Population Dynamics and Prey Relationships of an Exploited and Recovering Wolf Population in the Southern Yukon

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Abstract

Numerical and functional changes in wolf (*Canis lupus*) demography and prey relationships were studied between 1983-88 in a 12,970 km^2 area in the Coast Mountains of the southern Yukon. The wolf population size was reduced for 3 years (1983-85) in an effort to increase moose (*Alces alces gigas*) survival, then monitored for a 3-year recovery period (1985-88). At the same time, 54 wolves in 25 packs and 10 solitary wolves were captured, radio-instrumented and relocated 1,696 times, mostly during winter. During control, wolf numbers declined from 161 to 47, density fell from 12.4 to 3.6 wolves/1000 km^2 and average pack size declined from 8.6 to 3.6 wolves. Annual pack density did not change substantially during the study. Wolf numbers recovered to about 88% of original 1983 size after 3 breeding seasons. Wolf density and average pack size did not recover to early control values by the end of the study. The most intensive reduction of wolf numbers limited breeding opportunities, and pup numbers in the next winter fell sharply to levels that would suggest low exploitation. The high rate of population increase during the first recovery winter was primarily due to high ingress rates, with reproduction being secondary. Size of wolf home ranges increased by 3 times in the first recovery winter when small recolonizing packs occupied large home ranges. As competition for space increased the next year, pack home ranges declined to more normal sizes. Wolf condition improved following the first year of control, but fat levels indicated that wolves were not under-nourished during the study.

Seventy-nine percent of wolf-killed ungulates were moose and 18% were Dall sheep (*Ovis dalli dalli*). Predation on moose was mainly additive. Wolves took primarily moose calves, yearlings and middle-old age adults. These age classes were taken in higher proportions to their occurrence in the annual winter populations. No prey showed starved condition, based on marrow fat values. Wolves killed young through old age Dall sheep rams, but only older females were wolf-killed. Sheep predation by wolves was apparently linked to moose density in some wolf territories.

Moose, including neonatal calves, were the most important prey in summer. Winter predation and consumption rates were moderate to high compared to other studies. Small packs had disproportionately high winter predation rates compared to larger packs, and 3 of 4 pairs studied killed ungulates as frequently as packs of 5-7 wolves. The biomass of prey killed/wolf/day was 3 times higher for wolves in pairs than for wolves in larger packs. The exceptionally high predation rates of pairs were believed to be related to scavenger competition by ravens and increased exposure to vulnerable prey due to the larger home ranges that pairs occupied.

Moose:wolf ratios and the ungulate biomass:wolf index suggested that moose were likely declining at the beginning of this study. Other equations suggested a stable CM moose population was capable of supporting only 8-10 wolves/1000 km^2, 17-33% lower than the observed, early control density (12/1000 km^2). Surplus moose available to hunters was apparently negligible, assuming wolf predation rates were 8-10 moose/wolf/year.

Based on winter predation rates, wolves potentially removed 64% of moose calves during 2 winters and 11-14% of adults. Wolf predation on adult moose remained high during the first year of recovery when wolf numbers were lowest and, for unknown reasons, the predation rate on calves was also lowest. Wolf predation studies supported moose and sheep studies in the area that found the level of wolf reduction did not increase moose or sheep numbers, nor substantially improved recruitment rates of moose, sheep or woodland caribou (*Rangifer tarandus caribou*) in the area.

We found there was a 2:1 relationship between the number of wolves removed from the population and the number of ungulates saved from wolf predation. We show a functional response of wolves to increase their predation rates as pack size declines, and this can limit the benefits of wolf control to ungulate populations. We discuss the management of wolves as a tool to increase low density moose populations where wolves, grizzly bears and moose are sympatric is also discussed. We argue that management decisions regarding short-term wolf control should depend on the potential impact reductions would have on elevating moose calf survival to early winter. Recommendations are provided on how to conduct wolf control to maximize survival of moose during the winter.

INTRODUCTION

Similar to the history of wolves (*Canis lupus*) in many parts of North America during the past century, wolves in the Yukon Territory were indiscriminately managed as undesirable competitors for big game populations. There were various attempts to reduce Yukon wolf populations since the turn of the century. Wolf bounties were paid between 1920-33 and 1946-53, and strychnine poison was freely used by trappers and game guides throughout the 1920's-60's. The Yukon Game Branch conducted a systematic wolf poisoning program throughout the Yukon during the 1950's and 1960's in response to apparent declines in ungulate numbers (Smith 1983). Poisoning was most intensive in the Coast Mountains (CM) of the southwestern Yukon. Bait sites were not monitored in most years and little information was gathered on the numbers of wolves killed annually. According to game outfitters and resident hunters, the intensive poisoning in the CM was thought to have caused a decline in wolf numbers and a subsequent increase in ungulate populations. Poison use was discontinued after 1971 (Smith 1983) and wolves likely recovered to naturally-regulated densities by the mid 1970's.

In 1980, Larsen (1982) conducted the first systematic inventory of moose (*Alces alces gigas*) in the Coast Mountains. Continued surveys through the mid 1980's showed a moose population characterized by relatively low density (141--274 moose/1000 km^2) and low calf:cow (18-30:100) and yearling:cow ratios (4-22:100, Larsen et al. 1989*a*). Moose numbers rapidly declined in 2 areas in the Coast Mountains between 1981-84. Coincidentally, in October 1982 the number of wolf/livestock conflicts increased sharply in the Whitehorse area. A public paranoia of wolves developed throughout the fall and early winter, largely fueled by inaccurate and sensational media reporting. In response, the Yukon government allowed private aerial hunting of wolves in a 24,000 km^2 area in the southern Yukon including the CM, and limited wolf poisoning occurred near Whitehorse during the 1982-83 winter.

Wolf research studies began in January 1983, after wolf control had already begun. At the same time, Larsen et al. (1989*b*) investigated the factors limiting the moose population by studying samples of radio-instrumented cow and calf moose between 1983-86. They documented that moose population growth in the CM study area was primarily limited by grizzly bear (*Ursus arctos*) predation on neonatal calves and wolf predation was the secondary factor. In an attempt to increase moose numbers, Larsen and Gauthier (1985) proposed grizzly bear and wolf population reductions, and a hunting closure for antlerless moose.

The objectives of this study were to determine the effects of exploitation on the demography, distribution and physical characteristics of wolves. Manipulation of wolf numbers allowed us to investigate wolf predation ecology on moose, Dall sheep (*Ovis dalli*) and woodland caribou (*Rangifer tarandus caribou*) at various wolf densities. Numerical and functional aspects of wolf population recovery were investigated following control.

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N. Hulstein drafted maps and figures. D. Mossop, K. Jingfors, C. Promberger, B. Slough and R. Sumanik edited earlier drafts of the report and provided valuable criticisms.

Fixed-wing pilots H. Kitchen and B. Watson of Alkan Air, J. Ostashek and R. Pyde of Ostashek Outfitting, and T. Hudgin and J. Buerge of Aerokon Aviation flew safely and efficiently. T. Hudgin conducted most of the flying and was an especially keen observer. His special flying skills and dedication to this project were critical to its success. Wolf capture flights were piloted by M. Conant, D. Holden, P. Kelly and D. Makkonen of Trans North Air, J. Fletcher of Midwest Helicopters, and N. Graham and B. Meili of Capital Helicopters.

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STUDY AREA

Physiography and Vegetation

The size of the wolf study area varied from 7,616 km^2 in 1983, 11,046 km^2 in 1984, and 12,970 km^2 from 1985 through 1988 (Fig. 1). The area was divided into 3 regions: CM East, Center and West based on differences in chronology and intensity of wolf studies. CM Center (6,300 km^2) was the only area where wolf population data were annually collected from 1983 through 1988, and was also where radiotelemetry studies were concentrated. One year of wolf survey was missed in CM East (1984) and CM West (1983).

The study area is a portion of the Coast Mountain ecoregion (Oswald and Senyk 1977), characterized by mainly rugged sedimentary and intrusive mountains decreasing in elevation northward. The southern portion is glaciated with several ice-covered peaks > 2,400 m above sea level (a.s.l.). The northern portion is composed of remnant glacial formations and extensive mountain blocks surrounded by high rolling plateaus. About 70% of Coast Mountain terrain lies above treeline (Oswald and Senyk 1977). The mountains are drained by the headwater tributaries of the Yukon, Dezadeash and Tatshenshini Rivers. The Southern Lakes complex, a group of large montane lakes, transect the study area providing important movement corridors for wolves in winter.

The subalpine shrub community is mainly composed of dwarf birch (*Betula spp.*) and willow (*Salix spp.*) mixed with subalpine fir (*Abies lasiocarpa*). Lower elevations are characteristically mesic or arid, supporting white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Soapberry (*Shepherdia canadensis*) and willow dominate the shrub understory.

The climate is semi-arid, influenced by the orographic effects of the Coast Mountains. Annual precipitation ranges from 226-300 mm over most of the area. Precipitation is 2-3 times higher in the southwestern portion of the study area, averaging 761 mm (Oswald and Senyk 1977). Snow depths vary by latitude and elevation with the greatest accumulations at high elevations in the south, diminishing northward. Snow fall averages 431 cm along the Haines Road, 136 cm at Haines Junction, and 127 cm at Whitehorse (Dep. of Environ., Atmospheric Environmental Serv., unpubl. data). Snow above treeline is consolidated by wind and temperature fluctuation, and alpine ridges are blown free of snow throughout the winter. Snow depths on the valley floors range between 30-60 cm. Average annual temperature is between -1 to -3° C and winter temperature averages -12° C.

Wildlife Populations

Moose, Dall sheep, woodland caribou, and mountain goat (*Oreamnos americanus*) occupy most of the study area except for the highest, glaciated peaks in the southern area. Moose density ranged from 141-274/1000 km^2 (Larsen et al. 1989*a*), with the highest density in CM Center. The Coast Mountains were the most important moose hunting area during the 1970's and early 1980's (Larsen et al. 1989*a*). A Yukon-wide antlerless moose (cow and calf) season was opened from 1974 to 1982 in response to observations by hunters that moose numbers were high. Between 1979 and 1987, the sport harvest declined by 88% in the southwestern Yukon (Larsen et al. 1989*a*). Indian harvest has remained unregulated with no restriction on the season or the number and sex of ungulates taken. Voluntary reporting of Indian harvest began in 1987 (Quock and Jingfors 1988, 1989).

Dall sheep density was 262 non-lamb sheep/1000 km^2 in CM Center and West (Barichello et al. 1989*a*); sheep were absent in CM East. Mountain goats were sparsely distributed throughout the southern study area. Sheep and goat populations were likely stable throughout this study (N. Barichello, Yukon Fish and Wildl. Br., pers. comm.). Two small woodland caribou herds totalling 350 animals ranged throughout CM East and Center (Farnell 1982). Mule deer (*Odocoileus hemionus*) were uncommon and a small, introduced herd of 30-40 elk (*Cervus elaphus*) ranged along the northern boundary (Florkiewicz 1990). Beaver (*Castor canadensis*) and snowshoe hare (*Lepus americanus*) were uncommon during the study. The hare population crashed in the southern Yukon during February 1983 (Boutin et al. 1986). The ground squirrel (*Spermophilus parryii*) was common. Other large carnivores included grizzly (13-22/1000 km^2, Larsen and Markel 1989) and black bear (*Ursus americanus*). Smaller carnivores included the wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), coyote (*Canis latrans*) and red fox (*Vulpes vulpes*).

METHODS

Estimating Wolf Population Size

Wolf population studies were divided into 2 periods. The wolf control period included 1 November 1982 through 31 March 1985. Wolf population recovery studies began on 1 April 1985 and ended 1 April 1988. Six month winter periods are defined by the year of the last winter month. For example, the 1983 winter included the period 1 October 1982 through 1 April 1983.

CM Center was aerially censused for wolves each winter from 1983-88, CM West from 1984-88 and CM East in all years except 1984. Annual wolf numbers in unsurveyed regions were derived by extrapolating the average density from surveyed areas, assuming density was constant throughout the Coast Mountains each winter. For example, we assigned CM Center wolf density to CM West in 1983 because of the similarities in physiography and prey distribution, and the 1984 wolf density in CM West was not different from CM Center.

We used both aerial snow tracking techniques (Stephenson 1978, Gasaway et al. 1983) and radiotelemetry studies (Mech 1982) to annually estimate winter wolf population size. Snow tracking requires fresh snowfall (5-10 cm), followed by suitable light conditions to successfully follow fresh wolf trails and locate packs. Ideally, snow track surveys should be conducted over a short period using experienced observers in 2-3 aircraft to ensure wolf pack duplication does not occur (Stephenson 1978). One Cessna 185 and 2 PA-18 Supercubs were used. The Cessna 185 was useful for locating trails but it was less efficient for finding wolves and was dropped after March 1983. Our ability to intensively survey large blocks in a short period was restricted by low snow accumulations, winds obscuring trails in the mountains and the availability of only 1-2 suitable survey aircraft each winter. Consequently, we censused small blocks (500-3,000 km^2), the size depending on weather conditions. We relied on radiotelemetry to assist in identifying packs, delineating territories, and counting pack members. We concentrated our snow tracking effort in areas where radio-collared wolves were not present. Trappers in the area were sent a questionnaire in 1984 and 1985 to assist in determining wolf numbers and distribution, and various residents regularly reported wolf activities during the study.

Pack size was determined either by counting individuals in radio-instrumented packs or following trails until wolves were observed. Whenever a trail was followed and the pack was not located, the size was estimated from the number of separate trails counted. These methods provide minimum estimates of pack size. Wolf surveys were initiated in October or November following the first snowfall, except 1983 when surveying began in early January. It was not possible to complete wolf surveys until mid winter (15 January) of most years and early winter pack size was unknown for most uncollared packs in all years, except 1986 when wolf surveys were completed by late December. We calculated late winter (15 March) population size by the formula: A-B-C+D; where A = mid winter (January 15) population of wolves in packs, B = number of wolves killed between 15 January-15 March, C = number of radio-instrumented and associated wolves that died or left the pack in the same period, and D = estimated lone wolf population (10% of A). In wolf literature, there is little empirical data on the proportion of lone wolves in wild populations due to the difficulty of finding solitary wolves and knowing if they are temporarily separated from packs. We used a 10% value for lone wolves (Gasaway et al. 1983), but Fuller (1989) estimated that lone wolves may represent as much as 30% of a high density, saturated wolf population in Minnesota. Fuller (1989) found that lone wolves formed pairs during September-December. We believe that the majority of CM lone wolves had formed into new pairs by early winter due to the exploited state of this population (*see* Results and Discussion).

All wolf packs that ranged inside the fixed study area boundaries were considered residents, including packs that formed portions of their territories outside. Winter wolf densities were based on total area with no adjustment for excluding high elevation areas or lakes. Wolves commonly travelled in alpine areas hunting sheep, used mountain passes to move between valleys, and travelled on lake ice frequently.

Three observers and 3 pilots conducted all wolf surveys, minimizing potential survey biases (Stephenson 1978). Between 100-150 aircraft hours were annually spent snow tracking wolves and another 50-350 hours were annually logged during radiotelemetry studies for a total of about 1,700 aircraft hours spent during the study.

Estimates of wolf abundance have been calculated by various methods in the literature, all of which are non-statistical for they do not employ sampling. This disallows any probabilistic modelling or standardized replication (Fuller and Snow 1988). Over large areas, wolf density estimates have been made in conjunction with intensive radiotelemetry studies of wolves (Fritts and Mech 1981, Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987, Fuller 1989). Gasaway et al. (1983) used snow tracking techniques and Gasaway et al. (1990) combined both techniques to delineate territorial wolf packs and estimate abundance in interior Alaska.

By employing both techniques we suggest that our reported numbers are accurate minimum counts for the following reasons: 1) In our study area where territorial packs are spatially separated most of the time, we assumed that all packs could be located and counted by frequently searching all habitats and elevations zones. 2) The probability of locating wolves increased as sampling frequency increased. All areas were searched until wolves or their sign were found, or we were confident wolves did not use the areas. 3) Because wolves frequently travel long distances during winter, it was probable that experienced observers would intercept a trail and follow it until the pack was found or an estimate of pack size was made from separate trails counts. 4) By knowing the whereabouts of radio-collared packs throughout the winter we were able to intensively search where non-instrumented packs were ranging. This increased the probability of encountering new packs and minimized the possibility of duplicating packs. 5) Wolves and their trails were highly visible because most of the study area is above tree-line.

Wolf Control and Necropsy Studies

Wolf control was conducted between November 1982 and March 1985. Techniques included government poisoning (Strychnine) and aerial hunting, public aerial hunting, ground hunting and trapping. In the winter of 1983 (1982-83), government aerial hunting was limited to the Whitehorse city limits. The public was licenced to aerially hunt the study area only during the winter of 1983. Public aerial hunters were required to report all wolves killed and submit the carcasses for necropsy study. Poison use was limited to the Whitehorse area, but was discontinued after March 1983. Extensive aerial hunting was conducted during the winters of 1984 and 1985 throughout the study area. A Yukon Fish and Wildl. Br. helicopter crew shot wolves with 12 gauge shotguns then retrieved carcasses for necropsy study. Some packs were initially radio-collared. Once their general home ranges were established, all members were killed except certain radio-collared individuals. In an effort to increase trapper take, a $200 incentive was offered to all Yukon trappers for each wolf taken between 1983 and 1987. CM trappers and hunters were requested to submit carcasses of all killed wolves.

Wolf carcasses were necropsied following procedures by R. O. Stephenson (Alaska Dep. Fish and Game, pers. comm.). Wolves were measured for chest and neck circumference, and body length. Condition was assessed by depth measurements of subcutaneous fat at 3 sites (sternum, flank and rump), xiphoid fat weight, and a subjective index of mesenteric fat. A body fat index was calculated by the formula: xiphoid fat (g)/whole wolf weight (kg). Obvious infirmities, including broken legs and skull fractures were recorded and ribs were examined for breakages. The stomach was opened and contents were identified. Female reproductive tracts were removed and uteri were examined for signs of current or past reproductive activity, including swollen appearance and size of uterus, and evidence of placental scars. Ovaries were fixed in alcohol, sectioned at 1 mm intervals and examined for the presence of graffian follicles, corpora lutea of pregnancy (current), recent corpora lutea (last year) and corpora albacantia (historic).

A first premolar was extracted, decalcified (Linhart and Knowlton 1967), sectioned by cryostat, metachromatic stained (Thomas 1977) and cementum annuli counted to determine minimum age. Goodwin and Ballard (1985) determined that cementum techniques were not useful for separating wolf pups (< 12 months) from yearlings (12-23 months) because the first annulus is usually deposited between 20-22 months old. Pups were separated from yearlings based on the presence of an open root apical foramen (Parker and Maxwell 1986), dentition characteristics including deciduous teeth, incomplete eruption and anterior orientation of canines, absence of tooth wear and color staining. Secondary characteristics of pups include small undeveloped testes in males and uteri in females, small body size, pelt characteristics and the absence of epiphyseal closure at the distal end of the radius (Rausch 1967*a*). During the wolf control period (1983-85), the age and sex composition of each winter population was determined by pooling live, radio-collared wolves with dead wolves. In the first recovery winter (1986), pup and adult proportions were determined by capturing and radio-collaring wolves ($n = 25$) and counting the pup numbers in 13 packs (11 radio-collared packs, 2 observed packs).

A 1 kg sample of muscle tissue was removed from 34 necropsied wolves and studied by radiocesium techniques (Holleman and Luick 1978, Holleman and Stephenson 1981) to indirectly estimate the importance of caribou in the diet of CM wolves. The method relies upon the accumulation of fallout ^{137}Cs in potential prey species and the subsequent transfer of ^{137}Cs to wolves. To reference prey radiocesium levels in prey species in the southern Yukon, 7 woodland caribou, 3 moose and 2 Dall sheep were sampled during the winters of 1983-85.

Wolf Telemetry Studies

Wolf Capture and Observation

Wolf telemetry studies were also divided into control and recovery phases. Wolves were captured by helicopter darting, snaring and by purchasing live captured wolves from trappers. Snare closure was stopped at 350-375 mm. Snare setting techniques followed procedures by D. Grangaard (Alaska Dep. Fish and Game, pers. comm.). Snares were checked every 24-48 hours. Wolves were immobilized with a 5:1 mixture of Ketamine Hydrochloride (Parke-Davis, Brockville, Ont.) and Xylazine (Rompun, Cutter Laboratories, Mississauga, Ont.) delivered from a Capchur gun (Palmer Chemical and Equipment Co., Douglasville, Ga.) or hand injected. Most wolves received dosages of 10-15 mg Ketamine/kg body weight. Adults were usually selected for helicopter capture based on behavioural and physical characteristics because we expected them to remain in the pack longer than yearlings or pups. Darted wolves received minor injuries, and in most cases they rejoined their pack immediately. Captured wolves were weighed and measured, a premolar was extracted for ageing, or age was estimated as pup, yearling, or adult (≥24 months) based on previously described dental characteristics. Wolves were instrumented with radio-transmitter collars (150-152 MHz: Telonics, Mesa, Az.; Lotek, Aurora, Ont.; Austec, Edmonton, Alta.). Transmitters performed differently depending on the manufacturer; Telonics transmitter life and signal strength was superior, followed by Lotek, then Austec.

Radio-instrumented wolves were located from a PA 18 Supercub. At each location we recorded the time, the number of wolves seen and their activities, general habitat, elevation, and the presence of prey carcasses. Locations were plotted on 1:250,000 topographic maps in the field and later recorded as metric grid coordinates (to nearest 1 km). Movements and territory size of radio-collared wolves were calculated using Program Home Range 1.1 (Ackerman et al. 1989). Carbyn (1983) and Fuller and Snow (1988) showed that a minimum of 30 locations are required to completely describe wolf territories. Ballard et al. (1987) found 60 locations was the minimum number required. We calculated winter home range sizes for packs with ≥30 locations. To account for transiency and temporary dispersals, 95% convex polygons were calculated. Monthly and annual survival rates of radio-collared wolves were calculated by methods described by Trent and Rongstad (1974).

Predation Studies

During the winter, wolf kills were incidentally located during snow-tracking surveys, and during intensive monitoring of radio-collared packs to determine rates of predation. From the air, the sex of a moose carcass in early winter was determined by antler presence until bulls dropped their antlers in November/December. After this period, moose kills were not sexed from the air. Age was divided into calf and older based on the obviously smaller size of calf carcasses throughout the winter.

Cause of death during winter was separated as wolf predation, probable wolf predation, bear predation (to December), non-predator caused (including accidental death and starvation) or unknown cause. We separated wolf kills from wolf-scavenged animals by the presence of wolf and prey trails and fresh blood spoor that indicated wolves attacked and fed on the animal at the time of death. If a carcass was sternally recumbant we assumed the cause of death was not predation (Stephenson and Sexton 1974, Ballard et al.

1987). At each mortality site visited, the percentage of carcass remaining was subjectively estimated, the habitat type was noted and the sex of moose was determined by antler pedicel presence. A moose incisor bar was collected to determine age by cementum annuli (Sergent and Pimlott 1959) and a long bone was collected to assess marrow fat content by the dry weight method (Neiland 1970). Samples were collected during the winter and kept frozen, minimizing dehydration (Peterson et al. 1982). For Dall sheep, sex and age was determined by horn size and configuration, and number of horn annuli counted (Geist 1966).

Winter predation and consumption rates during the control period were assessed by the daily observations of 3 wolf packs between 5 February -1 April 1983. During wolf recovery, 8 packs and 2 lone wolves were studied daily between 9 February-3 April 1986, and 3 packs between 3 November-8 December 1986. Due to the variations in biomass of moose and Dall sheep we followed a kill rate method (Ballard et al.1987) that adjusts predation rates of various age and sex classes of ungulate species relative to the biomass of 1 adult moose equivalent (*m.e.* = 427 kg, Ballard et al. 1987). Average weights of prey varied between early and late winter (Appendix A). Predation rates were expressed as the no. of days/*m.e.* killed (adjusted days/kill).

Most studies of wolf consumption rates of moose (Peterson 1977, Fuller and Keith 1980, Peterson et al. 1984, Messier and Crete 1985, Ballard et al. 1987) have assumed that wolves ate all edible biomass (available), estimating 25% of moose carcass weights (Peterson 1977) were not available to wolves (i.e. skeleton, rumen, hide). Some researchers (Kolenosky 1972, Peterson 1977, Ballard et al. 1987) recognized scavengers removed some of the wolf-available biomass, but did not estimate amounts. A recent study in the Yukon indicates that the amount of prey consumed by wolves depends on the pack size. C. Promberger (Univ. of Munich, unpubl. data) presented ungulate carcasses to scavengers. By simulating wolf consumption he found that ravens (*Corvus corax*) removed 10% of wolf-available prey biomass from a pack of 10 wolves, 20% from a pack of 6, 50% from a pair and 66% from a lone wolf. We used these values to estimate moose consumption rates of wolves in various size packs. Weights of wolf-available biomass was estimated at 75% for moose, based on a bull moose weighed by Peterson (75%,1977) and a cow moose weighed by C. Promberger (76%, unpubl. data). The wolf-available biomass of sheep was also estimated at 75% based on Fuller (1989) for similar size white-tailed deer (*Odocoileus virginianus,* 74%). We assumed that wolves consumed all available sheep biomass, based on the small size of sheep and small number of ravens seen at sheep kills. Weights of available prey biomass also varied between early and late winter (Appendix A). Wolf consumption rates (kg consumed/kg of wolf/day) were based on the following average wolf weights during winter: 35 kg (n =135 wolves) for wolves in packs >2 (includes pups, yearlings and adults), 40 kg for adult pairs, 43 kg for solitary adult males and 36 kg for solitary adult females (Table 2).

Summer food habits were studied by collecting wolf scats from 7 denning sites of 4 packs between 1985-88 (post-control). Scat samples were individually bagged and autoclaved, and prey items were identified by comparing hair samples to reference material of prey species and by examining hair scale impressions (Adorjan and Kolenosky 1969, Kennedy and Carbyn 1981).

Data Analysis

Differences in frequency ratios were tested by chi-square tests (Rohlf 1984; SAS Inst. Inc. 1985). Mean differences were compared using t tests and nonparametric least likelihood ratios (SAS Inst. Inc. 1985). Correlations were tested using simple linear regressions (SAS Inst. Inc. 1985). Probability value of 0.05 was used for testing significance of relationships, unless otherwise stated.

RESULTS AND DISCUSSION

Radiotelemetry

Sixty-four wolves were radio-instrumented between February 1983-February 1987: 50 were darted by helicopter, 6 were snared by us, and 8 were captured in leghold traps or neck-snared by trappers. Fifty-nine wolves were captured once and 5 were captured twice. Handling-related mortality was 3%. One wolf died from dart penetration and 1 did not recover after being immobilized. Three wolves were radio-collared but their transmitters failed immediately after attachment. Fifty-five percent of instrumented wolves were adults ($n = 35$), 23% were pups ($n = 15$) and 22% were yearlings ($n = 14$). Overall sex ratio was 37 males and 27 females and did not differ significantly from 50:50 among pups, yearlings and adults.

The 64 radio-collared wolves included 10 lone wolves, 12 in pairs and 42 in packs of 3 or more. Thirty-six were instrumented during control and 28 during recovery. During the study we monitored 25 different pairs or packs that formed part or all their territory in the study area and 10 lone wolves (Fig. 2). The history of our contact with radio-collared wolves is summarized in Appendix B. An average of 8 packs (range 4-11) and 2-4 solitary wolves were monitored in each winter. Contact was lost with 18 wolves (28%), 15 due to known or suspected transmitter failures and 3 probably dispersed. Thirty-five (55%) died on the study area, 8 (13%) dispersed from the study area and eventually died, and 3 (4%) were alive in the area at the end of the study (Appendix C).

Radio-collared wolves or other pack members were observed on 77% of all telemetry locations. Wolf sightings were more frequent in winter (83%) than in summer (53%). Instrumented wolves were located most often between 10:00-14:00 hours (68%). The average period radio-collared wolves were monitored was 258 days, ranging from 1-1175 days. Seventy-one percent of wolves were monitored for less than 1 year, 25% for 1-2 years, and 4% for more than 2 years.

Wolf Population Dynamics

The percentage of study area wolf packs seen each winter ranged from 47-70%, and the proportion of packs that were collared ranged from 24-54% based on actual areas censused each winter. The annual number of resident packs, their minimum size and the method of enumeration are presented in Appendix D. Fig. 3 shows the annual distribution of both collared and uncollared wolf packs during each winter, including known and suspected territory areas. Packs that were annually reduced by more than 50% are also shown. Because the annual CM wolf population estimates were based on extrapolations from surveyed to unsurveyed areas in some years, we compared population trend data from the entire study area to CM Center, where complete wolf surveys were conducted in each year and radio-collared packs were present all winters.

Changes in Wolf Population Size and Age Composition

A total of 251 known wolves were killed by humans in the study area between 1983-85 and 4 died from unknown or natural causes. Reduction in wolf numbers varied by year and area (Table 1). Overall, the CM wolf population declined from 161 wolves in mid winter 1983 to 47 by March 1985 (71% decline), with the largest decline (81%) observed in CM Center (Fig. 4a, Table 1). Wolf density fell from 12.4 to 3.6 wolves/1000 km^2 (CM Center: 11.8 to 2.2 wolves/1000 km^2) and average pack size declined from 8.6 wolves to 3.6 wolves (CM Center: 8.4 to 2.6, Fig. 4b). Pack density (pairs included) varied little during the study ranging from 1.3-1.6 packs/1000 km^2 (18-20 packs:1984-88) in the study area and 1.3-1.7 (8-11 packs) in CM Center (Fig. 4c). The number of wolf packs remained high during and shortly after intensive control. In 1983 in CM Center, 0 of 8 packs were 2-3 wolves. In 1986, 9 of 11 packs were newly formed pairs (*n* = 6) or trios (*n* = 3).

During recovery the CM wolf population increased from 47 (March 1985) to 141 wolves (February 1988), and from 14 to 55 wolves in CM Center (Table 1, Fig. 4a). The slower recovery in CM Center was partially due to the complete removal of 2 packs (*n* = 9 and 4 wolves) involved in livestock depredations during the winter of 1987. Wolf density increased from 3.6 to 10.8 wolves/1000 km^2 (CM Center: 2.2 to 8.7) and mean pack size increased from 3.6 to 5.5 wolves/pack (CM Center: 2.6 to 5.8, Fig. 4b). Mean pack size remained below 1983 values, corroborating the population count that showed wolf numbers had not recovered fully by March 1988. On the Kenai Peninsula (Peterson et al. 1984) and south-central Alaska (Ballard et al. 1987) average pack size also declined as wolf harvest increased.

A total of 226 wolf age records (killed and radio-collared wolves) were collected between January 1983 through March 1986 (Fig. 5). The samples represented 43% of the total number of age records of wolves (*n* = 521) in the study area during the 4 years. In winter 1985 we aged 68% (93 of 137) of the wolves and 51% (37 of 73) in 1986, giving us especially detailed pictures of the wolf age composition in those years. Changes in age class proportions were observed but were significantly different for pups only (Fig. 5). Pups comprised an annual average of 34% (range 16-45%) of all wolves, yearlings averaged 24% (range 15-30%) and adults 43% (range = 33-54%).

Eighty-nine percent of wolves were aged to actual year classes (Fig. 6). Among the adults, wolves ≥5-years-old were uncommon (9%) and wolves ≥ 7-years-old were especially rare (3%). Seventy-seven percent of all adults were young (2 to 4-years-old). Age data supports the findings of Stephenson and Sexton (1974) in Alaska that few wolves survive beyond 7-years-old in exploited populations.

We observed annual declines in subsequent winter wolf population size when a minimum of 44% of the original size was removed (Table 1). When 71% of the original size was removed in late winter 1985, we observed a substantial decline in the 1986 population (32% of 1983 size). Our data support Keith (1983) who suggested that wolves can sustain annual harvests of up to 38%, and also support other studies that indicate the maximum sustainable harvest of most wolf populations is between 40-50% of the early winter population (Gasaway et al. 1983, Peterson et al. 1984, Keith 1983, Ballard et al. 1987, Gasaway et al. 1990).

Fuller (1989) concluded that a stable population would occur when total overwinter mortality was 35%, but he suggested that the rate could vary depending on the age composition of the harvest and the rates of dispersal in and out of exploited areas. If pups composed a high proportion of the harvest or immigration was rapid, then stability may occur at much higher harvest rates. We believe that public harvest techniques (trapping and hunting) select for young, inexperienced wolves, and can produce stability at relatively high harvest. Conversely, public harvest biases for the survival of adult wolves which maintains high reproductive potential in the population. To determine the effects of incomplete pack removals on wolf repopulation rates, we followed 5 radio-collared adult males that had all their pack members killed during late winter. In all cases, the wolves remained in their previous territories and found new mates before the next winter . In 3 of 4 cases when their packs were killed during the early breeding period, the males re-mated with new females immediately and produced pups the same spring, showing that reproduction potential is high in exploited wolf populations and can contribute to pack size stability when adult wolves are allowed the opportunity to breed.

The 1988 CM wolf population recovered to 88% of 1983 size, and CM Center population to 74% after 3 breeding seasons. Ballard et al. (1987) found wolf densities recovered to 81% of pre-control levels after 1 breeding season in a control area in Alaska

(7,262 km^2). Immigration rates may have been slower in CM because of poor wolf habitat to the west (Kluane icefields) and low wolf density to the north (3.2/1000 km^2, Baer and Hayes 1987), the larger wolf reduction area (12,970 km^2), and low survival rates of wolves during recovery caused by trapping and hunting (*see* Survival Rates and Mortality of Radio-collared Wolves).

In our study the annual rates of increase were highest during recovery (Table 1) when the average annual rate of increase was 1.77 (1.55-2.13). During initial wolf colonization of Isle Royale when food was abundant, competition low and ingress negligible, the average rate of increase was 1.39. Keith (1983) considered this rate to be the instrinsic rate (r_m) of increase. Rausch (1967*a*) predicted a maximum r_m of 2.30, given maximum reproduction, no mortality and stable age distribution. Ballard et al. (1987) and Farnell and McDonald (1991) reported rates of increase as high as 2.40-2.64 in highly exploited wolf populations. These high rates of increase can be explained by the higher relative importance of wolf reproduction and immigration to low density wolves. As wolf numbers decline and surviving wolves are allowed to breed, pup production will contribute to a greater proportion of the subsequent winter wolf numbers than at higher, unexploited wolf densities. Packard and Mech (1983) recognized that immigration contributed most to population increases when wolves were sparse. At extremely low density, the population value of an individual ingressing wolf is much greater than at higher density. Because the areas surrounding our study area supported naturally-regulated wolves, we expected emmigration rates were independent of wolf population size in the removal area, but successful immigration into the study area should have increased when wolf density and competition for space was lowest. Rapid recolonization and pairing by ingressing wolves also explain the stable number of packs that occupied our study area each winter.

Pups declined significantly from 45% in 1985 to 16% in 1986 following the greatest decline in population size (71%). Keith (1983) found the percentage of pups ranged from 30-73% in 9 exploited wolf populations and concluded that increased pup proportions were correlated to increased levels of exploitation. Ballard et al. (1987) observed 42-74% pups in public wolf harvests in an exploited wolf population in Alaska. In our study, pup proportion was highest in 1985 (45%) following 2 years of moderate wolf population reductions of 39-42% which supports the hypothesis of Keith (1983) that pup proportions increase in moderately exploited populations.

Ballard et al. (1987) speculated that if adult wolves are killed throughout the breeding period then reproduction is restricted and repopulation rates would be depressed. The most intensive reduction in CM wolf numbers happened in 1985 when wolves were killed from early winter through the March breeding period. This technique depressed breeding and pup proportions fell sharply the following winter (Fig 5). In 1985, 78% (14 of 18) of packs reproduced compared to only 39% (7 of 18) in 1986. Thus, arbitrarily using proportion of pups as an index of exploitation levels is not recommended because at very high exploitation rates pup production is negatively affected, and can decline to levels observed in unexploited populations. We believe that Keith's principles are limited to moderately exploited populations and are dependent on the sampling methods used. Public trapping and hunting is likely biased to taking pups (Fuller 1989), the most vulnerable age class. Therefore, age structure derived from public harvest then could cause an artificially inflated estimate of pups in the population. This could explain the large percentages of pups Ballard et al. (1987) found in the annual public wolf harvest in south-central Alaska.

Physical Characteristics of Wolves

Morphology

Adult male and female wolves differed significantly in weight, contour length, chest and neck circumference with males being heavier, longer and larger than females (Table 2).

Between male and female yearlings, sex-related differences were less obvious with females being significantly shorter in contour length and chest circumference, but of similar weight and neck circumference. Among males, yearlings weighed significantly less than adults and were shorter in length and neck circumference. Female yearlings did not differ in weight or any external measurements compared to adult females, indicating that CM females reach adult body weight and size by the end of their second year (yearling) but males do not. Parker and Luttich (1986) found both sexes of Labrador wolves reached adult weight and size by the end of the second year. They also found that males and females did not differ significantly in size or weight, recording lighter average weights for adult males (28-30 kg) than our adult males (43 kg). Adult Yukon males, being substantially larger, apparently require more time to achieve full body weight and size compared to the smaller *C. l. labradorius* in north-eastern Canada.

Sex Ratio

The sex ratio of pooled necropsied and radio-collared wolves was 81 males/100 females. This is the first study that has shown a disparate sex ratio favouring females. In other studies, ratios favoured males (Cowan 1947, Stenlund 1955, Rausch 1967*b* , Mech 1975, Nielsen 1977, Parker and Luttich 1986). Pullianen (1965) found a much greater proportion of males immigrating to unoccupied wolf range in Finland, but found equal sex ratios on established breeding range. We found no significant increase in the ratio of males in the study area during the winter following the most intensive removal. Mech (1975) found a higher percentage of male pups in a high density Minnesota wolf population as the food resources declined. Packard and Mech (1983) suggested fewer females would regulate the population during food shortages by providing fewer pairs to recolonize vacant territories. If male-skewed ratios are an indicator of food-stressed wolf populations, then the female-skewed ratio in the Coast Mountains indicates food supply was not limiting the wolf population during this study; a point supported by wolf physical condition and reproduction parameters, and wolf predation studies (*see* Winter Predation and Consumption Rates).

Reproduction

The average number of placental scars and fetuses among previously bred females was 4.4 ± 1.6 (n = 18, range 2-7) similar to the average of corpora lutea counts (4.6 ± 1.9, n = 20, range 2-10). Corpora lutea production was similar to counts by Gasaway et al. (4.3, 1983) and Peterson et al. (5.0, 1984), but less than counts of Ballard et al. (6.1, 1987), Parker and Luttich (6.8, 1986) and Rausch (7.3,1967*b*). Eighty-two percent of CM female wolves older than yearling showed evidence of being in estrous or had previous pregnancies, compared to 89% reported by Rausch (1967*a*) and 71% found by Gasaway et al. (1983). Ninety-three percent of females 2 years-and-older and all females older than 3 years were sexually active. We found no evidence that more than one female concurrently bred in each pack.

Evidence of ovulation as yearlings was observed in 3 of 7 two-year-old females but no yearlings sampled (n = 12) during the copulation period (early-mid March, Rausch 1967*a*) showed ovulation activity. Three yearlings killed during December and January showed pre-estrous follicle development. Ovarian activity was not found in any pups although the female reproductive system is capable of maturing at 10 months of age (Medjo and Mech 1976). Our data supports the finding by Rausch (1967*a*) and Parker and Luttich (1986) that showed wild wolves first breed at 22 months old; however, these individuals are rare.

Physical Condition and Injuries

We predicted that fat tissue deposits and general body condition would increase during the wolf control period in response to decreasing competition for prey. Xiphoid fat index increased significantly from an average of 2.4 (*n* = 32) in 1983 to 3.9 (*n* = 95) during 1984-85. Increasing trends in xiphoid fat levels were apparent in all age classes and sexes. Subcutaneous fat did not change and wolves showed moderate average depths (24-28 mm) in all years sampled. We conclude that fat tissue was lowest during the early control period, but fat levels did not suggest that wolves were nutritionally stressed.

The incidence of rib injury was 16% of 151 wolves examined, the same percentage found by Nielsen (1977) for Game Management Unit (GMU) 20A wolves in Alaska. In the Coast Mountains, the incidence of rib injuries was significantly different between sexes. Only 6% of all males (4 of 63) showed previous rib breakages (scars) compared to 24% of females (21 of 88). Rib scars were found in all female age classes including pups (5%), yearlings (3%), and adults (16%), but scars were found only in adult males. For the GMU 20A wolves examined by Neilsen (1977) the opposite was observed - 93% of all wolves with broken ribs were males. Moose were also the most important prey in GMU.20A but sheep were not available to most packs (Gasaway et al. 1983).

Rib breakage is most likely sustained during hunting activities. Injuries in the Coast Mountains can occur from being kicked by moose, butted by sheep, or falling from rocks while pursuing sheep. The higher frequency of rib scars in CM female wolves could be related to the differences in the roles of sexes during sheep hunting. Female wolves, being smaller and presumably quicker and more agile than males, may be more successful at chasing and killing sheep. On the other hand, larger and heavier males should be better adapted to killing moose. These data suggest that sex-related injury rates may vary regionally depending on the prey species composition.

Wolf Distribution and Territoriality

Home range analyses were based on 1,183 pack locations (1,689 individual collar locations) recorded from February 1983 through April 1988. Most wolf movement data were collected during winter except for 2 packs (Primrose, Alligator) studied during the summer of 1983. The 95% convex polygons of all packs studied during winter is shown in Fig. 3. Nine winter pack territories, 3 during control (1983-84) and 6 during recovery (1986-87), were considered fully-defined based on 30 or more locations, with a mean of 51 ± 20 locations (Fig. 7).

Summer and winter territories were of similar size. May through July territory size in 1983 for was 794 km^2 (*n* = 85 locations) for the non-denning Primrose pack and the 583 km^2 (*n* = 39) for the denning Alligator pack. Winter territories of 624 km^2 (Primrose, *n* = 96) and 752 km^2 (Alligator, *n* = 52) were recorded during 1983-84. Fuller (1989) also reported similar size summer and winter pack territories in Minnesota.

Intensive removal of wolves had a substantial effect on territory sizes of packs (Fig. 7). During early control (1983-84), winter territories averaged 630 ± 120 km^2 (*n* = 3) or 87 km^2/wolf. By the first winter of recovery (1986) when wolf density was lowest, average territory size increased to 1753 ± 988 km^2 (*n* = 3) or 539 km^2/wolf, then declined to 794 ± 513 km^2 (*n* = 3) or 143 km^2/wolf in 1987. Recolonizing wolves (2-3/pack) claimed disproportionately larger areas than larger packs. During the first recovery winter, the average territory area/wolf in small packs (2-3 wolves) was 582 ± 334 km^2/wolf (*n* = 3), 5 times greater than the average of 116 ± 80 km^2/wolf for larger packs studied in all winters (*n* = 6). Peterson et al. (1984) also found that recolonizing wolf pairs on the Kenai Peninsula had 3-4 times larger areas/wolf than members of larger packs. They also found that in the second year of recovery, the area/wolf declined as packs recovered to more normal sizes. We believe that during early recovery small packs exhibited uniquely large home ranges because they had not yet established the boundaries of their territories, and were free to travel widely because there was minimal space competition from other wolves. As CM and Kenai wolf density increased, intraspecific competition for space again restricted the size of wolf territories.

We compared our wolf population estimates with predicted sizes based on dividing the study area by the average area/wolf from radio-telemetry studies. We found the 2 techniques showed comparable results for 2 of 3 winters. In the winters of 1983 and 1984 the average territory area/wolf predicted 149 pack wolves + 15 lone wolves for a total of 164 wolves in the study area compared to our counts of 150-161 wolves . In 1986, territory area/wolf extrapolation expected only 26 wolves in the study area compared to 73 wolves counted. In 1987, territory area/wolf predicted 100 wolves compared to 111 counted. The large difference observed in 1986 can be explained by the large degree of home range overlap during this low density period which would result in underestimating wolf numbers.

Dispersal

Dispersal data was determined from 52 radio-collared wolves. Fifteen (29%) dispersed from the territory they were initially radio-collared in, similar to the 28% that Ballard et al. (1987) found. Males (7) and females (6) dispersed equally. One male and 4 females were not affiliated with other wolves before dispersing and were likely unaffiliated at the time of capture. The average age of dispersing males was 37 months (range = 23-51) and females 31 months (range = 12-83). Fifty-three percent dispersed during April-June, 26% during January-March and 20% during July-September.

The location and eventual fate of 12 dispersed wolves were known, including 8 that dispersed outside (Fig. 8) and 4 that relocated inside the study area. Six that dispersed outside died within a few months after emmigrating ,1 lived for 1 year, and 1 survived for 5 years. Within the study area 2 wolves dispersed into a vacant territory, paired and established a new pack. Two others successfully moved into existing packs. The average distance that wolves dispersed was 90 km (range 10-140).

During this study, long distance dispersals of wolves were documented between Alaska and the southern Yukon showing mixing of geographical races (Fig. 8). Radio-collared *C. l. pambasileus* wolves dispersed 450 km from interior Alaska (D. Kellyhouse, Alaska Dep. Fish and Game, pers. comm.) and 330 km from east-central Yukon to the Coast Mountains, which lies within the northern boundary of *C. l. columbianus* range. Study area wolves dispersed to Haines, Alaska, into *C. l. ligoni* range; to Atlin, B. C. in *C. l. columbianus* range; and to Kluane Lake in *C.l. pambasileus* range. These and other long distance movements in Alaska (Ballard et al. 1983) and northern Yukon (R. Hayes, pers. observ.) demonstrate the dynamic distribution of wolves in the Yukon and Alaska, confirming the phenotypical relatedness of the northwestern gray wolf (Nowak 1983).

Causes of Mortality and Survival Rates of Radio-Collared Wolves

Hunting and trapping mortality accounted for 55% (18 of 33) of radio-collared wolf deaths and 1 wolf was killed by an automobile. Natural mortality represented 21% (7) and another 21% died of unknown causes. Cause of death was confirmed for 2 natural mortalities. One was killed by a moose and the other wolf broke its leg during a sheep hunt and eventually was separated from its pack and starved. We did not observe intra-specific mortality among radio-collared wolves but we did suspect 4 were killed by other wolves, and radio-collared wolves killed other wolves on 2 occasions. Most wolf mortality (73%) occurred from September-March. The legal hunting season included 1August-15 June and the trapping season was 1 November-31 March. Hunters shot 6 of 9 radio-collared wolves during September-December and trappers killed 7 of 8 wolves during December-February. Natural mortality was equally distributed during winter (4) and summer (3).

Annual survival rates (by monthly intervals) of radio-collared wolves were calculated based on a biological year beginning on 1 June. The calculation of wolf survival rates included all radio-collared wolves except ones that were killed by us (*n* = 9). The annual survival rate averaged 0.40 between 1982-83 and 1987-88 but varied widely (0.68-0.16; Table 3). Average annual survival rates of this exploited population were lower than reported for the Kenai Peninsula (0.67; Peterson et al. 1984), south-central Alaska (0.59; Ballard et al. 1987) and Minnesota (0.64; Fuller 1989), but during the first 2 years of this study survival rates (0.64-0.68) were comparable. Wolf survival was lowest during the year of the most intensive removal (1984-85) and during the second (1986-87) and third year (1987-88) of wolf recovery. There was no increase in the proportion of wolves annually killed by the public after the first year, therefore we do not believe that changes in survival rates were related to harvest effort. More likely, the high exploitation rate in 1984-85 increased the mortality rates of surviving wolves by upsetting wolf social order and spatial relationships thereby increasing wolf vulnerability to harvest and other mortality factors. The ability of wolves to recover was depressed by the low survival rates of wolves during 1986-87 and 1987-88. Adult wolves that remained in the pack territories they were initially radio-collared in did not survive better (0.35) than adult wolves that dispersed (0.38), contrary to results from other studies (Peterson et al. 1984, Messier 1985), but similar to findings of Fuller (1989).

Subadult wolf survival rates were based on a small number of radio-collared wolf pup months (41 of 643; 6 %) and yearlings months monitored (93; 14%). Annual survival rates were widely disparate (0.0 for pups and 0.87 for yearlings) and seemed unreasonable. Annual subadult survival was recalculated by comparing the ratios of pups/yearlings and yearlings/2-year-olds (Fig. 6); for values of 0.55 for pups and 0.60 for yearlings.

Predation Ecology of Wolves

Between January 1983 and April 1988, 184 ungulate mortality sites were located in the study area: 171 in winter and 13 in summer. Seventy-one (39%) were observed from aircraft only and 113 (61%) were later visited. Seventy percent were killed by wolves and another 19% were probably wolf-killed. Non-predator mortalities (disease, starvation, injury) were 7%. Wolf-killed and probable wolf-killed moose were pooled based on no significant differences in the average adult moose age, sex ratio, and proportion of calves between the groups. Moose represented 79% of kills followed by Dall sheep at 18%. Caribou and mule deer were not important to CM wolves. We found only 1 kill of each species during the 6 years of study. Observations of wolves hunting are described in Appendix E.

Age, Sex and Condition of Wolf-killed Moose

CM wolves selected for calves, yearlings, and older moose. Moose calves accounted for 5-41% of moose prey annually killed by wolves (Fig. 9). Calves were killed at a significantly higher rate than they occurred in the populations in 1984 and 1987, based on fall moose surveys (Larsen et al. 1989*a*). Selection for calves has been documented in other wolf/moose studies (Fuller and Keith 1980, Peterson et al. 1984, Ballard et al. 1987). In contrast, the calf proportion of wolf-killed moose in winter 1986 represented only 5% (1 of 19 moose killed), significantly less (*P*= 0.06) than the composition index of 30 calves/108 adult moose (22%) incidentally recorded during winter wolf surveys. Although no systematic moose inventory was conducted in fall 1985, this index of high calf survival in late winter was verified by the relatively high proportion of yearlings in the moose population during fall of 1986 (10%; Jingfors and Markel 1987). Furthermore, in the same area we compared calf/adult moose ratios (22/135; 14%) from wolf surveys during February-March 1987 and found it was near the 17% calves observed during systematic moose surveys (Jingfors and Markel 1987) in November 1986. Therefore, we believe that our late winter calf/adult moose ratios were a reasonable estimator of calf proportions in winter.

We cannot explain why wolves killed so few moose calves during the winter of 1986. Average pack size was the smallest then (3.6 wolves/pack) but we did not observe any differences in calf predation among various size packs: ie. no calves were killed by 3 packs of 4-7 wolves and 1 calf was killed among 5 packs of 2-3 wolves intensively studied in late winter. In the east-central Yukon, moose calves made up 50% of the moose killed ($n = 61$) by 13 radio-collared wolf packs (9 pairs) during the first winter of population recovery (1990), following 7 years of intensive wolf control (R. Hayes, unpubl. data). We conclude that pack size in the CM was not limiting wolf predation on moose calves. Snow conditions and winter severity indices (Larsen et al. 1989*a*) could not explain low calf vulnerability that winter.

Yearling moose were also taken in a greater proportion than their availability in winter populations, representing 10% of wolf-killed moose compared to an average of 3.5±4.3% yearlings in the fall moose populations from 1982 through 1986. Wolves killed young adults in proportion to their low occurrence in the population and took proportionally less middle-age moose than were available, suggesting this last group was the least vulnerable to wolf predation. The age distribution of wolf-killed adults was the same for both sexes, and the pooled age distribution was significantly different than 89 cow moose (Fig. 10) captured in the study area (Larsen et al. 1989*a*). The proportion of young adult moose (2 to 4-years-old) killed by wolves was small (12%) and the same age class was uncommon among captured moose (9%). Seventy percent of captured cows were middle-aged (5 to 10-years-old) compared to 34% of wolf-killed moose. Old moose (11.to 17-years-old) was the largest age group (36%) taken by wolves compared to 18% of captured cows. Excluding yearlings, the average age of wolf-killed adult moose was 9.1 ± 4 years.

The age distribution of Coast Mountain wolf-killed moose was the same as found in south-central Alaska (Ballard et al. 1987), Isle Royale and pooled studies from Alaska and Alberta (Peterson et al. 1984) but different than on the Kenai Peninsula (Peterson et al. 1984) and interior Alaska (Gasaway et al. 1990) where higher proportions of old moose were killed (Fig. 11). There was a tendency to select for calves and older moose in the Coast Mountains, the Kenai Peninsula, and south-central Alaska. Middle-age CM moose were taken at a lower rate than their occurrence in the population, but were still important prey to wolves. Of the 52 adult moose kills that were sexed 42% were males. Bulls comprised an average of 27% of the adult population from 1981-86 (Larsen et al. 1989*a*), significantly lower than the wolf-killed sample indicating selection for bulls by wolves during winter.

Glover and Larsen (1988) concluded that CM moose were in good body condition during late winter, based on physical examination and blood parameters of 63 cows. Larsen et al. (1989*a*) reported an average birth rate of 112 calves/100 cows and a 27% twinning rate in the area, indicating a moose population in good nutritional condition (Glover and Larsen 1988). The nutritional condition of wolf-killed prey was determined by bone marrow fat levels, using ≤10% for calves and ≤20% for adults as standards for starvation condition (Stephenson and Johnson 1973, Peterson et al. 1984, Ballard et al. 1987). Thirty-two adult moose averaged 80% marrow fat (range 30-99) and 17 calves were lower, averaging 60% (range 25-83). This supports observations by Peterson et al. (1984) that calves in winter have lower fat reserves than adults because of rapid body growth requirements. Most of the marrow fat samples were collected from moose killed between February and March when adult and calf marrow fat levels are lower compared to early winter (Franzmann and Arneson 1976, Ballard et al. 1987). Peterson et al. (1984) found nearly half (48%) of wolf-killed moose calves and 4% of adults were malnourished on the Kenai Peninsula. In south-central Alaska, W. B. Ballard (Univ. Ariz., Tuscon;

pers. comm.) found 32% of calves and 2% of adults showed starvation levels of marrow fat. No CM adult or calf moose showed starvation levels, indicating wolves were preying upon a healthier moose population compared to Alaskan studies. Mech and Delguidice (1985) and Ballard et al. (1987) cautioned that marrow fat level was a 'one way' indicator of low physical condition; it did not indicate if an animal was in fair or good nutritional condition, nor did it show if an ungulate was diseased or injured. Notwithstanding, we found no evidence that wolf-killed calf and adult moose were in a starved condition, indicating that winter range or weather conditions did not predispose moose to wolf predation.

Dall Sheep

Our ability to detect sheep kills was limited by their small size, low contrast on snow, the short period wolves attended sheep kills, and the characteristically wind-blown conditions at most alpine kill sites. The detection of all but 1 dead sheep was dependent on locating radio-instrumented wolves close to sheep kill sites. Of 32 wolf-killed Dall sheep found during this study, 25 were non-lambs (78%), 3 were lambs (9%) and 4 (13%) could not be aged. We expected that some lamb kills were missed due to their small size.

Adult sex breakdown was 16 females (64%), 7 males (28%) and 2 unknowns (8%). Thirteen adults averaged 8-years-old (range = 3-13) with no significant difference between sexes. Sheep older than 7-years-old represented 77% (*n* = 10) of adults. We pooled our sheep age data with other Yukon studies where wolf-killed sheep ages were known (*n* = 24 from all areas: Hoefs et al. 1986, Sumanik 1987, Yukon Fish and Wildlife Br. unpubl. data, this study), and found a significant difference in adult age distribution between sexes. Overall, 35% of wolf-killed adults were males, with old and young males killed in equal proportions. The remaining 65% of adults were females greater than 7-years-old (Fig. 12). The absence of yearlings and young females may be an artifact of the small pooled sample size, but it can also be explained by sex-related behavioural differences. Female Dall sheep tend to be in larger nursery bands compared to ram group size (N. Barichello, Yukon Fish and Wildl. Br., pers. comm.). Cumming (1975) showed that clumping tends to decrease caribou vulnerability to predation providing predators do not clump in response. Similarly, large female group size in Dall sheep would enhance the survival of immature age classes and young adult females by providing increased surveillance. Rams tend to be more unpredictable in their use of range compared to females, potentially exposing them to more wolf predation losses throughout the winter. Barichello et al. (1987) found 4 of 12 radio-collared Dall sheep rams died during or immediately following the early winter rut in the northern Richardson Mountains, Yukon, and speculated that during the rut, ram activity and movements increase, leaving males more vulnerable to wolf predation.

By flying twice daily (12 hrs) Fuller (1989) determined that daily wolf locations (24 hrs) underestimated kill rates of white-tailed deer by at least 50%. Because adult deer weigh about the same (78 kg, Fuller 1989) as Dall sheep (73 kg; Nichols 1978), it was possible that our daily relocations underestimated sheep kill rates. Fuller (1989) found that no deer kills were visited for more than 24 hours, but both Sumanik (1987) and our study found that the average time spent on sheep kills exceeded 24 hours (*see* Winter Predation and Consumption Rates). We believe that Fuller (1989) was influenced by relatively poor observability of deer kills and wolves and their trails in forests. We conclude that daily locations of packs did not substantially underestimate wolf predation rates on sheep.

Caribou

During our study we found no wolf-killed caribou during winter and only 1 during summer. In interior Alaska, cesium levels in caribou ranged from 218-543 Bequerels (Bq)/kg, moose from 2-5 Bq/kg (Holleman and Luick 1978, Holleman and Stephenson

1981), and Dall sheep from 11-14 Bq/kg (Holleman and Stephenson 1981). We found similar values for interior Yukon ungulates: 7 caribou averaged 335 Bq/kg, 3 moose 5 Bq/kg and 2 Dall sheep 7 Bq/kg. By measuring radiocesium levels in study area wolves we also established that wolves infrequently killed woodland caribou. The average ^{137}Cs body burden of CM wolves in late winter was 14 ± 11 Bq/kg, well below the minimum value of 37 Bq/kg that indicates light wolf predation on caribou (D. Holleman, Inst. of Arctic Bio., Univ. Alaska, pers. comm.). The average radiocesium burden of wolves sampled inside annual caribou range was 28 Bq/kg (n = 10) which was significantly higher than the average of 9 Bq/kg (n = 24) for wolves outside the caribou winter range, but still relatively low, verifying our radiotelemetry studies that showed caribou were infrequently killed by wolves.

Wolf/Prey Biomass Relationships

Using relative biomass values for prey species from Keith (1983), our ungulate biomass/wolf index in 1983 was 134 based on 65 wolves and ungulate populations of about 750 moose, 150 caribou, 2060 sheep, and 175 mountain goats in a 6,000 km^2 area. Fuller (1989) compared 24 wolf studies and found wolf density was highly correlated with ungulate biomass. The Coast Mountain biomass/wolf index was the lowest index among studies where moose were primary prey (mean = 237±171,n = 10 studies, Fuller 1989). The regression equation provided by Fuller (1989) predicted Coast Mountain wolf density at about 8 wolves/1000 km^2 based on the CM biomass/wolf index. Actual density in the sample area was 11 wolves/1000 km^2 in winter 1983. Variances to the predicted wolf density can occur depending on whether the wolf population is increasing, decreasing or stable in relation to food supply. Mech and Karns (1977) Gasaway et al. (1983) and Peterson and Page (1983) showed a lag response of wolf numbers to decreasing ungulate densities.

Summer Food Habits

Analyses of 650 wolf scats collected from 4 denning sites between 1985-88 (n = 7 collections) showed moose were the most common prey item in scats (46%), followed by beaver, muskrat and small rodents (Table 4). Ungulate species accounted for 54% of all prey items found, compared to 59% for south-central Alaska (Ballard et al. 1987) and 75% moose prey for Kenai Peninsula wolves (Peterson et al. 1984). Using Floyd et al. (1978), we estimated that moose contributed 82% of the prey weight consumed during denning and combined ungulates species represented 91% of biomass consumed at dens (Table 5). Caribou were likely over-represented in their importance to denning wolves in the study area, for 5 of 7 collections were from dens within the range of the Ibex caribou herd. Most study area wolves did not have access to caribou prey. Other research indicates that scat collections can bias the importance of moose to wolf summer diet. Peterson et al. (1984) and Doyle et al. (in prep.) found that Alaskan wolves often visited winter moose kill sites during the summer. If scats from these scavengings were deposited at den sites, they would overestimate the contribution of moose to the summer diet, because no significant moose biomass would be contributed. Nevertheless, scat analyses suggest that moose were the most important prey of CM wolves and moose calves were a substantial portion. This is supported by Larsen et al. (1989 *a*) who found wolves killed 27% of radio-collared moose calves, with most wolf-related mortality occurring during the first 2 months following calving.

Winter Predation and Consumption Rates

We attempted to monitor the daily activities of a total of 14 packs and 2 lone wolves (436 pack days), during late winter 1984 (Period 1; 3 packs, 127 pack days) and 1986 (Period 2; 8 packs and 2 lone wolves, 212 pack days), and early winter 1987 (Period 3; 3 packs, 97 pack days). Overall we were unable to monitor an average of 11% (50) of the pack days during the 3 study periods (range 7-14%). The longest period missed between observations was 3 days. We were confident that most moose kills were seen due to the high visibility of wolf packs (91% sightings) and moose kills, and the average period packs spent at moose kills (3.7 days). Some Dall sheep kills likely were missed, but we do not think they would have contributed significantly to kill rates.

A total of 60 ungulate kills were found during predation rate studies, including 40 moose and 20 Dall sheep (Table 6). Two packs were intensively studied but were not included in the analyses of predation and consumption rates. The Primrose Mountain pair (Period 3) was excluded because it separated frequently and the Rose Creek pack was excluded because the wolves frequently visited dump sites and consumed a high portion of garbage.

Pack kill rates averaged 10.2 ± 5.3 adjusted days /kill (*n* = 3 packs, mean = 5.7 wolves/pack) during early control (Period 1), and 15 ± 6.4 days/kill (*n* = 9 packs, mean = 4.4) during the population recovery phase (Periods 2 and 3 combined), but the difference was not significant. Pack size and adjusted kill rates were not correlated (*r* = -0.18, *P*= 0.27, Fig. 13a) disagreeing with Ballard et al. (1987, Fig. 17) who found large packs killed ungulates more frequently than small packs. We believe that our results differed because of the larger number of pairs in our sample (*n* = 4 of 12 packs) compared to Ballard et al. (1987, *n* = 1 of 8) and the absence of large packs in our study. Predation rates were very high for 3 CM pairs and equalled the rates of some packs of 6-7 wolves. The pair studied by Ballard et al (1987, Table 14) also had a relatively high adjusted kill rate, only slightly lower than much larger packs. After excluding pairs we still found no correlation between pack size and adjusted kill rates (*r* = 0. 47, *P* = 0.23), showing that rates varied widely among normal size packs in this exploited population. The adjusted kill rate/wolf was found to be correlated to pack size (*r* = 0.57, *P* = 0.05, Fig. 13b) with wolves in pairs exhibiting the highest rates. The weight of prey biomass killed/wolf was negatively correlated to pack size (*r* = -0.70, *P* = 0.01, Fig. 13c), and wolves in pairs killed significantly more prey biomass daily (17.1 ± 5.8 kg/wolf) compared to members of larger packs (6.7 ± 3.7 /day). We conclude that in the highly exploited CM wolf population, predation rates were not related to pack size, and kill rates of small groups were as high as some medium size packs.

Wolf consumption rates were not correlated with pack size (*r* = 0. 40, *P* = 0.19) with wide variations observed for pairs and larger groups. Adjusted consumption rates ranged from 0.05-0.25 kg/kg wolf/day, the widest range observed in 6 studies where moose were the primary prey (Table 7). The extreme range was observed during recovery phase. Early control (Period 1) consumption averaged 0.16 ± 0.07 kg/kg wolf/day (*n* = 3 packs). Recovery period consumption was 0.13 ± 0.08 kg (*n* = 9 packs). The non-linear, unpredictable nature of wolf predation rates and wide-ranging consumption rates were likely related to social disruption that occurred during control and early recovery.

Consumption during recovery predicted the breeding success and fate of certain packs. Mech (1977) estimated the minimum intake for survival was about 0.06 kg prey/kg of wolf/day, and 0.13 kg for successful reproduction. The Hacky Sack pair enjoyed high consumption as a pair (0.14 kg) in Period 2. With 3 pups, their consumption fell to 0.05 kg in Period 3; all their pups died during that winter. The Primrose Mountain pair had a high daily consumption rate during Period 2 (0.12 kg/kg wolf), but during Period 3 the pair killed only 1 sheep then frequently split, making no kills. Both wolves travelled widely and both died before spring. The Moose Hollow pair had high daily consumption during both periods (0.18-19- kg/kg wolf) and successfully raised pups from 1986-1988.

Most CM wolves exhibited moderate to high consumption rates during all 3 winter periods studied, indicating that the low prey biomass/wolf index did not negatively affect consumption rates. We believe our consumption rates were more accurate than previously reported values, and recommend that future calculations of intake rates of wolves should be pro-rated by pack size to better estimate actual biomass consumed by wolves.

Messier and Crete (1985) and Ballard et al. (1987) found that the number of days wolves spent on adult moose kills (handling time) decreased as pack size increased. We found a similar negative relationship (r = -0.58, P= 0.004). Packs of 3-7 wolves spent an average 3.7 days (n = 15 kills, range 1-6) on adult moose; pairs spent 6 days (n = 7 kills, range 2-8). Coast Mountain packs spent more time on adult moose kills compared to wolves in south-central Alaska (2.7 days, Ballard et al. 1987) and northern Alberta (2.5 days, Fuller and Keith 1980). This may have been due to the lower wolf/ungulate biomass ratio in our study area, influencing wolves to more completely consume their prey.

Mean handling time for sheep kills was 1.7 ± 1 days (n = 16 kills) for all packs. The longest period a pack spent on a sheep carcass was 3 days. Lone wolves spent an average of 2.3 ± 0.5 days on sheep kills (n = 4). In Kluane Game Sanctuary, Yukon, Sumanik (1987) observed comparable sheep handling periods: 1.4 days for packs and 3 days for lone wolves.

Packs ≥ 3 wolves averaged 22 wolf feeding days (no. of days on kill x no. wolves in pack) per adult moose, significantly more than for pairs (12 days). Coast Mountain wolves spent considerably fewer wolf feeding days on adult moose than Quebec wolves (48.7 wolf-days, Messier and Crete 1985), but averaged 16 ± 2 wolf feeding days on moose calves, similar to Quebec wolves (12.5 days, Messier and Crete 1985).

The 2 lone wolves studied provided some insights into the ability of single wolves to kill large ungulates. Lone wolves killed a calf and a 2-year-old bull moose, and a 12-year-old Dall sheep ram. A lone wolf severely wounded a moose and tested it for 5 days before abandoning it. Consumption rates of lone wolves were high (Table 6), despite an estimated 33% of wolf-available biomass consumed by lone wolves. Scavenging varied between the 2 lone wolves studied; the Canyon lone female killed about 10 % of the prey she consumed, the remainder being scavenged. The Pass Creek lone male apparently killed all his prey.

It is not clear how prey availability and changing wolf density and distribution influenced the species and age of prey items killed by Coast Mountain wolves. Predation rates of exclusively moose-killing packs averaged 10.4 days/*m.e.* killed, significantly greater than for packs that killed both moose and sheep (18.6 days). Moose-killing packs consumed significantly more prey (0.17 kg/kg wolf/day) compared to moose/sheep-killing packs (0.09 kg/kg wolf/day). What factors then determine the predation strategy to hunt Dall sheep? Energetically, the strategy appears to be less productive, for sheep-killing packs killed and consumed less biomass than packs that only killed moose. Sumanik (1987) documented some of the lowest kill and consumption rates in the literature for sheep-killing wolves. He suggested that Dall sheep were a difficult prey to capture frequently enough to support wolves over extended periods. In CM, frequent wolf predation on sheep was pack-specific with only a few packs focused on sheep hunting (Primrose, Primrose Mountain, Hacky Sack). Our two lowest consumption rates (0.05 and 0.07 kg/kg wolf/day) were from 2 moose-sheep packs (Hacky Sack and Jo-Jo Lake) that both ranged in the same mountain block during the study, and spent much of their time in sheep habitat. Their territories also supported relatively low early winter moose density (140 moose/1000 km^2) compared to the neighbouring Kusawa and Moose Hollow packs (290 moose/1000 km^2), which exclusively killed moose and exhibited high kill and consumption rates. Messier and Crete (1985) speculated that 200 moose/1000 km^2 was the density threshold below which wolves could not survive in the absence of alternate prey. Sumanik (1987) implied that as moose density decreased, the importance of Dall sheep as a prey item increased. There is evidence in our wolf predation data to support the idea that alternate prey selection for sheep is dependent on moose density.

Predation Rates and Pack Size

Carbyn (1983), Ballard et al. (1987), Sumanik (1987) and this study reported that the highest per capita kill rates were for wolves in small packs. Carbyn (1983) speculated that straight line relationships between pack size and predation rates may not exist and our data shows this clearly. Why CM wolf pairs exhibited such high kill rates may be partially explained by 1) their greater exposure to prey and 2) greater scavenger competition compared to larger packs. By occupying much larger home ranges during the first winter of recovery, CM pairs were exposed to a larger prey population and a larger selection of potentially vulnerable individuals. C. Promberger (Univ. Munich, unpubl. data) showed that the prey biomass consumed by ravens is inversely related to wolf pack size. As wolf pack size increases, then the portion of prey consumed by wolves and the rate of carcass removal also increases because the number of wolf feeding days increases with pack size. With more members feeding, larger packs collectively spend more time/day attending their kills, minimizing scavenging opportunities.

The high adjusted kill rates of CM pairs challenge the idea that, for social carnivores, success in hunting large prey is lower for groups of 1 or 2 individuals compared to larger groups (Packer and Ruttan 1988). It also does not support Isle Royale wolf data that showed kill rates of moose is maximal at pack size of 5 wolves and that the rate of kill/wolf declines below 4 wolves per pack (Page 1989). Because the CM population was exploited and Isle Royale wolves were naturally-regulated the comparison may be inappropriate. The question remains whether kill rates of CM pairs will remain elevated as the exploited wolf population recovers to a normal, prey biomass-limited density.

This study has shown that individual kill rates for wolves in pairs was almost 3 times higher than for larger packs. Using the average kill rates of 17.1 kg/wolf/day for wolves in pairs, and 6.7 kg/wolf/day for larger packs, we modelled the expected change in daily prey consumption by CM Center wolves, based on annual variations in pack composition. In 1983, when pack composition was 8 packs >2 wolves (mean=8.4) and no pairs, the wolf population daily kill rate was potentially 450 kg (A). During 1986, when the total pack population was 43% of 1983 size and composed of 6 pairs and 5 packs > 2 wolves (mean=3.4), the daily kill rate was 319 kg - 71% of A. This demonstrates that there was a 2:1 relationship between wolf numbers removed and prey numbers killed. These projections also demonstrate the impacts of small pack predation rates and illustrate the problems of reducing wolf-caused mortality on ungulates during winter. Reducing the number of resident wolf packs produces the largest benefit to prey populations. By arbitrarily changing pack frequency to 4 pairs and 3 packs > 2 we projected a potential kill rate of 204 kg/ day (45% of A) for a wolf population 28% the size of 1983. This shows that pack frequency and the proportion of pairs in a population are both important factors in determining the impacts of wolf predation on wintering ungulates. Wolf pack composition can strongly affect the numerical relationship between wolves and their prey during periods of high human exploitation of wolves and should be included into wolf-ungulate management decisions.

Impacts of Wolf Predation on Ungulate Populations

We assessed the impacts of wolf predation during 3 winter periods (180 days) in 1984, 1986 and 1987 in CM Center where wolf predation rates were available and ungulates were regularly surveyed (Appendix F). We assumed that kill rates of wolves varied by pack size, and used the values for pairs and larger packs from the previous section. The proportions of ungulates killed were determined by calculating the number of moose and sheep available in CM Center where surveys showed reasonably stable numbers of both species during 1984-87. Numbers of ungulates killed by wolves during winter were based on 8% of winter wolf days monitored in 1984, 24 % in 1986, and 5% in 1987. Similar techniques have been used by Mech (1977), Fuller and Keith (1980), Messier and Crete (1985), Ballard et al. (1987), and Larsen et al. (1989*b*) to estimate ungulate population losses to wolf predation.

We compared our inductive projections against the results of ungulate studies concurrently conducted in the study area that deductively measured changes in moose, sheep and caribou population conditions in response to lowered wolf density. Larsen et al. (1989*a*) measured changes in annual fall moose population size and composition before, during and following the wolf control period. Barichello et al. (1989*b*) compared Dall sheep demography in a 210 km^2 area in CM Center where wolves were substantially reduced between 1982 and 1986, with a control study group 160 km to the northwest. R. Farnell (Yukon Fish and Wild. Br., unpubl. data) conducted annual fall rut counts on the Ibex caribou herd from 1983 through 1989 and we compared annual caribou calf proportions against wolf density to determine if caribou calf survival was correlated to wolf numbers.

Moose

Based on wolf predation rates, the proportion of the moose population removed by wolves was high in all 3 winters. Wolves potentially killed 11-14% of the wintering population of adult moose in all winters and removed 64% of the moose calves in 2 of 3 winters (Fig. 14, Appendix F). In 1986, when wolf numbers were lowest and moose calves were apparently least vulnerable to wolf predation, wolves shifted to adult moose, taking as many as in other winters when wolf numbers were much higher.

During our study, Larsen et al. (1989*b*) found that grizzly bears killed 58% of 119 radio-collared moose calves compared to 27% killed by wolves. These proportions were similar to results from studies in Alaska (Ballard et al 1991, Gasaway et al. 1990) where at reduced wolf densities, grizzly bear predation was the primary factor limiting moose calf survival and wolf predation was a secondary agent . Larsen et al. (1989*a*) compared CM moose population size and calf survival to 6 months old and found neither was correlated to wolf density changes, but did show that calves in wolf reduction areas had marginally (but significantly) higher survival rates than calves outside. Ballard et al. (1991) showed a correlation in spring wolf densities and subsequent autumn moose calf survival, but concluded that reduction in wolf numbers failed to substantially or rapidly improve calf survival rates. Gasaway et al. (1990) found no substantial change in calf or yearling survival 1 year following a 78% reduction in wolf numbers. Yearling survival in the CM could not be tested due to insufficient yearling data.

CM Center moose censuses showed a stable population between 1982-86. The combination of high rates of grizzly bear predation on adults and calves during summer (Larsen et al. 1989*b*) and by wolves throughout the year, in addition to an estimated 6-8% annual removal of the moose population by hunters (Larsen et al. 1989*a*) would suggest that moose numbers should decline. Because of the wide variances around moose population censuses (18-28%, 90% C.I.), the population could have declined annually, for the random stratified census technique (Gasaway et al. 1981) is unable to detect significant changes until a substantial difference over several years is observed.

How wolves impact moose population dynamics depends on whether prey mortality is additive or compensatory. Gasaway et al. (1990) defined predator-related mortality as additive to other mortality sources if "predators killed many moose that otherwise would have lived to reproduce" and compensatory if "a moose was killed that likely would have died from another cause before reproducing". Theberge (1990) argued that wolf predation becomes additive to other mortality sources when prey populations fall below the nutrient/climate ceiling. Following Gasaway et al. (1990), CM moose were considered vulnerable to compensatory mortality if their condition was poor (≤20% bone marrow fat) or they were very old (cows > 15 years and bulls > 12 years). We found no adults were nutritionally stressed in winter and only 1 of 29 cows and 2 of 15 bulls were very old. Moose condition studies (Glover and Larsen 1988) showed CM moose were below the nutrient/climate ceiling and apparently not predisposed to other mortality factors. This supports our conclusion that wolf predation on CM moose was mainly additive, and contributed to the low density of moose in the Coast Mountains.

Dall Sheep

During all 3 winter periods Dall sheep were a secondary prey species and wolf predation was not apparently limiting CM sheep demography. The proportion of sheep theoretically killed during winter ranged from 3-11% (Fig. 14, Appendix F). Because wolf predation on sheep was not uniform in all packs, the impacts varied among territories. Dall sheep were most important to wolves during the early winter (1987) when they represented 21% of the total prey biomass killed by two packs. This agrees with Barichello et al. (1987) who speculated that sheep vulnerability to wolf predation was highest during and following the rut. We believe that the estimated proportion of sheep removed during the 1987 winter was inflated due to the higher vulnerability of sheep during the early winter study period. Hoefs and Cowan (1979) determined a total annual sheep mortality of 18% during a long-term study of a neighbouring, stable sheep population in Kluane National Park. Assuming a similar mortality ceiling was regulating CM Dall sheep, we conclude that wolf predation alone was not limiting the sheep population, based on the low winter predation rates and the low frequency of sheep in wolf summer scats. This supports Barichello et al.(1989*b*) who found that annual sheep population size, lamb production and age structure were not correlated to changes in wolf numbers in our study area.

Other studies have suggested that wolf predation on thinhorn sheep can regulate sheep population dynamics. Murie (1944) speculated that wolf predation on young Dall sheep in Denali Park, Alaska, regulated sheep numbers during a period when caribou were unavailable to most wolves. Heimer and Stephenson (1982) correlated an increase in sheep populations in Alaska to reduced wolf densities but could not explain similar changes in areas outside wolf control. Sumanik (1987) found wolves could potentially limit sheep in Kluane, but believed wolf predation and consumption rates were so low they were negatively affecting wolf recruitment there.

Caribou

There was no significant change in Ibex caribou calf survival as wolf density declined, suggesting wolves were not an important source of mortality for caribou calves during summer, although scat data showed calves were killed by wolves. From 1983 through 1989 calf numbers in population counts of the Ibex herd averaged 23 ± 3% during fall (R. Farnell, Yukon Fish and Wildl. Br.; unpubl. data). R. Farnell (Yukon Fish and Wild. Br., pers. comm.) believed that subsistence hunting mortality on this small herd has been too high, causing it to remain stable or decline, despite the low impacts of wolf predation during this study.

Wolf and Moose Management Implications

Walters et al. (1981), Gasaway et al. (1983, 1990) and Messier and Crete (1985) argued that the impacts of wolf predation on moose populations increase as moose density declines. Ballard and Larsen (1987) reviewed the implications of predator-prey relationships to moose management and concluded that the effects of predators become increasingly important when combined with hunting. In the Coast Mountains, there is not sufficient historical data to establish why the moose population declined in some regions in the early 1980's. However, the impacts of unrestricted hunting on male, female and calf moose by sport and Indian hunters during the 1970's and early 1980's (in the absence of any population monitoring), was likely important. Gasaway et al. (1983) and Fuller (1989) cautioned that care must be taken in harvesting ungulates in areas where predators are naturally-regulated. Where predators are found in near natural densities, ungulate managers must account for natural predation losses before adjusting harvest levels to satisfy hunting interests. Otherwise, moose population instability will most certainly occur.

Because there is no fast-acting feedback mechanism to regulate wolf numbers to declining prey populations (Packard and Mech 1983) wolves can remain at relatively high density when food supply is low (Peterson and Page 1983, Ballard et al. 1987). We believe this was the case in the Coast Mountains in 1983 when the ungulate biomass/wolf index (134:1) was the lowest recorded for moose/wolf systems, but wolf density and predation rates were moderate, and reproduction and physical condition parameters showed a relatively healthy wolf population.

Fuller (1989) provided a series of formulas to determine values for wolf/moose ratios, ungulate biomass/wolf ratios, and the maximum wolf density that would result in a stationary moose population. He suggested that stability required a ratio of 35 moose/wolf and an ungulate biomass index of 210:wolf. During the first year of this study the moose:wolf ratio was only 10:1 and the biomass/wolf index was 135, suggesting that the moose population was unstable and declining. CM moose stability required a wolf density (*W*) range of 8-10 wolves/1000 km ^{2} based on the equation of Fuller (1989, page 32); with values of 1.42 for the potential rate of increase for CM moose (λ_p), 0.0135 moose/km^2 for average annual hunter kill rate (*S*) between 1979-89, and an estimated 8-10 moose killed/wolf/ year (*K*). The predicted density was 17-33% below the 12 wolves/1000 km^2 observed in 1983. Because we had a better confidence in estimating wolf kill rates in winter months, and moose population estimates are always conducted during early winter, we estimated wolf density that would result in a stationary early winter moose population in the Coast Mountains as:

$$W = \frac{E - U}{K}$$

when $E = 250$ (moose density in early winter/1000 km^2), $U = 219$ (moose density in spring before birth/1000 km^2) and $K = 4$ or 5 (number of moose killed/wolf from 1 November-1 May 1). The resulting theoretical density was 6.2-7.8 wolves/1000 km^2, well below the observed density.

Rearrangements of Fuller's equation (1989, page 33) showed there was no allowable harvest for moose hunters given the CM moose density,wolf density and the estimated annual wolf predation rate. Also, the density of 250 moose/1000 km^2 in the early 1980's was too low to ensure stability. Density should have been between 260-317 moose/1000 km^2 given the impacts of wolves and the reported harvest pressure. These analyses suggest the CM moose population was too small to support the wolf numbers without causing moose numbers to decline.

While the use of Fuller's equations are useful to model general ungulate management options in systems with naturally-regulated predator populations, we caution that the non-linear relationship between wolf numbers and predation rates can limit the application of his model for intensively exploited wolf populations. Wolf density must be lower than the predicted values for moose stability if the wolf population is composed of a high number of pairs or small groups, elevating annual wolf predation rates (*W*). We have already shown that the reduction of the wolf population size by more than 50% resulted in a decline of only 20-30% in the amount of prey biomass killed during winter.

The high kill rates of CM wolves during low wolf density complicated moose recovery efforts in the Coast Mountains and may have been important in other studies (Ballard et al. 1987, Gasaway et al. 1990). In these areas, no substantial increase of moose calf survival rates occurred following intensive wolf control. The reduction and fragmentation of exploited wolf packs pose some considerable problems to managing impacts of wolf predation on moose that have not been previously considered. Because exploited wolves are recolonizing and finding mates during the summer and fall, we believe that the important predation impacts of wolves occurs mainly during winter after pairs have been established. Larsen et al.(1989b) showed that wolves killed 27% of radio-collared moose calves throughout the year, but took most during the summer. We expect recolonizing single wolves will continue to take calves during the summer because of the rapid ingress and the vulnerability of neonatal moose calves to wolf predation. Intensive reduction of wolf numbers, therefore, may only minimally reduce wolf-related mortality on calves in summer.

Grizzly bear predation is another potentially confounding factor to moose population recovery. Where moose calf recruitment is limited by bear predation during the summer (Ballard et al. 1987, Gasaway et al. 1990, this study), the net benefits of lowered wolf numbers are reduced because, 1) the number of moose calves surviving to early winter is small and 2) the wolf predation rate on moose is independent of wolf density. In systems where bears may not be as important predators of neonatal calves, reduced wolf densities caused a substantial increase in calf survival by early winter as Gasaway et al. (1983) found in interior Alaska, and Jingfors (1988) observed in a wolf control area of the east-central Yukon.

This study and Larsen et al. (1989*a*) agree there was little chance that the low density CM moose population could escape the control by bears and wolves. Ballard et al. (1987) and Gasaway et al. (1990) argued that bears are not obligate carnivores and will not likely respond demographically to changes in moose density. However, recent studies by Schwartz and Franmann (1991) suggest black bear demography (ie. growth rates and cub survival) on the Kenai peninsula was influenced by the availability of high protein moose calves in spring. They also showed that black bear predation rates of neonatal moose was independent of moose density. If grizzly bears respond similarly to moose density changes, the combination of bear and wolf predation should maintain low moose density in the Coast Mountains for a long period, even after hunting mortality is near negligible.

In the absence of lethal grizzly bear control plans among wildlife management jurisdictions, can moose populations be released from low densities through a combination of short-term (3-5 years) wolf control, non-lethal management of bear predation on calves, and restrictions on human harvest? Where grizzly bears, wolves and moose are sympatric and wolf control has been applied, moose numbers have apparently failed to increase in response to large, short term wolf reductions, although some small increases in calf survival have been detected (Ballard et al. 1987, 1991; Larsen et al. 1989*a*, Gasaway et al. 1990).

There is some reasonable expectation that a long term (5-10 years), intensive wolf control (70-80% annual reduction), in conjunction with harvest restrictions could increase moose in the CM grizzly bear-wolf/moose system (Larsen et al. 1989*a*). However, their theoretical model is not adequate for it assumes that there is a 1:1 relationship in the number of wolves killed and the number of moose saved from wolf predation, which our study does not support. However, the high importance of wolves to CM moose demography does suggest that by substantially reducing wolf numbers for a long term, over-winter moose survival will increase. The question that remains is whether there would be a substantial increase in yearling recruitment over time to slowly release the moose population from the limitations of grizzly-bear predation on neonatal calves.

Reducing wolf numbers will have the most immediate positive effect on winter survival rates of moose, especially calves and yearlings, and our data suggest that extreme reduction levels (70-80%) are required to produce moderate increases in moose survival rates. Unless grizzly bear-related mortality on moose can be reduced, the annual calf populations surviving to winter have been shown to be too small to substantially and quickly increase moose recruitment rates (Ballard et al. 1987, 1991; Larsen et al. 1989*a*; Gasaway et al. 1990). We recommend that short-term wolf control should not be used to increase moose density in bear/wolf-moose systems because of the low expectation that calf survival to 5 months can be substantially increased. We agree with Gasaway et al. (1990) that attempts to non-lethally reduce bear-related calf mortality, in conjunction with wolf control, will have a greater chance of increasing moose. We also recommend that increased research into the effects of non-lethal control of bear predation on moose calves should be a priority of wildlife management jurisdictions that manage moose in wolf/grizzly bear systems. One technique may be diversionary feeding of bears during the summer calving period (Boertje 1990).

Short-term wolf control should only be applied by wildlife agencies when a large proportion of moose calves are expected to survive to early winter (ie. simple wolf/moose systems) and management programs should be adequately monitored to measure fall calf recruitment changes. When intensive manipulation of wolves fails to substantially increase calf survival in 2 successive years, agencies should be prepared to end wolf control, unless yearling survival rates are substantially increased at the same time. In management areas surrounded by naturally-regulated wolf populations, wolf control should be carried out to ensure numbers are reduced throughout the entire winter, including the late winter breeding period. This would minimize winter predation impacts of newly-formed pairs and reduce the chances of wolves immediately pairing, thereby depressing reproduction. The number of recolonizing packs should be held well below pre-control levels to maximize winter survival of moose. This would require that control programs be conducted in areas that are sufficiently large enough to ensure wolves cannot recolonize all vacant territories immediately. A 20-40% reduction in the number of wintering packs occurred in the east-central Yukon during 7 years of intensive wolf control in a 23,000 km^2 area (Farnell and Hayes 1991), but did not occur in the this study area (12,970 km^2). At the conclusion of wolf population reduction, wolves should be protected completely to allow these predators to recover to natural levels. This could be critical in the Yukon where human harvest may be insufficient to arrest herd growth, and the moose population could reach the nutrient/climate ceiling in the absence of wolf predation.

CONCLUSIONS

1. Wolf control removed 39% of the winter population in the Coast Mountains in 1983, 42% in 1984 and 71% in 1985. The wolf population declined after more than 40% of the winter population was removed, but a large decline occurred only after 71% were removed. Intensive removal had a negative effect on wolf recruitment with the proportion of pups being lowest after 71% reduction. Rates of increase were highest immediately following control, and were best explained by disproportionately high ingress rates into the lowest density wolf population. Wolves did not fully recover after 3 breeding seasons.
2. Most female wolves greater than 1-year-old (75%) and all females 3-years-and-older showed signs of current or past reproduction. There was evidence that a few yearling wolves bred successfully.
3. Wolf pack home ranges during early control were similar to other northern studies, but home range sizes increased after most wolves were removed. Small recolonizing packs occupied extensive ranges for 1 year, after which home ranges declined as pack sizes increased and competition for space restricted wolf movements.

4. Predation rates, reproduction and wolf physical condition data indicated wolves were not nutritionally-limited during early control, despite the lowest wolf/ungulate biomass ratio recorded for wolf/moose prey systems.
5. Moose were the most important prey for wolves, followed by Dall sheep. Wolf predation on moose was additive as wolves selected calves, yearlings and middle-old age moose. No wolf-killed moose were in poor physical condition based on marrow fat values. Including all known sheep killed by wolves in the Yukon, adult male sheep were killed in all age classes, but only females 8 years and older were killed. Behaviour differences between male and female sheep may explain the low vulnerability of young and middle age females to wolf predation.
6. Wolf scat analysis and moose calf radiotelemetry studies showed the summer diet of wolves was mainly moose, including neonatal calves. Wolf pack predation rates in winter were moderate-high during early control but fluctuated widely during early recovery. Pairs of wolves killed prey as frequently as larger packs and individual kill rates were 2-3 times greater for wolves in pairs compared to wolves in larger packs. Our data suggest that optimal wolf group size for foraging is 2 wolves in exploited populations.
7. We found that there was a 2:1 relationship in the number of wolves removed and number of ungulates saved from wolf predation. A 55% reduction of the early winter wolf population size resulted in a decline of only 20-30% in the prey biomass killed during winter. The high wolf predation rates at low wolf density, combined with high bear predation on calves, confounded any significant response in moose survival to wolf density changes.
8. Modelling wolf predation rates in winter with ungulate demography during control and recovery predicted the following: i) During 2 winters, wolves removed more than 60% of the moose calves that survived to fall and wolf predation in winter contributed to the exceptionally low yearling moose recruitment rates. ii) Wolves removed few calves during early recovery despite an apparent abundance of calves in the winter population. This calf cohort appeared to be highly resilient to wolf predation, but we cannot explain why. iii) Wolves again removed about half the calves in the second recovery winter. iv) 11-14% of adult moose were killed by wolves during all winters. When combined with moderate harvest rates and low recruitment, this would predict a declining moose population. v) Sheep removal rates were low compared to annual natural mortality in an neighbouring sheep population. Wolf predation on sheep was pack specific and wolves likely affected regional sheep populations differently. Wolf predation on sheep appeared to be related to availability of moose.
9. Moose:wolf ratio and prey biomass: wolf index predicted that the moose population was likely unstable and declining at the beginning of the study. Equations derived from moose population data, human harvest rates and wolf predation rates indicated wolf density should have been 17-33% less than we observed to sustain moose numbers in the Coast Mountains. Harvest rates were found to be excessive given the estimated impacts of wolves on moose calf and adult mortality.
10. Our wolf predation data supported concurrent moose and Dall sheep population studies that found the level of wolf reduction did not substantially increase recruitment rates or population size of moose, Dall sheep or woodland caribou.
11. Wolf predation on adult and immature moose during winter, and grizzly bear predation on calves during summer will likely maintain CM moose density at low levels for an indeterminate period. Moose recovery will require addressing natural predation losses and human harvest, especially in the lowest moose density areas near communities and along road corridors. Short term removal of wolves will likely have no substantial positive effect on moose populations, based on this and other studies in Alaska where moose, wolves and grizzly bears are sympatric. Short-term wolf control should be conducted only if calf survival to early winter can be increased substantially and rapidly.

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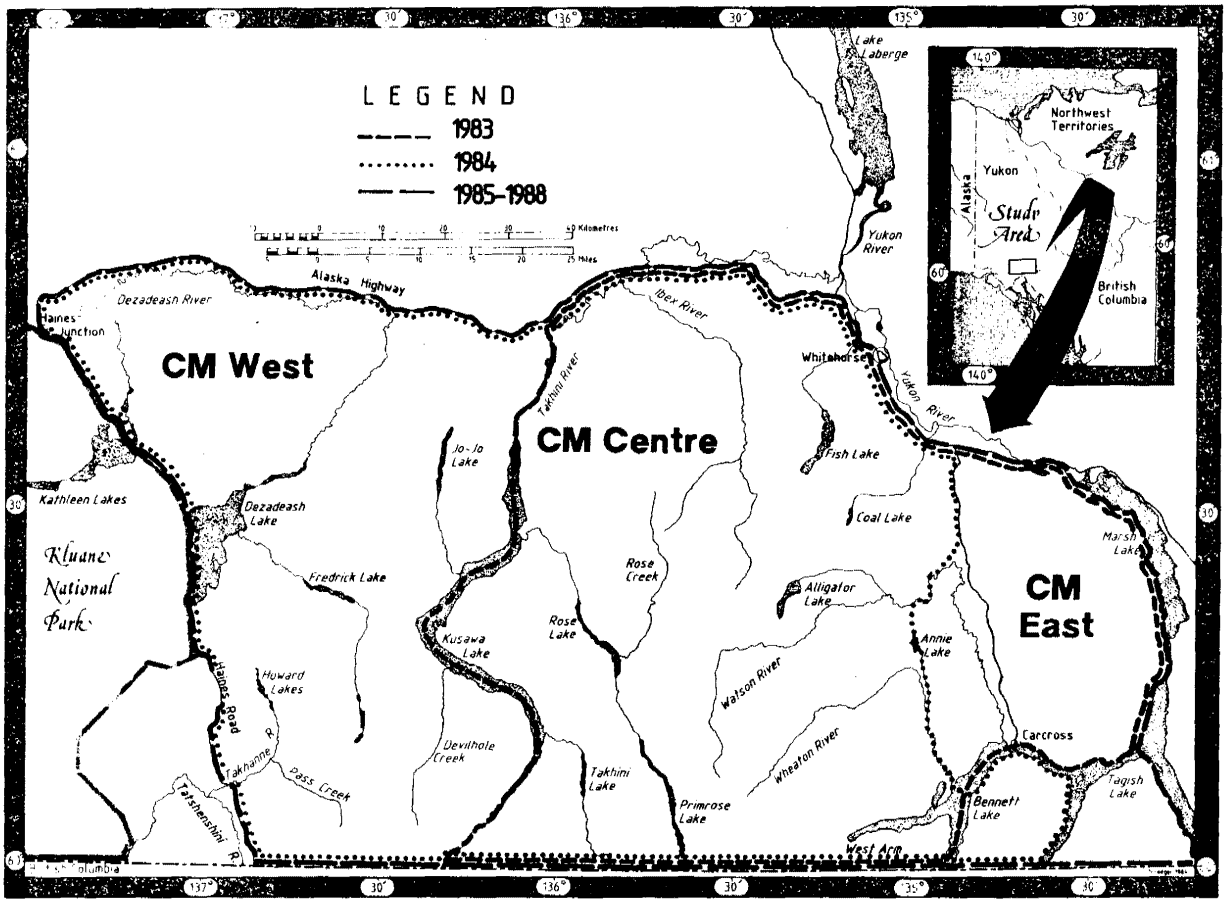

Fig. 1. The location of the Coast Mountain wolf study area in the southwestern Yukon, 1983-88.

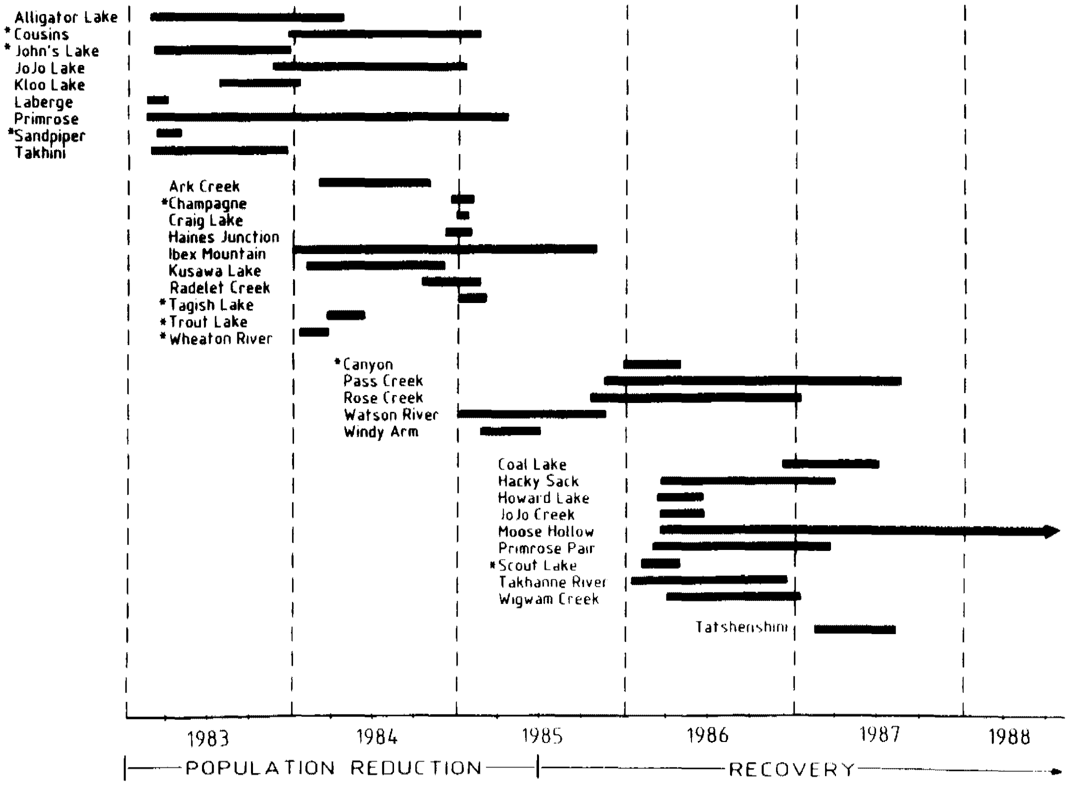

Fig. 2. The chronology of radio-transmitter contact with 25 wolf packs and 10 lone wolves (*) in the Coast Mountain study area. Canyon pack was a pair that split into 2 radio-collared lone wolves during monitoring.

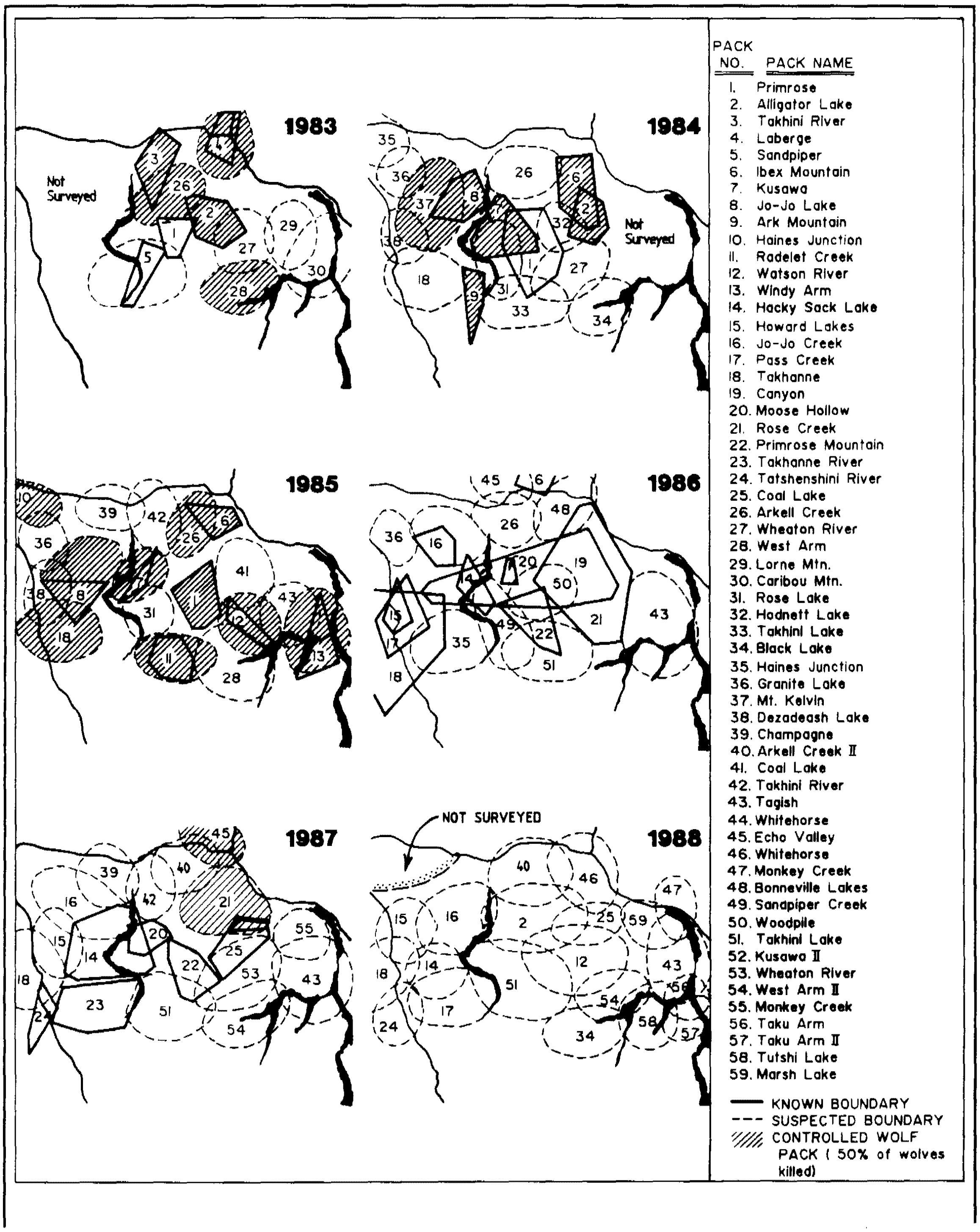

Fig. 3. Annual winter distribution of wolf packs in the Coast Mountain study area, 1983-88.

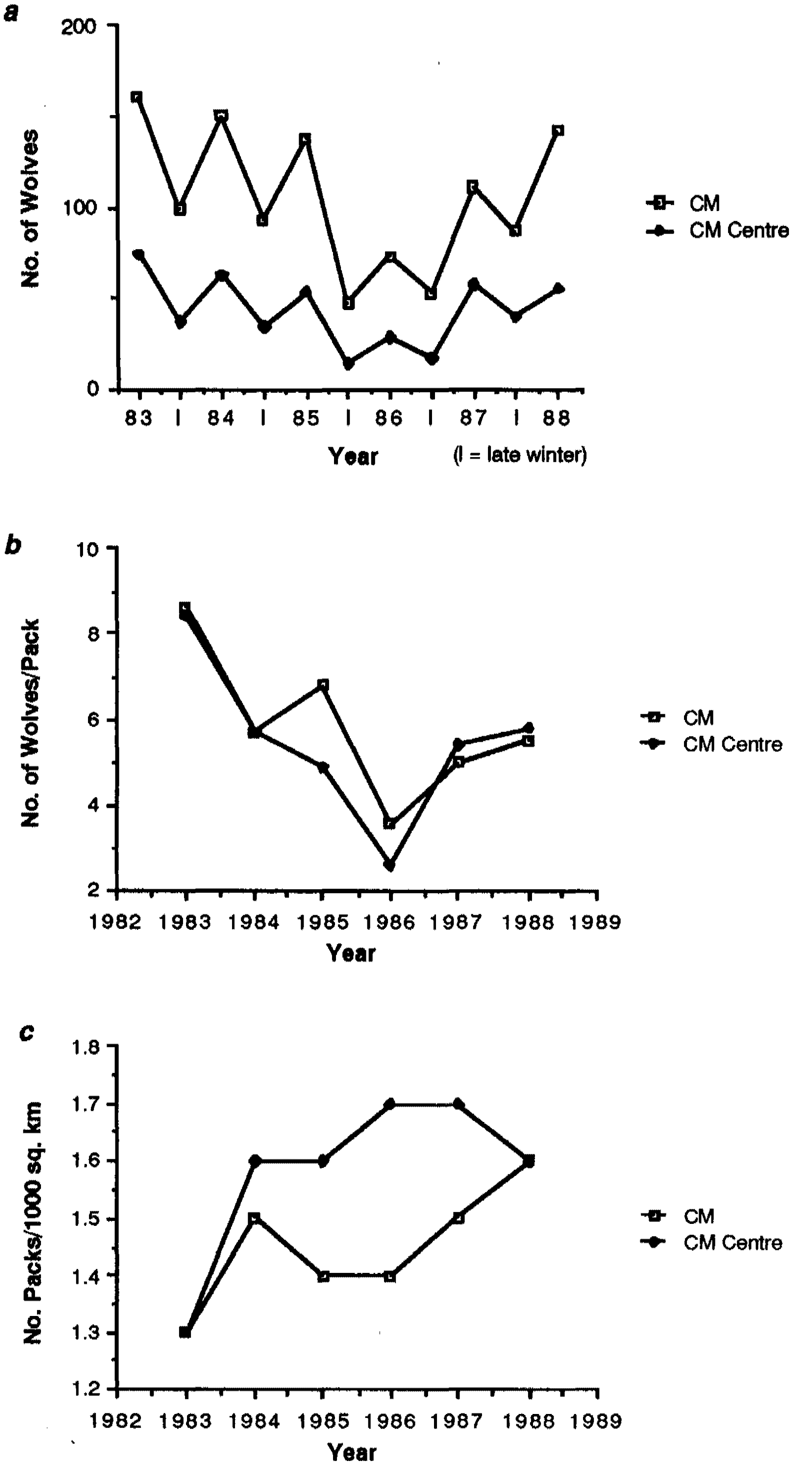

Fig. 4. Annual fluctuations in winter wolf population size (a), pack size (b), and pack density (c) in the Coast Mountain study area, 1983-88.

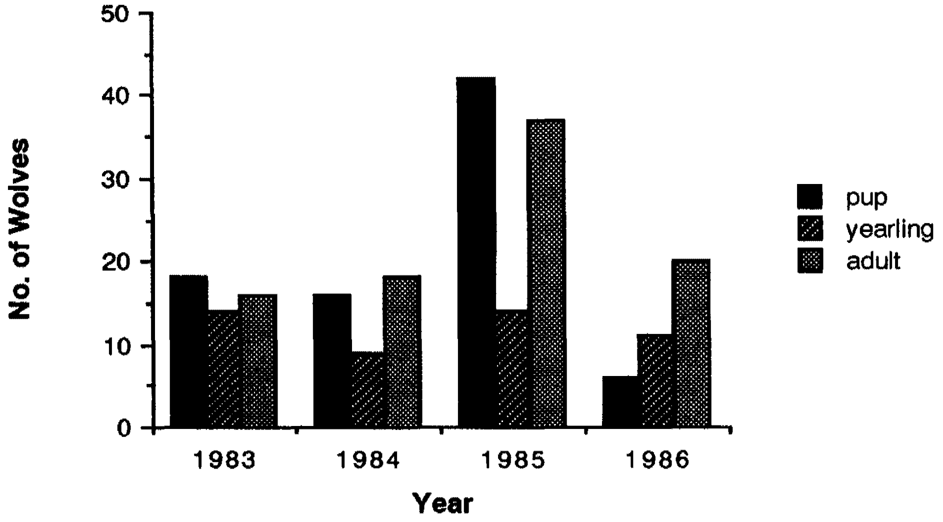

Fig. 5. Age class frequencies of 226 radio-collared or killed wolves studied during control (1983-85) and during the first winter of recovery (1986) in the Coast Mountains.

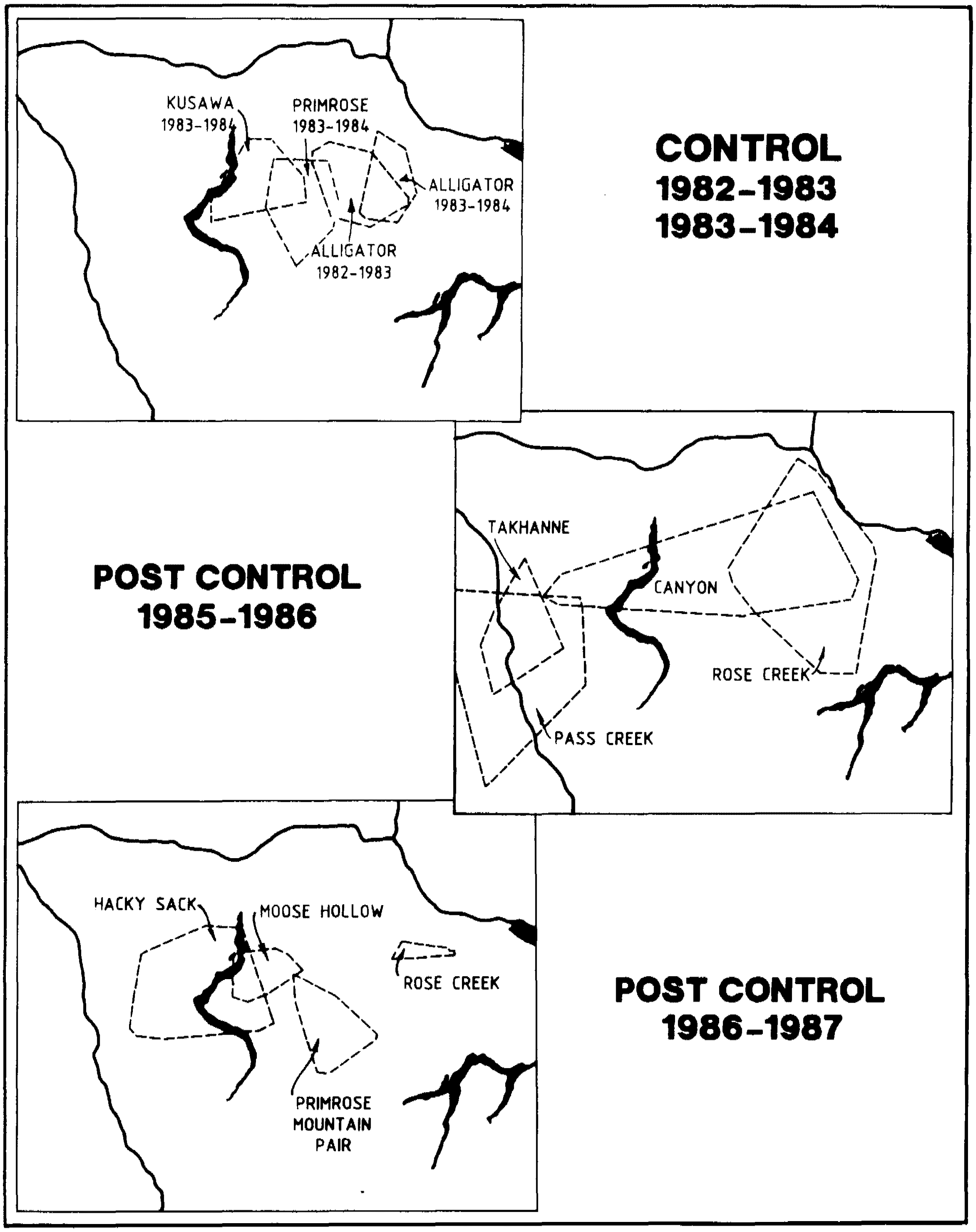

Fig. 7. Winter home ranges of Coast Mountain wolf packs located ≥ 30 times, during and following wolf control.

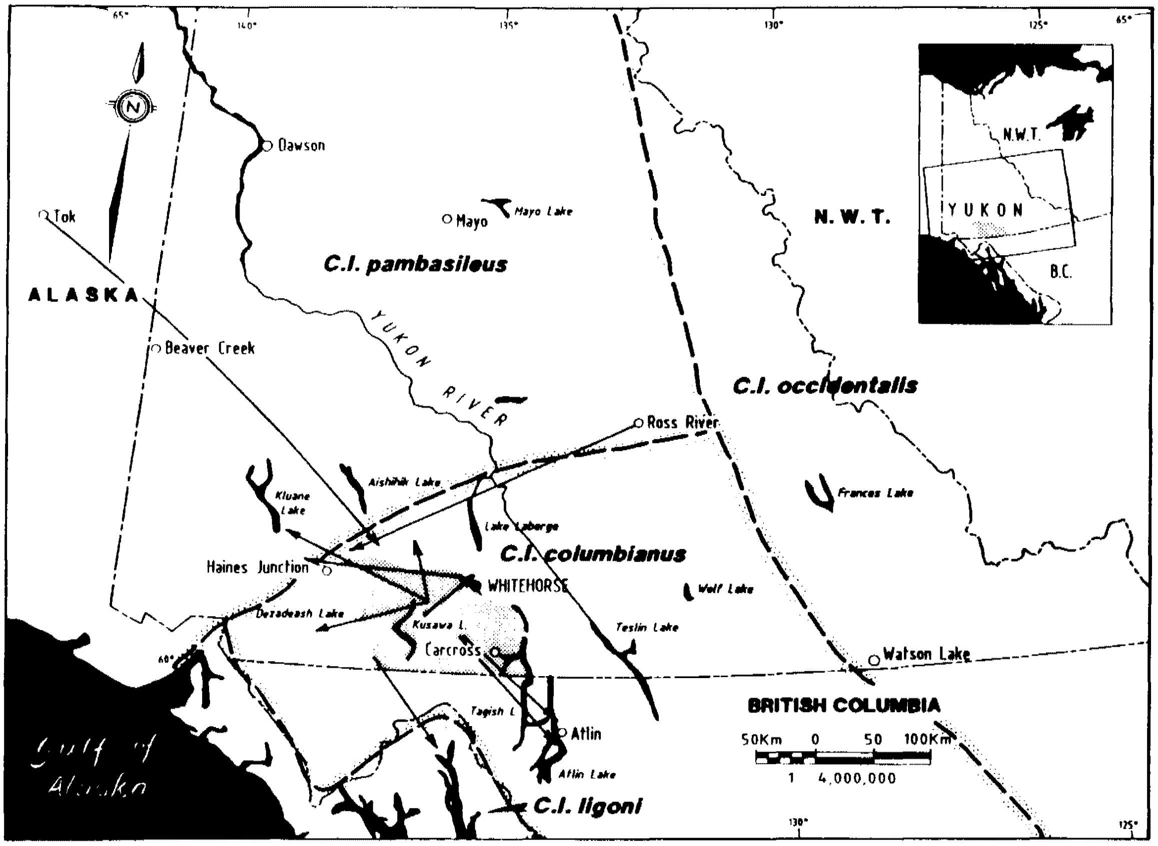

Fig. 8. Movements of radio-collared wolves to and from the southwestern Yukon between 1983-87. Subspecific wolf ranges are from Nowak (1983).

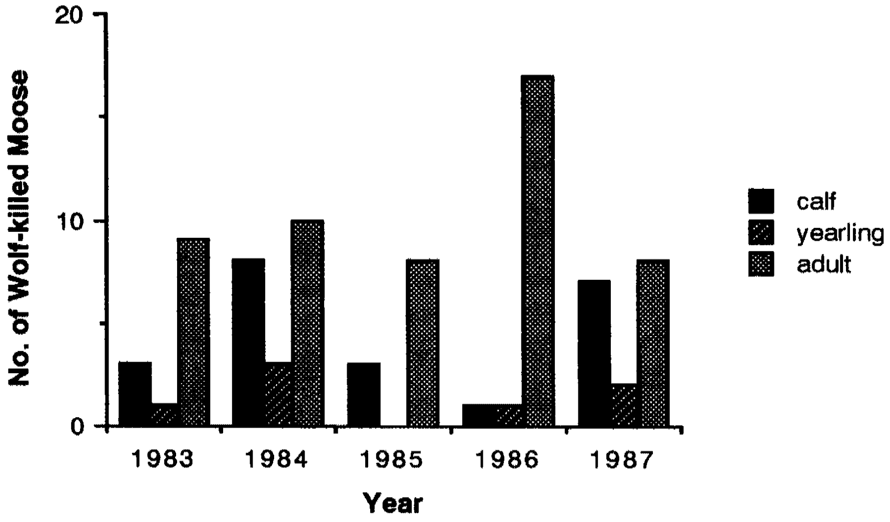

Fig. 9. Age classes of moose killed by wolves during each winter in the Coast Mountain study area, 1983-1987.

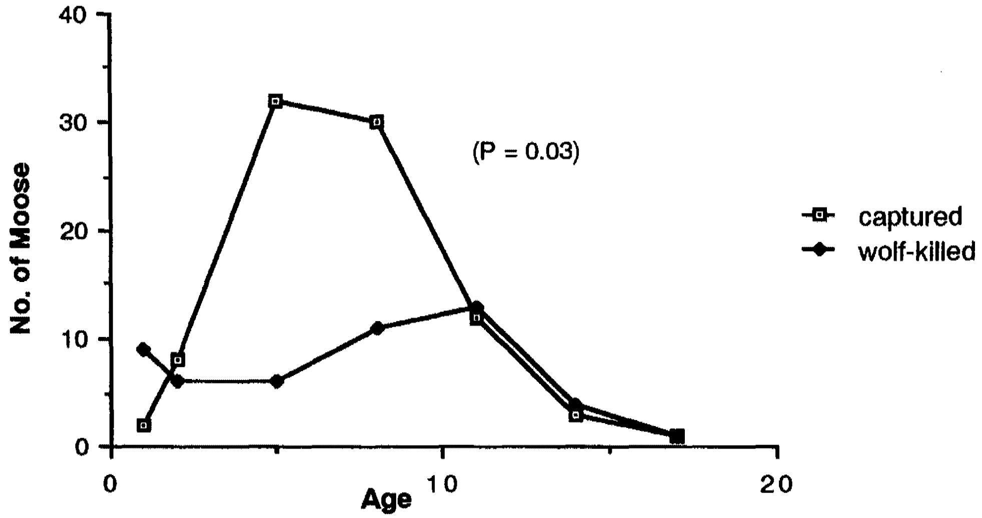

Fig. 10. Age distribution of all wolf-killed yearling and adult moose, and live-captured cow moose (Larsen et al. 1989*b*) in the Coast Mountain study area.

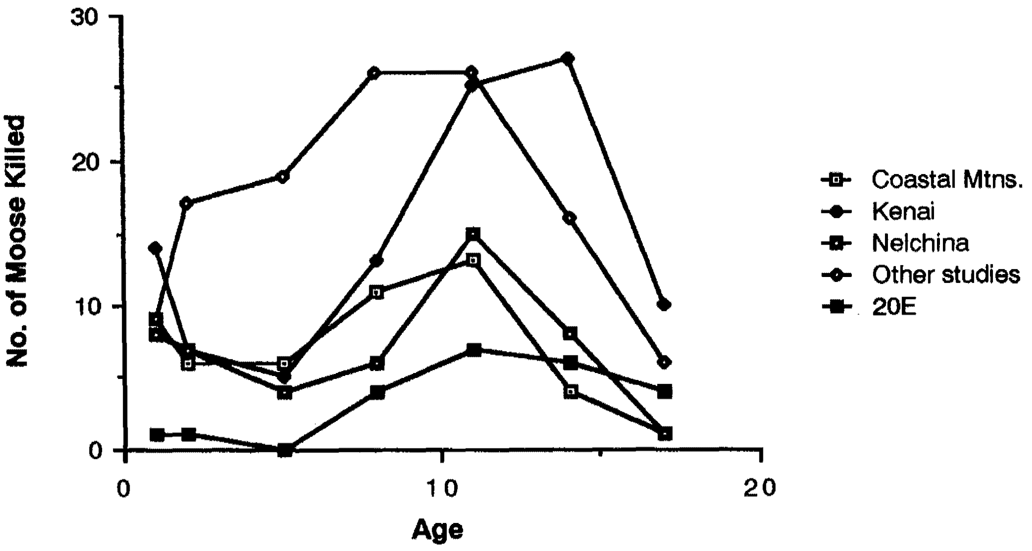

Fig. 11. Age distribution of wolf-killed adult and yearling moose from 5 wolf-moose studies in Canada and Alaska. Sources of data were as follows: Kenai Peninsula, Alaska and other studies (Peterson et al. 1984), Nelchina, Alaska (Ballard et al. 1987), Unit 20E, Alaska (Gasaway et al. 1990), and this study.

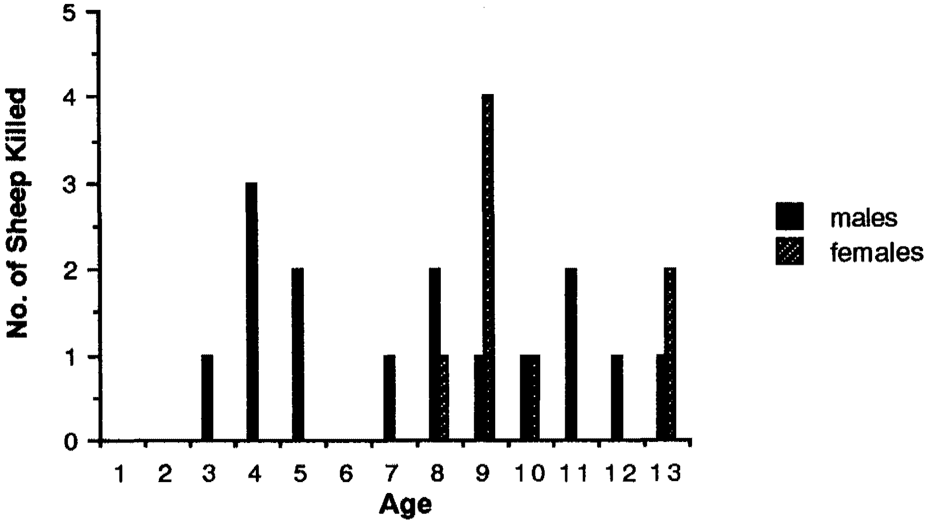

Fig. 12. Known ages of adult Dall sheep killed by wolves in the Yukon during the 1980's. Data from this study, Hoefs et al. (1986), Sumanik (1987) and B. Slough, Yukon Fish and Wildl. Br., (unpubl. observ.).

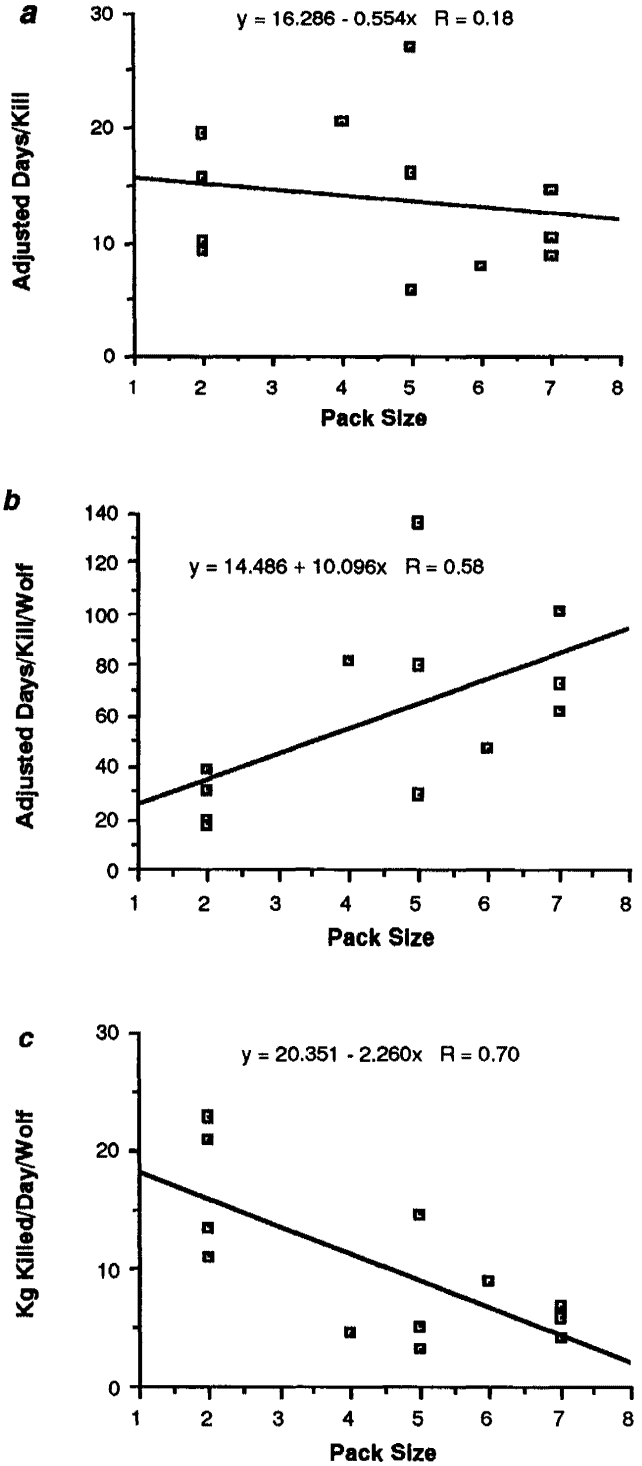

Fig. 13. Relationships between CM wolf pack size and adjusted days/kill (a), adjusted days/kill/wolf (b) and kg of prey killed/day/wolf (c).

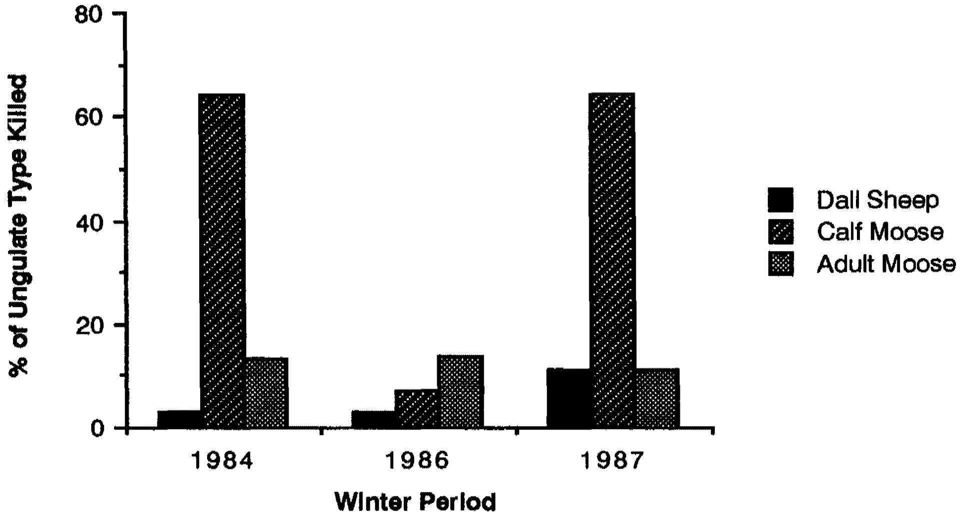

Fig. 14. Predicted rates of prey population losses caused by wolf predation during three 180-day winter periods in the CM study area.

Table 1. Annual winter wolf population data by Coast Mountain area, 1983-88.

Year		CM West	CM Center	CM East	Total
(Wolf Control Period)					
1983	total wolves[1]	[a]62[nc]	74[c]	25[c]	161
	number dead	20	37	5	62
	1983% dead	32	50	20	39
	% original pop. dead	32	50	20	39
1984	rate of increase	1.47	1.70	1.25	1.51
	total wolves	62[c]	63[c]	25[nc]	150
	number dead	27	28	2	57
	1984% dead	44	44	8	38
	% original pop. dead	44	53	8	42
1985	rate of increase	1.42	1.54	1.32	1.47
	total wolves	[b]50[c]	54[c]	33[c]	137
	number dead	[d]27	40	23	90
	1985% dead	[e]54	74	70	66
	% original pop. dead	[f]63	81	60	71
(Wolf Recovery Period)					
1986	rate of increase	1.69	2.00	-0.60	1.55
	total wolves	39[c]	28[c]	6[c]	73
	number dead	6	12	3	21
	1986% dead	15	43	50	29
	% original pop. dead	47	78	88	68
1987	rate of increase	1.39	3.56	2.60	2.13
	total wolves	46[c]	57[c]	8[c]	111
	number dead	8	17	0	25
	1987% dead	17	30	0	23
	% original pop. dead	39	46	68	47
1988	rate of increase	1.55	1.38	3.30	1.64
	total wolves[2]	59[c]	55[c]	27[c]	141
	% original pop. dead	5	26	0	12

[1] Total wolves in mid winter of each year.

[2] Only early winter population size estimated for 1988.

[c] Censused.

[nc] Not censused.

$$e = \frac{b-d}{b} - 1$$

$$f = \frac{b-d}{a} - 1$$

Table 2. Weight (kg) and external body measurements (mm) of adult and yearling wolves from the Coast Mountain study area.

Sex	Weight	S.E.	Contour[a]	S.E.	Neck[b]	S.E.	Chest[b]	S.E.
Adult[c]								
Male	43	1.9	1296	18	440	9	756	16
Female	36	1.1	1232	11	399	6	706	7
Yearling[d]								
Male	37	1.3	1251	11	423	11	733	19
Female	35	1.2	1197	11	412	19	675	22

[a] Contour length was the distance from the tip of the nose to the base of the tail along the back.

[b] Neck and chest circumference measurements were from skinned wolves.

[c] Data were from 19 males and 37 females.

[d] Data were from 10 males and 18 females.

Table 3. The average monthly and annual (June-May) survival rates of radio-collared wolves in the Coast Mountain study area.

	Wolf months (*N*)	Deaths (*N*)	Monthly survival rate	Annual survival rate
1982-83	38	1	0.973	0.68
1983-84	135	4	0.970	0.64
1984-85	122	8	0.934	0.21
1985-86	124	5	0.959	0.51
1986-87	167	11	0.934	0.22
1987-88	57	4	0.930	0.16

Table 4. Frequency of occurrence of 742 prey items found in 650 wolf scats collected from CM dens during August, 1985-88[a].

	No.	Moose			Caribou		Dall				Small		
Year	Items	Adult	Calf	All	Adult	Calf	Sheep	Beaver	Muskrat	Hare	Rodents	Birds[b]	Other[c]
1985	75	0	11	11	0	4	1	29	8	4	29	8	5
1986	278	36	11	47	5	1	0	27	4	4	9	2	1
1987	231	17	26	43	8	1	1	13	22	0	1	7	4
1988	158	28	35	63	6	1	5	10	9	0	1	1	4
Percentage		25	21	46	6	1	1	19	11	2	7	4	4

[a] Scats were collected from den sites of the Alligator Lake (1985, 1986), Jo-Jo Lake (1986,1987), Moose Hollow (1986, 1987, 1988) and Tatshenshini (1987) packs.

[b] Birds included ducks, grouse and passerines.

[c] Other prey included fox, wolverine, porcupine, fish and unknown type.

Table 6. Predation and consumption rates of wolf packs and lone wolves during late winter 1984 (Period 1) and 1986(Period 2), and early winter (1987), Coast Mount study area.

						PREDATION AND CONSUMPTION RATE				
		No.	Period (days)	No. of kills		Total kg	Adjusted	No. adj.days	Kg killed	Kg consumed
Period	Pack name	wolves	studied	moose	sheep	killed	days/kill[a]	/kill /wolf[b]	/wolf/day	/kg wolf/day [c]
1	Kusawa	7	56	9	0	2708	8.8	62	6.9	0.12
	Primrose	5	53	5	6	1408	16.0	80	5.1	0.10
	Ark Creek	5	17	3	0	1335	5.7	29	14.8	0.25
2	Pass Creek Loner	1	38	2	0	577	28	28	15	0.11
	Canyon Loner	1	41	0	1	75	241	241	1.8	0.12
	Hacky Sack	2	22	1	3	600	15.7	31	13.6	0.14
	Primrose Mountain	2	24	1	2	528	19.5	39	11	0.12
	Pass Creek	2	30	3	0	1260	10.2	20	21	0.24
	Moose Hollow	2	19	2	0	881	9.2	18	23	0.19
	Rose Creek[d]	3	36	1	1	NA	NA	NA	NA	NA
	Howard Lakes	4	22	1	0	400	20.5	82	4.5	0.11
	Takhanne River	7	41	4	0	1681	10.4	73	5.9	0.10
	Jo-Jo Lake	7	18	1	1	529	14.6	102	4.2	0.07
3	Primrose Mountain[d]	1-2	33	0	1	NA	NA	NA	NA	NA
	Hacky Sack	5	28	1	5	443	27	136	3.2	0.05
	Moose Hollow	6	36	6	0	1948	7.9	47	9	0.18

[a] Adjusted kill rates are based on no. of days it took wolves to kill 1 moose equivalent (427 kg, Ballard et al. 1987). See Appendix A for details of prey weights used. Unclassified moose and sheep were assumed to be adults.

[b] Calculated by multiplying the number of wolves in each pack x no. of adjusted days/kill.

[c] Consumption rates included estimates of biomass scavenged.

[d] The Rose Creek pack (Period 2) and Primrose Mountain pair (Period 3) were not included in predation and consumption rate comparisons (*see* Methods for rationale).

Table 5. Calculation of relative prey biomass from scats collected at natal dens in the Coast Mountains, 1985-88.

	Moose		Caribou		Dall Sheep	Beaver	Muskrat	Hare	Small Mammal	Bird
	Adult	Calf	Adult	Calf						
(A) Percentage occurrence of prey in scats	25	21	7	1	1	19	11	2	7	4
(B) Estimated average weight of prey /scat[a]	6.8	1.2	3.3	0.6	1.6	0.6	0.4	0.4	0.4	0.4
(C) A X B (kg)	170	24	20	1	2	12	5	1	3	2
Relative % biomass consumed (A X B/sum C)	71.5	10.2	8.3	0.3	0.7	5.0	1.8	0.4	1.1	0.7

[a] From Floyd et al. (1978). Assumed whole mammal weights from Ballard et al. (1987) except for Dall sheep (Bunnell and Olsen 1976). Consumable weights (kg) were as follows: adult moose (320) calf moose (39), adult caribou (145), calf caribou (12), adult Dall sheep (62), beaver (12), muskrat (1.4), snowshoe hare (1.8), squirrel (0.5), small rodent (0.1) and birds (0.7).

Table 7. Winter consumption rates of wolves from 6 North American studies where moose were the primary prey.

Study area	No. of packs studied	Consumption rate (kg prey /kg wolf/day)	Reference
Coast Mountains			
Period 1	3	0.12-0.25	
Period 2	7	0.07-0.24	
Period 3	2	0.05-0.18	
Northern Alberta	2	0.12-0.15	Fuller and Keith (1980)
South-central Ak.	4	0.13-0.22	Ballard et al. (1987)
Kenai Peninsula, Ak.	1	0.12	Peterson et al. (1984)
Quebec	14	0.09-0.12	Messier and Crete (1985)
Isle Royale, MI.	7	0.09-0.19	Peterson et al. (1977)[a] and unpublished data

[a] Cited in Peterson et al. (1984).

APPENDICES

Appendix A. The weights of moose and Dall sheep prey used in Coast Mountain predation rate studies.

Species	Winter Period	Age	Sex	Live Wt. (kg)[a]	Available kg[b]	Source
Moose	All	Adult	Male	454	340	Franzmann et al 1978
	All	Adult	Female	400	300	Franzmann et al 1978
	All	Adult	Unk.	427	320	Ballard et al. 1987
	Early	Calf	Unk.	181	136	Franzmann 1978
	Late	Calf	Unk.	150	113	Franzmann et al 1978
	All	Yearling	Unk.	278	209	Franzmann et al. 1978
Dall sheep	Early	Adult	Male	88	66	our calculation
	Late	Adult	Male	75	56	Bunnell and Olsen 1976
	Early	Adult	Female	58	44	our calculation
	Late	Adult	Female	49	37	Bunnell and Olsen 1976
	Early	Lamb	Unk.	30	23	Nichols 1978
	Late	Lamb	Unk.	25	19	Nichols 1978
	Early	Adult	Unk.	73	55	our calculation
	Late	Adult	Unk.	62	47	Bunnell and Olsen 1976

[a] Late winter calf weight was estimated from Franzmann et al. (1978, Fig. 3) showing slight decline from October to May. Early winter weights of adult and lamb Dall sheep were estimated to be 18% more than during late winter, based on lamb weight loss (Nichols 1978).

[b] Assumed that 75% of live weights of all prey types were potentially available to wolves.

Appendix B. The history of radio-collared wolves in the Coast Mountain study area, 1983-88.

Alligator Lake Pack

Contact was first made with this 12 member pack on 21 February 1983 when 2 members (1000, yearling female; 1040, yearling male) were collared. The alpha female (1150) was collared in early March. She produced a minimum of 5 pups during the 1983 denning season. The alpha male (1121) was collared on 23 May, then illegally shot on 27 June. The pack continued to disintegrate during the winter 1984 with both 1000 and 1040 dispersing and 6 other wolves disappearing between 2-21 February. Female 1150 found a new male in March which was shot by government aerial hunters on 19 March. Wolf 1150 was subsequently seen with the collared male 1181 of the Ibex pack on several occasions between 20 March and 12 April. She was eventually shot in late April, and found to be pregnant.

Ark Creek Pack

The Ark Creek pack was instrumented 29 February 1984 when the alpha male (1810) was captured. This 5 member pack was observed every 2 days until March 18, when all members except 1810 were shot. Wolf 1810 remained in the pack territory until at least October, after which the signal failed to transmit. A radio-collared wolf matching his description was seen in the area by an outfitter in the fall of 1985, in the company of another adult and 2 pups.

Canyon Pair

On 30 December 1985, a pair of wolves were located on a moose carcass near Primrose River canyon. The adult male (1114) was collared on that date and an adult female (1056) was darted 19 January 1986 at the same site. The wolves were not seen together again. Wolf 1114 died 23 February 1986 from neck injuries caused by a trapper's snare. Female 1056 wandered alone through the study area then dispersed in early April. Her collar and carcass were found on 10 June near Atlin, B.C. Cause of her death was unknown.

Champagne Lone Female

Wolf 1110, a 9-year-old female, was collared 23 December 1984, after being trapped several kilometers north of the study area, near Champagne village. She was snared in the study area by another trapper on 1 February 1985. At the time of her death she had a recently broken leg. She was apparently with other wolves at the time of her first capture, but was apparently alone when she died.

Coal Lake Pack

This pack began as a lone male wolf (1081) collared on 4 December 1986 at Coal Lake. A radio-collared pup (0999), 1 of 3 survivors from the Rose Creek pack (*see* Rose Creek pack), was also present. On 16 December, 2 uncollared wolves were seen with 1081 but both disappeared by 16 January 1987. On 17 February 1081 was in the company of a 4-year-old female. This wolf (1100) was collared on 27 March and denned at the Alligator Lake den site.

When located on 16 June, 1081 was 20 km east of the den in the company of an uncollared black wolf. Wolf 1100 was found dead from unknown causes at the den site. Wolf 1081 was relocated several time through 1987 and was seen with another wolf during December. In the spring of 1988, he was seen attending the den of the Moose Hollow pack.

Cousins Lone Female

This female (1141) was caught in a snare on 15 December 1983, 8 km north of Whitehorse. During our monitoring, she was never seen in the company of other wolves. She remained near the study area throughout 1984, mostly centered on the Whitehorse dump. Her fate after 16 February 1985 was unknown.

Craig Lake Pack

The 5 member Craig Lake pack was contacted on 30 December 1984, when a female pup (1160) was snared and radio-collared near Craig Lake while travelling with 5-6 other wolves. This wolf was relocated only once before she was killed by a trapper on 7 January 1985. Contact with the pack was not re-established. However, trappers took the remaining pack members during the winter.

Granite Lake Pack

This 3 member pack was located at Granite Creek on 27 November 1983 during aerial surveys of moose. On 28 November a yearling male (1110) was radio-collared. He was found dead at the capture site the next day. The wolf died of internal bleeding caused by dart penetration into the peritoneal cavity. Radio contact was not re-established with the pack.

Hacky Sack Lake Pack

This pack was first contacted on 14 March 1986 when 2 wolves, 1179 (adult male) and 1253 (yearling female), were captured near Kusawa Lake.

During the summer 1986, the pair denned in a rock cave near Jo Jo Lake raising 3 pups to early winter. Intraspecific conflict with the Moose Hollow pack and another uncollared pack resulted in the death of the 3 pups by the end of January 1987. Both signals were lost after 27 March 1987.

Haines Junction Pack

This 6 member pack was contacted on 4 December 1984 when 2 wolves were snared at the Haines Junction dump. Wolf 1350, a male pup, was instrumented and the other wolf, a 3-year-old male, had a broken femur from a previous injury and was destroyed. The pack was observed until late January 1985 when all pack members except 1350 were shot as part of the reduction program. Efforts to relocate wolf 1350 after 21 January failed.

Howard Lake Pack

This 4 member pack was first contacted at Howard Lake on 10 March 1986 when 2 wolves, 1079 (male pup) and 1099 (adult male), were radio-collared. Wolf 1079 died of a broken spine between 23-28 March at a moose kill site. A third member left the pack after 28 March. When seen at Dezadeash Lake on 31 March, only 1099 and a second wolf were present. The pair was last located on 2 June.

Ibex Mountain Pack

The Ibex Mountain Pack was radio-instrumented on 5 January 1984 when wolf 1181 (adult male) was captured in a leg-hold trap at the Whitehorse dump in the company of 3 other wolves. One wolf left the pack in February. This wolf matched the description of the male shot with the Alligator Lake female on 19 March (*see* Alligator Lake pack). Wolf 1181 joined briefly with the Alligator Lake female until late April, but spent most of his time alone near Whitehorse. Wolf 1181 was next located on 25 September 1984 with 6 pups and 1 adult female. The 7 wolves were shot between 13 November 1984 and 8 January 1985. Wolf 1181 was relocated north of the study area (Little River) during June 1985 attending a den. He was observed with 1 wolf on 21 November then shot by a home owner on 28 November near Whitehorse. There was a minimum of 4 wolves with him at the time.

John's Lake Lone Female

An adult female (1050) was captured in a leg-hold trap at John's Lake by a trapper in late February 1983. She was extremely emaciated and remained near the capture site until 22 March, when she moved about 15 km away. She remained there until May 5, then moved 50 km northeast (Lake Laberge) during June and July. She was found dead in the Whitehorse city limits on 22 December 1983, killed by a vehicle.

Jo-Jo Creek Pack

The Jo-Jo Creek pack was first contacted on 15 March 1986 when 3 wolves (1123, female yearling; 1244 and 1263, male pups) were radio-instrumented near Jo-Jo Lake. Wolf 1263 died before 28 May near Champagne and 1123 was found dead near the Alaska Highway in July. Causes of death were unknown. Wolf 1244 was located several times during the summer of 1986 near a den site that produced young. Contact with the pack was lost after 17 June. In March 1987, a 10-12 member pack believed to be this group was seen near Frederick Lake.

Jo-Jo Lake Pack

This 6 member pack was first contacted (alpha male, 1221) on 27 November 1983 north of Jo Jo Lake. On 19 January 1984, 3 members of the pack were aerially shot. Two more wolves were shot on 15 February. Wolf 1221 attended a den near Dezadeash Lake during the summer of 1984,but may not have sired the pups raised there. On 17 December 1985 all 6 wolves associated with this male were shot by government aerial hunters. After January 1985, contact was lost with 1221.

Kloo Lake Pack

The Kloo Lake pack was first encountered on 20 July 1983 when a 5-year-old black male (1190) was caught in a snare at the Haines Junction dump. The wolf was first monitored 20 December when it was found with 7 wolves on a moose kill near Haines Junction. The pack was located 3 more times and on 20 January 1984 wolf 1190 and 2 others were shot by a helicopter crew. The remaining 4 members escaped and contact with the pack was lost.

Kusawa Lake Pack

The Kusawa Lake pack was known from the 1983 winter wolf surveys. On 5 March 1983, 5 of 9 wolves were shot by a trapper in the central activity area of this pack. On 23 January 1984, a juvenile male (1821) was darted and radio-instrumented. This 7 member pack was monitored daily from 23 January to 1 April 1984 during winter predation rate studies. Five members of the pack were shot on 1 April, with only the alpha male and wolf 1821 surviving. The 2 wolves were located on 11 October 1984 accompanied by a young female wolf. On 26 November, 1821 and the female were killed and the alpha male was captured and radio-collared. The alpha male died from unknown, capture-related injuries.

Moose Hollow Pack

This pack was first located on 24 October 1985 in the old territory of the Kusawa Pack. On 28 October wolf 1075, an adult male from the Watson River pack of the previous winter, was recollared. The collar failed after 16 November and the pair was not located again until 18 March 1986. On this occasion, wolf 1005 (adult female) previously from the Windy Arm pack, was re-captured and re-instrumented (1166). The pair denned and produced 5 pups. A female pup (1111) was instrumented on 6 November 1986. The pack remained at 6 wolves through the winter. Six pups were produced during 1987 and pack size was 12 wolves to December 1987. Wolf 1166 raised pups in 1988 after 1075 disappeared and the Coal Lake male (adult, 1081) mated with her. Pack size during winter

1988-89 was 17. Wolf 1166 continued to raise pups into 1991, producing 6 consecutive litters. During her study period, her colour changed from gray to nearly pure white.

Pass Creek Pack

On 16 November 1985, 3 wolves were located at Pass Creek, and a 3-year-old male (1154) was instrumented. On 15 January 1986, a second male (1175, yearling) was captured and instrumented. During the period 9-22 February, 1154 travelled with an uncollared grey wolf. On 23 February, 1154 was seen with wolf 1216, a female collared in the Takhanne pack. Wolf 1175 travelled alone until 28 February, then left the pair again on 12 March 1986, remaining alone throughout the summer. Wolf 1154's transmitter failed during the summer, but the wolf was found on 5 September in the company of 1175. During the summer 1986, 1175 and 1216 separated and travelled alone. Wolf 1216 was seen on 18 November 1986 in the company of 2 new wolves (*see* Tatshenshini pack). Wolves 1154 and 1175 were seen together on 5 September for the first time since March 1986. On 19 November, they were located with a grey female on Ark Mountain. Wolf 1154 was recollared on 20 November. The pack remained together through the winter of 1987 and occupied a den near the Hendon River in the summer of 1988. On 10 September, 1154 was found dead from unknown causes. On 18 September 1988, wolf 1175 and a grey wolf were shot by an outfitter near Blanchard Lake, B.C. There were several wolves present at the time.

Primrose Mountain Pair

This pair began as a lone female (1224, 3-year-old) instrumented on 2 March 1986. She travelled alone until the end of May 1986. On 1 November she was with an adult male (1120, 2-year-old) subsequently captured 30 November. The pair were observed daily from 6 November to 8 December during predation rate studies. Wolf 1224 was found dead at the Mt. Skukum mine site on 27 January 1987. Wolf 1120 was last located in the area on 27 January. He dispersed and was found dead near Kluane Lake on 27 February. Cause of death of both wolves was unknown.

Primrose Mountain Pack

This 6 member pack was contacted on 11 February 1983, when a yearling male (0192) was captured. A second wolf was collared on 5 March (1100, male pup) and a third on May 26 (1830, adult male). The pack did not produce pups in 1983, remaining at 6 wolves during winter 1984 until 1100 separated from the pack after breaking a leg during a sheep hunt. He followed the pack for a short time then died in emaciated condition in October. The alpha female (1062) was collared in late April 1984, apparently pregnant. She did not produce pups and we believe we caused her to abort her pups by immobilizing her. In late September wolf 0192 was shot by a hunter. The 3 remaining wolves stayed together until late November when 1062 and another female were aerially shot. Wolf 1830 remained alone in the pack territory until mid-March 1985, when he joined with a new adult female (1085). She had been trap-injured earlier and died in late April. Wolf 1830 was not relocated after 26 March 1985.

Radelet Creek Pack

This group of 7 was first contacted 19 October 1984 on Primrose Lake, when a 3-year-old male (1840) was collared. From that date, a maximum of 5 wolves were seen together. Two pups were shot on 24 October 1984. A 5-year-old female was shot on 10 December. On 27 January 1985, a yearling male (1145) was instrumented while in the company of 1840 and another wolf. The last contact with the pack was on 19 February. Wolf 1145 was shot by a hunter on 20 March near the Hendon River. Wolf 1840 was not relocated after February.

Rose Creek Pack

This pack was first contacted on 25 October 1985, when a 5-year-old female (1133) and a 3-year-old male (0998) were radio-collared while in the company of wolf 1125 from the Watson River pack. From 9 February-29 March 1986, the pack was studied daily to determine predation rates. The pack later denned at Alligator Lake, producing 6 pups. During the fall of 1986, the pack remained near Cowley Lake and began to kill pets in the area. By 22 November all 3 collared adults and 3 pups were shot by residents. On 29 November the 3 remaining pups were found at the rendezvous site near Coal Lake. One of the pups (0999, male) was radio-instrumented. After his capture the pup remained near Coal Lake through December and became temporarily associated with the Coal Lake male. Wolf 0999 was trapped on 10 January 1987. It seems likely that all pups of the Rose Creek pack died that winter.

Sandpiper Lone Male

Wolf 1070 was an adult male radio-collared on 3 March 1983 near Rose Lake. At the time, the wolf was following 14 wolves that had come from the Haines Road area; 1 was shot by a trapper the same day. By March 15, the wolf was relocated alone on 5 occasions, travelling to the headwaters of Kusawa River in British Columbia. After March the wolf disappeared and was next located in August 1984 in the Tatshenshini River area, dead from unknown causes.

Sandpiper Lake Pack

An adult male (1045) and adult female (1203) were aerially captured near Sandpiper Lake on 24 October 1985, in the company of another wolf. Both transmitters failed immediately. The 3 wolves were seen again on 1 April 1986 in the same area, but attempts to recollar them were unsuccessful.

Scout Lake Lone Male

On 5 February 1986, a yearling male was captured in a snare and radio-collared. The wolf remained alone until 20 April, then the wolf dispersed to Haines Junction, about 160 km west, and was shot on 5 June 1991.

Tagish Lone Female

This juvenile female (1152) was snared and instrumented at the Tagish village dump on 30 December 1984. She remained alone between 4 January and 28 February, never travelling more than 10 km from Tagish. She was killed by a hunter on 28 February.

Takhanne River Pack

The 8 member Takhanne River pack was first located at Howard Lake on 15 January 1986. Two wolves were collared: an adult male (1094) missing his right rear leg below the femur, and a 2-year-old female (1216). By 9 February, 1216 had left the pack. On 1 April a yearling female (0130) was instrumented. Wolf 0130 split from the group during the summer and joined a black wolf by 18 November. Wolf 0130 died from unknown causes by 8 December. Wolf 1094 also travelled alone during the summer and was in the company of 7 wolves in early December. He was shot in January 1987 near the Haines Road.

Takhini Pair

Contact with this pair was established on 20 February 1983 when an adult female (1020) was trapped and radio-collared. A male wolf (1090) was radio-collared on 3 March. The wolves travelled together until March 26 when 1020 was shot near Kusawa Lake. Wolf 1090 was relocated alive between 13 May and 27 September, but died some time before 22 December. Cause of death was unknown.

Tatshenshini River Pack

The Tatshenshini River pack was initially contacted when wolf 1216, formerly of the Takhanne and Pass Creek packs, was located in the company of 2 wolves on 18 November 1986, near Wigwam Creek. Pack size was 3-4 wolves until 23 February. On 12 March, Wolf 1216 was with a 5-year-old male (1121) radio-collared the next day. The pair remained together and raised 3 pups in 1987. Wolf 1216's collar likely failed after 30 June 1987. Wolf 1121 was found dead near the Haines Road on 7 August 1987.

Trout Lake Lone Female

Wolf 1190 was snared on the Ibex River on 21 March 1984. This yearling female was probably travelling alone before capture. She dispersed from the study area sometime during the summer of 1984. Her signal was located near Aishihik Lake where she apparently died.

Watson River Pack

This 5 member pack was contacted on 31 January 1985 when a female pup (0321) was instrumented on the Watson River. On 21 March, 2 adult males were radio-collared: Wolf 1125, a 6-year-old and 1075, a 4-year-old. During the 1985 summer, radio contact was lost with 0321 after she apparently dispersed from the study area. The pack was not monitored until 25 October when 1125 was located with 2 new wolves, a 5-year-old female (1133) and a 3-year-old male (0998 *see* Rose Creek pack) .

On 28 October 1985, wolf 1075 was recollared near Kusawa Lake in the company of wolf 1005, a dispersed female from the Windy Arm pack. Together they formed the Moose Hollow pack.

Wheaton River Lone Female

This wolf (1081) was a yearling female captured in a snare set on 15 January 1984. At the time of capture she was probably following a 7-8 member pack travelling the Wheaton River. After her capture, she was not seen with other wolves, and soon drifted out of the area by 8 February, finally dispersing after March 9. She was snared by a trapper near Atlin B.C. on 30 December 1985 while travelling with a pack of 6-7 wolves. Her reproductive tract showed she had produced pups.

Whitehorse Pack

Initial contact was made on 19 February 1983, when a lone adult male (1160) was radio-collared near Lake Laberge. On March 5, 1160 was seen with 2 other wolves west of Whitehorse and a 4-year-old female (1080) was radio-collared. The wolves were killed on 7 March by government aerial hunters after dogs were reported killed in their vicinity the same day. All 3 wolves were young adults.

Wigwam Creek Pack

This pack was located on 1 April 1986, when a pair of wolves were found on upper Wigwam Creek, just west of the study area. A yearling male (0760) was collared. On 3 January 1987, wolf 0760 was snared by a trapper at Klukwan village, Alaska. The fate of the second wolf was unknown.

Windy Arm Pack

This pack was first contacted on 9 February 1985, when 2 of 14 wolves were shot by aerial hunters near Windy Arm of Tagish Lake. Although pack size was not clear, at least 25 wolves were associated between 9 February-27 March 1985. A yearling female (1005) was collared on 10 February. At the same time 6 wolves were aerially shot. On 26 March, 1005 was seen with 11 other wolves on Taku Arm of Tagish Lake. The next day 5 were shot and 5 others, including 1005, escaped into forest cover. Wolf 1005 was relocated alone during the summer 1985. Her collar failed sometime after 29 June and contact with her lost until 19 March 1986 when she was found at Kusawa Lake in the company of the former Watson River pack wolf 1075. Together they formed the Moose Hollow Pack.

Woodpile Pair

A yearling female was trapped at Rose Lake on 16 March 1986 in the company of another wolf. Her transmitter failed immediately.

Appendix C. Status of radio-instrumented wolves in the Coast Mountains study area, February 1983 through June 1988.

Pack name	Frequency	Sex	Age[a]	Capture date	Date last located	No. days active[b]	Date died[c]	Location of wolf or collar	Cause of death
Wolves dispersed and known dead									
Wheaton lone	151081	F	Y	150184	120384	705	201285	Atlin, B.C.	trapped
John's L. lone	151050	F	A	020383	151283	288	151283	Whitehorse	vehicle
Trout L. lone	151191	F	Y	210384	120484	231	071184	Dullmit Lake	unknown
Sandpiper Ck.	151070	M	A	030383	070683	530	140884	Carmine Mtn.	unknown
Canyon loner	151056	F	A	190186	200486	507	100687	Atlin, B.C.	unknown
Wigwam Creek	151760	M	Y	010486	181186	277	030187	Klukwan, Ak.	trapped
Scout Lake	151115	M	Y	050286	200486	74	050691	Haines Jct.	nuisance
Primrose Mtn.	151120	M	A	301186	270187	147	270787	Kloo Lake	unknown
Wolves suspected to have dispersed									
Alligator Lake	151040	M	Y	210283	100184	323			
Alligator Lake	151000	F	Y	210283	180483	56			
Watson River	150321	F	P	310185	210385	49			
Wolves dead in the study area									
Primrose	150192	M	Y	110283	240984	591	240984	Mud Lake	hunter
Primrose	170000	F	Y	110283	251184	653	251184	Rose Creek	control
Primrose	151100	M	P	050383	251185	631	251185	Mud Lake	natural
Primrose	151062	F	A	240484	251184	215	251184	Rose Creek	control
Primrose	151085	F	A	210385	150485	25	150485	Summit Creek	natural
Alligator Lake	151121	M	A	230583	270683	35	270683	Alligator Lake	hunter
Alligator Lake	151150	F	A	050383	240484	416	240484	Friday Creek	control
Kusawa Lake	151021	M	A	261184	271184	1	271184	Mt. Coudert	capture
Kusawa Lake	151821	M	P	230184	261184	308	261184	Mt. Coudert	control
Kloo Lake	151190	M	A	200783	200184	184	200184	Haines Jct.	control
Granite Lake	151110	M	Y	271183	271183	1	271183	Granite Lake	capture
Ibex Mountain	151180	M	A	050184	281185	693	281185	Takhini River	hunter
Champagne	151110	F	A	231284	010285	40	010285	Champagne	trapped
Tagish	151152	F	P	301284	130285	60	280285	Windy Arm	hunter
Craig Lake	151160	F	P	301284	040185	8	070185	Tagish	trapped
Radelet Creek	151145	M	Y	270185	190285	52	200385	Hendon River	hunter
Watson River	151125	M	A	210385	020386	346			
recollared	151114			020386	040986	194	120986	Cowley Lake	nuisance
Rose Creek	150998	M	A	251085	071086	347	071086	Cowley Lake	nuisance
Rose Creek	151133	F	A	251085	231186	394	231186	Cowley Lake	nuisance
Rose Creek	150999	M	P	301186	081286	41	100187	Watson River	trapped
Pass Creek	151175	M	Y	150186	100987	974	150988	Blanchard Lake	hunter
Pass Creek	151154	M	A	161185	300586	195			
recollared	151180			201186	100987	294	311087	Devilhole Creek	natural
Canyon	151114	M	A	301285	170286	49	170286	Fish Lake	snared
Takhanne River	151094	M	A	150186	131286	332	010187	Haines Road	nuisance
Primrose Mtn.	151224	F	A	020386	110287	346	120387	Wheaton River	hunter
Howard Lakes	151079	F	P	100386	230386	13	230386	Klukshu	natural
Jo-Jo Creek	151224	F	Y	150386	010486	78	010686	Dezadeash R.	natural
Jo-Jo Creek	151263	M	P	150386	010386	74	280586	Champagne	natural
Tatshenshini	151224	M	A	130387	070887	147	070887	Haines Road	unknown
Coal Lake	151100	F	A	270387	150587	49	150587	Alligator Lake	unknown
Laberge	151060	M	A	190283	070383	16	070383	Whitehorse	control
Laberge	151060	F	A	050383	070383	2	070383	Whitehorse	control
Takhini River	151020	F	A	200283	260383	34	260383	Takhini River	nuisance
Takhini River	151090	M	Y	030383	070983	188	070984	Mendenhall R.	unknown
Takhanne River	151031	F	Y	010486	081286	251	081286	Howard Lakes	natural

(Continued)

Appendix C. (Continued).

Pack name	Frequency	Sex	Age	Capture date	Date last located	No. days active
Signal failures						
Woodpile	151187	F	Y	160186	160186	1
Sandpiper Lake	151045	M	A	241085	241085	1
Sandpiper Lake	151203	F	A	241085	241085	1
Takhanne River	151216	F	A	150186	202856	36
recollared[d]	150430			010486	300687	455
Watson River	151075	M	A	210385	281085	225
recollared[d]	151144			281085	101185	13
Suspected signal failures						
Primrose Mtn.	151830	M	A	260583	260385	670
Jo-Jo Lake	151221	M	A	271183	180185	418
Cousins	151141	F	A	151283	160285	429
Ark Creek	151810	M	A	290384	201084	234
Radelet Creek	151840	M	A	191084	190285	123
Haines Jct.	151350	M	P	041284	210185	48
Howard Lakes	151099	M	A	100386	020686	84
Hacky Sack	151179	M	A	140386	270387	378
Hacky Sack	151253	F	A	140386	270387	378
Jo-Jo Creek	151244	F	Y	150386	170686	94
Wolves alive in study area						
Windy Arm	151005	F	Y	100285	290685	129
recollared[d]	151166			190386	060689	1175
Moose Hollow	151110	F	P	061186	311287	420
Coal Lake[d]	151081	M	A	041286	060689	915

[a] Age at capture: P= pups, Y=yearling, A=adult.

[b] Number of days collar was active and monitored.

[c] Death dates of certain wolves were assigned to the first date of relocation that death was suspected. In most cases, the actual death date was sometime earlier.

[d] Wolves changed pack affiliations. Watson River 151144 dispersed to found Moose Hollow pack with 151005 female, a dispersal from Windy Arm pack. Takhanne 151216 moved to Pass Creek pack, then Tatshenshini pack. Coal Lake 151081 replaced 151144 as the alpha male of Moose Hollow pack in spring 1988.

Appendix D. The annual mid winter composition of wolf packs in the Coast Mountain study area, 1983-88. Surveyed areas varied among years (*see* Fig. 1).

Pack name	No. of wolves	Count technique[a]
1983		
Takhini River	4	tr, rc
Arkell Creek	9	tr, pu
Laberge	9	tr, rc
Sandpiper Creek	15	tr, rc
Primrose	6	rc
Alligator Lake	12	rc
Wheaton River	7	tr
West Arm	5	tr, pu
Lorne Mountain	12	tr, pu
Caribou Mountain	7	tr
Total	86	
1985		
Champagne	3	pu
Granite Lake	5	vs, pu
Haines Junction	6	rc
Jo-Jo Lake	7	rc
Dezadeash Lake	5	tr
Takhanne River	19	vs, pu
Arkell Creek	4	tr
Coal Lake	2	tr, pu
Ibex Mountain	8	rc
Kusawa	3	rc
West Arm	5	tr
Primrose	5	rc
Rose Lake	3	tr, pu
Radelet Creek	7	rc
Takhini River	5	vs
Watson River	7	tr
Tagish	5	tr, pu
Windy Arm	25	tr, pu
Total	124	
1987		
Champagne	4	tr
Howard Lakes	4	tr
Hacky Sack Lake	5	rc
Jo-Jo- Creek	10	vs
Kusawa	2	tr
Pass Creek	3	rc
Takhanne River	2	rc
Takhanne	8	vs
Tatshenshini River	4	rc
Arkell	4	tr
Coal Lake	2	rc
Echo Valley	8	tr, pu
Moose Hollow	7	rc
Rose Creek	9	rc
Takhini Lake	8	tr
Wheaton River	7	tr
West Arm	5	tr, pu
Tagish	5	vs
Monkey Creek	2	tr
Primrose Mountain	2	rc
Total	101	
1984		
Arkell Creek	9	tr
Ibex Mountain	3	rc
Kusawa	8	rc
Alligator Lake	7	rc
Rose Lake	3	tr, pu
Primrose	6	rc
Hodnett Lake	4	tr
Takhini Lake	7	tr
Wheaton R.	7	tr
Black Lake	3	tr, pu
Haines Junction	7	tr
Granite Lake	3	vs, pu
Mt. Kelvin	10	vs
Jo-Jo Lake	6	rc
Takhanne River	19	tr, pu
Dezadeash Lake	6	tr
Ark Mountain	5	rc
Total	113	
1986		
Granite Lake	4	tr
Hacky Sack	2	rc
Howard Lakes	4	rc
Primrose Mountain	2	rc
Jo-Jo Creek	7	rc
Kluhini River	5	tr
Pass Creek	3	rc
Takhanne River	8	rc
Arkell Creek	4	tr
Bonneville Lakes	3	vs
Canyon	2	rc
Echo Valley	4	vs
Moose Hollow	2	rc
Rose Creek	3	rc
Sandpiper Creek	3	rc,vs
Woodpile	2	rc
Takhini Lake	2	tr
Tagish	5	tr
Total	65	
1988		
Tagish	8	tr, pu
Taku Arm	2	vs
Taku Arm	2	tr
Tutshi Lake	7	vs
Monkey Creek	3	tr
Marsh Lake	2	tr
Whitehorse	6	tr, pu
Arkell Creek	6	tr, pu
Moose Hollow	12	rc
Takhini Lake	7	vs
Coal Lake	2	rc
West Arm	6	tr, pu
Black Lake	4	tr

(Continued)

Appendix D. (Continued).

Pack name	No. of wolves	Count technique
1988 (continued)		
Watson River	6	vs
Jo-Jo Creek	12	vs
Pass Creek	5	vs
Hacky Sack	4	tr
Tatshenshini River	7	rc
Howard Lakes	6	tr
Takhanne River	5	rc
Total	112	

[a] The following codes explain the method of pack enumeration: rc was radio-collared, tr was trail count by wolf survey crew, vs was visual count by survey team and pu was public observation.

Appendix E. Wolf-ungulate encounters observed during the study.

We observed wolves attacking and killing 4 moose and attempting to kill 1 other. One female moose was killed by 5 wolves during winter, after the wolves forced the moose into a small meadow. The 2 radio-collared adults chased the cow then bit onto the head and rear of the moose. The moose spun the wolves around then collapsed with the wolves still attached. The 3 pups immediately attacked the cow but ran off when the cow stood up again. The 2 adults pulled it down 2 more times before killing it. On another winter moose kill, a group of 5 wolves surrounded a cow moose in the subalpine. Wolves in the rear repeatedly ran and bit at the flanks causing large bleeding wounds. The wolves moved away and laid down while the moose browsed some willows. By the next morning the moose was dead. We watched the same pack kill another cow moose by inflicting similar wounds, then rested nearby the moose for a day before killing it. A calf moose was mortally wounded by wolves during winter but its dam refused to leave the dying calf despite the wolves resting less than 5 meters away. The cow stood over the calf or within a few meter for 2 days following the calfs death while the wolves remained nearby. The wolves finally abandoned the calf after 48 hours then immediately killed a Dall sheep ewe. The pack apparently did not return to the calf kill that winter.

Two sheep hunts were observed but none were successful. Wolves hunting sheep have been rarely reported (Murie 1944, Child et al. 1978, Hoefs et al. 1986, Sumanik 1987) especially during winter. Murie (1944) and Sumanik (1987) speculated that wolves were most successful at killing Dall sheep when they approached them from above, forcing the sheep to run downhill into deep snow. In the Coast Mountains, a wolf pack killed Dall sheep on 5 separate occasions by either pushing the sheep from cliffs onto creek ice at the cliff base or overtaking them on the ice before the sheep could reach cliff safety. Sumanik (1987) observed wolves hunting Dall sheep during the winter on various occasions, concluding that little teamwork was evident among pack members during hunts. On 1 sheep hunt we observed from aircraft, a wolf pack chased a group of 20 sheep on a wind-blown plateau as the sheep ran for large rocks to escape. The wolves gained on the sheep at the base before all the sheep reached safety. The wolves individually chased various sheep, often pursuing them past other sheep that were hiding nearby in rocks. Eventually all sheep reached safety. On the second observation, a wolf pack approached a band of 50-60 sheep and chased them through a large boulder field. Both sheep and wolves had difficulty running through the rocks, at times walking and climbing to move through the boulders. Wolves individually pursued sheep, approaching some at close range but failing to capture any. We saw no evidence of coordination by wolves during sheep hunts.

Appendix F. Predicted impacts of wolf predation on sheep and moose populations during winters of 1984, 1986 and 1987 in CM Center. Periods are 180 days (October 1-March 31).

Period	No of wolves[a]	No. of pairs	Kg killed per day [b]	Biomass killed (kg)	Prey type[c]	% of total biomass	No. killed	No. available[d]	% pop'n. killed
Winter 1984	49	0	328	59,040	sheep	7	66	2060	3
					calf moose	25	98	152	64
					adult moose	68	94	750	13
Winter 1986	22	6	272	48,960	sheep	7	55	2060	3
					calf moose	3	10	152	7
					adult moose	90	103	750	14
Winter 1987	49	6	390	70.200	sheep	20	226	2060	11
					calf moose	30	97	152	64
					adult moose	50	109	750	11

[a] Wolf population size was the mid point between mid and late winter counts.

[b] Calculated by multiplying average kg killed/wolf/day x no. of wolves. Wolves in pairs had daily kill rates of 17.1 kg and other wolves averaged 6.7 kg.

[c] There was no breakdown between Dall sheep lambs and adults.

[d] Moose and sheep numbers were stable in this portion of study area (Larsen et al. 1989*a*, .Barichello et al. 1989*a*). Percentage of moose calves was 17% during each winter based on stratified random sample counts in 1984 and 1987. The 1986 value was estimated by averaging calf percentages from 1983, 1984 and 1986 (16.6%) then rounded off.

Renewable Resources