sedentary pups. Travel became more widespread by late summer and fall and remained extensive from November through February. The activity radius increased abruptly to a peak in March, when we observed frequent extraterritorial movements and dispersal. From March until June there was a rapid contraction in the range of pack movements. If the March peak caused by extraterritorial movements is ignored, pack movements within territories were most extensive in early winter when the entire pack traveled together. Shortly after the pups accompanied the adults on a regular basis, the packs typically fell into a pattern of wide-ranging movements, apparently visiting many parts of their territory for the first time since the previous winter.

One third (21 of 64) of the wolves we monitored dispersed from their original pack. Extraterritorial movements of pups were negligible, but radio-collared adults spent 16% of total monitoring time outside their home territory. Dispersing wolves rapidly colonize vacant territory (Fritts and Mech 1981), and thus dispersal is an important characteristic of wolf populations from both standpoints of management and population dynamics. Linked to a basic dispersal pattern was a variety of extraterritorial movements, ranging from brief exploratory forays to abrupt long-distance dispersal.

Lone wolves that have dispersed from their original pack travel along pack territorial boundaries and avoid established packs. Successful colonization requires both locating a suitable vacancy and bonding with a mate (Rothman and Mech 1979). In our study, with few exceptions, wolves that left their pack territories traveled alone. In 3 cases a pair of wolves left together, but in each case they later separated and traveled independently. Often dispersal was gradual, with a wolf breaking ties with its pack over a period of weeks. Van Ballenberghe (1983) also found that dispersing wolves may temporarily renew ties with their original pack. We followed a few wolves until they found vacant space and a mate, and established a new pack. Some wolves returned to their pack after odysseys lasting weeks, whereas others traveled out of our range. Wolf 214 left the Kenai Peninsula and was later killed 180 km away, in south central Alaska. Being more vulnerable in unfamiliar surroundings, a large proportion of dispersers were killed by humans (Appendix 9).

Many of the extraterritorial movements (31%) and eventual dispersal movements (27%) started in February, coinciding with the beginning of the breeding season (Fig. 19). Wolves in captivity show a peak in agonistic behavior during the breeding season (Rabb et al. 1967, Zimen 1976). Factors affecting the dispersal pattern of a population are poorly understood, but social interactions within packs are of ob-

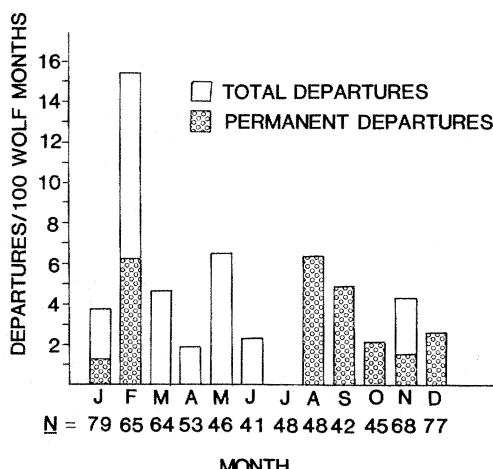


Fig. 19. Monthly frequency of extraterritorial movements of Kenai Peninsula wolves, 1976–81.

vious importance (Packard and Mech 1980).

Other studies have indicated that most dispersers left in late summer or early fall (Ballard et al. 1981b, Fritts and Mech 1981) or throughout the year (Van Ballenberghe 1983). Average pack size was larger in our study than in these others, and we speculate that a higher level of social stress in large packs might prompt more frequent extraterritorial movements during the breeding season. Aside from an unusually high frequency in February, extraterritorial movements of Kenai wolves (including dispersal) were well-distributed throughout the year.

Extraterritorial movements during and after the breeding season were most often exploratory, with the wolf usually returning to its pack. During January–May, only 5 of 20 extraterritorial movements resulted in permanent separation, whereas in other months 10 of 12 such movements resulted in permanent dispersal. This likewise suggests social stress in the breeding season as a motivating factor, although an unknown portion of "permanent" dispersers probably would have returned to their packs if they had not been killed.

Characteristics and Fate of Dispersing Wolves.—Although details of an individ-

ual wolf's social status were rarely known, we can be reasonably sure that no dispersers were alpha wolves. Yearlings and 2-year olds, unlikely to be dominant in relatively large packs, comprised 11 of 18 dispersers; of the 6 older dispersers, 4 (026, 039, 106, 212) were known subordinates.

The record of male 106 suggests that dispersal is closely tied to social status. We believe this wolf was the alpha male in a pack of 20 wolves (Swanson River Pack) prior to his capture in December 1976. The only black wolf in the pack, he was considered dominant because he actively scent-marked and often led the pack (Peterson and Mech 1975, Peterson 1977). After collaring, he assumed an obviously subordinate role. In another case reported by Rabb et al. (1967), an alpha wolf was unable to reassume its dominant role after being removed for a few days from a captive pack for experimental purposes. Less than 2 weeks after being collared, male 106 abruptly dispersed and eventually

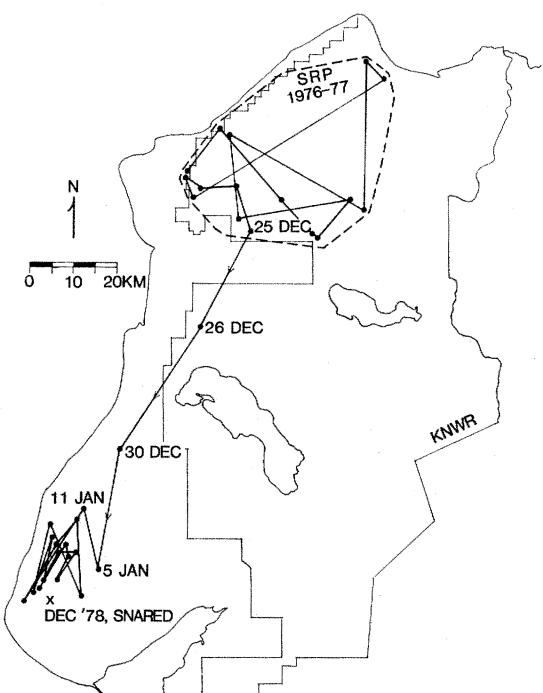


Fig. 20. Dispersal movements of male wolf 106, who left Swanson River Pack (SRP) on 25 December 1976 after losing dominant status.

founded a pack near the southern end of the Kenai lowlands (Fig. 20). We believe the change in social status was the primary motivation for this wolf to disperse. This was the only case in which we had any knowledge of proximal factors that might have prompted a wolf to leave its pack.

During 1976–80 there was a preponderance ($P < 0.025$) of males (10 of 12) among dispersers from study packs. However, when dispersers from 1980–81 plus 4 loners are added (totaling 13M:9F), the sex ratio was not significantly different from 50:50 ($P > 0.40$). Total monitoring time for adults of both sexes was virtually identical in this study. It is not clear whether the high proportion of dispersing males early in the study was an artifact or somehow was related to the large average pack size at that time. Other studies, generally involving smaller packs, report a male preponderance among dispersers (Mech 1970, Ballard et al. 1981b). There seemed to be a tendency for females to disperse a shorter distance than males. Of the 8 wolves that left the study area, only 1 was female; the probability of obtaining such a skewed sample from a population with an even sex ratio is 0.11.

Dispersing wolves are rarely pups (Fritts and Mech 1981). In the present study, only 1 radio-collared pup dispersed; male 462 left Swanson River Pack with 1 adult, which subsequently separated from the pup and dispersed to the south. The radio signal from the pup disappeared near the Kenai mountains.

Dispersers were highly vulnerable to hunting and trapping; of the 18 radio-collared wolves that left study packs, 10 died within a year and the fate of 2 was unknown. Six survived more than a year, and all but 1 of these were known to have developed associations with other wolves, usually by founding new packs; at least 4 of these 6 wolves eventually reproduced. Of the 4 lone wolves captured and radio-collared, 2 were killed by humans and the other 2 left the study area. Thus, at least 4 but not more than 8 of the 18 dispersers

in this study successfully reproduced outside their original packs.

The annual survival rate (Table 12) for radio-collared wolves outside their territories (0.38) was half that of wolves within their territories (0.73). Extensive travel in unfamiliar areas and a lesser tendency among dispersers to avoid settled areas probably explains this high mortality rate.

We inferred from their high vulnerability that dispersers constituted a significant proportion of the wolf harvest. We tried to determine pack origin for each wolf taken on the study area through our close monitoring of pack sizes and information on wolves killed (location, pelage color, sex and age, and reports of hunters and trappers). During the study, 18 (20%) of the 89 wolves killed on the study area were judged to be dispersers with an unknown origin. Additionally, 6 (7%) collared wolves that dispersed from study packs were killed on the study area. Thus, dispersing wolves comprised 27% of the wolf harvest on the study area.

Five dispersers eventually settled and began the process of pack formation. Male 106 left Swanson River Pack and traveled quickly to the southern end of the lowlands (Fig. 20). Within a month this wolf became associated with 2 others, and this trio was consistently together for the remaining 2 months of monitoring. The following winter, 6 wolves were reported in the area where 106 had settled, and he was eventually snared in the same area.

Wolves 026 and 212, both subordinate males in the Skilak Lake Pack (SLP), dispersed in the summers of 1977 and 1978, respectively. Male 212 had undertaken extraterritorial movements during the previous winter and earlier in the summer. After pairing with female 404 in vacant territory northeast of SLP territory, male 212 apparently never returned to his original pack. On the other hand, male 026 returned to SLP at least twice after pairing with female 134 in vacant territory northwest of the SLP. In early October 1977, about a month after pairing with wolf 134, wolf 026 returned to SLP

without his mate and fed on at least 1 fresh kill during his 2 weeks of renewed association with the pack. Then he departed and traveled with 134 in their new territory for about 10 days, but on 21 November he was again with the SLP, near the edge of SLP territory. Wolf 134 was moving away from the area, evidently after accompanying 026 to the boundary of SLP territory. This time 026 remained with SLP for about a week, fed on another fresh kill, and finally returned permanently to his new mate and territory.

Female 424 dispersed from Bear Lake Pack (BLP) in February 1980 and assumed the role of alpha female in the Skilak Lake Pack (SLP) about 6 weeks after the former SLP alpha female (402) disappeared. Female 424 died in a snare in early May 1980, shortly after giving birth to 6 pups. Three months later her sibling, female 420, dispersed from BLP to SLP, paired with the SLP alpha male, and in 1981 apparently raised a litter of pups successfully.

Extraterritorial Movements of Packs.—Wolf packs trespassing onto neighboring packs' territories is a common response to food shortage (Mech 1977b). However, Carbyn (1981) provided an account of 1 pack displacing another even when ample food was present. In our study, several extraterritorial movements of packs were documented, and none seemed associated with food shortage. In 1 case extraterritorial movements coincided with intensive hunting and trapping, as detailed below.

In 1977, Mystery Creek Pack I and Skilak Lake Pack both traveled briefly beyond their territorial boundaries in February and April respectively, and each was located as far as 18 km beyond their customary boundaries. As both packs killed moose on a regular basis within their territory throughout the winter, food shortage did not adequately explain these movements.

Extraterritorial travel by the Swanson River Pack (SRP) in winter 1978–79 was associated with frequent pack splitting and

a period of intensive airplane-assisted (land-and-shoot) hunting. The SRP began the winter of 1978–79 as a cohesive pack of 16 wolves. The pack split only temporarily after we darted 4 wolves on 1 December. The pack again split into groups of 6 and 12 on 11 December as 2 more wolves joined the pack. Two wolves were shot in 1 group on 23 December and 2 more in the other group on 2 January. On 2 January the 4 wolves remaining in 1 group left SRP territory, heading northeast through the territory of the nonradioed Point Possession Pack (PPP). On 4 January, 6 of 10 wolves in the other group left in the same direction, and only 4 SRP wolves remained in their territory. Both extraterritorial groups declined in number rapidly, some interchange between groups and dispersal were noted, and 2 wolves associated briefly with wolves in Mystery Creek Pack II. Six more wolves were shot during this time but only 1 seemed to be from SRP; we assumed the rest were members of the PPP. During 19–26 January, 10 wolves reunited within SRP territory; then 2 more were shot. In late February, 3 more wolves disappeared for unknown reasons. The remaining 5 wolves included 3 radio-collared pups. The following winter 2 uncollared yearlings were captured, and thus it is possible that all 5 remaining SRP members in March 1979 were pups. In April this group again traveled 30 km beyond their territory to the edge of the Kenai mountains before again settling down in SRP territory. These unusual movements possibly resulted from social disruption caused by intensive harvest, but a causal relationship could not be established. In any case, the movements of these wolves did not appear to be motivated by food shortage.

Relations with Bears

The Kenai Peninsula has long been noted for its abundant black bear populations (e.g., Chatelain 1950). Black bears were seen incidentally from the air more frequently than any other species except

moose during our study. From April to November 1977 and 1978, 104 black bears and 17 brown bears were observed.

Both brown bears and black bears frequently kill moose calves, and brown bears are capable predators on adult moose as well (Chatelain 1950, Franzmann et al. 1980, Ballard et al. 1981a). Wolves and bears were observed simultaneously near dead moose 12 times in 1977 and 1978; 5 of these observations involved brown bears.

Wolves and bears are capable of killing each other (Ballard et al. 1981b, Rogers and Mech 1981), but we rarely observed interaction between them, even near kills. Wolves seemed to defer to brown bears at kills but did not consistently do so for black bears.

Bears emerging from winter dens in April frequently scavenged the remains of dead moose, including a high proportion of wolf-kills. We examined over 100 carcasses of moose in early May 1977 and 1978. Fresh bear sign was commonly seen, and all carcasses were thoroughly scavenged.

Perhaps the greatest threat that bears pose to wolves would be at dens containing young wolf pups. On 9 May 1977 we observed 9 wolves in the Mystery Creek Pack holding a large brown bear at bay about 100 m from their den. The bear stood in a small forest opening, while the wolves were bedded or standing between the bear and the den. Twice, a single wolf darted in toward the side of the bear, who whirled around with snapping jaws. Finally, the bear ambled off into heavy forest growth, heading away from the den. On 5 May 1978, 6 members of the Skilak Lake Pack were observed following about 50 m behind a large male brown bear. The bear was traveling east about 7 km northwest of the pack's den. The alpha female was not with the pack at this time and may have been present at the den with newborn pups. The pack followed the bear for several hundred meters before turning back and retracing their path.

CONCLUSIONS

Our most important conclusions are those concerning the influence of harvest on wolf population dynamics. During the 5-year study, hunting and trapping increased from a relatively insignificant level to become the major form of mortality apparently regulating wolf density on the study area. Reported harvest averaged 30% annually, and annual mortality of radio-collared wolves was 32%. Average losses were ample to stabilize or even reduce a population with a high intrinsic rate of growth. Empirical data indicated that wolf density declined when harvest the previous winter exceeded 40% and increased when harvest was <35%.

We suggest that the primary influence of harvest on wolves was to lower average pack size. As average pack size declined, the pup proportion in the population increased because pup recruitment per pack was independent of pack size. Pack size reduction also resulted in a decline in pack territory size, and in extreme cases this created vacant territory for colonizing wolf pairs. Thus, we predict that, compared to unharvested populations, harvested wolf populations should consist of smaller packs, contain a higher number of packs per area, and include a higher total number of pups. We found no evidence of increased fertility or number of litters per pack as harvest increased.

Dispersal of wolves from packs played a key role in wolf population dynamics. Extraterritorial forays of individuals were most common during the February breeding season, but permanent dispersal from packs occurred throughout the year. Nearly all dispersing wolves were at least 1 year old and none was a dominant, or alpha, wolf. Being highly vulnerable to harvest, most dispersers were reproductively unsuccessful. However, those surviving to reproduce on the study area were instrumental in maintaining population density in spite of increased mortality.

Examinations of 206 wolf-killed moose revealed that wolf predation was strongly

age-selective. Calves were over twice as numerous among wolf-kills as in the population, indicating high calf vulnerability. Many yearlings also were killed, but otherwise most kills were of moose at least 12 years old.

Wolf predation on moose was selective on the Kenai, as in other studies, but the Kenai findings were unique in that wolves preyed more heavily on moose >12 years old, especially females spared by males-only hunting regulations. The winter nutritional stress evident among Kenai moose in our study is consistent with other studies (e.g., Oldemeyer *et al.* 1977). Most calves killed by wolves after January were in relatively poor condition, and most moose dying of malnutrition were calves. After March there was evidence also of progressive fat depletion in bone marrow of wolf-killed adult moose.

The Kenai National Moose Range (now the Kenai National Wildlife Refuge) was established in 1941 in order to protect wildlife habitat and promote development of exemplary management techniques for big game. The fortuitous return of wolves to the Kenai will surely complicate management, but it will also provide a rigorous test of human motivation to retain these large predators in their natural ecological role. Here wildlife managers will have a second chance. For them, balancing the ever increasing human demands on wildlife resources with maintenance of natural wildlife diversity presents a most pressing and difficult challenge.

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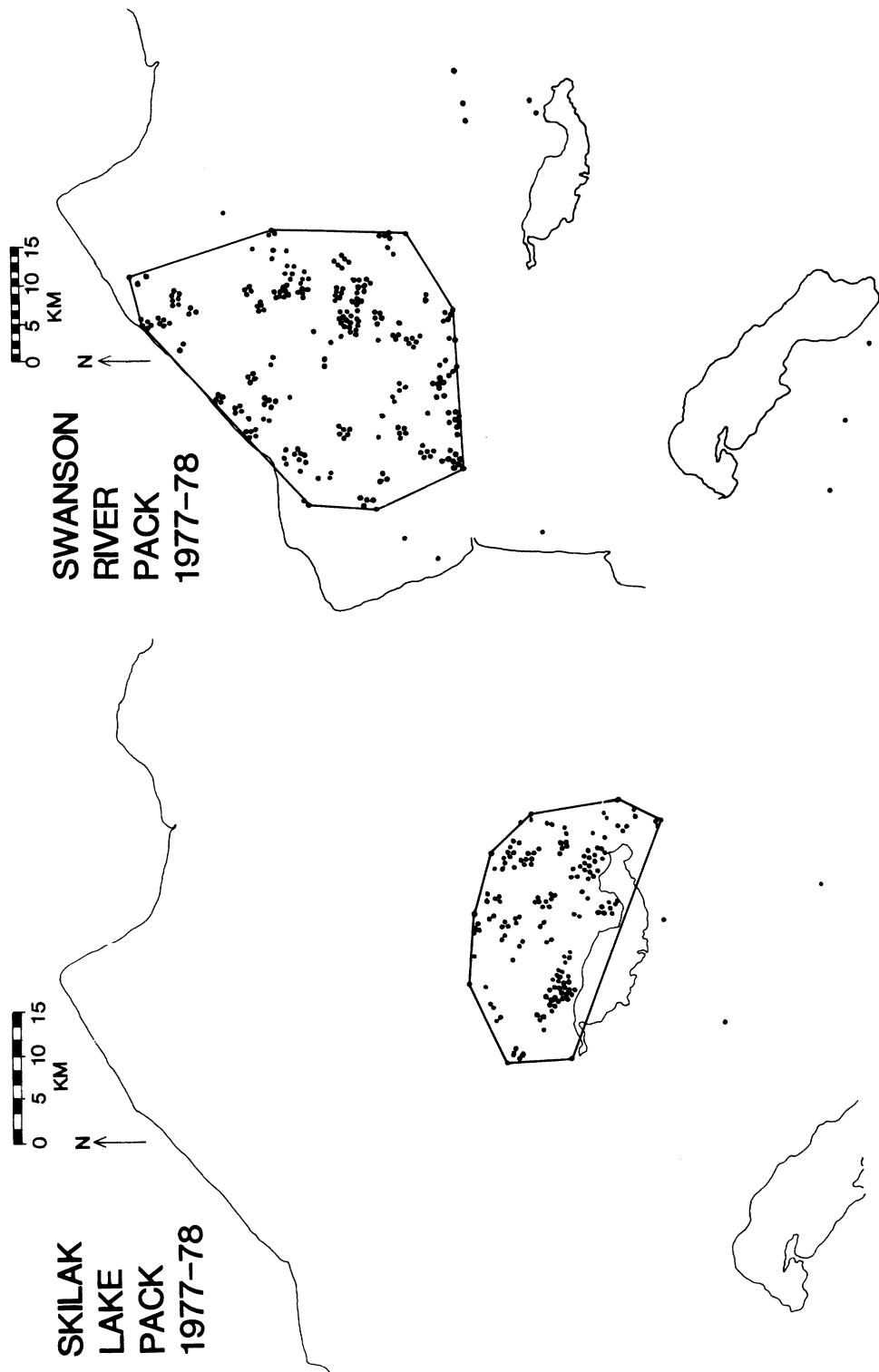
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APPENDIXES



Appendix 1. Examples of wolf pack territory polygons in relation to all locations for pack members. Locations outside the polygons represent extraterritorial movements.

Appendix 2. Details of annual census area boundary designations (Fig. 10).

- (1) We have assumed that interyear stability in pack size was associated with stability in territory. When packs exhibited interyear stability in size and general location, all locations from those years were used to derive a cumulative census area boundary (e.g., MCP I in 1976–77 and 1977–78, MCP II in 1978–79 through 1981–82, and KRP in 1977–78 through 1979–80).
- (2) Areas adjacent to pack territory polygons, which were not occupied by other packs and probably were used by radio-marked packs, were included in annual census areas. In some instances (e.g., MCP I in 1976–77, BICP and BCP in all years) territory polygons were known to be inadequate because at times packs could not be located within their respective polygons.
- (3) The census area near Mystery Creek Pack (MCP) I in 1976–77 was extended to include all locations of this pack in 1977–78 because the 1976–77 polygon was known to be inadequate.
- (4) The western boundary of the census area for all years (the area adjacent to Swanson River Pack, or SRP) was assumed to be constant and delineated by human settlement along the Cook Inlet shoreline.
- (5) The census area extension around the Killey River Pack (KRP) in 1977–78, 1978–79, and 1979–80 was delineated by all locations for KRP during these years. In 1980–81 KRP size and movements were both reduced; consequently, the adjacent western boundary of the census area was moved in to coincide with the 1980–81 KRP polygon and the eastern boundary was pulled in to just include the pack's traditional den site.
- (6) The Big Indian Creek Pack (BICP) and the Bear Creek Pack (BCP) were excluded from census areas in all years because of an inadequate data base. Frequently these packs were not located because of mountainous terrain.
- (7) In 1981–82 the northern boundary of the census area in the vicinity of the SRP and the Bear Lake Pack (BLP) was delineated by the most recent territory polygon available for these packs.
- (8) Dashed ellipses within designated census areas in 1980–81 and 1981–82 represent approximate locations of known-size packs for which territory polygons were unavailable. Infrequent fixes on radio-collared wolves in 1981–82 were consistent with previous data.

Appendix 3. Summary of data for wolves captured on the Kenai Peninsula, 1976–81.

Wolf number	Capture date	Sex	Wt (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)		Cause of tracking termination	Ultimate fate
							No. fixes			
022	14 Aug 76	F	29.0	Gray	Ad	Mystery Cr. I	465	92	Shed collar	Snared 15 Feb 78
026	22 Aug 76	M	38.1	Black	Ad	Skilak L.	351	103	Trans. failed	
026	9 Oct 77	M	45.8	Black	Ad	Skilak L.	717	190	Shed collar	Trapped Dec 81
039	9 Oct 76	F	34.5	Gray	Ad	Swanson R.	325	70	Trans. failed	Snared 5 Dec 79
049	18 Oct 76	F	38.1	Gray	Ad	Loner	101	23	Left study area	Unknown
102	8 Dec 76	F	23.6	Gray	Pup	Mystery Cr. I	364	56	Recaptured	
102	7 Dec 77	F	34.0	Gray	Ad	Mystery Cr. I	126	15	Trans. failed	Shot 3 Jan 79
104	8 Dec 76	F	29.5	Black	Pup	Mystery Cr. I	421	63	Trans. failed	Shot ca. 10 Mar 78
106	12 Dec 76	M	53.5	Black	Ad	Swanson R.	114	34	Trans. failed	Snared 16 Dec 78
108	16 Dec 76	F	19.5	Gray	Pup	Skilak L.	571	152	Trans. failed	Snared 17 Mar 79
110	16 Dec 76	M	29.9	Black	Pup	Skilak L.	250	69	Trans. failed	Unknown
112	3 Jan 77	M	45.8	Gray	Ad	Swanson R.	113	37	Left study area	Unknown
115	3 Jan 77	M	44.5	Gray	Ad	Swanson R.	595	165	Trans. failed	Shot 21 Dec 78
119	17 Jul 77	F	33.6	Gray	Ad	Swanson R.	107	25	Trans. failed	Snared 12 Dec 82
122	25 Jul 77	M	37.2	Gray	Ad	Swanson R.	128	35	Recaptured	
122	30 Nov 77	M	49.9	Gray	Ad	Swanson R.	170	59	Trans. failed*	Unknown
134	28 Sep 77	F	34.9	Gray	Ad	Bear L.	305	101	Recaptured	
134	29 Jul 78	F	34.0	Gray	Ad	Bear L.	239	60	Trans. failed	Unknown
136	2 Oct 77	F	30.8	Black	Ad	Skilak L.	72	28	Recaptured	
136	13 Dec 77	F	32.7	Black	Ad	Skilak L.	243	72	Killed	Shot 13 Aug 78
200	13 Dec 77	M	35.8	Black	Pup	Skilak L.	469	108	Killed	Shot 9 Sep 79
201	30 Nov 77	M	37.6	Gray	Pup	Swanson R.	406	114	Left study area	Shot Jun 79

Appendix 3. Continued.

Wolf number	Capture date	Sex	Wt (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
203	30 Nov 77	M	39.9	Gray	Pup	Swanson R.	302	93	Died	Distemper 13 Sep 78
206	6 Jan 78	M	50.3	Gray	Ad	Killey R.	115	24	Trans. failed	
206	12 Dec 79	M	45.5	Gray	Ad	Killey R.	270	39	Trans. failed	
206	10 Jul 80	M	45.5	Gray	Ad	Killey R.	4	1	Recaptured	
206	14 Jul 80	M		Gray	Ad	Killey R.	135	7	Killed	
208	27 May 78	F	29.5	Gray	Ad	Loner	151	6	Killed	Shot 26 Nov 80
210	6 Jan 78	M	35.4	Black	Pup	Killey R.	755	135	Killed	Shot 25 Oct 78
212	13 Dec 77	M	41.7	Black	Ad	Skilak L.	739	98	Recaptured	Shot 31 Jan 80
212	22 Dec 79	M	45.4	Black	Ad	Skilak L.	150	16	Trans. failed*	Unknown
214	7 Dec 77	M	34.9	Gray	Pup	Mystery Cr. I	40	8	Trans. failed	
214	29 Jul 78	M	39.9	Gray	Ad	Mystery Cr. I	242	12	Left study area	Snared Nov 80
216	7 Dec 77	M	45.4	Gray	Ad	Mystery Cr. I	96	20	Killed	Shot 13 Mar 78
218	7 Dec 77	M	29.5	Black	Pup	Mystery Cr. I	8	2	Trans. failed	Unknown
222	30 Nov 77	M	39.0	Gray	Pup	Swanson R.	250	69	Recaptured	
222	8 Aug 78	M	40.4	Gray	Ad	Swanson R.	174	48	Killed	Shot 27 Jan 79
225	26 May 78	F	34.0	Gray	Ad	B. Indian Cr.	397	30	Recaptured	Unknown
225	26 Jun 79	F	36.3	Gray	Ad	B. Indian Cr.	94	5	Trans. failed*	Capture death
262	12 Dec 78	F	36.3	Black	Ad	Killey R.	0	0	Killed	Unknown
264	12 Dec 78	M	43.1	Gray	Ad	Killey R.	135	25	Trans. failed*	Unknown
266	12 Dec 78	M	29.9	Black	Pup	Killey R.	399	71	Trans. failed*	Unknown
268	15 Dec 78	M	31.8	Black	Pup	B. Indian Cr.	726	27	Killed	Snared 30 Jan 81
270	15 Dec 78	F	32.7	Gray	Ad	B. Indian Cr.	35	3	Unknown	Unknown
276	9 Dec 80	M	28.1	Gray	Pup	Swanson R.	178	21	Transmitting	Last fix 5 Jun 81
278	9 Dec 80	F	29.0	Gray	Pup	Swanson R.	118	15	Transmitting	Last fix 6 Apr 81
280	9 Dec 80	F	28.1	Gray	Pup	Swanson R.	178	18	Transmitting	Last fix 5 Jun 81
402	27 Jul 78	F	38.1	Gray	Ad	Skilak L.	252	57	Trans. failed	
402	28 Jun 79	F	31.8	Gray	Ad	Skilak L.	201	32	Prob. killed	Unreported 15 Jan 80
404	12 Aug 78	F	30.8	Gray	Ad	Mystery Cr. II	322	35	Recaptured	
404	27 Jun 79	F	31.8	Gray	Ad	Mystery Cr. II	39	5	Trans. failed	Snared Mar 81
406	9 Oct 78	M	20.9	Black	Pup	Skilak L.	169	35	Killed	Snared 27 Mar 79
408	9 Oct 78	M	20.9	Black	Pup	Skilak L.	327	57	Killed	Shot 1 Sep 79
410	12 Jun 79	M	40.8	Black	Ad	Bear Cr.	357	38	Killed	Snared Feb 81
412	1 Dec 78	F	26.3	Gray	Pup	Swanson R.	343	82	Recaptured	
412	8 Nov 79	F	38.6	Gray	Ad	Swanson R.	67	25	Died	Distemper 15 Jan 80
414	1 Dec 78	M	29.5	Gray	Pup	Swanson R.	243	68	Trans. failed	
414	19 Jan 80	M	40.8	Gray	Ad	Swanson R.	130	13	Trans. failed	Shot 21 Jan 81
416	1 Dec 78	F	29.9	Gray	Pup	Swanson R.	33	16	Killed	Shot 2 Jan 79
418	1 Dec 78	M	32.2	Gray	Pup	Swanson R.	157	55	Trans. failed	
418	19 Jan 80	M	41.7	Gray	Ad	Swanson R.	6	4	Killed	Snared 25 Jan 80
420	11 Dec 78	F	33.1	Black	Pup	Bear L.	214	60	Trans. failed	
420	30 Nov 79	F	34.9	Black	Ad	Bear L.	123	37	Recaptured	
420	11 Jul 80	F	35.4	Black	Ad	Bear L.	313	37	Transmitting	Last fix 20 May 81
422	11 Dec 78	F	34.9	Black	Pup	Bear L.	344	72	Trans. failed	Snared Feb 81
424	11 Dec 78	F	32.7	Gray	Pup	Bear L.	141	48	Trans. failed	
424	3 Oct 79	F	35.4	Gray	Ad	Bear L.	226	55	Killed	
452	20 Jul 79	F	29.5	Gray	Ad	Bear Cr.	333	22	Trans. failed*	Snared May 80
454	7 Oct 79	F	31.8	Black	Ad	Skilak L.	140	32	Killed	Unknown
458	8 Nov 79	F	38.6	Gray	Ad	Swanson R.	36	5	Killed	Snared 24 Feb 80
462	8 Nov 79	M	28.1	Gray	Pup	Swanson R.	134	43	Left study area	Snared 14 Dec 79
464	30 Nov 79	M	40.8	Gray	Pup	Bear L.	145	23	Trans. failed	Unknown
466	11 Dec 79	M	38.1	Gray	Pup	Killey R.	111	31	Died	Malnutrition (?) Mar 80
470	30 Nov 79	M	33.6	Black	Pup	Bear L.	30	12	Unknown	Unknown
472	11 Dec 79	F	37.2	Black	Ad	Killey R.	393	46	Killed	Shot 8 Jan 81

Appendix 3. Continued.

Wolf number	Capture date	Sex	Wt (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
473	19 Jan 80	M	42.6	Gray	Ad	Swanson R.	63	9	Killed	Shot 22 Mar 80
476	22 Dec 79	M	32.2	Gray	Pup	Mystery Cr. II	365	25	Killed	Snared 21 Dec 80
478	22 Dec 79	M	31.8	Gray	Pup	Mystery Cr. II	0	0	Died	Capture death
480	11 Dec 79	F	35.4	Gray	Ad	Killey R.	80	22	Trans. failed	
480	16 Jul 80	F	36.3	Gray	Ad	Killey R.	231	8	Recaptured	
480	3 Mar 81	F	37.6	Gray	Ad	Killey R.	77	9	Killed	Snared summer 81
486	18 Jul 80	F	31.8	Black	Ad	Loner	11	2	Recaptured	
486	27 Jul 80	F		Black	Ad	Loner	0	0	Left study area	Unknown
488	18 Jul 80	F	33.6	Gray	Ad	B. Indian Cr.	145	9	Unknown	Unknown
490	19 Jul 80	F	35.4	Gray	Ad	Loner	233	13	Killed	Shot 17 Mar 81
494	3 Oct 80	M	43.1	Gray	Ad	Swanson R.	97	17	Trans. failed ^a	Unknown
801	2 Mar 81	M	34.0	Gray	Pup	Killey R.	110	9	Transmitting	Last fix 20 May 81

^a Probable transmitter failure, but definite evidence lacking.

Appendix 4. Kenai Peninsula wolf harvest summary.^a

Classification	Regulatory years							Total
	1974-75	1975-76	1976-77	1977-78	1978-79	1979-80	1980-81	
Game management unit								
15A	1	3	4	6	24	12	14	64
15B	0	1	2	6	4	14	1	28
15C	4	8	3	8	14	12	11	60
7	1	9	3	16	13	6	9	57
Sex								
Male	5	8	2	15	32	22	15	99
Female	1	13	10	18	23	20	19	104
Unknown	0	0	0	3	0	2	1	6
Age								
Adult	1	7	5	23	27	24	19	106
Pup	0	14	7	12	11	11	7	62
Unknown	5	0	0	1	17	9	9	41
Color								
Gray	3	14	7	21	36	20	20	121
Black	3	5	3	14	14	11	11	61
Brown	0	2	2	1	3	10	3	21
White	0	0	0	0	1	0	0	1
Unknown	0	0	0	0	1	3	1	5
Method								
Ground-shooting ^b	3	9	7	19	20	12	14	84
Trapping	1	8	5	6	22	18	7	67
Snaring	0	4	0	10	9	13	13	49
Other	0	0	0	1	3	1	0	5
Unknown	2	0	0	0	1	0	1	4
Total	6	21	12	36	55	44	35	209

^a Determined from ADF&G records.

^b Includes all harvest by airplane-assisted trappers.

Appendix 5. Individual pack summaries.

Pack	Observations
Swanson River Pack (SRP)	<p>Reports suggest that this pack was well established by 1974. Oilworkers reported 14 wolves here in 1974, R. Richey counted 15 tracks from this pack in 1975, and R. Richey and A. Johnson observed 11 wolves (10 gray, 1 black) in this pack in March 1976.</p> <p>Contact with this pack was initiated in October 1976 when subordinate female 039 was trapped, and continued almost without interruption until December 1981 via radios placed on 20 pack members. During 1976, the pack contained 1 black and 19 gray members, with the black wolf (male 106) the apparent alpha male. The alpha female (119) was captured in 1977 but was monitored for only 4 months before transmitter failure. In November 1978, the SRP contained 18 wolves, after 1 radioed male (203) died of distemper in September. During the winter of 1978–79, 7 wolves were shot and 1 radioed wolf dispersed from SRP. By winter's end only 5 wolves remained in the pack.</p> <p>In November 1979 the SRP contained 8 wolves (10 were observed once). Of these 8 wolves, 2 dispersed and were killed, 1 was killed within the home territory, and a radioed yearling (female 412) died of distemper. Three of the final 4 wolves remaining in this pack in January 1980 were radioed, and all 3 dispersed (2 were subsequently killed) leaving 1 probable pup of unknown fate from the original pack.</p> <p>Radio contact with wolves in the SRP territory was not re-established until October 1980, when an adult male (494) of unknown origin was captured. We then found the SRP territory to be occupied by a pack of 6 wolves, their all-gray color suggesting an origin in the old Swanson R. or Point Possession packs (the only all-gray packs observed in the study). Three pups (296, 278, 280) were radio-collared, and the remaining uncollared wolves appeared to be an adult female and a fourth pup. All locations for this group were within the 1979–80 SRP territory. In early winter 1981–82, the pack contained 7 gray wolves.</p>
Skilak Lake Pack (SLP)	<p>This pack of predominantly black wolves lived in a territory that straddled the Sterling Highway. Though containing as many as 12 wolves in early winter, the pack usually numbered 7–8 wolves during winter observations. Stability in this pack prior to our study is suggested by several observations of 7–8 wolves in this area in 1973 and 1974, including many black wolves. In 1976–80 the pack was led by the same alpha male and female. The alpha female (402) was a large, light gray wolf with heavily worn canine teeth. The alpha male was black, with graying sides and face that suggested advanced age. He was never captured, but both alpha wolves were readily recognized throughout the study.</p> <p>Even though highly accessible to hunters and trappers, this pack was affected little by harvest until 1978. In late 1978 we observed this pack at a maximum of 12 wolves, but it then declined to 1–2 wolves after 10 were killed over the next 2 seasons. At least 4 of these wolves were killed in the 1978–79 season, and the pack numbered 5 at winter's end. Only 2 pups were observed in 1979, and 2 adults were shot in September, leaving the alpha pair, a young adult female, and 2 pups in the pack. One pup and the young female were subsequently killed by trappers, and the radioed alpha female disappeared abruptly, possibly an unreported kill, leaving the alpha male and 1 pup in late February 1980. Yearling female 424, from the adjacent Bear Lake Pack, then paired with the alpha male. The pup disappeared, but 424 was snared in May just after giving birth to 6 pups (indicated by placental scars). Contact with the nonradioed alpha male was re-established when female 420, sister to female 424, dispersed from the adjacent BLP and paired with the SLP alpha male. From limited monitoring, we determined that this pair traveled together throughout the winter of 1980–81, confining their movements to the northern portion of the original SLP territory. The remaining SLP territory attracted several loners and wolves from the adjacent MCP II. Non-SLP members that were killed in traditional SLP territory include loner 490, BICP disperser 268, and MCP II wolves 404 and 476. In 1981 pups were produced by female 424 and the SLP alpha male, presumably, because the pack contained 8 wolves in early winter 1981–82.</p>
Mystery Creek Pack I & II (MCP)	<p>In 1972 and 1973, a pack of 4 gray and 4–5 black wolves was reported 5 times from the MCP territory, suggesting stability in this pack prior to this study. During 1976–77, the MCP I was a large pack of both black and gray wolves that inhabited both mountains and lowlands on the eastern edge of the KNWR. By 1977–78 this</p>

Appendix 5. Continued.

Pack	Observations
	pack had shifted to the east for unknown reasons and was located only a few times in early winter on the lowlands. Even during flights over its mountainous territory of the previous year we were often unable to locate any of the radio-collared wolves. Subsequently 3 wolves (including 104 and 216) were shot from the pack as they fed on a kill on Kenai Lake; therefore the MCP territory was extended to this point in our analysis. Contact with the MCP I was lost early in 1978 when all radio-collared wolves were killed, but reports indicated that this pack continued to occupy the eastern portion of its original territory.
	The vacant western portion of the MCP I territory was claimed by a new pair, 404 and 212, that formed the MCP II. Male 212 had dispersed from the adjacent SLP and female 404 may have been from the original MCP, because in 1979 she used the same den to raise pups that had been used by MCP I in 1977. She apparently had pups for the first time in 1979, very likely in the den in which she had been born herself, and 4 of her pups survived to early winter. This pack occupied most of the territory used by the MCP I in 1976–77.
	Male 214, a member of MCP I, dispersed from this pack in 1977–78. He returned in 1978–79 and traveled briefly with the MCP II pair, then departed again, traveled through the northern lowlands, and was last located in March 1979, traveling with a pack of at least 3 other wolves of unknown affiliation south of MCP territory. In November 1980, 214 was snared on the mainland about 125 km northeast of Anchorage (180 km straight-line from his origin in MCP I); he was accompanied by 4 other wolves when killed.
	We monitored only male 476 in MCP II during the winter of 1980–81, and this adult was not observed with other wolves. An ADF&G track count indicated 3 wolves traveling together in MCP II territory, and 476 was accompanied by 3 wolves when he was killed in December 1980. Thus we estimated early winter pack size at 4 for MCP II in 1980–81. Tracks of 7–10 wolves were observed in MCP II territory early in winter 1981–82.
Bear Lake Pack (BLP)	During 1976–77 the Moose River Flats seemed to be vacant territory located between the previous 3 packs. The SRP occasionally ventured into this low, boggy area but spent very little time there. During a 2-month period in late summer 1977, when his transmitter was inoperative, male 026 left the SLP, found a female mate (134), and became established on the Moose River Flats. Male 026 was re-radioed in October 1977, and female 134 was initially radio-collared at about the same time. From her color we knew this gray female was not from SLP but had no clue as to her origin. During the winter of 1977–78 the new BLP (wolves 026 and 134) traveled over the Flats and the adjacent rolling upland to the west. In the same winter the SRP shifted to the west, and the BLP simultaneously occupied the vacated portion of the SRP territory.
	During 1978 the BLP pair raised a total of 6 pups. Two pups disappeared in winter, but 4 more were raised in 1979, raising pack size to 10 in late 1979. During the winters of 1978–79 and 1979–80 the pack expanded steadily to the west, coincident with the retreat of the SRP.
Big Indian Creek Pack (BICP)	A lactating female (225) from the BICP was trapped and collared in May 1978. She was consistently located in the same area on a shrubby mountainside, which we presumed to be a den site. During the winter of 1978–79 we found a minimum of 12 wolves in this pack. Maximum pack size was difficult to determine because of frequent pack splitting and poor flying conditions in their mountainous territory. We assumed that BICP territory extended at least to the road to Hope. During the winter of 1979–80, we confirmed that BICP contained at least 15 wolves, because 11 were observed after a known harvest of 4 wolves. T. Spraker (ADF&G) observed a minimum of 17 wolves and once counted 22 tracks on the ground, which we used as maximum pack size. It is very likely that our estimate of 12 wolves the previous year was too low. In 1980–81, male 268 dispersed from BICP and was killed in SLP territory; female 488 traveled within BICP territory in 1980–81 but during limited monitoring was never observed with other wolves.
Killey River Pack (KRP)	Tracks of at least 17 wolves were seen south of the Kenai River in 1976. Two wolves were radio-collared in this pack (KRP) in January 1978, and that winter we found

Appendix 5. Continued.

Pack	Observations
	<p>13 wolves in this pack. During the following 2 years, maximum pack size was 14 and 15, respectively.</p> <p>During the 1977-78 and 1978-79 seasons this pack experienced little harvest, and pack size and territory changed little. In 1979-80, 15 wolves began the winter, but 8 were killed, 1 died (male 466), and 1 dispersed (male 210) to an apparent vacancy immediately west of KRP territory. In 1980 the pack raised 3 pups, and the pack numbered 8 wolves in early winter 1980-81. A year later (1981-82) 9-10 wolves were observed.</p>
Bear Creek Pack (BCP)	<p>Fourteen wolves were observed in 1970 on the "benchland" north of Tustumena Lake. One wolf was shot from a pack of 15 in August 1977 north of Tustumena Lake. The following winter we found kills and tracks from a large pack in the same area and tracked the pack to the southeast end of Tustumena Lake. In June 1979, male 410 was trapped and radio-collared north of Skilak Lake, and he subsequently returned to a pack just north of Tustumena Lake. A den site and rendezvous area were soon located, where an additional wolf, female 452, was trapped and radioed. During the winter of 1979-80 as many as 21 wolves were observed in this pack, and it was frequently out of range in the mountains to the east. Significantly, the pack was not located south of Tustumena Lake, where we earlier saw tracks of a large pack. Radio contact with BCP was lost in June 1980. Subsequently, male 410 was killed after dispersing to the southern lowlands.</p>
Loners	<p>Four female wolves that were not part of a pack were monitored briefly during the study. Female 486 left the study area immediately after she was radio-collared. Female 049 was caught in October 1976, along the pipeline access road between the territories of the MCP and SLP. She entered the mountains and could not be located for 2 weeks, then emerged again on the lowlands, and traveled widely across the study area. She spent most of her time on the lowlands in SRP territory and was occasionally quite close to this pack. On 22 November, she was located in dense spruce 0.8 km from 7 nonradioed wolves (probably part of SRP) resting on a lake. When we darted a wolf in this pack on 15 December, 049 was within 2-3 km of SRP. She was never seen with other wolves, and in January 1977 she re-entered the mountains and was not located again.</p> <p>Female 208 was trapped between MCP and BICP territories. One front leg was useless and held close to her chest. We could not extend the leg, and it seemed to swing loosely from the proximal humerus. Leg muscles were atrophied and her claws had grown in a complete circle, imbedding themselves in her foot. In spite of her single status and disability, she weighed almost 30 kg and was judged in good condition.</p> <p>We located 208 only infrequently during summer 1977 in the Kenai mountains, although in September she was found once near the Moose Research Center (MRC) on the lowlands. In October 1977, she entered a large enclosure at the MRC, probably by walking under a gate, and soon killed a tame, 5-month-old moose calf. We tried unsuccessfully to frighten her out of the pen with shotgun blasts. She would not leave the pen and, because 4 additional tame moose calves were in the pen, we were forced to shoot the wolf. She was still operating on 3 legs, and when her leg was rotated at the shoulder we could feel abnormal grating of bone in the joint. We found the shoulder joint shattered and, although bone remodeling was progressively fusing the joint, the leg was held in place by fibrous tissue. She weighed 35 kg with an empty stomach, and ample body fat confirmed she was in excellent condition.</p> <p>The last radio-collared loner, female 490, was captured in 1980 along the border between BLP and SLP. During the winter of 1980-81 she traveled within traditional SLP territory, usually in the vacated southern portion not occupied by the SLP alpha male and female 420. We never observed 490 with other wolves, but she apparently had brief associations. She was in the vicinity, along with at least 2 other wolves, when MCP II male 476 was snared in SLP territory. The person who shot female 490 in March 1981 reported another wolf at the same location the next day. When she was killed, 490 had a crippled rear leg and reportedly could not walk normally. She had lost a molar tooth some time previously and had broken 4 other molars recently. Her condition suggested that she had escaped from a trap or snare.</p>

Appendix 5. Continued.

Pack	Observations
Other packs	<p>Limited information on packs outside the study area was available from reports of other biologists and the general public, in addition to our own observations. Presumptive territories of these packs are presented in Fig. 11.</p> <p>After 1976–77 the SRP territory shrank to only a portion of its former extent. In 1978–79, we confirmed that other packs, the Point Possession Pack (PPP) and the Elephant Lake Pack (ELP), occupied the areas vacated by SRP. PPP and ELP became established just northeast and south of the reduced SRP territory, respectively. Both packs apparently developed since 1976–77. In 1978–79 the ELP contained at least 1 black and 2 gray wolves, and SRP pup 412 was once observed resting and then traveling with these 3 wolves. By 1978–79 the PPP was relatively large, and we estimated from tracks that at least 12 wolves were present. T. Spraker counted 16 tracks in this area once, but at a time when we could locate only 5 wolves in SRP. The SRP traveled extensively over what we considered to be PPP territory in 1978–79, but we had no evidence of temporary associations between the 2 groups. Both SRP and PPP were heavily harvested in 1978–79, and in 1979–80 the SRP was much reduced, and we found no sign of the PPP. In 1980–81, however, we saw 9 gray wolves and received another reliable report of 9 wolves in PPP, while during the same year 5 wolves were reported in ELP territory. Tracks of about 8 wolves were seen in ELP territory in 1981–82.</p> <p>A trapper familiar with the Kenai mountains east of MCP claimed to have tracked a pack of up to 12 wolves in the vicinity of the Alaska Railroad about 40 km southeast of Hope. Another trapper indicated that a small pack used an area southeast of Skilak Lake, and L. Nichols reported 10 wolves here before the present study.</p> <p>Information on wolf packs southwest of Tustumena Lake was only fragmentary. We indicated in Fig. 11 the area where male 106, who dispersed from SRP, eventually settled. Large packs were reported both northeast and northwest of the head of Kachemak Bay. As many as 9 wolves were reported near the southern extreme of the lowlands. Groups of wolves numbering up to 7 or 8 were commonly reported west of Tustumena Lake. Because the southern Kenai lowlands is heavily hunted (see Fig. 15), pack territories may be less stable and pack sizes smaller than on the study area.</p>

Appendix 6. Dynamics of wolf packs on Kenai study area.

Year and pack	Early winter pack size plus previous harvest ^a	Late winter pack size ^b	Reported harvest ^c
1976-77:			
Swanson River	20 + 1	13	1
Skilak Lake	9 + 2	7	2
Mystery Creek I	14	14	0
Total	43 + 3	34	3
1977-78:			
Swanson River	20	15	3
Skilak Lake	9	8	1
Mystery Creek I	16 + 1	8	6
Bear Lake	2	2	0
Killey River	13 + 1	11	1
Total	60 + 2	44	11
1978-79:			
Swanson River	18 + 1	5	8
Skilak Lake	12 + 2	5	5
Mystery Creek II	2	2	0
Bear Lake	8	6	0
Killey River	14	11	2
Big Indian Creek	12 ^d	10	2
Total	66 + 3	39	17
1979-80:			
Swanson River	10	1	3
Skilak Lake	5 + 2	1	5
Mystery Creek II	6	4	1
Bear Lake	10	6	1
Killey River	13 + 2	5	8
Big Indian Creek	22	10 ^e	5
Bear Creek	21	12 ^f	5
Total	87 + 4	39	28

Appendix 6. Continued.

Year and pack	Early winter pack size plus previous harvest ^a	Late winter pack size ^b	Reported harvest ^c
1980-81:			
Swanson River	6		0
Skilak Lake	2		0
Mystery Creek II	4 ^g est.		2
Bear Lake	6-10 est.		5
Killey River	8		3
Point Possession	9 ^h		3
Elephant Lake	5 ⁱ		1
Total	40-44		14
1981-82:			
Swanson River	7		
Skilak Lake	8		
Mystery Creek II	7-10 est.		
Bear Lake	9		
Killey River	9-10 est.		
Elephant Lake	8 est.		
Slikok Lake	8		
Total	56-60		

^a Preharvest level equal to maximum observed pack size in early winter (usually Nov or Dec) with reported harvest before that time added.

^b Usually maximum observed pack size in April.

^c Includes harvest of dispersers that had not successfully settled.

^d Minimum count, probably only of a portion of the pack. Excluded from most calculations.

^e Late winter pack size estimated from pack size of 11 determined 2 February 1980, minus 1 reportedly killed in March 1980. Pack not observed in late winter.

^f Pack not observed in late winter. Late winter pack size estimated from reported harvest of 5 plus assumed 17% unreported loss (4 wolves), the average for other packs during the study.

^g Track count by ADF&G; also the number present when male 476 was snared.

^h Nonradioed pack of 9 observed; also reported by seismic crew.

ⁱ Nonradioed pack of 5 observed.

Appendix 7. Reproductive status and teat development of adult female wolves captured on the Kenai Peninsula.

Wolf	Date examined	Teat description ^a	Remarks on age, ^b reproductive status
022	14 Aug 76	rear pair 3 × 3 mm, remainder inconspicuous	nulliparous, probably yearling
039	9 Oct 76	barely discernible, 3 × 3 mm	nulliparous, 2-4 years old (est.)
049	18 Oct 76	inconspicuous, 2 mm wide	nulliparous, probably yearling
102	7 Dec 77	inconspicuous	nulliparous, yearling
119	17 Jul 77	rear 6 teats engorged and pigmented, 25 × 12 mm	probably multiparous, young adult, alpha female; minimum 5 pups
134	28 Sep 77	rear 2 teats pigmented and engorged, 6 × 6 mm	primiparous or multiparous, 4-6 years old (est.)
134	29 Jul 78	rear 2 teats 10 × 8 mm; other 6 were 13 × 10 mm; hair loss on rear 4	alpha female of newly-formed pack; 6 pups seen in autumn
136	2 Oct 77	inconspicuous, 3 mm wide, unpigmented	nulliparous, 2-4 years old (est.)
208	27 May 78	rear 6 teats 10 × 10 mm, pigmented; hair loss on rear 4, not engorged, but expressed milk	loner, probably pseudopregnant, 4-6 years old (est.)

Appendix 7. Continued.

Wolf	Date examined	Teat description ^a	Remarks on age, ^b reproductive status
225	26 May 78	8 engorged, pigmented teats, 10 × 5 mm; hair loss on rear pair	no. pups unknown, 2–4 years old (est.)
225	26 Jun 79	8 pigmented teats, 20 × 15 mm; rear 4 missing hair and engorged	multiparous, 3–5 years old (est.)
262	12 Dec 78	inconspicuous	nulliparous, probably yearling, no uterine scars
270	15 Dec 78	5 × 5 mm	nulliparous, probably yearling
402	27 Jul 78	8 engorged, pigmented teats, 14–15 × 10–13 mm; hair loss on rear 2	multiparous, alpha female, 6–7+ years old (est.); 6 pups observed
402	28 Jun 79	6 engorged pigmented teats; rear 6 missing hair, 10 × 7 mm	multiparous, alpha female, 7–8+ years old (est.); 2 pups observed
404	27 June 79	6 engorged teats, 12 × 9 mm	primiparous, alpha female, 2 years old (est.); 4 pups seen
412	8 Nov 79	inconspicuous	nulliparous, yearling
420	30 Nov 79	inconspicuous	nulliparous, yearling
420	11 Jul 80	inconspicuous	nulliparous, 2 years old
424	3 Oct 79	inconspicuous	nulliparous, yearling
424	16 May 80	6 engorged teats 30 × 50 mm, unpigmented; no hair loss	primiparous, 2 years old, 6 placental scars
452	20 Jul 79	inconspicuous	nulliparous, probably yearling
454	7 Oct 79	inconspicuous	nulliparous, probably yearling
458	8 Nov 79	inconspicuous	nulliparous, probably yearling
472	11 Dec 79	inconspicuous	nulliparous, probably yearling
480	11 Dec 79	inconspicuous	nulliparous, probably yearling
486	16 Jul 80	inconspicuous	nulliparous, 2–4 years old
488	18 Jul 80	inconspicuous	nulliparous, 1–2 years old
490	19 Jul 80	inconspicuous	nulliparous, 2–4 years old

^a Dimensions given are length × width at base.^b Adults with tooth wear were assumed to be >2 years old. For these animals an age interval was estimated on the basis of tooth wear.

Appendix 8. Temporary associations of wolves from different packs.

Radio-collared wolves involved	Pack ^a	Date	Observations
112 and 022	SRP MCP I	22 Feb 1977	112 located within SRP territory with packmate, 10 km west of MCP I, which was at that time on the edge of SRP territory.
		26 Feb	Both located about 1 km apart in MCP I territory, each alone.
		3 Mar	112 located on a kill with at least 6–7 wolves from MCP I (including 022).
		5 Mar	112 seen traveling northwest, 3.4 km from 11 wolves of MCP I (with 022), still at kill where observed on 3 March.
		8 Mar	MCP I (with 022) at territory edge, examined scent post then ran to nearby SLP kill. Wolf 112 located 3 km north of MCP I (in MCP I territory).
112 and 201 and unidentified	SRP SRP MCP I	26 Feb 1978	Located in group of 15 wolves (MCP I) in MCP I territory. No unusual behavior noted as pack slowly traveled.

Appendix 8. Continued.

Radio-collared wolves involved	Pack ^a	Date	Observations
214 and 212 and 404	MCP I MCP II MCP II	27 Feb 8 Nov 1978	112, 210, and an unidentified gray wolf located together, still within MCP I territory. Location of MCP I not determined. Subsequently, wolf 210 returned to SRP while 122 traveled south, returning to SRP about a month later.
418 and 422 and 404 and 212	SRP SRP MCP II MCP II	17 Feb 1979 12 Jan 1979	212 and 404 located with gray wolf of unknown origin (possibly 214). While outside SRP territory, 418 and 422 associated with 404 and 212 while on a kill in MCP II territory. Three of the 4 observed together.
414 and unidentified	SRP ELP	2 Jan 1979	414 bedded and traveled briefly with a nonradioed group of gray wolves and 1 black wolf near their mutual territory boundary.
412 and 414 and 418 and unidentified	SRP SRP SRP ?	18 Apr 1979	When located in MCP II territory, 5 wolves from SRP were seen with an extra gray wolf of unknown origin. SRP consistently contained only 5 wolves before and after this observation, when inside their own territory.
115 and 216	SRP MCP I	13 Mar 1978	During a brief extraterritorial movement, 115 was located (not observed) with 216 inside MCP I territory.

^a ELP = Elephant Lake Pack; other pack abbreviations as in Appendix 5.

Appendix 9. Radio-collared wolves that dispersed from their original pack.

Wolf	Original pack ^a	Sex	Age	Date of final departure	Fate
026	SLP	M	3-5 years	Sep 1977	Established BLP with female 134
039	SRP	F	2-4 years	unknown	Killed Dec 1979 in SLP territory
106	SRP	M	3-5 years	Dec 1976	Settled successfully, southern Kenai lowlands
112	SRP	M	yearling	Apr 1977	Lost signal, southern Kenai mountains
201	SRP	M	yearling	Jan 1979	Killed Jun 1979 east side Kachemak Bay
206	KRP	M	5+ years	unknown	Killed Nov 1980 near Soldotna
210	KRP	M	2 years	Oct 1979	Killed Jan 1980 near Soldotna
212	SLP	M	2-4 years	Jul 1979	Established MCP II with female 404
214	MCP I	M	yearling	Dec 1978	Killed Nov 1980 on mainland
268	BICP	M	2 years	ca. Apr 1980	Killed Jan 1981 in SLP territory
410	BCP	M	2-4 years	mid-1980	Killed Feb 1981 southern Kenai lowlands
414	SRP	M	yearling	Feb 1980	Killed Jan 1981 southern Kenai lowlands
420	BLP	F	2 years	ca. Aug 1980	Replaced female 424 as alpha female in SLP; alive Dec 1981
424	BLP	F	yearling	Feb 1980	Replaced alpha female in SLP; killed May 1980
458	SRP	F	probably yearling	Nov 1979	Killed Dec 1979 in KRP territory
462	SRP	M	pup	Feb 1980	Unknown
472	KRP	F	probably yearling	ca. Sep 1980	Killed Jan 1981, southern Kenai lowlands
473	SRP	M	probably yearling	Feb 1980	Killed Mar 1980, northern side Tustumena Lake

^a Pack abbreviations are as follows: Skilak Lake Pack (SLP), Swanson River Pack (SRP), Killey River Pack (KRP), Mystery Creek Pack I (MCP I), Big Indian Creek Pack (BICP), Bear Creek Pack (BCP), and Bear Lake Pack (BLP).