WOLVES OF THE KENAI PENINSULA, ALASKA

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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. A prominent furbearer throughout the 19th century, Kenai wolves disappeared completely little more than a decade after a gold rush in 1895 and 1896 brought thousands of prospectors to the region. Unregulated killing and market hunting of native wildlife, together with extensive man-caused fires, effected changes in many important wildlife species in the early 1900's. Caribou (Rangifer tarandus) were eliminated, probably due to overharvest (Davis and Franzmann 1979), and populations of Dall sheep (Ovis dalli) and moose (Alces alces) were locally reduced, although moose populations ultimately increased in vast areas of fire-created habitat (Spencer and Hakala 1964). Poison was widely used to harvest furbearers and to eliminate large carnivores elsewhere early in this century and is believed responsible for apparent elimination of wolves from the Kenai (Peterson and Woolington, in press). Wolf populations were evidently greatly reduced by 1905 and probably extirpated by 1915. In southcentral Alaska there followed a period of intensive trapping, prompted by bounties instituted in 1915 for wolves and 1929 for coyotes (McKnight 1970). In 1948 a decade of federal wolf control began, which further reduced the wolf population on the southcentral mainland (Rausch and Hinman 1977). The combination of sparse prey for wolves in the mountains to the north, human control of wolf populations in this area, and the narrow avenue for recolonization of the Kenai were probably responsible for wolf absence until the late 1950's.

Federal wolf control efforts began to wind down before statehood in 1958, and under subsequent state management wolf populations in southcentral Alaska rapidly recovered (Rausch 1969). Simultaneously, isolated individuals were reported from the Kenai Peninsula in the early 1960's, with the frequency of sightings and the size of packs increasing steadily through the late 1960's. Wolves were reported from most accessible areas of the Kenai by the early 1970's and were generally well-established by approximately 1975.

The moose population on the Kenai National Wildlife Refuge (KNWR), administered by the U.S. Fish and Wildlife Service, declined by about 50% between 1970 and 1975, coincident with a series of severe winters (Oldemeyer et al., 1977; Bailey, 1978; Bangs and Bailey 1980). The uncertain relationships of the population decline to increased hunting pressure, severe winter weather, declining habitat quality, and predation by both wolves and black bears (*Ursus americana*) were acknowledged by the Alaska Department of Fish and Game (ADF&G) and the U.S. Fish and Wildlife Service (USF&WS), leading to a cooperative predator-prey study focusing on wolves, bears and early mortality of moose calves. Aspects of the moose calf mortality study were reported by Franzmann et al. (1980) and Ballard et al. (1981a), wolf-moose relationships are summarized by Peterson et al. (submitted), and bear studies by ADF&G are underway. This monograph focuses on the ecology and population dynamics of Kenai wolves.

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METHODS

Wolf population density, size and spatial distribution of wolf packs, patterns of wolf predation, and other aspects of wolf ecology were all determined from radio-collared wolves. Field work centered on year-round efforts to radio-collar and subsequently locate wolves in as many packs as possible. As the study progressed additional packs were monitored and the study area was enlarged, eventually including about half the estimated wolf population on the Peninsula.

We captured wolves in each pack in summer with leg-hold traps, while helicopter darting was used in early winter to collar several additional wolves in each pack. Trapping was limited to the period May through October, since feet of trapped wolves commonly freeze in winter. We usually darted during periods of complete snowcover in early winter, when packs were most cohesive.

Trapping was an effective way to catch adult wolves and provided the only means to examine wolves in the non-winter season. Traps employed to catch wolves were Newhouse 4, 14, and 114 double long-spring, equipped with a 2m 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).

When darting wolves we often deliberately chose pups because they were less elusive, remained in a pack for at least a year, and were seldom live-trapped in summer. Drugs were delivered by helicopter at close range in 3cc projectile syringes (Cap-Chur, Palmer Equipment Co.). Effective drug dose was about 3 times that used for trapped wolves; we used fixed drug doses of either 100mg Sernylan and 50mg Sparine or 40mg Sernylan and 220 mg Xylazine (Rompun, Chemagro, Kansas City, MO).

While most trapped wolves suffered minor cuts, none were disabled, and travel patterns and gait of trapped wolves usually appeared normal within a few days. Darted wolves usually sustained only a minor dart wound, although 2 darted wolves died, 1 suffered a broken leg and 1 was temporarily paralyzed after being hit in the spine.

We weighed and measured tranquilized wolves, taking standard body measurements plus canine length and testes or teat size. Up to 35ml of blood were drawn for laboratory analysis (Franzmann and Peterson, unpubl.). Most wolves were given intramuscular injections of 1,200,000 units of Bicillin (Wyeth) and supplementary vitamin injections to reduce the likelihood of capture-related infections and to compensate for possible disruption of travel and feeding patterns. We classified captured wolves as pup or adult by canine tooth appearance and, later, lower incisor wear. Pups captured in October still retained milk canines, while those caught in November or later showed various stages of permanent canine eruption.

We ear-tagged wolves with numbered yellow Rototags (Nasco, F. Atkinson, WI). Sixty-four wolves were fitted with radio-transmitter collars manufactured by either AVM Instrument Co. (Champaign, IL) or Telonics (Mesa, AZ); 16 wolves were captured twice, 2 wolves captured 3 times, and 1 captured 4 times. We located wolves regularly from aircraft (PA-18 Supercub or Cessna 185) by the method of Mech (1974). We monitored individual wolves in this way for up to 3 years, but the average length of coverage was 10 months. Tracking was terminated by premature transmitter failure in about half of the cases, and maximum life for any transmitter collar was 2 years.

We flew tracking flights about once/week in summer when wolves were only observed about 15% of the time, but almost daily in early winter when sightability of wolves approached 90% (Fig. 1). Average wolf sightability for the 3,600 wolf locations obtained from August 1976 through March 1980 was 60%.

Each time a wolf was located by radio-fix we circled the area and attempted to observe the wolf, count the wolves in the pack, and determine activity. In this way we located many prey carcasses utilized by wolves; we later examined most carcasses on the ground (Peterson et al. submitted). Whenever conditions permitted snow-tracking, we backtracked wolves as far as possible to determine travel patterns and find previous kills. Social status of some wolves was determined from individual histories or behavioral expression (Peterson 1977). We conducted limited aerial searches for unradioed packs adjacent to those being monitored regularly, but poor light and inadequate snow-tracking conditions usually precluded effective use of this technique.

Radioed wolf packs inhabiting lowland areas could be located during almost any flight, but flights in mountainous areas were often prevented or limited by low clouds or turbulence, so the size of pack territories determined from radiofixes was minimal for packs inhabiting mountains. In some analyses requiring knowledge of the entire range of packs in the mountains, we estimated approximate territory boundaries by considering radio-locations, reports of other observers, locations of harvested wolves, and probable wolf distribution in the mountains.

Observations of wolves in summer were too infrequent to provide a complete profile of summer food habits, so we collected wolf scats on an opportunistic basis between May and October. Since coyotes (*Canis latrans*) were present on the study area and coyote and wolf scats may be indistinguishable (Weaver and Fritts 1979), we collected only those scats that could be identified as wolf on the basis of tracks, or from known den and "rendezvous sites" (Murie 1944).

Wolf harvest by hunters and trappers was determined primarily from an ADF&G mandatory sealing program for all wolves taken. Age (pup or adult) of many wolves sealed was determined by ADF&G by examining epiphyseal closure in the radius (Rausch 1961) which, until 1978, was required to be left attached to the hide. We determined whether or not harvested wolves were from study area packs from kill location, color, age and sex of the wolf, changes in observed pack size, and contacts with hunters and trappers. We contacted as many successful hunters and trappers as possible in order to secure a sample of current Kenai wolf skulls. The Refuge solicited carcasses of all furbearers taken by trappers by offering a nominal payment for skinned carcasses, and several skulls and frozen carcasses were obtained in this manner.

To estimate wolf density, we considered all wolves that were included in packs, reflected by maximum pack size in early winter. This was a period of maximum pack cohesiveness and, with few exceptions, radioed wolves were found in packs in early winter. Even though we monitored packs almost daily in early winter, packs were sometimes observed at maximum size only once or twice, indicating that we were indeed including many wolves that were transient or irregular pack members. We considered pack territories to be defined by convex polygons including the outermost locations of each pack. Movements of dispersing wolves and occasional extra-territorial forays of packs were excluded. The space used by a pack from October through April was assumed to be the pack territory. In summer, with few exceptions, pack members were within their winter territory. Annual estimates of wolf density were calculated for a contiguous area where all wolf packs were monitored.

Our capture methods and sport harvest were both biased toward either pups or adult wolves and thus proved inadequate for estimating population age structure. We estimated pup:adult ratios for study packs by subtracting spring pack size from subsequent early winter pack size, then adjusting for summer and fall losses of adults to harvest, dispersal, and natural mortality.

Mortality rate and annual turnover within the wolf population were determined from individual histories of radioed wolves and from detailed monitoring of pack sizes during winter. Collared wolves, the ADF&G sealing program for harvested wolves, and KNWR trapper reports enabled us to determine the nature and extent of mortality factors.

STUDY AREA

Located between Prince William Sound and Cook Inlet in southcentral Alaska, the Kenai Peninsula (lat. 60 deg. N; long. 150 deg. W) lies just S of Anchorage (Fig. 2). Although 26,000 km^2 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 1500 m (with major icefields) dominate the eastern half, while the Kenai lowlands on the western half consist of a rolling plateau ranging from sea level to about 500 m near its southern end. Numerous bedrock fault-lines cross the landscape, the most notable delineating the eastern edge of the Kenai lowlands. Patterns of uplift and subsidence are pronounced, with the lowlands generally rising and the mountains settling into the sea (Plafker 1969). During the 1964 earthquake the eastern shore dropped several feet, while the downward displacement of the western shore was almost negligible (ibid).

Forest vegetation includes white and black spruce (*Picea abies* 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 near ocean influence. The altitudinal limit of trees in the mountains is approximately 500 m.

The study area encompassed Kenai lowlands and adjacent mountains north of Tustumena Lake; most of this area has burned during the last 100 years (Spencer and Hakala 1964; Davis and Franzmann 1979). Much of the 700 km^2 "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. The northern lowlands supported few moose until a 1947 fire burned 1,255 km^2 in this area. The extensive edge created by the 1947 burn and the characteristics of successional-stage vegetation that followed created optimum moose habitat over much of the northern lowlands, 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 moose population declined (Oldemeyer, et al. 1977). An additional 352 km^2 of mature forest burned in 1969 just NE of the town of Kenai. Although it lacks the interspersion of unburned stands that characterized the 1947 burn, the 1969 burn now produces considerable moose browse and seasonally attracts large numbers of moose (Bangs and Bailey 1980).

The moose population on the KNWR N of Tustumena Lake was estimated at 3,400, or a density of 0.5 moose/km^2 in winter (Bailey 1978), down from an estimated 9,000 - 10,000 in the late 1960's. Although moose undoubtedly support most of the Kenai wolf population, other ungulates with more restricted distributions may be locally important as prey outside the study area. Caribou were re-introduced in 1965 and 1966, resulting in 2 populations totaling perhaps 300 - 400 animals. A population of 100 or less inhabits the N lowlands, while the remainder inhabit the Kenai mountains SW of the town of Hope. Dall sheep and mountain goats (*Oreamnos americanus*) can be found throughout much of the Kenai mountains. Beaver (*Castor canadensis*) were not abundant on the study area, with fewer the 100 colonies estimated for the entire Refuge (KNWR files). Snowshoe hares (*Lepus americanus*) were sparse during the study after reaching high levels during 1971 - 1972 (Wolfe 1974).

Annual precipitation between 1944 and 1977 averaged 48 cm and was evenly distributed throughout the year (Bangs and Bailey 1980). Complete snow cover is usually present from late November to early April, although snow depth rarely exceeds 50 cm. Winter severity was above average from 1971 to 1975, largely due to below-normal temperatures and more persistent snow-cover (Bangs and Bailey 1980). During the study, winters were relatively mild, with frequent thaws and rain interspersed with wet snow. Even in mid-winter snow cover was often incomplete and snow was usually very dense and crusted from frequent thaws. Snow depth varied considerably over the study area; locally heavy snow accumulation was noted SE of Soldotna and E of the Swanson River oil field, while the area N of Skilak Lake typically had much less snow than elsewhere. High snow density and frequent snow crusts common on the Kenai tend to provide favorable hunting conditions for wolves in winter.

Of the 26,000 km^2 that comprise the Kenai Peninsula, 14,600 km^2 are included in the following federal land units: Kenai National Wildlife Refuge (7,972 km^2), Chugach National Forest (4,340 km^2), and recently-established Kenai Fjords National Monument (2,268 km^2). The peninsula is divided into 2 ADF&G Game Management Units, GMU 7 and 15, and GMU 15 is further divided into 15A, 15B, and 15C (Fig. 2a).

PHYSICAL AND MORPHOLOGICAL CHARACTERISTICS

Taxonomic Status

The earliest classification applied to Kenai wolves was that of Osgood (1901), who regarded Peninsula wolves as Canis occidentalis (Richardson), evidently because that was the closest formal designation in use at that time. Goldman (1944) undertook a complete revision of wolf classification in North America, and assigned the original Kenai wolves to a new subspecies, Canis lupus alces, based on skulls of 2 adult females and 3 male pups collected near Kachemak Bay in 1904:

> "This peninsular race reaches the maximum size attained by the species in North America. The skulls of 2 adult females are longer than those of any other examined and present other peculiarities pointed out. Skulls of three immature males are not widely different from those of pambasileus (interior Alaska wolves) of comparable age, but differ uniformly in the greater width of the supra-occipital shield. The new subspecies may range throughout the Kenai Peninsula, which at its base is narrowly connected with the mainland of Alaska. Specimens from north of Turnagain Arm of Cook Inlet are assignable to pambasileus. The principal natural prey of the Kenai wolf is doubtless the giant moose of the region. The large size of the wolf may be the result of adaptation enabling it to cope with so large an animal" (Goldman, 1944:423-424).

Skulls of both adult females examined were longer than any other of the 191 female skulls measured by Goldman. Pedersen (1978) reviewed the taxonomy of present wolf populations in Alaska. He has since compared current Kenai wolf skulls to others from both the original Kenai population and the present mainland population. Preliminary findings (S. Pedersen, per. comm.) are that the Kenai wolves are morphologically close enough to the Interior wolf (*C. l. pambasilieus*) to be considered as an ecological race of this subspecies. The variables measured by Goldman, when analyzed by multivariate statistical methods, did not provide a clear separation between the original Kenai and Interior wolves and Goldman's classification of *C. l. alces* was made from an insufficient sample. The original and present Kenai wolves are sufficiently similar to consider that they probably had a common origin among Interior wolves in southcentral Alaska.

Capture Data

Basic data for the wolves captured during the study, including 2 wolves that died during capture, are summarized in Table 1 and Appendix I. During 6,800 trap-nights, 23 wolves were trapped, with the remaining 54 captures by helicopter-darting.

Physical Condition

We evaluated seasonal variation in wolf condition from total weight and blood packed-cell volume (PCV). Males were larger than females (Table 2), so sexes were separated when assessing seasonal fluctuations. Body weight was significantly less in summer for both males ($P < 0.025$) and females ($P < 0.005$) and, with sexes pooled, blood PCV was less in summer (47.8) than winter (50.9) ($0.025 < P < 0.005$). Only one adult wolf was captured in both summer and winter: 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 general pattern as outlined.

While body weight and blood parameters may reflect nutritional status, these variations are superimposed on normal seasonal fluctuations. Studies of captive wolves fed *ad libidum* show summer declines in PCV (L. D. Mech, pers. comm.), so we cannot, on the basis of our present data, infer a relative food shortage in summer.

All wolves captured had permanent canine teeth except male pups 406 and 408, trapped on Oct. 9 with milk canines. All other pups, caught in November and December, had canine teeth in various stages of emergence. While upper canines were generally 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) while lowers averaged 21.9 mm (range: 20-26). Tooth eruption of pups 406 and 408 seemed delayed compared to pups of equal age in Minnesota (Van Ballenberghe and Mech 1975), but overall Kenai wolf pup weight and tooth eruption patterns appeared similar to Minnesota wolf pups.

We could not easily distinguish pups from adults during routine aerial observations in winter. During the first year of the study, pups in Skilak Lake Pack could be identified by their small size as late as 11 months of age, but this was unusual. Many pups were virtually indistinguishable from adults when darted in December, so we relied primarily on behavioral cues to single out pups for darting.

Color

Pelage color of Kenai wolves varied from very light gray to completely black. Typical gray coloration included many dark markings and bands, especially along the back, while belly and flanks were more uniformly light gray or brown. Black wolves often had considerable light coloration on belly and lower sides and, sometimes, a white patch on the chest. Often "black" pups that did not have a fully developed coat of black guard hairs appeared brown. Although 1 wolf sealed by ADF&G was recorded as "white", no white wolves were observed during the study.

About a third of the wolves on the study area were black, with the rest gray (agouti). Of the wolves we captured, 33% were black, equaling the 33% black proportion that was observed in all study packs in early winter. Among Kenai wolves sealed by ADF&G, 30% were described as "black" (Table 3).

The degree to which packs were genetically isolated from each other was apparent from the different color proportions observed in adjacent packs. Since average color proportions for the combined total of all study packs varied between years only form 32% to 39%, early winter color proportions for each pack during all years were combined to produce an average value for each pack (Table 3). Observed extremes occurred in the Swanson River Pack (almost entirely gray) and the adjacent Skilak Lake Pack (2/3 black).

Color proportions in individual packs that are substantially different from the population average of 30-40% black probably reflect very stable leadership for many years, as well as little genetic mixing with wolves from the population at large. Thus the Skilak Lake Pack, with the same alpha male (black) and female (gray) during all 4 years of the study (both wolves were rather old), exhibited the highest proportion of black wolves for any study pack. Litters born to gray parents were 100% gray, while those born to gray females and black males produced an average of 40% black: 60% gray offspring (Table 4). We had no known litters born to black females.

FEEDING ECOLOGY

We attempted to provide a general profile of annual predation patterns, although quantitative data on predation rate was obtained in winter only. Direct observations of wolves in winter provided the basis for determining predation patterns at this season, but this was not possible from June to September when visibility was restricted by leaf cover. Scat analyses provided the most direct indicator of food habits during summer, supplemented by some aerial observations.

Prey Species

Moose were the only significant prey for wolves on the Kenai lowlands and probably were the main prey for packs inhabiting the Kenai mountains as well. Based on direct observations of wolf-kills in winter, and indirect evidence from summer scat analyses, we concluded that wolves were supported by moose, especially old cow moose, on a year-round basis. Of the 201 moose kills we examined, mainly from the winter period, 47% were calves and the average age of the adults was 10.9 years. Only 4% of the 72 adult kills for which sex could be determined were males, all yearlings (Peterson et al. submitted).

We observed only one caribou that was consumed by wolves, a newborn calf apparently killed by male 115 NE of Kenai in 1977. During the study we received 3 reports of adult caribou killed by wolves, all along the western edge of the Kenai mountains. The only wolf pack on the Peninsula that could be supported significantly by caribou is the Big Indian Creek Pack, since the entire range of the mountain herd of 200-300 caribou falls within their territory. Wolf density in this area was higher than in adjacent areas, although the full extent of this pack's territory was only estimated from telemetry data plus limited reports of wolves in the mountains to the east. Moose do not seem more abundant here than in adjacent areas, so we consider locally-abundant caribou as a possible explanation for the apparently higher wolf density here.

The Mystery Creek Pack, adjacent to the Big Indian Creek Pack in the mountains, is probably more typical of wolf packs inhabiting the mountains. A few caribou may be available in the extreme northern part of this pack's territory, and several mountains with Dall sheep were within their territory, but these wolves were seldom found above tree-line and all kills examined for this pack were moose, usually killed at or below tree-line. Wolf distribution in the Kenai mountains, judging from reports of biologists and other observers, seems to be primarily related to availability of moose.

The lowland caribou herd may number no more than 100 animals and migrates between open boggy areas NE of Kenai (summer) and Moose River Flats (winter). Most calving is thought to occur near Kenai, although we observed a solitary cow and newborn calf on the Moose River Flats in 1977. These caribou usually inhabit areas rarely frequented by wolves, although their strongest habitat characteristic seemed to be open areas rather than absence of wolves. During the course of the study these caribou seemed to shift their winter concentration area into more rolling uplands to the S of the Moose River Flats, which coincided with 2 developments in this area. During 1976-77 and 1977-78, an area totalling 17.6 km^2 was mechanically crushed for KNWR moose habitat improvement, resulting in a large open area in the northern part of the Skilak Lake Pack territory immediately S of Moose River Flats. Also, in 1977 a pair of wolves became established on the Moose River Flats (Bear Lake Pack). In 1978-79 and 1979-80, most caribou observations occurred in the southern Moose River Flats and the adjacent crushed area, approximately between Skilak Lake and Bear

Lake packs. While our data were not conclusive, they do suggest that caribou tend to inhabit areas where the risk of predation loss is minimized, not unlike patterns of deer and wolf distribution in Minnesota (Mech 1977b).

In spite of extensive observations of wolves in areas frequented by lowland caribou, we observed no wolf distribution shifts in repsonse to movements of caribou, only 1 newborn calf killed by wolves, no known occurrence of caribou in summer wolf scats, and no indication that hunting efforts were directed at lowland caribou. We concluded that lowland caribou were unimportant in the diet of wolves, realizing that this does not mean that wolf predation is necessarily insignificant to this small caribou population.

The only observation of possible wolf predation on Dall sheep on the study area was by T. Bailey and V. Berns in February, 1977. They located the Skilak Lake Pack above treeline, near a carcass that appeared to be a sheep, though it was not clear if the wolves had killed the sheep. During that winter, extremely heavy snowfall and icing conditions in the Kenai mountains caused very high mortality amoung Dall sheep in this area (L. Nichols, pers. comm.), and it is likely that wolves were frequently scavenging sheep carcasses.

One observation of the Bear Lake Pack alpha pair in winter suggested a possible hunting strategy for hares. In an area of local hare abundance, we observed 1 wolf walking down a cutline while the other walked through the adjacent thick birch in the 1947 burn, paralleling the first wolf about 50 m away. Any hare that was flushed from thick vegetation by one wolf would be more readily caught on the cutline by the other wolf. Snowshoe hares were not abundant during the study, and we found no indications of significant reliance on hares.

Winter Predation Rate

Whenever we observed wolves we noted behavior and searched for prey remains. While most moose carcasses consumed by wolves were considered kills, some scavenging was evident. Moose calves sometimes died of malnutrition in winter, and during April and May wolves were frequently located at carcasses of moose that died of malnutrition or undetermined causes.

Here we are concerned with feeding patterns of wolves, while the impact of wolf predation on the moose population is considered elsewhere (Peterson, et al., submitted). Wolf behavior provided an important clue to recent predation. For example, wolves typically engorge at their first feeding and then sleep outstretched on their sides. Their subsequent motivation to hunt increases with the length of time since their last kill. Hunting motivation can be gauged approximately by pack behavior: wolves that are traveling but have recently fed tend to travel in loose formation, may engage in play, rest and defecate frequently, and seem to terminate chases of prey readily, while wolves that are hunting more seriously travel in close formation, often single file, rarely engage in play, and tend to travel upwind or crosswind (Mech 1966; Peterson 1977; Peterson, unpublished).

These generalizations were applied to determine actual predation rates for the Swanson River Pack for a 57-day period beginning Nov. 9, 1977. Weather permitting, the pack was usually located daily. If the pack had just made a kill, we often skipped the next daily location. Maximum pack size was 19-20 wolves, and the pack was relatively cohesive during this period. Visibility was good, and snow conditions often permitted back-tracking, so we believe a record of this pack's kills was determined for 51 days during the 57-day period (Table 5). Part of the pack was not monitored for the entire period, since the main body of the pack sometimes numbered only 12 or 15-16 wolves, so the kill rate we determined should be considered a minimum rate.

We estimated the total prey biomass available to the Swanson River Pack over the 51-day period from the sex and age data for the kills. Applying the weights of Peterson (1977) for edible portions of moose, we derived a prey consumption of 0.12kgper kg of wolf per day. This is near the low end of the range determined from other studies for wolf food consumption in winter (0.09 to 0.19 kg/kg/day, Peterson 1977 and unpublished; Fuller and Keith 1980). However, the average Kenai pack was 40% smaller than the Swanson River Pack in 1977 - 78, and since predation rates appear to be relatively independent of pack size, the average pack, if it killed moose at the same rate as the Swanson River Pack, would have 0.20 kg/kg/day of available food. Since the observed kill rate for SRP in 1977 - 78 was near the maximum observed for wolves preying on moose, probably higher than predation rates of most Kenai packs, average prey consumption was probably more on the order of 0.15 kg/kg/day, or 15% of body weight daily. A direct determination of predation rate for other 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 can be used to calculate a daily predation rate when the pack is located on an average interval of up to 6 days. This was used to determine predation rate for other packs that were located frequently during periods of uniformly good visibility (Table 6).

The average interval between kills in winter for packs of more than 2 wolves was 4.7 days, identical to the interval determined for 1 pack in 2 winters in NE Alberta (Fuller and Keith 1980) and essentially the same as the average interval of 4.3 days between kills made by Isle Royale packs between 1971 and 1980 (Peterson, unpublished).

It was evident that predation rates were relatively independent of pack size, at least for packs numbering 7-20 wolves, implying a poor correlation between absolute wolf density and extent of predation on moose. Of greater significance are the number of packs, or hunting units, and moose vulnerability. Mech (1977b) found that pack activity was better correlated with food available/pack rather than food/individual wolf, and Stephenson (1978) also indicated that predation rates seemed poorly correlated with pack size.

Our conclusions regarding predation rates were generally supported by prey utilization. Usually, most bones were well-cleaned of muscle and hide, while metacarpus and metatarsus were left unskinned. Pelvis and skull were usually left attached to the vertebral column, which was often intact, and legs were usually not disarticulated. Remaining from calf carcasses were usually upper toothrows, portions of the skull, mandibles, and several leg bones. Most major bones from adult moose were normally left intact. Between 1971 and 1980 on Isle Royale, utilization rates both higher and lower than this were observed, with carcass utilization inversely proportional to predation rate (Peterson, unpublished).

Based on edible prey weights from Peterson (1977), adult cow moose provide an estimated 2.3 times as much edible mass as calves, so the frequency of calves among wolf-kills does not reflect the relative importance of this age-class to wolves. While adult moose comprised 53% of the kills, they provided 71% of the biomass available to Kenai wolves in winter. Nonetheless, since calves lack effective defense apart from the provided by their mother, wolves usually prey heaviest on this age group.

Wolf-Moose Encounters

We observed 37 wolf-moose encounters in which wolves actively pursued moose (plus 14 other encounters not involving active pursuit by wolves). The defensive behavior of 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, while 14 others successfully rebuffed wolves by making a stand after initially running. Eight moose outran pursuing wolves. Significantly, wolves chased every moose that ran during their initial encounter (Table 7).

Portions of 2 successful chases of moose were observed. On Dec. 30, 1976, we located 6 wolves of the Skilak Lake Pack surrounding a wounded moose that was still standing. As the plane made a second pass, the moose was lying on its side and the wolves began to feed. The moose was a 14-yr-old cow and had been severely wounded on its right hindquarter near the anus, with considerable blood loss.

A successful chase was observed on Jan. 7, 1977, involving 18 wolves in the Swanson River Pack. When located, the wolves were chasing an adult moose back and forth along the length of a small lake, with the moose not yet wounded. After several minutes of running, wolves were able to bite into and hang onto the hindquarters area of the moose, an 8-yr-old cow. One wolf grabbed the moose's nose but was quickly shaken off. Soon the moose went down and was killed, about 12-15 minutes after the observations began.

The Swanson River Pack, numbering 19 wolves, was observed for about 2 hours on Dec. 24, 1976, while they hunted moose in the 1969 burn. At 1005 a bedded bull moose detected the approaching pack, arose and immediately ran off. The wolves gave chase, but gave up after they failed to gain any ground in a few hundred meters. At 1050 the pack traveled upwind toward a bedded cow and calf. As soon as the moose detected the wolves, they rose and ran down an open, frozen drainage. The wolves were able to maintain positions close to the rear of the cow and off to either side, but could not advance on the calf, running in front. After running hard for about 1 km, the moose turned into a burned stand of trees with many windfalls. The moose immediately slowed to a walk and the wolves began to encircle the pair. The cow lunged back and kicked out at wolves near her rear end as they entered the timber, and other wolves immediately closed in on the calf. The cow whirled around just in time to protect her calf, who was kicking with its front legs. After this close encounter, the cow and calf successfully fended off all wolves while they slowly made their way about 100 m to a point where they were almost completely encircled by fallen dead timber. Any wolf that would have tried to approach closely would have been without effective escape, and after a few moments the wolves left.

At 1140 the pack entered a stand of dense spruce where we could not follow their progress, but a yearling bull moose soon ran out the other side of the trees and continued running for about 300 m until it came to a cow moose, probably its mother. The pack encountered a bedded cow moose 5 minutes later that immediately broke into a run. The wolves were close behind, however, and the cow soon turned and faced the wolves. The wolves then turned away, the cow again ran off, and we terminated the observations.

Escape into water is a very effective defense against wolves, as indicated by the following observations.

1) On July 13, 1977, we observed wolf 422 near a lakeshore, by a brown bear feeding on a recently-killed moose calf. A cow moose stood in water about 30 m from the calf.

2) On April 24, 1978, male 026 made a large circle around an area of standing water in the Moose River Flats. About 50 m away, on a small area of tussocks in the middle of the water, stood a cow moose, intently watching the wolf. The moose had been wounded and was bleeding from the anal area. The fate of this moose was not determined.

3) On August 15, 1978, male 210 was located in a dense stand of conifers adjacent to a small pond. In the middle of the pond stood a cow and calf, both watching the wolf.

4) On Oct. 27, 1978, we located the alpha pair and 6 pups of the Bear Lake Pack just leaving a lake, where 20 m out in the water stood a cow and twin calves, grouped together and watching the departing wolves.

5) On Sept. 1, 1979, we observed 5 wolves of Swanson River Pack chase a moose for almost 0.5 km. The chase proceeded through mature timber and ended when the moose ran into a small lake and swam off, leaving the wolves at the shore.

6) On Nov. 8, 1979, we observed a moose crossing the Swanson River, while 8 wolves of Swanson River Pack waited on the opposite shore. Just after the moose reached shore, it swam back to the middle of the river, where it remained for 30 minutes after the wolves left.

Non-winter Predation Patterns

We relied largely on scat analyses to determine wolf predation patterns in non-winter months (Table 8). The formula developed by Floyd et al. (1978) can be used to determine, from the incidence of prey remains in wolf scats, the relative proportions of individual prey and prey biomass in the diet. Their study indicated that the percent frequency of occurrence, if used to estimate the biomass of prey consumed by a wolf, tended to overestimate the significance of small prey and underestimate the importance of larger prey. This can be readily seen in Table 9. Frequency of occurrence, in the studies reviewed, resembled relative numbers of moose taken more closely than relative biomass.

Application of the formula of Floyd et al. (1978) indicated that adult moose were generally far more significant in the wolf diet then calves, even though many more calves than adults were probably killed. This alters the common assumption that in summer wolves are highly dependent on moose calves, and consequently the appropriateness of the conversion formula should be considered carefully. Floyd et al. (1978) found a linear relationship between whole prey weight and weight of prey represented by each collectible scat, using prey ranging in size from a snowshoe hare up to an adult white-tailed deer weighing 75 kg. Whether or not this relationship holds for prey as large as adult moose weighing 350 kg or more is unknown, although Floyd et al. (1978), Fuller and Keith (1980), and Stephenson (1978) assumed that it did.

At least 2 factors might alter the relationship between prey weight and weight represented by each scat for large prey. First, wolves are far less likely to eat hide and hair from moose than from smaller prey, which would reduce the likelihood of producing an identifiable scat. Secondly, hair from adult moose is easily recognized, to the point where even a portion of a single hair in a scat is readily seen, which increases the likelihood of adult moose being recorded in scat examinations. These 2 biases tend to offset each other, however, so we believe that the conversion formula is still the best available means to interpret scat analyses.

Moose comprised the overwhelming majority of all prey remains found in summer scats, appearing in 77% of all scats examined. Snowshoe hare was found in 15% of all scats, beaver and other smaller rodents in 9% of all scats, and other items were rather insignificant. These proportions were essentially the same as the percent frequency of occurrence among all prey remains. (Table 8).

Judging from scat analysis from 1977 and 1978 combined, Kenai wolves rely on moose to about the same extent as wolves in many areas, and seem to rely on adult moose to a somewhat greater extent than elsewhere (Tables 9 and 10). We can only speculate on the reasons for the variation in reliance on calf moose in different areas, since data on relative abundance is not comparable between areas. Calves are preferred prey of wolves at all times of the year, so we would expect a direct relationship between calf abundance and predation on calves, but in fact the relationship may be altered by presence of alternate prey and perhaps such subtle influences as availability of escape habitat (water), condition of cow moose, etc.

The calculated proportion of the non-winter wolf diet (determined from scat analyses) comprised of adult moose is 81%, approximately the same as the 71% figure derived from winter observations. The relative number of calves and and adults killed in winter and non-winter were also similar, with calves comprising 47% of the winter wolf-kills examined and 58% of the moose killed in summer.

Contrary to the evidence from scat analyses, we observed few wolf-killed adult moose in summer during the study. Adult carcasses consumed by wolves in summer were repeatedly visited and consequently, even with limited visibility, we easily located such carcasses. If wolves were killing adult moose in summer at a rate even close to that documented for winter, we surely should have observed more evidence of this, for such kills would have been repeatedly visited by single wolves. Since scat analyses did not agree with our summer observations, we sought to resolve the discrepancy through additional indirect evidence.

Moose survival data from other studies suggest that predation losses in summer are much reduced from winter levels, indicating caution when drawing conclusions from scat analyses alone. From the frequency of occurrence of antlers in various stages of development among moose skulls found on Isle Royale, Peterson (1977) determined that the mortality rate of adult bulls was some 12 times greater in winter than summer. An estimated 94% of the adult bulls died between September and April, while 6% died from May through August. This is consistent with the predation loss pattern determined for 19 radio-collared adult moose that were killed by wolves while being monitored on a year-round basis (Hauge and Keith 1981; Coady 1974, 1976); 95% died during October-May, while 5% died in June-September. On the other hand, Ballard and Spraker (1979) determined that kill rates of yearling and older moose by 2 wolf packs in early summer were comparable to winter kill rates.

There are several important reasons for greater wolf predation rates in winter. Perhaps the most important is the advantage accruing from group hunting, which begins in earnest in October. It was not unusual for Kenai wolf packs to kill adult moose in October, after the adults and pups joined together and began traveling extensively. Wolves also gain some advantage from frozen lakes, which remove an important escape option for moose confronted by wolves, and from winter snow, if it is sufficiently deep and crusted to hamper moose and yet support wolves (Peterson and Allen 1974).

Observations suggested that some of the adult hair in summer wolf scats resulted from scavenging. Of the moose carcasses discovered from aircraft, the proportion that were judged fresh wolf-kills was much less in summer (16% of 50) than winter (80% of 214). Many of the carcasses visited by wolves in summer dated from the previous winter, and fresh carcasses of adult moose that were consumed in summer by wolves (e.g. road-killed moose along the Sterling Highway) were visited and re-visited over a much longer period than in winter. If the scat data accurately reflect relative proportions of calf and adult moose, and if our summer observations correctly portrayed predation patterns, then food availability must be substantially less in summer than winter.

Predation on Domestic Animals

Livestock is not common on the Kenai Peninsula, but some cattle and horses can be found along the Sterling Highway from Sterling to Homer, then N along the shore of Kachemak Bay to the head of the bay. Radioed wolf packs showed strong avoidance of areas settled by humans, but this was not the case with dispersing individuals. After leaving the SRP and traveling to the southern Kenai lowlands, male 201 was shot in June, 1979, after reportedly trying to enter a goose pen at Kachemak Bay. Likewise, after dispersing from the Killey River Pack, female 472 was observed and finally shot near an Anchor Point farm that had reportedly lost 2 head of stock and a dog to wolves.

Probably the largest concentration of livestock (primarily cattle) occurs at the head of Kachemak Bay, where wolves have been present since the late 1960's. The head of the local cattleman's association, B. Willard, confirmed that at times wolves were quite common in the valley, but indicated no serious predator losses among roughly 400 head of cattle that are run on state-leased grazing land in the valley floor. Only about 2 dozen cattle and perhaps 20 horses are left to overwinter in the valley. Although Willard has had cattle in the valley since 1960, he has not confirmed any losses to wolves among his livestock. Black bears, however, have killed some of his calves and he indicated that other owners have reported a few losses that might have been due to wolves. He regarded free-running dogs as a more serious disturbance to cattle than wolves.

POPULATION DYNAMICS

Growth of the Re-established Population

From historical references, Peterson and Woolington (in press) concluded that the original Kenai wolves were probably extirpated by 1915. Palmer (1938) indicated that a "small" wolf had been shot on Skilak Lake in 1928, although coyotes ("brush wolves") had just become established on the Kenai at the time.

A large gray male wolf was shot on Tustumena Lake in February, 1951, by J. Willard (pers. comm.) of Caribou Lake. The animal was missing a toe, and characteristic tracks of this individual has been seen in the Tustumena area for the previous 2 winters. We examined the hide of this wolf in 1976.

Aside from a vague track report in the Kenai mountains in the 1930's, these were the only reliable reports of wolves on the Kenai between 1915 and the late 1950's. Given the accelerated human activity and development on the Kenai following World War II, and the frequent aerial surveys over the Moose Range beginning in the late 1940's, we believe it is improbable that a remnant wolf population could have gone undetected.

At least 3 local residents familiar with wolves reported (pers. comm.) observations of wolves on the Kenai Peninsula in the late 1950's, and thereafter reports of wolves began to accumulate. An ADF&G biologist observed a wolf in 1961 during a moose survey, leading to a state closure of all wolf hunting and trapping on the Peninsula, effective July 1, 1962 (Le Roux 1971).

We assembled all reports of Kenai wolves prior to 1976 from ADF&G and KNWR files (Peterson and Woolington, in press). Most early sightings were between Skilak and Tustumena lakes. By 1968, wolves were also reported N of the Kenai River and S of Tustumena Lake, indicating an expanding population, and by 1970 about a dozen reliable sightings were recorded. Between 1970 and 1975 an additional 102 wolf observations were recorded, primarily by ADF&G and USF&WS

biologists. Packs containing more than 10 wolves were reported from all major areas of the lowlands, with an average of 4.4 wolves seen per observation. There can be little doubt that the wolf population expanded most rapidly between 1965 and 1975.

Between 1971 and 1977 ADF&G biologist P. LeRoux conducted several aerial surveys of Kenai wolves based on snow-tracking and direct observations. His estimates of the total Kenai population, summarized in Table 11, suggested a rapid increase in the wolf population in the early 1970's, a time of severe winters and substantial malnutrition mortality among Kenai moose (Oldemeyer, et al. 1977).

Wolf Density and Pack Territories

As wolves in additional packs were radioed, the study area was enlarged annually (Fig. 3). Wolf density in early and late winter and aspects of over-winter loss are presented in Table 12 for each pack, summarized in Table 13. From 1976 to 1978 wolf density across the study area increased from 14 to 18 wolves/1,000 km^2, declined by 1980 to about 14 wolves/1,000 km^2, then increased to about 19 wolves/1,000 km^2 in 1981.

Fluctuations were attributed to changes in study area as well as actual change in wolf density in portions of the study area. The core study area on the northern lowlands included packs (Swanson R., Bear L.) with the lowest observed density while the enlarged study area included packs with the highest wolf density (Big Indian Cr., Bear Cr.). While we believed the wolf population on the core study area was near saturation density in 1976, 2 new packs (Bear L., Mystery Cr. II) developed in vacancies that became apparent early in the study, providing some potential for further growth.

The principal source of wolf mortality was hunting and trapping, which increased steadily during the study. Wolf density declned in 1979 and 1980 in apparent response to peak harvest the previous year, then increased in 1981 after harvest declined. These correlations suggest that wolf density was controlled by harvest at the close of the study, and would increase to an undetermined level in the absence of harvest.

Average pack territory size was 622 km^2 (Table 14). Territory size was correlated ($r^2 = 0.854$, $\underline{P} < 0.001$) with pack size (Fig. 4). Thus as the Swanson R. and Skilak L. packs both declined, so did their territory. Since there was no evidence of fluctuation in wolf food supply for the Kenai study area as a whole, we discount this as an explanation for changes in territory size. Other studies have demonstrated territorial trespassing following a decline in food supply (Mech 1977b) and reduced territory size resulting from increased food supply (Peterson 1977). Haber (1977) demonstrated that territory size was inversely related to prey biomass.

Significantly, 2 pairs of wolves that became established in a vacancy claimed a territory equivalent in size to that of much larger packs. This suggests that a vacant "superterritory" (Verner 1977) may be required for successful establishment of a newly-formed pair. Areas used by 2 pairs in this study amounted to 1/2 - 2/3 that of the average pack. Likewise, Mech (1977b) reported that when a pack declined from 7 wolves to just the alpha pair, the pair still occupied most of their original territory.

Generalizing, we suggest that a pair of wolves require a superterritory for successful colonization, thereby providing an area with 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 prey size (Peterson 1977).

Substantial variations in wolf density in portions of the study area should be pointed out (Table 14). Intra-pack density varied from 1 wolf/24 km^2 to 1 wolf/78 km^2 for all packs except 2 newly-formed pairs, which established territories providing 200 km^2 and 154 km^2 per wolf, respectively. Lowest density for established packs was found on the northern lowlands in areas where there were no obvious concentrations of wintering moose. The average density for Swanson R. and Bear L. packs in 1979 and 1980 was 1 wolf/ 64 km^2. Higher wolf density within the Skilak L. Pack territory was well documented, averaging 1 wolf/40 km^2 over a 4-year period. Of the packs inhabiting mountain edges, territories of Mystery Creek Pack (I and II) and Killey River Pack were best documented. These packs (excluding Mystery Cr. Pack II in 1978-79 when only 2 wolves were present) averaged 1 wolf/50 km^2, a value which may not reflect all of the mountainous area used by these packs (calculated density should be considered a maximum estimate). The 2 packs that showed the highest density, Big Indian Creek Pack and Bear Creek Pack, were monitored relatively infrequently, yet the density values may still be relatively accurate since both pack inhabit areas of high relative prey density. The Big Indian Cr. Pack includes all of the known range of the mountain caribou herd of 200-300 animals, and broad mountain valleys in this area support moderate densities of moose (USFS 1978). The Bear Cr. Pack, when found outside of mountainous areas, was generally associated with treeline edge areas known to support high moose densities in winter. This pack also has access to the mountains NE and SE of Tustumena Lake, where 300-400 Dall sheep exist (KNWR files). In view of the imperfect data on the total range of these packs, we conclude that wolf density for these 2 packs can be only roughly estimated to be about 1 wolf/25-35 km^2.

Major Changes in Pack Territories

During the study most packs exhibited only minor annual changes in territory size and boundaries; a detailed chronology of each pack is provided in Appendix II. Provided here is a brief overview of major changes observed among study packs.

Mystery Creek Pack (MCP) I and II. In 1976-77 a large pack, MCP I, occupied a territory that included both lowlands and mountains N of the Kenai R., and in 1977 the pack established a den on the edge of the mountains. During the winter, 1977-78, this pack moved entirely into the mountains and apparently abandoned the lowlands and adjacent mountains occupied the previous year. All radioed wolves in MCP I were subsequently killed and contact with this pack was lost. During summer 1978 a radioed wolf pair occupied the vacant territory and in 1979 raised pups in the same den used by MCP I in 1977. This group, MCP II, used the same lowland and mountain areas utilized by the preceding pack.

Swanson R., Bear L., Pt. Possession and Elephant L. Packs (SRP, BLP, PPP and ELP). Containing 20 wolves in 1976, the SRP traveled over a major portion of the northern lowlands in 1976-77. During the course of the study, we followed the transition in this pack's territory from 1 pack containing 20 members to 4 packs with 26-30 members by late 1980. In 1977 a radioed wolf pair established the Bear Lake Pack in a vacancy just SE of SRP territory. Over the next 4 years the SRP moved progressively toward the west, while BLP assumed a large portion of the vacated area. We never found evidence that BLP agressively displaced the SRP, and could only speculate that SRP was shifting its activities toward the growing moose population in the 1969 burn, located in the western portion of their original territory. Two unradioed packs, Pt. Possession (PPP) and

Elephant Lake (ELP), subsequently became established in the northern and southwestern portions of the original SRP territory. Early in the winter of 1978-79, in an area only slightly larger than the original SRP territory, we found 18 wolves in SRP, 8 wolves in BLP, at least 10-12 in PPP (judged from tracks only), and a minimum of 3 in ELP (from direct observations), for a total of 39-41 wolves. Thus, wolf density in this local area had roughly doubled in 2 years. Since this type of rapid spatial re-organization and population growth was seen nowhere else on the study area, we speculate that it was not a continuation of population growth following colonization of the northern Kenai by wolves, but rather a localized phenomenon perhaps attributable to increasing moose density in the 1969 burn.

In 1978-79 the SRP and PPP were heavily harvested, and the SRP dropped from 18 wolves to just 5 members by spring. This pack increased to 8 members by the beginning of the next winter but declined to 1 wolf (probably a pup) by winter's end. Harvest, disease, and dispersal were all involved in the continued reduction during 1979-80. In October 1980 we found a pair plus 4 pups utilizing the reduced SRP territory, but could not establish if either wolf of the pair originated within SRP. Early in the 1980-81 winter we estimated 6-10, 9, and 5 wolves in BLP, PPP, and ELP, respectively, or a total of 26-30 wolves in the 4 packs.

Skilak Lake Pack (SLP). From 1976 until January 1980 this pack was led by the same alpha pair. SLP reached a maximum pack size of 12 early in the winter of 1978-79, but was then reduced to just the alpha male after 2 seasons of heavy harvest when at least 10 pack members were killed. In February 1980, within a month after losing his mate, the lone alpha male paired with dispersing female 424 from the adjacent BLP. This female was killed in May 1980 just after giving birth to 6 pups, which presumably did not survive. During the summer of 1980, the alpha male again paired with a dispersing female from BLP (420), and during limited monitoring in the winter of 1980-81 we determined that this pair used only a small portion of the original SLP territory. Significantly, since male 026 (a young male), father of BLP females 420 and 424, was probably the offspring of the SLP alpha male of long-standing (a graying underbelly and head suggested an old wolf), then 420 and 424 both paired with the equivalent of their grandfather.

After being reduced by harvest, SLP reduced the extent of its travels, and the original SLP territory functioned almost like a vacuum, attracting potential colonizers from other packs. In 1979-80 4 wolves judged to be non-SLP members were killed within the old SLP territory, and in 1980-81 a radioed lone wolf, 2 radioed MCP II wolves, and 1 radioed BICP wolf were all killed within the SLP territory.

Kenai Peninsula Wolf Population Estimate

An accurate estimate of wolf density is available only for the wolf study area on the northern lowlands. Here wolf density varied in different years from about 14 to 19 wolves/1,000 km^2. We suggested that, at least during the latter part of the study, wolf density on the study area was probably constrained by harvest. Containing packs that were both heavily and lightly harvested, the study area represents reasonably well the range of harvest pressure sustained by the wolf population across the Peninsula. However, wolf harvest for the entire Peninsula peaked in 1978-79 and 1979-80, while on the study area harvest continued to increase through the 1980-81 season. Consequently, by 1980, the effect of harvest on the entire Kenai wolf population was probably less then on the study area, where wolf density was about 14/1,000 km^2. Thus, we chose a wolf density of 16/1,000 km^2 as representative of early winter wolf density in 1980 for most of the available habitat on the Kenai.

Recognizing that a single "best estimate" of the entire Kenai wolf population may be of limited usefulness because of the potential for rapid change in any wolf population, we nonetheless feel obliged to set forth such an estimate, since the Peninsula is a discrete geographical entity and a total population estimate is of obvious management value. We divided the Peninsula into primary and secondary wolf habitat and non-wolf habitat on the basis of reported observations and harvest records, then applied wolf density estimates to the designated wolf habitat. Areas we considered to be non-wolf habitat were the following:

1) All glaciers and permanent icefields, comprising about 5,000 km^2, or almost 20% of the peninsula.

2) Areas heavily settled by humans in the central lowlands and the western shore along Cook Inlet.

3) The precipitous SE coast of the peninsula.

Estimated wolf distribution appears in Fig. 5. No wolf packs have been observed outside the area indicated in Fig. 5 as wolf habitat, although we had 1 report of wolf tracks along Nuka Bay and 1 was killed at Gore Point.

The Kenai lowlands and the portion of the study area within the Kenai mountains were considered primary wolf habitat with estimated density 16 wolves/ 1,000 km^2. An area of secondary wolf habitat was assumed to exist between primary wolf habitat and non-wolf habitat on the eastern side of the Peninsula, with assumed density half that of primary habitat.

The resulting estimate for the entire Kenai Peninsula is 185 wolves in early winter (Table 15). Wolf populations are often censused later in winter when better light conditions may exist for snow tracking; we estimate the midwinter population at 155 wolves, assuming a constant rate of overwinter loss averaging 32% (4-year average for the study area was 39%, reduced to allow for estimated survival of dispersing wolves).

Inadequate snowcover or snow heavily crusted by wind and thaws has usually precluded Peninsula-wide wolf censuses based on track observations. The only attempted complete census of Kenai wolves between 1976 and 1979 was in March 1977. LeRoux (1978) reported a minimum of 72-81 wolves in GMU 15 and 21-22 in GMU 7, based on observation of tracks, actual wolf observations, and trapper reports. Approximately 2/3 of the wolves on the study area were located during the census, and LeRoux (ibid) expanded his minimum estimate on the basis of the proportion of the area covered, the prevailing snow conditions, and the assumed proportion of wolves missed. The resulting "best estimate" was 95-120 in GMU

15, 21-22 in GMU 7, or a peninsula total of 116-142 in mid- to late-winter, somewhat less than our estimate.

Age and Sex Ratios

The estimated maximum proportion of pups in early winter increased from 35% to 50% in the course of the study, averaging 41% (Table 16). Spring-to-fall increases in pack size provided the basis for these estimates, with the following adjustment. The simple comparison of spring and fall counts could underestimate the number of pups produced that year as some adults probably dispersed or died during the summer. We monitored 46 wolves for at least 3 months between May and October. Five wolves dispersed and 1 died, suggesting a summer loss of 13% of the adults. Our pup:adult ratio was adjusted accordingly. Two other biases are unavoidable, and they act to offset the summer adult losses discussed above. A small but unknown number of adult wolves could disperse onto the study area. Also, it is likely that some adults were not counted in spring monitoring because of lower sightability and less pack cohesion. Since these latter biases are not quantifiable, the above pup:adult ratios should be considered maximal.

While the significance of unbalanced sex ratios among wild 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, since the sex ratio of adults in the recorded harvest between 1974 and 1980 was 99M:104F. There was conflicting data for pup sex ratio from the recorded harvest versus pups that were captured during the study. A significant excess of females (23M:39F) was recorded for pups harvested across the Peninsula ($\underline{X}^2 = 4.13$, $\underline{P} < 0.05$), but an excess of males (22M:10F) was evident in the pups we captured on the study area ($\underline{X}^2 = 4.5$, $\underline{P} < 0.05$).

Wolf harvest intensity during the study may have been higher on the study area than for the entire Kenai wolf population, since access for hunters and trappers was greatest there. If wolf density here was reduced by harvest, as we suggested, Mech's (1975) hypothesis would predict that pup sex ratio on the study area would favor females, or at least more so than the overall pup sex ratio on the Peninsula, but the available data suggest otherwise.

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 sex ratio of adults that we live-trapped in this study was heavily weighted toward females (7M:19F) ($\underline{X}^2 = 5.5$, $\underline{P} < 0.025$), with alpha females frequently caught. In 1978 lactating females in 4 contiguous packs were trapped and radioed, with 3 of the 4 known to be alpha females. In 1979, all 4 individuals were again trapped, and again all were lactating. While live-trapping in summer seemed selective for females, the sex ratio among wolves darted in winter (13M:9F) was not significantly different from 50:50 ($\underline{X} = 0.45$, $\underline{P} > 0.5$).

Aspects of Reproduction

The pattern and timing of reproduction for Kenai wolves followed the well-known pattern for this species. 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 when we knew the social standing of the mother. Although neither courtship behavior nor breeding were observed, and we had few pregnant females radioed in spring, other radioed wolves began frequenting dens in early May, so the breeding season was probably in late February or early March, assuming a 62-day gestation period (Mech 1970). Judging from a highly distended uterus and fresh placental scars, female 424 had given birth just before dying in a snare during May 6-13, 1980.

Six dens in 5 packs were examined after being abandoned by wolves (Table 17). Dens were most often dug out among the roots of large trees, and were consistently in mature forest, possibly to gain some relief from the almost continuous sunlight during the denning period. Both SLP and Killey R. Pack used the same dens in 3 consecutive years, indicating traditional use of preferred sites.

Pups were usually moved to a rendezvous site in late June or July, usually 1-2 km or less from the densite. Thereafter, pup activities centered around a succession of rendezvous sites, progressively farther from the den, as documented elsewhere (Joslin 1967; Carbyn 1975; VanBallenberghe et al., 1975; Peterson 1977).

Litter size for Kenai wolves during the study was about average for the species. We estimated litter size by examining uteri of 13 yearling and older females for placental scars. Only 4 wolves exhibited scars, including 1 wolf with 7 wide scars and 5 less prominent scars (we considered this as indicating 2 separate litters). The 5 litters thus indicated by placental scars averaged 5 pups/litter and ranged from 3 to 7 pups.

Spring-to-fall increases in pack size (Table 16) suggested that an average of 4.5 pups survived to fall in each pack (corrected total of 68 pups among 165 wolves in 15 packs). Coupled with an estimated litter size of 5 pups, this suggests that pup survival during the first 6 months of life was high during the study. Significantly, the number of surviving pups was unrelated to pack size (Fig. 6).

While wolf pups have bred in rare cases in captivity (Medjo and Mech 1975), most females first enter estrus as yearlings. We examined reproductive tracts from 5 known-age females at least 1 year old. Two yearlings had no placental scars, indicating that they had not bred as pups. Only 1 (424) of the others bred as a yearling; female 424 dispersed from the BLP and became the only breeding female in the SLP.

We assessed reproductive condition of live-captured female wolves from teat development (Table 18). Again, we found no instances of females breeding as pups. Three mature females (039 in 1976, 108, 136) that did not bear young were known to be socially subordinate.

The record of female 039 of SRP suggests a possible fate of subordinate wolves that mate within their pack. She was estimated to be 2-4 years old and a nonbreeder when captured in October, 1976. She was clearly a subordinate wolf, her peripheral ties to SRP evident 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 rendezvous site in more open habitat, we observed her with 7 pups. Thereafter, she was observed with no more than 2 pups which were seen for the last time on Aug. 13. At that time the pups were obviously growth-retarded and about half as large as 119's pups.

At the densite of 039 we found no scats, 1 moose calf scapula, and no trails leading into the area. We suspect that 039 had attempted to raise her pups alone, since we saw no other adults with her and movements of other radioed pack members showed almost no overlap with those of 039 (Fig. 7). While we can only speculate that her pups all died, we do know that they did not subsequently join SRP, since all 3 pups captured in SLP in November were large and no small pups were observed in the pack. Female 039's radio expired in late August, 1977, and we did not determine if she rejoined SRP. In 1979 she was snared S of SRP territory with no sign of pack affiliation.

It is a common observation that reproduction within a wolf pack, especially a large pack, rarely reaches its potential level. Peterson (1979) observed a female chased from a pack after mating but did not determine the eventual fate of the animal. In studies of captive wolves, Rabb (1967) and Packard and Mech (submitted) found that mate preferences and dominance relationships reduced the frequency of mating. We found that social relationships not only moderated mating frequency, but also affected relative success in pup-raising.

Annual Mortality

We used annual mortality for radioed wolves as an estimate for the study area population. The fate of all wolves radioed in December (N = 80) was determined for the following 12 months. During this time, summing over 5 years, 21 of these wolves died, implying a mortality rate of 26%. Most mortality was from harvest, and we believe most harvested wolves were properly reported to ADF&G. Since the remaining 60 wolves were not all monitored for a full year (average transmitter life was 9.8 months), some unreported harvest and natural mortality could have gone undetected, producing a slight underestimate of annual mortality. Sample sizes were not adequate for a breakdown by year or age, so we developed an estimate based on total tracking time for all wolves monitored.

An alternate estimate of annual mortality was obtained by dividing the total number of deaths of radioed wolves with operating transmitters by the number of wolf-years of monitoring. The result (43%) for our study is an overestimate of annual mortality, however, since most wolves were radioed just prior to the winter season when harvest loss was highest. To offset this bias, we added to total tracking time the period from May 1 (assumed birth date) to date of capture for each wolf. This would otherwise lead to an underestimation of mortality since obviously only surviving wolves were radioed. However, the resulting estimate of annual mortality, 26% (Table 19), is identical to our other estimate, so we have assumed that the 2 biases inherent in this approach are offsetting. The second method provides us with a more useful estimate of annual mortality for each year and better basis for comparing mortality of pups and adults.

Annual mortality for radioed wolves rose during each year of the study (Table 19). This mirrored the trend in wolf harvest on the study area except during 1980-81, when harvest dropped but radioed wolf mortality continued to increase. In 1980-81, 3 wolves with operating transmitters were killed in the partially vacant SLP territory, and the high losses among radioed wolves that year were not representative for the study area population.

Estimated annual mortality for adult radioed wolves (35%) was substantially greater than that of radioed pups (10%). We attribute this in a later section largely to the high mortality exhibited by dispersing adult wolves.

Mortality Factors

Mortality of radioed wolves (all at least 5-6 months old) indicated that harvest by hunters and trappers was the primary cause of mortality in this moderately exploited population. Of the 23 radioed wolves that died when transmitters were operating, 18 (78%) were killed by legal harvest, 3 (13%) died from natural causes, and 2 (9%) died from illegal or unknown causes.

Human Harvest

No legal harvest of Kenai wolves was allowed from July 1, 1962, until Nov. 1, 1974, when a sport hunting season was initiated and resulted in the shooting of 6 wolves. When a regular trapping season was added the next year, 21 wolves were taken on the Peninsula. Beginning in 1976-77, state wolf hunting and trapping seasons were identical to those in most of Alaska (Table 20).

Harvest Regulations and Data. For the first several years of legal harvest, ground shooting, often incidental to hunting for other species, constituted the principal harvest. As local knowledge about wolves increased, more wolves were taken by snares and traps, as well as "land-and-shoot" harvest. Under state regulations, wolves are considered both fur-bearers and game animals and, while it is illegal for hunters to use aircraft to locate wolves, trappers can legally locate furbearers from aircraft, land, and shoot them. Airplane-assisted "trapping" of wolves is a common practice in Alaska (VanBallenberghe 1981), and is compatible with the Federal Airborne Hunting Act of 1972 if the wolves are not herded or harrassed by aircraft. In 1977-78 and 1978-79, with large wolf packs that had not been intensively hunted, good snow conditions allowed land-and-shoot trappers to take 42% of the wolves harvested on the KNWR.

Taken together, snares and traps constituted the principal means of wolf harvest on the Kenai (Table 21). The relative importance of snares vs. traps may not be accurately reflected by the ADF&G sealing records. While ADF&G records report more wolves trapped than snared, during our study no radioed wolves were trapped while 15 were snared (2 radioed wolves that were trapped were released with the cooperation of the trapper).

Some harvest-related mortality is probably undetected, although we believe most wolves harvested on the Kenai were reported to ADF&G as required. There was only slight evidence of illegal aerial shooting of wolves, wolves stolen from traps and snares, and wolves left dead in the field. Three wolves, including radioed wolves 424 and 480, were found dead in abandoned snares.

Distribution of Harvest. Wolf harvest patterns were clearly linked to human access and visibility (Fig. 8). The only major treeless area on the Kenai lowlands is the plateau NW of Kachemak Bay, and wolves appear to be highly vulnerable there. Otherwise, most of the harvest was associated with roads, snowmobile trails, a gas pipeline crossing the Refuge, or rivers and lakes. Wolf harvest was highest in accessible portions of GMU 15A on the study area and also GMU 15C on the southern lowlands.

Pup Vulnerability to Harvest We sought to determine whether the proportion of pups in the harvest reflected the actual age structure of the population. Survival of radioed wolves suggested that adults were more vulnerable to harvest than pups, so we would predict proportionately fewer pups in the harvest than in the population. However, average pup proportion in the population during the study was estimated at 43%, comparable to 49% pups in the harvest, as determined by ADF&G sealing records for the years 1975-76 through 1977-78.

The above discrepancy could be due to inaccuracies in age determination or spatio-temporal incompatibility between the harvest and population samples. Until 1978 age (pup or adult) of harvested wolves reported to ADF&G was determined by epiphyseal closure in the radius leg bone (a requirement dropped after 1978). We suggest that a systematic examination of epiphyseal closure variability is needed, especially as related to growth retardation, and that possible errors in this aging technique be assessed. While the technique has been in use since it was introduced by Rausch (1961), there are no published data that can be used to assess its accuracy. We have most confidence in the survival data for radioed wolves, which suggested a lower vulnerability among study area pups than adults.

Harvest Trend. Wolf harvest on the study area and the entire Kenai Peninsula increased to a peak in 1978-79 and 1979-80, then declined in 1980-81 (Table 21). Except for 1980-81, harvest loss among radioed individuals showed a similar trend. We estimated the early winter wolf population on the northern lowlands by applying wolf density determined for study packs to the 3,566 km^2 of wolf habitat contained in GMU 15A and the N half of GMU 15B. Wolf harvest in this area was obtained from ADF&G records. The magnitude of annual harvest was indicated by the proportion removed from the early winter population. This ranged from 12% in 1976-77 to 41% in 1978-79 (Table 22).

Natural Mortality

Disease has recently been implicated in declines in other wolf populations (Chapman 1978; Carbyn in press). While wolves are exposed to canine distemper virus (CDV) in some areas of Alaska where they have contact with domestic dogs (Ritter et al., unpublished), wolf mortality to distemper had not been recorded in Alaska prior to this study, so we provide the following case histories:

1) Male 203 of the SRP died at the age of 16-17 months after being monitored for 10 months. Although the animal was rarely seen in the 3 months prior to its death in September, 1978, we detected nothing abnormal in its movement or associations with other wolves. On Aug. 1 we saw it investigating human refuse along a cutline 2.5 km NE of Kenai, an area frequented by local dogs. On Sept. 6 it was located at the site of its eventual death, with male 201, while male 222 was a few hundred meters away. None of the wolves were observed, and 203 may have already died. On Sept. 27, after repeated locations at the same site, we checked the area on the ground and found the carcass of the wolf floating in a shallow pond. The intact head was sent to the Alaska Rabies-Virology Unit, where foci of CDV were located within the brain, implicating distemper as the cause of death (D. Ritter, pers. comm.).

2) Female 412, also from SRP, died at the age of 20 months after being monitored for 13 months. On Jan. 1, 1980, it was located with 3 packmates on an old kill. On Jan. 2, 3, and 4, 412 and packmate 462 were both located at the same site, although only 1 wolf could be seen. Wolf 412 remained in the area after her packmates left, and on Jan. 12, Woolington checked the area on foot and found wolf 412 bedded, near the old kill. The wolf appeared ill, her hair was matted, and she walked away slowly when approached. On Jan. 15, when located from aircraft, the wolf was dead in the same location. The wolf had lost 13 kg since its capture 9 weeks earlier, but still possessed omental fat in thin, 3 mm layers, with 2 mm layering of fat along the ribs, suggesting acute rather than chronic deterioration. Tissues were tested by fluorescent antibody technique for CDV and infectious canine hepatitus virus. Bladder tissue was positive for CDV, while brain, kidney and liver were negative. The presumptive cause of death was again distemper (D. Ritter, pers. comm.).

In light of known mortality from distemper among SRP wolves, the decline of this pack between 1978 and 1980 may be circumstantially linked to loss from disease as well as human harvest. The death of 412 followed closely an outbreak of distemper among dogs in the Kenai-Soldotna area, immediately adjacent to the SRP territory. Two local veterinarians, G. D. Carter and R. D. McCarten, each reported seeing over 30 cases of distemper in dogs in September and October, 1979. Prior to this Dr. Carter had not seen over a half dozen cases of distemper per year for 3-4 years, and Dr. McCarten had seen about 5 cases in the previous 1-2 years.

The only other non-harvest mortality involved male 466, a KRP pup that was monitored for 3 months prior to its death. It traveled regularly with KRP until the end of February, 1980, then its movements became localized. On Apr. 8, packmate 472 was located with 466. We later examined the area on the ground and found the carcass of 466 lying beneath a spruce tree. The date of death was probably in March, so wolf 466 was likely dead when adult female 472 returned to the site. Total weight of the carcass was estimated at 20-22 kg., and the animal was quite emaciated. Its condition strongly suggested malnutrition as a contributing factor in its death, although possibly a secondary factor. A trapper caught several wolves from this pack in 1979-80, and gave us the carcass of a pup that seemed to be in very poor condition. The skinned carcass from the trapped wolf weighed only 19 kg (suggesting a live weight of about 25 kg), was emaciated, and had white spots of undetermined origin on the surface of the liver.

Wolf 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% annual 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 approximately 40% or less of the wolves present in early winter often lead to population declines the next year (Ballard et al. 1971; VanBallenberghe 1981; W. Gasaway, pers. comm.). After reviewing several studies, Keith (in press) suggested that harvests in excess of 30% of a wolf population might be expected to reduce wolf density the next year.

Our data suggest that a principal impact of harvest was the reduction of pack size (Fig. 9). We found that the number of pups produced was unrelated to pack size (Fig. 6), with probably just 1 litter of pups in each pack. Thus, the increased proportion of pups and proportion of breeding females in exploited wolf populations could simply result from constant litter size in smaller packs. Wolf density could be maintained in moderately harvested populations if additional packs (reproducing units) developed in vacancies created by reduced territory size of established packs. We found measured territory size and pack size to be directly correlated, at least for moderate or large-sized packs, and as harvest increased, so did the number of packs on the study area. The average space occupied by each pack (Table 13) was directly correlated with average pack size ($r^2 = 0.92$), and as average pack size declined and vacant territory appeared, additional packs developed. It is likely that only some of the new packs on the study area developed as a result of increased harvest, as both BLP and MCP II developed before harvest loss was very significant. In response to harvest 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 SRP contained 20 wolves and occupied a large territory. By 1980, the old SRP territory contained 3 packs (SRP, ELP, PPP) totaling 20 wolves, plus comprised a portion of BLP territory.

Responses in pack size and wolf density to specific harvest levels are suggested in Fig. 9. Wolf density continued to increase slowly from 1976 until late 1978, a period when harvest levels were less than 15%. During the next 2 years, following harvest of 41% and 36% of the population, wolf density declined. During the final year of the study, wolf harvest dropped to less than 30% and wolf density increased the following year. Average pack size declined from 15 to about 6 wolves in 4 consecutive seasons as harvest generally increased; pack size finally increased in 1981-82 after harvest declined. The estimated proportion of pups in study packs increased during the first 4 years of the study (Table 16). We had no data suggesting increased litter size in response to harvest, but the total number of pups increased as additional packs developed on the study area. Given the reduced average pack size at the close of the study, we concluded that wolf density could be maintained at the 1980-81 level with reported harvests of up to 30-35% of the early winter population. This figure will vary with changes in average litter size and dispersal patterns, as well as pack size.

The dispersal pattern of a wolf population will significantly affect its response to increased mortality. While we did not have a precise annual measure of dispersal, this was a major component of unreported overwinter loss (overwinter loss minus reported harvest). Unreported loss was highest during the 2 years of peak harvest, suggesting that dispersal might increase with increasing harvest. However, the correlation between harvest and unreported loss during the 4 years for which we obtained data was nonsignificant ($\underline{P} >$ 0.25). Fritts and Mech (1981) found high dispersal from small packs in an increasing wolf population. We would expect that the optimum reproductive strategy (maximizing individual fitness) for subordinate adult wolves in an increasing or heavily harvested population would be to disperse, provided ample vacant territory was available. Our limited data support the hypothesis of Packard and Mech (1980) that young wolves should disperse when population density is lower than saturation density and food abundant.

Some wolves which were killed within territories of monitored packs apparently originated elswhere. During all years of the study 18 (20%) of the 89 wolves reported 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. We consider the reported harvest on the study area as a suitable estimate of annual mortality for the population, even though dispersers originating off the study area are included, since the suggested 20% of the harvest comprised of dispersers with unknown origins offsets unrecorded mortality, which we found to be about 17% (4 out of 23 deaths for wolves with operating transmitters) during our study. This conclusion is supported by the agreement between the average harvest over 5 years (26%) and the estimated annual mortality rate for radioed wolves (26%) during these years. If harvest is accurately reported and early winter wolf density can be determined, use of the proportion harvested as an estimate of annual wolf mortality seems to be a valid management approach.

BEHAVIORAL ECOLOGY

While observations of wolves in this study were invariably from aircraft and of relatively short duration, aspects of wolf behavior were evaluated, especially as they relate to territoriality, pack cohesiveness, and relationships with non-prey species.

Observed Activity

Changes in wolf activity patterns have been linked to nutritional status, with increased sleeping and decreased amounts of travel during periods of poor hunting success (Mech 1977b). Kenai wolf activity in winter included traveling during 50% of the observations and sleeping during 15% (Table 23), approximately the same as Minnesota wolves at a high level of hunting success (ibid).

Seasonal patterns of activity reflected the tendency of wolves to travel during daylight hours more in winter (50%) than summer (29%). Sleep seemed to be associated with recent feeding, often recorded for packs near kills in winter. Observed activity was reduced in summer, with wolves resting during 50% of all observations. However, continuous monitoring of a few wolves at dens (Peterson, unpublished) suggested that in summer most travel was at night.

Pack Cohesiveness

An index to pack cohesion was developed, based on packs in which more than 1 wolf was radioed. 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 radioed in a pack, and were together during 6 out of 10 locations, the cohesion index would be 0.60. These data were analyzed on a monthly basis (Fig. 10). Packs were most cohesive in November and December; at this time all pups were traveling with the adults, and peripheral adults were most apt to travel with packs. As the breeding season in February and early March approached, pack cohesion declined, reaching a wintertime low in March which coincided with extraterritorial movements and dispersal. The return of some wolves to packs in April resulted in increased pack cohesion, then it dropped to a summertime low from June to September. Packs which consisted of only pairs or pairs and their pups exhibited higher pack cohesion at all times of the year and did not show as sharp a drop in cohesiveness during the breeding season.

Seasonal Variation in Use of Territory

Spatial distribution of wolf activity was determined with the aid of a mean radius of activity calculation. The mean radius of activity represents the average distance from all selected locations to the geometric center of these locations. While shapes other than circles may better represent animal home ranges and perhaps wolf territories, we chose the circle for a model to reduce the complexity of calculation and interpretation.

Since data from all years was pooled for each pack, only those packs on the lowlands that exhibited no annual shift in summertime activity areas (dens and rendezvous sites) were used for this analysis (BLP, KRP, and SLP). Packs inhabiting mountainous areas were not located frequently in summer and the mountains tended to prevent us from locating wolves that were distant from known centers of activity, so they were excluded from consideration.

Activity radii were shortest in June and July (Fig. 11), when adult activity was centered around relatively immobile pups. It increased steadily through late summer and fall, reaching a relatively stable high plateau from November through February. The activity radius increased abruptly to a peak in March, when we observed frequent extraterritorial movements and dispersal (initiated in February). From March until June there was a rapid contraction in the extent of pack movements. If the March peak caused by extraterritorial movements is ignored, we see that pack movements within their territory were most extensive in early winter when the entire pack was traveling together. Shortly after the pups accompanied the adults on a permanent 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.

Centers and circumscribed radii of activity are presented for each pack in Fig. 12. The breakdown in pack cohesion and territory stability is readily seen for the Swanson River Pack, contrasting with other packs where activity radii and centers of activity were similar among pack members.

Extraterritorial Movements

One of the most important characteristics of wolf populations, from the standpoints of both management and population dynamics, is the fact that vacant territory within a saturated wolf range is rapidly colonized by immigrants. In an area with contiguous pack territories, if a pack of wolves is eliminated or shifts its range significantly, other wolves will colonize the vacancy and, through subsequent reproduction, may bring wolf densities back to their former levels or lead to a population increase. Within a saturated wolf range, single wolves are invariably present, traveling along pack territorial boundaries, avoiding established packs, providing a potential nucleus for a new pack in any vacant area that is sufficiently large (Rothman and Mech 1979). These single wolves have dispersed from their original pack, either temporarily or permanently, and provide the potential for pack replacement or population increase.

We observed a broad range of movements that can be linked to a basic dispersal pattern, ranging from brief, exploratory, forays into areas adjacent to a wolf's pack territory to abrupt long-distance dispersal. Dispersal was often gradual, with a wolf breaking ties with its pack over a period of weeks. A few wolves were followed until they had found vacant space, a mate, and had begun a new pack. Some wolves returned to their pack after odysseys lasting weeks, or traveled out of range. Being more vulnerable in unfamiliar surroundings, a large proportion were killed by humans.

Group Size of Dispersers

With few exceptions, wolves that left their pack territories traveled alone. Several group movements by SRP outside their territory were recorded in this study, but we considered this quite unusual. In a few cases, 2 packmates departed together. BLP females 420 and 424 entered adjacent SLP territory together about 1 month after the death of the SLP alpha female. Female 420 soon returned to the BLP, but 424 remained behind and assumed the role of alpha female in SLP. After 424 was killed, female 420 returned to SLP and became the alpha female. Two males from KRP, 206 and 210, left their territory within a few days of each other, both traveling south, and were observed together scavenging a moose that had been killed by a resident pack of 8-12 wolves south of Tustumena Lake. They then separated again, returning to KRP within a few days of one another. Males 122 and 201 of SRP left their territory together in February, 1978, but 201, a pup, returned to SRP within a few days while 122 embarked on a month-long journey before returning to its pack.

Seasonal Variation

The bulk of all extraterritorial movements occurred in winter. Many of the extraterritorial movements (40%) and eventual dispersal (ca. 25%) movements were initiated in February, coinciding with the beginning of the breeding season. Studies of wolves in captivity have indicated 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 obvious importance. Other studies (Packard and Mech 1980; Ballard et al. 1981; Fritts and Mech 1981) have indicated that most dispersers left in late summer or early fall rather than in winter, suggesting different motivating factors in other populations. Average pack size was larger in our study than in these others, and we speculate that increased social stress in large packs might prompt more frequent dispersal during the breeding season.

Characteristics of Dispersing Wolves

Dispersing wolves were usually socially subordinate or yearling individuals (Table 24). While details of individual wolves' social status were rarely known, we can be reasonably sure that no dispersers were alpha wolves. Most dispersers were yearlings, unlikely to be dominant in relatively large packs; of the 6 dispersers older than yearlings, 4 (026, 039, 106, 212) were known subordinates.

The record of male 106 suggests that dispersal may be closely tied to social status. Prior to his capture in December, 1976, we believe this wolf was the alpha male in a pack of 20 wolves (SRP). Male 106 was easily distinguished as the only black wolf in the pack, and was considered dominant because he actively scent-marked and often led the pack (Peters and Mech 1975; Peterson 1977). After being removed briefly from the pack for collaring, he subsequently assumed an obviously subordinate role, not unlike the experience of Rabb et al. (1967) when they removed an alpha wolf from a captive pack for experimental purposes; the alpha wolf was returned to the pack but was not able to reassume its dominant role. Less then 2 weeks after being collared, male 106 abruptly dispersed, and eventually founded a pack near the southern end of the Kenai lowlands (Fig. 13). We believe the change in social status was the primary motivation for this wolf to disperse. This was the only case when we had any knowledge of proximal factors which might have prompted a wolf to leave its pack.

During the first 4 years of the study, there was a significant ($\underline{P} < 0.025$) preponderance of males (10 of 12) among dispersers from study packs. When dispersers in the final portion of the study plus 3 loners are added (13M:8F), however, the sex ratio was not significantly different from 50:50 ($\underline{P} < 0.40$). We don't know if the high proportion of dispersing males early in the study was caused by small sample size or somehow was related to the large average pack size at that time. Other studies, generally involving smaller packs, report male preponderance among dispersers (Mech 1970; Ballard et al. 1981). There seemed to be a tendency for females to disperse a shorter distance than males ($P = 0.30$); of the 10 dispersers that remained on the study area, 4 were females, but of the 8 wolves that left the study area, only 1 was female.

Eight of the 18 dispersers were thought to be yearlings, while the remainder was comprised mostly of young adults, based on tooth wear. Only 1 pup dispersed: male 462 left SRP with 1 adult, which subsequently separated from the pup and dispersed to the S. The signal from the pup disappeared near the Kenai mountains, so it probably entered the mountains. Fritts and Mech (1981) also found, with 1 exception, that dispersers were at least of yearling age.

Fate of Dispersing Wolves

Dispersers were highly vulnerable to harvest, with over half killed less than 1 year after leaving their home pack. Of the 18 radioed wolves that left study packs, 10 (56%) died within a year, 6 (33%) survived at least a year, and the fate of 2 (11%) was unknown. Of the 3 lone wolves we captured, 2 were killed and the third left the study area. Of the 6 radioed dispersers that survived for at least a year, all but 1 were known to have developed associations with other wolves, usually by founding a new pack; at least 4 of these 6 wolves eventually reproduced. Thus, depending on the reproductive success of the 3 dispersers with unknown fate, between 19% and 42% of the dispersers we monitored successfully reproduced.

The sample of radioed wolves provided a basis for estimating the extent of dispersal and a direct comparison of disperser vs. non-disperser mortality. We estimated that radioed wolves were located outside their home territory for about 11% of the total time they were monitored, or about 16% of the total monitoring time for adults only. One-third (21 of 64) of the wolves we monitored dispersed from their original pack. Radioed wolves outside their territory exhibited a mortality rate 5.3 times higher then wolves within their territory (9 deaths in 9.4 wolf-years of monitoring vs. 14 deaths in 78.2 wolf-years, respectively). Extensive travel in unfamiliar areas and a lesser tendency among dispersers to avoid settled areas probably explains their high mortality rate.

Five dispersers eventually settled and began the process of pack formation. Male 106 left SRP and traveled quickly to the S end of the lowlands (Fig. 13). 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, probably a new pack, 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, dispersed in the summer 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 NE of SLP territory, we did not locate 212 with his original pack again. Male 026 had not been located outside of SLP territory prior to dispersal, but his transmitter was inoperative during the 2 months when he paired with female 134 in vacant territory NW of the SLP. During his last summer in SLP, 026 visited the den area less frequently than other radioed wolves in the pack, suggesting weaker ties with other pack members. 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 SLP. Then he departed and traveled with 134 in their new territory for about 10 days, but on Nov. 21 he was again with the SLP, this time near the edge of SLP territory. Wolf 134 was moving away from the area, after apparently accompanying 026 to the edge of SLP territory. This time 026 remained with SLP for about 1 week, fed on another fresh kill, and finally returned to his new mate and territory, this time permanently.

Female 424 assumed the role of alpha female in SLP about 6 weeks after the former alpha female (402) disappeared. Female 424 died in a snare in early May, shortly after giving birth to 6 pups. Her sibling, female 420, then dispersed from BLP to SLP, paired with the SLP alpha male, and apparently successfully raised a litter of pups in 1981.

Extraterritorial Movements of Packs

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 territorial boundaries. Neither pack was observed because of heavy cover, but all 3 radioed wolves present in both packs were located on both locations, suggesting that most of the pack was present. We could not determine whether the packs made a kill outside their own territory. We do not believe that trespassing in this case was due to shortage of prey since both packs killed moose on a regular basis within their territory throughout the winter.

The movements of Swanson River Pack wolves outside their territory also did not appear to be motivated by food shortage within their territory. Extraterritorial movements of this pack in 1978-79 were associated with frequent pack splitting and a period of intensive airplane-assisted hunting. Since these movements were highly unusual, they will be considered in detail below.

The SRP began the winter of 1978-79 as a rather cohesive pack of 16 wolves (Fig. 14). We darted 4 wolves in the pack on Dec. 1, but they regrouped and once again began to travel as one unit. On Dec. 11, the pack split into groups of 6 and 12 wolves, implying that 2 other wolves joined the pack. Two wolves were shot on Dec. 23 and 2 more on Jan. 2. On Jan. 2 the 4 wolves remaining in 1 group left SRP territory, heading NE. On Jan. 4, 6 more wolves left in the same direction, and only 4 SRP wolves remained within their territory. Both groups declined in number rapidly, male 201 was located in both groups before dispersing S permanently, and 2 wolves (male 418 and female 422) associated briefly (Jan. 14) with the 2 wolves in MCP II. An additional wolf, shot on Jan. 10 north of SRP territory, was assumed to be from this pack. The 2 groups that traveled NE from Swanson River Pack territory moved through an area inhabited by the adjacent Pt. Possession Pack, an unradioed pack. Five additional wolves were shot in this area at about the same time as the SRP wolves were killed, but we assumed that wolves killed here were not SRP wolves unless they were radioed or associating with radioed SRP wolves.

Between Jan. 19 and 26, most remaining members of SRP reunited along the eastern edge of their territory briefly, just before 2 more were shot. The remaining 8 wolves remained together inside their territory until at least Feb. 21, then 3 disappeared for unknown reasons. The final 5 members were quite cohesive through April, but once again left their territory in early April and traveled to the edge of the Kenai mountains. Three of these 5 wolves were pups (412, 414, and 418) and the other 2 may have been pups (male 473 was probably a pup in 1978-79, since he appeared to be a yearling when caught in January 1980; female 458 was a probable yearling when subsequently caught in November, 1979) so all 5 wolves in the SRP in April 1979 may have been pups. The following fall the pack consistently numbered 8 wolves, but 10 were seen on Nov. 8, when 2 wolves were darted. This implies that either additional wolves were accepted into this pack or, more likely, we did not observe all the Swanson River Pack wolves that remained alive in spring, 1979.

Temporary Associations Among Wolves from Different Packs

Apart from cases involving new pack formation, we recorded 7 instances of 1 or more wolves associating with other packs or individuals from other packs (Appendix III). The only case that did not involve wolves from both Swanson River Pack and Mystery Creek Pack was on January 2, 1979, when male pup 414 from SRP was seen with 1 black and 2 gray wolves on Finger Lakes (first indication of Elephant Lake Pack). There were no black wolves in SRP. The 4 wolves were bedded on the lake, each separated by about 10 m from each other. Later the same day, 414 traveled single file with the other 3 as they traveled.

While most associations between wolves from different packs involved only a small number of wolves, twice we observed 1-2 wolves from SRP with all or most of the MCP. After a MCP extraterritorial foray on Feb. 22, 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 Mar. 3. 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 form MCP at the same site and male 112 traveling 3.4 km away, with 1 set of wolf tracks leading from the MCP to 112. About a year later 2 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.

Relations with Non-prey Species

Aside from their predatory role, wolves also have important relationships with several other species. In winter, ravens were constant companions at virtually every kill, and we observed ravens at times accompanying wolves in their travels. Overwintering eagles found a relatively constant source of food in wolf kills, especially when deep snow covered salmon carcasses along river banks. In 1977-78, between November and April, eagles were observed on 11 wolf kills, with up to 3 individuals present at 1 time. In the mountains, especially, wolverines scavenged wolf-kills; 1 jumped from a tree next to a wolf-kill we ground-checked near Soldotna in April, 1978.

Bears

The Kenai Peninsula has long been noted for its abundant black bear populations (e.g., Chatelain 1950). Aside from moose, black bears were observed incidentally from the air more frequently than any other species during our study. In 1977 and 1978, 104 black bears and 17 brown bears were observed. Since brown bears seemed to be associated with moose carcasses more frequently than black bears, these figures probably do not accurately reflect relative densities of the 2 species.

Both brown and black bears frequently kill moose calves, and brown bears are capable predators of adult moose (Chatelain 1950; Franzmann et al. 1980; Ballard et al. 1981;). Wolves and bears were both observed near dead moose 12 times in 1977 and 1978; 5 of these instances involved brown bears. An adult male black bear was observed feeding on an adult moose that he had apparently killed on May 2, 1978, the moose a 19.5 yr-old cow.

Wolves and bears are both capable of killing each other (Ballard et al. 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, and found fresh bear sign at many of them. Most were wolf-kills from sometime during the previous winter, and all carcasses were thoroughly scavenged.

Perhaps the greatest threat which bears pose to wolves would be at dens containing young wolf pups. On May 9, 1977, we observed 9 wolves in the MCP holding a large brown bear at bay about 100 m from the MCP den. The bear stood in a small forest opening, with the wolves 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 at any nearby wolf. We circled over the site for a few minutes, until the bear ambled off into heavy forest growth, heading away from the den. On May 5, 1978, 6 members of the SLP were observed following about 50 m behind a large male brown bear. The bear was traveling E and was located about 7 km NW of the SLP den. The alpha female was not with the pack at this time, and might well 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. On May 8, 1978, we observed a black bear standing at the radio-fix for a radioed coyote at the site where we believe she had just established a den. Her movements thereafter became highly nomadic, suggesting that the bear had killed her pups.

Other Canids

The historical abundance patterns of wild canids on the Kenai Peninsula strongly suggest intraspecific exclusion of smaller canids by larger species (Peterson and Woolington, unpublished). Coyotes were frequent scavengers at wolf-killed moose and locally were quite abundant, especially associated with settled areas. We documented 8 instances of wolves killing coyotes, and gathered circumstantial evidence suggesting that wolves may be capable of reducing coyote densities in some remote areas.

SUMMARY AND CONCLUSIONS

We studied wolf ecology and population dynamics on Alaska's Kenai Peninsula from 1976 to 1981. Sixty-four wolves were live-captured and radio-collared 81 times, providing 3,600 aircraft fixes, with wolves observed in 60% of the locations. Each year we monitored from 3 to 7 wolf packs with contiguous territories on the Kenai National Wildlife Refuge (formerly Kenai National Moose Range). The original Kenai wolf population was apparently extirpated by 1915 and wolves were virtually absent until the early 1960's when the Peninsula was probably re-colonized by immigrants from the southcentral mainland. Between 1965 and 1975 the wolf population expanded rapidly on the Kenai lowlands and adjacent mountains.

On the northern lowlands, wolves were supported primarily by moose, with few buffer species present. Adult moose, especially old cows, provided most of the prey biomass. The average kill rate in winter was 1 moose per pack every 4.7 days. Predation rates were not closely correlated with pack size, although a pack of 20 wolves provided the highest kill rate, 1 moose every 3.1 days. Daily food availability in winter was estimated at about 15% of body weight. Utilization of prey carcasses was typical for wolves preying on moose, indicating no unusual degree of moose vulnerability on the study area.

One litter of pups was typically produced by the alpha female annually in each pack. Apparent litter size (no. surviving young) averaged 4.5 pups/pack and, significantly, was unrelated to pack size. In one case when a subordinate female bore young, she apparently raised the pups by herself; the pups showed obvious growth retardation and probably died.

Mortality was predominantly human-caused, averaging 26% annually during the study. After 13 years of complete protection, wolf harvests were initiated in

1974. The impact of harvest generally increased during the study, amounting to 41% of the early winter wolf population in 1978-79. Wolf density on the study area was estimated at about 14 wolves per 1,000 km^2 in 1976 and 19 wolves per 1,000 km^2 in 1981. Wolf density increased when wolf harvest was less than 30% of the early winter population, and decreased when harvest loss exceeded 35%. We suggest that wolf density was controlled by human harvest, at least during the last portion of the study.

The principal effect of harvest was to decrease pack size. As harvest loss increased during the study, average radioed pack size declined from 15 wolves (in 1976) to about 6 (in 1980). Territory size fluctuated directly with pack size, so vacant space appeared as packs became smaller. New packs developed as dispersing wolves paired and colonized vacancies. Two colonizing pairs occupied areas 50- 75% that of average packs, suggesting that new pairs might require a superterritory for successful establishment. New packs became established following pack size reductions from harvest. Actual pup production increased only as new packs developed; this occurred on the study area probably in response to both harvest loss and natural population increase.

Wolf packs were least cohesive during summer pup-rearing and most cohesive in early winter, when packs traveled most widely within their territories. Dispersal of socially subordinate adults from packs occurred most frequently during the February-March breeding period, when cohesiveness of large packs declined sharply. One alpha male dispersed abruptly after losing his dominant status. Dispersing wolves were highly vulnerable to harvest loss, exhibiting a mortality rate 5.3 times higher than wolves within their pack territories. Limited data suggested that dispersal might increase with harvest loss. Dipsersal was a significant phenomenon on the study area, accounting for 16% of the total monitoring time for adult wolves and, ultimately, one-third of all radioed wolves. We estimated that dispersers comprised about 27% of the harvest on the study area.

While wolf density on the Kenai study area was relatively high for northern latitudes, moose provided high prey biomass in this area. Actually, the wolf:moose ratio on the Kenai was lower than that observed elsewhere (Peterson et al., submitted), and there may be potantial for natural increase in this predator population. Originally extirpated by man from the Kenai Peninsula, wolves recolonized the area during a period of favorable public attitudes toward wolves. It should be clear that, while wolves density may be ultimately linked to prey vulnerability and density, at present harvest probably determines wolf density to a major extent on much of the Kenai Peninsula. It is the responsibility of wildlife managers to provide for the future of prey and predator alike, as well as to serve diverse public needs associated with wildlife. The Kenai National Wildlife Refuge provides an outstanding wildlife management opportunity and challenge for the future.

LITERATURE CITED

BAILEY, T. N. 1978. Moose populations on the Kenai National Moose Range. Proc. N. Am. Mose Conf. Workshop, 14:1-20.

BALLARD, W. B., T. H. SPRAKER AND K. P. TAYLOR. 1981a. Causes of neonatal moose calf mortality in south-central Alaska. J. Wildl. Manage. 45(2):335-342.

____________, R. O. STEPHENSON AND T. H. SPRAKER. 1981b. Nelchina Basin wolf studies. Final reort, Projects W-17-8 through W-17-11, Fed. Aid Wildl. Res. 201 pp. (mimeo). Unpubl. rep., Alaska Dept. Fish and Game.

____________ AND T. H. SPRAKER. 1979. Unit 13 wolf studies. Unpubl. rep., Alaska Dept. Fish and Game. Fed. Aid Proj. W-17-8

BANGS, E. E. AND T. N. BAILEY. 1980. Interrelationships of weather, fire, and moose on the Kenai National Moose Range, Alaska. Proc. N. Am. Moose Conf. and Workshop 16:255-274.

CARBYN, L. N. 1975. Wolf predation and behavioral interactions with elk and other ungulates in an area of high prey diversity. Ph.D. thesis, Univ. Toronto. 233 pp.

____________. (in press). Incidence of disease and its potential role in the population dynamics of wolves in Riding Mountain National Park, Manitoba. Proc. Portland Wolf Symposium, August, 1979. Noyes Publications.

CHAPMAN, R. C. 1978. Rabies: decimation of a wolf pack in Arctic Alaska. Science 201:365-367.

CHATELAIN, E. F. 1950. Bear-moose relationships on the Kenai Peninsula. Trans. N. Am. Wildl. Conf. 15:224-233.

COADY, J. W. 1974. Interior moose studies. ann. Prog. Rep. Vol. II, Proj. W-17-6, Jobs 1.3R, 1.4R, 1.8R, and 1.11R. 12 pp. (mimeo).

__________. 1976. Interior moose and moose disease studies. Ann. proj. seg. rep., Vol. III, Proj. W-17-6 through W-17-8, Job 1.9R, Fed. Aid. Wildl. Res.

DAVIS, J. L. AND A. W. FRANZMANN. 1979. Fire-moose-caribou interrelationships. Proc. N. Am. Moose Conf. and Workshop 15:80-118.

FLOYD, T. J., L. D. MECH, AND P. A. JORDAN. 1978. Relating wolf scat content to prey consumed. J. Wildl. Manage. 42:528-532.

FRANZMANN, A. W., C. C. SCHWARTZ AND R. O. PETERSON. 1980. Moose calf mortality in summer on the Kenai Peninsula, Alaska. J. Wildl. Manage. 44(3):764-768.

FRITTS, S. H. AND L. D. MECH. 1981. Dynamics, movements, and feeding ecology of a newly-protected wolf population in northwestern Minnesota. Wildl. Monogr. No. 80:1-79.

FULLER, T. K. AND L. B. KEITH. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44(3):583-602.

GOLDMAN, E. A. 1944. Classification of wolves. Part II of S. P. Young and E. A. Goldman. The wolves of North America. Dover Publ., N.Y., 636 pp.

HABER, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Ph.D. thesis, Univ. Brit. Column. 786 pp.

HAUGE, T. M. AND L. B. KEITH. 1981. Dynamics of moose populations on the AOSERP study area in northeastern Alberta. J. Wildl. Manage. 45(3):573-597.

JOSLIN, P. W. B. 1967. Movements and home sites of timber wolves in Algonquin Park. Am. Zool. 7:279-288.

KEITH, L. B. (in press). Population dynamics of wolves. Proc. 1980 IUCN Wolf Symposium, Edmonton.

LeROUX, P. A. 1971. Wolf survey-inventory progress report for 1971. Ann. rep. survey-inventory activities, Fed. Aid Wildl. Res. (mimeo).

__________. 1978. Wolf survey-inventory progress report for 1976. in Hinman, R. (ed). Annual report of survey-inventory activities. Vol. VII. Proj. W-17-9, Fed. Aid in Wildl. Res. 194 pp. (mimeo).

McKNIGHT, D. E. 1970. The history of predator control in Alaska. Unpubl. report, Alaska Department of Fish and Game, 9 pp.

MECH, L. D. 1966. The wolves of Isle Royale. U. S. National Park Service Fauana Series No. 7, 210 pp.

__________. 1970. The wolf. Natural History Press. 384 pp.

__________. 1974. Current techniques in the study of elusive wilderness carnivores. Proc. 11th Intl. Cong. Game Biol. aa:315-322.

__________. 1975. Disproportionate sex ratios of wolf pups. J. Wildl. Manage. 39:737-740.

__________. 1977a. Wolf-pack buffer zones as prey reservoirs. Science 198:320-321.

__________. 1977b. Population trend and winter deer consumption in a Minnesota wolf pack. pp. 55-83 in R. Phillips and C. Jonkel (eds.). Proc. 1975 Pred. Symp., Bull. Montana For. and Cons. Exp. Sta., Univ. of Montana, Missoula. 268 pp.

MEDJO, D.C. AND L. D. MECH. 1976. Reproductive activity in nine- and ten-month-old wolves. J. Mammal. 57(2):406-408.

MURIE, A. 1944. The wolves of Mount McKinley. U.S. National Park Serv. Fauna Ser. No. 5, 238 pp.

OLDEMEYER, J. L., A. W. FRANZMANN, A. L. BRUNDAGE, P. D. ARNESON, AND A. FLYNN. 1977. Browse quality and the Kenai moose population. J. Wild. Manage. 41(3):533-542.

OSGOOD, W. H. 1901. Natural history of the Cook Inlet region, Alas American Fauna No. 21. U. S. Government Printing Office.

PACKARD, J. P. AND L. D. MECH. 1980. Population regulation in wolves. pp. 135-150 inCohen, M. N., R. S. Malpass, and H. G. Klein (eds.). Biosocial mechanisms of population regulation. Yale Univ. Press, New Haven, CT.

__________ , __________ AND U. S. SEAL. (submitted). Social influences on wolf reproduction (Canis lupus).

PALMER, L. J. 1938. Kenai Peninsula moose. Research Project Report, Bureau of Biological Survey. Sept.-Oct., 1938. Unpubl. report, Kenai National Moose Range files, 24 pp., typewritten.

PEDERSEN, S. 1978. Geographical variation in Alaskan wolves (Canis lupus L.). M.S. thesis. Univ. of Alaska.

PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Park Service Scien. Monogr. Ser. No. 11. 210 pp.

__________. 1979. Social rejection following mating of subordinate wolf. J. Mammal. 60(1):219-221.

__________ AND D. L. ALLEN. 1974. Snow conditions as a parameter in moose-wolf relationships. Naturaliste Canadien 101 (3,4):481-492.

__________ AND J. D. WOOLINGTON. (in press). The extirpation and reappearance of wolves on the Kenai Peninsula, Alaska. Proc. Portland Wolf Symposium, Aug. 1979. Noyes Publications.

__________ AND __________ AND T. N. BAILEY. (Submitted). Wolf-moose relationships on the Kenai Peninsula, Alaska. J. Wildl. Manage.

PLAFKER, B. 1969. Tectonics of the March 27, 1964 Alaska earthquake. U. S. Geol. Surv. Prof. paper 543-I. U.S. Government Printing Office, Washington, D.C. 74 pp.

RABB, G. B., J. H. WOOLPY, AND B. E. GINSBURG. 1967. Social relationships in a group of captive wolves. Amer. Zool. 7:305-311.

RAUSCH, R. A. 1961. Present status and possible future management of wolf populations in interior and arctic Alaska. Proc. Alaska. Sci. Conf. 12:28.

___________. 1967. Some aspects of the population ecology of wolves, Alaska. Amer. Zool. 7:253-265.

___________. 1969. A summary of wolf studies in southcentral Alaska, 1957-1968. Trans. N. Am. Wildl. and Nat'l Res. Conf. 34:117-131.

___________ AND R. A. HINMAN. 1977. Wolf management in Alaska -- an exercise in futility? Proc. 1975 Predator Symp., Montana Forest and Conservation Experiment Station, Univ. of Montana, Missoula. pp. 147-156.

REARDEN, J. 1980. Wolf management in Alaska. Alaska 46(5):30.

ROTHMAN, R. J. AND L. D. MECH. 1979. Scent-marking in lone wolves and newly formed pairs. Anim. Behav. 27:750-760.

SEAL, U. S., A. W. ERICKSON AND J. G. MAYO. 1970. Drug immobilization of the Carnivora. Int. Zoo Yearbook 10:157-170.

SPENCER, D. L. AND J. B. HAKALA. 1964. Moose and fire on the Kenai. Tall Timbers Fire Ecol. Conf. 3:11-33.

STEPHENSON, R. O. 1978. Unit 13 Wolf Studies. Ann. Prog. Rep. Vol. I, Proj. W-17-8, Jobs 14.8R, 14.9R, 14.10R, Fed Aid Wildl. Res. 73pp. (mimeo).

U.S. FOREST SERVICE. 1978. Environmental statement, Chugach moose-fire management program. Unpubl. report, Chugach National Forest. 146 pp.

VAN BALLENBERGHE, V. 1981. Population dynamics of wolves in the Nelchina Basin, southcentral Alaska. Proc. 1980 Worldwide Furbearer Conference, Frostberg, MD.

________________ AND L. D. MECH. 1975. Weights, growth, and survival of timber wolf pups in Minnesota. J. Mammal. 56(1):44-63.

___________, A. W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildl. Managr. 43:1-43.

VERNER, J. 1977. On the adaptive significance of territoriality. Am Nat. 111(980):769-775.

WEAVER, J. L. AND S. H. FRITTS. 1979. Comparison of coyote and wolf scat diameters. J. Wildl. Manage. 43(3):786-788.

WOLFE, M. L. 1974. An overview of moose coactions with other animals. Naturaliste Can. 101(4):437-456.

ZIMEN, E. 1976. On the regulation of pack size in wolves. Zeitschrift fur Tierpsychologie 40:300-341.

Table 1. Wolves captured on the Kenai Peninsula, 1976–81.

Number	Capture date M/D/Y	Sex	Wt. (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
022	08/14/76	F	29.0	G	Ad	Mystery Cr.I	465	92	Shed collar	Snared 02/15/78
026	08/22/76	M	38.1	B	Ad	Skilak L.	351	103	Trans. failed	Unknown
–	10/09/77	–	45.8	–	--	--	717	190	Shed collar	
039	10/09/76	F	34.5	G	Ad	Swanson R.	325	70	Trans. failed	Snared 12/05/79
049	10/18/76	F	38.1	G	Ad	Loner	101	23	Left study area	Unknown
102	12/08/76	F	23.6	G	Pup	Mystery Cr.I	364	56	Recaptured	Shot 01/03/79
–	12/07/77	–	34.0	–	Ad	--	126	15	Trans. failed	
104	12/08/76	F	29.5	B	Pup	Mystery Cr.I	421	63	Trans. failed	Shot ca. 03/10/78
106	12/12/76	M	53.5	B	Ad	Swanson R.	114	34	Trans. failed	Snared 12/16/78
108	12/16/76	F	19.5	G	Pup	Skilak L.	571	152	Trans. failed	Snared 03/17/79
110	12/16/76	M	29.9	B	Pup	Skilak L.	250	69	Trans. failed	Unknown
112	01/03/77	M	45.8	G	Ad	Swanson R.	113	37	Left study area	Unknown
115	01/03/77	M	44.5	G	Ad	Swanson R.	595	165	Trans. failed	Shot 12/21/78
119	07/17/77	F	33.6	G	Ad	Swanson R.	107	25	Trans. failed	Unknown
122	07/25/77	M	37.2	G	Ad	Swanson R.	128	35	Recaptured	Unknown
–	11/30/77	–	49.9	–	--	--	170	59	Trans. failed[1]	

Table 1. continued

Number	Capture date M/D/Y	Sex	Wt. (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
134	09/28/77	F	34.9	G	Ad	Bear L.	305	101	Recaptured	Unknown
-	07/29/78	-	34.0	-	--	--	239	60	Trans. failed	
136	10/02/77	F	30.8	B	Ad	Skilak L.	72	28	Recaptured	Shot 08/13/78
-	12/13/77	-	32.7	-	--	--	243	72	Killed	
200	12/13/77	M	35.8	B	Pup	Skilak L.	469	108	Killed	Shot 09/09/79
201	11/30/77	M	37.6	G	Pup	Swanson R.	406	114	Left study area	Shot 06/79
203	11/30/77	M	39.9	G	Pup	Swanson R.	302	93	Died	Distemper 09/13/78
206	01/06/78	M	50.3	G	Ad	Killey R.	115	24	Trans. failed	Shot 11/26/80
-	12/12/78	-	45.5	-	--	--	270	39	Trans. failed	
-	07/10/80	-	45.5	-	--	--	4	1	Recaptured	
-	07/14/80	-	--	-	--	--	135	7	Killed	
208	05/27/78	F	29.5	G	Ad	Loner	151	6	Killed	Shot 10/25/78
210	01/06/78	M	35.4	B	Pup	Killey R.	755	135	Killed	Shot 01/31/80
212	12/13/77	M	41.7	B	Ad	Skilak L.	739	98	Recaptured	Unknown
-	12/22/79	-	45.4	-	--	--	150	16	Trans. failed [1]	
214	12/07/77	M	34.9	G	Ad	Mystery Cr.I	40	8	Trans. failed	Snared 11/80
-	07/29/78	-	39.9	-	--	--	242	12	Left study area	
216	12/07/77	M	45.4	G	Ad	Mystery Cr.I	96	20	Killed	Shot 03/13/78

Table 1. continued

Number	Capture date M/D/Y	Sex	Wt. (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
218	12/07/77	M	29.5	B	Pup	Mystery Cr.I	8	2	Trans. failed	Unknown
222	11/30/77	M	39.0	G	Pup	Swanson R.	250	69	Recaptured	Shot 01/27/79
-	08/06/78	-	40.4	-	Ad	--	174	48	Killed	
262	12/12/78	F	36.3	B	Ad	Killey R.	0	0	Killed	Capture death
225	05/26/78	F	34.0	G	Ad	B. Indian Cr.	397	30	Recaptured	Unknown
-	06/26/79	-	36.3	-	--	--	94	5	Trans. failed[1]	
264	12/12/78	M	43.1	G	Ad	Killey R.	135	25	Trans. failed[1]	Unknown
266	12/12/78	M	29.9	B	Pup	Killey R.	399	71	Trans. failed[1]	Unknown
268	12/15/78	M	31.8	B	Pup	B. Indian Cr.	726	27	Killed	Snared 01/30/81
270	12/15/78	F	32.7	G	Ad	B. Indian Cr.	35	3	Unknown	Unknown
276	12/09/80	M	28.1	G	Pup	Swanson R.	178	21	Transmitting	Last fix 06/05/81
278	12/09/80	F	29.0	G	Pup	Swanson R.	118	15	Transmitting	Last fix 04/06/81
280	12/09/80	F	28.1	G	Pup	Swanson R.	178	18	Transmitting	Last fix 06/05/81
402	07/27/78	F	38.1	G	Ad	Skilak L.	252	57	Trans. failed	Unreported 01/15/80
-	06/28/79	-	31.8	-	--	--	201	32	Prob. killed	
404	08/12/78	F	30.8	G	Ad	Mystery Cr.II	322	35	Recaptured	Snared 03/81
-	06/27/79	-	31.8	-	--	--	39	5	Trans. failed	

Table 1. continued

Number	Capture date M/D/Y	Sex	Wt. (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
406	10/09/78	M	20.9	B	Pup	Skilak L.	169	35	Killed	Snared 03/27/79
408	10/09/78	M	20.9	B	Pup	Skilak L.	327	57	Killed	Shot 09/01/79
410	06/12/79	M	40.8	B	Ad	Bear Cr.	357	38	Killed	Snared 02/81
412	12/01/78	F	26.3	G	Pup	Swanson R.	343	82	Recaptured	Distemper 01/15/80
-	11/08/79	-	38.6	-	Ad	--	67	25	Died	
414	12/01/78	M	29.5	G	Pup	Swanson R.	243	68	Trans. failed	Shot 01/21/81
-	01/19/80	-	40.8	-	Ad	--	130	13	Trans. failed	
416	12/01/78	F	29.9	G	Pup	Swanson R.	33	16	Killed	Shot 01/02/79
418	12/01/78	M	32.2	G	Pup	Swanson R.	157	55	Trans. failed	Snared 01/25/80
-	01/19/80	-	41.7	-	Ad	--	6	4	Killed	
420	12/11/78	F	33.1	B	Pup	Bear L.	214	60	Trans. failed	Last fix 05/20/81
-	11/30/79	-	34.9	-	Ad	--	123	37	Recaptured	
-	07/11/80	-	35.4	-	--	--	313	37	Transmitting	
422	12/11/78	F	34.9	B	Pup	Bear L.	344	72	Trans. failed	Snared 02/81
424	12/11/78	F	32.7	G	Pup	Bear L.	141	48	Trans. failed	Snared 05/80
-	10/03/79	-	35.4	-	Ad	--	226	55	Killed	
452	07/20/79	F	29.5	G	Ad	Bear Cr.	333	22	Trans. failed[1]	Unknown
454	10/07/79	F	31.8	B	Ad	Skilak L.	140	32	Killed	Snared 02/24/80

Table 1. continued

Number	Capture date M/D/Y	Sex	Wt. (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
458	11/08/79	F	38.6	G	Ad	Swanson R.	36	5	Killed	Snared 12/14/79
462	11/08/79	M	28.1	G	Pup	Swanson R.	134	43	Left study area	Unknown
464	11/30/79	M	40.8	G	Pup	Bear L.	145	23	Trans. failed	Unknown
466	12/11/79	M	38.1	G	Pup	Killey R.	111	31	Died	Malnutrition(?) 3/80
470	11/30/79	M	33.6	B	Pup	Bear L.	30	12	Unknown	Unknown
472	12/11/79	F	37.2	B	Ad	Killey R.	357	46	Killed	Shot 01/08/81
473	01/19/80	M	42.6	G	Ad	Swanson R.	63	9	Killed	Shot 03/22/80
476	12/22/79	M	32.2	G	Pup	Mystery Cr.II	365	25	Killed	Snared 12/21/80
478	12/22/79	M	31.8	G	Pup	Mystery Cr.II	0	0	Died	Capture death
480	12/11/79	F	35.4	G	Ad	Killey R.	80	22	Trans. failed	Last fix 05/20/81
-	07/16/80	-	36.3	-	--	--	231	8	Recaptured	
-	03/04/81	-	37.6	-	--	--	77	9	Transmitting	
486	07/16/80	F	31.8	B	Ad	Loner	11	2	Transmitting	Unknown
-	07/27/80	-	--	-	--	--	0	0	Left study area	
488	07/18/80	F	33.6	G	Ad	B. Indian Cr.	145	9	Unknown	Unknown
490	07/19/80	F	35.4	G	Ad	Loner	233	13	Killed	Shot 03/17/81

Table 1. continued

Number	Capture date M/D/Y	Sex	Wt. (kg)	Color	Age	Original pack affiliation	Length of tracking period (days)	No. fixes	Cause of tracking termination	Ultimate fate
494	10/03/80	M	43.1	G	Ad	Swanson R.	97	17	Trans. failed[1]	Unknown
801	03/02/81	M	34.0	G	Pup	Killey R.	110	9	Transmitting	Last fix 05/20/81

[1]Probable transmitter failure, but definite evidence lacking.

Table 2. Whole body weights of Kenai Peninsula wolves.

	Average male weight (kg)	N	Average female weight (kg)	N	Probability of no sex difference
All adults	43.8	21	34.2	33	<0.10
All pups[1]	32.5	22	28.7	10	<0.001
Adults, summer[2]	40.3	6	33.2	16	<0.001
Adults, winter[2]	45.3	16	35.2	17	<0.001

[1]Pups captured between Oct. 9 and Dec. 22

[2]Summer defined as May-August, winter as September-April.

Table 3. Coat color proportions among Kenai wolves.

Color proportion among study packs, summed for all years:

Pack	No. gray (G):No. black (B)	Proportion G:B
Swanson River	73:1	99:1
Skilak Lake	13:28	32:68
Mystery Creek I & II	23:15	61:39
Bear Lake	10:10	50:50
Killey River	31:17	65:35
Big Indian Creek	15:11	58:42
Total	165:82	67:33

Color proportion (G:B) among harvested wolves[1] 70:30 (N = 203)

Color proportion (G:B) among live-captured wolves: 67:33 (N = 64)

[1]Wolves listed as "brown" on ADF&G sealing forms were pooled with gray wolves.

Table 4. Coat color inheritance patterns in Kenai wolves.

Pack, year	Color of presumed parents (female X male)	Color or observed pups (no. gray:no. black)
All gray parents:		
Swanson R., 1977[1]	G X G	5:0
Swanson R., 1977[2]	G X G	7:0
Swanson R., 1978	G X G	4:0
Swanson R., 1979	G X G	3:0
Total		19:0
Mixed color parents:		
Skilak L., 1977	G X B	1:2
Skilak L., 1978	G X B	2:4
Skilak L., 1979	G X B	2:0
Bear L., 1978	G X B	3:3
Bear L., 1979	G X B	3:1
Mystery Cr.II, 1979	G X B	4:0
Total		15:10

[1]Minimum number of pups surviving from litter born to wolf 119.

[2]Pups born to female 039, assuming her mate was from Swanson R. pack (all gray).

Table 5. Predation recorded for Swanson River Pack for 51 days in winter[1].

Date located (M/D/Y)	No. wolves[2]	Observed pack activity	Age and sex of moose killed
11/08/77	12	Feeding on fresh kill 142	7.5 yr cow
11/10/77		Feeding on fresh kill 285	1.5 yr bull
11/11/77	9	Group greeting near last kill, then began traveling	
11/12/77		Resting near standing moose, apparently not wounded	
11/16/77	12,6	Pack split into 2 groups, 24 and 38 km from previous location, each on a fresh kill(147 & 246)	15.5 yr cow 3.5 yr sex ?
11/18/77	12	Group of 12 resting and feeding at fresh kill 146	21.5 yr cow
11/20/77	12	Bedded near fresh kill 150, backtracked to previous location	1.5 yr cow
11/21/77	16	Just leaving last kill, 2 wolves chasing each other near rear of pack	
11/22/77		Resting after consuming fresh kill 148	6 mo calf
11/23/77	20	Traveling single file	
11/25/77		Feeding and resting near fresh kill 152	13.5 yr cow
11/26/77		Feeding and playing at previous location	
11/28/77		Resting, evidently en route from previous kill	
11/29/77		Traveling, appear to be hunting	
11/30/77	16	Still traveling, single file; darted 4 wolves	
12/01/77		Bedded in heavy cover, pack may be split	

Table 5. continued

Date located (M/D/Y)	No. wolves[2]	Observed pack activity	Age and sex of moose killed
12/02/77	15	Feeding and sleeping near fresh kill 155	6.5 mo calf
12/04/77	18	Sleeping while en route from last kill	
12/05/77	20	Sleeping and feeding at fresh kill 158	3.5 yr cow
12/06/77		Pack split evenly into 2 groups 13 km apart, both groups sleeping	
12/08/77	19	Traveling single file, with occasional play behavior	
12/09/77		Traveling in loose formation strung-out in small groups	
12/10/77	19	Initially resting near fresh kill 154, then began to travel	6.5 mo calf
12/12/77		Traveling in dense forest	
12/13/77		Still traveling	
12/15/77	18	Traveling away from old kill 146	
12/16/77		Bedded and resting, scats in area; suspect fresh kill but found none	
12/17/77	19	Traveling	
12/18/77	18	Feeding on fresh kill 77-149	remains of 2 calves found
12/22/77	19	Traveling	
12/23/77		Resting near fresh kill 205	12.5 yr cow
12/28/77		Traveling	
12/29/77		Bedded near fresh kill 161	13.5 yr cow
01/02/78	15	Bedded; backtracked to recent kill 159	7 mo calf

Table 5. continued

Date located (M/D/Y)	No. wolves	Observed pack activity	Age and sex of moose killed
01/03/78	15	Bedded	
01/04/78		Bedded near kill 159, now complete consumed	

[1]Six days (12/14-16, 12/21, 12/26-27) were subtracted from 57-day period of tracking due to inadequate coverage.

[2]Provided only for those locations when we obtained an accurate count of all wolves present.

Table 6. Predation rates for Kenai Peninsula wolf packs preying on moose in winter.

Pack and dates	No. loc.	No. kills found	Length of interval (days)	Ave. no. of wolves	Interval (days) between kills
Bear Lake, 1977-78 Nov 1 - Apr 28	66	12	179	2.0	21.7 days[1]
Bear Lake, 1978-79 Dec 19 - Mar 8	30	13	80	7.0	3.4 days[1]
Swanson R.,1977-78 Nov 8 - Jan 4	40	16	51	19.5	3.1 days[2]
Swanson R.,1978-79 Dec 11 - Mar 5	41	12	85	11.2	5.3 days[1]
Skilak L., 1977-78 Nov 8 - Jan 30	41	10	85	8.2	6.9 days[1]

[1]Calculated from formula developed by Fuller and Keith (1980).

[2]Table 5.

Table 7. Outcome of observed encounters between wolves and moose on the Kenai Peninsula.

Frequency	Outcome
Encounters involving active pursuit by wolves:	
5	Moose standing in water as wolves leave, initial details unknown.
6	Moose made stand as soon as wolves approached, wolves left.
14	Moose ran first, then turned and made a stand, wolves left.
8	Moose ran initially, eventually outrunning wolves.
2	Wolves seen just leaving moose, initial responses unknown.
2	Wolves succeeded in killing moose, initial responses unknown.
Encounters not involving active pursuit by wolves:	
1	Moose wounded but standing, wolves bedded or standing in general area.
3	Moose detect approaching wolves, depart before their arrival.
10	Wolves travel past standing moose, with no observed reaction from either predator or prey except close observation by both.

Table 8. Contents of 542 Kenai wolf summer scats[1].

Season	Prey remains as frequency of occurrence[2] (% frequency of occurrence)										
	Adult moose	Calf moose[3]	Unident moose	(Total moose)	Snowshoe hare	Muskrat/ beaver	Small rodent	Bird	Other[4]		Total
Spring & early summer (early May - June)	80 (30%)	60 (23%)	41 (16%)	(181) (69%)	46 (17%)	13 (5%)	15 (6%)	2 (1%)	4 (2%)	2 (1%)	263 (101%)
Mid-summer (July - mid-August)	46 (24%)	72 (37%)	38 (20%)	(156) (80%)	26 (13%)	6 (3%)	2 (1%)	4 (2%)	0 -	0 -	194 (100%)
Late summer (mid-August to October)	24 (18%)	48 (36%)	36 (27%)	(108) (80%)	10 (7%)	9 (7%)	6 (4%)	1 (1%)	0 -	1 (1%)	135 (100%)
Total				(445) (75%)	82 (14%)	28 (5%)	23 (4%)	7 (1%)	4 (1%)	3 (1%)	592 (101%)

[1]Collected from Skilak Lake den (1977,78), Mystery Creek den (1977), Bear Lake den (1978), Killey R. den (1978), 15039's den (1977), rendezvous sites of Skilak Lake and Swanson River packs, and fresh scats from roads and trails.

[2]Non-prey scat contents included wolf hair in 68 (13%) scats, moth larvae deposited on 77 (14%) scats, grass and other vegetation in 69 (13%) scats. Bone pieces found in 247 (47%) scats.

[3]By mid-August moose calves acquired a darker coat of hair that more closely resembles adult pelage, thus complicating calf/adult distinctions after that time.

[4]Represented in 1 scat each were salmon, insects, porcupine (Erithizon dorsatum), and a plastic bag.

Table 9. Comparative prey utilization in areas where moose constitute the principal prey, as indicated by scat analyses[1].

Area		Prey species	Relative number of prey	Relative prey biomass	Percent prey biomass
Alberta[2]					
Moose as % of total prey occurrence:	61%	Prey species:			
		Adult moose	1.00	1.00	86.5
% adult moose:	40%	Calf moose	0.69	0.10	8.5
		Beaver	0.85	0.03	2.3
% calf moose:	21%	S.S. hare	8.13	0.03	2.4
Kenai Peninsula, AK[3]					
Moose as % of total prey occurrence:	75%	Prey species:			
		Adult moose	1.00	1.00	80.7
% adult moose:	36%	Calf moose	1.38	0.20	15.9
		Beaver	0.28	0.01	0.8
% calf moose:	38%	S.S. hare	7.11	0.02	2.0
Nelchina Basin, AK[4]					
Moose as % of total prey occurrence:	51%	Prey species:			
		Adult moose	1.00	1.00	62.4
% adult moose:	15%	Calf moose	3.04	0.43	27.0
		Beaver	2.16	0.08	4.8
% calf moose:	35%	S.S. hare	27.27	0.09	5.8
Isle Royale, MI, 1958-61[5]					
Moose as % of total prey occurrence:	74%	Prey species:			
		Adult moose	1.00	1.00	61.1
% adult moose:	18%	Calf moose	4.03	0.57	35.0
		Beaver	1.47	0.05	3.2
% calf moose:	55%	S.S. hare	3.08	0.01	0.6
Isle Royale, MI, 1973[6]					
Moose as % of total prey occurrence:	47%	Prey species:			
		Adult moose	1.00	1.00	36.1
% adult moose:	7%	Calf moose	7.93	1.11	39.9
		Beaver	19.14	0.67	24.0
% calf moose:	40%	S.S. hare	0	0	0

Table 9. continued

[1]Only 3 principal prey species 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; relative prey numbers and biomass calculated according to the footnote in Table 10.

[2]Fuller and Keith (1980).

[3]This study.

[4]Stephenson (1978). The 3 prey species constituted 95% of the prey biomass. In the other studies, these 3 species provided essentially all of the prey biomass.

[5]Mech (1966).

[6]Peterson (1977).

Table 10. Summer reliance on moose by wolves, as indicated by scat analyses.

Area	% prey biomass provided by moose	Moose biomass ratio in wolf diet (adult/calf)[1]	Relative number of adult and calf moose (adult/calf)[1]
Alberta (Fuller and Keith 1980)	95%	10.2	1.45
Kenai Peninsula, Alaska (this study)	97%	5.1	0.72
Melchina Basin, Alaska (Stephenson 1978)	89%	2.3	0.33
Isle Royale, 1958-61 (Mech 1966)	96%	1.8	0.25
Isle Royale, 1973 (Peterson 1977)	76%	0.9	0.13

[1] The following whole prey weights (Franzmann et al. 1978 and Floyd et al. 1978) were used to derive estimates of prey weight represented by each scat using the formula of Floyd et al. (1978):

	Whole prey weight (kg)	Prey weight (kg) per scat (or prey occurrence)
Adult moose	350	7.38
Calf moose	50	1.38
Beaver	12.5	0.63
Snowshoe hare	1.2	0.41
Rodent, bird	0.1	0.38

Table 11. ADF&G estimates of the total Kenai Peninsula wolf population (LeRoux 1978 and pers. comm.).

Year	Estimated wolf population
1968-69	10
1969-70	10-15
1970-71	17-27
1971-72	27-39
1972-73[1]	40-71
1973-74	80-100
1974-75[1]	102-130
1975-76	116-160
1976-77[1]	116-142

[1]The estimated wolf population in Game Management Units 15A and 15B was 30-35 in 1973, 39-44 in 1975, and 36-42 in 1977.

Table 12. Dynamics of wolf packs on Kenai study area.

Pack	Early winter pack size[1]	Late winter pack size[2]	Reported harvest[3]
1976-77:			
Swanson R.	20+1	13	1
Skilak L.	9+2	7	2
Mystery Cr. I	14 min.	14	0
Total	43+3	34	3
1977-78:			
Swanson R.	20	15	3
Skilak L.	9	8	1
Mystery Cr. I	16+1	8 max.	6
Bear L.	2	2	0
Killey R.	13+1	11	1
Total	60+2	44	11
1978-79:			
Swanson R.	18+1	5	8
Skilak L.	12+2	5	5
Mystery Cr. II	2	2	0
Bear L.	8	6	0
Killey R.	14	11	2
Big Indian Cr.	12[4]	10	2
Total	66+3	39	17
1979-80:			
Swanson R.	10	1	3
Skilak L.	5+2	1	5
Mystery Cr. II	6	4	1
Bear L.	10	6	1
Killey R.	13+2	5	8
Big Indian Cr.	22	10[5]	5
Bear Cr.	21	12[6]	5
Total	87+4	39	28
1980-81:			
Swanson R.	6	-	0
Skilak L.	2	-	0
Mystery Cr. II	4[7] est.	-	2
Bear L.	6-10 est.	-	5
Killey R.	8	-	3
Pt. Possession	9[8]	-	3
Elephant L.	5[9]	-	1
Total	40-44	-	14

Table 12. continued

Pack	Early winter pack size[1]	Late winter pack size[2]	Reported harvest[3]
1981-82:			
Swanson R.	7	-	-
Skilak L.	8	-	-
Mystery Cr. II	7-10 est.	-	-
Bear L.	9	-	-
Killey R.	9-10	-	-
Elephant L.	8 est.	-	-
Slikok L.	8	-	-
Total	56-60	-	-

[1]Preharvest level equal to maximum observed pack size in early winter (usually November or December), with reported harvest before that time added.

[2]Usually maximum observed pack size in April.

[3]Including mortality of dispersers that had not successfully settled.

[4]Minimum count, probably only of a portion of the pack. Excluded from most calculations.

[5]Late winter pack size estimated from pack size of 11 determined Feb. 2, 1980, minus 1 reportedly killed in March 1980. Pack not observed in late winter.

[6]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.

[7]Track count by ADF&G; also the number present when male 476 was snared.

[8]Unradioed pack of 9 observed S of Pt. Possession, also reported by seismic crew.

[9]Unradioed pack of 5 observed near Elephant L.

Table 13. Estimated wolf density on the Kenai Peninsula study area.

	Year					
	1976-77	1977-78	1978-79	1979-80	1980-81	1981-82
Study area size (km^2)[1]	2,997	3,699	3,042	2,650	2,927	3,008
Total early winter wolf population[2]	43	60	54	44	40-44	56-60
Early winter wolf density (wolves/1,000km^2)	14.3	16.2	17.8	16.6	13.7-14.9	18.6-19.9
Average early winter pack size (N packs)	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)	999	740	608	530	418	501

[1]Annual study areas outlined in Fig. 5, determined by intensive monitoring of radioed packs from 1976-77 through 1979-80 and by traditional pack territories in 1980-81 and 1981-82.

[2]Maximum observed pack size in November and December (Table 12).

Table 14. Intra-pack wolf density on the Kenai study area, determined from early winter observed pack sizes and October-March territory[1].

	Year			
Pack	1976-77	1977-78	1978-79	1979-80
Swanson R.	$\frac{1556}{20} = 78$	$\frac{1313}{20} = 66$	$\frac{991}{18} = 55$	$\frac{563}{10} = 56$
Skilak L.	$\frac{325}{9} = 36$	$\frac{459}{9} = 51$	$\frac{473}{12} = 39$	$\frac{177}{5} = 35$
Mystery Cr. I & II	$\frac{711}{14} = 51$	$\frac{738}{16} = 46$	$\frac{308}{2} = 154$	$\frac{378}{6} = 63$
Bear L.	---	$\frac{400}{2} = 200$	$\frac{463}{8} = 58$	$\frac{684}{10} = 68$
Killey R.	---	$\frac{713}{13} = 55$	$\frac{475}{14} = 34$	$\frac{631}{13} = 49$
Big Indian Cr.	---	---	---	$\frac{534}{22} = 24$
Bear Cr.	---	---	---	$\frac{549}{21} = 26$

[1]Key to information provided: (Area (km^2))/(early winter pack size) = km^2 per wolf. Territory areas were determined for convex polygons enclosing known locations of pack members, except for the Bear Cr. territory, which was extended to include all likely territory (see text).

Table 15. Estimated early winter wolf population on the Kenai Peninsula in 1980, and the proportion included on the Kenai National Wildlife Refuge[1].

Area	Primary wolf habitat		Secondary wolf habitat		Unit totals	
	Size (km^2)	No. wolves	Size (km^2)	No. wolves	Size (km^2)	No. wolves
Game management unit 15	7,166	115	2,276	18	9,442	133
Game management unit 7	1,769	28	3,067	24	4,836	52
Total	8,935	143	5,343	42	14,278	185
Kenai National Wildlife Refuge (7,972 km^2, 70% occupied by wolves):						
	4,650	74	947	8	5,597	82

[1]Primary wolf habitat assumed to support 16 wolves/1,000 km^2, secondary habitat 8 wolves/1,000 km^2. Habitat delineated in Fig. 8.

Table 16. Wolf pup:adult ratios determined for study packs on the Kenai Peninsula[1].

	Year				
Pack	1977	1978	1979	1980	4-yr. total
Swanson R.	7/20	4/19	5/10	4/6*	
Skilak L.	2/9	6/14	2/7*	0/2*[2]	
Mystery Cr.	3/17	--	4/6*	--	
Bear L.	--	6/8*	4/10	--	
Killey R.	--	3/14	4/15	3/8*	
Uncorrected total	12/46	19/55	19/48	7/16	57/165
Corrected total[3]	16/46	23/55	22/48	7/16	68/165
Corrected pup:adult ratio	35:65	42:58	46:54	50:50	41:59

[1]Key to table: (Early winter pack size - spring pack size)/(early winter pack size + previous reported harvest). * denotes packs in which pups were determined by direct observation instead of spring-to-early winter increase in pack size.

[2]This pack was reduced to 1 adult male after the alpha female was snared in May 1980, shortly after giving birth to 6 pups.

[3]Adjusted for estimated 13% summer loss of adults when no. pups was estimated by spring-to-early winter increase in pack size.

Table 17. Characteristics of Kenai Peninsula wolf dens.

Pack	Year used	Description
Skilak L.	1977, 1978, 1979	Kenai lowlands, located on upland ridge in mature forest. Single hole under base of birch tree.
Mystery Creek I and II	1977, 1979	Edge of Kenai mountains, located at top of steep slope down to major drainage. Single hole under large aspen tree in mature forest.
Bear L.	1978	Located on sandy knoll surrounded by large, wet bog. Single hole dug into sand bank, in mature forest. Auxiliary den nearby.
Bear L.	1979	One hole 45-60 cm in diameter, facing west, on mound amidst fallen dead trees in mixed mature-1947 burn habitat.
Killey R.	1978, 1979, 1980	One hole 1 m across x 1 m deep at base of spruce tree on SW-facing slope. Wolves spent most of the time beneath dense mature spruce surrounding den.
Swanson R.	1977 (15039's den)	Located in mature forest, single hole beneath large birch tree.

Table 18. Reproductive status and teat development of adult female wolves on the Kenai Peninsula.

Wolf	Date examined (M/D/Y)	Teat description[1]	Remarks on age, reproductive status
022	08/14/76	rear pair 3x3mm, rest inconspicuous	nulliparous, prob. yrl.
039	10/09/76	barely discernable, 3x3mm	nulliparous, prob. 2-4 years old
049	10/18/76	inconspicuous, 2mm wide	nulliparous, prob. yrl.
102	12/07/77	inconspicuous	nulliparous, yearling
119	07/17/77	rear 6 teats engorged and pigmented, 25x12mm	probably multiparous, young adult, alpha female, minimum 5 pups present in autumn
134	09/28/77	rear 2 teats pigmented and engorged, 6x6mm	primiparous or multiparous, probably 4-6 years old
134	07/29/78	rear 2 teats 10x8mm, other 6 were 13x10mm, rear 4 teats showed hair loss	alpha female of newly-formed pack, 6 pups seen in autumn
208	05/27/78	rear 6 teats 10x10mm and pigmented, front pair very small, rear 4 teats showed hair loss, not engorged, though expressed milk	loner, probably pseudo-pregnant, probably 4-6 years old
225	05/26/78	8 engorged, pigmented teats, 10x5mm, rear pair missing hair	social status and number of pups unknown, probably 2-4 years old
225	06/26/79	8 pigmented teats, 20x15mm, rear 4 missing hair and engorged	multiparous, probably 3-5 years old
262	12/12/78	inconspicuous	nulliparous, prob. yrl., no uterine scars
270	12/15/78	5x5mm	nulliparous, prob. yrl.
402	07/27/78	8 engorged, pigmented teats, 14-15x10-13mm, rear 2 missing hair	multiparous, alpha female, probably 6-7+ years old, 6 pups observed in late summer

Table 18. continued

Wolf	Date examined (M/D/Y)	Teat description[1]	Remarks on age, reproductive status
402	06/28/79	6 engorged pigmented teats, rear 6 missing hair, 10x7mm	multiparous, alpha female, probably 7-8+ years old, 2 pups observed in late summer
136	10/02/77	inconspicuous, 3mm wide, unpigmented	nulliparous, probably 2-4 years old
404	08/12/78	inconspicuous, 2.5x2.5mm	nulliparous, prob. yrl.
404	06/27/79	6 engorged teats, 12x9mm	primiparous, probably 2 years old, alpha female in newly-formed pack, 4 pups seen in late summer
412	11/08/79	inconspicuous	nulliparous, yearling
420	11/30/79	inconspicuous	nulliparous, yearling
420	07/11/80	inconspicuous	nulliparous, 2 years old
424	10/03/79	inconspicuous	nulliparous, yearling
424	05/16/80	6(-8?) engorged teats 30x50mm, unpigmented, without hair loss	primiparous, 2 years old, 6 fresh placental scars
452	07/20/79	inconspicuous	nulliparous, prob. yrl.
454	10/07/79	inconspicuous	nulliparous, prob. yrl.
458	11/08/79	inconspicuous	nulliparous, prob. yrl.
472	12/11/79	inconspicuous	nulliparous, prob. yrl.
480	12/11/79	inconspicuous	nulliparous, prob. yrl.
486	07/16/80	inconspicuous	nulliparous, 2-4 yrs old
488	07/18/80	inconspicuous	nulliparous, 1-2 yrs old
490	07/19/80	inconspicuous	nulliparous, 2-4 yrs old

[1]Dimensions given are length x width at base.

Table 19. Annual mortality among wolves with operating transmitters[1].

Year	Pups		Adults		All wolves	
	No. deaths/ days coverage	Annual mortality (%)	No. deaths/ days coverage	Annual mortality (%)	No. deaths/ days coverage	Annual mortality (%)
1976-77	0/1460	0	0/2320	0	0/3780	0
1977-78	0/2419	0	1/4211	9	1/6630	6
1978-79	2/3860	19	4/5275	28	6/9135	24
1979-80	1/1630	22	9/6545	50	10/8175	45
1980-81	0/1460	0	6/2793	78	6/4253	51
Total	3/10829	10	20/21144	35	23/31973	26

[1]Annual mortality calculated from May 1 to April 30. "Days coverage" includes period between May 1 and date of collaring (see text). All mortality was human-caused except deaths of 1 adult in 1978-79 and 1 pup and 1 adult in 1979-80.

Table 20. Wolf hunting and trapping regulations, Kenai Peninsula.

Regulatory year	State hunting and trapping regulations, GMU 7 & 15				Federal modifications applicable to KNWR only
	Trapping season	No. wolves allowed per trapper	Hunting season	No. wolves allowed per hunter	
1962-73	No legal harvest; 8 wolves trapped incidently by lynx trappers in 1973-74.				
1974-75	no open season	---	Nov 1 - Feb 28	1[1]	none
1975-76	Nov 10 - Mar 31	no limit	Nov 1 - Feb 28	1[1]	KNMR south of Kenai River and Skilak Lake closed to taking of wolves
1976-77	Nov 10 - Mar 31	no limit	Aug 10 - Apr 30	2	Surfaces of Skilak and Tustumena lakes closed to wolf trapping
1977-78	Nov 10 - Mar 31	no limit	Aug 10 - Apr 30	2	Surfaces of Skilak and Tustumena lakes closed to wolf trapping
1978-79	Nov 10 - Mar 31	no limit	Aug 10 - Apr 30	2	none
1979-80 & 1980-81	Nov 10 - Mar 31	no limit	Aug 10 - Apr 30	2 in GMU7 4 in GMU15	none

[1] One wolf by permit only, unlimited number of permits available. Season to be closed by field announcement when 10 wolves had been taken (applicable to hunter take only).

Table 21. Kenai Peninsula wolf harvest summary[1].

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

[1] Determined from ADF&G sealing forms.

[2] Including all harvest by airplane-assisted trappers.

Table 22. Wolf harvest summary for Kenai National Wildlife Refuge and study area.

Regulatory year	Wolves killed on KNWR	Wolves killed in GMU 15A and N half GMU 15B	Wolves killed on study area[1]	Recorded harvest, study packs[2]	Harvest from study packs as % of early winter population[2]	Overwinter loss (%), study packs	Estimated wolf population on GMU 15A & N half GMU 15B[3]	Estimated proportion (%) harvested, GMU 15A and N half GMU 15B
1974-75	1	1	--	--	--	--	--	--
1975-76	4	4	--	--	--	--	--	--
1976-77	6	6	6	3	7%	21%	51	12%
1977-78	13	8	16	11	18%	27%	58	14%
1978-79	32	26	21	15	28%	46%	63	41%
1979-80	37	21	31	28	31%	61%	59	36%
1980-81	18	14	15	14	32-35%	--	49-53	26-29%

[1]Study area for each year shown in Fig. 5.

[2]Following are packs that were included in calculations, if data were available: SRP, SLP, MCP I&II, BLP, KRP, PPP, ELP (Table 12).

[3]Study area wolf density (Table 13) applied to 3,566 km^2.

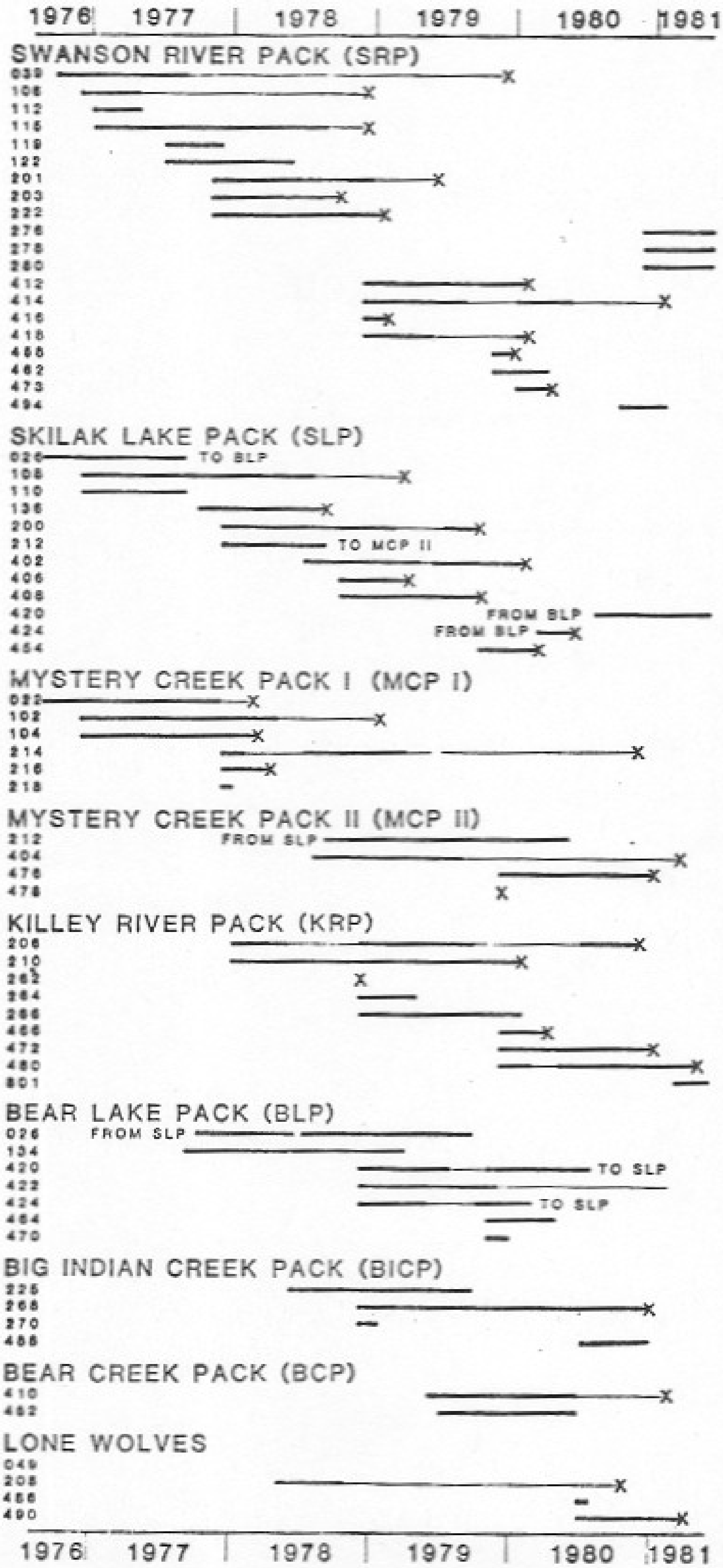
Table 23. Observed activity of radio-located wolves.

Season	% of total observations						N
	Resting	Sleeping	Traveling	Feeding	Courtship	Other	
Summer (Apr - Sept)	50%	6%	29%	9%	0%	7%	512
Winter (Oct - Mar)	24%	15%	50%	7%	0%	4%	1710

Table 24. Kenai wolves that dispersed from their original pack.

Wolf	Original pack	Sex	Age	Date of final departure	Fate
026	SLP	M	3-5 yrs	Sept 1977	Established BLP with female 134
039	SRP	F	2-4 yrs	unknown	Killed 12/79 in SLP territory
106	SRP	M	3-5 yrs	Dec 1976	Settled successfully, S Kenai lowlands
112	SRP	M	yrling	Apr 1977	Lost signal, S Kenai mountains
201	SRP	M	yrling	Jan 1979	Killed 6/79, E side Kachemak Bay
206	KRP	M	5+ yrs	unknown	Killed 11/80 near Soldotna
210	KRP	M	2 yrs	Oct 1979	Killed 1/80 near Soldotna
212	SLP	M	2-4 yrs	July 1978	Established MCP II with female 404
214	MCP I	M	yrling	Dec 1978	Killed 11/80, on mainland
268	BICP	M	2 yrs	ca.Apr '80	Killed 1/81 in SLP territory
410	BCP	M	2-4 yrs	mid 1980	Killed 2/81, S Kenai lowlands
414	SRP	M	yrling	Feb 1980	Killed 1/81, S Kenai lowlands
420	BLP	F	2 yrs	ca.Aug '80	Replaced female 424 as alpha female in SLP; alive 12/81 in SLP
424	BLP	F	yrling	Feb 1980	Replaced alpha female in SLP; killed 5/80
458	SRP	F	prob.yrl.	Nov 1979	Killed 12/79 in KRP territory
462	SRP	M	pup	Feb 1980	Unknown
472	KRP	F	prob.yrl.	ca.Sept '80	Killed 1/81, S Kenai lowlands
473	SRP	M	prob.yrl.	Feb 1980	Killed 3/80, N side Tustumena L.

APPENDIX I. Summary of 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.



APPENDIX II

Pack Summaries

wanson River Pack (SRP)

Reports of wolves within the Swanson River Pack's territory 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.

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, we determined that 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.

For the first 3 years of the study the SRP remained large, but gradually restricted its movements to the western portion of its original range, near the 1969 burn. Here there was evidence of an increasing moose population, or at least a concentration of moose (Peterson et al, submitted). While it seemed that the SRP was adjusting its movements to take advantage of better hunting conditions near the 1969 burn, we had no opportunity to test this idea. However, except for a slight shift in the territory of the Mystery Creek Pack, no other radioed pack exhibited a significant shift in territory during the study, so our explanation for changes in SRP territory seems reasonable.

In November, 1978, the SRP contained 18 wolves, after one 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, and by winter's end only 5 wolves remained in the pack. Their movements overlapped with those of the Pt. Possession Pack (unradioed) to the NE. Although we cannot exclude the possibility of interchange between the 2 packs, we regard this as an unlikely explanation for the decline in SRP. Free interchange between 2 large packs has never been documented; the interpack associations we observed in this study were all between 1 or 2 individuals and 1 large pack and were all quite transitory.

In November, 1979, we found 8 wolves (we once observed 10) in the SRP. 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.

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 Pt. Possession packs (the only all-gray packs observed in the study). Three pups (296, 278, 280) were darted and radioed, and the remaining uncollared wolves appeared to be an adult female and a fourth pup. All locations obtained for this group were within the 1979-80 SRP territory. In early winter, 1981-82, the pack contained 7 gray wolves.

Skilak Lake Pack (SLP)

This pack of predominantly black wolves lived in a territory that straddled the Sterling Highway east of Sterling. Though numbering as many as 12 wolves in early winter, the pack usually contained 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. From 1976 until 1980 the pack was led by the same alpha male and female. The alpha female was a very light gray wolf, so large that at first we assumed she was a male. Upon capturing her (402) we found that she was relatively old, indicated by rounded canines. The alpha male was black, with graying sides and face that suggested advanced age. We never captured him, but both alpha wolves were readily recognized through the study.

Even though highly accessible to hunters and trappers, this pack was affected little by human harvest during the first 2 years of the study. 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 one pup in late February, 1980. Yearling female 424, from the adjacent Bear Lake Pack, paired with the alpha male while the pup disappeared, but 424 was snared in May just after giving birth to 6 pups (indicated by placental scars). Contact with the unradioed 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, since the pack contained 8 wolves in early winter, 1981-82.

Mystery Creek Pack (MCP) I & II

During 1976-77, 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. In 1972 and 1973, a pack of 4 gray and 4-5 black wolves was reported 5 times from MCP territory, suggesting stability also in this pack prior to our study. By 1977-78 this 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 radioed wolves. Subsequently 3 wolves (including 104 and 216) were shot from the pack as they fed on a kill on Kenai Lake, so MCP territory was extended to this point in our analysis. MCP I female 022 was simultaneously snared on Ptarmigan Lake, east of Kenai Lake, but we could not determine if she had dispersed from the pack. We lost contact with MCP I early in 1978 when all radioed wolves were killed, but reports indicated that this pack continued to occupy the eastern portion of its original territory.

The vacant western portion of MCP I territory was claimed by a new pair, 404 and 212, that formed the Mystery Creek Pack II. Male 212 had dispersed from the adjacent Skilak Lake Pack, and we reasoned that female 404 was probably from the original Mystery Creek Pack, since 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 came to occupy most of the territory used by Mystery Creek Pack 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 NE of Lower Russian Lake (just S of MCP territory). In November, 1980, 214 was snared on the mainland about 125 km NE of Anchorage (175 km straight-line from his origin in MCP I), he was accompanied by 4 other wolves when killed.

We were able to monitor 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 she 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 the first winter of the study (1976-77) we identified the Moose River Flats as essentially 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 from SLP apparently left his pack, found a female mate, and became established on Moose River Flats. Male 026 was re-radioed in October, 1977, and female 134 was initially radioed at about the same time. From her color we knew this gray female was not from Skilak Lake Pack, but had no other clue as to her origin.

During the winter of 1977-78 wolves 026 and 134 traveled as a pair over the Flats and the adjacent rolling upland to the west, and became known as the Bear

Lake Pack (BLP). Over the course of the winter the SRP shifted to the west and the BLP simultaneously occupied this portion of SRP territory.

The Moose River Flats supported very few moose in winter, and while the lowland caribou herd wintered in this area, we never found any indication that the BLP killed any caribou. Instead they relied on moose found along the edge of the Flats. In spring a large influx of moose arrived on the Flats for calving, primarily migratory moose from the Kenai mountains (Bailey et al. 1978). During 1978 BLP denned on a small upland island in the middle of the Flats and raised a total of 6 pups. Two pups disappeared during their first 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)

The pack occupying the NE corner of the KNWR was monitored after May, 1978, when a lactating female (225) was trapped and collared on the edge of the mountains. She was consistently located in the same area on a shrubby mountainside, which we presumed to be a densite. 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 found radioed wolves from this pack as far E as the mountains E of Resurrection Creek. Since wolves often travel the Hope Road (A. Mars, pers. comm.), we assume the BICP territory extends at least to Six-mile Creek.

During the winter of 1979-80, we confirmed that BICP contained at least 15 wolves, since 11 were observed after a known harvest of 4 wolves. T. Spraker

(ADF&G) contributed several observations of this pack after radio-collaring a BICP wolf while capturing caribou. He observed a minimum of 17, 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 we never observed her with other wolves.

Killey River Pack (KRP)

Since tracks of at least 17 wolves were seen south of the Kenai River in 1976, we knew that a large pack inhabited this general area early in the study. Two wolves were first radioed in this pack in January, 1978, and that winter we found 13 wolves in this pack. During the following 2 years maximum pack size was 14 and 15, respectively.

During the 1977-78 and 1978-79 season this pack experienced little human harvest, and was very consistent in pack size and territory. While KRP wolves were located in the mountains as far as upper Benjamin Creek, they were usually on the lowlands near the Killey and Funny rivers. In 1979-80, after beginning the winter with 15 wolves, 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.

Bear Creek Pack (BCP)

The alpine tundra on the benchland north of Tustumena Lake had provided many of the wolf observations in the late 1960's and early 1970's, and 14 had been seen there in 1970. One wolf was shot from a pack of 15 in August 1977 along Bear Creek, and the following winter we found kills and tracks from a large pack in the same area, with tracks leading across the SE end of Tustumena Lake to the S side of Tustumena Glacier. In June 1979 male 410 was trapped and collared near Mystery Creek, and he subsequently returned to a previously unradioed pack just N of Tustumena Lake. A densite and rendevous 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 S of Tustumena Lake along Sheep Creek and the Fox River, 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 Deep Creek on the southern lowlands.

Loners

Three female wolves that were not part of a pack were monitored briefly during the study. 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 a couple weeks, then emerged again on the lowlands and traveled widely across the study area. She spent most of her time while on the lowlands in SRP territory, and was occassionally quite close to this pack. On Nov. 22, she was located in dense spruce 0.8 km. from 7 unradioed wolves (probably part of SRP) resting on a lake. When we darted a wolf in this pack on Dec. 15, 049 was within 2-3 km of SRP. She was never seen with other wolves, and in January, 1977, re-entered the mountains and was not located again.

Female 208 was trapped along the pipline between MCP and BICP territories. Her right 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.

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 then became aware of her presence in the square-mile pen. For 12 hours we stalked the wolf, firing shotgun blasts into the air whenever close to her in hopes of frightening her out of the pen. She would not leave the pen, and since 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. After removing the joint and cleaning the bones, we found that the shoulder joint had been shattered, and while bone remodeling was progressively fusing the joint, the leg was held in place by fibrous tissue. In spite of her disability, she weighed 35 kg with an empty stomach, and ample body fat confirmed she was in excellent condition.

The third radioed 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 with other wolves. She was in the vicinity, along with at least 2 other wolves, when MCP II male 476 was snared in

SLP territory. The individual who shot female 490 in March 1981 reported a second 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.

Unradioed Packs

Limited information on unradioed packs adjacent to the study packs was available from reports of other biologists and the general public, in addition to our own observations. Presumptive territories of unradioed packs are presented in Fig. 5.

After the first winter of the study, the SRP territory shrank to only a portion of its 1976-77 area. In 1978-79, we confirmed that unradioed packs, the Pt. Possession Pack (PPP) and the Elephant Lake Pack (ELP), occupied the areas vacated by SRP. PPP and ELP became established just NE and S 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 only from tracks that at least a dozen 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.

We learned of a pack that inhabited the Kenai mountains east of MCP from a trapper familiar with the area. He claimed to have tracked a wolf pack along the Alaska Railroad from Johnson Pass to Portage. The same pack ranged as far S as Trail Lake, and probably W to the Seward Highway. Once he counted 12 tracks from this pack, though usually fewer wolves were present.

Another trapper, a long-time resident who flew throughout the Kenai mountains, indicated that a small pack used the Resurrection River Valley between Seward and Lower Russian Lake. L. Nichols reported having seen 10 wolves in the northern part of this area before our study began.

We presumed that the MCP I continued to occupy much of their original territory, and in Fig. 5 indicated their presumptive territory as running from Juneau Lake and the American Pass area SE to Kenai Lake.

Information on wolf packs SW of Tustumena Lake was fragmentary at best. We indicated in Fig. 5 the area where male 106, who dispersed from SRP, eventually settled. Large packs were reported in Fox River Valley and adjacent Caribou Hills, possibly all the same pack. D. Hardy observed 9 wolves in 1977 along the upper Anchor River, so it is likely that a large pack inhabited the area NW of Kachemak Bay. Groups of wolves numbering less than 7-8 were commonly reported SW of Tustumena Lake and along tributaries of the Ninilchik River, so perhaps another pack inhabited this area. Since the southern Kenai lowlands is heavily hunted and many wolves were harvested in this area (see Fig. 8), pack territories may be less stable and pack sizes smaller than on the study area.

APPENDIX III. Temporary associations of wolves from different packs.

Radioed wolves involved	Pack	Description
112 15022	SRP MCPI	Feb 22, 1977: wolf 112 located within SRP territory with packmate, 10 km W of MCP I, which was at that time on the edge of SRP territory and 18 km outside MCP territory. Feb 26: 112 and 15022 (MCPI) located about 1 km apart in MCPI territory, each traveling alone. Mar 3: 112 located on a kill with at least 6-7 wolves from MCPI (15022 included). Mar 5: 112 seen traveling NW, 3.4 km NW from 11 wolves of MCPI (w/15022), still at kill observed on Mar 3. Mar 8: MCPI (w/15022) at territory edge, examined scent post then ran to nearby SLP kill. Wolf 112 located 3 km N of MCPI (in MCPI territory).
122 210 (no radios)	SRP SRP MCPI	Feb 26, 1978: wolves 122 & 201 located in group of 15 wolves (including minimum of 6 blacks, excluding the possibility that they were any pack other than MCPI) in MCPI territory. No unusual behavior noted as pack slowly walked around in forest opening. Feb 27: 122, 210 and an unidentified gray wolf located together, still within MCPI territory. Location of MCPI not determined. Subsequently wolf 201 returned to SRP while 122 traveled south, returning to SRP about a month later.
214 212 404	MCPI MCPII MCPII	Nov 8, 1978: 214 located with newly-formed pair, 404 & 212 (MCPII). 214 and 404 were very likely littermates in MCPI in 1977. Feb 17: 212 & 404 located with gray wolf of unknown origin (status of 214 unknown at this time).
418 422 404 212	SRP SRP MCPII MCPII	Jan 12, 1979: while outside SRP territory, 418 & 422 associated with 404 & 212, while on a kill in MCPII territory. Three of the 4 observed together.
414 (no radios)	SRP adjacent pack of 3 wolves	Jan 2, 1979: wolf 414 bedded and traveled briefly with an unradioed group of 2 gray wolves and 1 black wolf near their mutual territory boundary.

APPENDIX III. continued

Radioed wolves involved	Pack	
412 414 418 (no radio)	SRP SRP SRP	Apr 18, 1979: When located in MCPII territory, 5 wolves from SRP were seen with an extra gray wolf of unknown origin. SRP consistently contained 5 gray wolves before and after this observation, when inside their own territory.
115 216	SRP MCPI	Mar 13, 1978: During a brief extraterritorial movement, wolf 115 was located with wolf 216 in heavy timber inside MCPI territory.

Figure Captions

Fig. 1. Characteristic of wolf locations from aircraft. Upper graph shows the sightability of radioed wolves and the monthly distribution of all locations, while the lower graph shows the distribution of wolf locations according to time of day.

Fig. 2. (a) Map of the Kenai Peninsula, indicating locations mentioned in text. (b) State Game Management Units (GMU) in relation to major land management units.

Fig. 3. Wolf pack territories on the Kenai study area, 1976-77 through 1979-80. Pack territories are delineated by bold outline; also outlined is total study area for each year.

Fig. 4. Relationship between wolf pack size and territory size.

Fig. 5. Generalized map of radioed wolf packs (solid line) and speculative distribution of unradioed packs (broken line). Areas considered as primary and secondary wolf habitat are indicated.

Fig. 6. Relationship between pup production (Table 16) and pack size in spring. Uncorrected pup total used to avoid rounding error. Litter size of 6 pups assumed for Skilak L. Pack in 1980.

Fig. 7. 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.

Fig. 8. Distribution of reported wolf harvest between 1974-75 and 1979-80. Each dot represents one wolf killed and reported.

Fig. 9. Annual fluctuations in wolf density, pack size, and wolf harvest on the Kenai study area.

Figure Captions (continued)

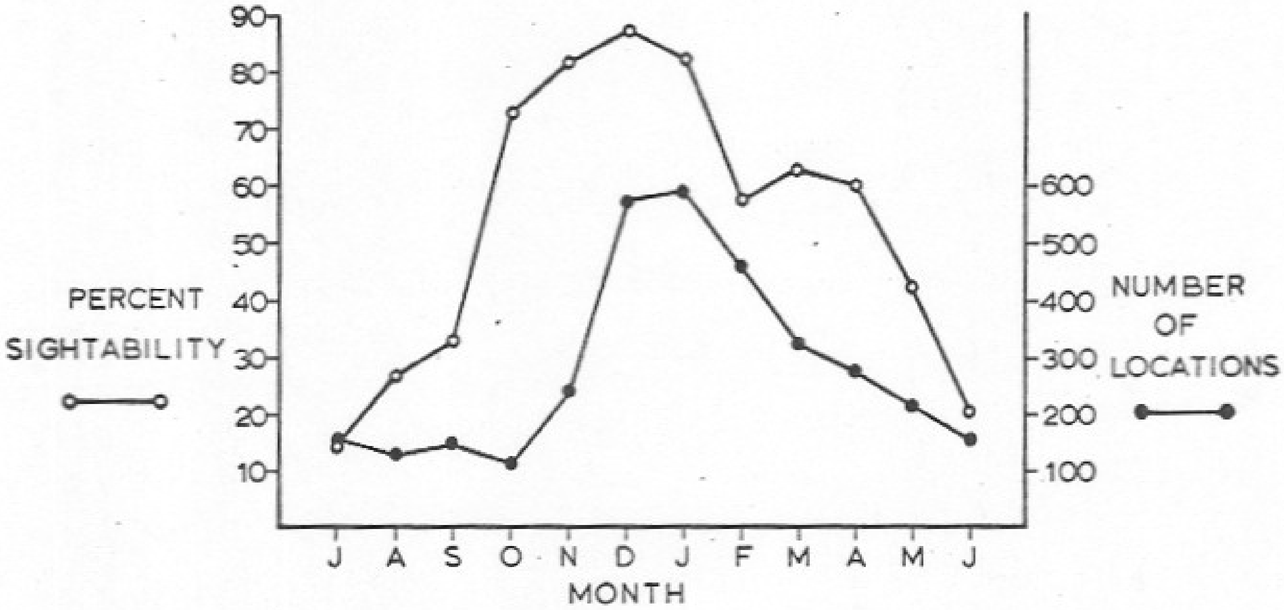
Fig. 10. Monthly distribution of wolf pack cohesion index for large and small wolf packs.

Fig. 11. Monthly mean radius of activity for radioed Kenai wolves.

Fig. 12. Centers and radii of activity for radioed wolves, 1976-77 through 1979-80.

Fig. 13. Dispersal movements of male 106, who left Swanson R. Pack after losing dominant status.

Fig. 14. Diagrammatic representation of Swanson River Pack during winter, 1978-79. Each vertical line represents one wolf, squares superimposed on the line indicates a direct observation, while superimposed circles indicate mortality. Shifts to right or left side signify extraterritorial movements. Dates of radiolocations indicated by horizontal bars on left-hand scale.


90
80
70
60
50
40
30
20
10
PERCENT
SIGHTABILITY
600
500
400
300
200
100
NUMBER
OF
LOCATIONS
J A S O N D J F M A M J
MONTH

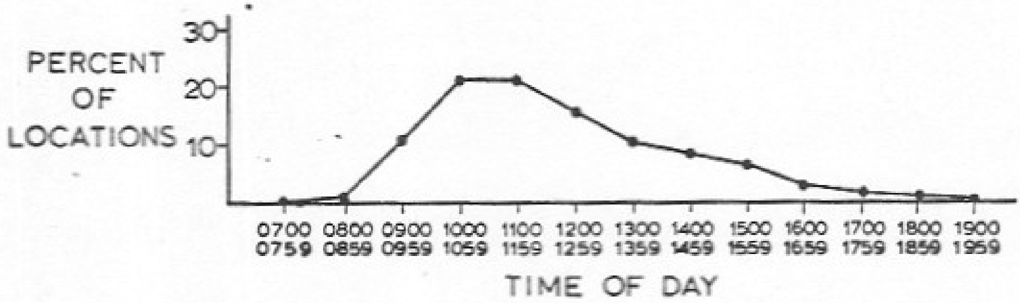

30
20
10
PERCENT
OF
LOCATIONS
0700 0800 0900 1000 1100 1200 1300 1400 1500 1600 1700 1800 1900
0759 0859 0959 1059 1159 1259 1359 1459 1559 1659 1759 1859 1959
TIME OF DAY

FIG. 1

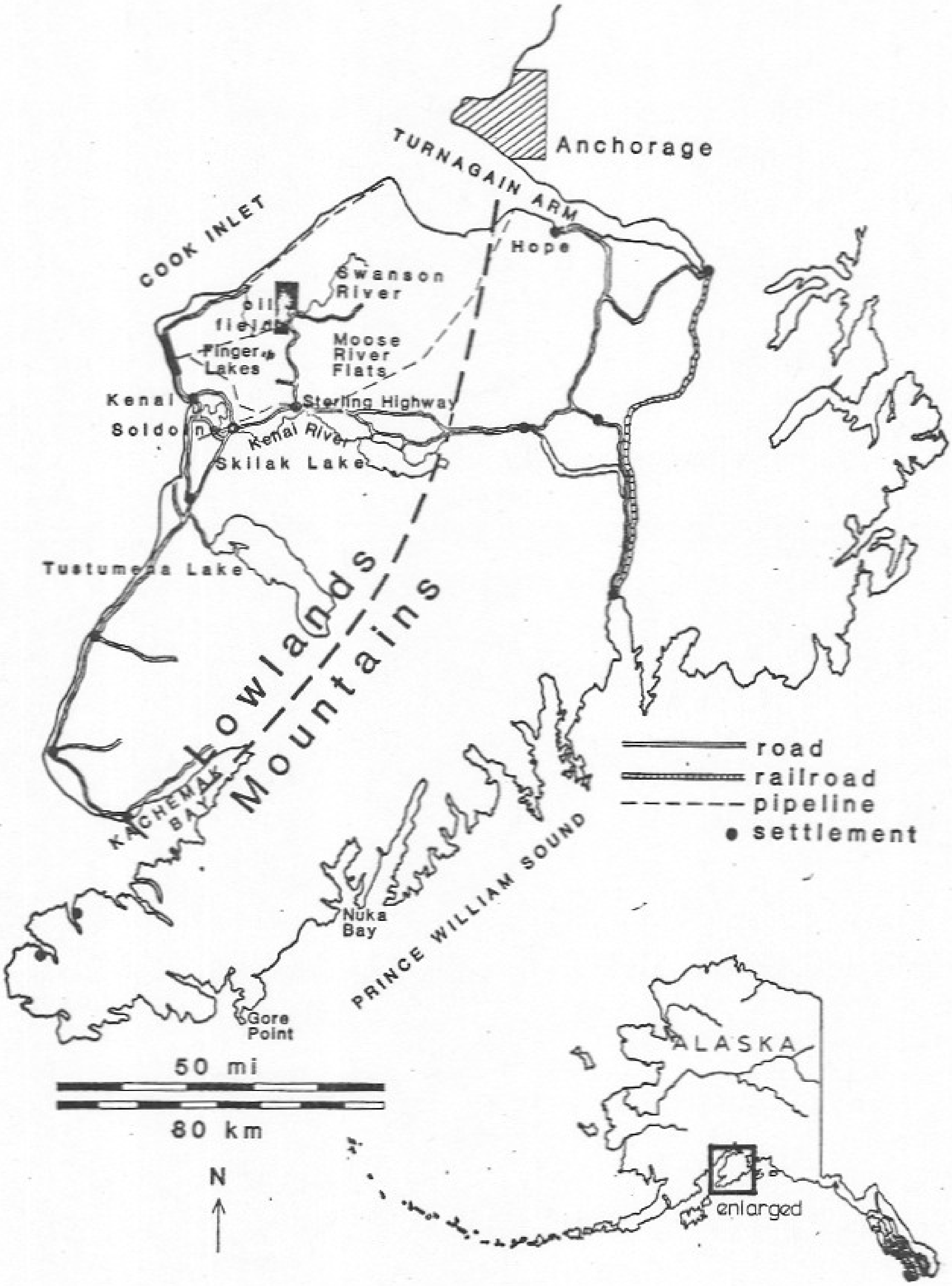

Anchorage
TURNAGAIN ARM
COOK INLET
Hope
Swanson River
oil field
Finger Lakes
Moose River Flats
Kenai
Sterling Highway
Soldotna
Kenai River
Skilak Lake
Tustumena Lake
Lowlands
Mountains
KACHEMAK BAY
PRINCE WILLIAM SOUND
Nuka Bay
Gore Point
road
railroad
pipeline
settlement
50 mi
80 km
N
ALASKA
enlarged

FIG.2a

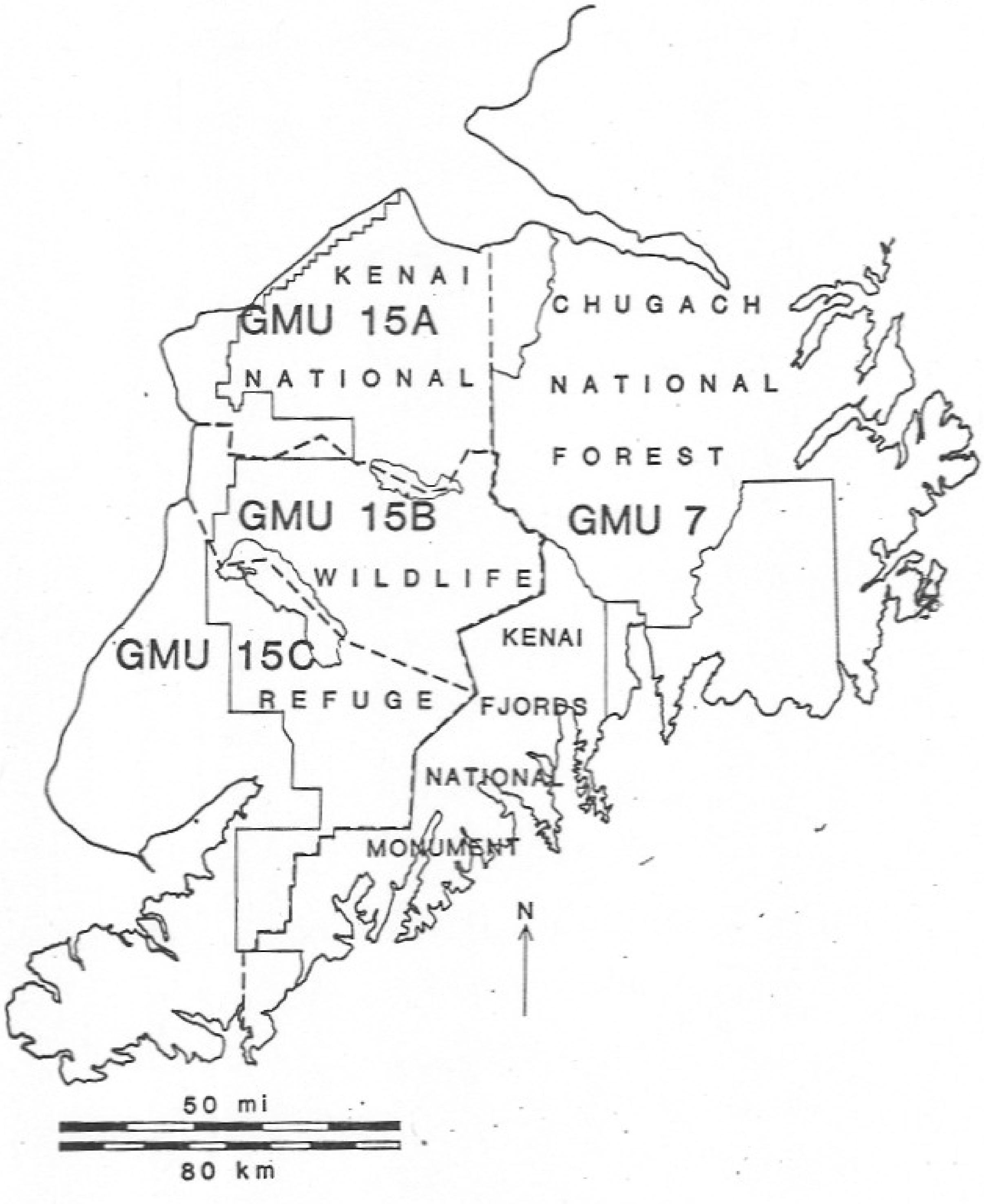
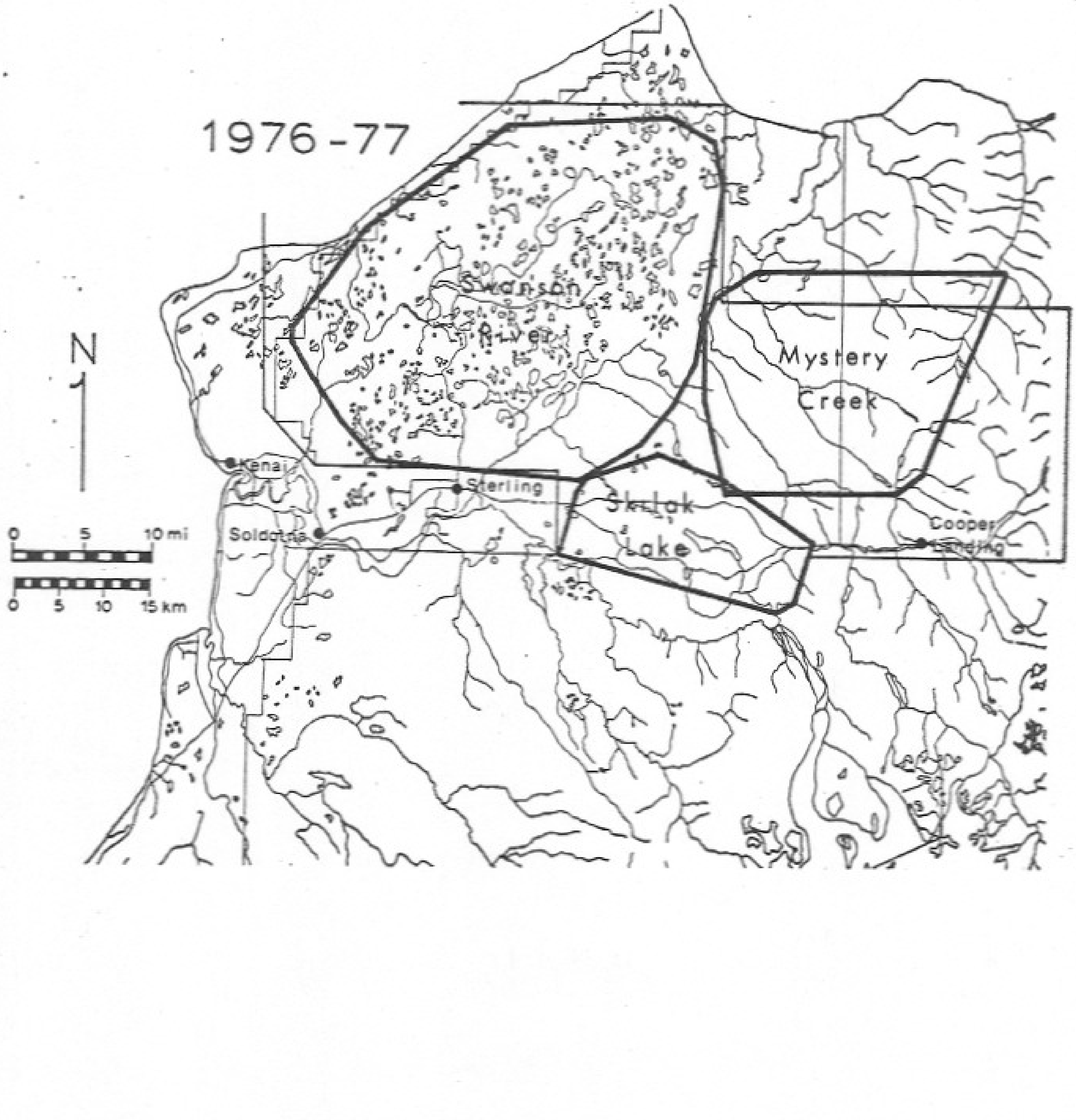

KENAI
GMU 15A
NATIONAL
CHUGACH
NATIONAL
FOREST
GMU 7
GMU 15B
WILDLIFE
GMU 15C
REFUGE
KENAI
FJORDS
NATIONAL
MONUMENT
N
50 mi
80 km

FIG. 2b



1976-77
N
Swanson River
Mystery Creek
Skilak Lake
Kenai
Sterling
Soldotna
Cooper Landing
0 5 10 mi
0 5 10 15 km

FIG. 3

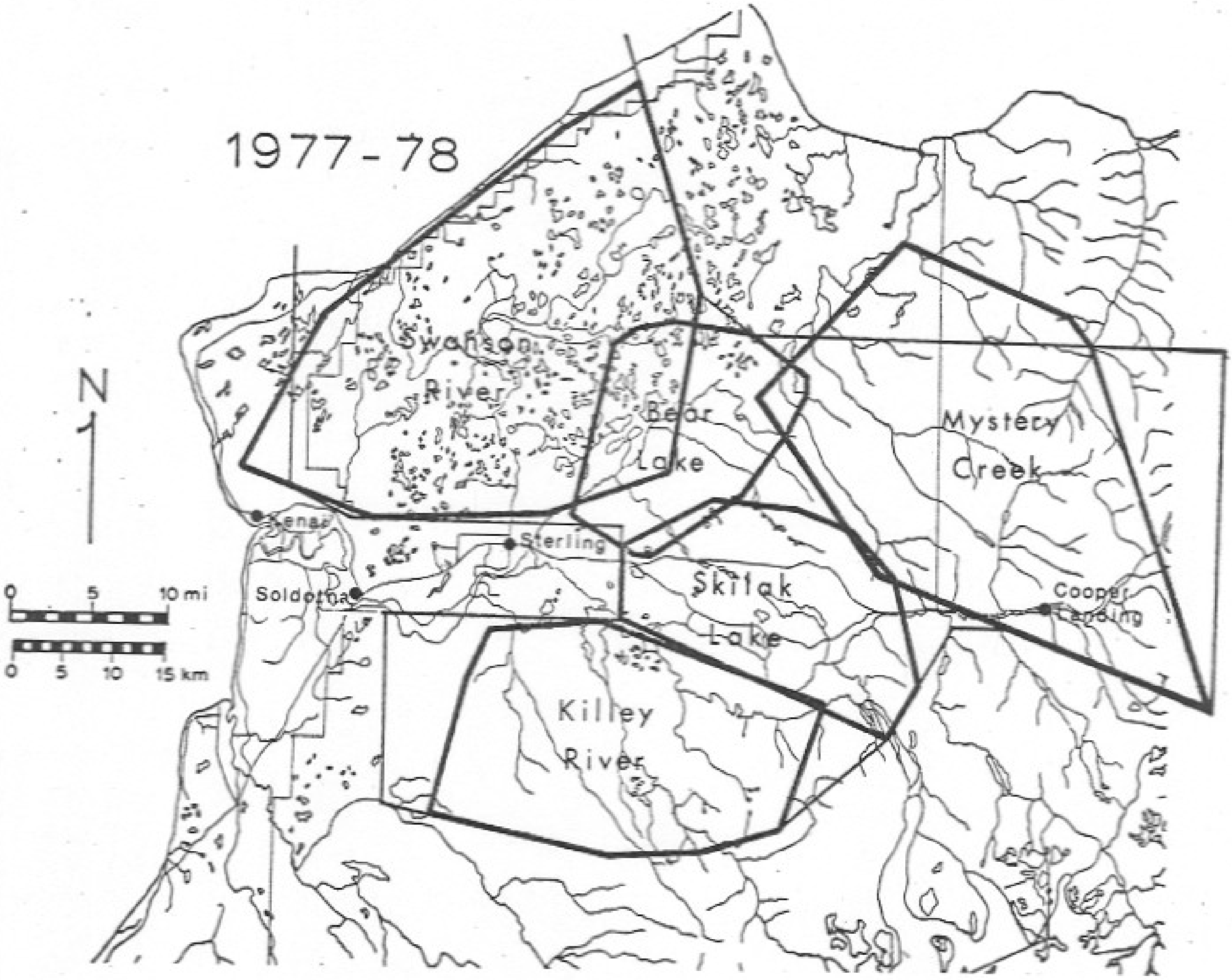

1977-78
N
0 5 10 mi
0 5 10 15 km
Swanson River
Bear Lake
Mystery Creek
Kenai
Sterling
Soldotna
Skilak Lake
Cooper Landing
Killey River

FIG. 8

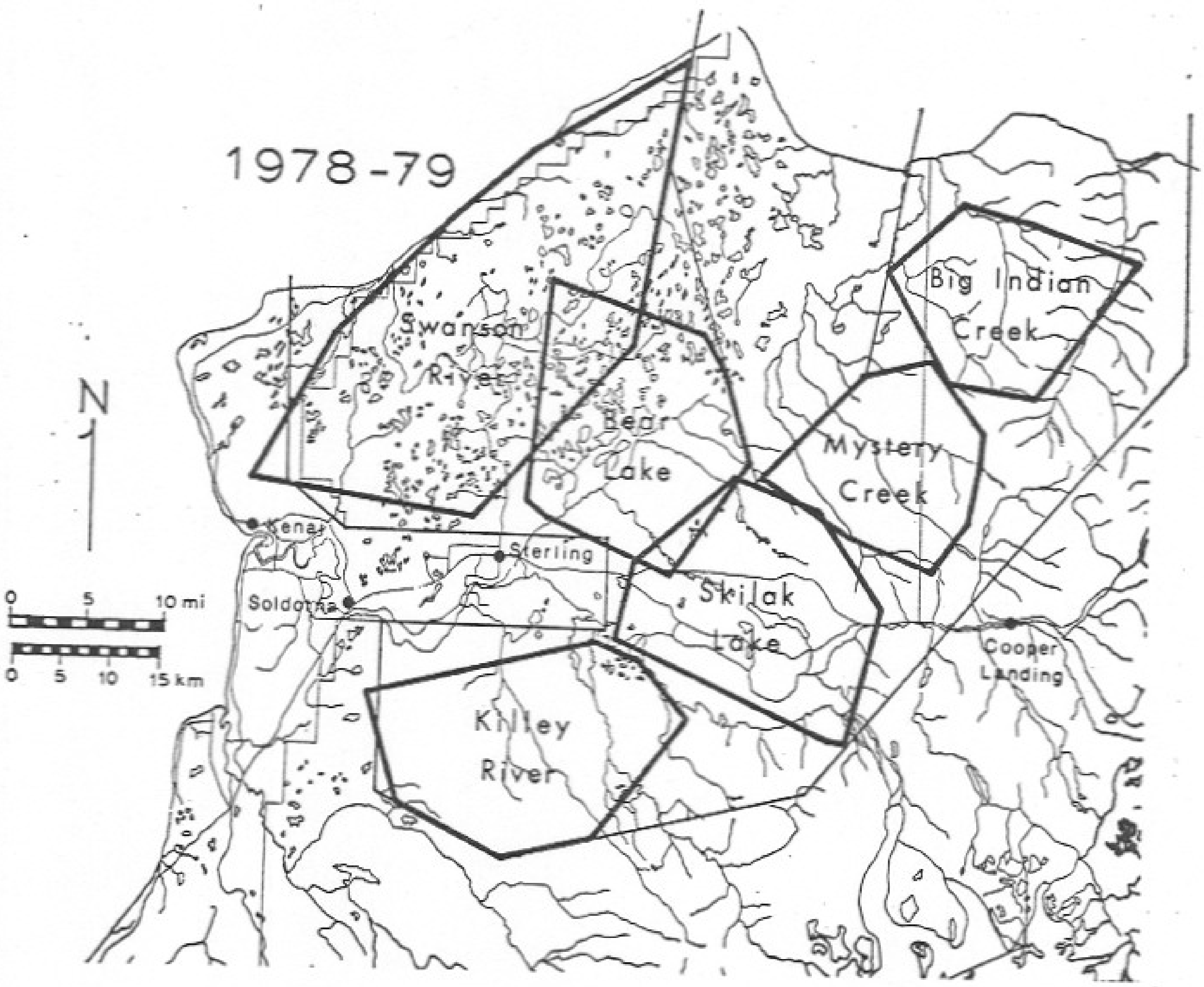

1978-79
Swanson River
Bear Lake
Big Indian Creek
Mystery Creek
Skilak Lake
Killey River
Kenai
Sterling
Soldotna
Cooper Landing
N
0 5 10 mi
0 5 10 15 km

FIG. 3c

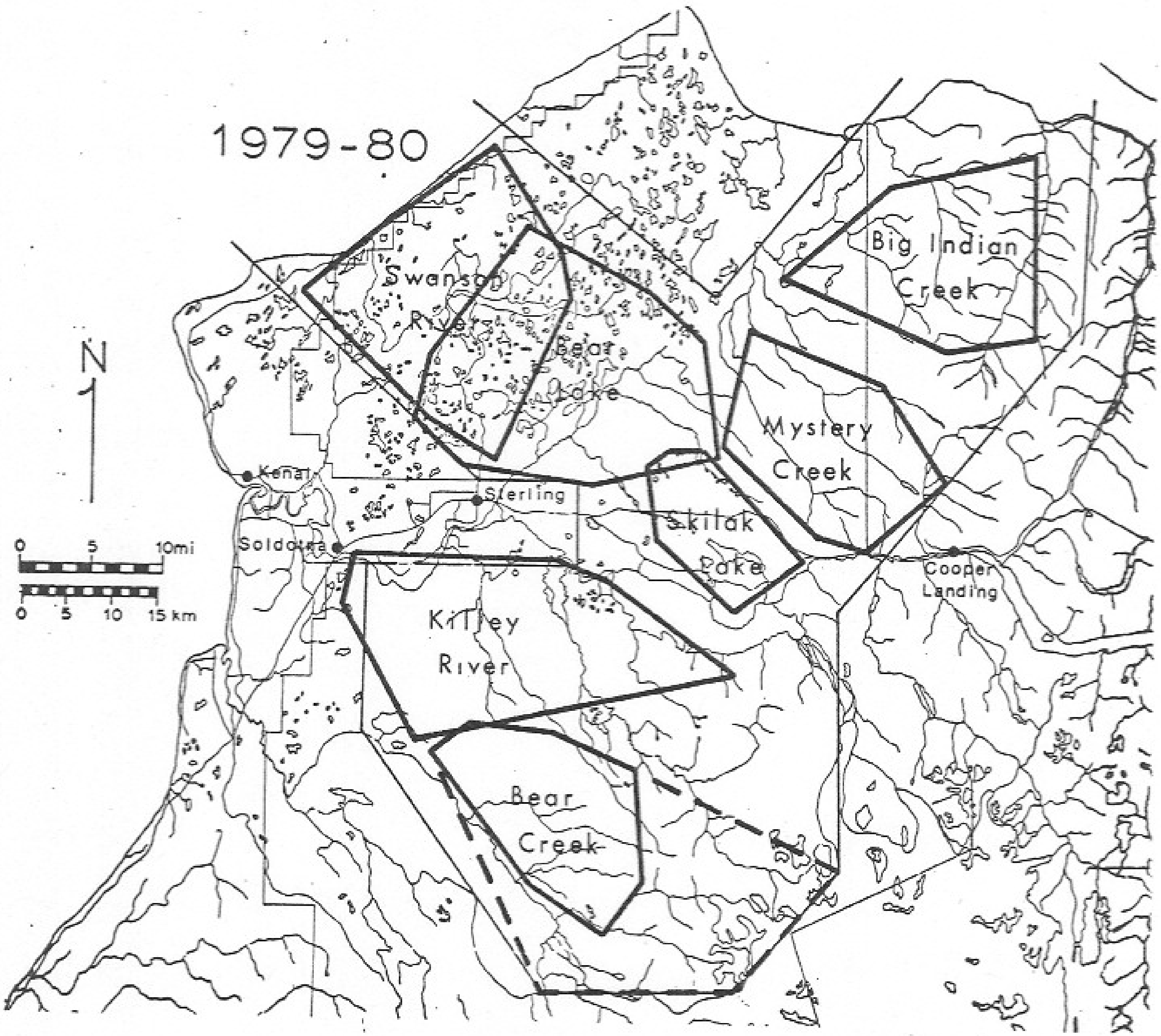

1979-80
N
Swanson River
Bear Lake
Big Indian Creek
Mystery Creek
Kenai
Sterling
Soldotna
Skilak Lake
Cooper Landing
0 5 10mi
0 5 10 15 km
Killey River
Bear Creek

FIG. 3c

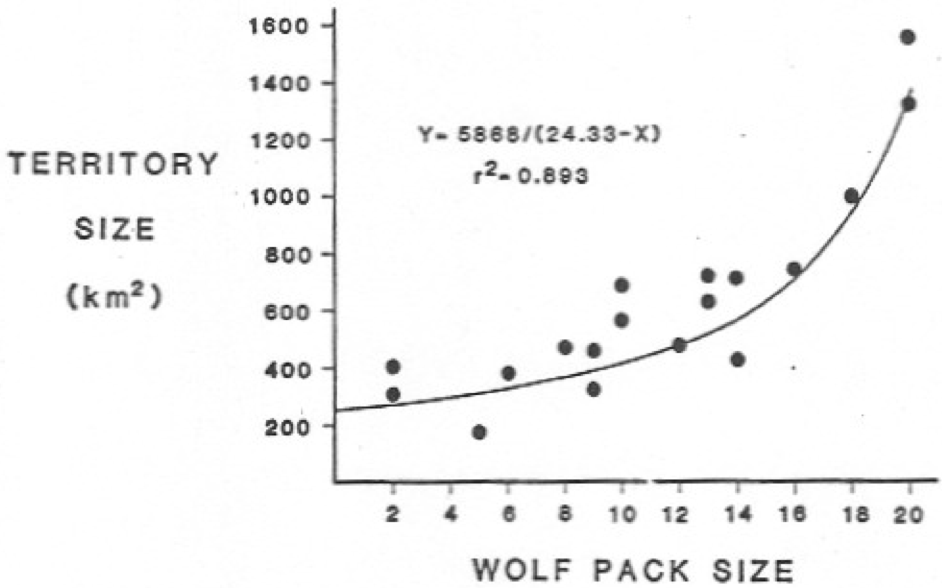

TERRITORY
SIZE
(km²)
1600
1400
1200
1000
800
600
400
200
Y= 5868/(24.33-X)
r²= 0.893
2
4
6
8
10
12
14
16
18
20
WOLF PACK SIZE

FIG. 4

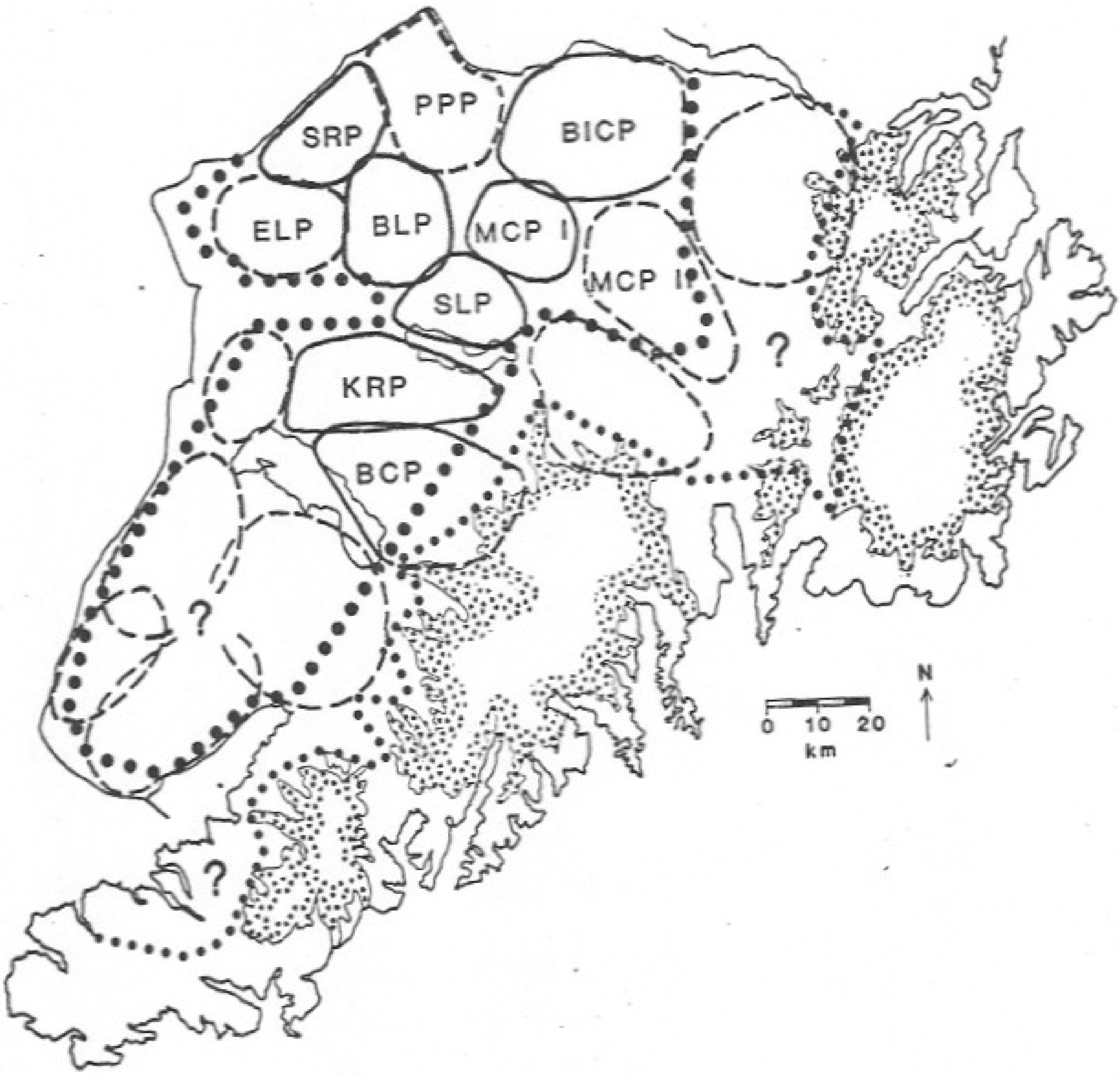


FIG.6

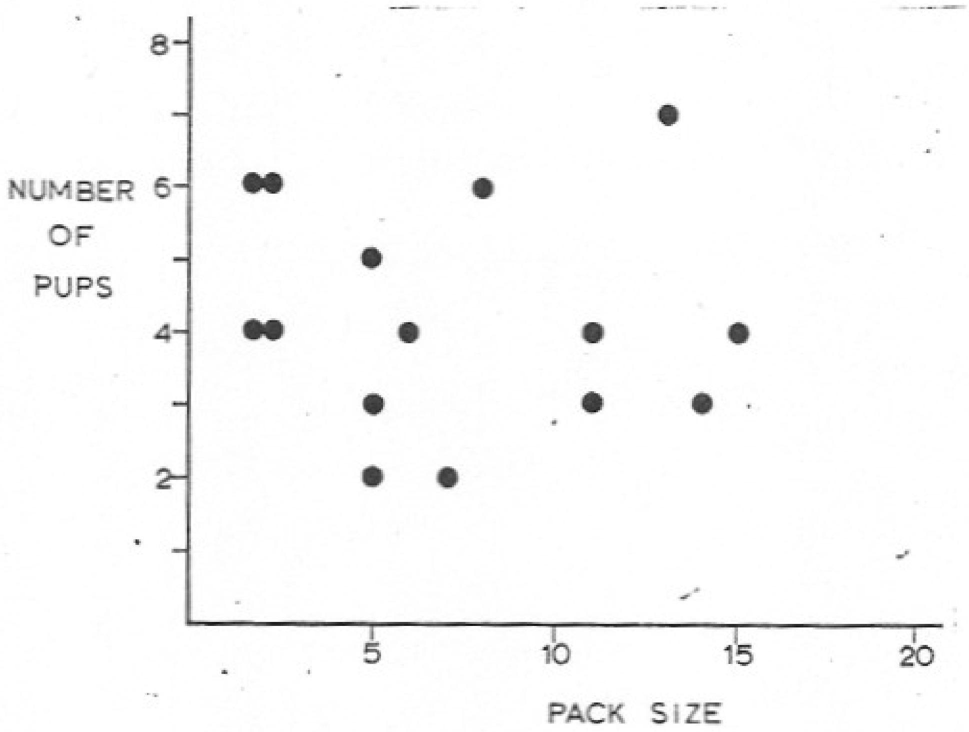


FIG.6

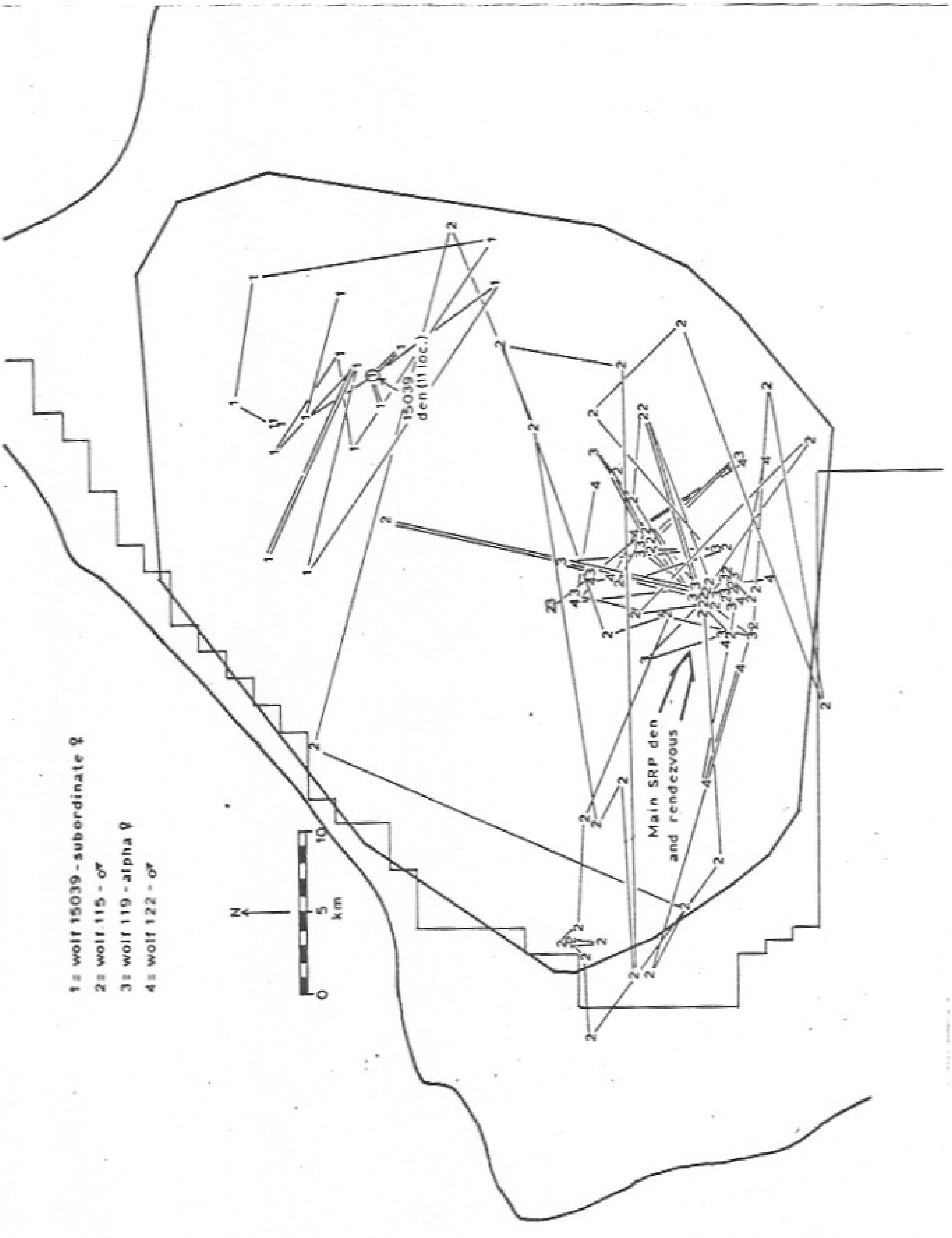

1= wolf 15039 - subordinate ♀
2= wolf 115 - ♂
3= wolf 119 - alpha ♀
4= wolf 122 - ♂
N
0 5 10
km
15039 den (11 loc.)
Main SRP den and rendezvous

FIG.

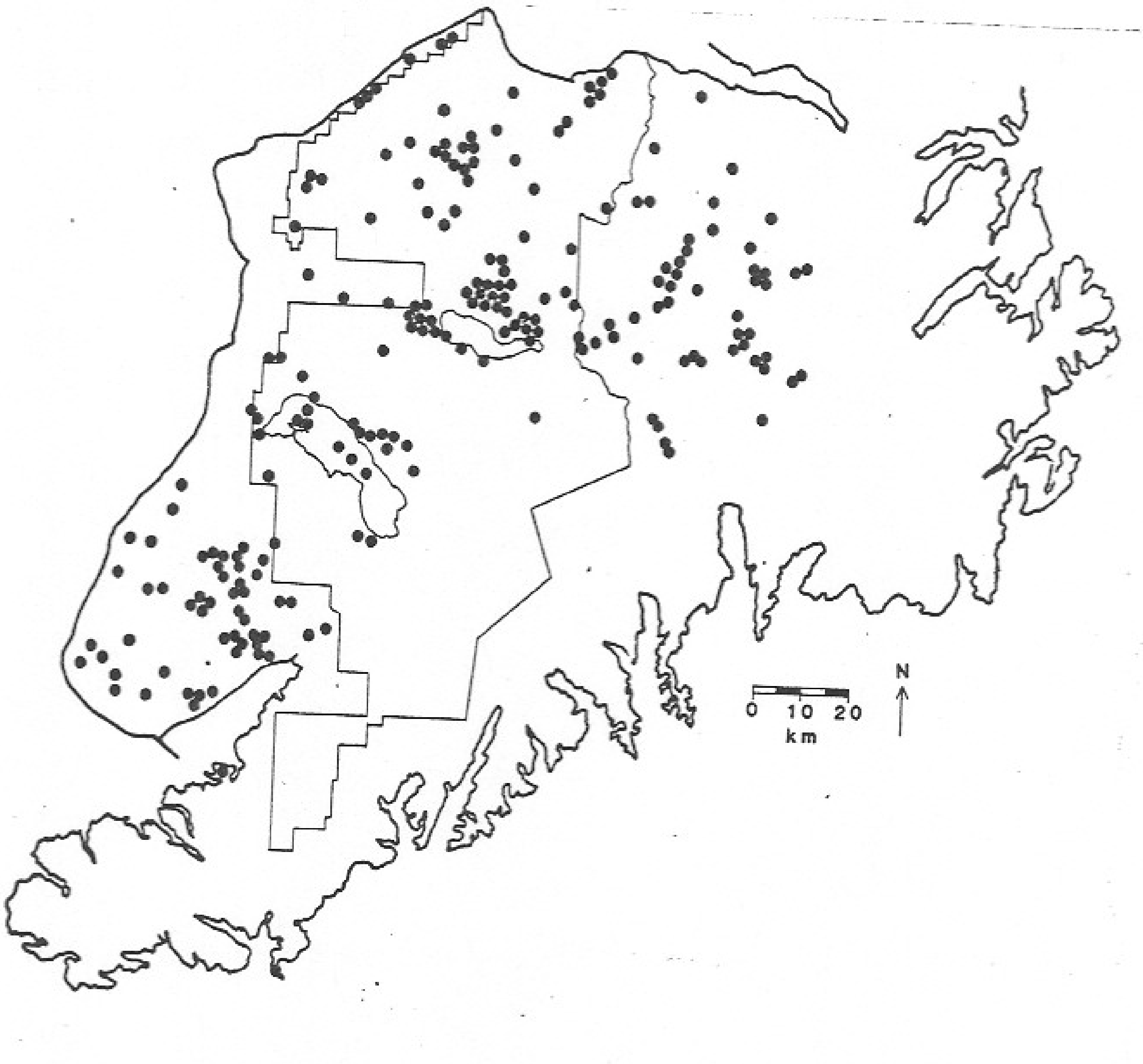


FIG. 1

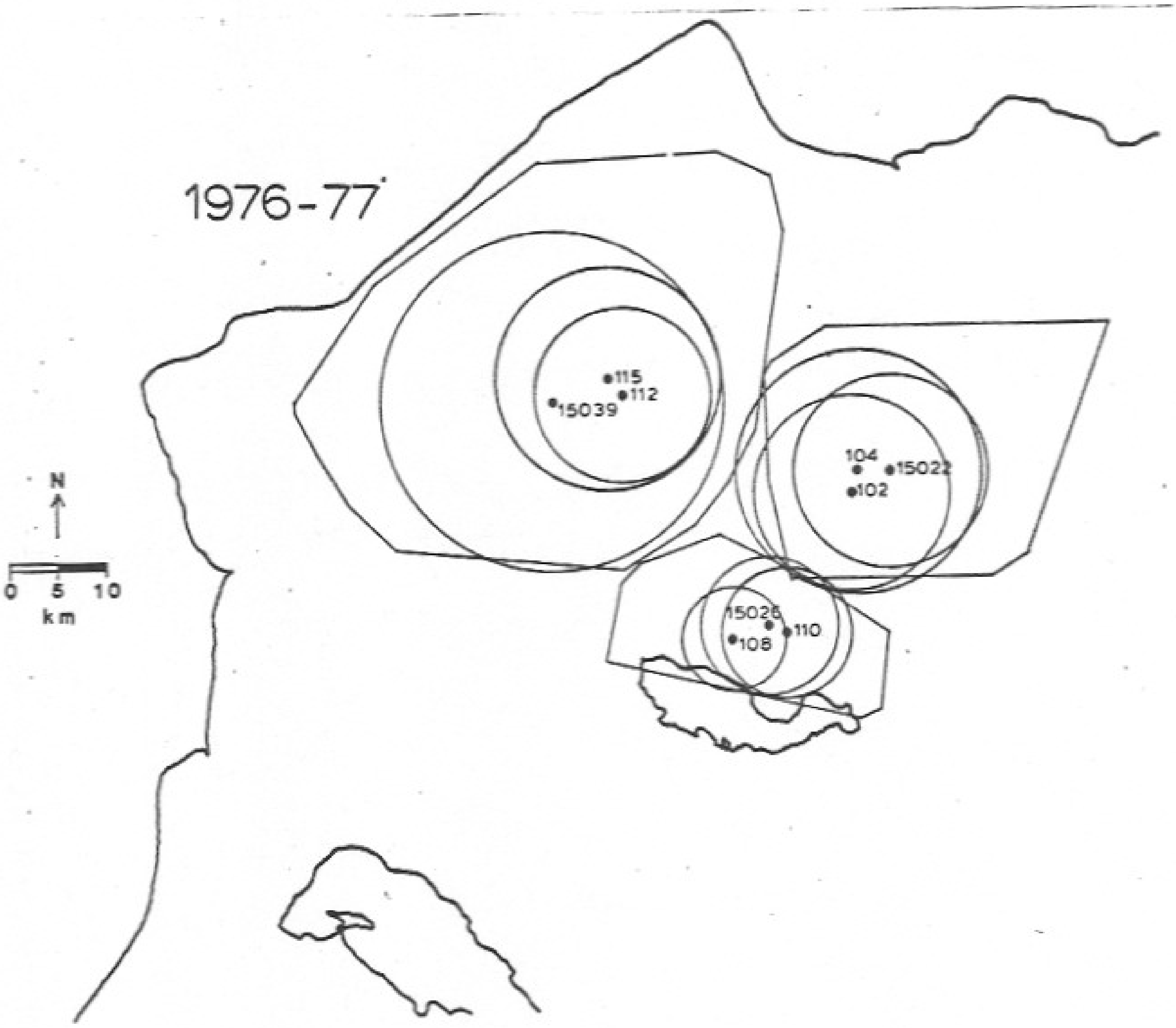


FIG 12

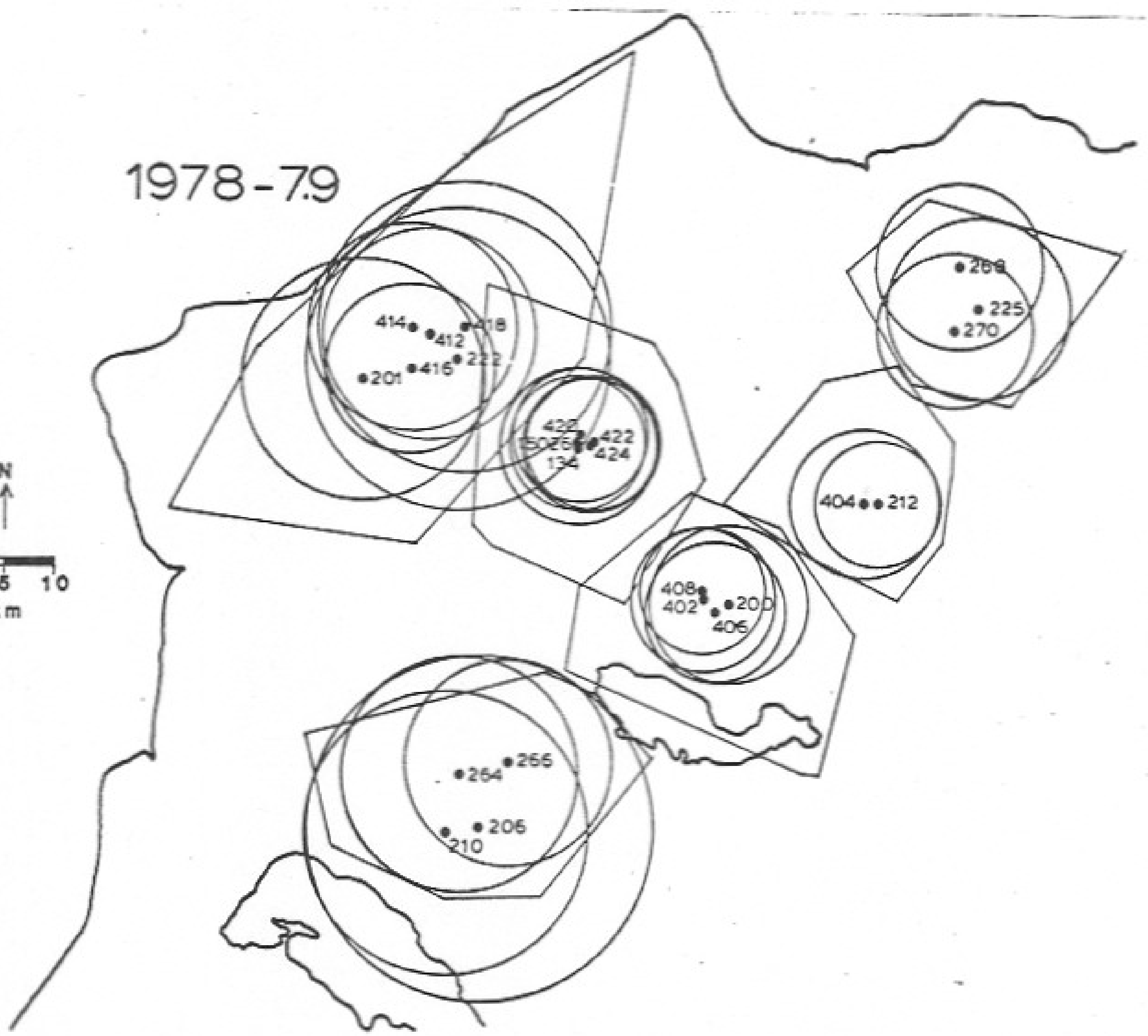

1978-79
N
0 5 10
km
414
412
418
201
416
222
420
422
424
134
268
225
270
404
212
408
402
200
406
264
266
206
210

FIG. 13:

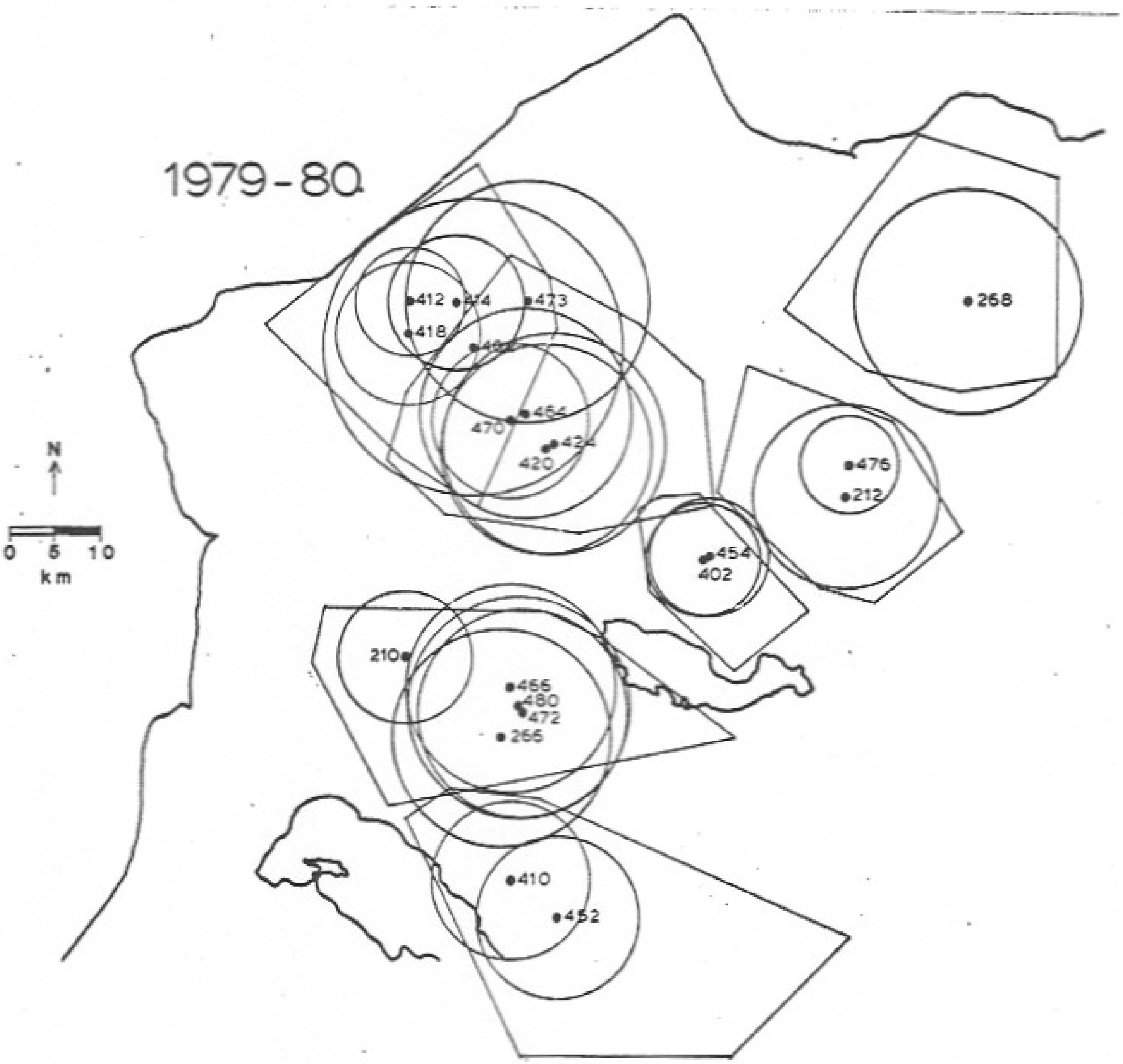

1979-80
412
414
473
418
462
464
470
424
420
268
476
212
454
402
N
0 5 10
km
210
466
480
472
266
410
452

FIG. 12d

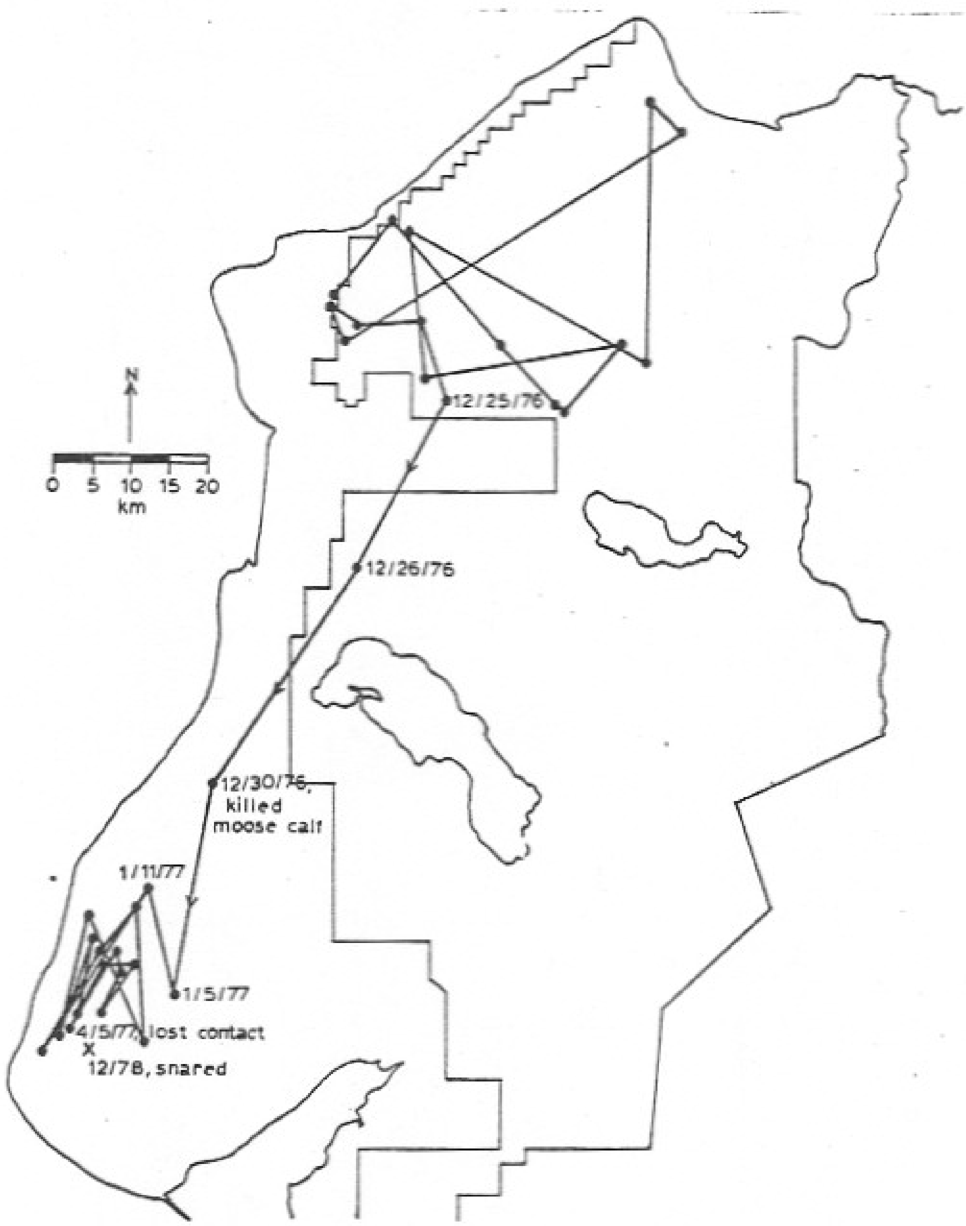

N
0 5 10 15 20
km
12/25/76
12/26/76
12/30/76, killed moose calf
1/11/77
1/5/77
4/5/77, lost contact
X
12/78, snared

FIG. 15

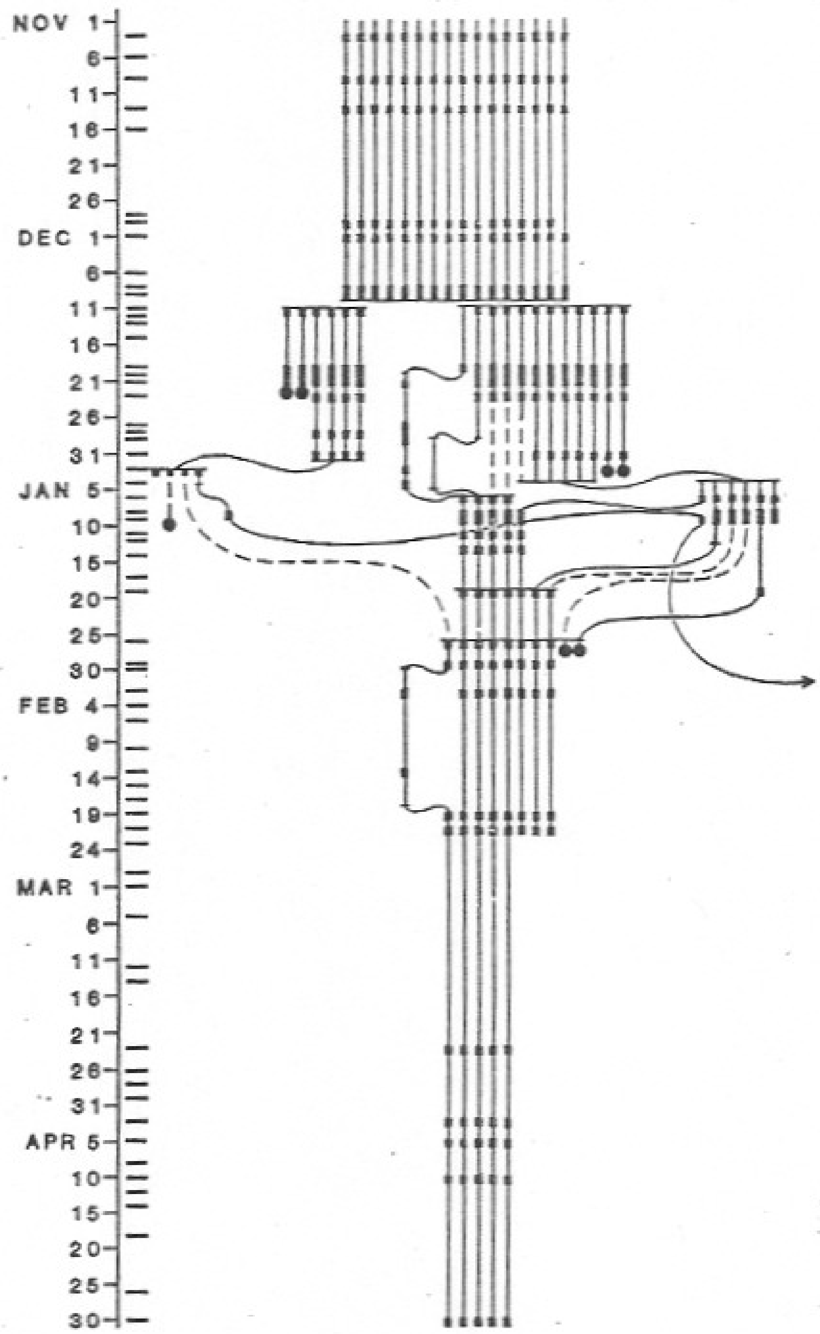

NOV 1
6
11
16
21
26
DEC 1
6
11
16
21
26
31
JAN 5
10
15
20
25
30
FEB 4
9
14
19
24
MAR 1
6
11
16
21
26
31
APR 5
10
15
20
25
30

FIG. 14