

ECOLOGY AND MANAGEMENT OF WOLVES IN THE PORCUPINE CARIBOU RANGE, CANADA 1987 TO 1993



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ECOLOGY AND MANAGEMENT OF WOLVES IN THE PORCUPINE CARIBOU RANGE, CANADA: 1987 TO 1993

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Summary

We conducted studies on wolves in the Canadian range of the Porcupine caribou herd from 1987 through 1993 to: 1) understand ecological relations with caribou and other ungulate prey, and 2) evaluate factors that affect wolf abundance, home range use, reproduction, recruitment, survival, dispersal, and predation.

Wolves exhibited two discrete behaviors. Tundra-dwelling wolves were migratory, following caribou long distances to seasonal ranges. Taiga-dwelling wolves were territorial, distributed on the landscape in relation to the seasonal presence of moose. Wolves on the Porcupine caribou herd range were apparently at a stable, low density during the study, with late winter density related to caribou availability. Wolf numerical response was primarily limited by caribou biomass, and reproduction had a strong effect on density. Dispersal rate was high and wolves dispersed long-distances compared to sub-Arctic Yukon areas. They showed a preference for caribou prey, a high prevalence of disease, and low denning success.

The annual number of wolves taken by hunters was linked to caribou hunting opportunities. Wolves were regionally overhunted in some years, but the long-term effect of harvest throughout the range of the herd was negligible due to irregular availability of the Porcupine herd among user communities. Concurrent research on predation rate by wolves on the Porcupine caribou winter range showed kill rate on caribou was about 30 caribou per wolf per year, and a predation rate model found wolves were not a primary factor limiting the size of the Porcupine caribou herd.

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Introduction

In this paper, we present results of ecological studies of wolves (*Canis lupus*) from 1987 to 1993 in the northern part of the Porcupine caribou herd (PCH) range in Canada. We studied wolves in a broad area of the Yukon North Slope and Mackenzie Delta, surrounding the North Slope settlement region of the Inuvialuit Final Agreement (IFA; Government of Canada 1984). The IFA, and Aklavik-Inuvialuit Community Conservation Plan (Anonymous 1993) support goals to manage all wildlife harvest on a sustainable basis, including for wolves. Wolves are important furbearers to the traditional culture and garment economy of the people of Aklavik, Fort McPherson, and Old Crow. Wolves are also traditionally hunted to help maintain a balance with other wildlife (Anonymous 1993).

Information about wolf population ecology is needed to determine sustainable harvest rates to ensure their long-term conservation. Wolves are at low densities throughout most of the Canadian Arctic. The current belief is that wolf numbers are limited by low seasonal food supply (Thomas 1995). Wolves in the Arctic are especially vulnerable to overhunting because of the open country, and easy access by snow machine (Hayes and Gunson 1995, Miller 1995, Thomas 1995, Ballard *et al.* 1997).

According to people of Aklavik, NWT, wolves are a predator of barren-ground caribou (*Rangifer tarandus groenlandicus*), moose (*Alces alces*) and Dall's sheep (*Ovis dalli*) in the North Slope settlement region. Caribou are a key part of the spiritual,

cultural and economic tradition of the Inuvialuit and Gwitch'in people. The PCH remains a highly valued food resource (Anonymous 1993), and it is one of the most studied herds in North America. Since the early 1970s, detailed research has included caribou movements (Fancy *et al.* 1989, Russell *et al.* 1992), herd demography (Whitten *et al.* 1992, Fancy *et al.* 1994) and range ecology (Russell *et al.* 1993). Understanding the role wolves play in limiting caribou, moose, Dall's sheep and muskoxen (*Ovibus moschatus*) is helpful for setting sustainable harvest levels for these ungulates.

Before our study, scientific information about wolves in the region was limited, although people in Aklavik believed wolves were migratory and followed the PCH for great distances (T. Arey, *personal communication*). Aklavik people also reported that there were many more wolves in the 1930s and 1940s. Wolves apparently declined due to poison programs in the 1950s, and then began to recover in the mid-1970s (Anonymous 1993). During the 1970's, researchers in the north Yukon (Doll 1974, Ruttan 1974, Ruttan and Wooley 1974) reported wolf sightings as part of Gas Arctic wildlife studies, but little was known about wolf movements or general ecology. It was unknown if Arctic wolves in the Yukon and NWT migrated to follow caribou, or if they were territorial, similar to wolves in the other parts of the Yukon (Sumanik 1987, Hayes *et al.* 1991) and Arctic Alaska (Garner and Reynolds 1986, Dale *et al.* 1994, Ballard *et al.* 1997). Hayes and

Barichello (1986) believed wolves in the PCH range were limited by low food supply caused by shifting distribution of caribou, and low availability of moose, mountain sheep and muskoxen.

Objectives

The objectives of our studies were to:

1. Periodically estimate wolf abundance to determine population trend in the area
2. Determine wolf seasonal movements and food habits
3. Determine rates of reproduction, dispersal, survival, and the causes of wolf mortality
4. Estimate the importance of human hunting on wolf demography
5. Describe den ecology
6. Assess the prevalence of diseases in limiting wolf abundance
7. Estimate prey selection and predation rates of wolves on the PCH

Hayes and Russell (2000) previously addressed Objective 7. They reported kill rate by wolves on caribou then developed a predation rate model to assess the importance of wolves on PCH demography. We summarize and discuss the results of their model.

Study area

People, Settlements and Land Management

There are ~1,700 people living in three communities that follow a traditional caribou-hunting lifestyle (Figure 1). Aklavik (population: 633, Statistics Canada 2011) is a community of mainly Inuvialuit and Gwitch'in First Nation peoples. Inuvialuit use the Yukon Arctic coast, Mackenzie Delta and North Slope drainages for subsistence hunting and gathering. Gwitch'in in Aklavik use the Mackenzie Delta and Richardson Mountains. Gwitch'in of Fort McPherson (792) mainly use the Richardson Mountains south of the Rat River. Old Crow (245) is a Vuntut Gwitch'in community that traditionally uses most of the Porcupine River drainage in the Yukon.

Local people told us that we should expect that wolves would move long distances to annually follow the PCH, so we chose a broad study area surrounding the North Slope settlement area. The Arctic Wolf Study Area (AWSA, Figure 1) intersects five land management areas, including the Inuvialuit Final Agreement settlement lands (30,000 km²), Vuntut Gwitch'in (7,444 km²) and Tetlit Gwitch'in (1,554 km²) settlement lands, Ivvavik (10,170 km²) and Vuntut National Parks (4,350 km²).

Physiography, Vegetation and Climate

The AWSA includes four discrete Ecoregions (Oswald and Senyk 1977): the Northern Mountains, the Coastal Plain, the Old Crow Basin, and Berry Creek. The following descriptions of physiography, vegetation and climate are from Oswald and Senyk (1977).

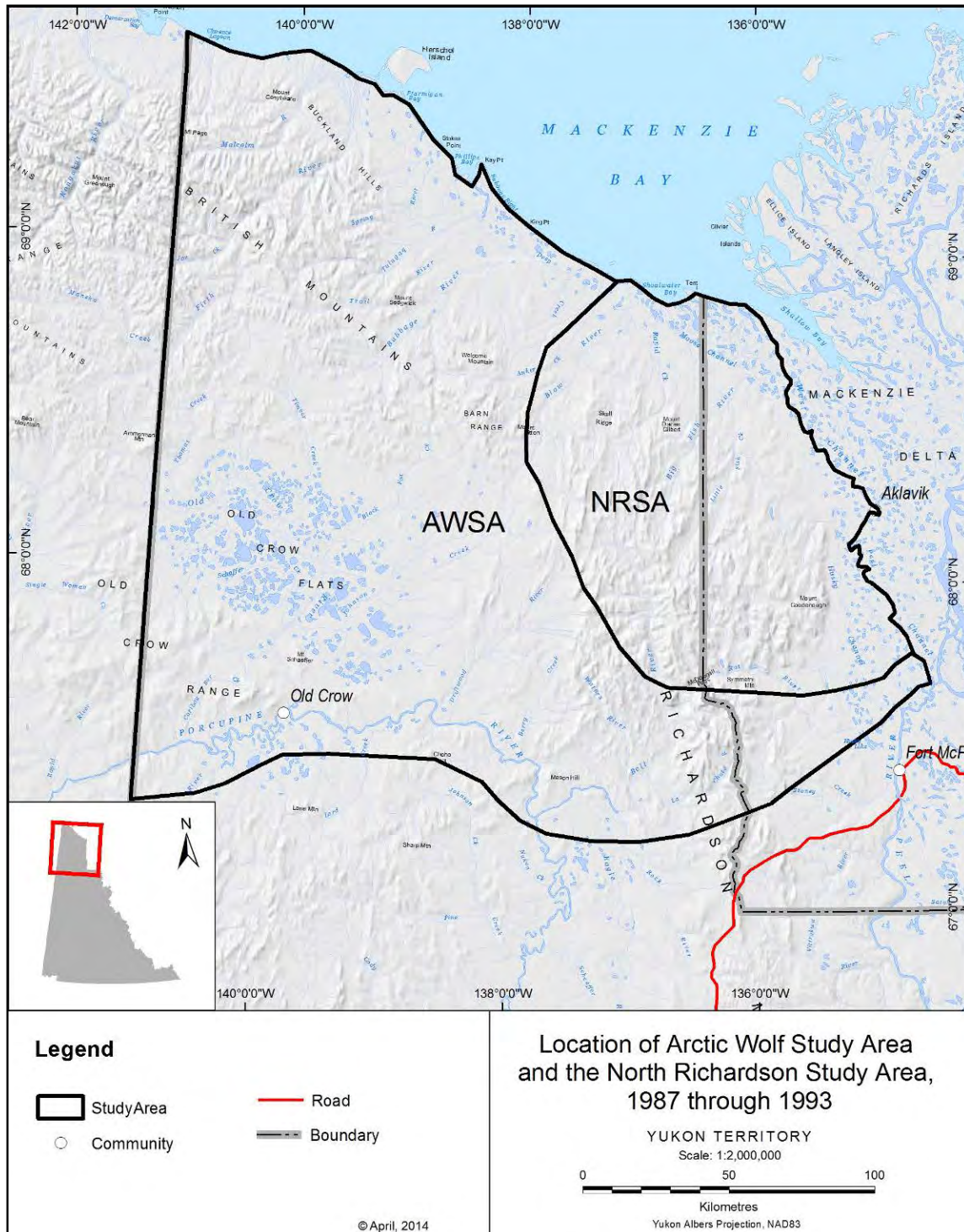


Figure 1. Location of Arctic Wolf Study Area (AWSA, 1987 only), and North Richardson Study Area (NRSA) from 1987 through 1993.

Most of the northern Yukon was a glacial refugia and is within the zone of continuous permafrost. The Northern Mountains Ecoregion includes most of the British and Richardson Mountain ranges. Elevations commonly exceed 1,500 m above sea level (asl). Most of the 20 km wide Coastal Plain Ecoregion lies below 150 m asl. The British Mountains and Yukon Coastal Plain include three major watersheds: the Firth, Babbage and Blow Rivers. The Willow, Rat, Fish and Bell Rivers drain the Richardson Mountains. For this report, the North Slope includes all the watersheds draining to the Arctic Ocean between the Big Fish River, NWT, and west to the headwaters of the Malcolm River, Yukon.

The 2,000 km² Old Crow Basin Ecoregion is an extensive complex of thermokarst lakes drained by the Old Crow River. The Berry Creek Ecoregion forms the western flanks of the Richardson Mountains. It is rolling terrain with uplands below 600 m asl and valleys below 300 m asl. The ecoregion is drained by the Bell, Porcupine, Eagle and Driftwood Rivers.

Most of the Northern Mountains and North Slope ecoregions are treeless, except along protected valleys where there are isolated stands of black spruce (*Picea mariana*), white spruce (*Picea glauca*) and balsam poplar (*Populus balsamifera*). The main vegetation is sedge (*Carex* sp.) and cottongrass (*Eriophorum* sp.) tussock tundra. Dwarf birch (*Betula* sp.), willow (*Salix* sp.) and alder (*Alnus* sp.) are found on warmer sites. Cooler sites support

ericaceous (acid-loving) shrubs, willows and various forbs.

The lower elevations of the Porcupine River watershed are transitional taiga composed of black and white spruce, paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and balsam poplar along riparian areas. In the broader valleys, spruce is sparse and stunted. The northern limit of spruce and balsam poplar forests are found on the Bell, Driftwood and Old Crow Rivers. Shrub birch and willow dominate most forest openings and the under story. Sedge and cottongrass tussocks dominate poorly drained lowlands and the higher elevation zones.

The AWSA receives about 250 mm of precipitation annually, except in the Richardson Mountains where 375 mm is normal. The mean annual temperature ranges from -9 to -12 °C.

After 1988, we focused wolf studies in the 15,000 km² Northern Richardson Mountains Study Area (NRSA), bounded by the Blow and Bell Rivers to the West, the Mackenzie Delta to the East, the Rat River to the South, and the Arctic Coast to the North (Figure 1).

Wildlife Populations

Between 1983 and 1989, The Porcupine caribou herd increased from 135,000 to 178,000 animals; an annual rate of increase of 1.05 (λ). Between 1989 and 1992, the herd declined to about 160,000 caribou ($\lambda=0.97$, Fancy *et al.* 1994). The annual home range of the PCH has been studied since 1970, with most of the seasonal range use determined by conventional VHF and satellite radiotelemetry techniques (Russell *et*

al. 1992). The PCH traditionally calves on, or near, the Arctic National Wildlife Refuge (ANWR) in northeastern Alaska then spends the post-calving and summer periods traveling along the Yukon Coastal Plain. The herd migrates to various traditional wintering areas in the Richardson Mountains, Eagle Plains, Ogilvie Mountains or the southern Brooks Range in Alaska. During our study, caribou wintered in AWSA each year, but numbers and regional distributions varied annually (Russell *et al.* 1993). The Northern Richardson Mountains and the Yukon North Slope were important wintering areas in most years.

Moose range throughout the AWSA, but they are uncommon in the Northern Mountains and Yukon Coastal Plain, especially during winter (Smits 1991). In November 1989, Smits (1991) counted 237 adult moose in the Richardson Mountains and adjacent Yukon Coastal Plain. Mossop (1975) estimated about 1,000 moose seasonally migrated in spring to the rich wetlands of the Old Crow Basin, then returned to winter in the southern slopes of the Brooks Range in Alaska. About 900 Dall's sheep were counted in the Richardson Mountains in 1986 (Barichello *et al.* 1987), and about 100 sheep range along the Firth and Malcolm Rivers in Ivvavik National Park (N. Barichello, *personal communication*). C. Smits (Yukon Fish and Wildlife Branch *unpublished*) counted 157 muskoxen on the Yukon Coastal Plain in 1993, part of an increasing herd that was introduced in Alaska in 1969 (Youngman 1975).

Other predators in the AWSA include polar bears (*Ursus maritimus*) that range along the Yukon coast in winter. Brown bear (*Ursus arctos*) are found throughout the AWSA (Nagy 1990), and black bear (*Ursus americanus*) are limited to the forest taiga lowlands. The three bears are thought to be at low density. Wolverines (*Gulo gulo*) range throughout the area. Arctic fox (*Alopex lagopus innuitus*) are restricted to the north coastal areas (Youngman 1975). Ravens (*Corvus corax*) are common, scavenging from carcasses of ungulate kills.

Methods

Estimating Change in Wolf Abundance

We defined study periods by the wolf biological year beginning on 1 May when wolves den in Arctic Alaska (Haugen 1987). For example, 1987 ended 30 April, and 1988 began 1 May. During April 1987, we flew wolf snow-tracking surveys (Stephenson 1978) throughout the AWSA, and in the NRSA in April 1989 and 1993. Surveys were flown in a PA 18 Supercub and Cessna 170 in 1987; a Maule LR7 in 1989; and a PA 18 Supercub and Maule LR7 in 1993. In all years a helicopter crew (Bell 206B) also snow-tracked while capturing wolves. Estimates of wolf abundance were based on total counts (Hayes 1995) that derive a minimum population size with no estimate of precision.

Stephenson (1978) showed experienced wolf trackers located three times as many wolves as

inexperienced observers did. To ensure efficient searching, we combined crews so that at least one experienced tracker was on board each aircraft. In taiga areas, our flight routes followed riparian areas where moose were mainly found in winter (Smits 1991). In caribou winter range, we flew transects about 500 m apart and searched for wolves along the periphery of herds where wolf tracks could be followed.

After a fresh wolf trail was located, we followed it until the wolves were found, or the minimum group size was estimated by track counts. Whenever possible, trails were backtracked to determine activities. Stephenson (1978) recommended wolf surveys should be done a few days following a snowfall of 5 cm. A snowfall of about 5 cm fell in Old Crow on 31 March, 1987 (Atmospheric and Environment Services), 10 days before we began surveying. Another 2 cm of snow fell during the count. We found snow conditions were ideal for snow-tracking throughout the area, including on the North Slope where powder snow and unusually calm conditions prevailed, allowing us to follow snow trails and find packs.

Tracking conditions were generally windblown and poor on the North Slope portion of the NRSA in 1989 and 1993, but conditions were good in the Rat, and Bell River drainages. In both years, we had to fly the North Slope watersheds many times to eventually locate packs.

Radiotelemetry and Home Range Use

Members of all wolf packs seen during 1987 through 1993 were radio-collared. When we found a pack, at least two wolves were immobilized by the helicopter (Bell 206B) crew using Capchur equipment (Palmer Chemical and Equip. Co., Douglasville, Ga.). In 1987, 31 wolves were administered a mixture of Ketamine Hydrochloride (Parke-Davis) and Zylazine (Rompun, Cutter Laboratories) at a ratio of 6:1, for an average concentration of 12 to 13 mg (Ketamine)/kg of wolf. After 1987, captured wolves received an average Zoletil (A. H. Robins) dose of 8.3 mg/kg, based on an average wolf weight of 40 kg. We selected adult wolves for capture because we expected that they would remain with packs longer than juvenile wolves would. Adults were separated by their different appearance and social behavior compared to juveniles (Hayes *et al.* 1991).

Captured wolves were sexed and weighed. We aged wolves as yearling, two years-old, or three years-old and older, based on tooth size, coloration, carnassial wear and canine eruption patterns (Van Ballenberge and Mech 1975). We extracted a pre-molar from five older wolves and determined their ages using cementum techniques (Sergeant and Pimlott 1959, Hayes *et al.* 1991). We attached conventional VHF radio-collars on wolves (Telonics, Mesa, Arizona), and followed standard radiotelemetry procedures for relocations (Mech 1974).

We located radio-collared wolves in spring (March and April), summer (June through August), and fall (October and November) from 1987

through 1989 to determine seasonal distribution. To adequately describe wolf home ranges requires 30 to 60 independent annual locations (Messier 1985a, Fuller and Snow 1988, Ballard *et al.* 1987, Hayes *et al.* 1991). We could not always determine annual home ranges using conventional telemetry because the study area was too large, and wolf seasonal movements were unpredictable. Consequently, we were unable to collect enough radiolocations to describe seasonal or annual home ranges. Because many of our wolf packs did not hold fixed home ranges, we used 100% area polygons determined by Geographical Inventory System analyses to describe the area used by radio-collared packs, regardless of the number of transmitter locations (L. Crooks, Yukon Fish and Wildlife Branch). All locations were pooled to estimate cumulative home ranges from April 1987 and ending April 1990. We separated wolves into two ecological types: *Tundra* wolves ranged mainly above treeline, and made long-range seasonal home range shifts to follow caribou. *Taiga* wolves occupied smaller, discrete home ranges below treeline in a mosaic of light forest and tundra, where low-density moose provided year-round resident prey.

Reproduction, Survival, Dispersal and Disease

Den sites were visited in June and August 1987 through 1989 to estimate reproduction, and to describe the habitat characteristics of den areas. Pup survival was monitored during fall flights (September to November) when they could be easily

distinguished from the adults by their smaller size and subordinate behavior (Harrington *et al.* 1983, Peterson and Page 1988). Survival rate was calculated using a Kaplan-Meier (KM) procedure, modified for staggered entry of radio-collared animals. Bounds on survival estimates were obtained using censoring methods of Pollock *et al.* (1989a, 1989b). We defined a wolf to have dispersed if it permanently left its original pack territory and either formed a new pack, or it joined an existing one (Messier 1985b).

We sampled blood from twenty live wolves between 1988 and 1994 to test for serologic presence of disease. We extracted 10 to 20 ccs of blood from lingual or cephalic veins. Blood was centrifuged and the serum separated, then frozen and analyzed for disease antibodies by R. Zarnke, Alaska Department of Fish and Game (ADFG), Fairbanks. Serologic tests followed methods of Zarnke and Ballard (1987).

Mortality and Harvest Rate of Wolves

Radio-collared wolf mortalities were separated into human or natural causes. We assumed that a wolf died of natural causes if they were not reported killed by trappers or hunters. We expected that most hunting mortalities were reported through wolf carcasses submitted to NWT Renewable Resources officers each winter. We assessed the proportion of wolves that were trapped and hunted by comparing the annual reported kill with the number of wolves alive in the NRSA in April 1987, 1989 and 1993.

Table 1. Wolf survey results from late winter 1987, 1989, and 1993 for North Richardson Study Area (NRSA). See Appendix 2 for locations of wolves killed by hunters *.

		Year		
		1987	1989	1993
Packs	Number of Packs	5	10	6
	Total Number of Wolves in Packs	29	52	24
	Mean Pack Size	5.8	5.2	4
	Number Reported Killed (Before Census)	16*	2*	12*
	Pack Wolves in April	41	54	32
	Lone Wolves	4	5	3
	Total Number of Wolves	45	59	35

Characteristics of Wolf Predation

We collected a total of 489 adult and pup scats at six wolf dens to determine food habits between May and August. Scats were first autoclaved and then we randomly collected a sample of guard hairs and washed them in separate solutions of ETOH and Methyl Salicylate. Gelatin hair impressions were made and compared to hair collections of common mammals found in the northern Yukon. Large mammals were identified to species from scat from three of six dens. In the other three dens, moose and caribou were not separated. Small mammals were identified to genus. Birds were identified to order using downy barbule keys (Day 1966).

During winter monitoring studies, we randomly visited a sample of wolf-killed ungulate carcasses by helicopter. Sex was determined by moose antler pedicels, and by antler configuration and jaw diastema length for caribou. We collected an incisor

bar to age moose to the year (Sargent and Pimlott 1959), and a longbone was taken for estimating physical condition of moose and caribou using marrow fat indices (Neiland 1970). Hayes and Russell (2000) reported on the results of wolf predation rate studies on caribou, including daily kill rate, age and physical condition of killed animals, and percent of the PCH annually killed by wolves.

Results

Change in Wolf Population Size

In April 1987, 116 wolves occupied the AWSA including: 88 wolves in 20 packs (Figure 2), 17 wolves reported killed by hunters before our April count, and 11 lone wolves (estimated as 10% of pack wolves from Mech 1973). Average density in the AWSA was 2.3 wolves per 1,000 km². Pack density was 0.4 packs per 1,000 km². Mean pack size was 4.4 wolves \pm 0.6 (SE), ranging from 2 to 12 wolves. Thirteen packs (65%) were small, numbering four wolves or less (Figure

2). Mean pack size in the western study area (Porcupine River and British Mountains) was 3.2 wolves ($n = 12$ packs), significantly less ($T = 2.7$, $df = 9.2$, $P = 0.03$) than 6.3 wolves ($n = 8$ packs) in the Richardson Mountains and east portion of the North Slope (see Figure 2).

To assess change in population size, we compared wolf numbers in the NRSA in April 1987, 1989 and 1993 after harvest by hunters had ended (Table 1). The number of wolves and packs increased from 1987 to 1989 then fell to the lowest densities in 1993. During the study years, wolf density varied from 2.4 to 4.1 wolves per 1,000 km², and packs from 0.4 to 0.7 packs per 1,000 km².

The movement of tundra wolf packs in and out of the NRSA can explain the change in abundance among the three study years (Table 1), but wolf harvest may have been important in reducing wolf numbers

in 1993. The number of packs increased from five (0.4 packs per 1,000 km²) in April 1987 when only a few thousand caribou were present (Russell *et al.* 1992) to 10 packs (0.7 packs per 1,000 km²) in 1989 when many thousands of caribou wintered in the Northern Richardson Mountains (Russell *et al.* 1993). PCH caribou wintered near Aklavik in 1991 and 1992 when a total of 69 wolves were reported taken by hunters (see Appendix 2) in the NRSA. This high harvest over the two winters could have caused the sharp decline in 1993 when the fewest packs were subsequently found. We found no differences ($T=0.5$, $df = 14$, $P = 0.6$) in mean pack size in 1987 ($n = 8$ packs, mean = 5.2 wolves) compared to 1989 ($n = 8$ packs, mean = 6.4). There was no difference in pack size in 1989 compared to 1993 ($T=1.0$, $df=9$, $P = 0.3$).

Table 2. Home range polygon information for taiga and tundra wolf packs, 1987-1993.

Taiga Packs	Cumulative Area (km ²) Traveled	No. of Radio-collar Locations	Tundra Packs	Cumulative Area (km ²) Traveled	No. of Radio-collar Locations
Frost Camp	201	10	Trout Lake	1,223	18
Eagle River	202	10	Malcolm River	1,814	8
Cadzow Lake	473	4	Babbage	2,304	20
Blow River 450	552	9	Firth River	2,863	27
Two Ocean	565	35	Blow River	8,639	211
Rat River	781	71	Trail River	11,092	42
Driftwood River	1,014	22	Trout Lake	13,983	88
Lord Creek	1,185	9	Bell River	16,099	57
Rat River 2	1,399	24			
Berry Creek	1,840	27			
Little Flats	3,586	22			

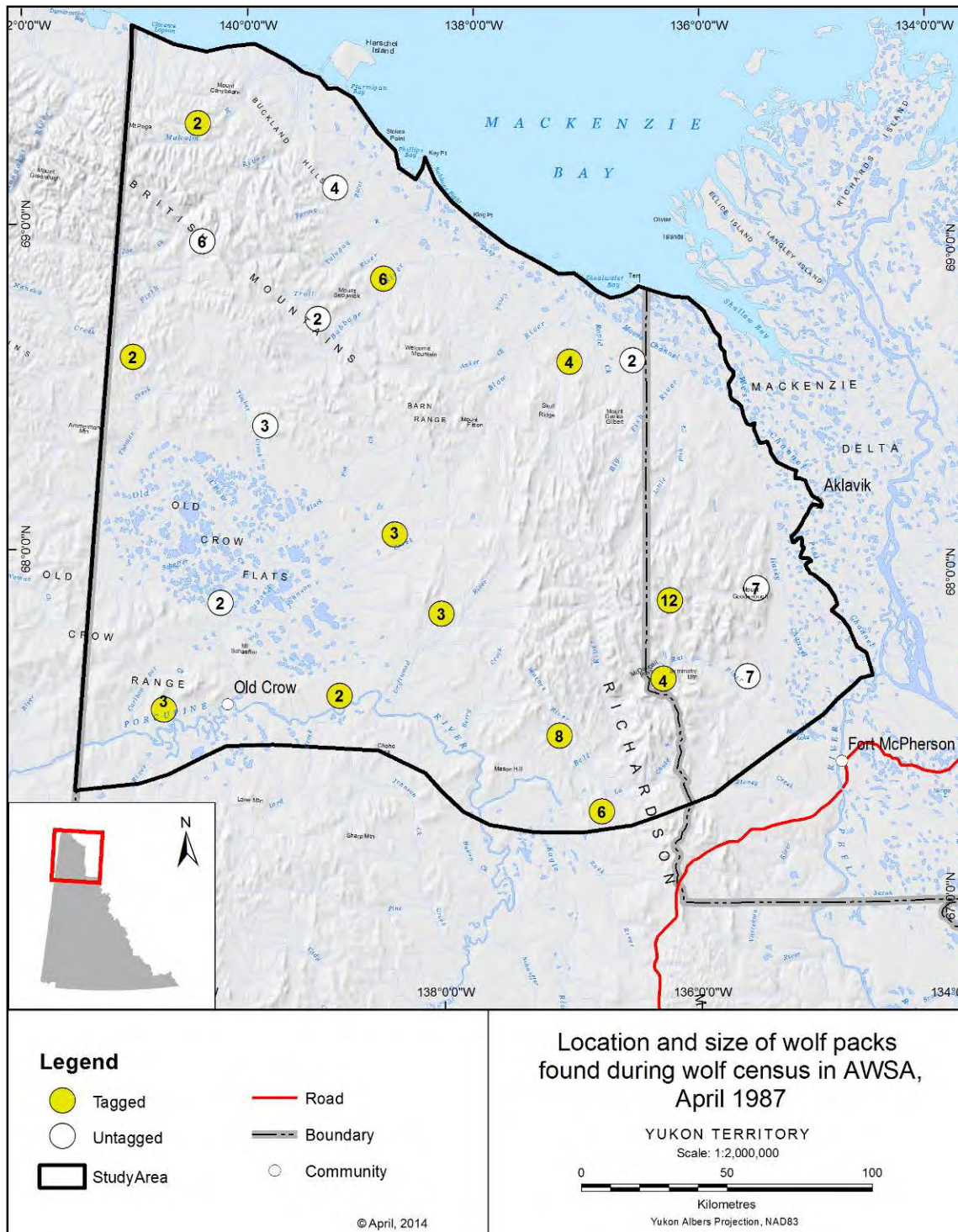


Figure 2. Location and sizes of wolf packs found during the April 1987 count in the AWSA.

Five packs grew to large sizes (range 10 – 17 wolves), but none remained large for more than one winter. The Blow River pack was 17 wolves in November 1988, but then it split into at least two groups of 12 and 3 – 5 wolves by March 1989, when contact was lost with the larger group. The Rat River pack was 11 wolves in early winter 1988, however it had split into groups of 6 and 3 wolves by March 1989. In both cases of splitting, the newly formed packs lived near their original packs. The Bell River pack was 12 wolves in April 1987, and we knew that it reproduced in summer 1987. Six months later, only the breeding male and a new female remained in the original range. In December 1987, we found the rest of their pack had separated, and were traveling in the Waters River – Mason Hill area in east Porcupine River drainage. During winter 1989, the Trout Lake pack fell from 10 to 5 wolves, and the Trail River pack fell from 17 to 10 wolves.

Radiotelemetry and Home Range Use

We monitored the life history of 51 radio-collared wolves for various periods (Appendix 1). We captured 48 wolves that were members of 20 packs between December 1986 and March 1989. We caused the death of four (8%) wolves during capture including: one from unknown drug complications, one from hyperthermia, and we dispatched two wolves after they were severely injured by darts separating the spinal columns. We also established contact with two radio-collared wolves that dispersed into the AWSA from the

Gates of Arctic National Park and Preserve in Alaska (L. Adams, US National Parks Service, *personal communication*). G. Weiler (US Fish and Wildlife Service, *personal communication*) found a radio-tagged wolf from the Malcolm River pack traveling with an uncollared wolf in eastern Alaska.

We monitored 27 radio-collared males and 24 females. Nine were pups (17%), 17 were yearlings (33%) and 25 were adults (49%, \geq two years old). All radio-collared wolves were associated with packs at the time of capture. Mean winter weight of adult males was 47.4 ± 3.0 (SE) kg ($n = 8$), yearling males 43.5 ± 1.8 kg ($n = 9$), adult females 42.5 ± 1.9 kg ($n = 9$), and yearling females averaged 38.1 ± 2.3 kg ($n = 6$).

Because of the long wolf movements and the large size of AWSA, we could not maintain regular contact with most wolves, especially those in the far west study area. After 1987, we limited our radio-tagging to packs in the NRSA. We collected an average of 58 ± 23 (SE) total radio-collar locations for tundra packs, and 22 ± 5 (SE) for taiga packs between 1987 and 1993.

Mean home range size (100% polygon) of 11 taiga wolf packs (Figure 3) was $1,310 \text{ km}^2 \pm 369$ (SE), compared to $7,254 \text{ km}^2 \pm 2,112$ (SE) for 8 tundra packs (Figure 3, Table 2). Three tundra packs traveled more than $10,000 \text{ km}^2$ during the three years of telemetry studies. Tundra wolves made long distance home range shifts each winter to follow caribou (Figure 3), and were often found concentrated among wintering caribou. For example, in November

1988, four radio-tagged packs were within a few kilometers of each other

along the Fish River, where thousands of caribou were wintering.

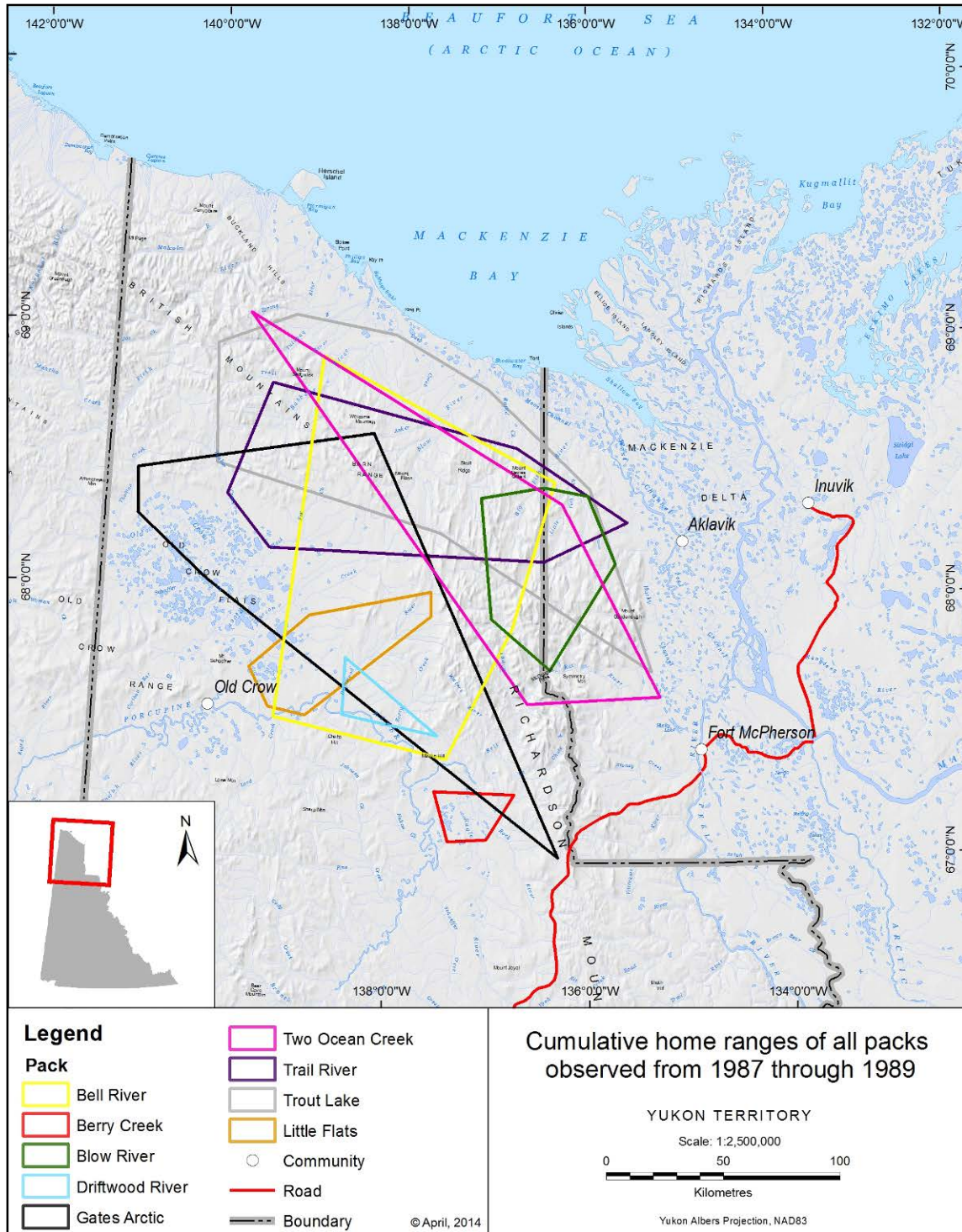


Figure 3. Cumulative home ranges of wolf packs observed from 1987 through 1989.

Taiga wolves did not shift home ranges for long periods to follow caribou (Figure 3) and their pack territories were apparently spaced in relation to moose distribution. For example, four taiga wolf packs wintering below tree line in the Richardson Mountains and three wintering in the upper Porcupine River did not follow migrating caribou, and killed moose when caribou left from their home ranges. Tundra packs, on the other hand, made extensive movements to follow caribou, and most killed only caribou during our study.

Reproduction, Survival, Mortality Causes, and Dispersal

We found 20 natal wolf dens (Figure 4). Half of the dens were located within 20 km of the northern limit of trees. Eight dens were on open tundra and 12 were in transitional taiga forest. Tundra den sites were typically on elevated, dry sites that were previously excavated by ground squirrels or foxes, which initially warmed and dried the permafrost soil, and allowed wolves to excavate and develop den sites further (S. Smith, Agriculture Canada, *personal communication*). In the taiga, most

dens were dug under the boles of spruce trees or willow stands on mesic sites where the warming action of the roots defrosted the soil to adequate depths for den development. Dens were usually exposed to sun and near a source of water.

We measured reproduction during 32 denning events. Packs successfully reproduced 17 times (53%). Breeding success varied among years, ranging from 33 to 79%, but reproductive success was not significantly different among years (Pearson chi-square = 5.1, $df = 2$, $P = 0.08$). We found no differences in reproduction rates between tundra and taiga packs (Yates corrected chi-square = 1.8, $df = 1$, $P = 0.3$). Successful breeders raised an average of 4.3 pups \pm 0.3 (SE) to October.

We documented complete litter losses twice. The Firth River pair (tundra) lost an unknown number of pups after the breeding female died from unknown causes in July 1988. At the Berry Creek den (taiga), a grizzly bear killed four wolf pups in 1989 (Hayes and Baer 1992). Hayes and Mossop (1987) documented two unsuccessful predation attempts by grizzly bears on pups at the Trout Lake den on the Babbage River.

Table 3. Annual survival rate for all wolves, by year.

Year	No. At Risk	No. of Deaths	Survival	No. Censored	No. New Added	Variance (survival)	95% CI	
							Lower	Upper
1987	26	6	0.77	4	12	0.0053	0.63	0.91
1988	28	4	0.86	11	6	0.0037	0.74	0.98
1989	19	4	0.68	2	0	0.0078	0.50	0.85
1990	13	1	0.66	4	0	0.0113	0.41	0.83

Annual survival rates were not different (Pearson chi-square = 1.3, *df* = 3, *P* = 0.73), averaging 0.73 ± 0.05 (SE) (Table 3). Wolves older than four years had significantly lower survival rates than younger wolves did (K-M log-rank test, chi-square = 7.25, *df* = 1, *P* < 0.01, Table 4).

The average age that radio-tagged wolves died was 5.0 ± 0.7 (SE) years old, with no difference between sexes (*t* = 0.17, *df* = 20, *P* = 0.86). Twelve of 47 wolves (26%) died from natural

causes, and 12 were trapped or shot. We did not relocate wolves frequently enough to document seasonal rates of mortality. Radio-collared wolves had the highest risk of being trapped or shot in late winter (February through April) when eight (75%) were taken. There was no difference in the proportion of radio-collared wolves that were shot, or that died of natural causes (Pearson chi-square = 0.94, *df* = 2, *P* = 0.63).

Table 4. Annual survival rate for wolves, by age class.

Age in Years	No. At Risk	No. of Deaths	Survival	No. Censored	Variance	95% CI	
						Lower	Upper
Yearling	7	1	0.86	0	0.015	0.62	1.09
Two	20	3	0.85	6	0.001	0.70	0.99
Three	21	4	0.81	2	0.006	0.65	0.96
Four	15	1	0.93	5	0.039	0.81	1.05
Five	10	5	0.50	0	0.02	0.28	0.72
Six	8	3	0.63	1	0.02	0.36	0.89
Seven	5	2	0.60	0	0.03	0.27	0.93
Eight and Older	8	3	0.63	0	0.2	0.36	0.89

Table 5. Frequency of wolf-killed ungulates, by year.

Year	No. Of Ungulates Killed			No. Kills	
	Moose	Caribou	Unknown	Visited on Ground	% Visited
1987	18	15	1	7	20
1988	0	5	1	1	17
1989	3	39	0	18	43

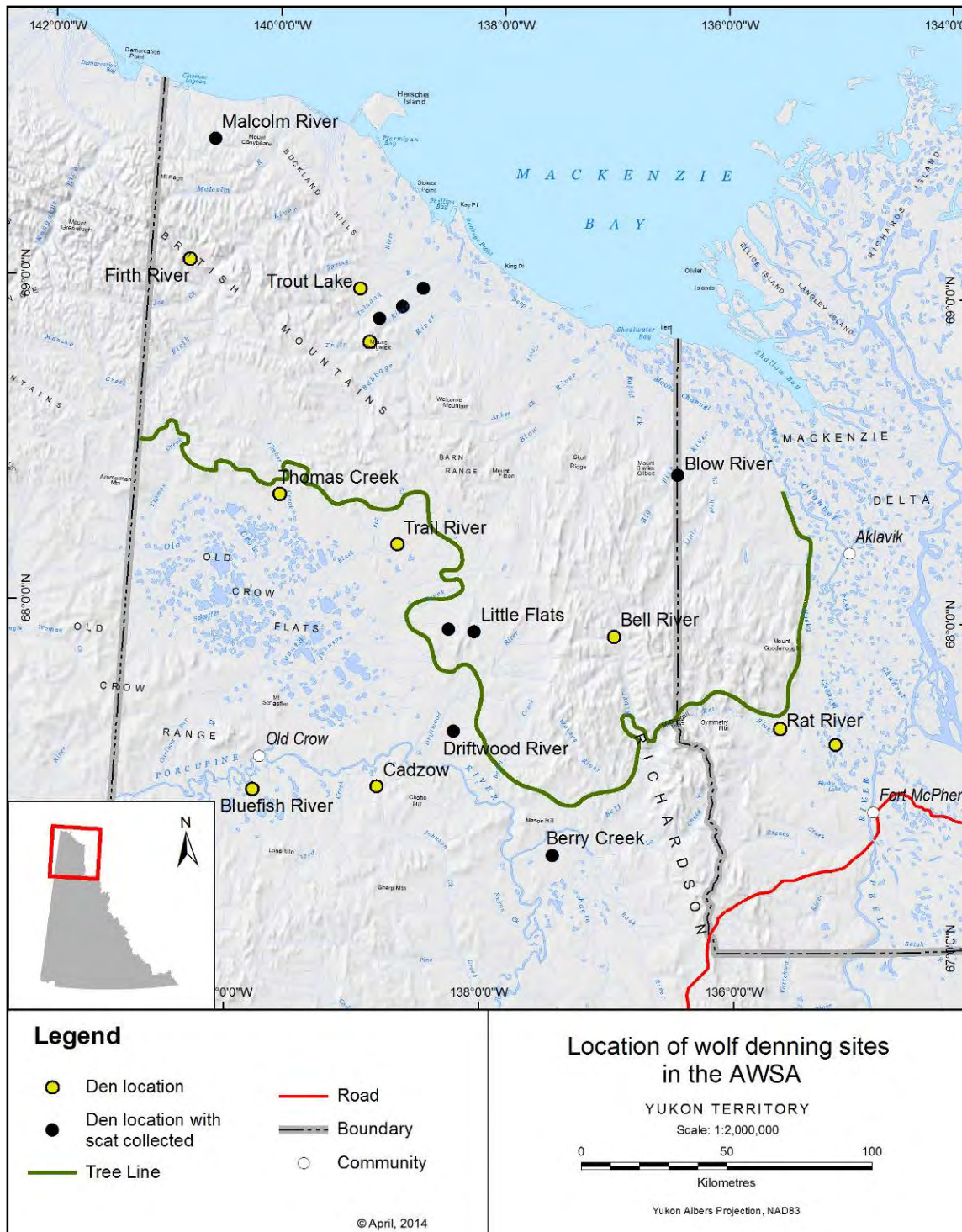


Figure 4. Locations of wolf den sites in the AWSA.

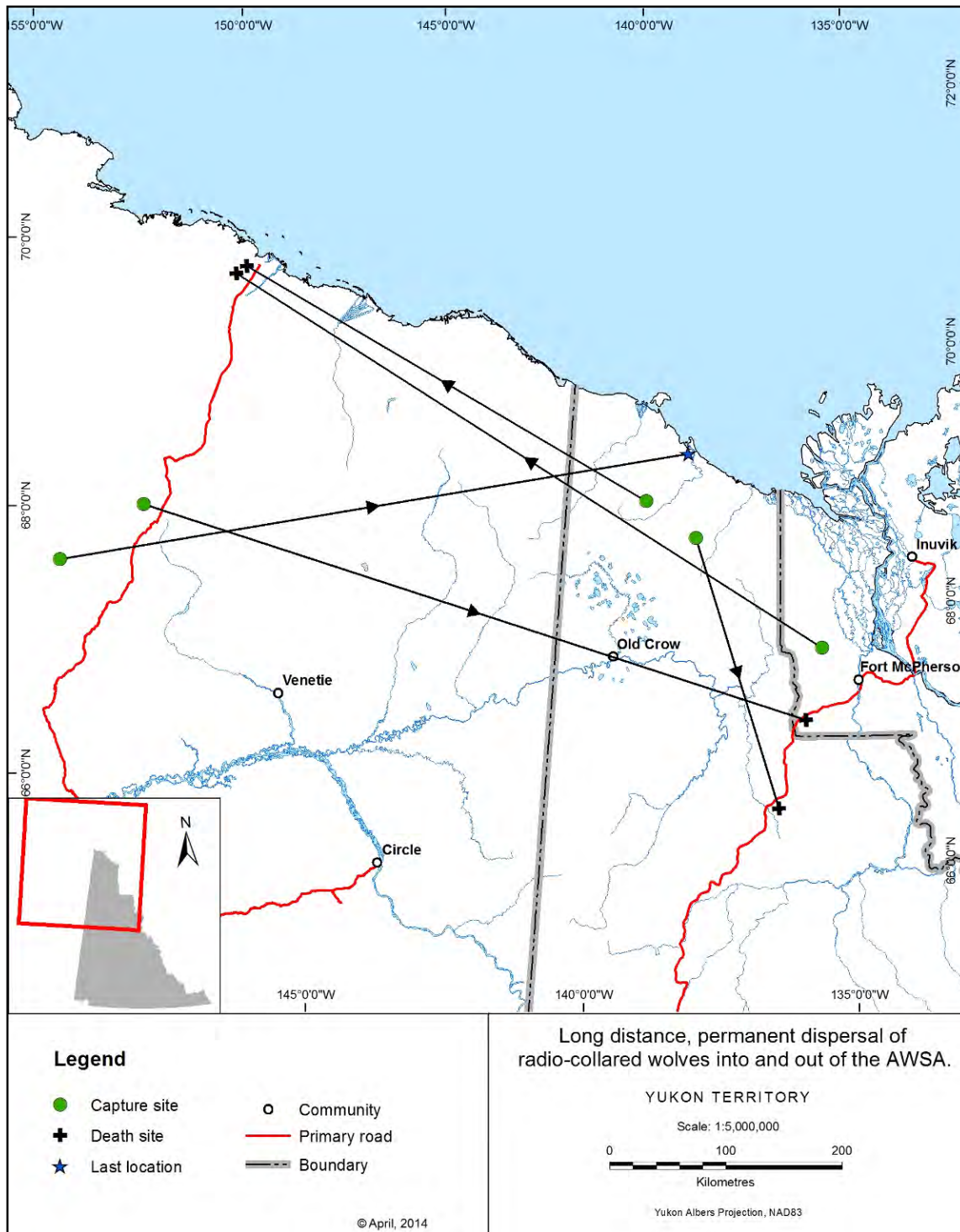


Figure 5. Dispersals of radio-collared wolves into and out of the study area.

Twenty-one of 44 (47%) radio-collared wolves were censored (contact lost for unknown reasons) during the study. We examined for age-

dependence and found a higher censorship rate among young adults between two to four years-old (23%) compared to wolves five years-old and

older (3%) (Fisher exact test [two-tail], $df = 1$, $P = 0.03$)—suggesting that dispersal explained a significant portion of the censored wolves.

We recorded three males and one female making permanent long distance dispersals of over 300 km (Figure 5). Two males dispersed from the Gates of the Arctic National Park and Preserve, Alaska (L. Adams, *personal communication*), traveling more than 500 km before pairing with females in the AWSA. A young male and female independently dispersed from the study area to Prudhoe Bay, Alaska, where they were eventually shot, after traveling distances of 400 and 600 km. Two males and one female dispersed from natal packs to form new pairs within the AWSA. Two of the four wolves that lost their mates dispersed and paired again.

Tundra wolves ($n = 10$) traveled a mean linear distance of 154 km (SE = 50) between initial capture and death sites, further ($T = 2.2$, $df = 17$, $p = 0.04$) than the mean distance of 20 km for taiga wolves ($n = 7$, SE = 7) (Figure 6). Males comprised 73% (8 of 11 wolves) of wolves that traveled more than 150 km. We could not tell if most of these wolves dispersed alone then died, or if they dispersed with other pack members. In some winters, we were unable to locate some tundra packs anywhere in the AWSA. We believe that these packs followed caribou to southern winter ranges because, by the next year, the packs were found again in the AWSA. Long distance movements of tundra wolves were also verified when hunters killed a wolf from the Blow River pack in 1993 and

a wolf from the Bell River pack in 1992, after the wolves had moved to caribou wintering areas 150 – 200 km from their initial capture.

Characteristics of Wolf Predation

Between 1987 and 1990, we found 82 wolf-killed ungulate carcasses, including 59 caribou, 21 moose, and two unknown ungulates. Most moose were killed in the taiga areas, and most caribou were killed in the tundra zone, north of treeline (Figure 7).

Moose represented 26% of ungulate kills located during telemetry studies (Table 5). Most moose were found in late winter 1987 when we followed eight radio-collared taiga packs in the Porcupine River drainage. At the time, few caribou were present. After 1987, we focused our study on tundra wolves in the NRSA that mainly killed caribou. We visited 26 wolf-killed carcasses (Table 5). The mean age of 11 adult caribou was 6.1 ± 0.7 (SE) years old. Average marrow fat for adult moose was $61\% \pm 0.4$ (SE, $n = 4$), and $71\% \pm 4$ (SE, range 11 to 94%, $n = 14$) for adult caribou. Only one caribou was near starvation (below 20% marrow fat) at the time it was killed by wolves.

Moose or caribou were found in 55% of summer wolf scats, and small mammals were found in 26% of scats (Table 6). Beaver or muskrat, were important in the Blow River, Little Flats and Trail River packs which dened near wetlands. Waterfowl were also important to the Trail River and Little Flats packs, which dened in the highly productive Old Crow Flats wetlands.

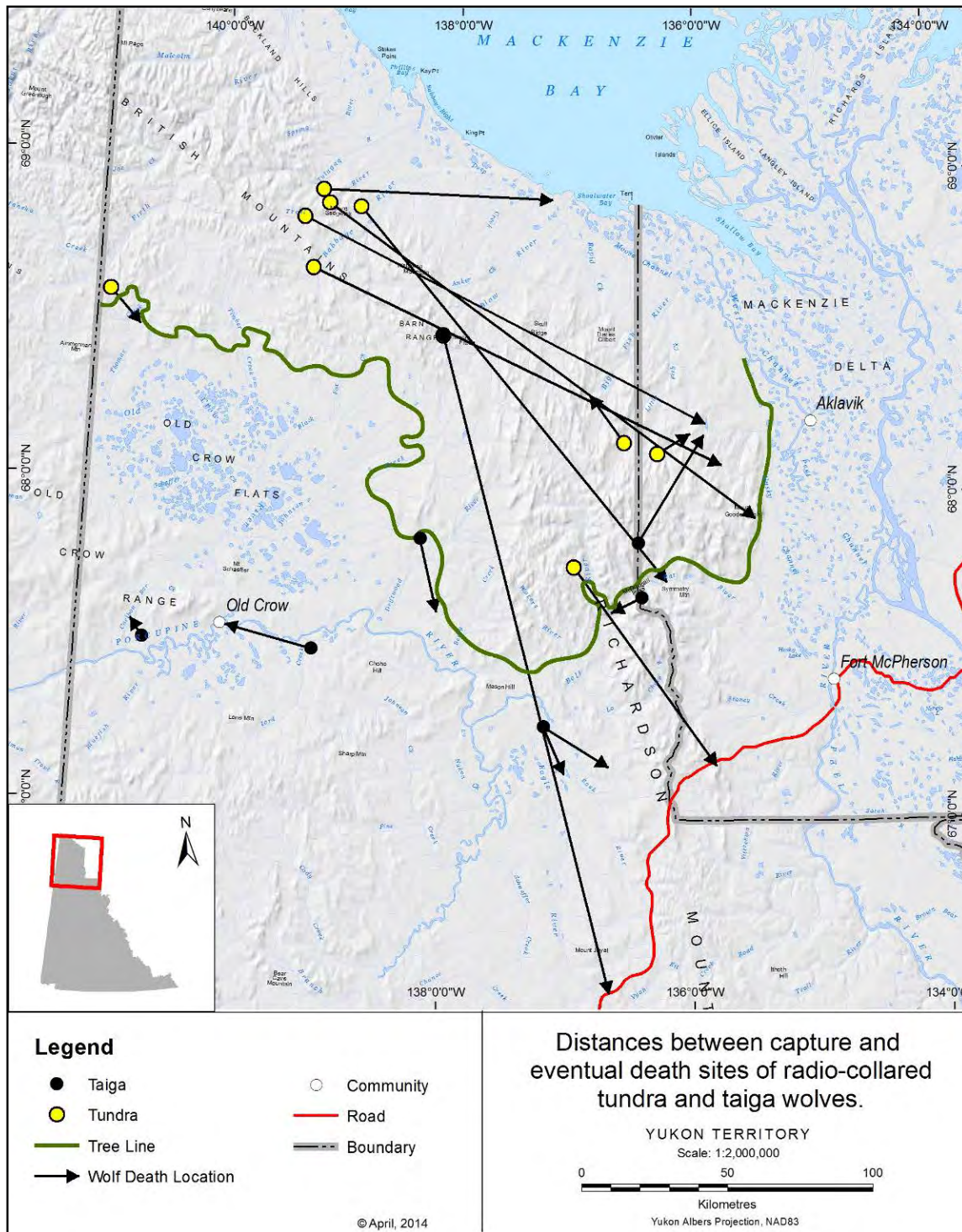


Figure 6. Distances between capture and death sites of radio-collared tundra (TN) and taiga wolves (TA).

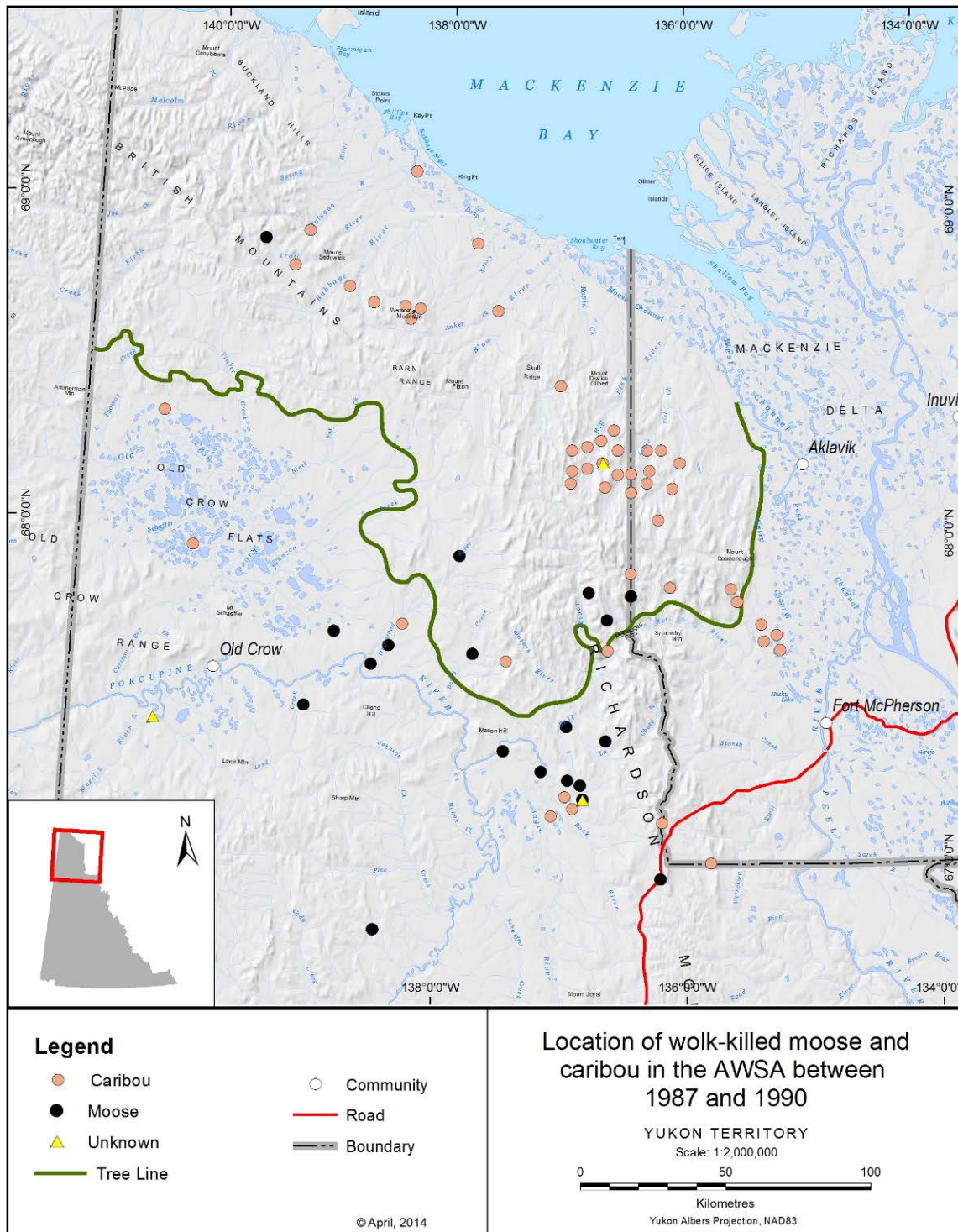


Figure 7. Locations of wolf-killed moose and caribou found between 1987 and 1990.

Table 6. Frequency of prey items from wolf scats collected from three taiga and three tundra dens.

	<u>Tundra</u>			<u>Taiga</u>			Total
	Blow River	Malcolm River	Trout Lake	Berry Creek	Little Flats	Trail River	
Number of Scats	100	13	95	48	67	166	489
Number of Items	111	14	121	69	125	182	622
Moose	47	39	ns	ns	15	ns	
Caribou	7	31	ns	ns	38	ns	
Unknown Ungulate			77	52		13	
All Ungulates	54	70	77	52	53	13	
Beaver or Muskrat	49				42	42	
Snowshoe Hare	1				2		
Squirrels and Microtines		8			9		
Furbearers*	1				2		
All small mammals	51	8	0	0	55	42	
Birds	1			6	66	17	
Fish						1	
Insects					11		
Bears					2		
Unknown	5	31	81	4	10	4	

* not separated by species

Infectious Diseases

We tested for six wolf disease agents from 20 wolves (Table 7). There was a high antibody prevalence of infectious canine hepatitis, parvovirus and distemper viruses, indicating widespread exposure to these disease agents. Brucellosis and tularemia antibodies were moderate. Coronavirus was not present among sampled wolves.

Harvest of Wolves

Hunters reported killing 121 wolves from 1987 through 1993 in the NRSA (Appendix 2). Average annual wolf harvest was 17 wolves \pm 5 (SE, range 2 to 39, 7 winters). Sex was reported for 105 wolves, including 64 males and 41 females. One hundred and two wolves were aged including 50 pups (49%), 19 yearlings (19%) and 33

Table 7. Frequency of diseases in AWSA wolves.

Disease	Number Tested	Number Positive	Percent Positive
Canine Distemper Virus	20	13	65
Infectious Canine Hepatitis	5	5	100
Canine Parvo Virus	4	3	75
Canine Coronavirus	5	0	0
Brucellosis	14	4	29
Tularemia	20	6	30

adults (32%). Aklavik hunters took an average of 13 ± 3 (SE) wolves each winter, mainly on the North Slope drainages of the Richardson Mountains between Aklavik and the Blow River (see maps in Appendix 2). Fort McPherson hunters reported killing 5 ± 2 (SE) wolves each winter, mainly along the Dempster Highway north of Eagle Plains to the Yukon/NWT border (Appendix 2).

We compared annual number of wolves killed in the NRSA with caribou satellite collar information each winter in the study area (Brad Griffiths, *unpublished*). Wolf harvest by Aklavik and Fort McPherson hunters was strongly dependent on the nearness of caribou to the two communities (Log-Likelihood Ratio, chi-square = 71.8, $df = 6$, $P < 0.001$), suggesting wolves were incidentally taken when people were caribou hunting.

The highest reported wolf harvests were 30 in 1991 and 39 in 1992 (Appendix 2). Based on the maximum population count of 59 wolves in April 1989, we estimate the harvest rates were at least 50% in 1991, and 66% in 1992. Harvest exceeding 30-40% of a wolf population is considered unsustainable (Keith 1983). In 1993, 35 wolves were counted in the area, suggesting the high harvest in 1991 and 1992 caused wolves to decline in 1993. We examined 78 hunter reports to assess wolf-hunting success. Hunters reported seeing average packs of 3.2 ± 0.3 (SE) wolves ($n = 76$ observations). They successfully shot 1.4 ± 0.1 (SE) wolves per encounter. There was no difference in success in relation to wolf pack size. When hunters encountered smaller packs

(2-5 wolves) they killed an average of 1.3 ± 0.1 (SE), but took only 1.9 ± 0.3 (SE) wolves from packs of six wolves or more.

Discussion

Wolf Movements, Home Range Use, Dispersal and Survival Rates

Our study supports previous research that found wolves on barren-ground caribou ranges seasonally shift home ranges to follow caribou to and from winter range (Banfield 1954, Kelsall 1968, Kuyt 1972, Stephenson and James 1982, Thomas 1995, Ballard *et al.* 1997, Clarkson and Liepens *unpublished*). Long distance home range shifting was apparent only among tundra wolves. The separation between migratory and fixed territorial behavior was roughly divided at treeline. Tundra wolves traveled significantly larger home ranges than did taiga wolves. They also traveled greater distances between initial capture and death sites, showed stronger home range overlap in the fall and winter, and tundra wolves followed and hunted caribou over moose. Taiga wolves preyed on low-density moose year-round.

Tundra wolves follow caribou because there is not enough other ungulate prey to support them, especially during winter. Most moose that summer on the North Slope leave to winter in taiga areas (Smits 1991). Few moose, muskoxen and Dall's sheep winter on the North Slope, limiting prey for tundra wolves.

We believe the low abundance of other ungulates prohibits tundra wolves from establishing territories,

and forces them to seasonally follow Porcupine caribou. We also found evidence that tundra packs were tolerant of each other, despite extensive home range overlapping. In 1989, when most of the Porcupine herd wintered in the NRSA, wolf pack density was two-fold higher than in years when caribou were lightly distributed there (1987 and 1993). This supports Parker (1973), Kuyt (1972), Thomas (1995), Clarkson and Liepens (*unpublished*) and Kolpashcoiv (*unpublished*) findings of 2-3 fold increases in wolf densities on winter ranges of barren-ground caribou herds in Canada and Siberia. We did not observe lower survival when wolves concentrated on caribou winter range, similar to Clarkson and Liepens (*unpublished*) on the Bluenose herd range to the east.

We detected a loose separation of the wintering areas occupied by tundra packs. As we followed radio-collared wolves from the air we noted caribou movements. We found tundra packs generally moved in the same direction following caribou, traveling through the same areas, but sometimes at different times. This allowed packs to remain apart as caribou moved, reducing opportunities for inter-pack conflicts. However, in mid-winter when caribou were not moving far, we saw packs sharing the same locations on the North Slope at the same time, similar to findings of Clarkson and Liepens (*unpublished*) in the Bluenose herd range.

Below treeline, wolves showed more typical territorial behavior, and were distributed in relation to moose and Dall's sheep, similar to Arctic wolves in Alaska (Garner and

Reynolds 1986, Dale *et al.* 1994, Ballard *et al.* 1997). During the winter of 1987, the only period that we were able to sample predation of taiga wolves, we observed wolves only killing moose. We did see taiga wolves switching to caribou when the PCH migrated through their territories in early winter in other years. However, we did not observe taiga wolves leaving home ranges for extended periods to follow caribou, but we did see temporary shifting in some taiga packs as they followed migrating caribou. All packs returned to their home ranges before mid-winter.

Dispersal is an important mechanism that regulates wolf pack size (Fritts and Mech 1981, Gese and Mech 1991, Hayes 1995). We observed only young adult wolves dispersing. At the same time, we also documented a high censorship rate of young adults, indirect evidence they had high dispersal rates out of natal packs. Our results also confirm that long distance dispersals are common among Arctic wolves in the Porcupine caribou range (Garner and Reynolds 1986), northern Alaska (Stephenson and James 1982, Stephenson *et al.* 1995) and NWT (Clarkson and Liepens *unpublished*). Tundra wolves in the AWSA dispersed, or moved greater distances than taiga wolves did, and movements were apparently associated with traveling caribou. Five of six known wolves appeared to be alone when they dispersed, then they subsequently met opposite-sex wolves then paired with them.

Pairing of unrelated wolves is the primary mechanism of new pack formation (Fritts and Mech 1981, Hayes *et al.* 1991, Hayes 1995). Conditions are optimal for Arctic

wolves to form new breeding pairs because:

1. Arctic wolf density is low and competition for space is low
2. Home ranges commonly overlap in winter, increasing the chances of contacting unrelated wolves
3. Tundra wolves are apparently more tolerant of unrelated wolves compared to territorial wolves
4. Tundra wolves disperse long distances, increasing opportunities for contacting unrelated wolves

Males moved longer distances than females, supporting other Arctic wolf studies (Pullianen 1982, Stephenson and James 1982, Clarkson and Liepens *unpublished*). We also found that the direction of dispersal was limited by geography (Pullianen 1982). None of our radio-collared wolves moved east across the Mackenzie Delta during the seven year study. At the same time, Clarkson and Liepens (*unpublished*) saw no dispersals west across the Delta among 137 radio-collared wolves on the Bluenose caribou herd range. We believe the large wetlands in the lower Mackenzie River Delta are a substantial barrier to dispersal in summer and fall, when wolves tend to abandon their natal packs (Gese and Mech 1991, Ballard et al. 1997). In the early 1980s, one radio-collared wolf dispersed from the Arctic National Wildlife Refuge in Alaska, passed through our study area then traveled across the Mackenzie Delta (Garner and Reynolds 1986), suggesting wolf genetic mixing sometimes happens across various Arctic caribou herd

ranges in North America (Lehman *et al.* 1992).

Annual average survival rate (0.73) was higher than for an increasing wolf population in northwestern Alaska (0.59 to 0.65, Ballard *et al.* 1997). Survival rate of radio-collared yearlings was 0.86; about 25% higher than in six exploited wolf populations (mean 0.61: Fritts and Mech 1981, Peterson *et al.* 1984, Messier 1985a, Ballard *et al.* 1987, Fuller 1989, Hayes *et al.* 1991), and similar to a rapidly increasing population in the central Yukon (0.81: Hayes 1995). Survival rate of adult wolves were equally high, (0.81 to 0.93) until wolves reached five-years old, then survival declined sharply to between 0.50 and 0.63—similar to the average of 0.59 observed in other exploited populations (*see* Hayes 1995). We conclude that juvenile survival was high and adult survival was similar to other Yukon wolves.

Thus, we believe that a main factor limiting the wolf population size during our study was low reproduction.

Factors Limiting Pack Size and Reproduction

Wolves in the AWSA were unable to sustain large pack sizes for long, and the declines could not be associated with documented mortalities. Wolf packs seem to have a social capacity limit of about 13 wolves, which is independent of food supply (Mech 1970, Zimen 1976). The inability of AWSA packs to remain large for long is probably due to the unpredictable availability of caribou prey throughout the year.

It is advantageous for wolves in large packs to split into smaller groups because per capita food supply increases substantially as pack size declines (Hayes *et al.* 1991, Thurber and Peterson 1993, Hayes 1995, Ballard *et al.* 1997). The small pack sizes in the AWSA was not due to especially low survival rates of yearlings or adults, thus, it must be caused by low reproduction, because wolf packs are mainly composed of adult wolves and their pup and yearling offspring (Zimen 1976, Packard and Mech 1980, Hayes 1995).

Small wolf packs were common in the AWSA and also in ANWR (Garner and Reynolds 1986). We could expect small packs to be more common than large packs because: 1) smaller packs are optimal for foraging on transient caribou that have relatively small biomass and unpredictable distributions; and 2) subordinate wolves in large packs are socially restricted from breeding (Packard and Mech 1980). If these two points are true then more breeding opportunities should happen when a pack splits. It follows that when reproduction or pup survival is low in PCH wolves (our study, Garner and Reynolds 1986), pack size will tend to be small because fewer pups will survive to become adults.

In most wolf populations, yearlings rarely breed although they are sexually able (Packard and Mech 1980). But Parker and Luttich (1986) found that 60% of yearling females were bred in Arctic Quebec and Labrador. High dispersal rates of young wolves in our study support Parker and Luttich's (1986) observation of early breeding among

Arctic wolves. We suggest that Arctic wolves release juveniles earlier than in other areas to compensate for the lower chance of litters surviving due to unpredictable availability of caribou prey.

Boertje and Stephenson (1991) showed that blastocyst reproduction in wild female wolves is reduced when food supply declines, thus we should expect that in the Arctic reproductive potential should be low when tundra wolves den far from caribou summer areas. Garner and Reynolds (1986) believed that the small pack sizes in the ANWR were caused by low ungulate supply inhibiting reproduction. In the NWT, adult wolves killed and ate their pups when food was low (Williams 1990). Wolves in the AWSA successfully denned about 50% less when compared to Hayes (1995), who found 71-93% annual den success in the central Yukon, where moose were the main prey. Other factors may also limit pup survival in the AWSA.

Rabies killed pups at Arctic dens in Alaska (Chapman 1978, Garner and Reynolds 1986, Ballard *et al.* 1997). In our study area, brown bears were known to prey on wolf pups at dens (Hayes and Mossop 1987, Hayes and Baer 1992). Thus, inadequate food, disease, and bear predation on pups at dens are some possible causes of low reproduction.

Changes in Wolf Density

Wolf density (2.3 wolves per 1,000 km²) in April 1987 was similar to the eastern Brooks Range, Alaska, (1.4 wolves: Garner and Reynolds 1986; 2.0 to 3.0, Stephenson 1994), the western Brooks Range (2.6 to 4.2,

Carrol 1994), northwestern Alaska (1.5 to 4.4, Ballard *et al.* 1997) and the Taimyr Peninsula of Siberia (1.5 to 2.5, L.A. Kolpaschicov *unpublished*). Density in the AWSA was lower north of treeline (1.4 wolves per 1,000 km²) compared to taiga areas (3.7 wolves per 1,000 km²), similar to tundra/taiga wolf distributions in other Arctic areas (Stephenson 1994, Carrol 1994, Kolpaschicov *unpublished*). By comparison, in the southern Yukon where wolves prey mainly on moose, wolf densities are 3-7 times higher ranging from 6-18 wolves per 1,000 km² (Baer and Hayes 1987, Hayes and Baer 1987, Hayes and Bowers 1987, Hayes and Baer 1989, Hayes *et al.* 1991, Hayes 1995).

We were unable to determine what caused the increase in wolf abundance in the NRSA between 1987 and 1989, or the subsequent decline in 1993. The decline followed high wolf harvest in 1991 and 1992, but we were unable to separate the effects of changing caribou distribution and wolf harvest among the three count years.

Ballard *et al.* (1997) reported a three-fold decline in wolf abundance in northwestern Alaska was caused by a combination of rabies and heavy harvest of wolves. We did not monitor wolves in the NRSA between 1990 and 1992, so we could not determine if epizootic rabies happened, or if wolf survival declined as a result.

Factors Affecting Wolf Numerical Response

The availability of ungulate prey biomass is a determinant of wolf numerical response (Keith 1983, Fuller 1989, Messier 1994). Dale *et al.*

(1994) argued that caribou have a stronger influence than moose do on wolf numerical response. They suggested that this dependence showed wolves have evolved to prey on caribou. We examined wolf numerical response in relation to PCH abundance using a formula of Fuller (1989).

Fuller provided an equation to estimate wolf density (W) that could result in a stationary ungulate population, given a specific ungulate density (U), annual hunter kill rate per km² (S), potential rate of increase of prey (λ_p) and annual rate of kill by wolves (K):

$$W = \frac{(U(\lambda_p - 1) - S)}{K} \cdot 1000$$

To solve for this equation, we estimated Porcupine caribou herd size at 178,000 animals (Fancy *et al.* 1994) in a mean annual range of 250,000 km² (Russell *et al.* 1992), giving an estimate of 0.72 for U ; 1.30 for λ_p (Bergerud 1983); 0.175 for S (unpublished data), and 29 caribou per wolf per year for K (Hayes and Russell 2000). The resolved density (W) was 2.7 wolves per 1,000 km²; compared to our observation of 2.3 wolves per 1,000 km² in the AWSA in 1987. Although the analysis is limited, it suggests caribou biomass is a main determinant of wolf abundance in the north Yukon.

Relations of Wolves to Caribou and Moose

Wolves in the range of the PCH prefer caribou, similar to Arctic wolves in Alaska (Dale *et al.* 1994, 1995, Ballard *et al.* 1997) and NWT (Clarkson and

Liepens *unpublished*). Wolves exhibit a weak prey-switching response, which means they continue to hunt their preferred prey even when other ungulates outnumber main prey (Hayes 1995), or preferred prey are almost absent (Mech and Karns 1977, Dale *et al.* 1994, Ballard *et al.* 1997).

There are few alternatives for tundra wolves because there are few other ungulates north of treeline. There are only small pockets of wintering moose, Dall's sheep and muskoxen available in the British and Barn Mountains, and along the Yukon North Slope. As a result, there is no ecological advantage to stay and defend these prey resources from other wolves. Tundra wolves have adapted by leaving to follow transient caribou, and by adopting social tolerance of other wolves that allow the predators to share caribou prey.

But it is not just a matter of where wolves live in relation to treeline that determines whether they will be migratory or territorial. Neighboring tundra wolves on the North Slope in ANWR are territorial in the Brooks Range where moose and Dall's sheep are more common than in the AWSA (Garner and Reynolds 1986). Broad u-shaped valleys are more common in the North Slope drainages of ANWR, supporting broad riparian shrub zones (personal observation) that provide good moose winter range. By comparison, the British and Barn mountains in the AWSA have limited riparian shrubs and few moose, and no sheep are found east of the Firth River drainages (Hayes and Barichello 1986). Muskoxen are limited to the far northwestern drainages of the North Slope. In short, wolves cannot stay in

the North Slope drainages and survive there.

On the other hand, taiga wolves display a plastic switching response that allows them to exploit caribou when they become available (our study, Dale *et al.* 1994, Ballard *et al.* 1997). We believe that taiga wolves prefer caribou because they account for the greatest portion of available ungulate biomass year-round (Ballard *et al.* 1997). Ballard *et al.* (1997) observed when caribou are not available, wolves turned to hunting low-density moose. Our results are consistent with Ballard *et al.* (1997), but contrary to Hayes (1995) who found that wolves in the central Yukon did not switch from hunting moose to preying on much more abundant woodland caribou during late winter. In the central Yukon, moose are at 2-3 times higher density than in AWSA. It is ecologically adaptive for these wolves to remain hunting moose, even when there are more caribou prey available (Hayes 1995).

Predation Rate by Wolves on Caribou

Hayes and Russell (2000) estimated the annual kill rate of PCH wolves was 29 adult caribou per wolf, similar to wolves in Arctic Alaska (Dale *et al.* 1994) and Northwest Territories (Clarkson and Liepens *unpublished*). Apparent consumption rate was 5.6 kg of caribou per wolf per day, similar to Alaska (5.3 kg of moose and caribou, Ballard *et al.* 1997) and NWT (4.4 kg caribou, Clarkson and Liepens *unpublished*).

Based on these kill rates, Hayes and Russell (2000) constructed a

model to estimate annual wolf predation rate on the PCH (% adult caribou killed). The model predicted that wolves removed 7,600 adult caribou each year—or about 6 – 7 percent of the PCH in the early 1990s.

The predation rate model of Hayes and Russell (2000) was based on late-winter kill rates and did not account for neonatal calves. Their model estimated wolves took 16% of adult-size caribou from calving through late summer, when caribou seasonal ranges were smallest and wolf home ranges were most limited by the requirement to feed pups at dens. The greatest portion of adults (84%) was theoretically killed when caribou expanded their range use during fall migration, winter, and spring migration, providing prey access to many more wolves. The model supported Bergerud (1974), and Thomas (1995) who argued that caribou space away in spring and summer to minimize their exposure to large carnivores (Bergerud 1989).

Effects of Infectious Diseases on Wolves

The importance of infectious diseases among wild wolves is not well understood because mortalities are often among neonatal wolves and researchers rarely see morbidity (Carbyn 1982, Bailey *et al.* 1995, Brand *et al.* 1995). Only two diseases are known to have caused mortality among wild wolves: rabies (Chapman 1978, Garner and Reynolds 1986, Theberge *et al.* 1994, Ballard *et al.* 1997) and canine distemper virus (Carbyn 1982, Peterson *et al.* 1984). Captive wolves have died from canine parvovirus (Mech and Fritts 1987) and

probably from brucellosis infections (Neiland 1975). Ballard *et al.* (1997) found rabies limited wolf abundance in northwestern Alaska. In their study, the disease killed pup and adult wolves, confirming earlier studies (Davis *et al.* 1980). Theberge *et al.* (1994) found rabies killed a high proportion of radio-collared wolves in Algonquin Park, Ontario. Rabies was a known cause of mortality among PCH wolves in the 1970s and 1980s (Chapman 1978, Garner and Reynolds 1986, G. Weiler *unpublished*). Cyclic outbreaks of rabies in Arctic fox, the primary reservoir of the disease, happen about every three to four years in the Arctic.

An epizootic outbreak in foxes was reported in northeast Alaska in 1984 and 1985 (Garner and Reynolds 1986). Wolves declined by 26%, but numbers did not decrease in subsequent years (Garner and Reynolds 1986). If rabies were important during our study period, then we should have seen an increase in mortality among wolves in 1989-90, when the next peak cycle was expected in the PCH range. During this time, we observed an 18% to 23% decline in wolf survival rates, but the difference was not significant (Table 3). Ballard *et al.* (1997) observed a 15% decline in wolf survival rates during the same years in northwestern Alaska and were able to associate the decline with rabies outbreak.

Garner and Reynolds (1986) believed that rabies transmission is limited by the avoidance of wolf packs from contacting each other. Chapman (1978) believed that rabies can be an important mortality agent among

certain packs, but he also believed that dispersal and reproduction in Arctic wolves rapidly replaces mortally infected wolves in Alaska. We believe that rabies transmission in the PCH range could be rapid given the high degree of mixing of wolf packs during late winter. At the same time, the low wolf density in the North Slope reduces the potential for rabies to transmit among packs, buffering tundra wolves from regional infection—especially during summer when wolf movements are restricted and the disease is most prevalent (Ballard *et al.* 1997). We conclude there is some evidence that rabies could have caused a decline in survival rates and wolf density during our study, but we could not detect it using our study methods.

Caribou are the primary reservoir for brucellosis and wolves can be infected by feeding on infected caribou (Neiland 1975). Brucellosis was detected in 4% of the PCH (Zarnke 1993). Brucellosis causes reproductive failure in caribou; Neiland (1975) and Neiland and Miller (1981) showed that it could cause reproductive failure among wolves. We found a moderate (29%) *Brucella* antibody prevalence from a sample of 14 wolves tested. Positive brucellosis titers are also frequent among caribou-hunting wolves in Arctic Alaska (45%, Neiland 1975, 16%, Zarnke 1993). There are no studies showing brucellosis causes death among wild wolves.

Canine distemper virus (CDV) prevalence was 71%, well above the average of 10% for wolves in Alaska (Zarnke 1993) and 41% in other parts of the Yukon (R. Zarnke *unpublished*). Like brucellosis, CDV mainly affects

reproduction and pup survival (Carbyn 1982), but it is hard to detect in a wild wolves (Bailey *et al.* 1995). Most wolves in North America exhibit good recruitment rates; therefore, distemper is probably not an important mortality agent of pups. However, the low productivity of wolves in the AWSA during our study (53%) could be related to the high CDV infection rate.

The five wolves that we sampled for Infectious Canine Hepatitis Virus (ICHV) were positive, similar to the high infection rates in Alaska (Zarnke 1993), and other parts of the Yukon (R. Zarnke *unpublished*). ICHV is an enzootic infection and, to date, there have been no reported mortalities in wolves (Brand *et al.* 1995).

Canine Parvovirus (CPV) is a recent disease of wolves, rapidly spreading through Alaska and Yukon wolves in the 1980s (R. Zarnke *unpublished*). CPV has caused mortality among captive wolves (Mech and Fritts 1987), but it is not believed to have caused wild wolf populations to decline. However, a wolf die-off was linked to a CPV outbreak among dogs on Isle Royale, Michigan (Brand *et al.* 1995). Like other diseases, the chance of detecting CPV-induced mortalities in the wild is improbable unless it is at epidemic levels.

We conclude that both ICHV and CDV are enzootic and do not appear to be important in limiting wolf population size in the AWSA, or in other parts of Alaska (Zarnke and Ballard 1987) or Yukon (R. Zarnke *unpublished*). The low reproduction rate among AWSA wolves could be linked to rabies (Chapman 1978, Garner and Reynolds 1986), CDV, or

brucellosis affecting neonatal pup survival. We found no evidence that mean pack size or wolf numbers were reduced in subsequent years due to disease events. In summary, we saw no evidence disease limited wolves on the PCH range, but we did not monitor wolves enough to detect effects of a regional rabies epidemic in 1990-1991.

Effects of Human Harvest on Wolves

Most wolves in the AWSA were killed while people were subsistence hunting for caribou. The risk of wolves to being hunted was higher when caribou were present and people spent more time on the land hunting. When caribou hunters saw wolves or found fresh sign, they usually stopped hunting caribou to pursue wolves.

Our study wolves were less vulnerable to hunters than in other parts of the Arctic. In the AWSA, hunters removed 24% of collared wolves compared to 37% in the Bluenose caribou range (Clarkson and Liepens *unpublished*), and 69% in northwestern Alaska (Ballard *et al.* 1997). Wolves in the adjacent Bluenose range are highly vulnerable to hunters because the terrain is flat and treeless with little chance of escaping, making it easy to find and track wolves (personal observation, Clarkson and Liepens *unpublished*). In the Northern Richardson Mountains, the terrain is steep and rugged, restricting hunting of wolves to the valley lowlands. Wolf hunting increased in our study in spring when snow conditions improved for snow machine travel, similar to other Arctic

areas (Ballard *et al.* 1997, Clarkson and Liepens *unpublished*).

Our results show that when hunters encounter packs, only a few wolves are killed. The risk of a wolf being killed increased the smaller the pack size was. Hunters took 1 to 2 wolves during most hunts regardless of the number of wolves encountered. Among larger packs, most members escaped being shot when encountered by hunters on snow machines.

We calculated the effect of harvest on PCH wolves throughout the herd range by including harvest data from Alaska (see Morgan 1989, 1990, Abbott 1991, 1992, 1993, Hicks 1994). In territorial wolves, maximum sustainable harvest is 30 to 40% of early winter numbers (Keith 1983, Gasaway *et al.* 1983, Peterson *et al.* 1984, Hayes *et al.* 1991, Gasaway *et al.* 1992, Hayes 1995). Between 1987 and 1993, hunters killed an average 45 wolves (range 27 to 82) in all parts of the herd's range. This represents about 6% of the PCH wolf population.

Local wolf harvest rates in the NRSA exceeded sustainable levels in 1991 and 1992, when 50-66% of taiga wolves were killed. However, wolf harvest declined again in 1993 when fewer caribou wintered there, and wolf-hunting effort was lower, so we expect wolves recovered. Unlike territorial (taiga) wolves, it is difficult to determine how hunting affects numerical response of tundra wolves because their distribution depends on where caribou are any given year. In the NRSA, harvest was apparently high, but we could not separate the regional effect of local wolf harvest with the natural shifting of packs as they followed caribou.

In some Arctic areas, the concentrating of wolves on caribou winter ranges can greatly increase the risk of large numbers of wolves being over-hunted (Thomas 1995, Ballard *et al.* 1997). A remarkably high wolf harvest happened in Coppermine, NWT, when hunters killed 850 wolves during a winter when the Bathurst caribou herd wintered nearby (Hayes and Gunson 1995). Miller (1995) believed that wolves on the Canadian Arctic islands were chronically over-hunted, and that on most islands wolves were well below the 'carrying capacity' based on ungulate prey supply.

In summary, three factors limit the risk of long term over-exploitation of PCH wolves by hunters. First, The PCH unpredictably shifts its winter distribution annually, reducing the long-term availability of migratory tundra wolves to communities in the herd's range. Wolves are hunted incidentally to caribou, so if caribou are not close to a community during winter, then hunters do not search and pursue wolves as often as when caribou are available. Second, much of the PCH range is mountainous or forested, providing escape features for wolves to avoid being shot or trapped. Third, there are few people living on the PCH winter range, limiting the exposure of wolves to hunting. These features combine to provide a buffer that likely ensures human exploitation has a minor effect on the long-term population dynamics of wolves in the PCH range.

Data Quality

We acknowledge certain factors limited our ability to study wolf ecology.

1. We could not maintain regular contact with tundra wolf packs in all years, making it difficult to accurately determine wolf movements and predation ecology - especially in spring and fall when wolves and caribou were moving long distances.
2. We observed a high censorship rate of radio-collared wolves, limiting our abilities to confidently estimate survival and dispersal rates.
3. Our estimates of annual and age-specific survival rates were based on small samples that violate certain assumptions of the staggered entry method (Pollock *et al.* 1989a).
4. We do not have a clear understanding of the cause of low reproduction, which appears to be the main factor limiting the size of wolf packs and wolf density in the area.
5. We did not follow wolves from 1990 through 1992, when a rabies induced population decline happened in adjacent areas in Alaska.
6. At three of six dens, wolf scat analysis was insufficient to distinguish moose from caribou prey, restricting our analysis of summer predation.

Nevertheless, our results are consistent with other Arctic wolf studies that found a migratory behavior among tundra-dwelling wolves associated with barren-ground caribou. Wolves on the PCH range

were at a naturally low density, but at predicted abundance according to available moose-caribou biomass. Tundra wolves had a strong preference for caribou prey. Taiga wolves hunted mainly moose, and they were territorial, with much smaller home ranges than tundra wolves. Pack sizes were small in all parts of the study area. Both tundra and taiga wolves showed a high prevalence of disease antibodies, high dispersal rates of young wolves, and low breeding success. Wolf predation was not a primary factor limiting the size of the Porcupine herd during our study.

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An earlier slideshow version of this study is available at <http://www.wmacns.ca/images/slideshows/wildlife/wolf/index.html>.

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APPENDIX 1 STATUS OF RADIO-COLLARED WOLVES IN THE AWSA FROM JUNE 1986 THROUGH MAY 1993

Wolf age classes include adults (2+ years old) and yearlings (<2 years old).

Pack	Type	Wolf No.	Date radio-collared	Date Found Dead	Sex	Age	Fate
Malcolm River	Tundra	3001	18 June 1986	18 June 1986	M	Ad.	Capture mortality
		3002	19 June 1986		F	Ad.	Unknown
		1102*	14 Aug. 1987		F	Ad.	Unknown
Bell River	Tundra	3008	11 Apr. 1987		M	Ylg.	Unknown
		3009	11 Apr. 1987	15 Mar. 1992	M	Ad.	Hunter mortality
		3011	12 Apr. 1987		M	Ylg.	unknown
		3032	23 Apr. 1988	25 Mar. 1989	F	Ylg.	Recapture mortality
Fish River	Tundra	3047	25 Mar. 1989		F	Pup	Unknown
		3017	13 Apr. 1987	14 Apr. 1987	F	Ad.	Capture mortality
		3018	13 Apr. 1987	30 Apr. 1987	M	Ad.	Hunter mortality
Trout Lake		3019	14 Apr. 1987		F	Ad.	Unknown
		3020	14 Apr. 1987	20 Feb. 1990	M	Ad.	Natural mortality
		3027	19 Apr. 1987	16 Nov. 1989	M	Ad.	Natural mortality
		3028	19 Apr. 1987	9 Feb. 1988	M	Pup	Hunter mortality
		3036	25 Apr. 1988	24 Mar. 1993	F	Ylg.	Hunter mortality
		3040	25 Apr. 1988		F	Pup	Unknown
		3048	24 Mar. 1989		M	Ylg.	Unknown
Blow River	Tundra	3025	19 Apr. 1987		F	Ad.	Unknown
		3026	19 Apr. 1987	30 Oct. 1992	F	Pup	Hunter mortality
		3035	24 Apr. 1988		M	Ad.	Natural mortality
		3043	25 Mar. 1989		M	Pup	Unknown
		3044	25 Mar. 1989		F	Ylg.	Unknown
		3045	25 Mar. 1989	14 Nov. 1989	F	Ylg.	Natural mortality
		3046	25 Mar. 1989		M	Pup	Unknown
Firth River	Tundra	3029	20 Apr. 1987	11 Jul. 1988	F	Ad.	Natural mortality
		3030	20 Apr. 1987		M	Ylg.	Unknown
		0765**	12 Sep. 1987		M	Ad.	Unknown
Gates of Arctic	Tundra	0985**	4 Oct. 1987	28 Feb. 1992	M	Ad.	Hunter mortality
Trail River	Tundra	3037	5 Apr. 1988	6 Mar. 1992	F	Ylg.	Hunter mortality
		3038	5 Apr. 1988		M	Ylg.	Unknown
		3039 D	25 Apr. 1988	15 Sep. 1988	M	Ylg.	Hunter mortality
Babbage Pair	Tundra	3041	25 Apr. 1988	14 Nov. 1989	M	Ylg.	Natural mortality
Old Crow	Taiga	3003	29 Dec. 1986	1 Mar. 1987	M	Ylg.	Trapper mortality
Eagle River	Taiga	3004	10 Apr. 1987	30 Jul. 1987	F	Ad.	Natural mortality
		3005	10 Apr. 1987	30 Jul. 1987	M	Ad.	Natural mortality
Little Flats	Taiga	3006	10 Apr. 1987		F	Ad.	Unknown
		3007	10 Apr. 1987		F	Ad.	Unknown
Two Ocean Cr.	Taiga	3010	11 Apr. 1987	31 Mar. 1992	M	Pup	Hunter mortality
		3014	11 Apr. 1987	14 Jun. 1988	M	Ad.	Natural mortality
Berry Creek	Taiga	3012	12 Apr. 1987		F	Ad.	Unknown
		3013	12 Apr. 1987		F	Pup	Unknown

Driftwood R.	Taiga	3015	13 Apr. 1987	12 Jun. 1988	F	Ad.	Natural mortality
		3016	13 Apr. 1987		M	Ad.	Unknown
Frost Pack	Taiga	3021	15 Apr. 1987	25 Apr. 1988	F	Ylg.	Natural mortality
		3022	15 Apr. 1987	23 Mar. 1988	M	Ad.	Killed by wolves
		3023	15 Apr. 1987	15 Apr. 1988	M	Ylg.	Capture mortality
Lord Creek	Taiga	3024	15 Apr. 1987	19 Nov. 1988	M	Ad.	Hunter mortality
		3031	20 Apr. 1987		F	Ad.	Unknown
Rat River	Taiga	3033 D	4 Apr. 1988	9 May 1993	F	Pup	Hunter mortality
		3034	4 Apr. 1988		M	Ylg	Unknown
		3042	6 Apr. 1988		F	Ad.	Unknown

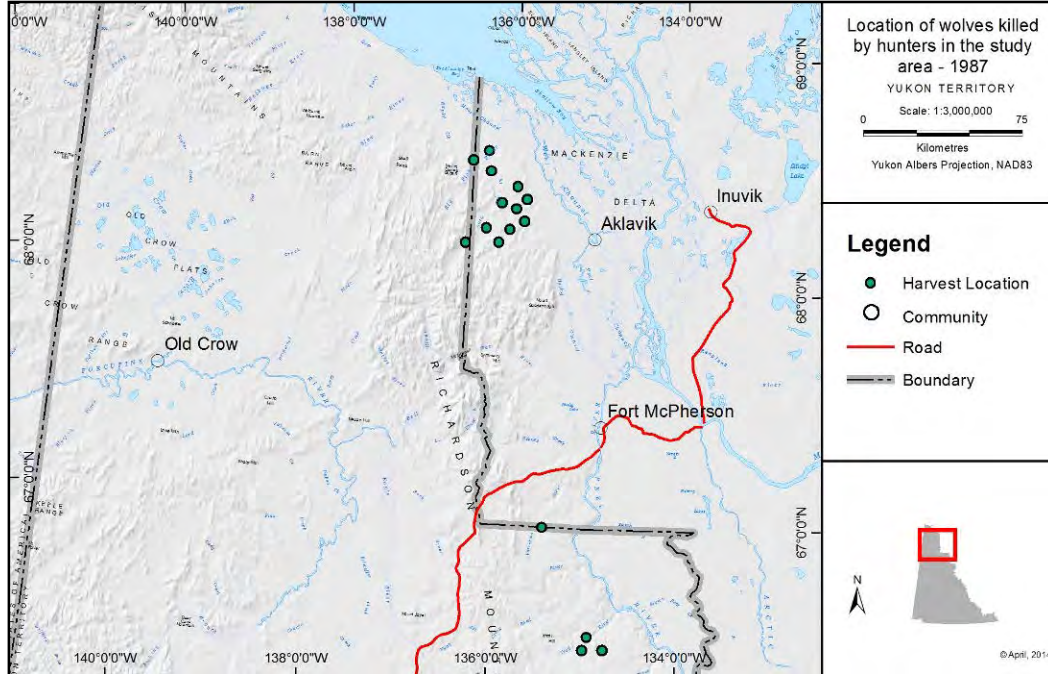
* radio-collared by G. Weiler, ANWR, Alaska

** radio-collared by L. Adams, US National Parks Service, Alaska

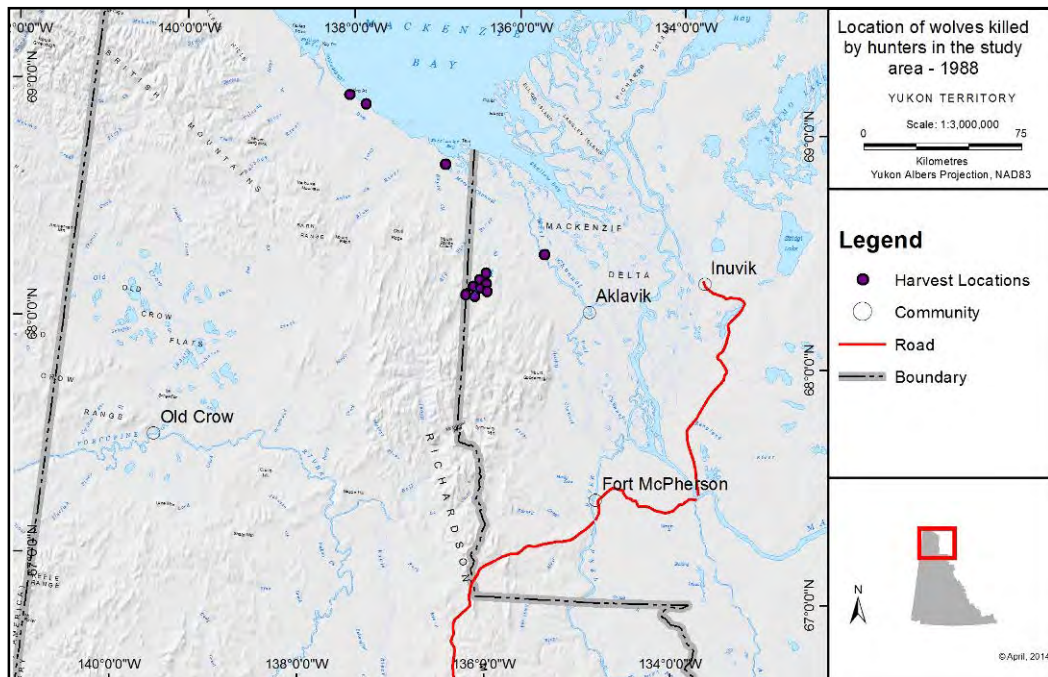
D Dispersed from study area to Prudhoe Bay, Alaska, then shot by hunters

APPENDIX 2 LOCATION OF HUNTER KILLED WOLVES BY YEAR

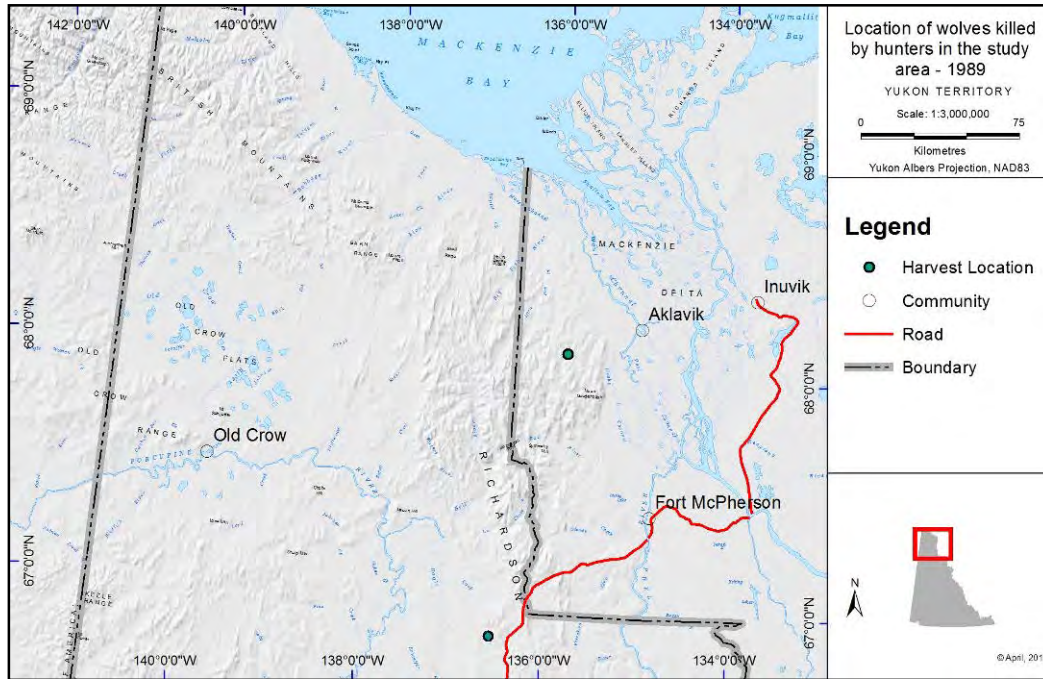
1987



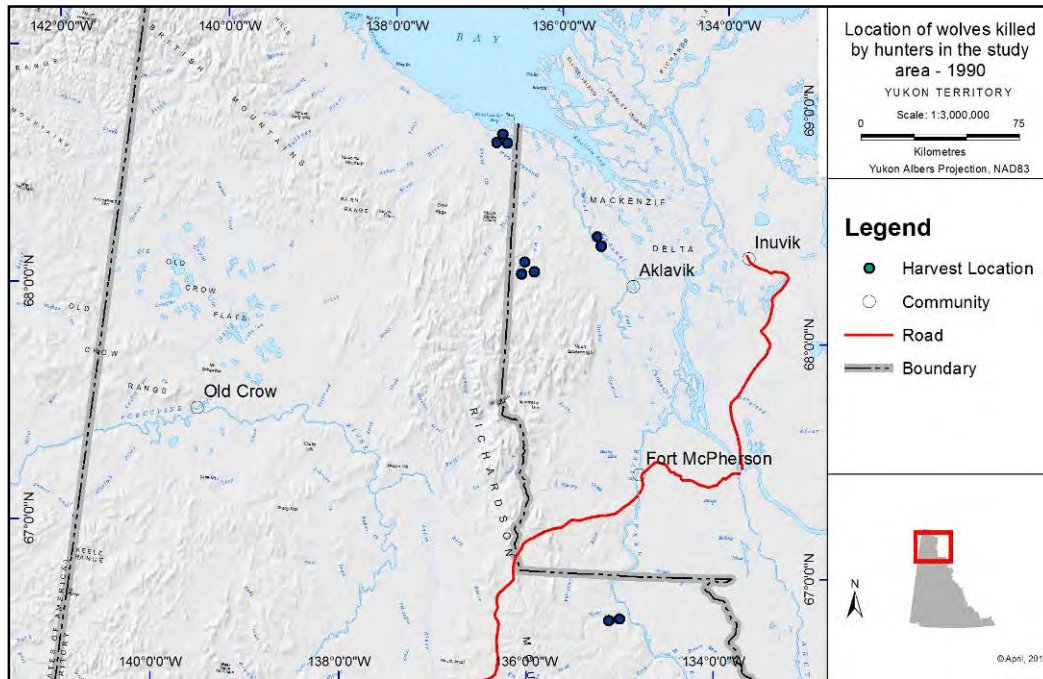
1988



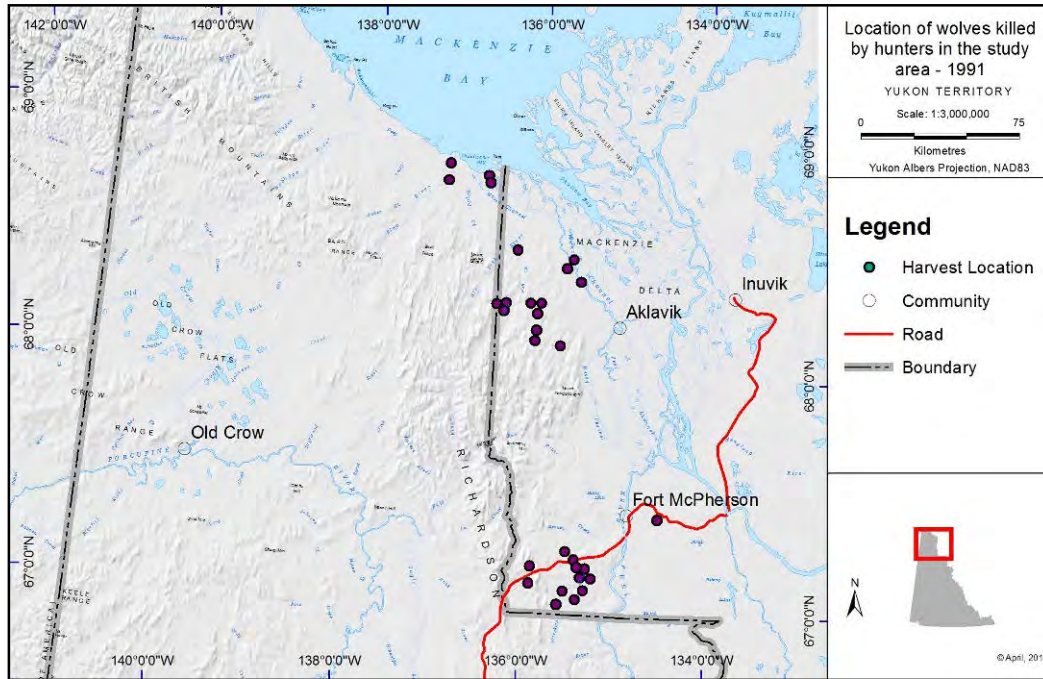
1989



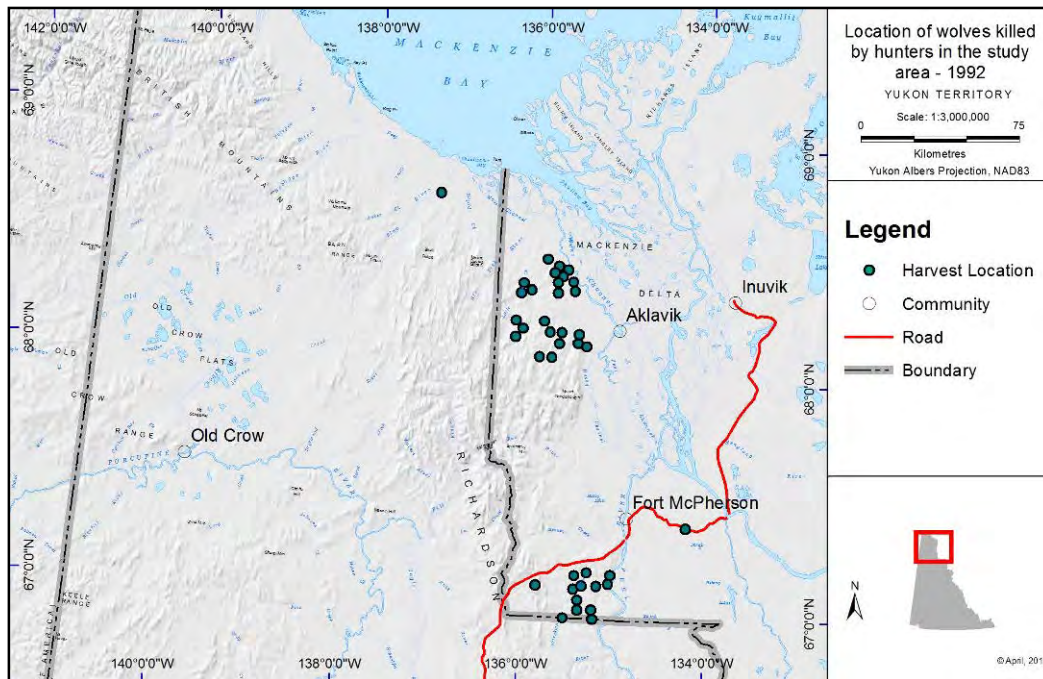
1990



1991



1992



1993

