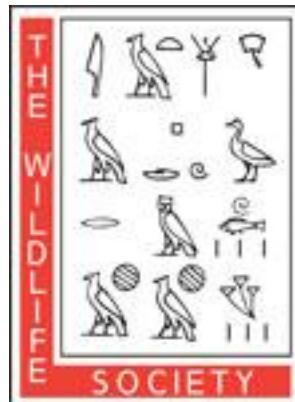


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## Ecology of an Exploited Wolf Population in South-Central Alaska

Author(s): Warren B. Ballard, Jackson S. Whitman and Craig L. Gardner

Source: *Wildlife Monographs*, Jul., 1987, No. 98, Ecology of an Exploited Wolf Population in South-Central Alaska (Jul., 1987), pp. 3-54

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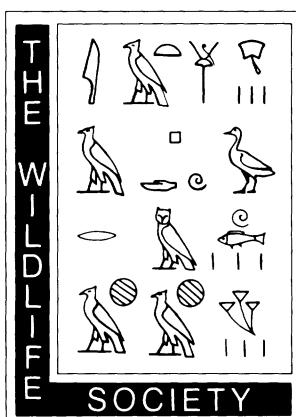
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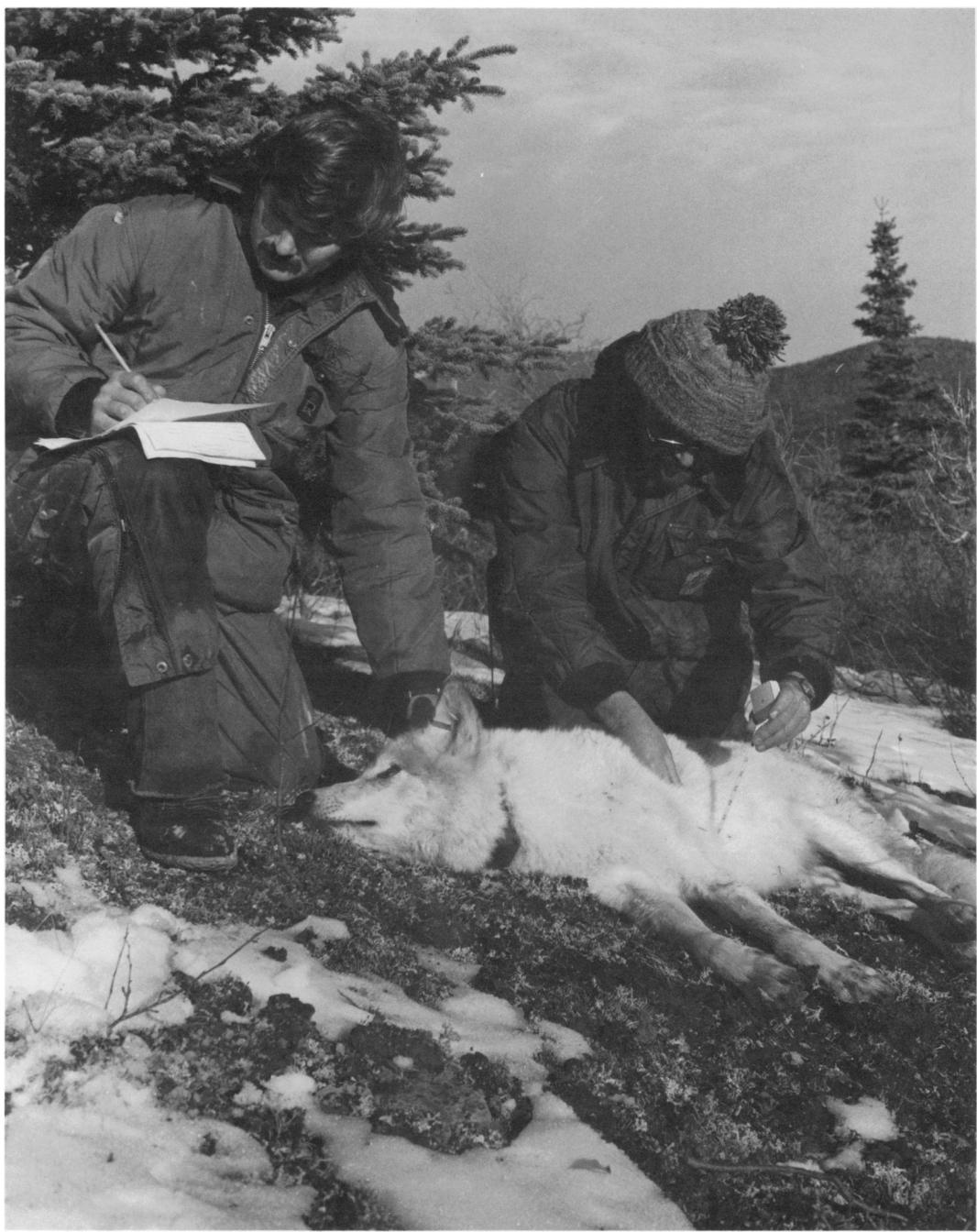
## ECOLOGY OF AN EXPLOITED WOLF POPULATION IN SOUTH-CENTRAL ALASKA

by

WARREN B. BALLARD, JACKSON S. WHITMAN,  
AND CRAIG L. GARDNER

JULY 1987

NO. 98



FRONTISPICE. Ted Spraker (left) and the senior author record physical measurements of an immobilized wolf. (Photo by Russ Dixon)

# ECOLOGY OF AN EXPLOITED WOLF POPULATION IN SOUTH-CENTRAL ALASKA

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**Abstract:** During April 1975 through April 1982, 151 gray wolves (*Canis lupus*) in 30 packs were captured and radio-collared in a 61,600-km<sup>2</sup> area of south-central Alaska. Area traversed by wolf packs was correlated with number of radiolocations, pack size, and density of ungulate prey. Territory sizes of packs located >60 pack days averaged 1,645 km<sup>2</sup>. Pack areas (located <60 pack days) and territories did not normally overlap, but, when overlaps occurred, packs were separated temporally. Wolves did not follow migratory movements of moose (*Alces alces*) or caribou (*Rangifer tarandus granti*) outside of their pack areas but did follow elevational movements of moose within their areas. Twenty-eight percent of 135 wolves dispersed from their original area. Dispersal occurred mainly during April through June and October through November. Seventy-four percent of dispersers were males. Twenty-two percent of all wolves that dispersed were accepted into existing packs. Parturition in south-central Alaska occurred during May. Natal dens usually were abandoned between late June and late July. Earlier abandonment resulted from human disturbance. Average distance between dens of neighboring packs was 45 km.

Wolf densities ranged from 10.3/1,000 km<sup>2</sup> in autumn 1975 to 2.6/1,000 km<sup>2</sup> in spring 1982. Mean annual litter sizes in November varied from 3.7 to 7.3 pups. At least 3 packs (7%) produced 2 litters at separate den sites. Intraspecific strife and other natural factors caused 20% of the annual wolf mortalities; the remaining mortalities resulted from legal and illegal human harvest. Harvest by humans >40% or total mortality >50% of autumn wolf numbers resulted in a population decline. During 1976 through summer 1978, 60 wolves were killed in the 7,262-km<sup>2</sup> Susitna River Study Area to determine the effects of reduced wolf densities on moose survival. Spring wolf densities were reduced from precontrol levels by 42% to 58% annually. Annual rates of increase ( $\lambda$ ) of wolves during years of control ranged from 0.57 to 0.81. When reduction efforts were terminated, wolf densities quickly increased with annual rates of increase ranging from 1.04 to 2.40.

Wolf packs were observed at 439 kills; 70% were moose. Wolves preyed upon moose calves slightly less or in proportion to their occurrence in the moose population during late May through October. Proportionately more calves were killed by wolves during winter, but adult moose were overall the most common prey (38% of the kills). Caribou were the second most common prey. The condition of wolf-killed moose, as reflected by bone marrow fat, was similar to that of moose that died from incidental causes; the latter were assumed to represent the average condition of moose in the population. Adult cow moose killed by wolves were relatively old in relation to cow moose live-captured from the population, but were probably healthy. Wolf predation rates during summer (based on biomass equivalent to 1 adult moose) ranged from 1 kill/7 to 16 days/pack, whereas winter rates ranged from 1 kill/5 to 11 days/pack. Large packs killed ungulates more frequently than smaller packs. Kill rates per wolf, however, were greater for smaller packs. Wolf-killed ungulates usually were heavily utilized by wolves. During winter, 7.1 kg of food were available per wolf per day, and the length of time wolves remained at a kill site depended upon pack size and amount of prey.

Spring wolf densities were negatively correlated with subsequent autumn moose calf : cow ratios, suggesting that reduced wolf densities improved survival rates of calf moose. Calf moose mortality studies indicated that predation by brown bears was the most important calf mortality factor. Estimates of moose recruitment compared with estimates of annual mortality from wolf predation during 1980-81 and 1983-84 within the Susitna River Study Area suggested that wolves were not preventing moose population growth at that time.

**WILDL. MONogr. 98, 1-54**

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## INTRODUCTION

Game Management Unit 13 (GMU 13), which encompasses the Nelchina and upper Copper and upper Susitna River basins, has been one of the most important moose hunting areas in Alaska for 3 decades. During 1963-74, approximately 18% of the reported statewide moose harvest occurred in the area (Ballard and Taylor 1980). The area also has been popular for nonconsumptive uses of wildlife.

Prior to 1953, few data on wildlife populations in GMU 13 were available. The moose population probably increased through the late 1940's and 1950's and peaked about 1960 (Bishop and Rausch 1974). Severe winters in 1961-62, 1965-66, and 1971-72 resulted in high moose mortality (Stephenson and Johnson 1972, 1973; Bishop and Rausch 1974). Moose population indices indicated a general decline in recruitment (calves:100 cows) during intervening years of mild winters, and the population continued to decline.

The winter of 1971-72 apparently had a particularly severe impact on the moose population (Stephenson and Johnson 1972, 1973). Moose harvests were reduced

through bull-only hunting seasons initiated in 1972, and efforts to identify the causes of low recruitment were initiated in 1975. Bishop and Rausch (1974) and McIlroy (1974) reviewed available data and concluded that snow depth, range quality, and hunting may have contributed to the population decline but were probably not the primary causes of low recruitment.

An extensive program of wolf poisoning and aerial hunting, conducted by the federal government during 1948-53, apparently resulted in low wolf densities and a period of moose population growth (Rausch 1967, 1969). In 1953 only 12 wolves were believed to remain in the area (Rausch 1969). Following termination of the program, wolf numbers increased to approximately 125 by 1961 when the moose population reached its peak. Wolf numbers may have increased to a peak of 350-450 by 1965 when the moose population was declining (Rausch 1967, 1969; Bishop and Rausch 1974). These moose and wolf population trends and the high occurrence of calf moose hair in wolf scats (Stephenson and Johnson 1972, 1973) suggested that predation by wolves was a major factor

contributing to the decline of the moose herd.

An understanding of the moose population decline was complicated by the presence of other potential predators, especially brown (*Ursus arctos*) and black bears (*Ursus americanus*), and such alternative prey species as barren-ground caribou, Dall sheep (*Ovis dalli*), beaver (*Castor canadensis*), and snowshoe hare (*Lepus americanus*). Because poison was used to reduce wolf numbers, it was suspected that bear numbers had been reduced inadvertently and they increased upon termination of the program. Caribou numbers declined from about 71,000 in 1962 to approximately 10,000 in 1973 (Pitcher 1982). The contribution of predation to the caribou decline was unknown, and contrasting views as to its importance exist (Bergerud 1980, Van Ballenberghe 1985).

In 1975 a wolf study was initiated to determine food habits and territory size, to examine population dynamics, and to determine the impacts of wolves on moose. This monograph focuses primarily on results of wolf studies conducted during 1975 through April 1982, but also includes pertinent data from concurrent related studies on moose and brown bear during 1975 through 1984.

**Acknowledgments.**—R. O. Stephenson and V. Van Ballenberghe were responsible for the first year of the wolf study. Their findings were presented by Stephenson (1978b), and their data have been included and, where appropriate, credited in this report. Stephenson also made a number of valuable suggestions on earlier drafts of the manuscript and was quite helpful during the early stages of the study. S. D. Miller and A. F. Cunning contributed substantially to the study by assisting with field investigations and data analyses, sharing ideas, and editing many drafts of the manuscript. Other individuals who deserve recognition for their contributions to the study include K. Adler, S. Albert, L. Aumiller, T. Balland, D. Cornelius, J. Dau, S. Eide, J. Foster, A. Franzmann, E. Goodwin, J. Hughes, D. McAllister, L. Metz, R. Rausch, R. Ridgeway, K. Schneider, R.

Somerville, T. Spraker, K. Taylor, R. Tobey, J. Vania, and J. Westlund. Constructive criticism on earlier drafts also was provided by R. Bishop, A. Franzmann, W. Gasaway, P. Hessing, R. Kramer, W. Martin, S. M. Miller, S. Peterson, K. Schneider, R. Tobey, and B. Townsend. S. M. Miller advised on statistical procedures and assisted with many analyses. K. Adler, S. Lawler, and I. Parkhurst typed several drafts of the manuscript. C. Hepler prepared the figures.

We thank pilots A. Lee of Lee's Air Taxi and K. Bunch of Sportsman's Flying Service for the many safe hours of flying they provided. Both donated their time on many occasions to ensure the project's success. V. and C. Lofstedt, Kenai Air Service, piloted helicopters for various tagging operations. Both were always willing to participate in any aspect of the project at any time. W. Gasaway, A. Cunning, and D. Timm were a source of encouragement for completing this project. The manuscript was greatly improved as a result of the constructive criticism provided by S. H. Fritts, D. M. Hebert, L. B. Keith, and R. L. Kirkpatrick.

## STUDY AREA

The study was conducted in GMU 13 (Fig. 1), an area of 61,600 km<sup>2</sup>. Thirty-one percent (18,800 km<sup>2</sup>) of the area lies above 1,220 m elevation, which is considered poor year-round habitat for ungulates and wolves (Ballard and Taylor 1980). Wolves were killed by Alaska Department of Fish and Game (ADF&G) personnel during 1976 through 1978 in an area of 7,262 km<sup>2</sup> within GMU 13, referred to as the Susitna River Study Area (SRSA) (Fig. 1). Wolf, moose, and bear studies were conducted during 1975 through 1984 in the SRSA and in the southern and eastern portions of GMU 13.

The climate of GMU 13 resembles that of interior Alaska, except that temperatures are slightly milder and precipitation slightly greater (Skoog 1968). Temperatures range from an average of 14 C in July to -21 C in December (Bishop and Rausch 1974). Average annual precipita-

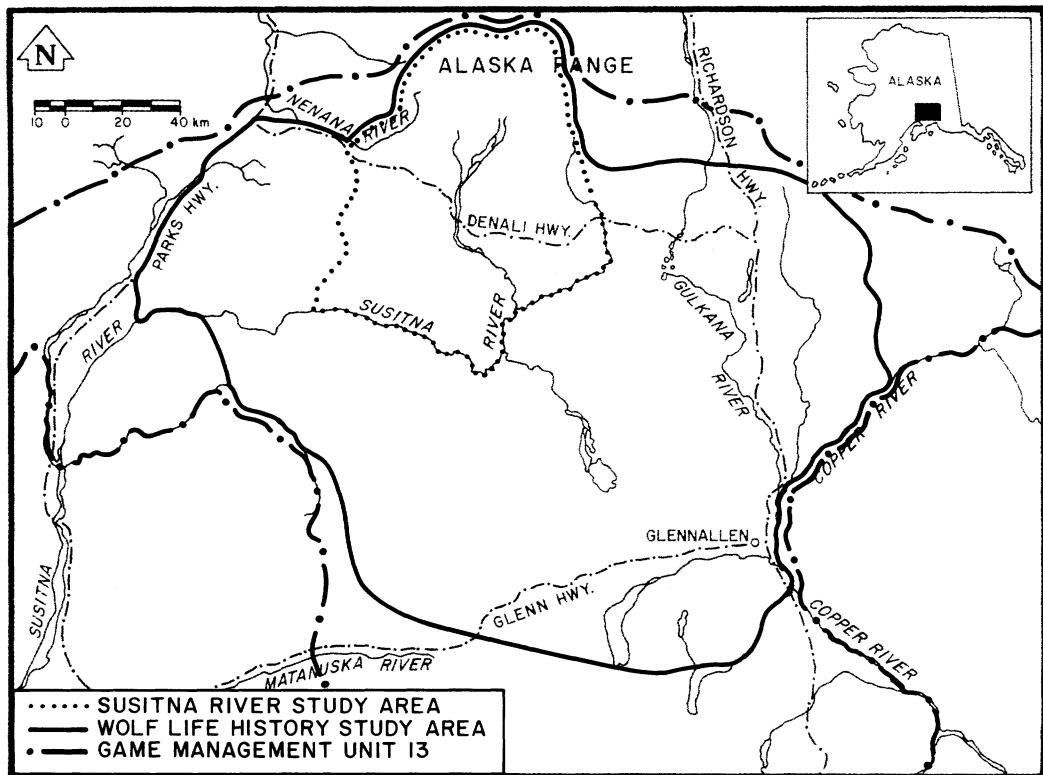


Fig. 1. Boundaries of Game Management Unit 13 and predator-prey study areas in south-central Alaska during 1975 through 1982.

tion is 24 cm. Winter snow depths at Gulkana (eastern edge of study area) range from 76 to 173 cm (Skoog 1968). However, both temperature and precipitation are quite variable within GMU 13.

Physiography and vegetation types within GMU 13 are diverse. Skoog (1968) divided GMU 13 into 15 caribou range units and described the vegetation and climate of each. Generally, the area is surrounded by the Alaska, Chugach, Talkeetna, and Wrangell Mountain Ranges. The ranges form watersheds for the Copper, Susitna, Matanuska, and Nenana River systems. Vegetation varies from alpine tundra and rock/ice areas in the mountains to dense spruce (*Picea* spp.) forests dotted with lakes and ponds in the lowlands. Skoog (1968) reported that 31% of the area was covered with spruce forest; 36% with dwarf arctic and shrub birch (*Betula nana* and *B. glandulosa*), dwarf

heath (comprised of *Cassiope* spp., *Empetrum* spp., *Ledum* spp., *Vaccinium* spp., and *Arctostaphylos* spp.), and sedge (*Carex* spp.) meadows; 15% with 8 other vegetation types consisting primarily of alder (*Alnus crispa*), rough fescue (*Festuca altaica*), and willows (*Salix* spp.); and 18% supported no vegetation. Willows, the most important moose winter forage, occurred in nearly all vegetation types but were most abundant in riparian areas. Since about 1930, an estimated 38% of the spruce forest has been burned (Skoog 1968). No major fires have occurred in GMU 13 within the last 30–40 years. Although much of GMU 13 is roadless and sparsely populated, it is traversed by 4 major road systems: the Richardson, Glenn, Parks, and Denali Highways. Much of GMU 13 is accessible by all-terrain vehicle, snowmobile, or light fixed-wing aircraft. Numerous trails exist as a result of oil exploration.

## METHODS

### Wolf Studies

Wolves were captured for **radio collaring** by darting from a helicopter, using drugs and methods described by Ballard et al. (1982a). Three additional live wolves were purchased from trappers.

During 1975 through 1977, wolves and adult moose were equipped with adjustable machine-belt radio collars manufactured by AVM Instrument Company (Champaign, Ill.). During 1978 through 1982, adjustable radio collars constructed of fiberglass and urethane manufactured by Telonics, Inc. (Mesa, Ariz.) were used. Radio-collared individuals were located and, when possible, visually observed from fixed-wing aircraft using the methods described by Mech (1974). Monitoring intensity varied from pack to pack, but locations were usually obtained at least twice each month during winter. Initially, a portable receiver (LA-12) manufactured by AVM Instrument Company was used to track instrumented wolves. Later, a programmable scanning receiver manufactured by Telonics, Inc. was used.

Ages of captured and released wolves were determined from tooth eruption and wear. Ages of wolves observed but not handled were estimated from relative size and other criteria described by Jordan et al. (cited by Mech 1970). Age and sex compositions of some packs were not ascertained until the animals had been killed by hunters or trappers. Hunters and trappers were encouraged to provide carcasses of wolves taken in GMU 13 by an offer of \$10/carcass. Ages of harvested wolves were determined by combinations of tooth eruption and wear, cementum age (Goodwin and Ballard 1985), and epiphyseal closure on the radius and ulna (Rausch 1967). In all cases wolves were classed as pups (<1 year old), yearlings (between 1 and 2 years old) and adults ( $\geq 2$  years old). Ovaries and uteri of females were examined for evidence of reproductive activity (Rausch 1967). Annual survival rates of radio-collared wolves were calculated as described by Trent and Rongstad (1974).

Areas occupied by individual wolf packs were computed for 4 time periods that coincided with changes in area boundaries, numbers of wolves, establishment and study of new packs, and differences in study objectives. The periods were (1) April 1975 through June 1976, a period that included the loss of several packs killed as part of an experimental wolf reduction program, (2) July 1976 through June 1978, while wolf reduction efforts continued, (3) July 1978 through June 1980, when substantial shifts in pack areas and boundaries occurred following termination of wolf reduction efforts, and (4) July 1980 through April 1982, a period following high rates of harvest by the public. Area traversed by individual wolf packs (called territories only if pack located  $> 60$  pack days) was determined by plotting all radiolocations for individual packs and connecting the outermost observations (minimum convex polygon) excluding extraterritorial forays and obvious dispersals (Mohr 1947). The average of at least 3 independent measurements with a polar planimeter was used to compute the size of each area. Total area included the outermost locations in all study years and provided the largest estimates of pack area. High use areas were identified by examining annual plots of all pack relocations.

Spring and autumn wolf densities in GMU 13 were estimated by extrapolating known numbers of wolves within radio-marked packs to other portions of GMU 13 with similar habitat where observations were more limited. Active wolf dens, located through observations of radio-marked wolves or during associated flying, were inspected on the ground after the wolves vacated (Ballard and Dau 1983). The vicinity of each den was searched, scats collected, and food remains identified. Scats were individually autoclaved and analyzed using previously described techniques (Stephenson and Johnson 1972). Hair-scale impressions (Adorjan and Kolenosky 1969) were used to confirm identifications of uncertain prey remains by comparisons with known samples imprinted on a slide containing clear fingernail polish.

During wolf radio-tracking flights, prey carcasses associated with wolves were assumed to have been killed by wolves. If other predators such as bears were observed with the wolves and the species that made the kill could not be determined, or the carcass exhibited characteristics typical of other causes of death (Stephenson and Johnson 1973, Ballard et al. 1979, and Ballard and Gardner 1980), wolf predation was not assumed to be the cause of death. Cause of death was classified as winter-kill (starvation) when there was no evidence of predation or accidental death. These moose were usually lying on their sternums with numerous pellet groups nearby, suggesting that such animals had been there several days prior to death. Sex of adult moose and caribou killed by wolves or other predators often was judged from fixed-wing aircraft by presence and shape of antlers. Wolf-killed prey were classified as calves, yearlings, or adults using combinations of body size, pelage, antler morphology, and presence of vulval patch (Peterson 1955, Skoog 1968). Calves and yearlings were aged to the nearest month, assuming a 1 June birthdate (Ballard and Taylor 1980; Ballard et al. 1981a,b).

Ungulate carcasses were examined on the ground when possible, and cause of death was determined according to methods described by Stephenson and Johnson (1973) and Ballard et al. (1979). Mandibles and femurs or other long bones were collected from each carcass for marrow fat determination, which was used as an index of physical condition. When only mandibles were available, long bone fat was estimated based on equations provided by Ballard et al. (1981a). Bone marrow fat content was assessed by the dry-weight method (Neiland 1970). Ages of moose killed were estimated from tooth eruption and cementum annuli using methods described by Sergeant and Pimlott (1959). Caribou were aged by tooth eruption and wear (Skoog 1968).

During winters 1978–79, 1979–80, and 1980–81 and summers 1977, 1978, and 1981, an attempt was made to locate and examine all kills made by selected radio-

collared wolf packs during a 2–3-month period. In winter, these packs were radio-tracked from fixed-wing aircraft at least every other day and were backtracked to their previous locations. Packs were monitored twice daily in summers 1977 and 1978, usually between 0600–1100 and 1600–2200 hours. In summer 1981, monitoring frequency was once per day. In an effort to maintain several packs at stable numbers for predation rate studies, portions of GMU 13 were periodically closed to hunting and trapping of wolves (Eide 1979, Tobey 1980).

An attempt was made to kill all wolves inhabiting the SRSA during 1976 through 1978 by shooting from either helicopter or fixed-wing aircraft. Our objective was to determine the effect of wolf removal on moose survival. Carcasses of wolves removed from the experimental area were necropsied, aged, and assessed for nutritional condition and reproductive status (Nielsen 1977). Repopulation of the removal area was documented by radio marking and monitoring activities of colonizing wolves, and by periodic wolf censuses (Stephenson 1978a). The latter censuses were conducted from fixed-wing aircraft after fresh snowfall by following wolf tracks until wolves were sighted or until tracks separated to allow numbers to be determined.

### Moose Studies

During 1976 through 1984, radiotelemetry was used to study moose movements and population dynamics in several parts of GMU 13. Moose were captured and processed according to methods described by Gasaway et al. (1978). Ages were estimated from tooth eruption and wear and by examination of cementum annuli (Sergeant and Pimlott 1959). Moose home ranges and survival rates were determined using methods described earlier for wolves.

Sex and age composition were surveyed each autumn beginning in the early 1950's (Bishop and Rausch 1974) within specific areas (Fig. 2). These low-intensity surveys were the basis for minimum estimates of

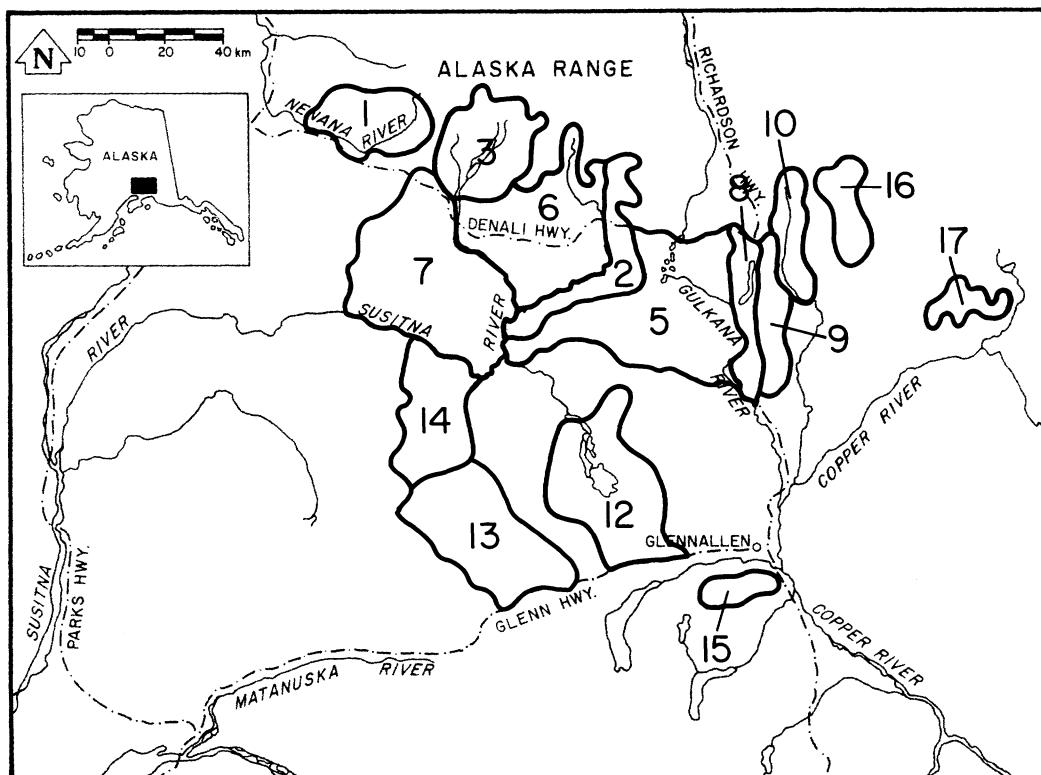


Fig. 2. Boundaries of fall moose sex-age composition count areas within Game Management Unit 13.

moose density in count areas. In autumn 1980 and 1983, moose numbers were estimated for portions of GMU 13 using quadrat-sampling techniques described by Gasaway et al. (1981).

### Statistical Tests

Statistical differences in means and ratio data were tested with *t* tests and chi-square analyses, respectively (Snedecor and Cochran 1973). Differences among mean ages of adult moose and marrow fat values (arcsin transformation) of calves and adults that died from various causes were analyzed using analysis of variance and Student-Newman-Keuls procedures (Sokal and Rohlf 1969). The *G* test of heterogeneity was used to compare adult age structures of moose killed by wolves. Analysis of covariance was used to test differences in wolf predation rates based on intervals

between flights. Unless stated otherwise,  $P < 0.05$  was required for statistical significance.

### CAPTURE AND TELEMETRY RESULTS

One hundred fifty-one wolves were captured and radio-collared in GMU 13 during April 1975 through April 1982 (Appendix 1). One hundred twenty-two wolves were captured once, 18 were captured twice, 10 were captured 3 times, and 1 was captured 4 times. Four wolves died during capture or handling: 1 drowned, 1 was fatally injured by the dart, and 2 died from drugs (Tobey and Ballard 1985).

Sex and age composition of the captured wolves was 45 adult males, 29 adult females, 10 yearling males, 8 yearling females, 28 male pups, and 30 female pups. One wolf was not sexed or aged. The adult

Table 1. Sizes of areas traversed by wolf packs studied in Game Management Unit 13 of south-central Alaska during April 1975 through April 1982.<sup>a</sup>

Pack name	1975-76 <sup>b</sup>		1976-78		1978-80		1980-82		Total km <sup>2</sup>	
	Km <sup>2</sup>	Pack days monitored (N)	Km <sup>2</sup>	Pack days monitored (N)	Km <sup>2</sup>	Pack days monitored (N)	Km <sup>2</sup>	Pack days monitored (N)	≤60 pack days <sup>c</sup>	>60 pack days <sup>c</sup>
Brushkana Creek	1,212	34							1,212	
B-S Lake							60	14	60	
Butte Lake	3,077	31							3,077	
Deadman Lake	280	38							280	
Deep Lake	1,816	47	1,419	72	1,015	26				2,145
Delta River	746	17							746	
Eureka							1,000	10	1,000	
Ewan Lake	2,238	121								2,238
Fish Lake							1,101	29	1,101	
Hogan Hill	1,469	115	894	48	469	13				1,546
Jay Creek			746	38			303	12	912	
Keg Creek	1,119	137	1,072	87	275	16				1,311
Lower Maclarens River							117	13	117	
Maclarens River	723	52							723	
Mendeltna Creek			1,448	128						1,448
Middle Fork			1,331	25						1,331
Portage Creek							751	12	751	
St. Anne Lake			1,028	41	948	35	948	28		1,329
Sinona Creek #1	1,119	95	780	48						1,222
Sinona Creek #2			609	16	381	11			694	
Snodgrass Lake							816	12	816	
Susitna Lake					1,197	129	1,453	95		1,453
Susitna-Sinona					736	28	1,208	10	1,236	
Talkeetna River							117	5	117	
Tolsona Ridge					2,216	85	2,541	83		2,541
Tyone River			655	35	782	115				943
Watana Creek							1,917	134		1,917
Total packs <sup>d</sup>	9	10		9			13		15	11
$\bar{x}$ territory size	1,191	998		891			948		740	1,645
SE	198	99		194			203		109	149

<sup>a</sup> Packs monitored >60 pack days were considered to have their territory sizes fully defined.

<sup>b</sup> Data from Stephenson (1978b).

<sup>c</sup> Pack day defined as 1 day when 1 or more pack members were located  $\geq 1$  occasions.

<sup>d</sup> Excludes Butte Lake Pack comprised of 3 males.

sex ratio differed ( $P = 0.06$ ) from 50:50, perhaps due to capture bias. In an effort to select a pack member that would not disperse, a deliberate effort was made to capture a large male first. There were no differences in sex ratios of captured wolves among years.

During April 1975 through April 1982, 151 radio-collared members of 30 individual packs (a pack is defined as  $\geq 2$  wolves) were individually located from fixed-wing aircraft on a combined total of 4,810 occasions (Appendix 2). These flights resulted in 8,970 wolf sightings (collared + uncollared) and a total of 2,274 pack days (a pack day is defined as 1 day on which  $\geq 1$

pack members were located on  $\geq 1$  occasions). Radio contact with individual packs averaged 531 days (range 76–1,830) (Fig. 3). The average number of locations per pack was 78 (range 5–240). Average interval between flights was 6.8 days (range 2.9–18.1).

## BEHAVIOR

### Pack Areas

Areas traversed by wolf packs varied greatly in size, ranging from 60 km<sup>2</sup> for a pair of wolves to 3,077 km<sup>2</sup> for a pack of 3 nondenning males (Table 1). Total min-

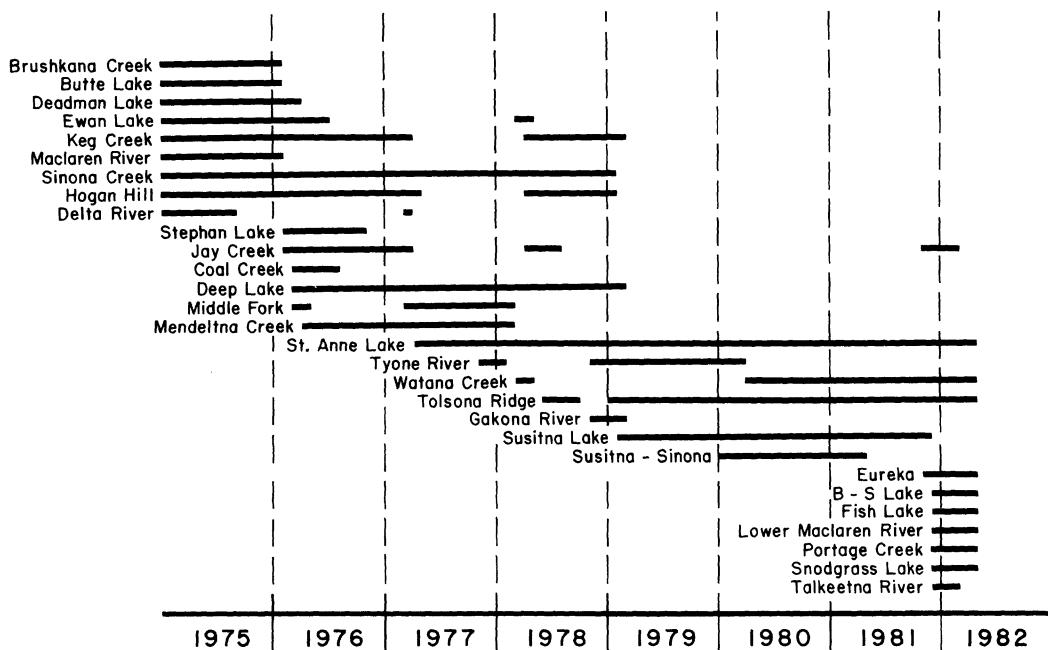


Fig. 3. History of radio contact with individual wolf packs studied in Game Management Unit 13 during April 1975 through April 1982. Solid line indicates period radio contact was maintained. Individual wolf histories are given in Appendix 1.

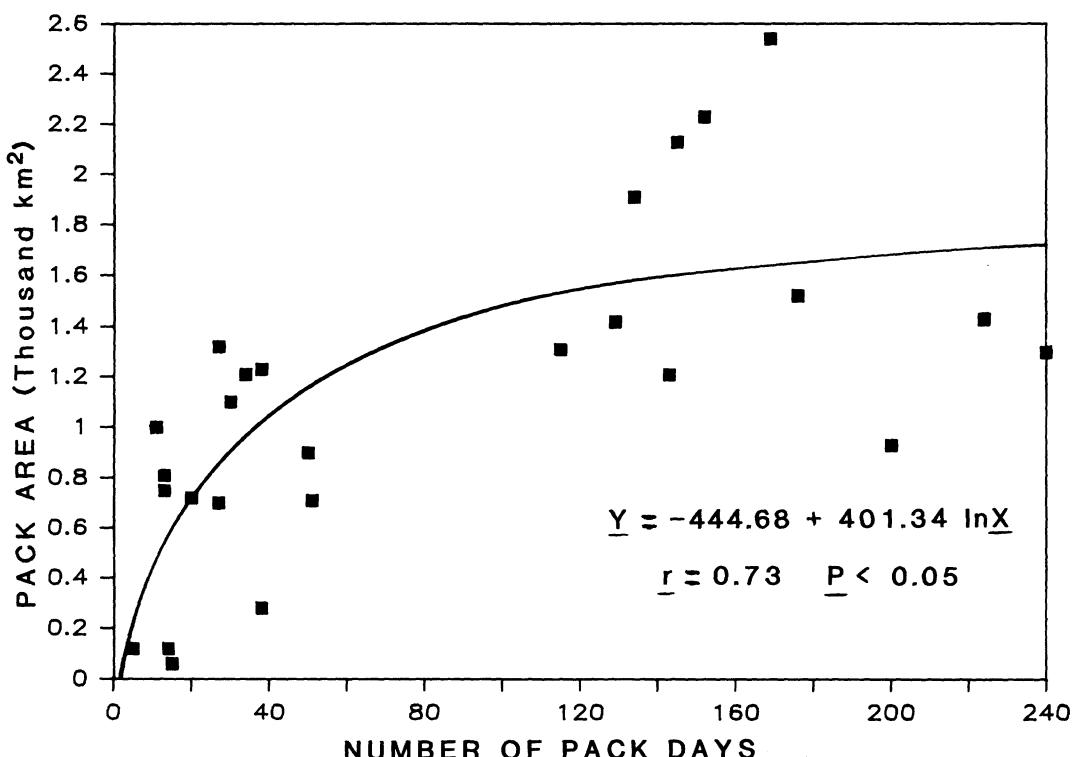


Fig. 4. Relationship between numbers of days radio-marked wolf packs were located and sizes of areas traversed during 1975 through spring 1982 in Game Management Unit 13 of south-central Alaska.

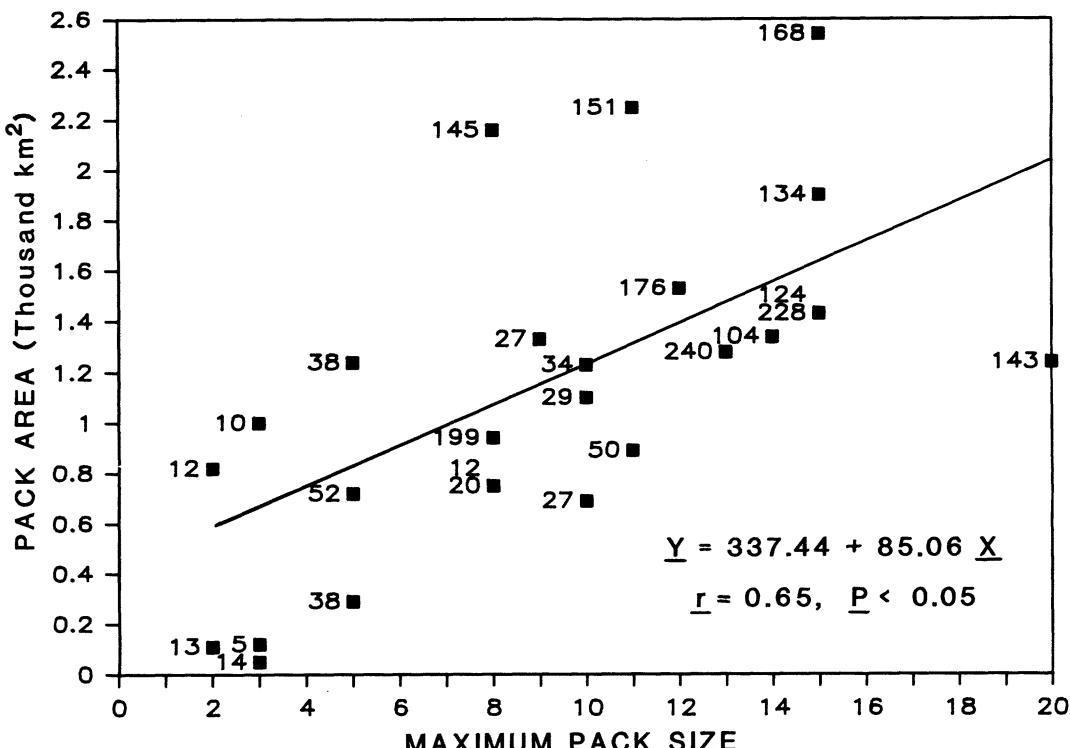


Fig. 5. Relationship between maximum autumn pack sizes and sizes of areas traversed by radio-marked wolf packs during 1975 through 1982 in Game Management Unit 13 of south-central Alaska. Number of days each pack was monitored is in parentheses.

imum area (Mohr 1947) traversed by individual wolf packs was correlated ( $P < 0.05$ ) with both number of days packs were monitored (Fig. 4) and autumn pack size (Fig. 5). Areas were stratified into 2 groups based on number of days monitored. Size of areas for packs located  $>60$  pack days were not correlated ( $P > 0.05$ ) with either number of days monitored ( $r = 0.26$ ) or autumn pack size ( $r = 0.10$ ), suggesting that the size of these areas was fully defined. These latter areas are referred to as territories. Eleven territories were considered defined, ranging in size from 943 to  $2,541 \text{ km}^2$  ( $\bar{x} = 1,645 \text{ km}^2$ ). These territories were larger ( $P < 0.05$ ) than 15 pack areas ( $\bar{x} = 740 \text{ km}^2$ ) traversed by packs located  $<60$  days (Table 1). The size of these latter pack areas was correlated ( $P < 0.05$ ) with number of days monitored ( $r = 0.50$ ) and autumn pack size ( $r = 0.57$ ). Thirty-three percent of the packs located

$<60$  pack days were relatively small ( $\leq 3$  wolves) or, if large ( $\geq 4$  wolves), were not located throughout an entire year (70%). Similar relationships among number of locations, pack size, and size of occupied areas have been reported in Minnesota (Fritts and Mech 1981) and on the Kenai Peninsula, Alaska (Peterson et al. 1984), where territory sizes were much smaller. Territory sizes (located  $\geq 60$  pack days) reported in this study were relatively large compared with those reported elsewhere in North America. Wolf territory sizes in GMU 13 corresponded with those estimated by Harestad and Bunnell (1979) based on body weight and trophic level.

Territory size was also influenced by prey availability. Deep Lake, Ewan Lake, and Tolsona Ridge Packs had the largest territories of the denning packs, averaging  $2,308 \text{ km}^2$  ( $SE = 120$ ). These packs were responsible for 51% of the caribou kills

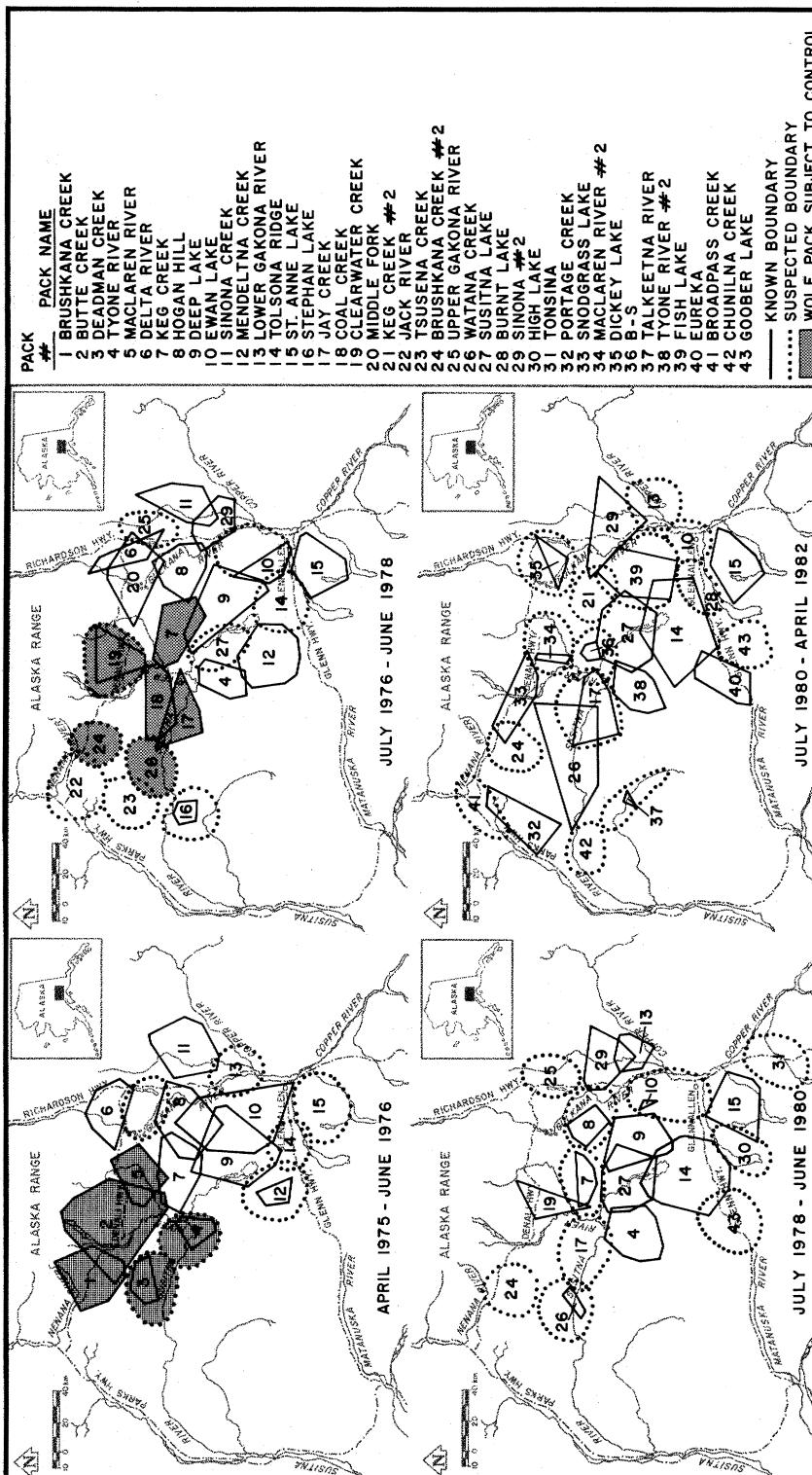


Fig. 6. Distribution and area boundaries of wolf packs studied within Game Management Unit 13 of south-central Alaska during April 1975 through April 1982. Data for 1975–76 from Stephenson (1978a). Number of days each pack was monitored during each time period is provided in Table 1.

observed during 1975 through 1980. Moose densities in these packs' territories were relatively low ( $0.09$  moose/ $\text{km}^2$ ), whereas caribou numbers were variable each year depending on the wintering location of the Nelchina caribou herd. These territories were characterized by flat terrain and a relatively homogenous spruce-bog forest that is considered poor moose habitat. We suspect that relatively large territories were the result of low densities of moose, the preferred ungulate prey during this study (see Food Habits).

**Distribution and Stability.**—Areas occupied by wolves were distributed continuously throughout GMU 13 in areas  $\leq 1,220$  m elevation (Fig. 6). Although several pack areas contained habitats  $> 1,220$  m elevation, wolves were rarely observed there even during summer. It appears that the absence of moose and caribou during winter, and vulnerability to aircraft-assisted hunting, render such areas in GMU 13 uninhabitable to wolves. Losses or additions of packs between 2 time periods were due to elimination or drastic reduction in pack size by hunters and trappers or previous failure to detect existing packs. Previous wolf location and distribution data were useful in predicting where colonizing pairs or packs might be found that had not yet been detected. For example, the Susitna Lake, Tolsona Ridge, Fish Lake, and Jay Creek Packs were initially located by searching likely but apparently unoccupied areas between known pack locations.

The general distribution of wolf packs was similar before and after wolf reduction (Fig. 6). During winter 1975–76, most members of 5 packs were killed in the SRSA. Over the next 2-year period, the area was colonized by singles and pairs, most of which also were killed. No wolves were killed by ADF&G after 1978, and singles and pairs repopulated the area. During 1980 through spring 1982, recolonization continued through immigration and reproduction, and territory boundaries were estimated.

Distribution and territory boundaries of wolf packs seem to be strongly affected by interaction with other packs and by dis-

tribution and density of prey (Peters and Mech 1975, Mech 1977, this study). For example, the Mendeltna Creek Pack was either eliminated or greatly reduced by aircraft-assisted hunting early in 1978. During the subsequent 2 years, members of the adjacent Tolsona Ridge Pack, which may have included 1 or 2 descendants of the Mendeltna Creek Pack, expanded their range westward into the old Mendeltna Creek Pack territory. Ultimately, the Tolsona Ridge Pack abandoned the southeast portion of its original territory, and by 1982 this pack occupied the previous Mendeltna Creek Pack territory. The Tolsona Ridge wolves had moved to an area of higher moose density ( $0.08$  vs.  $0.4$  moose/ $\text{km}^2$ ) based on autumn moose composition counts. During 1982–83, a pair of wolves colonized the original Tolsona Ridge Pack territory.

The sex-age composition of remaining pack members following heavy harvests also influenced whether an area continued to be occupied (W. Ballard, unpubl. data). If a single yearling or adult female ( $N = 3$ ) survived, she generally remained in the same but smaller area, attracted a new mate, and attempted to reproduce. Single males ( $N = 3$ ), however, usually dispersed and attempted to colonize vacant habitat or joined existing packs. If remaining pack members were only pups ( $N = 4$ ), they made extensive forays away from their original territory and eventually dispersed (75%) as yearlings. Other wolf sex and age combinations normally remained in the area.

**Overlap.**—Even though obvious dispersals and forays were excluded from area analyses, considerable overlap of pack areas and territories occurred (Fig. 6). Many overlaps resulted from the method used to depict territory and pack area boundaries (Mohr 1947). Overlap did occur along territory or pack area edges, but that overlap was usually separated by season of use. Also, many of the overlaps occurred along peripheral areas that were frequented less often than core areas (Fig. 7).

Annual variations in pack area or territory boundaries also were evident (Fig.

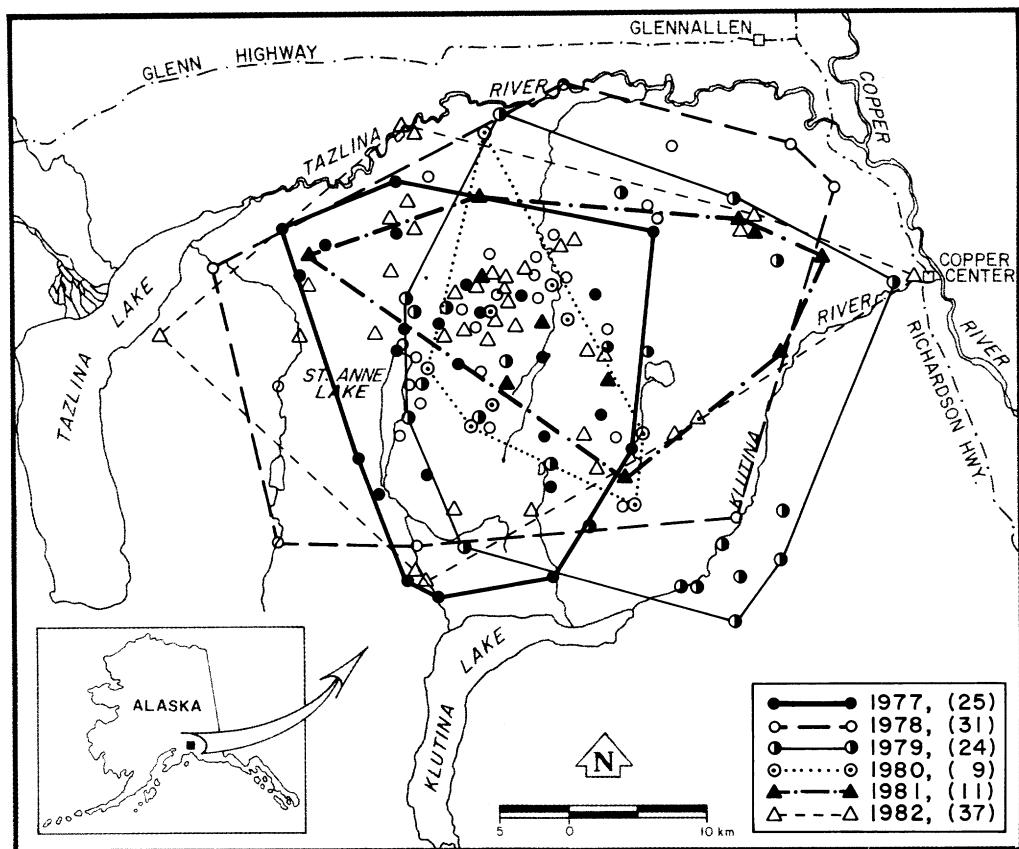


Fig. 7. Annual locations and territorial boundaries of St. Anne Lake wolf pack in south-central Alaska during fall 1977 through 1982 depicting use of core and peripheral areas. Number of days pack was monitored each year is in parentheses.

6, Table 1). Wolf packs appeared to change their use of peripheral areas, whereas the use of core areas was similar each year. This pattern was evident for the St. Anne Lake Pack (Fig. 7), except during 1980 and 1981 when too few relocations were obtained to measure use of peripheral areas. Other packs whose territories were considered fully defined ( $N = 10$ , Table 1) also exhibited the same general pattern of territory use (Fig. 6). Haber (1977) in nearby Mt. McKinley National Park (now Denali National Park and Preserve) believed that territory boundaries of unexploited packs remained stable (in at least 1 case, 1 segment of 2 territories was purportedly defined within a few meters) over relatively long periods. In northwestern Minnesota, Fritts and Mech (1981) recorded shifting

boundaries resulting from establishment and abandonment of territories in an increasing wolf population. Territorial boundaries could be relatively stable from year to year in unhunted, saturated populations where prey abundance remains relatively stable. However, in heavily exploited populations like those in GMU 13 or increasing populations as in northwestern Minnesota, shifts in territory boundaries are probably common, due to adjustments with other packs, changes in pack members, and changes in prey density.

In other parts of North America, territories are maintained through howling, scent marking, aggression, and avoidance (Peters and Mech 1975, Mech 1977, Peterson 1977, Harrington and Mech 1979). Territory sizes reported in those studies,

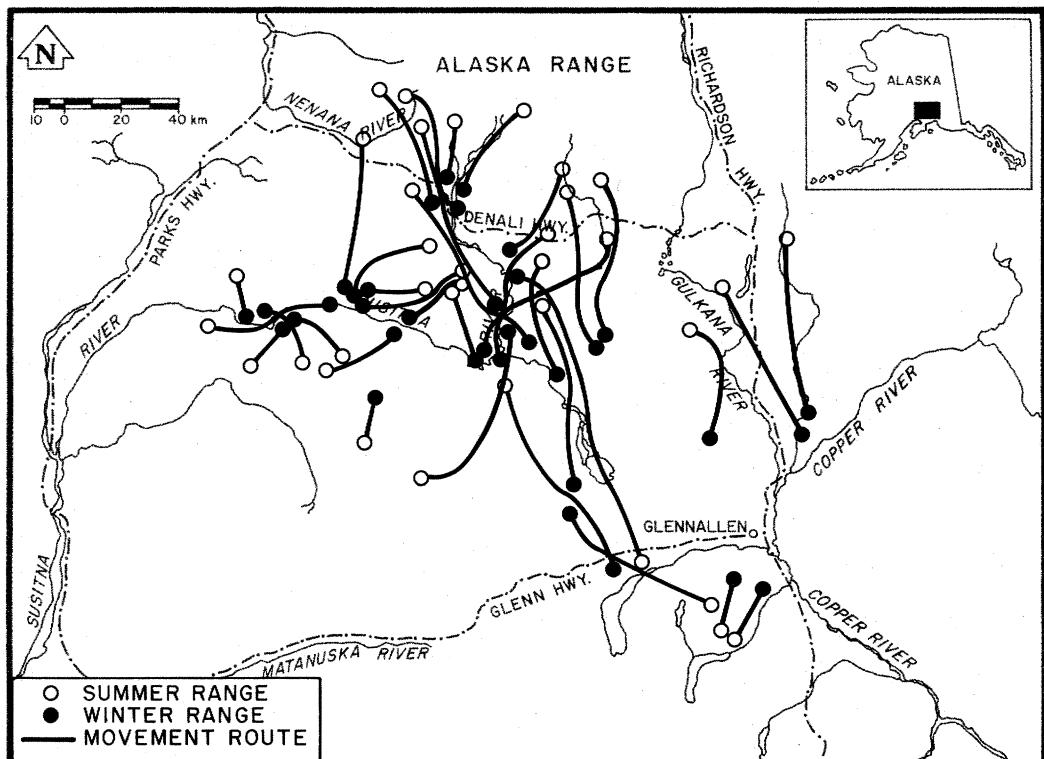


Fig. 8. Seasonal movement patterns of migratory radio-collared moose in Game Management Unit 13 of south-central Alaska from 1975 through 1982.

however, were considerably smaller than those reported here, and rates of harvest by humans were much lower. Regardless of territory size, those same mechanisms undoubtedly help to maintain territories in GMU 13.

*Pack Areas in Relation to Movements of Ungulate Prey.*—During October 1976 through April 1982, movements, productivity, and mortality of moose were investigated in the areas where wolves were studied. Over 3,500 aerial relocations were obtained on 207 radio-collared moose ranging in age from 6 months to 19 years.

Moose typically migrated from summer range to winter range in November. In some years these migrations occurred as early as October or as late as January and appeared to be initiated by the first heavy snowfall. Not all moose migrated each year. During winters of low snowfall, many remained on summer range. Initiation of

spring migration was not as clearly defined as that of autumn migration. Some moose began migrating as early as April, whereas others calved in wintering areas before migrating in midsummer. Once spring migration began, movement to summer range usually took 4–6 weeks. Distances between summer and winter home ranges of migratory moose ranged from 16 to 93 km (Fig. 8).

Seasonal and total home range sizes of GMU 13 moose were considerably larger than those reported elsewhere in North America (Ballard and Taylor 1980; Ballard et al. 1980a,b). Total area occupied by individual radio-collared adult moose averaged 224 km<sup>2</sup>, ranging from 4 to 2,911 km<sup>2</sup>. Average summer (Apr–Sep) and winter (Oct–Mar) home ranges were 129 km<sup>2</sup> and 125 km<sup>2</sup> in size, respectively.

In addition to resident moose, migratory moose (Fig. 8) traveled through wolf pack

territories (Fig. 6) during both spring and autumn. Wolf packs did not follow these migratory moose beyond their established pack territories. Thus, there were large seasonal variations in moose densities within some pack areas. However, all wolf pack areas were occupied year-round by some nonmigratory moose.

The seasonal and elevational distribution of wolves closely followed those of their principal prey, i.e., moose. Average monthly elevations of the Watana Pack in 1981–82 were significantly correlated ( $r = 0.89$ ,  $P < 0.05$ ) with the elevational distribution of 9 adult nonmigratory radio-collared moose (Fig. 9), which were representative of a larger population of nonmigratory moose within the pack's territory. Lowest mean elevation for both wolves and moose occurred in February, with both species inhabiting progressively higher elevations through October. Although wolves did not follow the movements of migratory moose, they apparently responded to movement of both resident and migratory moose within their territory.

Availability of caribou to wolves also fluctuated seasonally during the study (Fig. 10). The Nelchina caribou herd usually wintered on the Lake Louise flats from Tyone Creek east to the Copper River. Smaller numbers also occurred on the Gakona and Chistochina Rivers, Monahan Flats, Chunilna Hills, the upper Talkeetna River, and the Alaska Range (Pitcher 1982). Calving occurred in late May, primarily from Kosina Creek to the Oshetna River, after which most females inhabited the northern and eastern slopes of the Talkeetna Mountains between 1,000 and 1,800 m altitude (Pitcher 1982). Because most of the herd was concentrated on the calving grounds (Fig. 10), the bulk of the herd was unavailable to most wolf packs, which were widely distributed throughout the study area (Fig. 6). Bull caribou were scattered throughout large portions of GMU 13 during calving and began mixing with the female segment of the herd during autumn.

In areas of North America where mi-

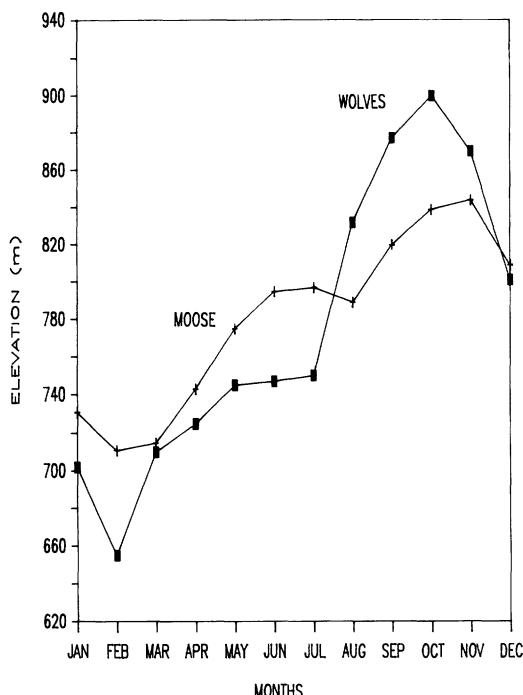


Fig. 9. Average monthly elevations of 9 adult radio-collared moose occurring within the territory of the Watana wolf pack in relation to average monthly elevations of radio-collared Watana wolf pack members during 1981–82.

gratory caribou compose most of the wolf diet, wolves are known to follow caribou as they migrate to both summer and winter range (Kelsall 1957, Kuyt 1972, Parker 1973). Spatial relationships of such migratory wolf packs on both summer and winter caribou range are poorly understood. GMU 13 wolves did not follow caribou during this study, probably because moose were sufficiently abundant in most areas to provide the bulk of their prey (see Feeding Ecology). Also, during the early years of this study, caribou numbers were relatively low. Because of the migratory habits of the area's caribou, wolves would have to become less territorial if they were to depend heavily upon caribou as prey.

### Dispersal

Excluding 4 wolves killed during tagging and 12 killed during experimental removal within GMU 13, 38 (28%) of 135 were known to have dispersed from the

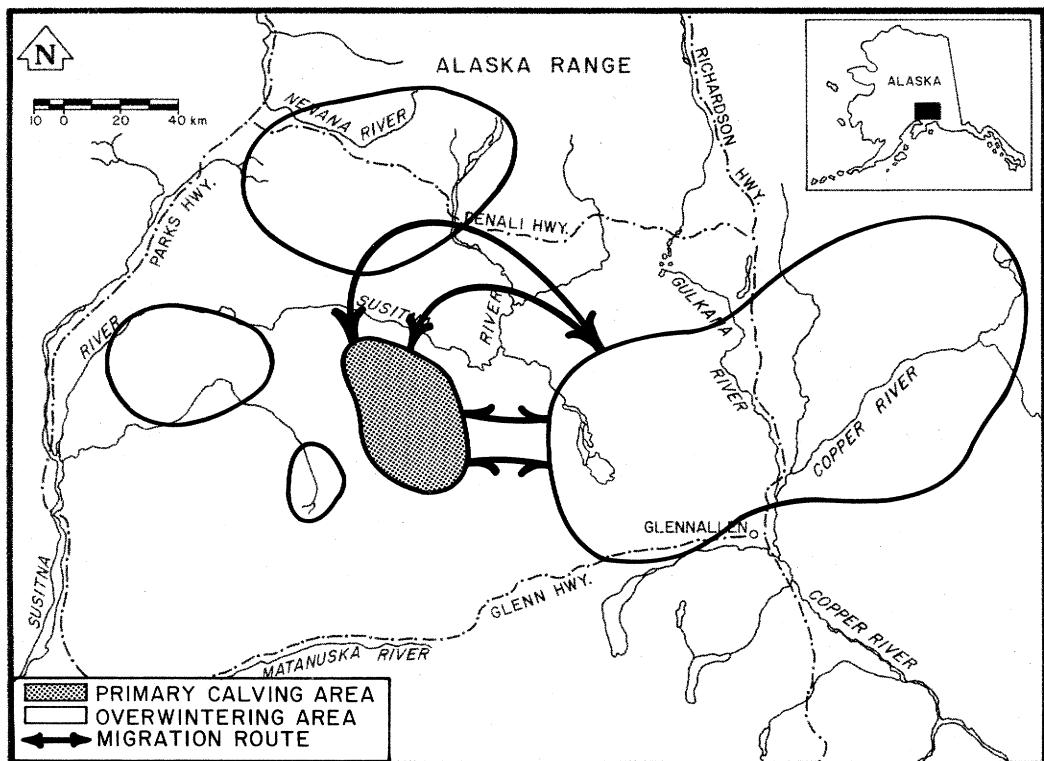


Fig. 10. General seasonal movement patterns of Nelchina Basin caribou during 1975 through 1982 (modified from Pitcher 1982).

pack area in which they were originally captured. More male (28) than female (10) ( $P < 0.05$ ) wolves dispersed (Appendix 1). Average estimated age of dispersing males (30 months) vs. females (33 months) was not significantly different. Forty percent of female and 50% of male dispersers were  $\leq 24$  months of age.

Wolves dispersed from their territories during all months of the year, but most (57%) dispersed during April through June and October through November. Straight-line distances moved by dispersing wolves ranged from 23 to 732 km. The longest movement was made by 2 radio-collared males from the St. Anne Lake Pack between April 1978 and March 1979 (Ballard et al. 1983). Although this dispersal distance was less than the distance reported for a single wolf that moved 917 km, from Minnesota to Saskatchewan (Fritts 1983), it represents the longest dispersal distance

reported for a group of wolves. Excluding this record movement, females dispersed farther ( $\bar{x} = 114$  km) than males ( $\bar{x} = 84$  km) ( $P < 0.05$ ).

Twenty-three (61%) of the 38 dispersing wolves were accompanied by 1 or more wolves following dispersal. At least 8 appeared to be pair-bonded in formerly vacant areas. Another 15 were accompanied by 2–6 wolves when last observed, and at least 8 of these were apparently accepted into existing packs. There were several instances when wolves left a pack, apparently dispersing, but returned. Forays of this type have been reported elsewhere (Peterson 1977, Fritts and Mech 1981).

Temporary associations among members from different packs were observed on 20 occasions. Such associations often preceded permanent dispersal from the original territory. Temporary associations sometimes resulted in wolf mortality, par-

ticularly when the associations included >2 members from 1 or both packs. At least 7 wolves (5 males, 2 females) were killed by other wolves. Both females that were killed were nondispersing members of small packs ( $\leq 4$ ) within their own territories when the conflicts occurred. Possibly the residing pack was unable to defend against intruding wolves because of its small size. In comparison, all 5 male deaths occurred during trespass into neighboring territories of packs comprised of at least 7 or more members. Two of these deaths occurred at moose kills within an overlap area between 2 packs, suggesting competition for food may have been a factor. Although the reasons for friendly meetings and temporary acceptance or rejection of foreign wolves are not known, fatalities more often occurred when pack sizes were relatively large ( $\geq 7$  wolves). Large packs would probably consist of an alpha pair and possibly several other adults that could be less tolerant of foreign individuals than smaller packs that may contain no adults.

Only 2 lone wolves not associated with a pack were encountered during this study and 1 eventually became a pack member. Most single radio-collared wolves eventually became members of other packs, either through pairing with another single wolf or through integration into an existing pack.

The average size of packs from which wolves emigrated was larger than those to which they immigrated ( $\bar{x} = 7.6$  vs. 2.8,  $P < 0.05$ ). These observations suggest that pack size influenced dispersal and acceptance of dispersing wolves.

Literature on North American wolves contains few references to dispersal. Fritts and Mech (1981) documented several examples of dispersal in a newly protected population in northwestern Minnesota. In that study, movements of loners, dispersers, and newly formed pairs were greatly influenced by established packs. This was also true in GMU 13 where most dispersers colonized vacant areas adjacent to occupied areas. There also appeared to be higher rates of dispersal from areas of relatively low ungulate densities (W. Ballard, unpubl. data).

Fritts and Mech (1981) suggested that acceptance of lone wolves by established packs helped maintain pack structure and resulted in a stable social system within an increasing wolf population. This may be important for wolves in GMU 13 where packs consist of <3 adults and 5–6 pups. Exploitation of these packs during and following the March breeding season could result in a loss of 1 or 2 adult members. This loss of adults could result in a reproductive failure that year and the following year, even though exploitation levels were below maximum based upon pack size alone. Such packs probably would have an unstable or less rigid social system than found in an unexploited population, creating a social environment favoring acceptance of foreign individuals. Rapid acceptance of dispersers in these situations would be advantageous and could minimize inbreeding.

### Activities of Wolves at Den and Rendezvous Sites

As in other areas of North America, reproducing packs focused their activities around dens and rendezvous sites (home-sites) during spring and summer. Wolves were observed at dens as early as 13 April, and most were regularly visiting dens by late April or early May. Wolf dens generally were situated near the center of territories. Average distance among 38 neighboring dens was 45 km (SE = 3.1 km), which is similar to the 40 km reported in north-central Alaska (Stephenson and Johnson 1973). Average annual distances between active wolf dens during 1975 through 1981 did not differ.

Pups were first observed from fixed-wing aircraft at dens or rendezvous sites from 1 June to 15 September. Late sightings of pups at and away from dens were the result of infrequent radio contact or dense vegetation. Mech (1970) indicated that wolf pups were commonly observed outside dens at 3 weeks of age. Clark (1971) observed 10-day-old pups outside dens on Baffin Island, and J. Foster (pers. com-

Table 2. Spring and fall wolf numbers from adjacent study packs used to calculate wolf density and population estimates for Game Management Unit 13 of south-central Alaska from spring 1975 through spring 1982.

Pack names	Spring 1975 <sup>a</sup>	Fall 1975 <sup>a</sup>	Spring 1976 <sup>a</sup>	Fall 1976	Spring 1977	Fall 1977
B-S Lake			8	5	2	8
Deep Lake						8
Ewan Lake	7	11	5	5	3	5
Fish Lake						
Hogan Hill	7	9	7	5	5	8
Keg Creek	7	13	5	8	1 <sup>c</sup>	1
Mendeltna Creek			5	9	7	15
Middle Fork		11	9	9	3	3
St. Anne Lake		11	8	8	8	14
Sinona Creek	7	11	11	20	2	8
Susitna Lake						
Tolsona Ridge				4		7
Tyone River			6	6	8	12
Subtotal	28	66	64	79	39	81
No. lone wolves (10%)	3	7	6	8	4	8
Total	31	73	70	87	43	89
Sample area (km <sup>2</sup> )	5,004	7,104	9,889	11,088	9,889	11,088
Density (wolves/1,000 km <sup>2</sup> )	6.2	10.3	7.1	7.9	4.4	8.0
Population estimate for GMU 13 wolf habitat <sup>d</sup> (37,985 km <sup>2</sup> )	235	390	269	298	165	305

<sup>a</sup> Data from Stephenson (1978b).

<sup>b</sup> Area and pack numbers not included in density calculations because of uncertainties concerning home-range size.

<sup>c</sup> Keg Creek pack reduced by experimental removal.

<sup>d</sup> Excludes 7,252-km<sup>2</sup> wolf-removal area, glaciers, and areas above 1,220 m elevation; density in study area directly extrapolated to land area.

mun.) indicated that pups of captive wolves began going outside the den at 16 days.

Aerial observations of pup emergence and wolf-den usage patterns suggested that

parturition occurred from mid- to late May in south-central Alaska. Ground observations at 2 den sites suggested that parturition occurred by 1 and 11 May in 1980 and 1981, respectively. These observations and differences in sizes of pups from different litters indicate parturition occurred throughout the month of May in south-central Alaska.

Natal dens ( $N = 24$ ) usually were abandoned during July ( $N = 13$ ), with dates ranging from 4 June to 1 August. The earliest movements (4 and 9 Jun) resulted from human disturbance. No pup mortality resulted from the human disturbance. Distance between natal den and first rendezvous ( $N = 10$ ) site ranged from a few hundred m to 14 km. In at least 2 instances packs moved to a second rendezvous site in August or early September. These latter sites were occupied for periods of several days. In general, pups began traveling regularly with adults between late August and mid-September.

Data on summer activity patterns of wolf packs were collected at 1 den site in 1977

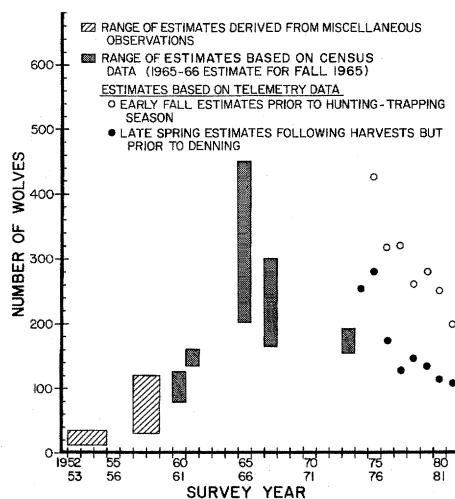


Fig. 11. Range of wolf population estimates in Game Management Unit 13 of south-central Alaska from 1952-53 through 1981-82. Lower ends of bars represent minimum estimates based on counts of individuals and tracks, whereas upper ends reflect maximum estimates.

Table 2. Continued.

Spring 1978	Fall 1978	Spring 1979	Fall 1979	Spring 1980	Fall 1980	Spring 1981	Fall 1981	Spring 1982
3	3	2	2					3
3	3	4	7					
				2	9	6	10	
8	12	1					9 <sup>b</sup>	5
2	8							
0	0							
0	1		5		2		7	
8	7	4	8	3	6	4	9	7
4	10	2	2	4	5	2	2	2
2	10	7	13	4	10	3	3	2
3	10	7	16	9	16	8	14	4
1	2	2	9	4	2	0	2	1
34	66	29	62	26	48	23	40	24
3	7	3	6	3	5	2	4	2
37	73	32	68	29	53	25	44	26
11,663	11,142	8,948	10,249	9,350	9,350	9,350	9,350	9,930
3.2	6.6	3.6	6.6	3.1	5.7	2.7	4.7	2.6
121	249	136	252	118	215	93	162	96

and 1978, concurrent with aerial summer predation studies. Six radio-collared wolves (3 in each pack) were located on 93% of 340 total relocation attempts during late May and June of 1977 and 1978. At least 1 radioed wolf from each pack was located at the den or rendezvous site on 55% of 316 relocations. The alpha female in 1 pack was radio-collared, and she accounted for 57% of 129 relocations of wolves at the den site for that pack. Away from the den site, wolves were more solitary during summer than during fall and winter; 55% of 143 and 6% of 142 relocations of radio-collared wolves were observed alone during summer and the remainder of the year, respectively. Even though wolves were more solitary away from the den site during summer than winter, the presence of adult males (presumed alpha males) was a contributing factor to the type and age of prey killed during summer. Adult males were involved in 92% ( $N = 12$ ) of the fresh kills involving calf moose or larger prey. Although yearlings ( $N = 3$ ) hunted alone, they were largely unsuccessful and scav-

enged old kills ( $N = 3$ ) or killed small prey ( $N = 2$ ). This suggests that in studies of summer predation, all adult members of each study pack should be radio-collared to aid in locating all ungulate kills.

## POPULATION DYNAMICS

### Wolf Densities

**Historical.**—The status of wolves in GMU 13 prior to 1948 is largely unknown. Reports of early explorers indicate that wolves and their ungulate prey were scarce in the late 1800's (Skoog 1968). By the 1930's, wolves were more common according to early residents (Murie 1944, Vogel 1977). C. McMahan, a resident and pilot in GMU 13 since 1941, reports that wolves were common during the 1940's and were increasing.

Between 1948 and 1974, wolf numbers in GMU 13 were estimated by various investigators, including Burkholder (1959), Atwell (1964), Rausch (1967, 1969), C. McIlroy (unpubl. data), and Van Ballen-

berghe (1981). Rausch (1967, 1969) summarized estimates prior to 1969 and concluded that extensive predator control, begun in 1948 by the U.S. Fish and Wildlife Service, reduced wolf numbers to a low of about 12 in 1953. After wolf control ceased, wolves increased steadily to a peak of 350–450 by 1965 (Rausch 1967, 1969). By 1967, wolf numbers had declined to a maximum of 300 or less, apparently due to hunting (Rausch 1967, 1969). The next population estimate was made by C. McIlroy (unpubl. data) who estimated that 207 wolves were present in March 1974. Van Ballenberghe (1981) correctly questioned several of the earlier estimates because of discrepancies in size of study areas. He also proposed several revisions of previous estimates, but these were poorly supported by available evidence (Bergerud and Ballard 1987). Based upon examination of Rausch's (1967, 1969) original and summarized data, several valid points raised by Van Ballenberghe (1981), Bergerud and Ballard (1987), and this study, the above general trend (Fig. 11) is the most logical explanation of wolf population changes.

**Present Study (1975–82).**—Beginning in 1975, wolf populations in GMU 13 were estimated by extrapolating densities derived from known numbers in continuous radio-marked packs to the entire GMU (Table 2). Dispersals and extraterritorial movements were not included in density calculations. Both autumn (postdenning, prehunting) and spring (posthunting, pre-denning) population estimates and densities were calculated to depict within-year fluctuations due to natality and mortality. Ten percent of the population was assumed to be composed of lone (mostly dispersing) wolves (Stephenson 1975). The number of packs and the land area from which estimates were derived varied between years because contact with some packs was intermittent. The estimates included all of GMU 13 except the SRSA, glaciers, large lakes, and all areas above 1,220 m elevation (Fig. 1). This method provides the most realistic estimate of density because neither wolves nor their prey

regularly inhabit areas above 1,220 m elevation in this region. The potential problem with the method was exclusion of some Dall sheep habitat from the estimates. Study packs were never observed on sheep kills and sheep were rarely represented in summer wolf scats; therefore the resulting error is believed to be minimal.

Wolf densities in GMU 13 (excluding the SRSA and areas >1,220 m elevation) varied from 10.3 wolves/1,000 km<sup>2</sup> in autumn 1975 to 2.6/1,000 km<sup>2</sup> in spring 1982. Lower spring densities reflected losses due to trapping, hunting, dispersal, and natural mortality, whereas autumn densities reflected pup production and immigration. From spring 1975 to spring 1982, wolf densities in radio-marked packs declined by 58% (Table 2). Autumn densities exhibited a similar trend, declining by 54%. From autumn to spring each year during 1975 through 1982, wolf numbers declined an average of 47% (range 31–60%). Annual increases from late spring (following hunting but prior to denning) to autumn (prior to hunting and when best estimates of pup production are available) averaged 72% and ranged from 11% to 106%.

Extrapolation of wolf density estimates (Table 2) to available wolf habitat (areas ≤1,220 m elevation) in GMU 13 (including the SRSA) yielded total population estimates ranging from 426 wolves in autumn 1975 to 109 wolves in spring 1982 (Fig. 11). Wolf population levels were highest in 1975–76 and declined each year thereafter due to aircraft-assisted ground shooting and Department wolf control. Annual finite rates of increase for autumn population estimates averaged 0.88 (range 0.77–1.01) during 1975–82.

Recent GMU 13 wolf densities were compared with those reported elsewhere in North America (Table 3). Reported wolf densities in Alaska ranged from approximately 10 to 15 wolves/1,000 km<sup>2</sup> southeastern Alaska (Atwell et al. 1963) to about 3 wolves/1,000 km<sup>2</sup> in the Brooks Range (Stephenson 1975). Wolf densities in GMU 13 occur near the midpoint of this range. However, in 1975 the density was similar to that reported on the Kenai Peninsula,

Table 3. Reported wolf densities in North America.

Location of study area	Source	Wolves/1,000 km <sup>2</sup>	Size of study area (km <sup>2</sup> )
Coronation Island, Alaska	Merriam 1964	128 <sup>a</sup>	78
Isle Royale, Michigan	Peterson 1976	84	544
Northwest Territories	Kuyt 1972	56	995
Isle Royale, Michigan	Mech 1966	38–56	544
Manitoba and Saskatchewan	Parker 1973	28–50 <sup>b</sup>	3,300
Superior National Forest, Minnesota	Van Ballenberghe <i>et al.</i> 1975	42	1,857
Algonquin Park, Ontario	Pimplott <i>et al.</i> 1969	39	2,590
Superior National Forest, Minnesota	Olson 1938	39	6,449
Superior National Forest, Minnesota	Mech 1973	36	10,886
Beltram Island State Forest, Minnesota	Fritts and Mech 1981	7–30	313–2,584
Superior National Forest, Minnesota	Stenlund 1955	23	10,619
Kenai Peninsula, Alaska	Peterson <i>et al.</i> 1984	11–20	2,671–4,401
Mt. McKinley National Park, Alaska	Haber 1968	9–16	3,885
Southeast Alaska	Atwell <i>et al.</i> 1963	10–15	19,425
Tanana Flats, Alaska	Stephenson 1977	11	18,130
Nelchina Basin, Alaska	This study 1975–82	3–10	5,004–11,663
Saskatchewan	Banfield 1951	5–10	
McKinley National Park, Alaska	Murie 1944	8	5,180
Nelchina Basin Study Area, Alaska	Rausch 1967	8	51,800
Northeast Alberta	Fuller and Keith 1980	7	25,000
Northwest Territories	Kelsall 1957	3–7	1,243,200
North-central Brooks Range, Alaska	Stephenson 1975	3–6	9,324
West Canada	Cowan 1947	4	10,878
West Canada	Carbyn 1975	4	1,536
Baffin Island, Canada	Clark 1971	3	4,662
Manitoba, Saskatchewan, and Northwest Territories	Parker 1973	2	282,310

<sup>a</sup> Artificial situation—4 wolves transplanted to Island.<sup>b</sup> Wolves concentrated on caribou winter range.

Alaska (Peterson *et al.* 1984), whereas in recent years densities have been similar to the low levels reported for the Brooks Range (Stephenson 1975).

## Productivity and Survival

Litter sizes as indicated by counts of placental scars in 16 adults  $\geq 3$  years old averaged 6.1 (SE = 0.5). Exceptionally high productivity was noted in 2 females ( $\geq 2$  years old) containing 9 fetuses each. Productivity as indicated by counts of corpora albicantia ( $\bar{x} = 6.4$ , SE = 0.6), placental scars, and fetuses was similar to that reported by Rausch (1967) for all of south-central Alaska during 1957 through 1966. However, productivity was higher than recently reported by both Gasaway *et al.* (1983) for interior Alaska ( $\bar{x} = 4.3$  placental scars/female) and Peterson *et al.* (1984) for the Kenai Peninsula, Alaska ( $\bar{x} = 5.0$  placental scars/female). In the former area,

early winter wolf densities were similar ( $\bar{x} = 5.9/1,000 \text{ km}^2$ ), but moose densities were lower ( $192/1,000 \text{ km}^2$ ) than in GMU 13. In the latter area, wolf ( $\bar{x} = 14.3/1,000 \text{ km}^2$ ) and moose ( $800/1,000 \text{ km}^2$ ) densities were higher.

Minimum estimates of mean litter size also were available from observations of selected packs in early summer (Table 4). Pack litter sizes ranged from 2 to 9 pups. Litters were larger in early June and July than in November suggesting that some pup mortality occurred during summer. Average pup survival rate during the first 6 months of life based upon average observed litter sizes could have been as high as 0.97 (Table 4). However, if an initial litter size of 6.5 was assumed (Rausch 1967), pup survival to 1 November in GMU 13 was estimated at 0.82 (Table 4). Considerable variation in mean litter size per pack among years (range 3.7–7.3 by 1 Nov) was observed. The lowest survival (1975–76)

**Table 4.** Annual wolf pup production, litter size, and calculated rates of pup survival for selected radio-collared wolf packs from birth to approximately 1 November 1975–81 in south-central Alaska.

Year	No. of packs	No. of pups		Mean litter size/pack		Range of early summer litter size	Survival rate 1 May–1 Nov <sup>a</sup>
		Early summer	1 Nov	Early summer	1 Nov		
1975 <sup>b</sup>	7	27	26	3.9	3.7	2–6	0.571
1976	4	23	21	5.8	5.3	3–6	0.808
1977	4	26–28	25	6.5–7.0	6.3	5–8	0.962
1978	5	28	28	5.6	5.6	3–8	0.862
1979	3	19–22	19–22	6.3–7.3	6.3–7.3	6–9	0.974
1980	3	18	18	6.0	6.0		0.923
1981	2	12	12	6.0	6.0		0.923
Total	28	153–158	149–152	5.5–5.6	5.3–5.4	2–9	0.819

<sup>a</sup> Assumes an initial litter size of 6.5 pups/adult wolf (Rausch 1967).

<sup>b</sup> Data from Stephenson (1978b).

occurred during the highest spring densities (see Table 2); this suggests that recruitment to autumn populations may be partially density dependent. However, both moose and caribou numbers were lowest that year; therefore nutrition may have influenced wolf productivity (Fritts and Mech 1981, Keith 1983) or pup survival.

Wolf packs generally produce 1 litter of pups/year. During our study of 41 pack litters with well-documented histories, at least 3 packs (7%) produced 2 litters by different females at separate dens in 1 year. A fourth instance of 2 litters in a pack may have occurred, but the second female died during capture activities prior to parturition. If this female had produced pups, the incidence of 2 litters/pack would have been 10%.

Van Ballenberghe (1983) concluded that conditions necessary for multiple litter production in wolves (large territories with several potential den sites, adequate numbers of prey, and low human exploitation) occur rarely. Our data do not support his hypothesis. Territory sizes for 2 of 3 twin-litter packs (Sinona Creek and Mendeltna Creek) were average for GMU 13, whereas the third area (Eureka Pack) was relatively small (1,000 km<sup>2</sup>). However, the size of the latter area was based on only 20 locations. All pack areas in GMU 13 contain numerous old and potential wolf den sites (Ballard and Dau 1983). There were no significant differences in numbers of wolves per pack between those which produced

1 or 2 litters. Also, there was no relationship ( $r = 0.10, P > 0.05$ ) between numbers of adults per pack in spring and numbers of pups surviving to November each year. This latter finding was similar to that of Peterson et al. (1984) on the Kenai Peninsula, Alaska, but different from that of Harrington et al. (1983) in Minnesota. Harrington et al. (1983) reported that for 2 wolf populations there was a relationship between pack size and litter size, but the direction of the relationships apparently varied in relation to prey availability. Reasons for the differences in correlation between the Alaska and Minnesota studies are not known. Although reductions in human-caused mortality may enhance conditions (more adult females per pack) for production of multiple litters at relatively low densities, the opposite appears true at higher wolf densities when prey may be relatively less abundant (Mech 1970, Peterson 1977, Packard and Mech 1980, Fritts and Mech 1981).

Harrington et al. (1982) concluded that in North America the frequency of multiple litters in the wild was greater than previously thought, ranging from 22% to 41%. In the present study, 7–10% of the packs produced multiple litters. Multiple litters would be advantageous in allowing a wolf population to quickly increase following high mortality, but such litters have not been documented in saturated or increasing unexploited populations (Mech 1970, Peterson 1977, Fritts and Mech

Table 5. Annual wolf survival rates by age class as determined from radio-collared wolves in south-central Alaska 1975–82.

Harvest year	Adults		Pups		Yearlings		All ages			
	No. wolf-months monitored	Annual survival rate	No. wolf-months monitored	Survival rate	No. wolf-months monitored	Annual survival rate	No. wolf-months monitored	Survival rate		
	Nov-Apr	Annual <sup>a</sup>	Nov-Apr	Annual <sup>a</sup>	Nov-Apr	Annual	Nov-Apr <sup>b</sup>	Annual		
1975–76 <sup>c</sup>	92	0.768	9	0.221	0.126	15	1.000	116	0.68	0.656
1976–77	134	0.577	12	0.593	0.479	22	0.572	168	0.51	0.557
1977–78	154	0.447	16	0.288	0.277	28	0.257	198	0.40	0.364
1978–79	156	0.490	35	0.584	0.503	29	0.656	220	0.41	0.481
1979–80	113	0.581	13	0.619	0.603	69	0.703	195	0.48	0.605
1980–81	153	0.728	11	0.300	0.277	54	0.799	218	0.42	0.676
1981–82	249	0.643	42	0.397	0.366	100	0.785	391	0.49	0.587
Total or weighted $\bar{x}$	1,051	0.591	138	0.432	0.354	317	0.681	1,506	0.48	0.551

<sup>a</sup> Rates for entire year were computed by multiplying the first survival rate by the survival rates from May to Oct from Table 4.

<sup>b</sup> Survival from 1 Nov through Apr = no. wolves observed in late spring ÷ no. observed in previous fall.

<sup>c</sup> Data from Stephenson (1978b).

1981). Therefore, multiple littering may represent a form of compensatory natality in heavily exploited wolf populations. Although the frequency of multiple littering is probably greater than previously thought, our data suggest that the estimate proposed by Harrington et al. (1982) may be too high.

Annual wolf survival rates (Table 5) were determined by the following 2 methods: (1) survival rates of all radio-collared wolves (excluding those removed during reduction programs) were calculated by age class according to methods described by Trent and Rongstad (1974) and (2) numbers in radio-marked packs during autumn were compared with those present in late spring just prior to denning. The first method assumes that radio-collared wolves were representative of the population. The second method assumes that immigration and emigration were equal.

Annual survival of radio-collared adult ( $\geq 2$  years) wolves from 1975–76 through 1981–82 averaged 0.59 (range 0.45–0.77) (Table 5). Adult survival was similar to that of yearlings (0.68) and both exceeded pup survival rates, which averaged 0.35 (range 0.13–0.60). The average annual mortality rate of all radio-collared wolves was 0.45 (1.00 – 0.55). Survival rates based upon losses from radio-collared packs were similar to those estimated from individual radio-collared animals (Table 5). Compari-

son of observed finite rates of increase in other North American wolf populations (range 1.15–1.46, Keith 1983) with mortality rates and finite rates of increase observed in this study (range 0.77–1.01, Table 2) suggests that mortality was sufficiently high to cause the population to decline.

## Mortality

Wolf mortality was classified as (1) trapped (snared or caught by leg-hold trap), (2) ground shot (landing aircraft and shooting during the same day), (3) aerially shot from aircraft (legal only in 1971–72), (4) experimental removal by ADF&G personnel (shooting from helicopter or fixed-wing aircraft), and (5) other (automobile collisions, natural mortality, and collaring mortalities). Illegal aerial harvests after 1971–72 were added to the ground shooting category because exact numbers were not known and probably reported as shot from the ground.

**Human-caused Mortality.**—Trapping was the most common harvest method from 1972–73 through 1975–76, accounting for 59% of the total harvest (Table 6). Beginning with the 1976–77 hunting season, ground shooting became more common, accounting for 55% of the total harvest from 1976 through 1978–79.

Table 6. Reported wolf harvests for Game Management Unit 13 of south-central Alaska, 1971–72 through 1981–82.

Method of harvest	1971–72	1972–73	1973–74	1974–75	1975–76	1976–77	1977–78	1978–79	1979–80	1980–81	1981–82	Totals	Annual mean
Trapped	43	57	53	60	48	25	51	20	35	30	23	445	41
Ground shot	22	20	22	41	36	49	68	47	10	16	28	359	33
Aerial shooting	46	0	0	0	0	0	0	0	0	0	0	46	4
Experimental removal	0	0	0	0	29	23	7	1	0	0	0	60	6
Other	0	3	0	2	1	5	2	1	2	0	4	20	2
Totals	111	80	75	103	114	102	128	69	47	46	55	930	85

The 1977–78 wolf harvest was the highest recorded for GMU 13 since 1968 when the hunting and trapping season was opened. Only 6% of the 1977–78 harvest was due to ADF&G wolf reduction efforts in the SRSA. Most of the increase could be attributed to the increased efficiency of 2 or 3 aircraft-assisted hunters (Alaska regulations allow trappers to land and shoot wolves from the ground on the same day as airborne); during 1976 through 1980, their harvest ranged from 12% to 61% of the total GMU 13 annual harvest. Beginning in 1979–80, trapping again became the most common method of harvest. During 1976 through 1980, successful trappers took an average of 1.5 wolves/season (range 1–6), whereas aircraft-assisted hunters averaged 3.4 wolves/season (range 1–23).

Sex ratios of harvested wolves were not significantly different from 50:50 annually or in total. According to harvest records, pups composed 42–74% of the annual harvest ( $\bar{x} = 80$ ), averaging 57% (SE = 4.4) from 1975 through 1982. Examination of 225 wolf carcasses during 1976 through 1982 revealed a similar pattern, annually averaging 62% pups (SE = 7.1).

The annual population dynamics of individual radio-collared wolf packs were examined by comparing annual overwinter mortality (Table 2), caused primarily by hunting and trapping, with annual finite rates of increase (Fig. 12). Mortality levels and rates of increase were inversely correlated ( $r = -0.73$ ,  $P < 0.01$ ), indicating that this wolf population was being controlled primarily by human harvest. An overall mortality rate of 50% from all causes would allow wolf packs to remain stable

(Fig. 12). Excluding natural mortality, which accounted for 20% of the wolf mortality (10% of population, see next section), human exploitation in excess of 40% of the autumn population would cause a population decline. For individual packs the exact number would vary considerably depending on the sex and age composition of each pack and the timing of the harvest. Heavily exploited packs are composed of only a few adults and several pups; therefore any additional adult mortality could greatly affect reproductive success.

Keith (1983) concluded that wolves could sustain annual harvests of 23–38% and that stationary populations, whether exploited or not, were composed of 40% pups by autumn or winter. Increasing and decreasing exploited wolf populations, however, would have larger percentages of pups. Results reported here are in basic agreement with Keith's (1983) conclusions. The average maximum sustainable harvest indicated by GMU 13 data (40%) and those examined by Keith (1983) and Peterson et al. (1984) are somewhat lower than the 50% or more mortality suggested by Mech (1970) as required to reduce wolf densities.

Although GMU 13 wolf population growth has been controlled primarily by human harvest, other forms of mortality also may have affected this wolf population. For example, subtraction of known hunting and trapping losses from autumn population estimates (Table 2) leaves an average of 46 wolves (SE = 9.6) unaccounted for each year. As indicated in the next section, the discrepancies were largely the result of natural mortality.

#### *Mortality of Radio-collared Wolves.—*

Of 151 radio-collared wolves (Appendix 1), 4 (3%) died during capture activities and 14 (9%) were killed as part of reduction programs in either GMU 13 or elsewhere (Table 7). Thirty-five (23%) were alive as of 30 April 1982, 28 (80%) of which were first captured during the last year of study. Capture-related mortalities, experimental reductions, and survivors thus accounted for 53 (35%) of 151 radioed wolves. The fates of an additional 70 wolves (45%) were known (Table 7) and those of 18 others (12%) were suspected. The fates of 10 wolves (7%) were unknown. Suspected and unknown fates included illegal harvest, dispersal, and radio failure. Illegal harvest was suspected when skinned carcasses of wolves were found shortly after radio signals were lost. In these cases, radiocollars were not returned, and evidence suggested that over half had been shot from aircraft. Wolves classified as "suspected dispersal" had earlier made movements outside of their territories, and final radiolocations also were outside previously used areas.

Harvest by humans (excluding experimental removal and collaring mortality) was the largest cause of death among radio-collared wolves. Legal (46%) and illegal (34%) human harvest made up 80% of the total mortality. Remaining losses were attributable to intraspecific strife (11%) and such miscellaneous causes as drownings, starvation, vehicle collisions, and injuries by moose (9%). In spite of the

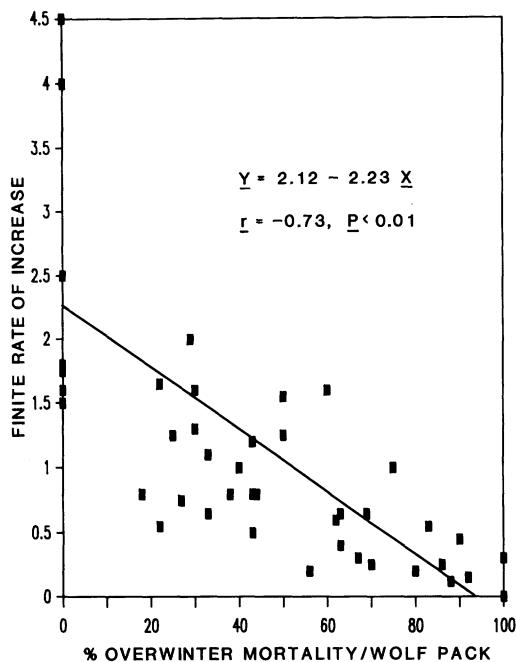


Fig. 12. Comparison of annual rates of mortality per pack (fall to spring) to finite rates of increase ( $\lambda$  from fall to fall) for radio-collared wolf packs studied in Game Management Unit 13 of south-central Alaska during 1975 through 1981.

comparatively high level of human-caused mortality, the natural mortality rate observed in this study was relatively high in relation to observed wolf population densities and to other North American studies (Mech 1970, Peterson 1977, Carbyn 1982, and others).

Table 7. The fate of 151 radio-collared wolves in south-central Alaska, April 1975 through April 1982.

Harvest year	Alive on 30 Apr 1982	Experimental removal	Trapped	Ground shot	Known illegal harvest	Suspected illegal harvest	Known dispersal	Suspected dispersal	Missing, cause unknown	Killed by wolves	Capture-related mortality	Other mortality	Total
1975-76*	0	6	2	0	0	2	0	0	3	1	1	1	16
1976-77	0	6	0	3	0	1	4	2	0	1 <sup>b</sup>	1	1	19
1977-78	2	0	0	11	1	0	3	0	0	1	0	1	19
1978-79	1	1 <sup>c</sup>	1	7	0	3	3	1	4	1	0	3	25
1979-80	4	0	1	1	3	0	3	1	1	2	0	0	16
1980-81	16	1 <sup>d</sup>	2	2	0	2	0	0	1	1	0	0	25
1981-82	12	0	1	2	6	6	0	0	1	1	2	0	31
Total	35	14	7	26	10	14	13	4	10	8	4	6	151

\* Data from Stephenson (1978b).

<sup>b</sup> Killed by either bear or wolf.

<sup>c</sup> Killed in wolf reduction program in GMU 20A.

<sup>d</sup> Killed in wolf reduction program in GMU 20E.

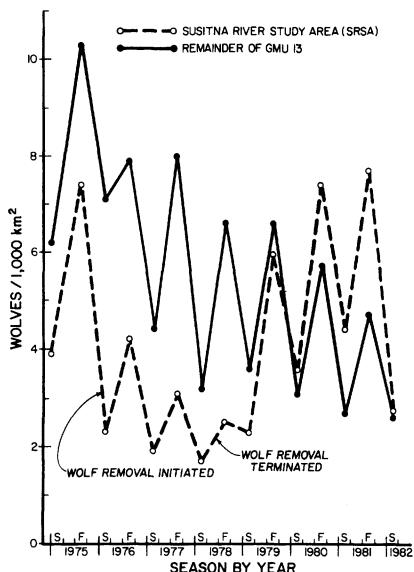


Fig. 13. Comparison of annual wolf density in Susitna River Study Area to wolf densities within the remainder of Game Management Unit 13 during 1975 through spring 1982.

**Experimental Wolf Reduction and Repopulation.**—During January 1976 through July 1978, 60 wolves were removed from the SRSA by ADF&G personnel as part of a wolf control program. During this period, 9 additional wolves were reportedly removed from the area by public hunting and trapping. Boundaries of the area and specifics of the removal program have been described by Ballard et al. (1981c) and Ballard and Stephenson (1982).

Immediately prior to initiation of wolf removal in 1976, wolf densities in the SRSA ( $7,262 \text{ km}^2$ ) ranged from 4 wolves/ $1,000 \text{ km}^2$  in spring 1975 to 7 wolves/ $1,000 \text{ km}^2$  in autumn 1975. During the experiment, spring densities (before whelping) were reduced by 42–58% from precontrol levels. Annual wolf density fluctuations from autumn to spring were similar to that in the remainder of GMU 13 except that densities were considerably lower in the SRSA (Fig. 13). While control was in effect, spring densities were an average of 57% lower than in the remainder of GMU 13, ranging from 47% in spring 1978 to 67% in 1976.

Several wolves immigrated into the

SRSA during the wolf reduction experiment, and annual effort was required to maintain low wolf densities (Ballard and Stephenson 1982). Prior to termination of wolf control, annual finite rates of increase (based on autumn population estimates) ranged from 0.57 to 0.81. Once the experiment terminated in July 1978, the wolf population quickly increased due to immigration and reproduction. The finite rate of increase from autumn 1978 to autumn 1979, after control efforts terminated, was 2.40, an apparent record rate of increase for a wolf population in North America. Thereafter, the finite rate of increase in 1979–80 and 1980–81 was 1.23 and 1.04, respectively. The area was open to public hunting and trapping throughout the period of study, and several wolves were killed. By 1981–82 the wolf population was limited by public hunting and trapping with 55% of the autumn 1981 population being harvested.

## FEEDING ECOLOGY AND BEHAVIOR

### Food Habits

**Aerial Observations.**—During April 1975 through April 1982, radio-collared wolves were observed at 439 kills (Table 8); 91% were ungulates. Smaller prey species (e.g., snowshoe hares) were undoubtedly underestimated during aerial observations.

Moose composed 70% of the observed kills. During May and June calves composed 30% of the classified moose kills ( $N = 53$ ). During these months, newborn calves made up 38–48% of the population (W. Ballard, unpubl. data). Thus wolves appeared to be taking calves less or in proportion to their occurrence in the moose population. This conclusion was supported by scat analyses (next section).

Wolves continued to take calves in proportion to availability through October. During July–October (1975–82), 14% of the moose killed ( $N = 56$ ) were calves, and they composed 12–20% of the moose counted in November surveys during 1975–82. Most neonatal mortality had oc-

Table 8. Wolf kills discovered while monitoring radio-collared wolves in Game Management Unit 13 of south-central Alaska, April 1975 through April 1982.<sup>a</sup>

Month of observations	Calf moose <sup>b</sup>		Yearling moose <sup>b</sup>		Adult moose	Unclassified moose	Calf caribou	Adult caribou	Unclassified caribou	Beaver	Miscellaneous prey <sup>c</sup>	Totals
	N	Age in months	N	Age in months								
May	7	0.1	4	12	10	5	1	2	1	1	2	33
Jun	9	1	6	13	17	3	0	2	1	1	7	46
Jul	2	2	4	14	14	0	2	1	0	2	1	26
Aug	4	3	0	15	8	2	0	7	0	1	2	24
Sep	1	4	0	16	11	0	1	1	1	0	3	18
Oct	1	5	0	17	11	6	0	2	1	0	3	26
Nov	7	6	0	18	9	5	0	6	5	0	6	38
Dec	4	7	0	19	13	4	2	1	3	1	1	29
Jan	11	8	0	20	22	0	0	13	2	0	1	49
Feb	10	9	0	21	17	0	1	6	4	1	4	43
Mar	15	10	1	22	17	5	0	8	3	0	2	51
Apr	18	11	3	23	16	3	1	9	4	2	0	56
Total	89		20		165	33	8	58	25	9	32	439 <sup>d</sup>
Percent	20		5		38	8	2	13	6	2	7	101

<sup>a</sup> Data for 1975–76 from Stephenson (1978b).

<sup>b</sup> Estimated age based on assumed birthdate of 1 Jun (Ballard and Taylor 1980).

<sup>c</sup> Includes snowshoe hare, birds, beaver, etc.

<sup>d</sup> Forty kills (9%) shared with 1 or more brown bear.

curred prior to July (Ballard et al. 1980b) so the reduced use of calves reflected, in part, a decrease in their availability.

During November–April, calf moose were selected disproportionately to their occurrence in the moose population. Calves made up 40% of the classified wolf kills ( $N = 163$ ) during November through April but represented only 12–20% of the moose counted in November. This result suggests increased vulnerability of calves due to several winter-related conditions such as snow cover (Peterson 1977).

Estimates of the proportion of yearlings in the autumn moose population were less accurate than for other age classes and only yearling bulls could be identified. Beginning in 1980, hunters were not allowed to harvest yearling bulls. Subsequently, an estimate of percent yearlings in the population was obtained by assuming equal sex ratios and doubling counts of yearling bulls. Using this method in 1980 and 1981, yearlings composed 11–15% of the November moose population in GMU 13. However, because of the large number of calves produced at parturition and subsequent high rates of calf mortality in late May and June (Ballard et al. 1981b), the actual percentage of yearlings in the herd at parturition

was probably lower than that in autumn. During May through July, yearling moose composed 19% of the classified wolf kills ( $N = 73$ ). This finding suggests that yearlings may have been killed disproportionately to their occurrence in the moose population.

Adult moose were the most common prey, accounting for 38% of the 439 observed kills. Based upon the findings of no selection for calves and slight selection for yearlings, adult moose apparently were preyed upon in approximate proportion to their occurrence in the population during May through October. Thereafter, they were killed less frequently with proportionately more calves being killed. Adults were not as vulnerable as calves during periods of snow cover.

Caribou were the second most important prey, composing 21% of all kills. Sex ratios of adult caribou kills observed from the air and those examined on the ground were not significantly different from those estimated during aerial composition surveys (Pitcher 1982).

Dall sheep were not important prey during the study. No identifiable sheep kills were observed although sheep remains were occasionally found in summer wolf

Table 9. Incidence of food remains in wolf scats collected at wolf den and rendezvous sites during 1975 through 1981 in Game Management Unit 13 of south-central Alaska.

Food types	1975 <sup>a</sup>		1976		1977		1978		1979		1980		1981		Total	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Adult moose	261	14.5	50	6.7	32	4.4	42	5.0	20	5.9	96	13.2	24	6.2	525	9.4
Calf moose	604	33.6	392	52.7	417	57.4	394	47.0	136	40.4	314	43.1	87	22.3	2,344	42.1
Adult caribou	30	4.0	7	1.0	15	1.8	17	5.0	25	3.4	31	7.9	125	2.2		
Calf caribou	54	7.3	34	4.7	34	4.1	36	10.7	12	1.6	19	4.9	269	4.8		
Beaver	237	13.2	36	4.8	38	5.2	118	14.1	18	5.3	32	4.4	37	9.5	516	9.2
Muskrat	12	0.7	18	2.4	27	3.7	42	5.0	10	3.0	20	2.7	24	6.2	153	2.7
Snowshoe hare	439	24.5	58	7.8	35	4.8	59	7.0	26	7.7	46	6.3	21	5.4	684	12.3
Parka squirrel	24	1.3	4	0.5	2	0.3	1	0.1	0	0	0	0	0	0	31	0.5
Microtine rodents	31	1.7	17	2.3	26	3.6	16	1.9	19	5.6	25	3.4	37	9.5	171	3.0
Other <sup>c</sup>	62	3.5	16	2.2	41	5.6	38	4.5	30	8.9	82	11.3	66	16.9	335	6.0
Vegetation	32	1.8	33	4.4	46	6.3	37	4.4	6	1.8	19	2.6	5	1.3	178	3.2
Unidentified	13	0.7	36	4.8	41	5.9	43	5.1	19	5.6	57	7.8	39	10.0	248	4.4
Totals	1,795	100.0	744	99.9	726	99.9	839	100.0	337	99.9	728	99.8	390	100.0	5,559	99.8

<sup>a</sup> Data from Stephenson (1978b).<sup>b</sup> Adult and calf caribou combined.<sup>c</sup> Other includes birds, insects, egg shells, wolf, red squirrel, and unidentified ungulate.

scats (*see* next section). Sheep were distributed throughout GMU 13 in habitats above 1,220 m. Although study packs generally inhabited elevations <1,220 m elevation, at least 9 pack areas contained habitat where sheep periodically or regularly occurred. For example, during 1976 through 1982, 130–209 sheep were counted annually within the Watana, Jay, and Coal Creek Pack areas (Fig. 6), but no sheep kills by these packs were identified. In other sheep habitats, such as the Talkeetna Mountains, wolves were uncommon. Wolves that periodically attempted to colonize portions of these areas usually did so where small bands of caribou overwintered. There, wolves were more vulnerable to human harvests because of sparse vegetation and extensive snow cover.

In nearby Denali National Park and Preserve, Dall sheep were preyed upon by wolves, but to a much lesser degree than caribou and moose (Murie 1944, Haber 1968). Murie (1944) suggested that predation on sheep was probably proportionately greater when wolf populations were relatively large. Wolf densities declined during our study, and much of the sheep habitat in GMU 13 was not occupied by wolves.

**Scat Analyses.**—Wolf scats were collected from den and rendezvous sites during 1975 through 1981. Food habits data obtained in this way provided a comparison with wolf kills noted from aircraft during spring and summer. As with aerial observations, analysis of scats showed that moose were the most common (52%) prey item (Table 9). Adult moose made up 9% of the prey and calves 42%. Ungulates of all species made up only 59% of the food items, and the remainder consisted of smaller prey that were less detectable from aerial observations during summer. When occurrence of food items was transformed to weight and number of prey using an equation developed by Floyd et al. (1978), calf and adult moose composed about 81% of the biomass consumed by wolves while at den and rendezvous sites (Table 10).

Mech (1977) determined that 1 Minnesota wolf pack declined after a winter

Table 10. Percent weight and numbers of individual prey consumed by wolves from mid-May through mid-July each year as determined from wolf scats collected at den and rendezvous sites in Game Management Unit 13 of south-central Alaska, 1975 through 1981.

Prey	Prey consumed														
	1975		1976		1977		1978		1979		1980		1981		
	Kg/ <sup>a</sup> scat <sup>a</sup>	% wt <sup>b</sup>	N <sup>c</sup>												
Adult moose <sup>d</sup>	8.98	67.7	132	40.2	90	32.7	45	36.6	37	39.2	44	62.7	61	44.2	34
Calf moose <sup>e</sup>	1.16	20.7	435	41.5	1,013	55.4	829	44.6	490	34.6	427	26.6	285	20.8	175
Adult caribou <sup>f</sup>	3.28	9.0	59	2.6	11	4.8	14	12.2	40	6.0	17	21.0	48		
Calf caribou <sup>f</sup>	0.62	1.4	97	3.1	246	2.4	117	2.1	75	5.7	229	0.5	17	2.4	66
Beaver <sup>g</sup>	0.63	4.3	286	2.1	160	2.7	126	7.3	250	2.5	96	1.5	50	4.8	126
Muskkrat <sup>h</sup>	0.41	0.1	59	0.7	476	1.3	542	1.7	520	0.9	309	0.6	179	2.0	470
Snowshoe hare <sup>i</sup>	0.42	5.4	2,494	2.2	1,163	1.7	551	2.4	571	2.4	642	1.4	324	1.8	329
Squirrel <sup>j</sup>	0.39	0.3	498	0.1	190	0.1	116	Tr <sup>k</sup>	26	0.0	0	0.0	0	0.0	0
Microtine rodent <sup>l</sup>	0.38	0.3	2,490	0.6	5,710	1.1	6,420	0.6	2,570	2.5	12,030	0.7	2,920	2.9	9,540
Totals	99.9	6,491	99.5	9,107	100.0	8,757	100.1	4,553	100.0	13,817	100.0	3,853	99.9	10,788	

<sup>a</sup> From Floyd et al. (1978); calculated by equation  $Y = 0.38 + 0.02X$ .

<sup>b</sup> Derived for each prey species by following formula: Y times no. scats for each prey species (from Table 9) divided by total kg of all species eaten.

<sup>c</sup> Derived by multiplying spring wolf population estimates from Table 2 times consumption rate of 5.8 kg/wolf/day times 61-day period times % weight of prey species consumed divided by weight of individual prey species.

<sup>d</sup> Assumed weight = 427.5 kg (from Franzmann and Bailey 1977).

<sup>e</sup> Assumed weight of 1-month-old moose calf computed as follows: newborn weight = 18.0 kg (from Franzmann et al. 1980a) with assumed weight gain of 1.0 kg/day for 21 days = 39.0 kg.

<sup>f</sup> Assumed weight of adult and calf caribou = 145.0 and 12.1 kg, respectively (from Skog 1968).

<sup>g</sup> Assumed weight = 12.1 kg (from Floyd et al. 1975).

<sup>h</sup> Assumed weight of muskrat and snowshoe hare = 1.4 and 1.8 kg, respectively (from Burt and Grossenbacher 1964).

<sup>i</sup> Assumed weight of squirrel and rodents = 0.5 and 0.1 kg, respectively (from Stephenson 1978b).

<sup>j</sup> Trace  $\leq 0.1\%$ .

when only 3.0–3.4 kg/wolf/day of food was killed, increased at 5.8 kg/wolf/day, and remained stable at 3.6 kg of food/wolf/day. Because wolf numbers were capable of increasing in GMU 13 and Mech's (1977) higher consumption estimate was closest to that found in this study (see Predation Rates, Winter), 5.8 kg of food/wolf/day was used as an estimate of consumption for conversion of scat data. Calculated values for percentage of each prey type killed by weight (Table 10) when wolves were present at either den or rendezvous sites (61-day period) were applied to this daily consumption rate. The numbers of each prey species killed were then calculated using mean weights of each prey species (Table 10). There were large annual variations in the estimated numbers of individual prey species killed by wolves based on extrapolations from scat analyses (Table 10). During 1975 through 1981, the estimated number of ungulate prey killed by wolves annually in GMU 13 during mid-May through mid-July ranged from 34 to 132 adult moose, 175 to 1,013 calf moose, 11 to 59 adult caribou, and 17 to 246 calf caribou.

*Age and Condition of Prey.*—One hundred forty remains of moose were examined *in situ* during this study to determine age, sex, and physical condition at time of death. An additional 79 examined in GMU 13 by Stephenson and Johnson (1972, 1973) and N. Steen (unpubl. data) during 1971 through 1974 were included in our analysis. Ninety-three percent of these moose died during December through May. Cause of death was assigned to 1 of 6 categories: (1) wolf predation ( $N = 137$ ); (2) incidental, including road kills, tagging mortalities, illegal and nuisance kills ( $N = 37$ ); (3) winter kill or starvation ( $N = 30$ ); (4) unknown causes ( $N = 8$ ); (5) brown and black bear predation ( $N = 5$ ); and (6) unknown predator ( $N = 2$ ).

Bone marrow fat of moose examined during this study reached relatively high levels by autumn and early winter ( $\bar{x} = 86\%$  for adults and 31% for calves). Fat levels for adults began declining in February ( $\bar{x} = 79\%$ ) and reached their lowest

during June ( $\bar{x} = 42\%$ ). No calf marrow fat values were obtained during late summer or autumn months, but fat levels were apparently declining by January, reaching their lowest level by April ( $\bar{x} = 17\%$ ). Similar patterns of marrow fat deposition and depletion have been described for moose on the Kenai Peninsula, Alaska (Franzmann and Arneson 1976, Peterson et al. 1984).

This and previous studies in GMU 13 (Stephenson and Johnson 1972, 1973) indicated that wolf predation was disproportionately heavy on calf moose during winter. Of particular importance, however, was the physical condition of individual moose upon which wolves were preying. If calves in poor condition were going to die regardless of whether they were killed by wolves, such losses would be nonadditive or indicate compensatory mortality, and wolf predation would have little or no significant effect on total mortality. If wolves killed healthy calves that would otherwise have survived, wolf predation would be additive mortality, and such predation might limit moose population growth.

Marrow fat levels of calf moose killed by wolves ( $\bar{x} = 31\%$ ) were not different from calves that died from incidental causes ( $\bar{x} = 24\%$ ), but were higher than those dead from starvation ( $\bar{x} = 12\%$ ,  $P < 0.05$ ) (Fig. 14). Marrow fat levels of starved calves also were lower ( $P = 0.07$ ) than those of calves that died from incidental causes. Franzmann and Arneson (1976) and Peterson et al. (1984) suggested that marrow fat values below 10% indicated starvation. In our study, 5 of 21 (24%) calves that were classified as starvation mortalities had fat  $> 10\%$ . These latter calves could have died from other causes but at least 3 of 5 were found lying on their sternum, which is purportedly a reliable indication of starvation (Stephenson and Johnson 1973). Other factors could have been involved in some of these calf deaths, but they were not killed by predators.

Marrow fat values and ages of adult cow moose that died of various causes during 1970 through 1982 were compared. No

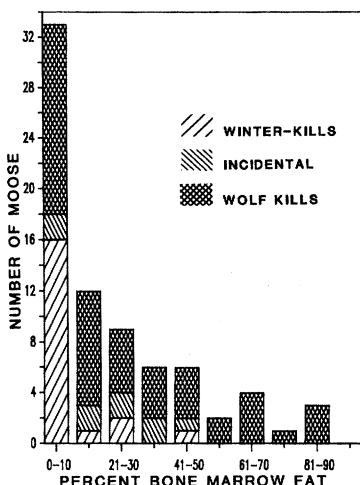


Fig. 14. Bone marrow fat in long bones of calf moose dying from wolf predation, incidental causes, and starvation within Game Management Unit 13 from 1970 through spring 1982.

differences were found between marrow fat levels of adult cow moose that died of incidental causes ( $\bar{x} = 79\%$ , SE = 4.8) and those killed by wolves ( $\bar{x} = 77\%$ , SE = 2.1). Adults that starved ( $\bar{x} = 52\%$ , SE = 15.3) had lower fat values ( $P < 0.05$ ) than adults killed by wolves and incidental causes.

Ages of dead cow moose were compared with cow moose live-captured during 1976 through 1982. Wolf-killed adult cows averaged 9.5 (SE = 0.7) years of age, whereas tagged adult cow moose averaged 7.7 (SE = 0.3) years of age (Fig. 15). Wolf-killed adults were older ( $P < 0.05$ ) than either tagged adults or moose that died from incidental causes ( $\bar{x} = 5.4$ , SE = 1.1) but younger than moose thought to have succumbed to starvation ( $\bar{x} = 14.5$ , SE = 0.7,  $P < 0.05$ ). Adults dead of starvation also were older ( $P < 0.05$ ) than tagged cows, and both types were older than those that died from incidental causes.

The age distribution of wolf-killed adult moose in GMU 13 was not different from age distribution of those killed by wolves on the Kenai Peninsula, Alaska (Peterson et al. 1984). Consequently, data from both Alaskan studies were pooled and compared with the age distribution of wolf-killed yearling and adult moose from Isle Royale, Michigan (Fig. 16) to determine

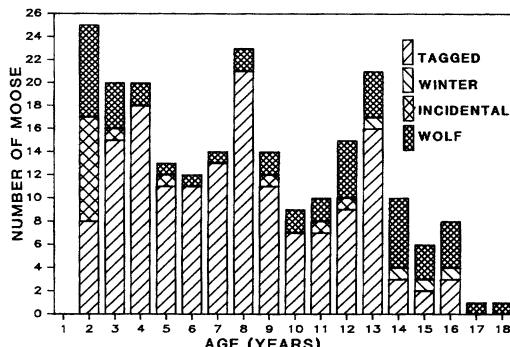


Fig. 15. Ages of adult cow moose by cause of death in relation to live-captured moose within Game Management Unit 13 from 1970 through 1982.

if differences occurred in the types of moose killed. Differences were found ( $P < 0.05$ ) between the 2 age distributions, with proportionately more yearlings and older adults killed by wolves in the Alaskan studies. Reasons for these differences are not known, but Peterson et al. (1984) suggested that middle-aged moose on the Kenai Peninsula may have been more resistant to wolf predation due to late onset of physical degeneration.

The tendency of wolves to kill calves and old adult moose has been reported elsewhere in the literature (Mech 1966, Peterson 1977, Gasaway et al. 1983, Peterson et al. 1984). The nutritional condition of wolf-killed moose in this study, as reflected by bone marrow fat, was similar to that of moose that died from incidental causes; the latter were assumed to represent the average condition of moose in the population. Based on bone marrow fat data alone, wolves were preying on calf and adult moose that were in better nutritional condition than moose that had apparently starved to death. However, statements concerning animal condition are often "one way" in that it is easier to detect debilitating conditions than to state with confidence that an animal was completely "healthy" (Mech and Delgiudice 1985). Undoubtedly, some of the classified kills were complicated by unknown debilitating factors, but there was no evidence to suggest that moose killed by wolves in the present study were unhealthy or abnor-

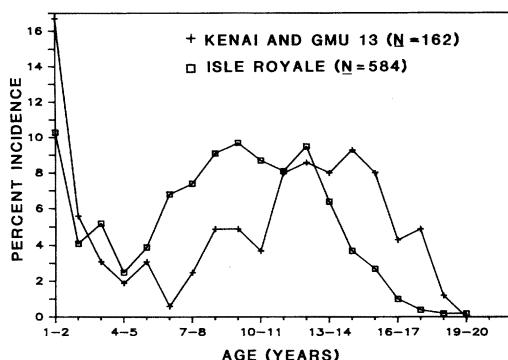


Fig. 16. Ages of adult moose killed by wolves from Isle Royale, Michigan, in comparison to those killed by wolves in this study (Game Management Unit 13) and the Kenai Peninsula, Alaska (from Peterson et al. 1984).

mal. On the Kenai Peninsula, Peterson et al. (1984) found that wolves preyed heavily on relatively old adult moose that had a high frequency of debilitating factors (33%) but were not malnourished. Wolves also preyed heavily on calves, but, in contrast to our study, a high proportion of the calves were malnourished (36% of kills had  $\leq 10\%$  marrow fat).

Twenty-four of 27 (89%) dead caribou examined during this study were killed by wolves. The mean age of wolf-killed adult caribou was 4.9 (SE = 0.6 years, range 1.5–10+ years). Because the caribou herd was increasing throughout the study period, the

low mean age of wolf-killed caribou may not reflect selection for any specific age class.

Percent marrow fat of wolf-killed adult caribou was variable, ranging from 8 to 81% ( $N = 21$ ). The small number of caribou that died from causes other than wolf predation precluded comparison of physical condition with those killed by wolves. Fifty-seven percent of the wolf-killed caribou were examined during the severe winter of 1978–79 (Eide and Ballard 1982). The large number of caribou carcasses examined during that winter reflected the increased vulnerability of caribou due to excessive snow accumulation (Eide and Ballard 1982).

## Predation Rates

Predation or kill rate is defined as the mean number of days per ungulate kill per pack. Because wolves usually consumed most or all edible flesh, estimates of consumption rates of flesh are similar to estimates of kill rates in terms of biomass unless indicated otherwise. Calculation of biologically meaningful predation rates was confounded in this study, as in many others, because of differences in size of ungulate prey. For example, calf moose have received equal weight with adult moose

Table 11. Summer predation rates of 4 wolf packs during 1977 through 1981 in south-central Alaska.

Pack name	Period located daily	No. days located	Wolves per pack	Kills found	Kills found <sup>a</sup> (adjusted to adult moose equivalent)	Observability of radio-marked wolves (%)	Kg prey/wolf/day <sup>a</sup>	Unadjusted predation (days/kill)	Adjusted predation rate <sup>a</sup> (days/kill)
Mendeltna Creek	27 May–15 Jul 77	50	7	11	6.8	84	6.3	4.5	7.3 <sup>b</sup>
Hogan Hill	28 May–21 Jun 78	25	8	6	2.7	85	4.4	4.2	9.2
Watana Creek	10 May–23 Jun 81	45	8	6	2.9	55	2.6	7.5	15.7
Watana Creek <sup>c</sup>	10 May–28 May 81	19	3	4	2.6	95	14.4	4.8	7.5
Mean		35	6.5	6.8	3.7	80	5.3	5.1	9.3

<sup>a</sup> Assumes unclassified caribou were adults and that unidentified kills were calf moose. Yearling brown bear weighs 45 kg (from Spraker et al. 1981) of which 75% is consumable, yielding 34 kg. Biomass of available food based upon following assumptions: weight of adult moose = 427 kg (from Franzmann and Bailey 1977) and yearling moose = 197 kg (from Franzmann and Arneson 1973, 1975) of which approximately 75% (from Peterson 1977) is available as food, yielding 321 kg and 148 kg, respectively. Adult caribou were assumed to weigh 145 kg (from Skoog 1968) with 75% consumable, yielding 109 kg of flesh. Newborn calf moose weighs 13 kg (from Ballard and Taylor 1978) and gains weight at rate of 1.3 kg/day (from Franzmann and Arneson 1973). Therefore, 15-day-old calf weighs 32 kg of which 90% is consumable, yielding 29 kg. Based on kg of edible flesh of 1 adult moose, the following species receive the following values for calculation of predation rates: adult moose = 1.0, yearling moose = 0.46, adult caribou = 0.34, newborn calf moose = 0.09, and yearling brown bear = 0.20.

<sup>b</sup> Includes 6 kills where 1 or more brown bears were present and 1 yearling brown bear was killed and eaten (Ballard 1982).

<sup>c</sup> Three wolves dispersed from original Watana Creek Pack.

and caribou, even though the amount of flesh available from each kill is substantially different. This problem was resolved for both summer and winter by adjusting predation rates based on biomass of edible flesh by species and age class so that the total number of kills was equivalent to 1 adult moose. For example, in other studies if 1 wolf pack had killed 1 calf moose, 1 adult caribou, and 1 adult moose within a 20-day period during winter, the kill rate would have been 1 kill/6.7 days. However, with the new method, the adjusted kill rate would be 1 kill/11.1 days because calf moose and adult caribou provide less edible meat than adult moose (see footnotes in Tables 11 and 14).

**Summer.**—To assess summer predation rates, 3 wolf packs were aerially located daily during late spring and summer of 1977, 1978, and 1980 in conjunction with studies of moose calf mortality and brown bear predation (Ballard et al. 1981c, 1982b). The lowest estimates of predation rates were obtained when observability of the wolves was lowest. Summer kill rates for packs with high observability (Table 11) were comparable to rates observed during winter. Even with excellent observability, some kills (especially small prey) were undoubtedly missed; therefore, actual summer predation rates were higher than those reported here. Predation rates for the Mendeltna Creek Pack may have been inflated because brown bears also were present at 6 of 11 kills, which confounded identification of which predator species made the kill. Regardless of which species was responsible, both eventually fed on the carcass (Ballard 1982). The Mendeltna Creek Pack may actually have had lower kill rates because they were able to scavenge bear kills; however, this does not indicate a lower consumption rate. If wolves were able to scavenge 50% of each kill, the kg of available food per wolf per day (Table 11) still falls within the ranges of predation and consumption rates reported for wolves during winter (next section). Calculated weights (kg) of prey per wolf per day for the other 3 packs also were similar to those obtained during winter (next section) and

are within the range of winter kill rates reported elsewhere (Mech 1970, 1977; Peterson 1977; Fuller and Keith 1980). Therefore, summer and winter predation rates (next section) are similar.

Peterson et al. (1984) concluded that predation rates were substantially lower in summer than winter on the Kenai Peninsula, Alaska, and consequently the wolves were in poorer condition and were primarily scavenging in summer. This speculation was based on the finding that Kenai wolves weighed less in summer, had lower hematological values, and had a lower number of observed kills per pack than during winter. Although these conditions warrant further study, the lower predation rates recorded by Peterson et al. (1984) were probably the result of low observability (15% observability of radio-collared wolves from aircraft in summer) and increased summer reliance on smaller prey.

**Winter.**—During 1979 and 1980, 5 wolf packs were aerially located every other day in late winter to determine species of prey and predation rates. Fixed-wing aircraft were used to backtrack each pack to their previous location to determine if kills occurred between relocation flights. If 50% or more of a kill was consumed, the kill was assumed made 1 day earlier. Because wolves were not tracked daily, some kills may have been missed. However, tracking conditions were typically good, and a large number of missed kills was unlikely. Regardless, estimated predation rates should be viewed as minimal.

The length of time a pack remained at a kill site was related to prey size and number killed (Table 12). The longest average period a pack remained at a kill ( $\bar{x} = 3.8$  days, range 2–5 days) occurred when both a cow and calf moose were killed. There was, however, considerable variation among packs. For example, the Tyone Creek Pack of 2 wolves remained at calf moose kills longer ( $\bar{x} = 4.0$  days) than other packs, whereas the Susitna Lake Pack of 9 wolves remained at adult moose kills the longest ( $\bar{x} = 3.3$  days). Average length of time wolves remained at adult moose kills was 2.7 days, which was similar to dura-

Table 12. Time spent in days at ungulate kills by 5 wolf packs during late winter 1979 and 1980 in south-central Alaska.

Pack name	Pack size	Year	Adult moose			Calf moose			Adult caribou			Calf and adult moose pair		
			N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range
Susitna Lake	9	1979	3	3.3	2-6	8	2.0					3 <sup>a</sup>	3.3	2-5
Tyone River	8	1980	2	2.0		5	3.0	1-8	1	2.0		1	5.0	
Susitna Lake	7	1980							4	2.0				
Susitna Lake	4	1980				2	2.0		2	3.0	2-4			
Tyone River	2	1979	5	2.6	1-6	2	4.0	3-5						
Weighted $\bar{x}$				2.7			2.5			2.3			3.8	

<sup>a</sup> Includes 1 cow and long yearling pair.

tions reported by Fuller and Keith (1980) for a wolf pack of 9-10 wolves in Alberta ( $\bar{x} = 2.5$  days). Wolves in GMU 13 ( $\bar{x}$  pack size = 6.0) remained at calf moose kills longer ( $\bar{x} = 2.5$  days) than wolves in Alberta ( $\bar{x} = 1.5$  days). Wolves remained at adult caribou kills an average of 2.3 days. Although correlations between pack size and length of time spent at kills were not significant, the smallest pack appeared to remain at kills longer and return to old kills more often than larger packs. For all packs, intervals between kills were greatest when larger prey had been killed (Table 13).

Smaller packs had longer intervals ( $\bar{x} = 5.2$  days) between adult moose kills than larger packs (range 1.5-2.0 days). Following calf moose kills the interval between kills ranged from 0 to 8 days for all packs. One pack of 9 wolves had a mean interval of only 0.1 day following calf kills, whereas packs of 4 and 2 wolves had means of 1.0 and 3.8 days, respectively. These intervals are less than those reported in Alberta where wolf packs did not make another kill for 3.6 and 5.8 days following calf and adult moose kills, respectively.

Substantial differences in diets existed both within and between winters for the 5 intensively studied packs (Table 14). Caribou were more abundant in the Susitna territory in 1980 than in 1979 and were preyed upon more heavily by wolves. With 1 exception, use of carcasses was uniformly heavy; thus the calculated prey biomass at each kill could be considered indicative of consumption. The Tyone pair frequently revisited kills over an extended period. The kills were heavily scavenged by ravens (*Corvus corax*) and red foxes (*Vulpes vulpes*). Excluding the Tyone pair, which killed 14.9 kg prey/wolf/day, consumption rates ranged from 4.5 to 8.0 kg/wolf/day. Pack size and consumption rates were inversely correlated ( $r = -0.91$ ,  $P < 0.05$ ) with smaller packs having more food available per wolf.

Observed rates of food consumption fall within the range of values reported elsewhere in North America where wolves prey primarily on moose. Peterson (1977) reported food availability of 4.4-10.0 kg/wolf/day for Isle Royale wolves during 1971 through 1974, whereas in Alberta, Fuller and Keith (1980) reported rates of

Table 13. Days between ungulate kills for 5 wolf packs during late winter 1979 and 1980 in south-central Alaska.

Pack name	Pack size	Year	After adult moose			After calf moose			After adult caribou		
			N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range
Susitna Lake	9	1979	4	2.0	0-6	7	0.1	0-1			
Tyone River	8	1980	2	1.5	0-3	4	4.0	1-8	2	3.0	2-4
Susitna Lake	7	1980	1	2.0					3	3.3	0-7
Susitna Lake	4	1980				1	1.0		2	0.0	
Tyone River	2	1979	5	5.2	0-11	4	3.8	0-8			
Weighted $\bar{x}$	6.0			3.3			2.1			2.3	

4.9 and 6.1 kg/wolf/day for 1 pack during 2 winters.

In northwestern Minnesota where whitetailed deer (*Odocoileus virginianus*) composed about 90% of the wolf diet by number, Fritts and Mech (1981) suggested that members of wolf pairs had higher rates of kill per wolf than larger packs. In GMU 13, adjusted kill rates per wolf were negatively correlated ( $r = -0.98$ ,  $P < 0.05$ ) with number of wolves per pack. Pairs had the largest kill rate per wolf. Pairs had more food available and remained at kill sites longer because it took them longer to consume a kill. Although the Tyone pair potentially had 30 kg of flesh available per day, actual availability was less due to scavenging by other species.

Peterson (1982) suggested that packs  $\geq 7$  wolves preyed upon ungulates at relatively constant rates regardless of differences in pack size. Adjusted pack kill rates and pack size for 5 wolf packs in GMU 13 were compared with those from Alberta (Fuller and Keith 1980) and Kenai Peninsula, Alaska (Peterson et al. 1984) (Fig. 17). All data were collected from intensively monitored radio-collared packs with high observability. Alberta data (Fuller and Keith 1980) were adjusted for the smaller size of moose in that area (from Peterson 1977). Pack size and adjusted kill rates were correlated ( $r = -0.77$ ,  $P < 0.01$ ); thus large packs kill ungulates more frequently than smaller packs (Fig. 17).

**Year-round.**—Mean kill rates, based upon numbers of kills observed per flight

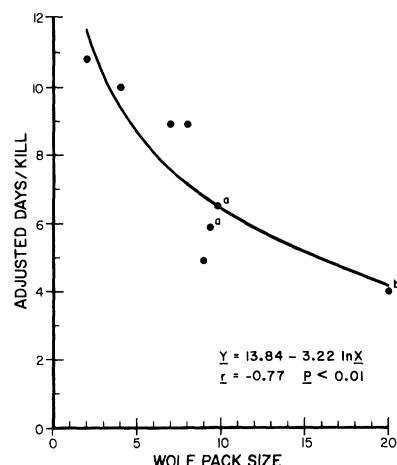


Fig. 17. Comparison of pack size with adjusted kill rates (1 adult moose equivalent) of wolf packs in Alaska and Canada, 1977–80. <sup>a</sup> Calculated from Fuller and Keith (1980) using mean pack size. <sup>b</sup> Calculated from Peterson et al. (1984).

for all packs but unadjusted for prey size, ranged from 1 kill/2.4 to 12.7 days and averaged 1 kill/5.4 days. Adjusted rates were lower, ranging from 1 kill/4.9 to 15.3 days, and averaged 1 kill/8.3 days. Fuller and Keith (1980) suggested that calculation of predation rates based upon average number of kills located per relocation would exaggerate kill rates because packs often remained at kill sites longer than 1 day. Therefore, the chance of observing them at a kill was greater than the actual kill rate. They determined that for 1 pack during 2 winters the average number of kills observed per flight remained constant at intervals exceeding 6 days between

Table 14. Kills observed, available prey per wolf per day, and estimated predation rates for 5 wolf packs intensively radio-tracked during late winter 1979 and 1980 in south-central Alaska.

Pack name	Pack size	No. days monitored	No. kills			Kg prey available/wolf/day <sup>a</sup>	Unadjusted days/kill	Adjusted days/kill <sup>b</sup>
			Adult moose	Calf moose	Adult caribou			
Susitna Lake	9	62	8	10	0	4,048	7.3	3.5
Tyone River	8	54	3	6	1	1,960	4.5	5.4
Susitna Lake	7	21	1	0	4	757	5.1	4.2
Susitna Lake	4	16	0	2	2	514	8.0	4.0
Tyone River	2	64	5	2	0	1,901	14.9	9.1
Total	30	217	17	20	7	9,180		10.8
Mean	6.0	43.4	3.4	4.0	1.4	2,053	7.1	4.9
								7.6

<sup>a</sup> Assumes 75% of prey biomass consumable, yielding following weight of food: adult moose = 321 kg, calf moose = 148 kg, and adult caribou = 109 kg.

<sup>b</sup> Calculated by assigning prey the following values based on biomass of edible flesh: adult moose = 1.0, calf moose = 0.46, and adult caribou = 0.34.

flights. We detected significant differences (analysis of covariance,  $P < 0.05$ ) in slopes of regression lines of kill rates among packs for flight intervals of 1–7 days. Correlation coefficients ( $r$ ) among packs ranged from 0.14 to 0.92 for linear, curvilinear, and logarithmic relationships in comparison with Fuller and Keith's (1980) log linear relationship of 0.93. Consequently, it was impossible to develop 1 correction factor for packs with 1–7-day intervals between flights. Although a correction factor based on intervals between flights would be desirable, additional investigation appears necessary to develop correction factors for packs of varying sizes.

All methods of estimating kill rates assume that all kills were observed. In this study there was large variation in observability among pack areas, and for some packs a large number of kills could have been missed. Also, it was possible to undercount kills at sites where multiple kills had been made, particularly kills of cow-calf pairs when all radio-collared wolves were at 1 kill site. At 10% of the kills brown bears were also present, and it was usually not determined which predator actually made the kill. Both average adjusted (adult moose equivalent) and unadjusted kill rates were similar to those obtained during intensive observation when intervals between flights were 1 day. Perhaps some of the biases and problems described by Fuller and Keith (1980) might be overcome by monitoring large numbers of packs over long periods. However, if accurate predation rate estimates are desired, investigators should strive to minimize intervals between wolf relocation flights.

## IMPACTS OF WOLVES ON THE MOOSE POPULATION

Impacts of wolf predation on the moose population were to be assessed by comparing calf and adult moose survival among areas with different wolf densities. As this study progressed, public wolf harvests outside the SRSA increased, and this caused a wolf population decline. Even though wolf densities averaged 57% lower in the

SRSA during the years of wolf control than in the remainder of GMU 13, wolf densities in both areas reached relatively low levels by spring 1978 (1.7 and 3.2 wolves/1,000 km<sup>2</sup> in the SRSA and remainder of GMU 13, respectively). Wolf densities in the SRSA were correlated ( $r = 0.37, P = 0.10$ ) with those in remainder of GMU 13 during spring 1975 through spring 1982 and for years (1976–78) of ADF&G wolf control ( $r = 0.88, P < 0.01$ ). Relatively low wolf densities in both the SRSA and remainder of GMU 13, combined with lack of moose population estimates before wolf control and biases associated with annual moose sex and age composition transects (Caughley 1974), provided inadequate data for evaluating the impacts of wolves on the moose population. However, there were other indicators that suggested reduced wolf densities may have increased moose survival.

Spring wolf densities in the SRSA were negatively correlated ( $r = -0.46, P = 0.13$ ) with subsequent autumn moose calf : cow (>2 years old) ratios from spring 1975 through spring 1982 (Fig. 18). A stronger negative correlation was evident during 1975 through 1978 when wolf control was occurring ( $r = -0.90, P < 0.05$ ). A similar relationship existed in the remainder of GMU 13 where ADF&G wolf control was not conducted but where wolf densities declined from public hunting and trapping. These correlations suggest that reduced wolf densities may have contributed to increased calf survival.

While wolf control was in progress, the causes of calf moose mortality were determined directly in 1977 and 1978 by radio collaring and monitoring 120 neonatal calves (Ballard et al. 1979, 1981b). Fifty-five percent of the radio-collared moose calves died during the first 6 weeks of life. Predation accounted for 86% of the natural deaths with predation by brown bears accounting for 91% of these deaths. Wolves, which were present at relatively low densities (2.7/1,000 km<sup>2</sup>), accounted for only 4–9% of the predation mortalities (Ballard et al. 1981b). Therefore, at relatively low wolf density, wolf predation was

of secondary importance as a calf moose mortality factor.

Additional estimates of the impacts of wolf predation on the moose population were derived by comparing estimates of adult and yearling moose killed by wolves in the SRSA in 1980–81 and 1983–84 with moose population estimates and survival rates of radio-collared moose. Comparison of recruitment in relation to numbers of adults killed by wolves provided an indication of whether the moose population was being limited by wolf predation. A similar method of evaluating the impacts of wolves on moose was used by Fuller and Keith (1980) in northeastern Alberta.

Estimates of moose mortality due to wolf predation for each year were divided into 3 time intervals based on changes in wolf population levels due to reproduction, mortality, and diet. The time intervals were (1) 1 June through 15 July, (2) 16 July through 31 October, and (3) 1 November through 31 May. Intervals 1 and 3 encompassed the wolf denning period (May through early Jul). Because pups were small, no food consumption was allocated until they were weaned. Interval 2 encompassed the postdenning period and represented the highest level of the wolf population (adults plus pups prior to hunting and trapping season) during the year. Pups were assumed to require 50% of the adult food requirements (Kuyt 1972). Interval 3 encompassed the wolf population's highest level during the year (prior to hunting and trapping season) and also the lowest level (posthunting and trapping season). Consequently, the midpoint between the 2 population estimates was used to provide an average number of wolves during winter. Pups were assumed to have food requirements similar to those of adults during this interval.

Estimates of percent biomass of moose consumed by wolves for interval 1 were based entirely on scat analyses according to methods described by Floyd et al. (1978). The analyses indicated that about 35% and 47% of the annual prey biomass was composed of calf and adult moose, respectively. Estimates of percent biomass during

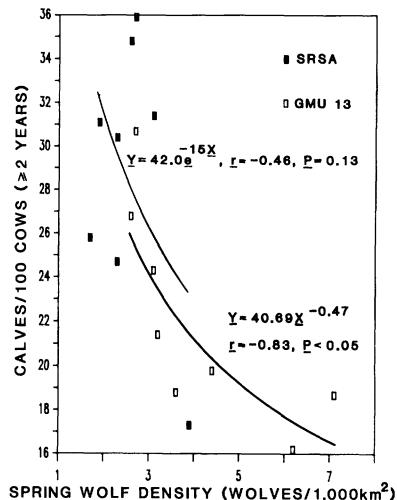


Fig. 18. Relationship of fall moose calf : cow ratios with previous spring wolf densities within the Susitna River Study Area and the remainder of Game Management Unit 13 of south-central Alaska during 1975 through 1982.

intervals 2 and 3 were determined from kills observed while monitoring radio-marked packs. Calf and adult moose composed 12% and 73% of the prey biomass during interval 2, and 17% and 68% during interval 3. For all 3 time intervals wolves were assumed to consume 7.1 kg prey/wolf/day during winter. Numbers of moose killed were estimated from average weights for each age class by time interval (derived from literature) and total biomass estimates.

Between 1 June 1980 and 31 May 1981, wolves were estimated to have killed 78 adult and yearling moose in a 2,435-km<sup>2</sup> portion of the SRSA (Appendix 3). This was equivalent to about 6% of the adults and yearlings present on 1 June 1980, which was considerably less than the recruitment of new yearlings the following spring (24%). Therefore, during 1980–81, wolf predation did not prevent growth of the moose population. However, yearling moose recruitment in 1980–81 was probably higher than normal as a result of a mild winter and a temporary 60% reduction of brown bear density (bears were translocated from area) in portions of the SRSA during 1979 (Ballard et al. 1980b, 1982b). Reduced bear densities resulted in

**Table 15.** Comparison of wolf and moose density estimates in late spring prior to moose parturition within the Susitna River Study Area from 1980 through 1984.

Density	1980	1981	1983	1984
Wolves (No./1,000 km <sup>2</sup> )	3.6	4.4	3.5	2.1
Moose (No./1,000 km <sup>2</sup> )	591	675	675	719
Moose/wolf	164	153	193	342

increased survival of calf moose in 1979 (Ballard et al. 1982b) but may have continued to affect moose survival the following year because only 60% of the adult bears returned to the area (Miller and Ballard 1982a,b). Regardless, these analyses suggest that wolf predation did not prevent the moose population from increasing during 1980–81.

During 1983–84 wolves were estimated to have killed 97 adults and yearlings in a 3,735-km<sup>2</sup> area of the SRSA (Appendix 4). This figure represents about 4% of the adults and yearlings present on 1 June 1983. As in 1980–81, estimated mortality from wolf predation was considerably less than estimated recruitment in spring 1984 (19%), indicating that wolf predation was not limiting moose population growth in that area.

Keith (1983) and Gasaway et al. (1983) examined the moose : wolf ratios necessary for wolf predation to stabilize a moose population. Based on an average potential finite rate of increase for moose (excluding hunting by man) of 1.16 calculated for the SRSA from Appendixes 3 and 4, Keith's (1983) model predicts that a ratio of 132 moose : wolf prior to calving would be sufficient to produce a stationary moose population if kill rates equaled 8.1 adult moose/wolf/year. Calculated moose : wolf ratios from late spring 1980 through late spring 1984 (Table 15) were not low enough to stabilize growth of this moose population.

Whether moose : wolf ratios were low enough for wolf predation to stabilize or cause a decline in the moose population prior to 1976, when this study began, remains unknown. However, wolf densities

were greater prior to 1976 than in either 1980–81 or 1983–84, and moose densities and recruitment were substantially lower as indicated by autumn moose sex and age composition surveys (ADF&G files, Anchorage). At the lower population and recruitment levels, wolf predation could have been a more important factor in preventing moose population growth even though numerically wolves were responsible for less moose mortality than were brown bears (Ballard et al. 1981b, 1982b, unpubl. data).

## Wolf and Prey Relationships

Within the past 2 decades, the diverse relationships between wolves and their prey have become better understood. Pimlott (1967), Keith (1974), and Bergerud (1983) concluded that in pristine North American ecosystems large predators generally controlled moose, deer, and caribou numbers. Numerous studies (Mech and Karns 1977; Bergerud 1978, 1980; Olson 1979; Gasaway et al. 1983; Keith 1983; Ballard and Larsen 1986) concluded that wolf predation could maintain declines in prey species or at least hold prey densities at low levels for extended periods. During this study, reductions in wolf numbers failed to dramatically and quickly improve calf survival; thus, other mortality factors became suspect. Calf mortality studies were initiated, and we now know that either brown bear (Ballard et al. 1981b), black bear (Franzmann et al. 1980b), or wolf (Gasaway et al. 1983) predation can produce the pattern of calf mortality observed in GMU 13.

No sensitive, fast-acting feedback mechanism regulates numbers of wolves relative to declining prey densities (Packard and Mech 1980). Because bears, unlike wolves, are not obligate carnivores, the regulatory feedback between bear and ungulate populations would be even looser and less sensitive than that acting on wolves. This phenomenon could increase the frequency and severity of predator-sustained declines in ungulate populations and decrease the likelihood that ungulate populations would escape control by predators

under natural conditions (Gasaway et al. 1983). The interrelationships in this predator : prey complex appear to lead to prolonged periods of ungulate scarcity. This could largely account for the scarcity of moose and caribou that has historically occurred in Alaska (Coady 1980, Gasaway et al. 1983). It is clear that maintaining at least moderate densities of wolves, bears, and their ungulate prey will be a complicated matter for wildlife managers attempting to provide for increasing human demands.

## CONCLUSIONS

1. Sizes of wolf pack areas were correlated with number of radiolocations, number of days an entire pack was located, and pack size. Distribution and density of ungulate prey influenced size of pack areas. Size of pack areas was not fully defined until each pack had been monitored >60 pack days. These latter areas were termed territories and averaged 1,644 km<sup>2</sup> (SE = 149). Wolves were distributed throughout areas <1,220 m elevation. Changes in distribution and boundaries of pack areas resulted from human exploitation and presence of other wolf packs. Pack areas (including territories) usually did not overlap, but when overlaps occurred they were normally separated by season of use. Annual variation in use of peripheral areas was observed. Wolves did not follow migratory moose or caribou across pack area boundaries but did follow seasonal elevational movements of moose within them.
2. Periodically, members of individual wolf packs were observed in temporary association with other packs. Such encounters usually preceded dispersal, but sometimes these associations resulted in wolf mortality, particularly when >2 wolves/pack were involved. About one-fourth (28%) of the radio-collared wolves dispersed from their original territory, and males commonly dispersed more than females. Dispersal most often occurred during spring and autumn. Dispersing wolves attempted to colonize vacant habitat, although 8 (21%) were accepted into existing packs. Most "lone" wolves were dispersers apparently attempting to locate vacant habitat and/or suitable mates.
3. Den sites usually were located near the center of pack areas, and the average distance between dens of adjacent packs was 45 km. Wolves began frequenting den sites by mid-April. Parturition occurred throughout the month of May. Den sites usually were abandoned in July, and 1–2 rendezvous sites were used through August.
4. Predator control greatly reduced wolf densities in GMU 13 in the early 1950's. When control ceased, wolf numbers gradually increased and probably peaked in 1965, with maximum estimates ranging from 350 to 450. By autumn 1975, the population was estimated at about 425 wolves.
5. Wolf densities ranged from 10.3 wolves/1,000 km<sup>2</sup> in autumn 1975 to 2.6/1,000 km<sup>2</sup> in spring 1982. Annual changes in density resulted from intensive hunting and trapping, wolf control, natural mortality, and dispersal. Wolf numbers declined during the study and reached a low of 109 by spring 1982. Observed wolf litter sizes ranged from 2 to 9 pups. Average litter size at implantation, based on counts of placental scars, was 6 pups. Mean litter size per pack in late summer varied from 3.7 to 7.3 pups with smallest litters occurring during years of highest wolf and lowest moose densities. At least 3 packs (7%) produced 2 litters at separate dens. There was no relationship between numbers of adults per pack in spring and numbers of pups surviving to November each year.
6. Annual adult wolf survival rates varied from 0.45 to 0.77, averaging 0.59. Yearling wolf survival rates were similar to those of adults, and both exceeded pup survival rates, which averaged 0.36. Mortality from all sources

- in excess of 50% of autumn numbers resulted in population declines. Intra-specific strife and other natural causes composed 20% of annual wolf mortality whereas the remaining mortality resulted from legal (46%) and illegal (34%) harvest. Human harvests >40% of autumn wolf numbers caused wolf population declines. Annual finite rates of increase for the wolf population, within portions of GMU 13 not subjected to wolf control, ranged from 0.77 to 1.01. This wolf population was limited by human exploitation.
7. During 1976 through summer 1978, wolf numbers were reduced by ADF&G wolf control in a 7,262-km<sup>2</sup> portion of GMU 13. Wolf numbers were reduced by about half from pre-control levels. Wolves annually repopulated the area through immigration and reproduction. While control was occurring, annual finite rates of increase ranged from 0.57 to 0.81. When control ceased, the wolf population increased with annual finite rates of increase ranging from 1.04 to 2.40. Within 1 denning season following termination of control, wolf densities recovered to within 81% of precontrol levels.
  8. Wolf packs were observed on 439 kills, 70% of which were moose. Ten percent of the kills were shared with brown bears. During late spring through midautumn, wolves preyed on moose calves slightly less or in proportion to their occurrence in the population. During the remainder of the year, moose calves were preyed upon proportionately more than their occurrence in the moose population. Yearling moose may have been killed disproportionately to their occurrence during May through July. Caribou were the second most important wolf prey. Analysis of wolf scats collected from den and rendezvous sites generally supported data collected by aerial observation during late spring and early summer.
  9. Percent marrow fat of wolf-killed calf and adult moose was similar to those that died from incidental causes, which presumably represented the average range of conditions of moose in the population. Percent marrow fat of wolf-killed moose was significantly higher than moose that died from starvation. Wolf-killed adult cow moose were older than live-captured moose or those that died from incidental causes. Relatively old adults and yearling moose made up a higher proportion of the wolf kills from GMU 13 and the Kenai Peninsula, Alaska, than at Isle Royale, Michigan.
  10. Wolf predation rates based on biomass equivalent to 1 adult moose were similar between winter and summer. Summer predation rates ranged from 1 kill/5 to 16 days/pack, whereas winter rates ranged from 1 kill/5 to 11 days/pack. Larger packs killed ungulates more frequently than smaller packs, but kill rates per wolf were higher for smaller packs. During winter, wolves killed and consumed 7.1 kg of prey/wolf/day. The length of time a pack remained at a kill depended on the size and number of kills and pack size. Small packs remained at kills longer than large packs. Packs remained at calf and adult moose kill sites an average of 2.5 and 2.7 days, respectively.
  11. Impacts of reduced wolf densities on the moose population were difficult to assess. Autumn calf : cow ratios were negatively correlated with the previous spring wolf population, suggesting that moose recruitment had improved as a result of lower wolf densities. Calf moose mortality studies indicated that predation by brown bears was of greater magnitude than predation by wolves.
  12. Comparison of yearling moose recruitment rates in 1980–81 and 1983–84 with estimated mortality due to wolf predation indicated that wolf predation was not preventing moose population growth at that time. Examina-

tion of moose:wolf ratios suggested that in the mid-1970's wolf predation may have been more important in limiting growth of the moose population.

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Received 1 April 1986.

Accepted 6 January 1987.

## APPENDIXES

Appendix 1. Status of wolves radio-collared in Game Management Unit 13 of south-central Alaska during April 1975 through April 1982.<sup>a</sup>

Original pack affiliation	I.D. number	Date radio-collared	Age <sup>b</sup>	Color	Sex	Weight (kg)	Radio-locations (N)	Month and year radio contact lost or mortality occurred	Ultimate or suspected fate as of 30 Apr 82 <sup>c</sup>
Brushkana Creek	983	20 Apr 75	Adult	Black	F	41	31	Jan 76	?
B-S Lake	367	07 Dec 81	Adult	Gray	F		14		Alive
B-S Lake	368	07 Dec 81	Adult	Gray	M	43	14		Alive
B-S Lake	405	11 Apr 82	Adult	Gray	M	45	3		Alive
Butte Lake	984	20 Apr 75	Adult	Black	M	46	23	Jan 76	ADFG control
Deadman Lake	981	20 Apr 75	Adult	Gray	M	42	35	Mar 76	ADFG control
Deadman Lake	982	20 Apr 75	Adult	Gray	F	49	28	Mar 76	ADFG control
Deep Creek	067	22 Mar 76	Adult	Gray	M	46	46	Mar 77	ADFG control after dispersal (48)
Deep Lake	993	22 Mar 76	Adult	Gray	F	43	58	Oct 76	Dispersal suspected (32)
Deep Lake	009	29 Oct 76	Adult	Gray	F	39	87	Feb 79	Killed by Susitna wolves
Deep Lake	096	13 Nov 77	Adult	Gray	M	50	11	Jan 78	Ground shot
Deep Lake	204	10 Apr 78	Pup	Gray	M	45	18	Jul 78	Dispersal
Deep Lake	212	19 Nov 78	Adult	Black	M	42	10	Feb 80	Ground shot after dispersal (56)
Delta River	997	06 Jun 75	Adult	Gray	M	44	21	Nov 75	Natural mortality; cause unknown
Delta River	998	06 Jun 75	Pup	Gray	M	23	1	Jan-Mar 75	Trapped
Delta River	063	21 Mar 77	Adult	Gray	M	33	4	Mar 77	Dispersal (192)
Delta River	064	21 Mar 77	Adult	Gray	F	47	2	Apr 79	ADFG control in Unit 20A after dispersal (192)
Eureka	352	15 Nov 81	Yearling	Gray	F	34	10		Alive
Ewan Lake	990	15 Apr 75	Adult	Gray	F	39	148	Oct 76	Dispersal (46)
Ewan Lake	991	04 Nov 75	Adult	Gray	M	39	11	Jan 76	Killed by St. Anne wolves after dispersal (32)

## Appendix 1. Continued.

Original pack affiliation	I.D. number	Date radio-collared	Age <sup>b</sup>	Color	Sex	Weight (kg)	Radio-locations (N)	Month and year radio contact lost or mortality occurred	Ultimate or suspected fate as of 30 Apr 82 <sup>c</sup>
Ewan Lake	992	04 Nov 75	Pup	Gray	M	25	17	Dec 75	Trapped
Ewan Lake	151	16 Mar 78	Pup	Gray	F	29	6	Mar 78	Killed by moose
Ewan Lake	219	17 Nov 78	Pup	Gray	M	24	4	Mar 79	Trapped after dispersal (128)
Fish Lake	326	14 Apr 81	Adult	Gray	F	42	25		Alive
Fish Lake	327	14 Apr 81	Pup	Gray	M	43	21		Alive
Fish Lake	329	17 Apr 81	Pup	Gray-blk	F	26	14	Feb 82	Trap-related starvation
Fish Lake	350	14 Nov 81	Adult	Gray	F	36	14		Alive
Fish Lake	351	11 Nov 81	Pup	Gray	F	27 <sup>d</sup>	14		Alive
Gakona River	999	18 Mar 76	Adult	Gray	M	50	2	Aug 76	Auto collision
Gakona River	217	16 Nov 78	Adult	Gray	F	45	3	Dec 78	Ground shot
Gakona River	218	16 Nov 78	Adult	Black	M		6	Feb 79	Ground shot
Hogan Hill	987	06 Jun 75	Yearling	Gray	F	31	104	Jan 79	Ground shot
Hogan Hill	988	05 Nov 75	Adult	Gray	M	40	62	Apr 77	Dispersal (64)
Hogan Hill	202	08 Apr 78	Adult	Gray	M	49	52	Jan 79	Ground shot
Hogan Hill	205	09 Apr 78	Pup	Gray	M	37	51	Jan 79	Ground shot
Hogan Hill	206	09 Apr 78	Pup	Gray	F	36	37	Sep 78	Dispersal suspected (46)
Jay Creek	355	30 Nov 81	Pup	Gray	M		7	Feb 82	
Jay Creek	356	30 Nov 81	Pup	Gray	F	31	7	Feb 82	Illegally shot
Jay Creek	357	30 Nov 81	Pup	Gray	F		7	Feb 82	Illegally shot
Jay Creek	358	30 Nov 81	Pup	Gray	M		7	Feb 82	Illegally shot
Jay Creek	365	06 Dec 81	Adult	Gray	F	41	5	Feb 82	Illegally shot
Keg Creek	986	20 Apr 75	Adult	Black	M	45	101	Mar 76	Illegal aerial shooting
Keg Creek	083	20 Apr 75	Adult	Gray	M	43	191	Feb 78	Ground shot after dispersal (72)
Keg Creek	002	20 Apr 75	Adult	Black	F	37	147	Jul 76	ADF&G control after dispersal (40)
Keg Creek	068	21 Mar 76	Adult	Black	F	42	74	Mar 77	ADF&G control
Keg Creek	201	21 Mar 76	Yearling	Gray	F	34	71	Feb 79	Illegal aerial shooting
Keg Creek	010	29 Oct 76	Pup	Gray	F	24	23	Mar 77	ADF&G control
Keg Creek	011	29 Oct 76	Pup	Gray	M	24	24	Mar 77	ADF&G control
Keg Creek	203	09 Apr 78	Adult	Gray	M	47	53	Feb 79	Illegal aerial shooting
Lower MacLaren	369	05 Dec 81	Adult	Black	F	34	13		Alive
MacLaren River	985	21 Apr 75	Adult	Gray	F	35	51	Jan 76	ADF&G control
Mendeltna Creek	007	29 Oct 76	Adult	Black	F	33	124	Feb 78	Ground shot
Mendeltna Creek	008	29 Oct 76	Pup	Gray	M	24	119	Nov 77	Killed by Tyone wolves after dispersal (22)
Mendeltna Creek	095	13 Oct 77	Adult	Gray	F	39	13	Feb 78	Ground shot
Mendeltna Creek	090	13 Oct 77	Pup	Gray	M	23	13	Feb 78	Ground shot
Middle Fork	996	21 Mar 76	Yearling	Gray	F	36	2	May 76	Unknown
Middle Fork	062	21 Mar 76	Pup	Gray	F	29	3	Mar 77	Collaring mortality
Middle Fork	078	21 Mar 76	Pup	Gray	M	30	2	Jan 78	Ground shot
Middle Fork	061	21 Mar 76	Pup	Gray	M	31	24	Jan 78	Ground shot
Middle Fork	085	28 Apr 77	Pup	Gray	F	37	18	Feb 78	Ground shot
Portage Creek	361	02 Dec 81	Adult	Gray	M	50 <sup>d</sup>	9		Alive
Portage Creek	362	02 Dec 81	Adult	Gray	F		5	Apr 82	Suspect illegally shot
Portage Creek	363	02 Dec 81	Pup	Gray	F		10		Alive

## Appendix 1. Continued.

Original pack affiliation	I.D. number	Date radio-collared	Age <sup>b</sup>	Color	Sex	Weight (kg)	Radio-locations (N)	Month and year radio contact lost or mortality occurred	Ultimate or suspected fate as of 30 Apr 82 <sup>c</sup>
Portage Creek	364	02 Dec 81	Pup	Gray	F	27 <sup>d</sup>	3	Jan 82	Suspect illegally shot
Portage Creek	403	10 Apr 82	Adult	Gray	F	48	2		Alive
Portage Creek	404	10 Apr 82	Pup	Gray	F		2		Alive
Snodgras Lake	366	06 Dec 81	Yearling	Gray	F	43	9		Alive
St. Anne Lake	086	28 Apr 77	Pup	Gray	M	41	3	May 77	Dispersed (?)
St. Anne Lake	088	28 Apr 77	Adult	Gray	M	45	37	Jun 78–Mar 79	Drowned after dispersal (51)
St. Anne Lake	087	28 Apr 77	Pup	Gray	M	37	4	May 77	Dispersal (48)
St. Anne Lake	093	11 Oct 77	Adult	Gray	M	40	8	Feb 78–Sep 79	Natural mortality; unknown after dispersal (128)
St. Anne Lake	094	12 Oct 77	Adult	White	F	33	79		Alive
St. Anne Lake	118	10 Feb 78	Adult	Gray	M	42	9	Apr 78	Dispersal (732)
St. Anne Lake	209	26 Feb 78	Pup	Gray	F		26	Apr–Dec 79	Starvation after dispersal (128)
St. Anne Lake	207	10 Apr 78	Pup	Gray	M	48	10	Apr 78	Dispersal (732)
St. Anne Lake	208	10 Apr 78	Pup	Gray	F	38	9	Aug 78–Sep 79	Dispersal (141)
St. Anne Lake	292	31 Mar 79	Pup	Gray	M	34	15	Jun 80	Dispersal (?)
St. Anne Lake	293	31 Mar 79	Adult	Gray	M	42	9	Jan 80	Dispersal (145)
St. Anne Lake	314	14 Oct 80	Adult	Black	M	43	16		Alive
St. Anne Lake	353	16 Nov 81	Yearling	Gray	M	42	7		Alive
St. Anne Lake	354	15 Nov 81	Pup	Gray	F	33	8		Alive
Sinona Creek	989	20 Apr 75	Adult	Gray	F	39	85	May 76	Unknown
Sinona Creek	038	05 Nov 75	Adult	Gray	M	48	70	Feb 77	Ground shot
Sinona Creek	048	05 Nov 75	Adult	Gray	M	39	108	Jan 79	Unknown
Sinona Creek	049	14 Mar 77	Adult	Gray	M		2	Mar 77	Ground shot
Sinona Creek	084	28 Apr 77	Adult	Gray	F	51	32	Dec 78	Ground shot
Sinona Creek	213	16 Nov 78	Pup	Gray	F	27	4	Dec 78	Suspect illegal harvest
Sinona Creek	214	16 Nov 78	Pup	Gray	F	27	3	Dec 78	Ground shot
Stephan Lake	016	19 Feb 76	Adult	Gray	F	34	24	Oct 76	Killed by bear or wolf
Susitna Lake	227	06 Feb 79	Pup	Gray	M	45	24	Apr 79	Probable radio failure
Susitna Lake	228	06 Feb 79	Pup	Gray	M	45	43	Apr 79	Probable radio failure
Susitna Lake	229	06 Feb 79	Pup	Gray	M	43	77	Jan 82	Killed by Tolsona wolves after dispersal (77)
Susitna Lake	230	06 Feb 79	Pup	Gray	M	45	47	Jan 80	Unknown
Susitna Lake	294	28 Mar 79	Pup	Gray	F	36	27	Apr 79	Unknown
Susitna Lake	295	25 Mar 79	Adult	Gray	F	43	153	Nov 81	Unknown
Susitna Lake	296	25 Mar 79	Adult	Gray	M	49	53	Mar 80	Killed by wolves
Susitna Lake	302	20 Feb 80	Pup	Gray	F		111	May 81	Killed by Watanawolves
Susitna Lake	303	20 Feb 80	Yearling	Gray	M	36	9	Mar 80	Killed by wolves
Susitna Lake	305	13 Apr 80	Adult	Gray	M	45	45	Mar 81	Ground shot
Susitna Lake	306	13 Apr 80	Pup	Gray	M	39	59		Dispersal (77); alive
Susitna Lake	330	17 Apr 81	Yearling	Gray	M	44 <sup>d</sup>	26		Dispersal (182); alive

## Appendix 1. Continued.

Original pack affiliation	I.D. number	Date radio-collared	Age <sup>b</sup>	Color	Sex	Weight (kg)	Radio-locations (N)	Month and year radio contact lost or mortality occurred	Ultimate or suspected fate as of 30 Apr 82 <sup>c</sup>
Susitna Lake	349	13 Nov 81	Yearling	Gray	M	50	51	Feb 81	Killed by ground shooting
Susitna Lake	331	17 Apr 80	Yearling	Gray	M	48	31	Apr 81	ADF&G control in GMU 20 after dispersal (182)
Susitna-Sinona	312	14 Oct 80	Pup	Gray	F	21	3	Nov 80	Trapped
Susitna-Sinona	313	14 Oct 80	Adult	Gray	M	48	17		Dispersal (83); alive
Talkeetna River	359	02 Dec 81	Adult	Gray	M	33	4	Feb 82	Suspect illegal harvest
Talkeetna River	360	02 Dec 81	Yearling	Black	F	41	4	Feb 82	Suspect illegal harvest
Tolsona Ridge	210	08 Jun 78	Adult	Gray	M	47	63		Dispersal (96); alive
Tolsona Ridge	220	22 Jan 79	Pup	Black	F	32 <sup>d</sup>	133		Alive
Tolsona Ridge	289	28 Mar 79	Pup	Gray	F	26		Dec 79	Dispersal suspected
Tolsona Ridge	290	28 Mar 79	Pup	Gray	M	38	24	Oct 79	Dispersal suspected
Tolsona Ridge	291	28 Mar 79	Pup	Gray	F	32	5	Dec 79	Trapped
Tolsona Ridge	315	16 Oct 80	Yearling	Gray	M	37	41	Nov 81	Recapture mortality
Tolsona Ridge	316	16 Oct 80	Adult	Gray	M	44	25	Apr 81	Unknown
Tolsona Ridge	328	14 Apr 80	Yearling	Gray	F	32	14		Dispersal (70); alive
Tolsona Ridge	347	11 Nov 81	Pup	Gray	M		7	Apr 82	Suspect illegal harvest
Tolsona Ridge	348	11 Nov 81	Yearling	Gray	M	43	6	Apr 82	Suspect illegal harvest
Tsusena Creek	994	20 Feb 76	Adult	Gray	M	39	4	May 76	Unknown
Tsusena Creek	199	17 Feb 76	Adult	Gray	F	36	64	Feb 82	Illegally shot after dispersal (199)
Tsusena Creek	056	19 Mar 77	Adult	Gray	M	42	1	Mar 77	Suspect illegal harvest
Tsusena Creek	057	19 Mar 77	Pup	Gray	F	33	1	Mar 77	Suspect illegal harvest
Tyone Creek	001	18 Feb 76	Adult	Gray	M	47	37	Jul 76	ADF&G control
Tyone Creek	995	16 Feb 76	Adult	Gray	F	36	15	Mar 76	ADF&G control
Tyone Creek	097	15 Nov 77	Adult	Gray	M	51	5	Jan 78	Ground shot
Tyone Creek	098	15 Nov 77	Pup	Gray	M	42	8	Feb 78	Illegal aerial hunting
Tyone Creek	099	15 Nov 77	Adult	Gray	M	51	5	Jan 78	Ground shot
Tyone Creek	115	10 Feb 78	Adult	Gray	F	42	2	Feb 78	Ground shot
Tyone Creek	116	10 Feb 78	Adult	Gray	M	51	20	Oct 78	Dispersal (96)
Tyone Creek	117	10 Feb 78	Adult	Gray	M	48	2	Feb 78	Ground shot
Tyone Creek	215	18 Nov 78	Adult	Gray	M	46	81	Mar 80	Illegal harvest
Tyone Creek	216	17 Nov 78	Adult	Gray	F	41	68	Mar 80	Illegal harvest
Tyone Creek	298	20 Feb 80	Pup	Gray	F	38	42	Dec 80	Suspect illegal harvest
Tyone Creek	299	20 Feb 80	Pup	Gray	F	37	37	Jan 81	Trapped after dispersal (256)
Tyone Creek	300	20 Feb 80	Pup	Gray	M	42	54		Dispersal (104); alive

## Appendix 1. Continued.

Original pack affiliation	I.D. number	Date radio-collared	Age <sup>b</sup>	Color	Sex	Weight (kg)	Radio-locations (N)	Month and year radio contact lost or mortality occurred	Ultimate or suspected fate as of 30 Apr 82 <sup>c</sup>
Tyone Creek	301	20 Feb 80	Pup	Gray	M	45	14	Mar 80	Illegal harvest
Tyone Creek	317	16 Oct 80	Adult	Black	M		5	Dec 80	Suspect illegal harvest
Watana Creek	197	20 Mar 78	Adult	Gray	M		5	Apr 78	Dispersal
Watana Creek	308	24 Apr 80	Adult	Gray	F	41	114		Alive
Watana Creek	309	19 Apr 80	Pup	Gray	F	36	14	Apr 82	Recapture mortality
Watana Creek	310	23 Apr 80	Adult	Gray	M	46	67	Feb 82	Ground shot
Watana Creek	311	23 Apr 80	Yearling	Gray	M	51	18	Aug 80	Ground shot
Watana Creek	323	07 Mar 81	Pup	Gray	F	42	64		Alive
Watana Creek	324	07 Mar 81	Pup	Gray	F	41	57		Alive
Watana Creek	325	07 Mar 81	Pup	Gray	M	50	55		Dispersal (112); alive
Watana Creek	344	10 May 81	Yearling	Gray	M	29	35		Dispersal (109); alive
Watana Creek	345	10 May 81	Yearling	Gray	M		50		Alive
Watana Creek	346	10 May 81	Yearling	Gray	F	35	55		Alive
Watana Creek	400	09 Apr 82	Adult	Gray	M	54	2		Alive
Watana Creek	401	09 Apr 82	Adult	Gray	M		2		Alive
Watana Creek	402	09 Apr 82	Pup	Gray	F	39	2		Alive

<sup>a</sup> Data for 1975–76 from Stephenson (1978b); does not include 1 capture-related mortality.<sup>b</sup> Pup <12 months; Yearling 12–23 months; Adult ≥24 months.<sup>c</sup> When dispersal was suspected or occurred, known distance is given in km in parentheses.<sup>d</sup> Estimated weight.

Appendix 2. Summary of location observations of radio-collared wolf packs in the Susitna and Nenana River basins of south-central Alaska from April 1975 through April 1982.

## Appendix 2. Continued.

Pack	Combined no. radio-collared wolves	Combined no. individual radio-locations	No. wolf sightings	No. pack days <sup>a</sup>	Pack	Combined no. radio-collared wolves	Combined no. individual radio-locations	No. wolf sightings	No. pack days <sup>a</sup>
Brushkana Creek	1	31	109	34	Middle Fork	5	49	60	27
B-S Lake	3	31	38	14	Portage Creek	6	31	47	12
Butte Lake	1	23	41	31	St. Anne Lake	14	240	478	104
Coal Creek	1	19	18	18	Sinona Creek	7	304	844	170
Deadman Lake	2	63	67	38	Snodgrass Lake	2	21	20	12
Deep Lake	6	210	343	145	Stephan Lake	1	24	16	24
Delta River	4	27	43	20	Susitna Lake	14	667	1,004	224
Eureka	2	20	22	10	Susitna-Sinona	3	48	99	38
Ewan Lake	5	181	354	151	Talkeetna River	2	8	7	5
Fish Lake	6	111	103	29	Tolsona Ridge	10	343	1,172	168
Gakona River	3	11	13	8	Tsusena Creek	4	16	7	1
Hogan Hill	5	306	746	176	Tyone River	15	401	622	199
Jay Creek	6	85	147	50	Watana Creek	14	517	544	134
Keg Creek	8	568	958	240	Totals	156 <sup>b</sup>	4,810	8,970	2,274
Lower Maclarens River	1	13	16	13					
Maclarens River	1	51	119	52					
Mendeltna Creek	4	391	913	128					

<sup>a</sup> Pack day defined as 1 day when 1 or more pack members were located >1 occasions.<sup>b</sup> Does not correspond with total number of wolves radio-collared because some wolves became members of other packs.

**Appendix 3.** Estimation of numbers of adult and new yearling moose on 1 June 1980 in relation to estimates of recruitment (proportion of new yearlings) and mortality through 31 May 1981 within a 2,435-km<sup>2</sup> portion of the Susitna River Study Area.

Purpose of calculation	Data required for calculations	Calculated values
To estimate no. of adult and yearling moose on 1 Jun 1980 in 2,435-km <sup>2</sup> portion of SRSA.	No. of new yearlings alive on 1 Jun 1980 = (fall 1980 yearling moose pop. est. <sup>a</sup> × mortality rate <sup>b</sup> ) + fall 1980 yearling pop. est. <sup>a</sup> + est. wolf predation <sup>c</sup> ) = (287 × 0.049) + 287 + 6 =	307
	No. of adult cows alive on 1 Jun 1980 = (fall 1980 cow pop. est. <sup>a</sup> × mortality rate <sup>b</sup> ) + fall 1980 cow pop. est. <sup>a</sup> = (925 × 0.024) + 925 =	947
	No. of adult bulls alive on 1 Jun 1980 = (fall 1980 bull pop. est. <sup>a</sup> × mortality rate <sup>b</sup> ) + fall 1980 bull pop. est. <sup>a</sup> + hunting mortality <sup>d</sup> = (76 × 0.000) + 76 + 63 =	139
	Total no. adult cows and bulls + wolf predation <sup>c</sup> = 947 + 139 + 22 =	1,108
	Total adults and new yearlings alive on 1 Jun 1980 = 1,108 + 307 =	1,415
To estimate recruitment (proportion of new yearlings) to census area moose population on 1 Jun 1981.	No. of adults (bulls + cows) alive on 1 Jun 1981 = (fall 1980 est. <sup>a</sup> × survival rate <sup>b</sup> ) – est. wolf predation <sup>c</sup> = (1,001 × 0.989) – 38 =	952
	No. of yearlings becoming adults on 1 Jun 1981 = (fall 1980 est. <sup>a</sup> × survival rate <sup>b</sup> ) – est. wolf predation <sup>c</sup> = (287 × 0.985) – 11 =	272
	Total no. adults and yearlings becoming adults = 952 + 272 =	1,224
	No. calves becoming new yearlings on 1 Jun 1981 = (fall 1980 est. <sup>a</sup> × survival rate <sup>b</sup> ) – est. wolf predation <sup>c</sup> = (441 × 0.952) – 25 =	395
	Proportion of new yearlings in moose pop. on 1 Jun 1981 = 395 ÷ (395 + 1,224) =	0.24

<sup>a</sup> Numbers of moose in early Nov 1980 were estimated from intensive aerial census (Gasaway et al. 1981). Nov 1980 total moose population estimate was 1,728 ± 182 (90% CI) comprised of the following estimated sex and age composition: yearlings = 287, calves = 441, adult cows ≥2 years of age = 925, and adult bulls ≥2 years of age = 76 (W. Ballard, unpubl. data).

<sup>b</sup> Seasonal survival and mortality rates from 1 Jun through 31 Oct 1980 and from 1 Nov 1980 through 31 May 1981 based on radio-collared moose (W. Ballard, unpubl. data) using Trent and Rongstad (1974) method of calculation. All rates exclude wolf predation, which was estimated independently.

<sup>c</sup> Wolf densities and estimated numbers of moose kills/time interval for 2,435-km<sup>2</sup> moose-census area were as follows: 1 Jun through 15 Jul 1980—3.6 wolves/1,000 km<sup>2</sup>, kill estimated at 3 adults and 1 yearling; 16 Jul through 31 Oct 1980—7.4 wolves/1,000 km<sup>2</sup>, kill estimated at 19 adults and 5 yearlings; and 1 Nov 1980 through 31 May 1981—5.9 wolves/1,000 km<sup>2</sup>, kill estimated at 38 adults, 11 yearlings, and 25 calves (W. Ballard, unpubl. data).

<sup>d</sup> Hunting mortality derived from mandatory harvest reports. Uncorrected for nonresponse bias.

**Appendix 4.** Estimation of numbers of adult and new yearling moose on 1 June 1983 in relation to estimates of recruitment (proportion of new yearlings) and mortality through 31 May 1984 within a 3,735-km<sup>2</sup> portion of the Susitna River Study Area.

Purpose of calculation	Data required for calculations	Calculated values
To estimate no. of adult and yearling moose on 1 Jun 1983 in 3,735-km <sup>2</sup> portion of SRSA.	No. of new yearlings alive on 1 Jun 1983 = (fall 1983 yearling moose pop. est. <sup>a</sup> × mortality rate <sup>b</sup> ) + fall 1983 yearling pop. est. <sup>a</sup> + est. wolf predation <sup>c</sup> = (470 × 0.049) + 470 + 9 = No. of adult cows alive on 1 Jun 1983 = (fall 1983 cow pop. est. <sup>a</sup> × mortality rate <sup>b</sup> ) + fall 1983 cow pop. est. <sup>a</sup> = (1,596 × 0.024) + 1,596 = No. of adult bulls alive on 1 Jun 1983 = (fall 1983 bull pop. est. <sup>a</sup> × mortality rate <sup>b</sup> ) + fall 1983 bull pop. est. <sup>a</sup> + hunting mortality <sup>d</sup> = (173 × 0.000) + 173 + 153 = Total no. adult cows and bulls + est. wolf predation <sup>c</sup> = 1,634 + 326 + 33 = Total adults and new yearlings alive on 1 Jun 1983 = 1,993 + 502 =	502 1,634 326 1,993 2,495
To estimate recruitment (proportion of new yearlings) to census area moose population on 1 Jun 1984.	No. of adults (cows + bulls) alive on 1 Jun 1984 = (fall 1983 est. <sup>a</sup> × survival rate <sup>b</sup> ) - est. wolf predation <sup>c</sup> = (1,769 × 0.989) - 43 = No. of yearlings becoming adults on 1 Jun 1984 = (fall 1983 est. <sup>a</sup> × survival rate <sup>b</sup> ) - est. wolf predation <sup>c</sup> = (470 × 0.985) - 12 = Total no. adults and yearlings becoming adults = 1,707 + 451 = No. calves becoming new yearlings on 1 Jun 1984 = (fall est. <sup>a</sup> × survival rate <sup>b</sup> ) - est. wolf predation <sup>c</sup> = (556 × 0.952) - 28 = Proportion of new yearlings in moose pop. on 1 Jun 1984 = 501 ÷ (501 + 2,158) =	1,707 451 2,158 501 0.19

<sup>a</sup> Numbers of moose in early Nov 1983 were estimated from intensive aerial census (Gasaway et al. 1981). Nov 1983 total moose population estimate was  $2,795 \pm 306$  (90% CI) comprised of the following estimated sex and age composition: yearlings = 470, calves = 556, adult cows  $\geq 2$  years of age = 1,596, and adult bulls  $\geq 2$  years of age = 173 (W. Ballard, unpubl. data).

<sup>b</sup> Seasonal survival and mortality rates from 1 Jun through 31 Oct 1983 and from 1 Nov 1983 through 31 May 1984 based on radio-collared moose (W. Ballard, unpubl. data) using Trent and Rongstad (1974) method of calculation. All rates exclude wolf predation, which was estimated independently.

<sup>c</sup> Wolf densities and estimated numbers of moose kills/time interval for 3,735-km<sup>2</sup> moose-census area were as follows: 1 Jun through 15 Jul 1983—3.5 wolves/1,000 km<sup>2</sup>, killed 5 adults and 1 yearling; 16 Jul through 31 Oct 1983—6.7 wolves/1,000 km<sup>2</sup>, killed 28 adults and 8 yearlings; and 1 Nov 1983 through 31 May 1984—4.4 wolves/1,000 km<sup>2</sup>, killed 43 adults, 12 yearlings, and 28 calves (W. Ballard, unpubl. data).

<sup>d</sup> Hunting mortality derived from mandatory harvest reports. Uncorrected for nonresponse bias.