University of Alberta

Population dynamics and limitation of wolves (*Canis lupus*) in the Greater Pukaskwa Ecosystem, Ontario

by

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Abstract

Ungulate biomass and human-caused mortality limit growth of wolf populations across North America. These factors were addressed in a study of 25 radio-collared wolves in and adjoining Pukaskwa National Park. The mean annual finite rate of increase (0.96) suggested that the population growth of wolves was limited and declining slightly. I tested the hypotheses that wolves were primarily limited by ungulate biomass and human-caused mortality. Average index of ungulate biomass (208 ± 33) was low, occurrence of natural mortality high (9 of 17 wolves) and rate of food consumption variable. Occurrence of human-caused mortality was high (8 of 17), but comparable with other studies. These data suggest that both ungulate biomass and human-caused mortality are limiting factors for wolves in the study area, although ungulate biomass may be more important. Based on these and other P5 data, I qualitatively predict the long-term viability of wolves in the study area.

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Chapter 1. Introduction

Background

Pukaskwa National Park and the Pukaskwa Predator Prey Process Project

Pukaskwa National Park (PNP) was founded by Parks Canada in 1978 to "…protect for all time, a representative example of Central Boreal Uplands and the Great Lakes shoreline…" (PNP Management Plan 1995). Initially the Park planned to develop more than 400 km of hiking trails, a hotel and a road that would be used to access campgrounds throughout the Park. These plans were initiated with the construction of a 40-km coastal hiking trail. At that time, concerns were raised about increasing human and wolf (*Canis lupus*) access to bands of woodland caribou (*Rangifer tarandus tarandus)* that lived along the coast and within the Park (F. Burrows, PNP Resource Management Specialist, pers. comm.). Furthermore, Park managers and biologists realized that little was known about the general ecology of woodland caribou, wolves and moose (*Alces alces*), even though these species were of conservation and economic interest to Parks Canada and the Ontario Ministry of Natural Resources (OMNR). Therefore, Parks Canada research goals were based on learning more about these three species.

Accordingly, researchers began gathering data on caribou, wolf and moose relationships and population dynamics in PNP (Bergerud et al. 1983, Bergerud 1985, 1989). The studies relied heavily on aerial and ground surveys because no animals were radio-collared in the Park. Despite this shortfall, two putative relationships of wolves and their prey were described:

1) Caribou were spatially separated from moose and wolves. Moose and wolf densities were highest inland, particularly in the northeastern section of the Park and adjacent provincial land. In these areas, fire and cut-overs created abundant early successional forage for moose, which then became prey for wolves. Caribou used the rugged coastal region where wolves were mostly absent (Bergerud 1985).

2) Predation by wolves appeared to limit the increase of the moose population in PNP (Bergerud et al. 1983).

The Pukaskwa Predator Prey Process Project (P5) was initiated in 1994 as a continuation and expansion of the work by Bergerud et al. (1983) and Bergerud (1985, 1989). Although these studies provided many insights into predator-prey relationships in the PNP, information important for management was lacking. Without radio-collared animals, details on animal movements, distribution and other population dynamics were missing. Also, little information was collected outside PNP, where industrial and other human activities were rapidly increasing. The effects of these developments on caribou, wolves and moose were unknown. Thus, caribou, wolves and moose continued to be the focus of P5 research.

The general objective of P5 was to assess the status of ecological integrity within PNP, which appeared to be increasingly influenced by the extent and proximity of human activities. Consequently, research was expanded from PNP to include the Greater Pukaskwa Ecosystem (GPE). P5 emphasized collaborative research and planning with all levels of government and the private sector.

Rationale of P5

Legislation and policy of National Parks require that managers make decisions that protect biodiversity, priority areas and ecological processes. A cost-efficient approach is to identify and maintain the habitat needs of focal species whose spatial and ecological requirements encompass those of many other species (Eisenberg 1980, East 1981, Noss 1995). Carnivores are candidate focal species because they use large areas and are at the top of many food chains (Hummel 1990, Foreman 1992, Paquet and Hackman 1995, Noss et al. 1996). Recent work in the Central Canadian Rockies suggests that large carnivores are effective focal species (Paquet et al. 1996).

In addition, large carnivores have ecological roles that make them useful focal species. For example, predators may directly influence prey populations and exert top-down control of food-chains. This was the case on Isle Royale where McLaren and Peterson (1994) found strong evidence of top-down control of a food chain by wolves; growth rates of balsam fir were regulated by moose density, which in turn was controlled by wolf predation. This top-down regulation is apparently replaced by bottom-up influences only when stand-replacing disturbances such as fire or large windstorms occur at times when moose density is already low (McLaren and Peterson 1994). Predators are also mechanisms for natural selection. The wolf, as an obligate predator with a large range, probably exerts significant evolutionary pressure on antlered and horned prey (Peek and Carnes 1996).

Given that large carnivores play such important roles in ecosystems, some biologists (Eisenberg 1980, Noss 1995, Paquet and Hackman 1995, Noss et al. 1996) consider them useful indicators of the health or ecological integrity of an ecosystem. For example, landscapes that retain viable populations of large carnivores are often ones where natural vegetation predominates, where most native species can still be found, and where ecological processes operate essentially as they have for a long time (Noss et al. 1996). However, given that some areas containing large carnivores are impoverished or damaged biologically (for instance, from logging), a more reasonable supposition is that landscapes with large carnivores have relatively intact food webs and, thus, a high potential for ecological integrity (Noss et al. 1996).

Goals and Objectives of P5

P5 was initiated within the context of Parks Canada's legislated mandate, namely, to protect and maintain the ecological integrity of a dynamic system that ensures the long-term viability of all native components (Burrows et al. 1996). The primary goal of P5 was to address questions concerning ecological integrity within the GPE by integrating data on predator-prey relationships and population dynamics with information on natural processes, land-use and wildlife management activities. The gray wolf was chosen as a major component of the research. The primary goal of the wolf study was to examine the effects of natural processes, land-use, and wildlife management activities inside and outside the Park on predator and prey relationships (Burrows and Cherepak 1994). The ecological issue of the wolf study was to determine how human activities affect biological processes and persistence of wolf populations (Burrows et al. 1996).

Specific objectives of P5 were to determine: "1) What natural and human land-use features facilitate or impede predator and prey movements?; 2) How the altered dynamics of habitat patch-size, geometry and juxtaposition affect predator and prey relationships?

i.e., clear-cut size, habitat quality, stand age/condition; 3) If wildlife management objectives in and outside the park affect predator and prey relationships? *i.e.*, (*Alces alces*) densities, exotics, hunting, trapping; 4) The interactions among objectives 1, 2, and 3?" (Burrows et al. 1996).

Four researchers and a primary investigator are doing P5 research. Peter Krizan, Acadia University, studied the "effects of human land development, landscape characteristics and prey density on the spatial distribution of wolves on the north shore of Lake Superior" (Krizan 1997). Frank Burrows, Lakehead University, is studying "the effects of landscape disturbance on moose density, home range and recruitment in the Greater Pukaskwa Ecosystem, ON" (M.S. in progress). Graham Neale, University of Montana, is studying "the spatial separation of caribou, moose and wolves in the Greater Pukaskwa Ecosystem, ON" (M.S. in progress). I studied population dynamics and limitation of wolves in the Greater Pukaskwa Ecosystem, ON. Dr. Paul Paquet is the primary investigator and he is incorporating all P5 data into a decision-support model that integrates ecology, sociology and economics. The model will be used for environmental decision-making in the GPE (Burrows et al. 1996).

Present Study Rationale

In 1996, P5 researchers documented low reproductive success and high mortality of adult wolves in and dispersing from the GPE. They did not reach a definitive conclusion about a population decline or its potential causes. Researchers, however, postulated that low food availability and high mortality from human influences could be negatively affecting the growth of the wolf population in PNP and to some extent, in the GPE (Burrows et al. 1996).

P5 researchers were concerned because a declining population of wolves could adversely affect the ecological integrity of PNP and surrounding areas. Moreover, Parks Canada is required to ensure that all populations of native species remain viable within the constraints of natural changes. Clearly, further research was needed into the suspected decline in wolf numbers.

Accordingly, I conducted a study from March 1997 – September 1998 on the use of prey by wolves in the GPE. This included data on densities, distribution (home range sizes and locations, pack sizes) and population dynamics of wolves (*e.g.*, reproduction, mortality, dispersal). I used these and other related P5 data to assess population limitation and probability of long-term viability of wolves in the GPE.

Introduction to Population Limitation

Birth, death, immigration and emigration are essential demographic parameters in any study of population dynamics. Interactions between these parameters determine whether populations increase or decrease over time. Increases occur when birth and survival (and perhaps immigration) exceed death and emigration. Decreases occur in the opposite situation. Estimating these rates of change and determining factors responsible for these changes are fundamental problems of population dynamics.

Rates of change in animal numbers are produced by the interaction of limiting and regulating factors. Limiting factors refer to processes that quantifiably affect population growth (Messier 1991); *i.e.*, cause changes in the number of individuals that are produced or lost from a population. Specifically, they influence growth (*i.e.*, rate of increase) by affecting rates of birth, death or movement (Keith 1974). In doing so, these factors induce annual changes in the rate of increase and, by extension, in animal numbers (Watson and Moss 1970). Limiting factors can be stochastic (= random, in this case, density-independent) or with reproducible density relationships (density-dependent). These limiting processes set the position of the population equilibrium; *i.e.*, production (inputs from births and immigrants) equals losses (outputs from deaths and emigrants). In contrast, regulating factors refer to any density-dependent processes that ultimately keep populations within normal ranges of density (Murray 1982, Fowler 1987). These regulating processes cause a population to return to its equilibrium. Thus, regulating factors are a subset of limiting factors characterized by negative feedback mechanisms that depress population growth as animal numbers increase. In summary, any factor, density- dependent or density-independent, which causes a change in production or loss is limiting. Only those factors, however, that are demonstrably density-dependent may be regulatory (Sinclair 1989).

Identifying limiting and regulating factors and assessing their importance are central endeavors for managers of animal populations. In theory, important limiting and regulating factors can be identified and manipulated for population management. In this study, I identified limiting and not regulating factors. Consequently, I use the context of limitation rather than regulation to assess the relative importance of factors in changing wolf population growth or density.

To assess whether a population is limited, one first needs to determine the rate of increase of the population. Caughley (1977) discussed several methods of calculating rate of increase and defined several different measures. The finite rate of increase or the coefficient of annual growth (λ) is the ratio of numbers in two successive years. In contrast, exponential rate of increase (r) is the natural logarithm (ln) of the finite rate of increase. The mean annual finite rate of increase can be calculated by taking the antilogarithm of the mean exponential rates of increase for the population (Fuller 1989).

The next step to assess whether a population is limited involves comparing the measured to the maximum rate of increase possible. The rate of increase of different animal populations likely differs according to variable environmental and ecological factors. Few populations, however, achieve a maximum rate of increase. The maximum rate for wolves ($r = 0.304$, $\lambda = 1.36$) was calculated by Keith (1983) based on the highest reproductive and survival rates reported from studies on wild wolves. He corroborated the results by comparing the estimate with data from wolves that colonized Isle Royale National Park, 1952 – 1959 ($r = 0.304$, $\lambda = 1.39$). These were also likely maximum rates of increase because few individuals with abundant food initiated the population (Keith 1983). However, both rates are still much lower than a theoretical exponential rate of 0.833 ($\lambda = 2.30$) given maximum reproduction (Rausch 1967), a stable age distribution and no deaths. Obviously, rates of increase of wolves are greatly depressed even in the most favorable environments (Keith 1983).

By comparing the rate of increase of wolves in the study area with the maximum rate predicted by Keith (1983), it is apparent that the population in the study area is limited in annual growth. In the study area between 1995 - 1998, the mean annual finite rate of increase was 0.96 (Chapter 4, page 41), which is well below the assumed maximum rate of increase, 1.36. Not only is 0.96 well below the maximum rate of increase, but 0.96 indicates that the wolf population was declining slightly. The factors responsible for the low rate of increase should be assessed.

The problem of identifying and assessing limiting factors may be somewhat less complicated for wolves because in North America, they appear to be limited by two main factors: ungulate biomass (Van Ballenberghe et al. 1975, Mech 1973, 1977a, 1977b, Fuller and Keith 1980, Packard and Mech 1980, Keith 1983, Messier 1985a, 1987, Peterson and Page 1988) and human-caused mortality (VanBallenberghe 1981, Gasaway et al. 1983, Keith 1983, Peterson et al. 1984, Fuller 1989, Paquet et al. 1996, Noss et al. 1996). Assuming that wolves in the study area are similar to other North American populations, and based on preliminary P5 data, a reasonable assumption is that these same factors may be limiting the growth of the wolf population.

Rationale for Predictions

Ungulate biomass can affect rates of population increase and resulting densities of wolves. Building on work of Keith (1983), Fuller (1989) reviewed 25 studies of North American wolf and prey populations and found that rates of increase of wolf populations were most affected by relative availability of ungulate biomass (directly influencing survival of pups <6 months old) and human-caused mortality. He concluded that regardless of prey type or stability of wolf populations, average wolf densities were clearly correlated with the biomass of ungulates available per wolf. Furthermore, he found that the ungulate biomass index per wolf was highest for heavily exploited (Ballard et al. 1987) or newly protected (Fritts and Mech 1981) wolf populations and lowest for unexploited wolf populations (Oosenbrug and Carbyn 1982, Mech 1986) or those where ungulates are heavily harvested (Kolenosky 1972).

Based on this, wolf populations not heavily influenced by human-caused mortality are characterized by a low index of ungulate biomass per wolf. These populations typically have a low rate of increase. Accordingly, food probably limits population growth. Conversely, wolf populations incurring high human-caused mortality may have a high index of ungulate biomass per wolf. These populations should have a higher rate of increase resulting from greater pup production and survival. Consequently, exploited wolf populations are more likely to be limited by human-caused mortality.

The index of ungulate biomass per wolf indicates how much food is available to wolves. The index, however, does not account for ungulate vulnerability, which is an important factor affecting wolf survival. Vulnerability can seldom be used when calculating availability because factors that affect vulnerability are rarely predictive (Fuller 1988).

Nonetheless, indices of biomass available to wolves can be corroborated with data from consumption rates of prey. These rates indicate how often and how much prey are used by wolves. Consumption rates may be accurate indicators of prey use by wolves because rates include: 1) weight of wolves; 2) consumable portions of carcass. Most researchers estimate that the consumable biomass of moose is 75 % its live weight (Peterson 1977, Carbyn 1983, Messier and Crête 1985, Ballard et al. 1987, Sumanik 1987, Hayes et al. 1991, Thurber and Peterson 1993, Dale et al. 1995);
3) actual percent of carcass consumed. Pimlott et al. (1969), Mech (1977a) and Carbyn (1983) found carcasses of wolf kills abandoned during deep snow years. Similarly,

Potvin (1987) found that rate of deer carcass use by wolves was higher when deer were scarce or during mid-winter because hunting was difficult for wolves. Rates of use were lower (*i.e.*, <80 %) in March and April because deer in poorer physical condition were easier prey; 4) portion of carcass lost to scavengers, particularly ravens. Promberger (1992) found that large groups of juvenile ravens removed up to 37 kg of food/day from fresh ungulate carcasses. Furthermore, he felt that these flocks of juvenile ravens were likely more important competitors with small than large wolf packs because fewer wolves consume kills more slowly than larger packs.

If we assume consumption rates are accurate indicators of food use by wolves, rates can be compared to minimums necessary for survival and reproduction. Mech (1977b) determined that 0.06 kg/kg wolf/day is the minimum consumption rate required for wolves to maintain their body weight in winter. He also determined that 0.13 kg/kg wolf/day is the minimum rate required for all individuals to survive and rear pups successfully. Hence, consumption rates, describing food use, can be used to indicate if food is limiting the population growth or density of wolf populations.

One final piece of evidence can be used to assess population limitation by ungulate biomass or human-caused mortality. Mortality of adult wolves is important. In areas where ungulate biomass is low, researchers have noted that starvation and intraspecific aggression are more common. For instance, in southwestern Quebec, Messier (1985a) noted that wolves with fewer prey incurred more deaths from natural causes, namely starvation and intraspecific aggression. Similarly, Mech (1977a) noted that starvation and intraspecific aggression increased as prey availability declined in Minnesota. However, Mech (1977a) noted that only pups seemed to starve.

Based on mortality it is difficult to quantify population limitation by food because results vary among studies. On Isle Royale, annual mortality from starvation and intraspecific strife (both related to low food availability) ranged from 18 – 57 % during a 20-year period (Peterson and Page 1988). In populations where some human-caused mortality occurs, and thus compensates for natural mortality (starvation, accidents, disease and intraspecific strife), about 8 % of individuals greater than 6 months of age can be lost each year (Ballard et al. 1987, Fuller 1989). Some researchers have accepted this variability and decided that any sign of starvation among adult wolves means that food is limiting population growth (Fritts and Mech 1981, Ballard et al. 1997, P. Paquet, pers. comm.). This assumption is reasonable given that adults typically are the last members of the population that are affected by food shortage (Eberhardt 1977) and as such, may be the most sensitive indicators of food shortage.

Wolves dying from malnutrition or intraspecific strife may be signs that food is limiting population growth; however, the effects of food shortage may not show themselves directly. That is, if wolves were not getting enough food, they may not perish from starvation but might become weakened and more subject to diseases, parasites and other stress factors. Collectively then, in context with other predictions that support food limitation, a high incidence of deaths from natural mortality (malnutrition, intraspecific strife, disease) could strengthen an argument for food limitation.

Mortality of adult wolves can also be used to assess population limitation by human-caused mortality. These causes include legal harvest (Fuller and Keith 1980, Keith 1983, Gasaway et al. 1983, Messier 1985a, Ballard et al. 1987, 1997, Peterson et al. 1984, Potvin 1987, Bjorge and Gunson 1989, Fuller 1989, Hayes et al. 1991, Pletscher et al. 1997), illegal harvest (Fritts and Mech 1981, Fuller 1989, Pletscher et al. 1997), vehicles on highways (Berg and Kuehn 1982, Potvin 1987, Fuller 1989, Paquet 1993, Parks Canada 1994, Forbes and Theberge 1995, Paquet and Hackman 1995, Thiel and Valen 1995, Bangs and Fritts 1996,) and trains on railroads (Paquet 1993, Parks Canada 1994, Paquet and Hackman 1995, Paquet et al. 1996).

Quantifying population limitation by human-caused mortality is difficult. Various researchers have suggested different annual mortality rates that they feel control growth of wolf populations. However, the annual rate of mortality that causes a population decline in wolves is unknown. Furthermore, many researchers consider only harvest (hunting or trapping) when they calculate mortality rates that cause wolf population declines. Mech (1970) concluded that an annual harvest of 50 % or more was necessary to control wolf populations based on pup-adult ratios but did not distinguish between harvest and natural mortality. Keith (1983) reviewed studies of 13 exploited populations and determined that harvests exceeding 30 % of fall populations resulted in population declines. Fuller (1989) found that annual rates of wolf increase vary in direct response to rates of mortality and where wolves are killed by humans, harvests exceeding 28 % of autumn or early winter populations might result in a population decline. He concluded that the population would stabilize with an overall annual mortality rate of 0.35 or a human-caused mortality rate of 0.28. Hence, the exact relationship between the annual rate of mortality from all human causes (harvest, collisions with cars and trains) and population limitation or decline in wolves is uncertain.

Another piece in the puzzle is that growth rates of wolf populations are affected by the amount of food available and age structure of the population (Keith 1983). For example, several studies (VanBallenberghe 1981, Gasaway et al. 1983, Keith 1983, Peterson et al. 1984, Ballard et al. 1987, Fuller 1989) have found that wolf populations can be limited by harvest levels of 20 - 40%, but that the lower rate has a more significant effect in an area with low ungulate biomass (Gasaway et al.1983). Peterson et al. (1984) and Fuller (1989) found evidence that harvest effects vary with time and population structure. For instance, if productivity was high, and consequently the ratio of pups to adults was high, the population could withstand a higher overall mortality because pups (non-producers) make up a disproportionate amount of the harvest (Fuller 1989). Furthermore, net immigration or emigration may mitigate the effects of harvest (Fuller 1989).

I did not calculate annual rates of wolf mortality in this study because few wolves were radio-collared. However, I can infer that high mortality from human causes would at least limit the population of wolves. If the index of ungulate biomass per wolf was high, limitation from human-caused mortality would be suspect.

The thesis addresses three objectives:

1) To quantitatively assess the trend in wolf numbers (*i.e.*, declining, stable, increasing) in the study area,
2) To determine if ungulate biomass or human-caused mortality was primary in limiting the population growth of wolves in the study area, 1994 – 1998 and
3) To predict the long-term viability of these wolves.

To meet the first objective, I review and discuss data on densities and population dynamics of wolves.

To meet the second objective, I used an objective hypothesis-testing framework. I hypothesized that:

H1: Wolves in the study area were primarily limited by ungulate biomass.

H2: Wolves in the study area were primarily limited by human-caused mortality (examples: hunting, trapping and mortality by vehicles and trains).

If wolves were primarily limited by ungulate biomass, the following predictions should be true:

1) The average index of ungulate biomass per wolf will be low. Specifically, if food is limiting and ungulates are not heavily harvested, the average index of ungulate biomass per wolf should be below 225. This is the highest index of ungulate biomass per wolf from a review by Messier (1994) of various moose-wolf ecosystems across North America where moose were the dominant prey (Figure 1-1, Table 1-1). Assuming that these wolf populations are limited by food (*i.e.*, moose), the strength of this prediction lies in where the index of biomass falls in relation to the rest of North American studies. If the index is below 225, I will assume that wolves are primarily limited by food.

2) Consumption rates per wolf will be low. Specifically, consumption rates will be below 0.13 kg/kg wolf/day, which is the minimum consumption rate required for individuals to survive and rear pups successfully (Mech 1977b).

3) Occurrence of natural mortality will be high. Specifically, natural mortality will be an important cause of death in the study area.

If I am able to reject the food limitation hypothesis, human-caused mortality remains as a reasonable cause for population limitation. If human-caused mortality was the primary factor limiting wolf population growth (*i.e.*, it is not possible to evoke alternative causes for limitation) the following predictions should hold:

1) The average index of ungulate biomass per wolf will be high. Specifically, if human-caused mortality is limiting the population, and assuming ungulates are not heavily harvested, average index of ungulate biomass per wolf will be above 225.

2) Occurrence of human-caused mortality will be high. Specifically, if humans are limiting this population, activities such as hunting and trapping, along with mortality on roads and rail lines, will be an important cause of death in the study area.

To meet the third objective, I review and discuss data on population dynamics, predator-prey relationships and associated resiliency profiles of wolves.

Chapter 2. Study Area

My study area comprised 4500 km^2 in the western half of the GPE (Figure 2-1). The study area was delineated by wolf locations from 1994 - 1998. The GPE comprises an area of 10,000 km^2 that includes PNP and surrounding areas (Figure 2-1).

Two distinct physiographic regions, coastal and interior, occur within the study area. The coastal region is characterized by rugged topography with elevations varying from 189 m to 650 m at sea level. Many lakes and rivers occur in the area, reflecting a natural patchy environment. The interior region is a flat plateau characterized by a heavily eroded mountain landscape scoured by continental glaciers (Poitevin et al. 1989). Average elevation inland is higher than on the coast.

Mean annual precipitation is 737 mm along the coast and 644 mm inland. Winter and summer temperatures range from –13 °C - 14.6 °C for the coastal area and –17 °C - 15.9 °C inland (Poitevin et al. 1989). Ice cover on Lake Superior ranges annually from 5 - 100 % (Skibicki 1994).

Two biophysical land classification units occur within the study area; Central Boreal Uplands and Great Lakes St. Lawrence Lowlands (Gimbarzevsky et al. 1978). The Central Boreal Uplands predominate, whereas the Great Lakes St. Lawrence Lowlands occur at the southeastern corner of the study area.

Vegetation on the coast of Lake Superior and inland is mixed with associations of balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), eastern white cedar (*Thuja occidentalis*) and trembling aspen (*Populus tremuloides*), with occasional red maple (*Acer rubrum*) and other hardwoods more locally abundant in the southeastern corner of the study area. Both terrestrial and arboreal lichens occur in the study area. Terrestrial lichens include reindeer lichens, *Cladonia mitis*, *C. rangiferina* and *C. alpestris*. Arboreal lichens include *Usnea cavernosa*, *U. comosa*, *U. dasypoga*, *Alectoria jubata*, *A. nidulifera* and *Evernia mesomorpha*.

Predatory mammals include the gray wolf, black bear (*Ursus americanus*), red fox (*Vulpes vulpes*), lynx (*Lynx canadensis*), river otter (*Lontra canadensis*), fisher (*Martes pennanti*), American marten (*Martes americana*), mink (*Mustela vison*) and weasel (*Mustela* spp.). Coyotes (*Canis latrans*) are rare.

Potential prey species for wolves include moose, woodland caribou, snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), mink (*Mustela vison*), southern red-backed vole (*Clethrionomys gapperi*), meadow vole (*Microtus pennsylvanicus*), deer mouse (*Peromyscus maniculatus*), southern bog lemming (*Synaptomys cooperi*) and red squirrel (*Tamiasciurus hudsonicus*). White-tailed deer (*Odocoileus virginianus*) are rare.

Pukaskwa National Park is a 1878 km^2 wilderness (Figure 2-1). Within the study area and GPE, timber harvest, mines, towns and associated infrastructure occur outside PNP (Figure 2-2). Large stands of merchantable hardwood and coniferous forests surround PNP. Companies that operate under sustainable forestry licenses manage all forests. The White River Forest (Figure 2-2) is managed by Domtar Forest Products. The company and mill are located in the town of White River (Figure 2-2). The Black and Pic River Forests (Figure 2-2) are managed by Fort James-Marathon Company, Inc., located in the town of Marathon (Figure 2-2). The Wawa Forest is divided into two sections (Figure 2-2), the first of which is managed by Clergue Forest Products, Inc.

whose company and mill are located in the town of Wawa. The second section of the Wawa forest is Algoma Central Railway property.

Extensive road building has occurred throughout the study area and GPE to assist logging. Roads in the White River Forest are particularly extensive (Figure 2-2). Although most roads are passable by two-wheel drive vehicles, much of the traffic consists of pickup and logging trucks.

In addition to merchantable timber, abundant gold and mineral deposits are also found in the study area and GPE. One of the largest gold mines in North America, the Hemlo Gold Field (Figure 2-2), is located north of PNP. Two smaller gold mines, Eagle River and Magnacon Mines, are located east of PNP (Figure 2-2). Most mining activity occurs underground, with exploration roads above.

In addition to extensive timber and mining operations, five human settlements are within the area: Marathon (5,500 inhabitants), White River (2,000), Heron Bay (150), Pic River First Nation (400) and Mobert First Nation (300) (Figure 2-2). All towns and native reservations have local dumps that are on-site repositories for waste. Most are not fenced. The Marathon town dump is fenced on three sides (Krizan 1997).

Summary of Prey

Moose

Moose are a recent component of the mammalian predator-prey system along the north shore of Lake Superior. Before 1900, wolves and woodland caribou constituted the predator-prey system for large mammals (Clarke 1938, Snyder 1938, Snyder et al. 1942, DeVos and Peterson 1951). This composition changed when moose began to colonize the coastal boreal forest of Lake Superior at the end of the 1800's as a result of forestry operations and natural range expansion (Peterson 1955, Bergerud 1974). Today, moose densities in the study area and GPE are low to moderate and vary from 0.104 to 0.280 moose/km^2 (Table 2-1, Figure 2-3).

Woodland Caribou

Woodland caribou are native to the study area and GPE. Historically, they occupied much of the north shore of Lake Superior (Clarke 1938, Snyder et. al 1942, DeVos and Peterson 1951). Since the 1900's, numbers and distribution of caribou have declined steadily (DeVos and Peterson 1951; Cringan 1956) due at least in part to hunting, poaching, fire, habitat fragmentation, logging, increased predation (because of increasing moose and deer numbers), disease and human disturbance (Klein 1968, Anderson 1971, 1972, Bergerud 1974, Bergerud et al. 1984). Caribou are currently found in small bands along the coast. Putatively they avoid high densities of moose and wolves inland and take advantage of low snow depths (Bergerud 1985).

Caribou numbers have been monitored along the coast of PNP since 1972. Minimum counts are made using aerial line-transect techniques (Burnham et al. 1980). Counts include animals seen by observers and estimates of additional animals from tracks and other physical sign. From 1972 - 1988, the number of caribou in PNP ranged from 15 - 31 (Bergerud 1989). From 1993 - 1997, numbers ranged from 6 - 14 (Wade 1993a, 1995, 1997, 1999a).

Caribou numbers have not been systematically monitored throughout the rest of the GPE. Occasional sightings suggest that caribou are not restricted to the coast.

Nevertheless, the highest concentrations of caribou in the GPE are still believed to be coastal (Figure 2-4).

Beaver

Current estimates of the number of beaver in the study area and GPE are unavailable. Densities in PNP are likely decreasing because the forest is mature with coniferous species replacing more palatable deciduous species. Conversely, beaver are likely more common and widespread outside PNP because activities of industry maintain forests in early successional stages. Perhaps the best indicator of beaver availability is the healthy beaver trapping industry that exists outside PNP on the north shore of Lake Superior.

Chapter 3. Methods

Wolf population density, size and spatial distribution of packs, patterns of predation and other aspects of wolf ecology were determined from radio-collared animals. Fieldwork centered on year-round efforts to radio-collar and subsequently locate wolves in as many packs as possible. Approximately 85 % of the study population were monitored at the height of the study (1997 - 1998).

Capture and Handling

All capture and handling operations (1994 - 1997) were approved by an Ontario Ministry of Natural Resources Wildlife Animal Care Committee. Permits were renewed on an annual basis. Permit numbers were 1995 – 13, 1996 – 13, 1997 – 13, 1998 – 13. Wolves were captured in summer using leg-hold traps (*n* = 21) and in early winter using a net-gun from a helicopter (*n* = 5).

Trapping was limited to the period May through October because feet of trapped wolves commonly freeze in winter. Net-gunning occurred during periods of complete snow cover in winter when wolves were more commonly observed in packs.

Other P5 researchers and I captured wolves using Newhouse® or McBride® Number 14 OS traps (Woodstream® Corp.) in blind sets with lures. To reduce injuries, traps were modified with 1.8 mm offset jaws, rubber jaws, drag chain springs and a swivel attachment of the drag chains. To limit the capture of non-target species, traps were outfitted with spring tension pans (M-Y Enterprises), which prevents traps from being sprung unless the direct weight is >9 kg. Traps were set along roads and game trails in areas closed to public access or with appropriate signs. Traps were visually checked once, and when possible, twice daily.

In addition to trapping wolves, the Helicopter Wildlife Management team (575 E. 4500 S., Salt Lake City, UT 84107) and P5 researchers captured wolves using a net-gun from a helicopter. A Hughes 500 helicopter and hand-held 30-06 rifle firing blanks with cup-mounted nets were used for captures. A spotting plane was used for reconnaissance.

Wolves captured in traps or by using net-guns from helicopters were immobilized with Telazol® [tiletamine hydrochloride (HCL) and zolazepam HCL, A.H. Robins Co., Richmond, VA] administered by intramuscular injection with a jabstick. Wolf rectal temperature, pulse and respiration were closely monitored throughout the procedure. Immobilized wolves were examined for injuries, equipped with conventional VHF (Lotec®, Aurora, ON) transmitters, weighed, sexed and aged. Wolves were classified as pups (<12 months old starting Apr 1), yearlings (12 - 24 months old) or adults (>24 months old). Pups were classified by tooth eruption patterns and body size (Van Ballenberghe and Mech 1975). Yearlings were classified based on assumed age ($n = 1$) from their tooth wear, reproductive status and pack history (Fuller 1989).

Radio-collared wolves were released and monitored closely for 1 week to confirm they had not been adversely affected by capture and radio-collaring. Behaviours monitored included movement and re-association with other wolves post-capture.

Biotelemetry

The target frequency for locating each radio-collared wolf was four times/month in summer (Apr - Sept) and six to eight times/month in winter (Nov - Mar) (Burrows et al. 1996). Wolves were located by plane using a portable receiver (Lotek® SRX-400, 150.00 - 154.00Mhz), right-left switch boxes and paired 3-element Yagi antennae mounted on the wing struts of a fixed-wing aircraft (Cessna 185). A Global Positioning System (Garmin® 55 Aviation) unit was used to estimate wolf positions (White and Garrott 1990, Nams and Boutin 1991). Locations were recorded in Latitude, Longitude (deg/min/sec) and later converted to Universal Transverse Mercator (UTM, 1927 datum) using Geocalculator® software. For all locations, the transmitter frequency, observer, date, time of location, number of wolves, color of wolves and presence of pups were recorded. Additional information on topography, vegetation overstory, crown closure and proximity to cut-overs was recorded (Burrows et al. 1996) (Appendix A). Mean error of telemetry (difference between observed and true location) was calculated by using data we collected when regularly locating stationary transmitters placed throughout the study area (Burrows et al. 1996). Location data were downloaded into a Geographical Information System (GIS[Tydac SPANS®]) for display and analysis of wolf movements.

Ground-locations supplemented aerial locations throughout the winters of 1994 - 1995 and 1997 - 1998 (Nov - Apr). Portable receivers (150.000 - 153.000Mhz), a roof-mounted omni-directional antenna or a hand-held 3-element Yagi antenna (Lotek®) were used for ground telemetry. Locations were determined by triangulation or, when possible, by direct observation. Mean bearing error of ground locations was determined by regularly locating stationary transmitters placed throughout the study area. Data recorded from ground locations were the same as for the aerial locations.

Home Ranges

Ranges V® software (Kenward and Hodder 1996) was used to calculate year-long (Apr 1 - Mar 31) home range sizes from all pack relocations using 95 % minimum convex polygons (MCP) (Mohr 1947). All obvious extraterritorial forays and dispersals were excluded from the analyses (Ballard et al. 1997). These forays and dispersals were not included because they are not part of the normal area of activities and should not be considered part of the home range (Burt 1943). Some of these movements are easily identified but less obvious dispersals and forays are more difficult to define. This justifies the use of the 95% MCP, which gives an objective, repeatable method for purposes of comparisons among studies (White and Garrott 1990).

For each pack I used one wolf/year to represent the annual home range of the pack. This is reasonable because radiolocations from one wolf can be considered indicative of the whole pack (Kolenosky and Johnston 1967, Fuller and Keith 1980, Fritts and Mech 1981, Ciucci et al. 1997) provided that a high level of association exists between pack members. In the present study, this condition was confirmed by aerial observations of packs during telemetry flights.

Telemetry locations were classified according to accuracy into four categories. Class one, two, three and four locations were those within 100 m, 100 - 250 m, 250 m - 450 m and greater than 450 m from the true location, respectively. Only class one aerial and ground locations were used in the home range analysis.

Accuracy of aerial and ground locations for the entire study was 150 m, which was the highest mean error of telemetry obtained by any P5 researcher. To account for the 150-m error, I changed the 'fix resolution' from the RangesV® software default of 1 m to 150 m. This resolution is used to set the width of the boundary strip that is included in polygon edges and areas (Kenward and Hodder 1996, R. Kenward, pers. comm.). I left the scaling parameter at the software default of 1 m, which means that each coordinate unit is 1 m from the next.

Home ranges were assumed to be defined when the observation-area curve formed an asymptote (Kenward and Hodder 1996). By using this definition, I addressed the main disadvantage of using the MCP method, specifically that size of the home range estimate increases indefinitely as the number of locations increases (Jennrich and Turner 1969).

I calculated annual (Apr 1 - Mar 31) home range sizes for packs and individuals between 1994 - 1998. I partitioned these results into packs using or not using refuse from dumps found in towns or on reservations. Next, I calculated the sizes of annual home range areas per wolf per pack between 1994 - 1998. I partitioned these results into wolf packs using or not using refuse from dumps.

Density, Pack Sizes and Population Growth

Density of wolves/1000 km^2 was calculated by determining intra-pack densities (home range size/number of wolves in pack) of radio-collared wolves and averaging these densities per year to determine a study area density (Potvin 1987, Bjorge and Gunson 1989, Okarma et al.1998). The sizes of annual home ranges were calculated and the number of wolves in a pack was based on a mid-winter estimate (maximum number, Jan 15 - Feb 15). In two cases where the annual home range could not be properly defined owing to insufficient data, I used the boundary of the previous or subsequent year

(Messier 1985a). The time period of these estimates is comparable to that of Fuller (1989) who calculated annual wolf density in early (Nov - Dec) and late (Mar) winter and averaged these results to get an annual winter wolf density (wolves/1000km^2). I did not add 10 % wolves to account for lone or single wolves (Stephenson 1978; Ballard et al. 1987, 1997; Fuller and Snow 1988) because I used average intra-pack density as an estimate of population density.

Estimates of density based on intra-pack densities could be considered biased in two ways: 1) estimates could be lower than actual because lone wolves were not included. This might be important because studies of exploited populations report large numbers of lone wolves and pairs of wolves (Peterson et al .1984, Hayes et al. 1991, Ballard et al. 1987, Gasaway et al. 1992); 2) estimates based on intra-pack densities may be higher than those based on the census area approach (Messier 1985a, Ballard et al. 1987, 1997, Fuller and Snow 1988, Fuller 1989), which often includes interstices between pack home ranges. Peterson et al. (1984) found that estimates from the intra-pack density method were on average 1.27 times higher (SE = 0.10) than estimates from the census area approach, though results were correlated ($r^2 = 0.61$). Despite these potential biases, densities of wolves in this study were similar to estimates made by another P5 researcher who used the census area approach based on radio-collared and non-radio-collared wolves (G. Neale, pers. comm.).

Pack sizes were determined by recording numbers of wolves observed during aerial locations and by ground-track counts when possible. A pack was defined as a group of two or more wolves that traveled together for more than 1 month (Messier 1984). Pack size was determined for three time intervals: late fall (maximum number of wolves recorded in Nov - Dec), early winter (maximum number of wolves observed between Jan 15 - Feb 15) and late winter (maximum number of wolves observed in Mar). Fall counts were used to determine presence of pups and to provide a maximum estimate of the number of adult-size wolves present each year; whereas, winter estimates provided a minimum estimate of the population size.

Population growth was estimated using finite rates of increase (λ) determined from the ratio of successive yearly density estimates. Mean annual finite rate of increase was calculated by taking the antilogarithm of the mean exponential rate of increase ($r = \ln \lambda$) for the population (Fuller 1989). Measures of population growth will be biased because intra-pack density estimates only account for an increase in the number of wolves per pack and not an increase in the number of packs. However, pack sizes are small in the study area. Accordingly, changes in pack size may be the most important element in recognizing if the population is increasing. Hayes and Harestad (1999a) reported that increase in a post-control wolf population was achieved in three stages: 1) immigration of pairs and in-shifting of whole packs from outside the control area to rapidly fill vacant territorial space; 2) packs growing quickly to a size (8 - 10 wolves) similar to that in other wolf populations that rely heavily on moose for food, and some packs growing large and splitting into two adjacent packs; and 3) the population appeared to reach a stable state (annual finite rates of increase approached 1.00). During this study, the study area had established territorial packs. The likelihood of other packs moving in and displacing active packs is low (P. Paquet, pers. comm.). Thus, population increase would most likely occur within individual packs.

Dispersal

I assumed that a wolf dispersed if it permanently left its original pack and formed a new pack or joined an existing one (Messier 1985b). Dispersal dates were the median date between the date of last known occurrence within the original territory to when the dispersing wolf was known to be absent from that territory or was located in another territory (Ballard et al. 1997). Dispersal dates are estimates because in some cases a few months elapsed before the wolf was relocated. Hence, a reported median dispersal date may have a large degree of error. The number of wolves that dispersed is reported as percent of the radio-collared population.

Reproduction

We did not observe wolves at dens during this study. Dense vegetation and the secretive nature of wolves precluded accurate visuals of wolves in groups during the summer months. Visual observations of wolves were not obtained until October or November, at which time wolf pups are hard to distinguish physically from adults. Hence, successful year-specific reproduction was ascertained when: 1) pups were captured in spring; or 2) a pack increased in size from March to the following December, providing that sites of focal activities (*e.g.*, pup-resting areas) were observed in the intervening time (Messier 1985a). These dens and rendezvous sites were ascertained when movements became localized in April through July or when lactating females or their pups were captured during spring wolf trapping efforts. Potential denning and rendez-vous areas were checked in early fall to confirm these sites. Unsuccessful reproduction (*i.e.*, no or failed reproduction) was ascertained when: 1) a pack did not demonstrate focal activity sites in the summer; or 2) a pair remained together from March to the following December. There was one instance for which assertion of reproduction was uncertain. Results are reported for each pack by year.

Indices of Moose Biomass Available to Wolves

I assumed that moose were the main prey for wolves in the study area since caribou numbers are so low (Wade 1993a, 1995, 1997, 1999a, Figure 2-4). I followed Fuller's method (1989), which included information on moose density (moose/1000km^2), a moose index (6 after Keith 1983, Fuller 1989) and wolf density (wolves/1000km^2). By multiplying moose density by moose index (6) and dividing by wolf density, an index of ungulate biomass per wolf was calculated.

For the study area, I determined an index of moose biomass available per wolf in each pack per year. First, I calculated a single moose density per management unit across years (1995 - 1999). Assuming that there was little or no change in moose density between yearly estimates, I averaged results from two (21A, 21B, 33) or three years (PNP) between 1994 and 1999 (Table 3-1).

Next I weighted survey estimates according to percent of home range in each management area. I then calculated the indices of moose biomass available per wolf Fuller (1989) per pack. For example, in 1995 - 1996, 53 % of the home range of the White River Pack was in WMU 21B and 47 % was in WMU 33. The index of moose biomass [(number of moose/1000km^2) • 6] was [0.53• (1620) + 0.47 • (1152)]. The index of moose biomass available per wolf was [(1461.0/1000 km^2)/(5.8 wolves/1000km^2)]. In 1997 - 1998, 100 % of the home range of the Swallow Pack was in PNP so the index of moose biomass was [1.0 • (1152)]. The index of moose biomass available per wolf was [(1152.0/1000 km^2)/(10.0 wolves/1000km^2)]. I arranged these indices by packs within years, then averaged within and across years (1995 - 1996, 1996 - 1997, 1997 - 1998) to determine a yearly and overall mean index of moose biomass available per wolf in the study area. Furthermore, I averaged indices from each pack across years to examine differences in moose biomass available for each pack.

Prey Use

As noted, I assumed that moose were the main prey species for wolves. However, I also documented other species that were consumed. Information from scat collection, carcass collection and kill and consumption rates were used to characterize predator-prey relationships in the study area.

1) Scat collection

Wolf scats were collected by three P5 researchers. P. Krizan and G. Neale collected wolf scats from packs living inland ($n = 232$), 1994 - 1997. G. Neale collected scats along the coast ($n = 44$), February 1993 – May 1997. I collected scats from inland ($n = 20$) and coastal wolves ($n = 9$), November 1997 – March 1998.

P. Krizan and I used the same protocol for collecting scats inland in that scats were collected opportunistically throughout the study area. Only one scat was collected at each wolf kill site to avoid bias in scat collection. Each scat was labeled with an identification number, date, UTM coordinates, species and general location. Our protocol differed in that I sent frozen, labeled scats to the Big Sky Laboratory (PO Box 0776, Florence, MT 59833-0776). Prey remains were identified by macroscopic examination and comparison with known material and hair-scale impressions (Adorjan and Kolenosky 1969). Each scat was autoclaved, washed and then sorted to identify contents. Hair, teeth, claws and hooves were identified to species. Results were recorded in tally form using the following categories: adult moose, calf moose, adult caribou, adult deer, beaver, snowshoe hare, black bear, coyote, mink, meadow vole. Four scats contained garbage and two contained goose feathers but were not included in the summary. Results represent percent of total scats that contained each type of food. In contrast, P. Krizan analyzed the contents of scats he and G. Neale collected (Krizan 1997). Krizan summarized the data using pie charts (Krizan 1997) representing percentages of prey items found in scats.

The sampling protocol was different for scats collected along the coast by G. Neale and I. Most scats were collected while we hiked the coastal trail. Thus, we collected all scat found, regardless of age or location. We both labeled all scats with an identification number, date, UTM coordinates, species and general location. Furthermore, frozen, labeled scats were sent to the Big Sky Laboratory for analysis of contents. Results represent percent of total scats that contained each type of food.

2) Carcass collection

Moose carcasses were sampled from March 1995 - October 1998 (Appendix B). These included carcasses of radio-collared and non-radio-collared moose. Causes of death included predation by wolves, natural causes, trains, vehicles on highways and hunters. Sex and age were recorded and femur marrow collected when possible (see next section for more detail on observations made, samples collected and analysis of samples). Sex and age-class distribution data were summarized and the percent of fat in the marrow was calculated as per Neiland (1970). I used the non-parametric Mann-Whitney test to determine if the percent fat of moose killed by wolves was the same as percent fat of moose that died from other causes. Only one caribou carcass was found and no marrow samples were obtained. The caribou was age 14 when it died from natural causes. No white-tailed deer carcasses were found.

3) Rates of kill and consumption of prey by wolves

The rates of killing and consumption of large prey by wolves were studied by aerial and ground observation during a 6-week period, February - March 1998. Two packs, Bremner River and Rein Lake, were also followed between January and March 1998. The Bremner River Pack was located 57 times between January 18,1998 and March 27, 1998 (69 days) and the Rein Lake Pack was located 57 times between January 8, 1998 and March 26, 1998 (79 days). Other packs located were the White River Pack, 22 times between February 11, 1998 and March 20, 1998 (38 days) and the Swallow River Pack, 22 times between February 9, 1998 and March 22, 1998 (42 days). The Park pack (called the Swallow River Pack) was only located by aircraft with some limited ground observations to confirm whether they had made kills in certain areas. Other packs were followed by aircraft and via ground-based telemetry. Scats were collected regularly from one pack (Bremner River); these samples were used to supplement data on kill and consumption rates for this pack.

The number of wolves present at the kill was determined by visual observations from the air or by counting track numbers on the ground. Feeding sites that were located from the air and from ground-based tracking were visited and examined in detail when wolves had moved from the kill (usually after 1 week). At these sites, carcasses were examined to determine species of the carcass and other characteristics such as sex, physical condition and time and cause of death (Appendix B). Sex was determined by the presence of antler pedicels or vulva patch. Physical condition was determined by recording any debilitating abnormalities and by calculating percent fat from marrow of mandibles or long bones (Neiland 1970, Sergeant and Pimlott 1959).

The time and cause of a moose death were determined at the kill site. Causes of death included wolf-killed, hunter-killed, starvation or unknown. Evidence that wolves killed an animal included an obvious chase sequence in the snow or evidence of a struggle, including damaged vegetation, extensive blood on snow or canine slash marks on the animal (Haber 1977). Natural deaths were classified by absence of struggling (typically with signs such as carcass on sternum with folded legs, rumen frozen whole in body, low bone marrow fat) (Messier 1984). Scavenged animals included train and road-kills that showed clear evidence of impact, animals that fell through the ice and drowned, road-killed animals set out as bait to catch wolves and animals killed by other predators.

The rate of killing of large prey by wolves was calculated from the number of animals killed per tracking period (Messier 1985a). In this analysis I considered only tracking sessions in which pack locations were not separated by more than 54 hours. In a few instances, locations were separated by 72 hours. The wolves, however, made a kill or visited a dump the day they were relocated. These periods were retained in the analysis because it is unlikely these wolves made another kill. To confirm this, wolves were tracked on the ground. Additionally, previous P5 research has indicated that these small packs of wolves stay at food locations, on average, for 4.6 days (Krizan 1997). Similarly, Messier and Crête (1985) found that in winter, when small packs of wolves used a moose carcass from a predation or natural mortality event, they stayed in the vicinity (often sleeping beside it) up to 3 weeks. Messier and Crête (1985) felt that wolves in their study area could use carcasses for long times because pack sizes were small. Despite these two findings, kill rates in the present study should be considered minimums as wolves were not relocated every day and some small prey such as deer (fawns and adults), caribou calves, beaver and other smaller prey items may have been missed. Kill rates are reported as ungulates killed/wolf/100 days. By determining kill rates, I was then able to calculate consumption rate of prey by wolves.

Consumption rates were calculated based on kill rates and average weights of wolves and prey. Whole wolf weights were calculated from the average of radio-collared wolves and other wolves found dead in the study area. I excluded pups from this calculation and used only weights of adult wolves. No weights of yearlings were recorded.

The average edible weights of moose and beaver prey were assumed to be 330, 261, 114 and 13 kg for adult male moose, adult female moose, young-of-the-year moose and beaver, respectively (Peterson 1977, Thurber and Peterson 1993). These consumable prey weights are estimated at 90 % of whole weight for all prey except adult moose (75 % as in Fuller and Keith (1980) and Peterson et al. (1984). The edible weight does not include bones (without marrow), rumen contents or hide (Peterson 1977).

I assumed the average weight of white-tailed deer was 40 kg for fawns, 70 and 65 kg for yearling males and females, respectively, and 105 and 69 kg for adult males and females, respectively (Kolenosky 1972, Forbes and Theberge 1996). Ninety percent of fawn and 80 % of adult and subadult deer carcasses were considered edible (Pimlott 1967, Forbes and Theberge 1996).

Two consumption rates were calculated for the Bremner River Pack, one using scat-content results and the other without. Two consumption rates were calculated for the Swallow pack, one using a suspected additional ungulate kill and the other without. The additional kill may have been made during a 5-day period when no locations were made owing to inclement weather. All consumption rates are reported as kg prey/wolf/day and kg prey/kg wolf/day.

Mortality and Survival of Radio-Collared Wolves

The starting date of the survival study was August 20, 1994 (date when first wolf was captured) and the end date was December 31, 1998. Relocations of the wolves became less frequent and irregular after this date.

Wolves were re-located from time of capture until mortality or disappearance of the radio-signal occurred. For known deaths I estimated the date of mortality to the nearest day using field evidence. When evidence was unavailable, day of mortality was deemed the midpoint of the interval between the last day the wolf was known alive and the day that it was discovered dead. The cause of mortality was often identified on site and when possible, was confirmed by necropsies performed by Dr. Doug Campbell, Canadian Cooperative Wildlife Health Center, University of Guelph, ON.

I calculated the cumulative survival of radio-collared wolves ($n = 25$) using the Kaplan-Meier (K-M) product limit estimator and Minitab (Version 12) software. The cumulative survival was calculated for a 3-year period beginning August 20, 1994. One wolf was not included in the analysis ('Abbey') because he was shot by trappers while in the research trap.

Assumptions of the K-M model are: 1) sex and age classes are randomly sampled; 2) survival times are independent for the different animals; 3) time of death will be known to the nearest day (therefore, use of continuous-time survival distributions seems justified); 4) the censoring mechanism is random or non-informative (*i.e.*, not related to animal's fate and ultimate survival time); 5) newly tagged entries (left truncation) are assumed to have the same survival function (survival rates per unit time) as previously tagged animals; and 6) radio-collaring does not influence survival (Lagakos 1979, Pollack et al. 1989a, 1989b). My data likely fail the second assumption because of the strong social nature of wolves. For example, the death of a parent should reduce the survival rate of its pups and yearlings. Pollack et al. (1989a) stated that violation of this assumption will not cause bias but will produce smaller variances for survival probabilities than occur in nature.

Sample sizes were too small to use Cox's proportional hazards model and determine the influence of important covariates (such as age and sex) on survival. Furthermore, cause-specific mortality was not calculated; hence, mortality was described using percents. One major assumption I made is that the proximate cause of death determined was the ultimate cause of death. I am unable to assess the relative importance of other factors that may have been involved.

Mortality of Non-Radio-Collared Wolves

Data on wolves killed by trapping activities include anecdotal reports of number of wolves killed in the study area, winter 1994 - 1998. Data on wolves killed by vehicles include number of wolves killed on Highway 17 in the study area, October 1995 - August 1998. No prior information was available. I was unable to collect information on wolves killed on the railroad in the study area and no prior information was available.

Chapter 4. Results

Twenty-six wolves were captured and radio-collared ($n = 25$) or tagged ($n = 1$) between 1994 - 1997. Four wolves were captured twice, one wolf captured three times and another four times. Radio-collared wolves were not adversely affected by capture because wolves moved normally and re-associated with other wolves following capture. Two packs were followed in 1994 - 1995, four in 1995 - 1996, four in 1996 - 1997 and six in 1997 - 1998. The average weight of wolves ($n = 25$) was 32.3 kg (Table 4-1).

Home Ranges

Sizes of annual home ranges (Figures 4-1 - 4-4) of 13 packs were adequately described in this study (Table 4-2); *i.e.*, the observation-area curve was asymptotic and locations were obtained throughout the year (Table 4-2). The annual home ranges of 14 wolves were described (Appendix C).

For both packs and individuals, sizes of annual home ranges were not correlated with number of relocations ($r_s = 0.521$; $0.05 > p > 0.02$); hence, estimates accurately assessed areas used by wolves.

Home range sizes of packs and home range areas/wolf were variable. Results were separated for packs that frequented dumps and those that did not. Means and standard errors were calculated. There was no difference so data were pooled. The average annual home range size (based on 95 % MCP) was 388 ± 48 km^2 ($n = 13$, range, 101 - 644 km^2) (Table 4-2). The average home range area/wolf (based on 95 % MCP) was 139 ± 25 km^2/wolf (Table 4-2).

Most packs used the same areas annually (Figure 4-5). Three notable exceptions were: 1) the Rein Lake Pack, which expanded its home range in November 1996 (Figure 4-3) to include the dump in the Mobert First Nation townsite (Figure 2-2). In 1997, the pack shifted its entire home range east (Figure 4-4) to include the dump in the town of White River (Figure 2-2). As this pack changed configuration of its home range, another pack (Bremner River) occupied the abandoned areas (Figure 4-4), likely moving in from the north or east; 2) the Cascade Lake Pack (Figure 4-2), which disappeared in January. Of the two radio-collared wolves in this pack, one died as a result of inter-pack aggression and the other starved. When this pack disappeared, there was no further sign of wolves in the area. However, the Swallow River Pack included in its home range (Figure 4-4) some of the old home range of the Cascade Lake Pack; 3) the Black River Pack used the dumps at Marathon and Heron Bay (Figure 2-2) in 1994 - 1995 (Figure 4-1), but shifted to using only the Heron Bay dump, 1995 - 1998 (Figures 4-2, 4-4).

Areal expanse of home ranges increased by year for all four packs with wolves captured during more than 1 year (Table 4-3). In these packs, one wolf (Cassidy) expanded her home range to include a dump, a second wolf (Sam) dispersed in June 1995 and then again between May 1997 - January 1998 to an area outside the GPE, and a third wolf (Aldo) dispersed from the GPE in November 1995.

Density, Pack Sizes and Population Growth

Intra-pack density did not change over time. Reported densities were 7.9, 9.6 and 7.2 wolves/1000km^2 in 1995 - 1996 ($n = 4$ packs), 1996 - 1997 ($n = 4$ packs) and 1997 - 1998 ($n = 6$ packs), respectively. Furthermore, mean annual finite rate of increase between 1995 and 1998 was 0.96 (Table 4-4), which suggests this population was decreasing slightly.

Packs using dumps as food sources did not differ in size from packs that did not use dumps. Hence, data were pooled to determine average early winter pack size (Jan 15 - Feb 15), which was 3.5 ± 0.5 (n = 14 pack years) (Table 4-2). (Late fall, early and late winter pack sizes from 1994 - 1999 are reported in Appendices D and E)

The number of wolves in all packs remained stable or declined, 1994 - 1998, except the Neys and Swallow River Packs, whose numbers fluctuated annually (Table 4-5). The Neys Pack relied heavily on dumps for food (Krizan 1997). The Swallow River Pack (the pack in PNP) failed to reproduce while monitored.

Dispersal

Six of 26 (23 %) radio-collared wolves dispersed from the study area (Table 4-6). Four were males, two were females and all were between 1 and 4 years of age. One, ('Sam') joined a pack adjacent to his natal home range (Black River Pack). 'Sam' later made a second dispersal to Terrace Bay, 70 km from his natal home range. All six wolves dispersed to areas with higher moose densities. None dispersed into PNP.

Five of the six dispersing wolves died; three from human causes, one from disease and one from unknown causes. At the end of the study the fate of one wolf that dispersed was unknown. This wolf was last seen on February 15, 1997 with another wolf feeding at a dump in Manitouwadge, 70 km north of study area.

Reproduction

Between spring 1994 and spring 1998, wolves reproduced successfully in 8 of 22 pack-years (Table 4-7). Of the eight, four were wolves in packs that relied heavily on food from dumps and four were from packs that did not. Of the 13 instances where wolves failed to reproduce, five were wolves in packs that used dumps and eight were from packs that did not. The estimates of successful reproduction are maximum estimates. On two occasions, I assumed that wolves had reproduced because of large numbers of wolves in the packs during the following early fall and winter.

Indices of Moose Biomass Available to Wolves

The annual mean indices of moose biomass per wolf varied little between 1995 - 1998 (average 208 ± 33) (Table 4-8), but indices varied considerably among individual packs (Table 4-9). The Rein Lake and White River Packs had the highest indices, respectively; whereas, the Bremner River, Black River, Swallow River and Neys Packs had the lowest indices, respectively.

Prey Use

1) Scats

Results were variable for contents in wolf scats collected by different P5 researchers. Krizan (1997) found that beaver and moose comprised the largest portion of the diet of inland wolves (36.2 and 35.3 %, respectively). Evidence of caribou was found in only1 of 232 scats. In contrast, Neale (M.S. in progress) reported that beaver and caribou hair was most common and moose less common in scats collected along the coast. Thirty-four %, 41 % and 18 % of wolf scats contained evidence of caribou, beaver and moose, respectively. At least 10 species of vertebrates were represented in scats that I collected (Tables 4-10a,b). Adult moose and caribou were the food items most frequently found in scats (Table 4-10a) collected inland. Conversely, only evidence of moose was found in scats (Table 4-10b) collected along the coast. No evidence of caribou was found.

2) Carcasses

Seventy-eight moose carcasses were examined. Wolves killed thirty-one. Forty-seven were killed by hunters or vehicles or died of natural causes. Percent fat in marrow of moose killed by wolves and those that died from other causes were not significantly different ($U_{0.05(2)}$, 16, 11 = 117; $0.20 > p > 0.10$). I examined these same data using means and standard errors and found no difference between percent fat in marrow of moose killed by wolves and moose that died from other causes (moose killed by wolves; mean ±SE = 0.66 ± 0.07; moose dead from other causes; mean ± SE = 0.77 ± 0.06).

Moose killed by hunters, vehicles on roads or that died of natural causes tended to be younger than moose killed by wolves. Wolves killed 31 moose between 1995 - 1998 (9 males, 14 females, 8 unknown sex). Of these, exact ages of 30 were determined (Figure 4-6). Forty-seven moose (18 males, 19 females, 10 unknown sex) were killed by hunters, vehicles on roads or died of natural causes. Of these, exact ages of 35 were determined (Figure 4-7).

3) Rates of kill and consumption

Rates of kill and consumption were calculated for four packs (Table 4-11). The Swallow River and Bremner River Packs killed and consumed more ungulates than the other packs. The White River and Rein Lake Packs killed and consumed no ungulates. However, the White River Pack scavenged from moose that were killed by vehicles on the road or railroad, from snare sets and from other wolf kills. Similarly, the Rein Lake Pack scavenged from refuse in the town dump for White River (Figure 4-4). Unfortunately, I was not able to estimate the amount of biomass consumed via scavenging.

Mortality and Survival of Radio-Collared Wolves

As of December 31, 1998, 17 of 26 wolves radio-collared or tagged between 1994 - 1998 were dead, four were alive and five were missing (Table 4-12). Median survival time was 689 days or 1.9 years post-collaring.

Eight of 17 wolves died from human causes. Trains killed three, three were snared and two shot. Nine wolves died from natural causes. Two starved, two were killed by other wolves, four died from disease (three from mange and one from blastomycosis) and one died from unknown natural causes (Table 4-13).

Survival of radio-collared wolves decreased between 1 and 3 years post-collaring (Table 4-14). Wolves had a 32 % chance of dying in the first year, a 30 % chance of dying in the second year and a 57 % chance of dying in the third year. These data likely reflect survival in the study area, because they include seven of the eight known packs in the study area between 1994 - 1998 (Figure 4-8). The only pack that was not radio-collared appeared in March 1998 in the northeastern section of the park, an area previously unoccupied by wolves.

Mortality of Non-Radio-Collared Wolves

During winter 1994 - 1995, at least 10 wolves were snared and died at the Marathon town dump (R. Renner, local trapper, pers. comm.). In addition, trappers in White River reported killing 16 wolves in 2 months at the town dump during the winter of 1995 - 1996 (D. Morin, local trapper, pers. comm.). During a 3-year period, October 1995 - August 1998, at least seven wolves were killed in the study area by vehicles on Highway 17 between Neys Provincial Park and the town of White River (Appendix F).

Chapter 5. Discussion

Wolf Numbers: Increasing, Decreasing or Unchanging?

Studies of population dynamics seek to understand how rates of increase are determined, and thus how numbers are controlled over time (Keith 1983). Rates of increase are mediated through births, deaths, immigration and emigration and these four factors determine whether populations increase or decrease over time. Increases occur when birth and survival (and perhaps immigration) exceed death and emigration. Elucidation of these four demographic parameters is fundamental to any study of wolf population dynamics.

Analysis of wolf demography is simplified if we assume that immigration and emigration are negligible or counterbalanced. Then, analyzing wolf population trends, similar to analyzing other mammalian trends, can be based on three reductions in the population each year: 1) a decrease in natality; 2) mortality of juveniles (*e.g.*, under age 1); and 3) mortality of adults (Sinclair 1973).

Two of these factors may be responsible for the decline in wolf numbers in this study. There is no question that reproductive success (*i.e.*, natality) of this population was poor. The 36 % reproductive success is the lowest on record. In other studies, success has ranged between 45 and 93 % (Messier 1985a, Potvin 1987, Peterson et al. 1998). Adult survival was also low; *i.e.*, 17 of 26 wolves were dead from various natural and human causes from 1994 - 1998.

Unfortunately, I could not calculate annual survival rates and this makes it difficult to quantify whether the level of mortality in this study was sufficient to cause the population to decline. However, some predictions can be made based on the cumulative survival of wolves. Using the annual rate of mortality predicted for the first year (32 %) in this study as a hypothetical annual mortality rate and comparing it with annual rates of mortality from other studies, one can infer whether the rate of mortality was sufficient to cause a decline in wolf numbers.

There is no agreement among researchers on the annual rate of mortality that causes a population decline in wolves. However, Keith (1983) and Fuller (1989) reviewed several wolf studies across North America and concluded that harvests exceeding 28 - 30 % of fall populations resulted in population declines. Fuller (1989) further concluded that wolf populations would stabilize with an overall annual mortality rate of 35 %. He felt, however, that the effects of harvest could vary with time and population structure. Specifically, a population comprised of a high percentage of pups could withstand substantially higher mortality. Given this, it seems likely that a combination of low reproductive success and high rates of adult mortality caused the decline in wolf numbers in this study.

Population Limitation

Both ungulate biomass and human-caused mortality limit the rate of growth of the wolf population in the study area. Of the two, ungulate biomass may be the more important limiting factor.

The 'average index of ungulate biomass per wolf' was below 225. These data support the food limitation hypothesis for wolves in the study area. Though the population as a whole has a low average index of biomass available per wolf, some wolf packs do not. There are two possible explanations for this. First, the use of dumps by some packs resulted in indices that were variable according to pack. For example, the Neys Pack used dumps regularly for food from 1995 - 1998 (Table 4-9) and had low indices of biomass available per wolf; whereas the Rein Lake Pack had high indices in 1996 – 1997 and 1997 – 1998, when it frequented dumps (Table 4-9). This variability occurred because home range sizes differed according to pack. Size of the Neys Pack home range was small and the Rein Lake Pack normal when compared with other sizes of home ranges in this study (Table 4-2). Accordingly, number of moose available within each home range was variable.

The second explanation is moose may be distributed heterogeneously in the study area. Mech and Karns (1977) and Peterson (1977) found that in low and declining prey populations, prey distribution will be heterogeneous and subsequently, some packs of wolves will have more prey than other packs.

The above information suggests that the average index of biomass per wolf may be at best a coarse measure of food availability that can be used to assess the food limitation hypothesis. Unfortunately, there are other problems with using biomass indices. First, I was unable to accurately determine how much biomass each pack of wolves had available in home ranges. I relied instead on survey estimates of moose based on random stratified sampling techniques (Gasaway et al. 1986). These estimates are based on areas much larger than home ranges (Figure 2-3). Furthermore, they are imperfect measures of density of moose. Nonetheless, random stratified surveys are the current standard (Timmerman and Buss 1997) used to monitor and manage moose populations across North America. As such, survey data are the best available on densities of moose.

The second problem with using biomass indices is that estimates are based on winter densities of moose and wolves. Consequently, the influence of food available in summer is ignored. Winter needs are critical for survival of adult wolves and subsequent production of pups in spring, but summer needs are important for survival of pups (Mech 1977a).

The third problem is I have no quantitative data on amount of food acquired by wolves in dumps. I can only account for the biomass (moose) available in wolf home ranges. It is possible, however, that even without these moose, wolves receive enough food from dumps to avoid limitation by food. There is little information from North America or Europe regarding how much biomass is available in dumps but the amount likely varies according to location and season. For example, in this study, most carcasses in dumps were available during the hunting season. Throughout the year, however, animals killed by vehicles on highways or railroads were also deposited in dumps (pers. observ.)

The final problem with biomass indices is that, whereas moose were assumed the major prey for wolves in the study area (Krizan 1997), other prey such as caribou and beaver were ignored. Caribou likely do not represent a significant food item for wolves because their numbers are so low. Between 1993 – 1999, park biologists estimated there were 6 – 14 caribou in PNP (K. Wade, pers. comm). Furthermore, main concentrations of caribou were clustered along the coast of Lake Superior. Rarely, caribou were sighted further inland (Figure 2-4).

Nonetheless, data from scat contents presented conflicting and variable evidence regarding the above view namely, the relative importance of moose and caribou to diets of wolves in the study area. Krizan (1997) found that moose were most highly represented in scats of inland wolves. Indeed, he found little evidence of caribou. I found that moose were more highly represented than caribou in scats of inland wolves. Only moose, however, were represented in scats from coastal wolves. No evidence of caribou was found. Neale (M.S. in progress) found that caribou were more highly represented than moose in scats of coastal wolves.

It is difficult to reconcile all inconsistencies. The most important conflicting data include: 1) Krizan (1997) examined many scats from throughout the inland study area and found no evidence of caribou. I examined relatively few scats from inland and found evidence of caribou in the diet of wolves; 2) I found no and Neale (M.S. in progress) found some evidence of caribou on the coast. Granted, there is bias in the data from scats collected along the coast in that all scats were collected. Thus, caribou are likely over-represented in these data. Given this, however, it is surprising that I found no evidence of caribou along the coast.

Perhaps the best way to reconcile these inconsistencies regarding the relative importance of moose and caribou to the diet of wolves is by using other observational data. Despite the fact that in the study area, caribou are only systematically monitored along the coast, sightings further inland are rare (Figure 2-4). Furthermore, during P5, between 1994 and 1999, unequivocal evidence was found of only two caribou killed by wolves in the study area. One caribou, found in March 1994, was an adult and the other, found in February 1999, a calf (K. Wade, pers. comm). Between 1984 and 1999, there were a total of 7 suspected caribou kills that have been observed (K. Wade, pers. comm.).

These data support the view that moose are the main prey item for wolves and caribou are an opportunistic source of food for wolves.

Caribou may still be important particularly to wolves living along the coast. These wolves may choose caribou over moose since caribou are smaller, thus preferred ungulate prey for wolves (Holleman and Stephenson 1981, Bergerud and Ballard 1988, 1989). In the Rocky Mountains where there is a diverse ungulate prey base, Weaver et al. (1996) found much plasticity by individual packs in killing different species of prey in sequence. Prey vulnerability and wolf predation differ among areas and years according to herd size, terrain, snow depth and forest cover (Huggard 1993a, 1993b, 1993c, Weaver 1994, Paquet 1993, Paquet et al. 1996).

Beaver may also be important food for wolves, although beaver have not been shown to control the distribution or numbers of wolves (National Research Council 1997). In the P5 study, evidence of beaver was found in scats of wolves throughout the study area (Krizan 1997, Neale M.S. in progress, this study). In fact, Krizan (1997) found that beaver were found in scats more often than other ungulate prey. This is misleading because beaver contribute much less biomass because of their size. Nonetheless, beaver are still an important prey item. They may, however, be more important to packs of wolves outside PNP. Densities of beaver are unknown in the study area but may be lower in PNP (= mature forest with coniferous species replacing more palatable deciduous species) and higher outside PNP (= forests in early successional stages because activities of industry) (F. Burrows, pers. comm.). The importance of beaver may also change seasonally because they are less vulnerable in winter than summer (Meleshko 1986). Finally, the importance of beaver could change during times when large prey are not abundant. In Ontario, Messier and Crête (1985) and Forbes and Theberge (1996) found that beaver were important secondary prey when deer were not abundant.

Given these problems, the index of biomass may be a coarse indicator of the amount of food available per wolf. Nevertheless, the index provides useful information to support the food limitation hypothesis when used in conjunction with other predictors. Furthermore, the index is useful because: 1) it is based on winter densities of moose, which are believed to be the most important prey for wolves in the study area; 2) estimates of moose in each home range are based on the best available data, despite their limitations. Finally, densities of moose in the study area were all lower than the 0.4 moose/km^2 threshold below which Messier (1987) determined wolves would struggle to subsist. Furthermore, some wolf packs occur where moose density is below the 0.2 moose/km^2 threshold required to maintain wolf populations in moose-dominated ecosystems of eastern boreal forests (Messier 1985a).

The second prediction, 'consumption rates will be low', might support the food limitation hypothesis but not strongly. Wolves require a minimum consumption rate of 0.13 kg moose/kg wolf/day for individuals to survive and rear pups successfully (Mech 1977b). If wolves in this study were limited by food, consumption rate should have been below 0.13 moose/kg wolf/day. This was not the case for two of four packs in this study. In winter 1997 – 1998 the Swallow River and Bremner River Packs (Table 4-11) consumed at least 0.13 kg moose/kg wolf/day. All wolves in the Swallow River Pack survived, but they did not reproduce in that year or the following year (Table 4-7). Wolves in the Bremner River Pack whose fate was known survived and reproduced 2 years in a row (unpubl. data). This pack was tracked extensively and there were no known deaths from malnutrition. It is possible that wolves could have dispersed and died later because there was a drop in pack numbers from nine to three over the winter (Appendix D). These results suggest that both packs were not limited by food. However, for the Swallow River Pack, cause for failed reproduction remains unknown.

The remaining two packs (White River and Rein Lake Packs) did consume less than 0.13 moose/kg wolf/day suggesting that packs were limited by food. This seemed to be the case for the White River Pack because the dominant female failed to reproduce the following spring and died later in the summer. 'Moon' was extremely emaciated when killed by other wolves (D. Campbell, pers. comm.). These data may not strongly support the food limitation hypothesis for two reasons: 1) The White River Pack was a pair and as such, their rates of consumption were likely highly variable (Hayes et al. 1999). The degree to which this variability influences winter survival is unknown; 2) I cannot account for food these wolves obtained from scavenging. The Rein Lake Pack may also have been limited by food because they consumed less than 0.13 moose/kg wolf/day. Unfortunately, these data do not provide strong evidence to support the 'consumption rate prediction' because wolves fed regularly at a dump. Quantitative data on amount of food consumed are lacking. In summary, data for these two packs weakly supported the prediction.

The above data do not strongly support the food limitation hypothesis. Two additional factors, however, should be considered. First, the efficacy of Mech's (1977b) consumption rate estimate has never been tested. The estimate was derived from one pack of wolves in Minnesota (Mech 1977b) and a synthesis of data from captive (Mech and Frenzel 1971, Kolenosky 1972) and wild (Mech 1970, Kuyt 1972) wolves. As such, these figures may not accurately indicate limitation by food although other researchers have used them (Fuller and Keith 1980, Messier 1984, Bjorge and Gunson 1989, Hayes and Harestad 1999b). Second, consumption rates do not account for losses to scavengers such as ravens. These losses might be particularly important to small packs (*i.e.*, those that predominated in this study). Promberger (1992) concluded that the amount of biomass removed from ungulates by ravens was inversely related to wolf pack size. He estimated that ravens could remove 50 % of ungulate biomass from a pair of wolves, 33 % from a pack of six and 10 % from a pack of 10 or more wolves. At present, most researchers do not compensate for biomass lost to ravens though many believe it is important (Carbyn 1983, Messier and Crête 1985, Ballard et al. 1987, Fuller 1989, Hayes et al. 1991, Thurber and Peterson 1993, Dale et al. 1995, Hayes et al. 1999). In summary, though data on consumption rates do not strongly support the food limitation hypothesis, interpretation is confounded by the reliability of Mech's (1977b) consumption estimate and unaccounted losses of biomass to ravens.

Data supporting the third prediction, 'occurrence of natural mortality will be high', strongly support the food limitation hypothesis. Although I was unable to determine cause-specific mortality rates, more than half (9 of 17) of known mortality of radio-collared wolves in this study was from natural causes. Consequently, the occurrence of natural mortality in this study was high compared to other North American studies (Mech 1970, Peterson 1977, Carbyn 1982, Peterson et al. 1984, Ballard et al. 1987, Hayes et al. 1991).

Of the three causes of natural mortality, occurrence of starvation and intraspecific strife may be linked to low availability of food (Mech 1977a, Messier 1985a). Two adult wolves from different packs starved, one of which was a dominant female. Mech (1977a) suggested that alpha animals should be the last members of a pack to be affected by malnutrition. He felt that malnutrition would affect young animals exclusively, while helping to preserve established breeders by competition. Messier (1985a) also found evidence of adult wolves starving under conditions of low food supply. Specifically, the incidence of death from malnutrition was higher in a wolf population where availability of prey was low than in a population where availability of prey was high (Messier 1985a).

Two wolves from different packs were killed by conspecifics. One, 'Solita', was killed when her entire pack trespassed in an adjacent home range. The other, 'Moon', was killed at the edge of her home range. Messier (1985b) found that wolves changed their home range boundaries and increased extraterritorial excursions to areas with deer when moose density was low (*i.e.*, <0.2 moose/km^2). Similarly, Mech (1977a, 1977b) found that intraspecific strife, together with malnutrition, accounted for 58 % of adult mortality during a decline in numbers of white-tailed deer.

Disease cannot be linked with certainty to low availability of food but the relationship makes sense intuitively. A population of wolves encountering lack of food should be more vulnerable to disease than one with more food available. Furthermore, food shortage leading to nutritional stress could combine with disease factors to increase the significance of otherwise innocuous or sublethal conditions (Brand et al. 1995). In this study, disease killed four of eight wolves that died of natural causes. Two others

('Moon', 'Spirit') that died from other causes were diseased at the time of death. This level of disease-related mortality has not been reported previously for wolves. In other studies, from 2 – 21 % of wolf mortality has been attributed to disease (Carbyn 1982, Peterson et al. 1984, Fuller 1989, Ballard et al. 1997). In most studies, no disease-related mortality has been reported (VanBallenberghe et al. 1975, Mech 1977a, Fritts and Mech 1981, Messier 1985a, Potvin 1987, Ballard et al 1989, Hayes et al. 1991, Meier et al. 1995, Pletscher et al. 1997). Ballard et al. (1997) concluded that occurrence of rabies was a significant factor in a decline of wolves from Alaska. In that study, rabies-caused mortality was 21 %.

In this study, wolves died from sarcoptic mange (*n* = 3) and blastomycosis (*n* = 1). Sarcoptic mange is a rarely reported, but sometimes common, disease of wolves (Todd et al. 1981, Bornstein et al. 2000). Based largely on circumstantial evidence, several researchers believe that mange may be an important regulating factor in wild canid populations (Pike 1892, Murie 1944, Cowan 1951, Green 1951, Todd et al. 1981).

Blastomycosis is a chronic fungal disease that affects the pulmonary system of humans and dogs, and occasionally other animals (Jungerman and Schwartzman 1972, Stroud and Coles 1980, Legendre et al. 1981, Thiel et al. 1987). Blastomycosis is enzootic in Minnesota (Schlosser 1980) and Wisconsin (Sarosi et al. 1979, McDonough and Kuzma 1980) but until now, had not been reported from other wolf populations in North America.

Collectively then, natural causes of mortality in this study, resulting in deaths of over half the radio-collared wolves, support the food limitation hypothesis. Furthermore, when both ungulate biomass and causes of death are considered together, food appears to be an important factor that is limiting the population growth of wolves in the study area.

In this study, human-caused mortality limited the growth of the wolf population. Human-caused mortality, however, may not be as important as food in limiting the rate of growth. The first prediction, 'average index of ungulate biomass per wolf will be high', was not supported for the entire population. The prediction, however, was supported for two packs of wolves. Both were located north of PNP where human-caused mortality is more likely to occur (Burrows et al. 1996). In the White River Pack, wolf numbers dropped from nine to two during the first winter they were monitored (1994 - 1995). Pack numbers did not increase during the study. Similarly, numbers in the Rein Lake Pack dropped from six to three during winter, 1994 - 1995. Numbers remained low until the pack disappeared in winter, 1997 - 1998. The cause of decline of both packs is not well documented. Thus, neither can be reliably attributed to human causes.

The second prediction, 'occurrence of human-caused mortality will be high', was supported. Human causes (hunting, trapping, vehicles on roads and railways) accounted for just under half the mortality (8 of 17 wolves) of radio-collared wolves in this study. Clearly, human-caused mortalities are important but not in comparison with other studies where human-caused mortality was assumed to be the primary limiting factor (*i.e.*, 69 - 80%; Peterson et al. 1984, Ballard et al. 1989, 1997).

In this study, reported numbers of wolves killed by trappers and hunters might be minimal. Some trappers suspended their activities during P5 (D. Morin, R. Renner and L. Horth, all local trappers, pers. comm.). These trappers have been reported to take a minimum of 10 wolves (Marathon townsite dump, winter, 1994 - 1995) and a maximum of 16 wolves from dumps (White River townsite dump, winter 1995 - 1996) (R. Renner and D. Morin, pers. comm.). Hunters reported killing two wolves though only when questioned by Park wardens (K. Wade, PNP Park Warden, pers. comm., W. Michano, PNP Park Warden, pers. comm.). In summary, if mortality of wolves from hunting and trapping was under-represented during this study, limitation by humans could be even more important than presently considered.

In summary, only one of the two predictions for the human-caused mortality hypothesis was supported. Thus, human-caused mortality appears to be an important factor that is limiting the population growth of wolves in the study area. Regarding the relative importance of the two limiting factors, based on ungulate biomass alone, it appears that food is more important. With current short-term data and without statistical analysis, however, this conclusion is tentative at best.

Regardless of which factor is more important, both may adversely affect reproduction and therefore the population growth of wolves. In this study, wolves successfully reproduced in 36 % of possible occasions compared to 45 – 93 % noted in other areas (Messier 1985a, Potvin 1987, Peterson et al. 1998). The low reproduction recorded does not support the 'ungulate biomass' or 'human-caused mortality' hypotheses because both can cause low reproduction.

Lack of food can cause failed reproduction by wolves, but only when food is extremely scarce. More often, percentage of pups and mean number of pups per pack are affected. For example, Fuller (1989) found that the index of ungulate biomass per wolf is positively correlated with the percentage of pups and the mean number of pups per pack. Specifically, a high index may allow high pup survival (Fuller 1989). Similarly, Boertje and Stephenson (1992) found that when prey became scarce, litter sizes were reduced. Suppression of estrus (*i.e.*, no reproduction), however, occurred only when prey were extremely scarce.

In this study I was unable to determine if wolves produced pups that died soon after birth or no pups at all. However, lack of denning suggests that no pups were produced. This could mean that availability of food was low if we consider a situation in Minnesota. During a 5-year period of decline in deer numbers, increasingly fewer pups survived and eventually no pups were produced (Mech 1977a). Reduced reproduction related to food shortages was also noted by Eberhardt (1977) who detailed the following chain of events that occur in mammalian populations: 1) decreased survival of young; 2) delayed maturity; 3) reduced reproduction; 4) increased adult mortality. In this study, lack of reproduction could have been caused by low availability of food.

High mortality of wolves from human causes can cause failed reproduction but only when wolves are heavily exploited or suffering high mortality from different causes. The relationship, however, is not intuitive. If we assume exploited populations have a high index of ungulate biomass available per wolf, high pup production (greater number pups per litter) and survival should occur (Fuller 1989). As a result, the population should increase. However, the reverse situation may occur in circumstances where wolves are heavily exploited. In Alaska, Gasaway et al. (1983) found no increase in percent pups after exploitation and felt packs may have been left with no breeding-age individuals of one or both sexes. Similarly, in the Yukon, mate mortality caused reproductive failure of pairs at least nine times during the study (Hayes and Harestad 1999a). Researchers concluded that adult mortality was important in limiting wolf recruitment during the first 2 years of recovery post-control. The same thing could be happening to wolves in this study. That is, breeding partners may be rare because pack sizes are small. In this study, lack of reproduction may have occurred because of human-caused mortality.

Another concern is that with few packs reproducing, the age structure of the population may be skewed towards older animals that may not be as fecund as younger animals. The effect of age distributions on population declines has not been previously documented in wolves but has been documented in moose populations from Isle Royale (Page 1989). There, when recruitment was reduced to low levels and prolonged, prime-age classes were robbed of replacements necessary to sustain them. Eventually the age distribution became heavily skewed toward older animals with high mortality and low fecundity, and a population decline was inevitable (Page 1989). This same pattern may follow for wolves in the study area although meaningful comparisons between moose and wolves may be limited given differences in life history characteristics.

Shortfalls and Alternatives to My Analysis

In this study I was able to document two factors known to limit wolf populations across North America. I also tested to see which was more important in limiting population growth in the study area. A major shortfall of this study is I relied on a mensurative experiment to test my hypotheses. No manipulations were done and the hypotheses stood or fell on the basis of observations that defined the predictions. There were no replicates or controls, hence statistics were not used to demonstrate that chance played a part at a sufficiently low probability. As a result there exists substantial ambiguity in my conclusions. This is not to say that the analysis was not useful, only that the certainty of my conclusions suffered from limitations of the study. Observations need to be repeated at different times and in different locations.

An alternative approach that would allow more robust conclusions would be to employ a long-term study. Accordingly, two approaches could be used: 1) An experimental design that involves systematic removal of limiting factors while observing subsequent changes in the population growth relative to control areas (Boutin 1992); 2) Study a population at a single density and evaluate the relative importance of factors that might affect the population growth. The analysis could be guided by criteria outlined by Keith (1974): 1) For each factor, identify its immediate demographic effect(s) and compare its impact with other factors; 2) For each factor, describe its interaction with other factors in terms of additive, compensatory or modifying effects.

As an example, Messier (1991) examined the effects of factors that were limiting moose and deer in Minnesota. He furthered his analysis by determining if limiting factors had regulatory power by adhering to Keith's (1974) third criterion, which was to characterize the action of factors in relation to population density. Messier (1991) had long-term data sets for predator-prey relationships. He found that 30 years of data provided an adequate sample on which to base conclusions. Conversely, 10 years of data were insufficient and conclusions were not strongly supported. This example demonstrates the importance of long-term studies.

In my analysis, unlike Messier (1991), I could not determine whether limiting factors were regulatory. Clearly, understanding the role of regulating factors is important for population ecologists and wildlife managers. Whereas limiting factors may be responsible for annual fluctuations and can be manipulated to set the equilibrium, regulating factors determine the long-term viability of the population by causing it to return to equilibrium (Sinclair 1991). Consequently, regulating factors need to be determined in order to predict how populations will change under new conditions (Boutin 1992).

Furthermore, I was unable to describe any interaction between limiting factors in terms of additive, compensatory or modifying effects. Additive or cumulative effects of low food and current levels of human-caused mortality could be important.

This study also may have been limited because I did not directly address intrinsic factors that may affect population dynamics. Populations are limited intrinsically (or are self-regulatory) if mechanisms such as territoriality, dispersal and reproductive suppression reduce population growth before resource limitation (Lidicker 1978, Tamarin 1983. In contrast, populations are limited extrinsically if their numbers are controlled by weather, disease, predators, food or other environmental factors external to the population.

Packard and Mech (1980) examined the issue of intrinsic regulation or limitation (*i.e.*, what sets the upper limits of wolf populations) of wolves in detail. They concluded that: 1) many behavioral constraints to population growth were ultimately dependent on available food resources; 2) social factors controlled density more directly through intraspecific strife and imposition of limits on the number of breeding females, and indirectly through unequal distribution of food resources among pack members (Packard and Mech 1980). If this is the case, my analysis of the importance of food in limiting the rate of growth of wolves may have been sufficient.

I also did not address extrinsic factors such as weather or inter-specific competition with black bears. Messier (1991) considered only weather in his analysis but found it to be insignificant.

Long-Term Viability of Wolves

Assuming that ungulate biomass and human-caused mortality continue to occur at the present levels, the probability of long-term viability (*i.e.*, 100 years) of wolves in this study may be tenuous. The mean annual finite rate of increase (0.96) suggests the population is declining slightly. For example, in 1997 – 1998, the population comprised approximately 26 wolves. In 72 years, this same population could number <10 wolves based on current trends. It is not prudent, however, to base further management decisions on this trend alone. Without long-term demographic data, we cannot be sure that this trend will continue. Instead, 0.96 may have occurred during a local population decrease (for example, owing to frequency dependence adjustment) (Dias 1996). Thus, further analysis of P5 data is necessary.

Quantitative population viability analyses address the likelihood of a population's persistence over a specified period under specified conditions (Gilpin and Soulé 1986, Boyce 1992). Analyses define minimum viable populations, namely, populations large enough to permit "long-term" persistence despite genetic, demographic and environmental uncertainties (Shaffer 1981). To predict population persistence, parameters necessary include such population-specific factors as reproductive rate, survivorship and genetic effective population size (Noss et al. 1996). Other parameters include genetic diversity, demographic stochasticity, environmental stochasticity, long-term stages in plant succession, natural catastrophes and social dysfunction (Fritts and Carbyn 1995). P5 data provide baseline information to address some these of parameters. Data are limited, however, because of the short-term nature of the study. Consequently, I cannot perform a quantitative population viability analysis. Nonetheless, I can make a qualitative prediction based on P5 data and known life history characteristics of wolves.

These characteristics enable wolves to respond to natural and human-induced disturbances by conferring resilience (Weaver et al. 1996). Resilience has been defined as the " ability to absorb disturbance and still maintain the same relationship between populations or state variables (Holling 1973) and "the degree to which an entity can be changed without altering its minimal structure (Pickett et al. 1989). Thus, resilience can be thought of as a property of a system, whereas persistence is the outcome (Weaver et al. 1996).

The resiliency profile of wolves includes three basic mechanisms. First, wolves display remarkable behavioural plasticity in using different prey and habitats (Mech 1991). Wolves are able to substitute one resource for another in the face of environmental disturbance, thereby ameliorating flux in food availability (Weaver et al. 1996). In the Rocky Mountains, wolves living amongst a high diversity of ungulate species can be viewed as "expanding specialists". Specifically, wolves specialize on vulnerable individuals of large prey (elk and moose) yet readily generalize to common prey (usually deer) (Weaver et al. 1996).

In this study, multiple prey species were not universally available to wolves. Thus, behavioural plasticity may do little to confer resilience. Furthermore, plasticity was negative for wolves in that they readily used dumps for food. High mortality was incurred at dumps and predator-prey relationships were changed (Krizan 1997, unpubl. data).

Second, wolves are able to compensate demographically. This compensation, under certain circumstances, enables wolves to respond to increased rates of juvenile or adult mortality with increased reproduction and/or survival, thereby mitigating demographic fluctuations (Weaver et al. 1996). Naturally, dominant wolves are able to reproduce at a very young age (= 2, Mech 1970) and will usually reproduce every year thereafter (Weaver et al. 1996). Age at reproductive senescence has not been well documented but few females survive to reproduce past age 9 (Mech 1988). Wolves also display remarkable ability to recover from exploitation. For example, during a wolf reduction program in the Yukon, wolves recovered to pre-reduction densities within 5 years (Hayes and Harestad 1999a). Wolves immigrated into the study area during early recovery, followed by increases in pack size from reproduction (Hayes and Harestad 1999a).

In this study, reproductive success was very low (8 of 22 pack-years) suggesting that naturally, wolves are not compensating for mortality and dispersal. Only one instance of immigration into the study area was suspected (pers. observ.) although immigration of wolves can be difficult to detect (P. Paquet, pers. comm.). Finally, since pack sizes are small (3.5), ungulate biomass available is low (208) and few wolves are reproducing, the age structure of the population is likely skewed towards older animals. Thus, the population may not readily recover from high levels of human-caused mortality (Fuller 1989).

The final mechanism that confers resilience to wolf populations is dispersal. When dispersal is successful, vanishing local populations are rescued from extirpation (Brown and Kodric-Brown 1977) and functional connectivity of metapopulations is established (Hansson 1991). Wolves have tremendous dispersal capabilities and as a result, "connectivity" of populations is high. Dispersing wolves typically establish territories or join packs within 50 - 100 km of the pack in which they were born (Fritts and Mech 1981, Fuller 1989, Gese and Mech 1991, Wydeven et al. 1995). Some wolves, however, move longer distances. For example, Fritts (1983) observed a wolf that traveled at least 917 km.

In this study, dispersal success was low (17 %) compared to other North American studies (range: 27 – 85 %) (Weaver et al. 1996). This suggests that colonization success, at least outside of the study area, may be low. Given this, it is reasonable to assume that success within the study area could also be low. Human activities are widespread (Figure 2-2) and human-caused mortality is documented (8 of 17 wolves). Additionally, there was little documented immigration into the study area (P. Paquet, pers. comm.).

Collectively then, data from this study suggest that resilience of wolves to natural changes and human disturbance may be low. Consequently, probability of persistence and long-term viability may be tenuous.

Chapter 6. Conclusions

Analysis of wolf demography in the Greater Pukaskwa Ecosystem revealed that mean annual finite rate of increase was 0.96. This means that the annual population growth was limited and declining slightly. Putative factors responsible for this included low natality and adult mortality.

Assuming that population growth was limited, I assessed the relative importance of ungulate biomass and human-caused mortality. These are the two main factors known to limit other wolf populations across North America. I concluded that both played major roles in limiting the population growth of wolves in the GPE, although ungulate biomass may be more important. Conclusions related to the relative importance of each factor were tentative because long-term data were not available and I could not determine statistically which limiting factor was more important. Furthermore, limiting factors could interact to influence population growth. Additive or cumulative effects of low food and current levels of human-caused mortality could be important.

Nonetheless, based on the short-term data collected by me and other P5 researchers and known life history characteristics of wolves, I predict that the probability of long-term viability of this wolf population might be tenuous. I suggest that resilience of wolves to natural and human-caused disturbances in the GPE may be low because: 1) species diversity of ungulates is low; 2) wolves use dumps where they incur high mortality; 3) reproductive success is low; 4) the age structure is likely skewed towards old animals; and 4) there may be little immigration.

Results from this study add a new dimension to predator-prey research, namely the detailed examination of factors that limit wolf populations. Most detailed analyses of limitation in predator-prey systems involve prey populations: moose, deer, elk and caribou. In these studies, the proximate goal is to identify and manipulate limiting factors. The ultimate goal is to increase prey populations, often for human harvest.

Limitation of wolves has only been considered in detail on Isle Royale (Peterson 1998). There, wolves have been isolated geographically from mainland wolves since the 1940's (Wayne et al. 1991). Consequently, Isle Royale offers an, as of yet, unique opportunity to study wolves. Specifically, roles played by demographic stochasticity and genetic isolation in limiting wolf population growth can be examined.

In Canada wolves do not exist currently as isolated populations. This suggests that now would be an opportune time to study wolf population limitation in detail. Consequently, we could predict how populations will change when encountering future pressures. The time is even more opportune given the ever increasing human population, demand for natural resources and building of human infrastructure, all of which will only threaten viability of wolves in the future.

Chapter 7. Tables

Table 1-1. Estimated moose densities[a], moose biomass index and winter wolf density for wolf populations using moose predominantly as prey in various parts of North America (From Messier, 1994).

Locations and year(s) of sampling	Moose density (no./1000km^2)	Moose biomass index	Winter wolf density (no./1000km^2)	Moose biomass index per wolf	Reference
Carmacks, Yukon, 1982	40	240	2	120	Gasaway et al. 1992
Dromedary Mountain, Yukon, 1982	60	360	10	36	Gasaway et al. 1992
East Alaska, 1981	90	540	8	68	Gasaway et al. 1992
Central Alaska, 1986	90	540	3	180	Gasaway et al. 1992
Aishihik, Yukon, 1982	110	660	3	220	Gasaway et al. 1992
East Alaska, 1987	120	720	4.5	160	Gasaway et al. 1992
Nisutlin, Yukon, 1986	130	780	10	78	Gasaway et al. 1992
Mayo, Yukon, 1988	140	840	10	84	Gasaway et al. 1992
East Alaska, 1990	140	840	9	93	Gasaway et al. 1992
South-central Yukon, 1983	150	900	13	69	Gasaway et al. 1992
Central Alaska, 1976	180	1080	15.6	69	Gasaway et al. 1983
Central Alaska, 1986 - 1987	190	1140	6	190	Gasaway et al. 1992
Central Alaska, 1980	190	1140	8	142.5	Gasaway et al. 1992
Central Alaska, 1986	190	1140	15	76	Gasaway et al. 1992
East Denali National Park, Alaska, 1984	220	1320	5.9	224	Singer and Dalle-Molle 1985, Singer 1987
Southwest Quebec, 1980 - 1984	230	1380	8.2	168	Messier 1985a, Messier and Crête 1985
Northeast Alberta, 1975 - 1978	230	1380	11.1	124	Fuller and Keith 1980
South-central Yukon, 1983	260	1560	11.8	132	Larsen et al. 1989, Hayes et al. 1991
East Denali National Park, Alaska, 1966 - 1974	270	1620	12.7	128	Singer and Dalle-Molle 1985, Van Ballenberghe 1987
Northwest Ontario, 1975 - 1979	300	1800	11.9	151	Bergerud et al. 1983
South-central Alaska, 1975	330	1980	10.3	192	Ballard et al. 1987, Ballard et al. 1991
Southwest Quebec, 1980 - 1984	370	2220	14.8	150	Messier 1985a, Messier and Crête 1985
Teslin burn, Yukon, 1984	420	2520	18	140	Hayes and Baer 1986, Gasaway et al. 1992
Kenai Peninsula, Alaska, 1976 - 1982	800	4800	14.2	338	Peterson et al. 1984
Northwest Alberta, 1979 - 1980	1300	7800	22.1	353	Bjorge and Gunson 1989

[a] I did not use data from Isle Royale because results are from a closed population of wolves. Furthermore, I did not use the low-density results reported by Messier (1984) because these were never published along with the values for medium and high densities of wolves.

Table 2-1. Densities[a] of moose in the Greater Pukaskwa Ecosystem, 1993 - 1999. Data are from Wade (1993b, 1996, 1999b) and A. Bissett, pers. comm., 1999.

	Wildlife Management Unit			
Year	21A	21B	33	Pukaskwa National Park
1993				0.216 ± 0.037[b]
1994	0.2 ± 0.024	0.22 ± 0.023	0.28 ± 0.016	
1996				0.104 ± 0.042
1997	0.25 ± 0.031		0.26 ± 0.033	
1998		0.22 ± 0.031		
1999				0.257 ± 0.089

[a] Based on aerial surveys using stratified random sampling (Gasaway et al. 1986).

[b] Moose/km^2 ± standard deviation moose/km^2.

Table 3-1. Adjusted densities and biomass indices of moose for management units throughout the Greater Pukaskwa Ecosystem, 1993 - 1999.

Management Unit	Average moose density (moose/km^2)	Moose biomass index (number moose/1000km2) * 6
21A	0.225[a]	1350
21B	0.220[b]	1320
33	0.27[c]	1620
PNP	0.192[d]	1152

[a] Data averaged from 1994 and 1997.
[b] Data averaged from 1994 and 1998.
[c] Data averaged from 1994 and 1997.
[d] Data averaged from 1993, 1996 and 1999.

Table 4-1. Sex and weight of adult wolves from the study area. Measurements are from wolves that were radio-collared (No. 1 - 18) as well as wolves that were found dead (No. 19 - 25) in the study area, 1994 - 1998.

Wolf	Sex	Weight (kg)
1. Paulina	f	28.0
2. Nellie	f	29.0
3. Aldo	m	36.5
4. Cassidy	f	32.0
5. Mojo	m	32.0
6. Solita	f	25.0
7. Mika	f	27.0
8. Ana	f	35.0
9. Star	m	60.0
10. Sam	m	45.0
11. Ronja	f	30.0
12. Makade	m	50.0
13. Hale	m	39.0
14. Luz	m	39.0
15. Maiingan	f	26.5
16. Moon	f	23.5
17. Spirit	m	40.0
18. Charlie	m	27.5
19. 283 - 98	m	34.0
20. 279 - 98	f	22.0
21. 336 - 96	m	20.5
22. 337 - 96	f	17.8
23. 014 - 97	m	27.0
24. 242 - 96	m	27.0
25. 244 - 96	m	34.0
	Average	32.3

Table 4-2. Sizes of annual home ranges and home range areas per wolf of 13 packs of wolves in the study area, 1994 - 1998.

Year	Pack	Radio-collared wolf	Number of wolves in pack[a]	100% MCP[b] (km^2)	95% MCP[b] (km^2)	*n*	Area/wolf[c] (km^2)
1994 – 1995	Black River[d]	Sam	6	283	156	53	26
	Rein Lake	Cassidy	3	310	249	38	83
1995 – 1996	Black River[d]	Aldo	4	548	388	55	97
	Rein Lake	Cassidy	3	600	533	58	178
	Neys[d]	Sam	3	269	244	96	81
	Cascade Lake	Solita[e]	1	204	170	26	170
1996 – 1997	Rein Lake[d]	Cassidy	2	561	557	39	279
	Neys[d]	Leo	6	113	101	96	17
	White River	Moon	2	407	345	37	173
1997 – 1998	Black River[d]	Maiingan	4	468	450	74	113
	Rein Lake[d]	Thunder	2	692	600	87	300
	White River	Moon	2	589	498	65	249
	Bremner River	Chaba	6	760	644	93	107
	Swallow River	Makade	5	567	500	62	100
	Pooled Mean		3.5	455	388	63	139
	SE		0.45	52	48	6.3	25

[a] Maximum pack size, January 15 – February 15.

[b] The sizes of home ranges were described using the minimum convex polygon method (MCP) (Mohr 1947).

[c] Based on 95% MCP.

[d] Packs that used town dumps or dumps on reservations.

[e] Home range size and home range area per wolf were not included in pooled means because the area was not fully defined; *i.e.*, the observation-area curve was asymptotic but locations were not obtained throughout the year.

Table 4-3. Increasing sizes of annual home ranges of wolves in the study area, 1994 - 1998.

		95% MCP[a] (km^2) (*n*)			
Wolf	Pack	1994 - 1995	1995 - 1996	1996 - 1997	1997 - 1998
Sam[b]	Black River/Neys	156(53)	244(96)	248(85)	
Aldo[c]	Black River	149(56)	388(55)		
Cassidy[d]	Rein Lake	249(38)	533(58)	557(39)	
Moon	White River			345(37)	498(65)

[a] The sizes of home ranges were described using the minimum convex polygon method (MCP) (Mohr 1947).

[b] Wolf dispersed and joined a new pack (Neys Pack) east of the study area.

[c] Wolf dispersed from the GPE in November 1995.

[d] Wolf expanded her home range in November 1996; extension included a dump.

Table 4-4. Density of wolves in winter (Jan 15 – Feb 15) and annual rates of population change in the study area, 1995 - 1998.

		Annual rate of population increase	
Winter	Density (wolves/1000km^2)	Finite (lambda)	Exponential (r = ln lambda)
1995 - 1996	7.9		
1996 - 1997	9.6	1.22	0.199
1997 - 1998	7.2	0.75	-0.288

Table 4-5. Annual numbers of wolves in packs in the study area, 1994 - 1998. The number of sightings made is in parenthesis.

	March pack size[a]				
Pack	1994	1995	1996	1997	1998
Neys		3(4)	4(2)	2(2)	4(2)
Black River	4(2)	4(2)	4(2)	3(4)	
White River	2(2)[b]	2(4)	2(2)	2(9)	2(2)
Rein Lake	3(4)	3(3)	1(2)	1[b]	0
Bremner River				3(3)[b]	
Swallow River			5(2)[b]	3(3)	4(1)
Cascade River		1(4)	0		

[a] Maximum number of wolves seen in March.

[b] Pack sizes were confirmed by track-counts made from the ground.

Table 4-6. Median dispersal date[a], dispersal location, sex and age of radio-collared wolves that dispersed from the study area, 1994 - 1998.

Wolf	Median dispersal date[a]	Sex	Age at dispersal	Dispersal location
Sam[b]	23 Jun 1995	m	1	Neys Provincial Park
	24 Apr 1997		3	Terrace Bay
Aldo	10 Nov 1995	m	4	Manitouwadge
Paulina	7 Dec 1994	f	3	Terrace Bay
Mojo	3 Dec 1994	m	3	North or White Lake
Charly	9 Oct 1997	m	1	Dubreville
Chaba	27 Jun 1998	f	3	Pokei Lake

[a] Median date between the time when the wolf was occupying its old home range and the time when the wolf dispersed from its old home range.

[b] Wolf dispersed twice.

Table 4-7. Reproductive success of wolf packs, 1994 - 1998.

	Year				
Pack	1994	1995	1996	1997	1998
Black River	+[a]	--[a]	--	+	+
White River	+[b]	--	--	--	--
Rein Lake	+[b]	--	--	--	--
Neys			+	--	?
Bremner River				+	+
Swallow River				--	--

[a] + = reproduced successfully.
-- = did not reproduce successfully.

[b] This pack likely reproduced successfully because many wolves (9 - 10) were seen in late fall (Nov - Dec).

Table 4-8. Indices of moose biomass available per wolf in the study area, 1995 - 1998.

Year	Pack	Weighted moose biomass/1000km^2	Density of wolves/1000km^2	Moose biomass index per wolf
1995 - 1996	Black River	1304.7	10.3	127
	White River	1461.0	5.8	252
	Rein Lake	1361.7	5.6	243
	Cascade Lake	1152.0	5.9	195
	Neys	1350.0	12.3	110
			Mean	185
1996 - 1997	Black River	1383.6	8.9	155
	White River	1461.0	5.8	252
	Rein Lake	1453.9	3.6	404
	Neys	1350.0	59.4	23
			Mean	209
1997 - 1998	Black River	1383.6	8.9	155
	White River	1444.2	4.0	361
	Rein Lake	1620.0	3.3	491
	Neys	1350.0	19.8	68
	Swallow River	1152.0	10.0	115
	Bremner River	1546.2	9.3	166
			Mean	226
	Overall Mean			208
	SE			33

Table 4-9. Indices of moose biomass available per wolf, listed by pack, in the study area, 1995 - 1998.

	Indices of moose biomass available per wolf			
Pack	1995 - 1996	1996 - 1997	1997 - 1998	mean
Rein Lake	242	404	491	379
White River	252	252	361	288
Cascade Lake[a]	195	n.a.	n.a.	n.a.
Bremner River	n.a.	n.a.	166	n.a.
Swallow River	n.a.	n.a.	115	n.a.
Neys	110	23	68	67

n.a. means not available.

[a] This biomass value is only an approximate value because the home range size used in the calculation may not be fully defined. i.e. the observation-area curve formed an asymptote but the wolves were not monitored for one full year; they were only monitored between July 1995 and January 1996.

Table 4-10a. Diet composition of wolves living inland in the study area, June 1996 - April 1998, based on examination of 20 scats[a].

Food item	% of total scats examined that had food item
beaver	6
adult caribou	23
adult moose	35
black bear	6
adult deer	3
coyote	3
snowshoe hare	10
calf moose	6
vole	3
mink	3

[a] One scat contained pieces of garbage but data from this scat are not included in summary.

Table 4-10b. Diet composition of wolves living along the coast in the study area, June 1996 – April 1998, based on examination of 9 scats.

Food item	% of total scats examined that had food item
beaver	0
adult caribou	0
adult moose	60
black bear	10
adult deer	0
coyote	10
snowshoe hare	20
calf moose	0
vole	0
mink	0

Table 4-11. Rates of kill and consumption of prey by wolves in the study area, winter 1997 - 1998.

Pack	Kill rate (Ungulates per wolf per 100 days)	Consumption rate (kg prey/wolf/day)	Consumption rate (kg/kg wolf/day)
Swallow River	2.4	6.5[a]	0.20[a]
	3.2[d]	9.2[bd]	0.28[bd]
Bremner River	1.7	3.7[c]	0.11[c]
	2.0[e]	4.3[ce]	0.13[ce]
White River	0.0	0.0	0.0
Rein Lake	0.0	0.0	0.0

[a] Rate is calculated assuming 100%, 75% and 75% of three carcasses were consumed, respectively. Field evidence justified using these percentages to represent the amount of each carcass that was consumed by wolves.

[b] Rate is calculated assuming 100%, 100%, 75% and 75% of four carcasses were consumed, respectively. Field evidence justified using these percentages to represent the amount of each carcass that was consumed by wolves.

[c] Rate is calculated assuming 100% of the carcasses were consumed. Field evidence justified using these percentages to represent the amount of each carcass that was consumed by wolves.

[d] Rate is calculated including additional data from a suspected ungulate kill.

[e] Rate is calculated including additional data from evidence of ungulates and beaver found in wolf scats.

Table 4-12. Mortality and survival of wolves radio-collared in the study area, 1994 - 1998.

Pack	Wolf	Capture date	Status of wolves at end of study
Black River	Nellie	20 Aug 1994	dead (20 Oct 1994)
	Sam	22 Aug 1994	dead (4 Jan 1998)
	Aldo	26 Aug 1994	unknown (left study area 10 Nov 1995)[a]
	Maiingan	25 Jun 1997	dead (27 Dec 1998)
	Spirit	24 Jun 1997	dead (14 Oct 1997)
White River	Paulina	16 Sep 1994	dead (6 Dec 1994)
	Ana	29 Aug 1995	dead (1 Nov 1996)
	Moon	18 Feb 1996	dead (9 Aug 1998)
	Bremner	5 Aug 1997	alive[b]
Rein Lake	Cassidy	30 Sep 1994	dead (1 Feb 1997)
	Star	16 Feb 1996	dead (4 Feb 1997)
	Abbey	3 Oct 1994	dead (3 Oct 1994)
	Thunder	16 Jul 1997	dead (27 Dec 1998)
	Mojo	3 Oct 1994	dead (10 Feb 1996)
Bremner River	Chaba	16 Jul 1997	dead (11 Jul 1998)
Swallow River	Makade	8 Apr 1997	unknown (dropped collar on 13 May 1997)
	Luz	9 Apr 1997	alive[b]
	Hale	9 Apr 1997	unknown (collar malfunction on 3 May 1997)
Cascade River	Solita	15 Jul 1995	dead (26 Dec 1995)
	Mika	20 Jul 1995	dead (28 Jan 1996)
Neys	Louie	21 Aug 1994	dead (15 Dec 1994)
	Charly	22 Jul 1996	dead (18 Jan 1998)
	Ronja	26 Jul 1996	alive[b]
	Leo	12 Jul 1996	alive[b]
	Shy	20 Jul 1996	unknown (dropped collar on 29 Aug 1996)
Lone wolf	Aspen	5 Jul 1997	unknown (collar malfunction on 11 Dec 1997)

[a] This wolf was last seen alive with another wolf at a dump near Manitouwadge in February, 1997.

[b] December 31, 1998 is the last date of observation.

Table 4-13. Causes of death of wolves radio-collared in the study area between 1994 - 1998.

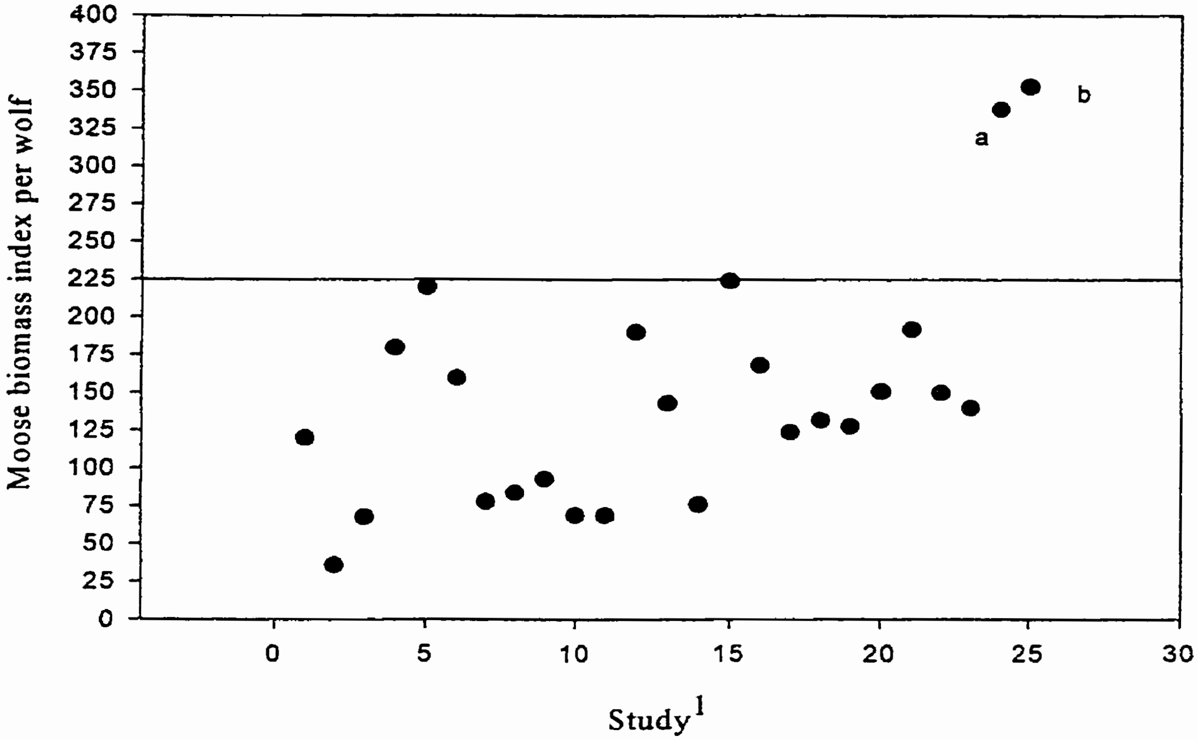
Pack	Wolf	Cause of death
Human causes of death of wolves in the study area:		
Black River	Maiingan	Train
	Spirit	Shot
White River	Paulina	Train
	Ana	Snared
Neys	Louie	Snared
	Charly	Train
	Sam	Snared
Swallow River	Abbey	Shot
Natural causes of death of wolves in the study area:		
Black River	Nellie	Starvation
White River	Moon	Inter-pack aggression
Rein Lake	Cassidy	Mange
	Star	Mange
	Thunder	Mange
	Mojo	Blastomycosis
Bremner River	Chaba	Unknown[a]
Cascade Lake	Solita	Inter-pack aggression
	Mika	Starvation

[a] The cause of death of this wolf was unknown but, based on field evidence, I assumed that it died from natural causes because there was no evidence of human activity in the area.

Table 4-14. Cumulative survival of wolves radio-collared in the study area, 1994 - 1998.

Interval (days)		Conditional probability of Mortality	Standard error	Survival probability	Standard error
Lower	upper				
0	365	0.32	0.10	0.68	0.10
365	730	0.30	0.15	0.48	0.12
730	1095	0.57	0.26	0.20	0.14

Chapter 8. Figures



a = These data are from the Kenai Peninsula (Alaska) that was colonized by wolves in the mid-1970's; hence, wolf numbers may still be increasing. Furthermore, Peterson et al. (1984) felt that wolf density was regulated by harvest, the dominant form of mortality.

b = These data are from the Simonette River (Alberta) where 17 of 20 dead wolves were a result of human activity. Average overwinter loss of these wolves was 30%, which may have been sufficient to limit the population growth (Keith 1983).

Figure 1-1. Indices of moose biomass available per wolf for wolf populations across North America that use moose predominantly as prey.

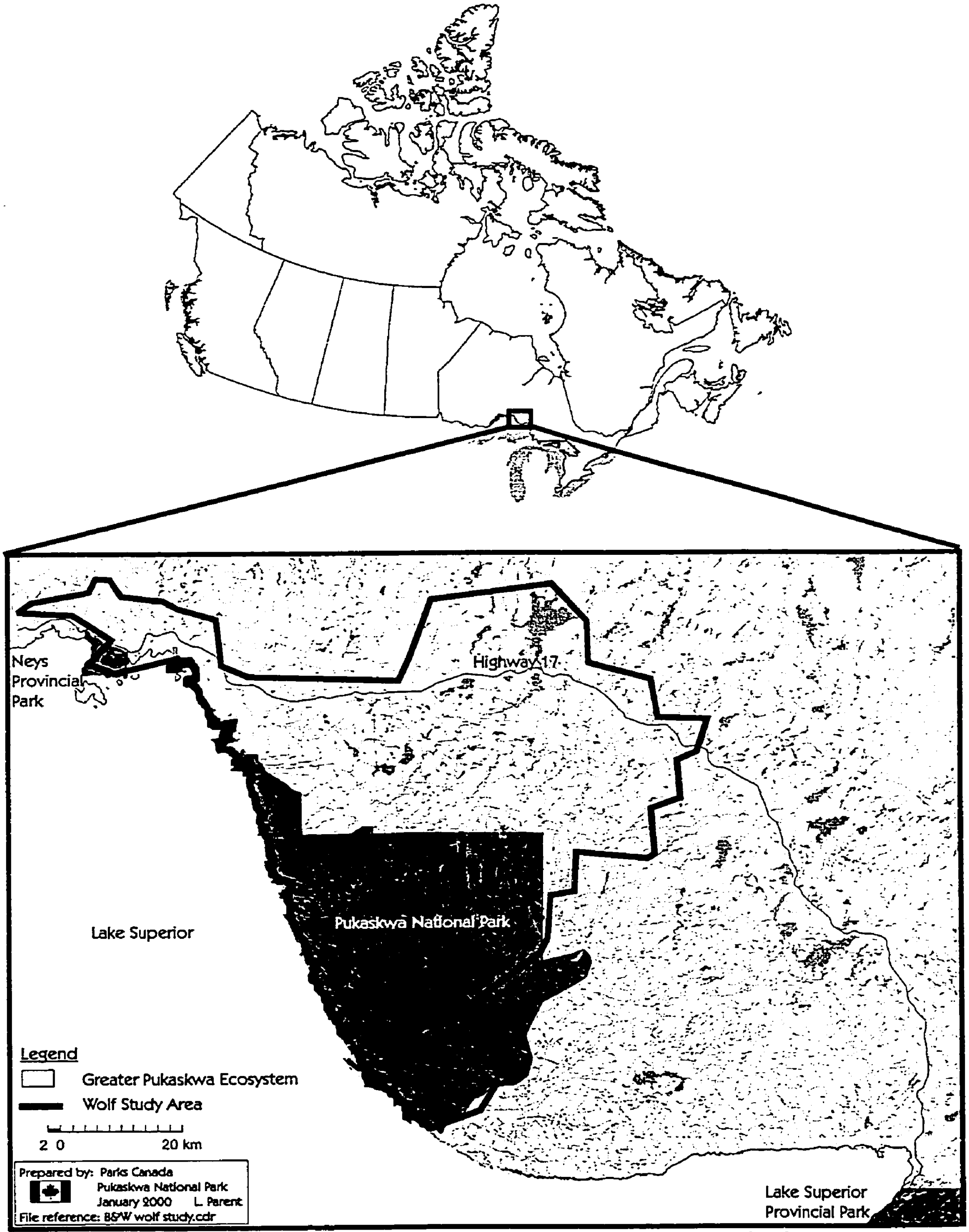


Figure 2-1. Location of the wolf study area within the Greater Pukaskwa Ecosystem, Ontario, Canada.

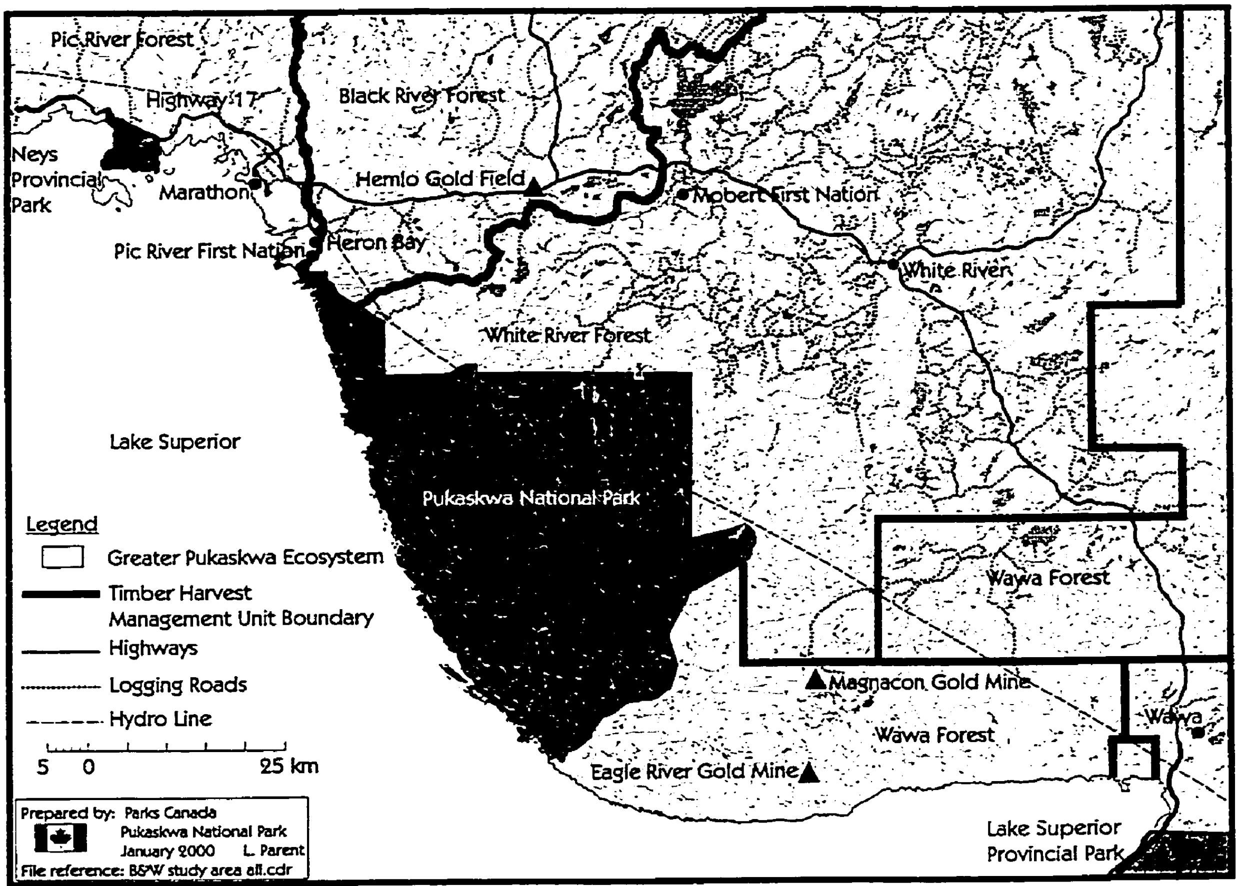


Figure 2-2. Timber harvest management units, mines, towns and associated infrastructure in the Greater Pukaskwa Ecosystem, Ontario, Canada.

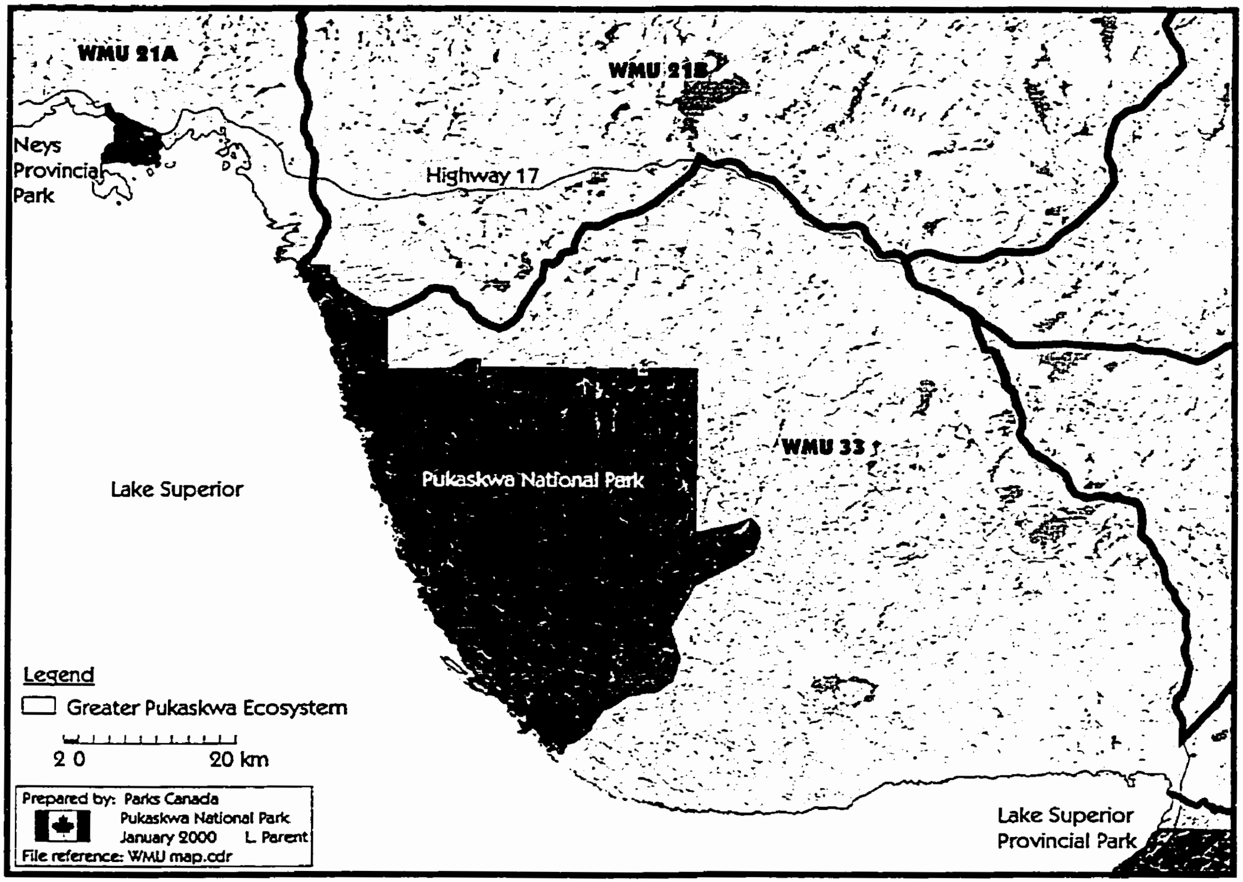


Figure 2-3. Location of Wildlife Management Units in the Greater Pukaskwa Ecosystem, Ontario, Canada.

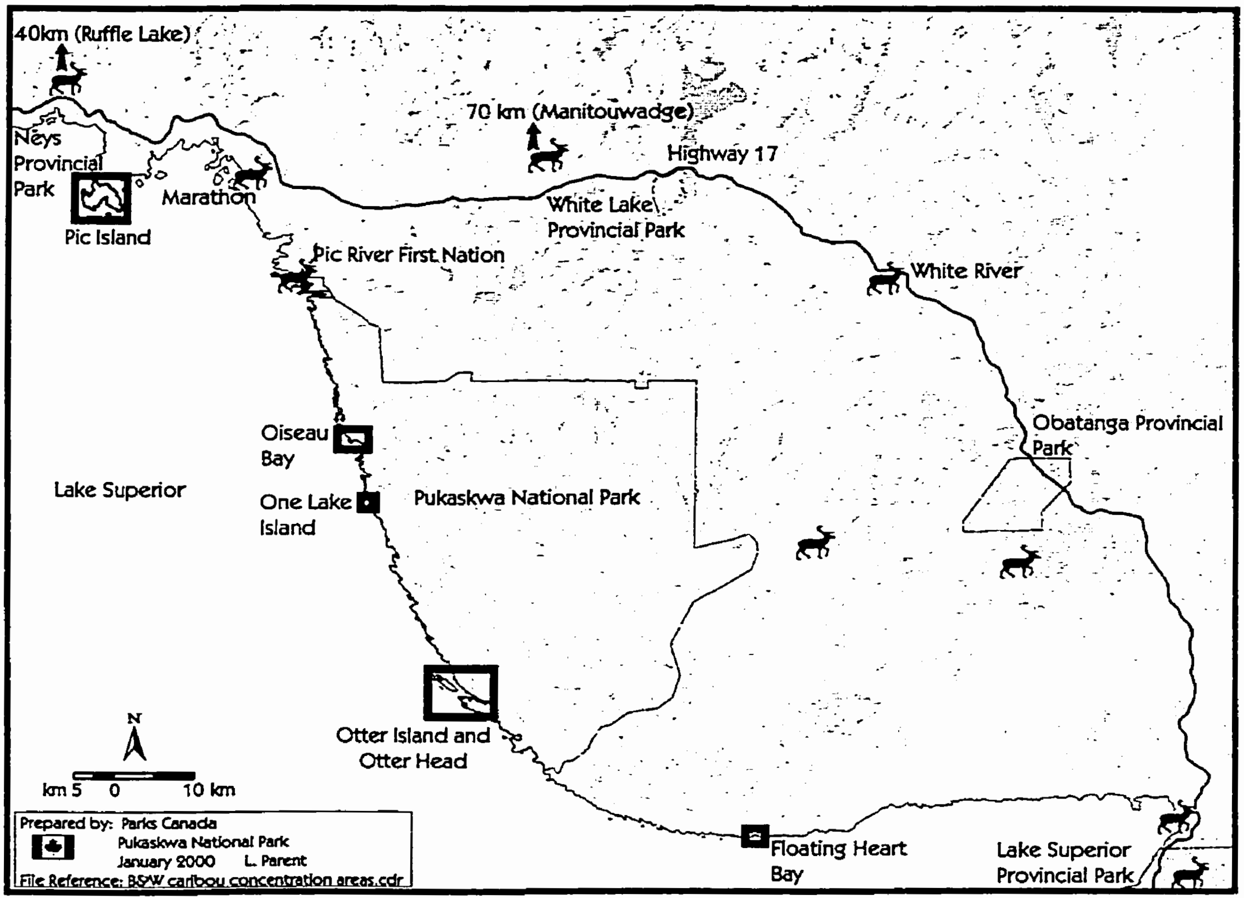


Figure 2-4. Areas of concentration (▣) and other confirmed sightings (🦌) of woodland caribou in the Greater Pukaskwa Ecosystem, 1996 - 1998 (from G. Neale, M.S. Thesis, 1999).

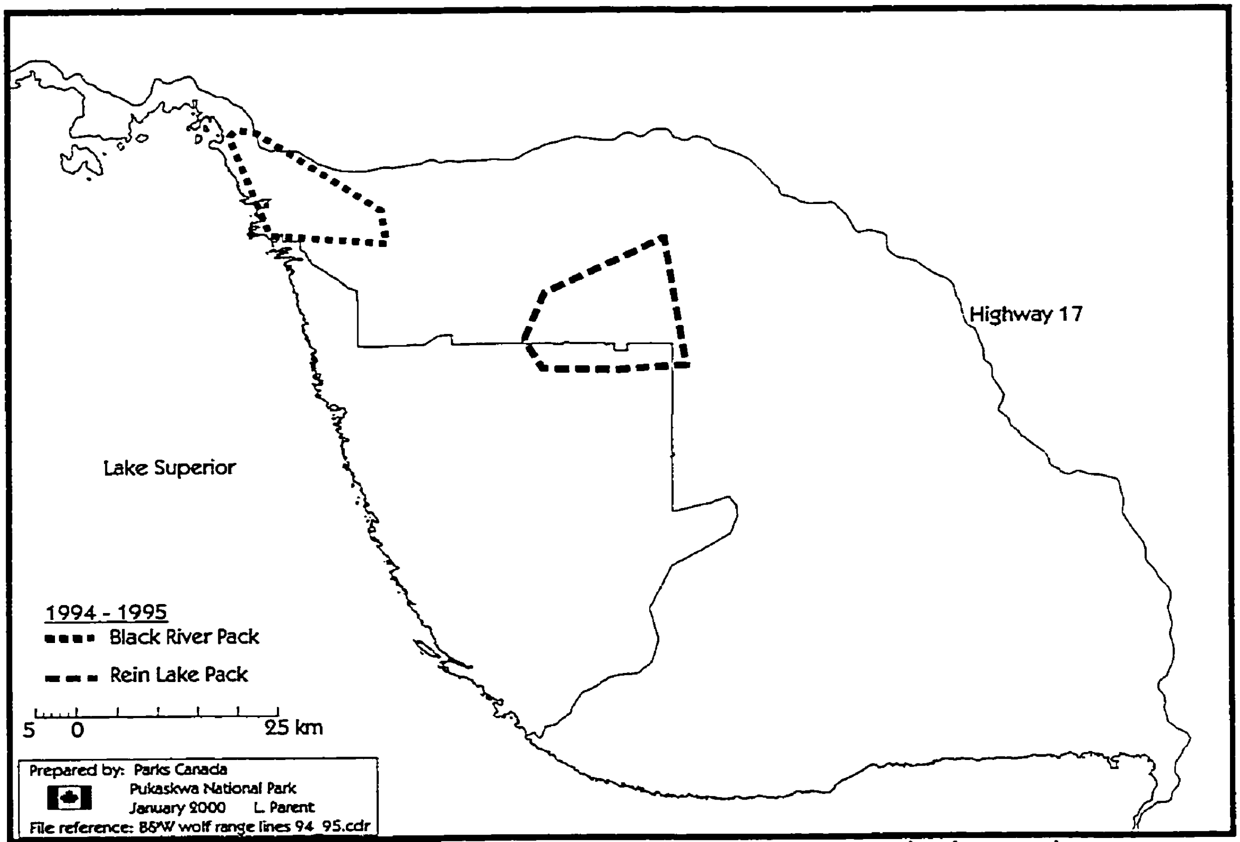


Figure 4-1. Annual (Apr 1 - 1 Mar 31) home ranges of wolves in the study area, 1994 - 1995.

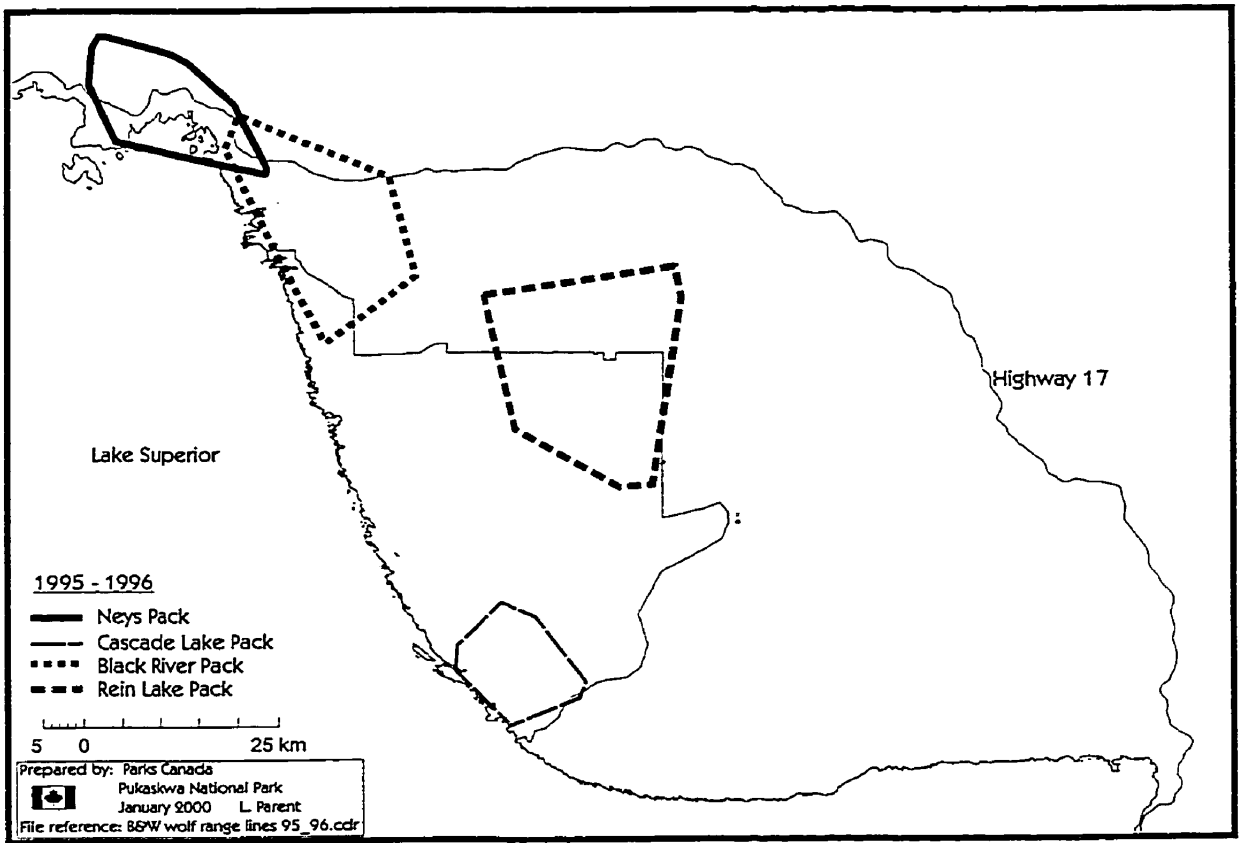


Figure 4-2. Annual (Apr 1 - Mar 31) home ranges of wolves in the study area, 1995 - 1996.

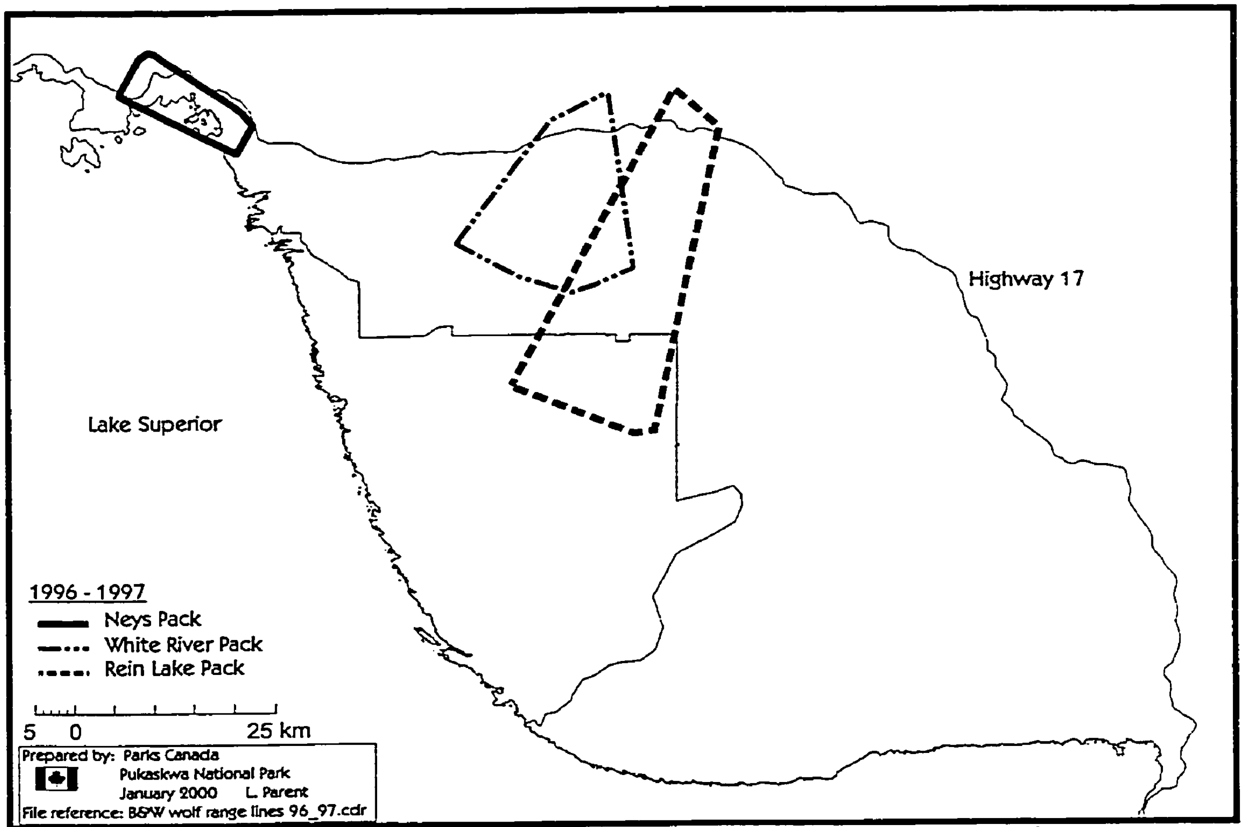


Figure 4-3. Annual (Apr 1 - Mar 31) home ranges of wolves in the study area, 1996 - 1997.

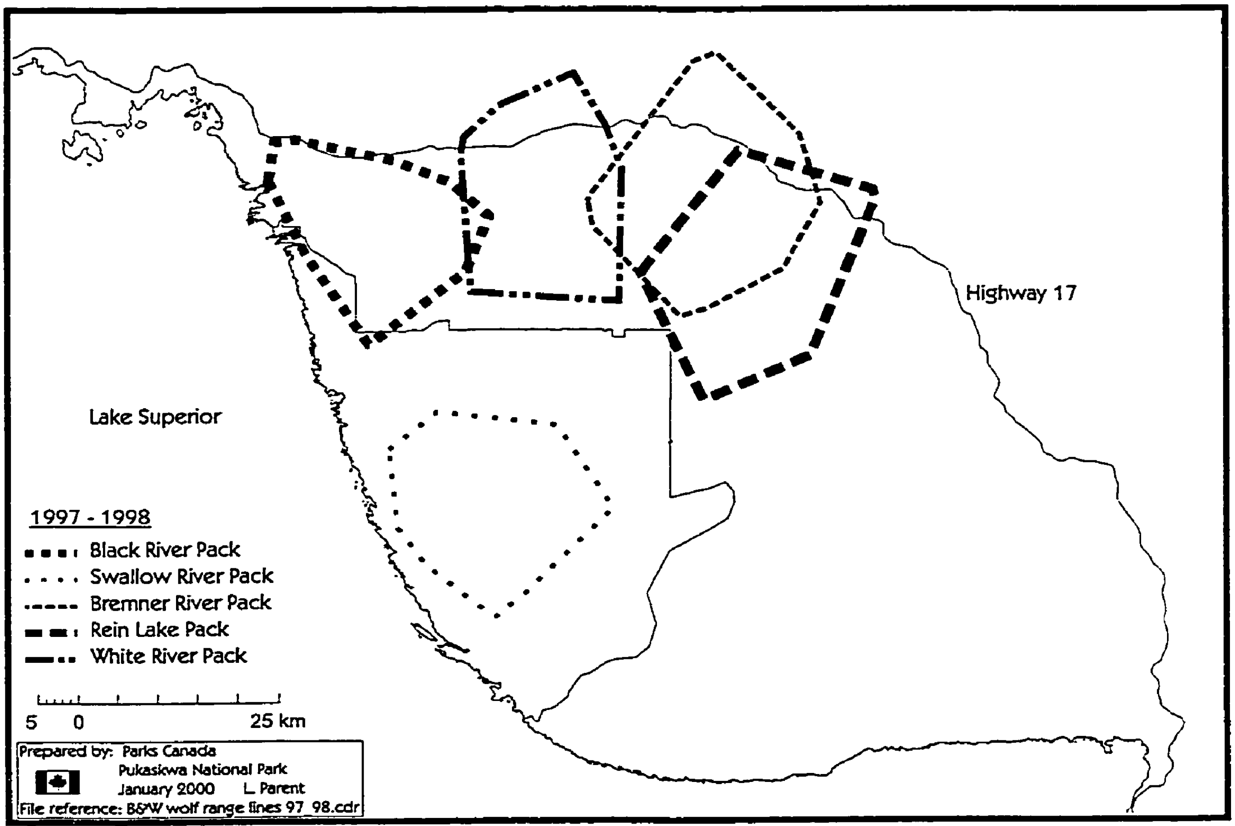


Figure 4-4. Annual (Apr 1 - Mar 31) home ranges of wolves in the study area, 1997 - 1998.

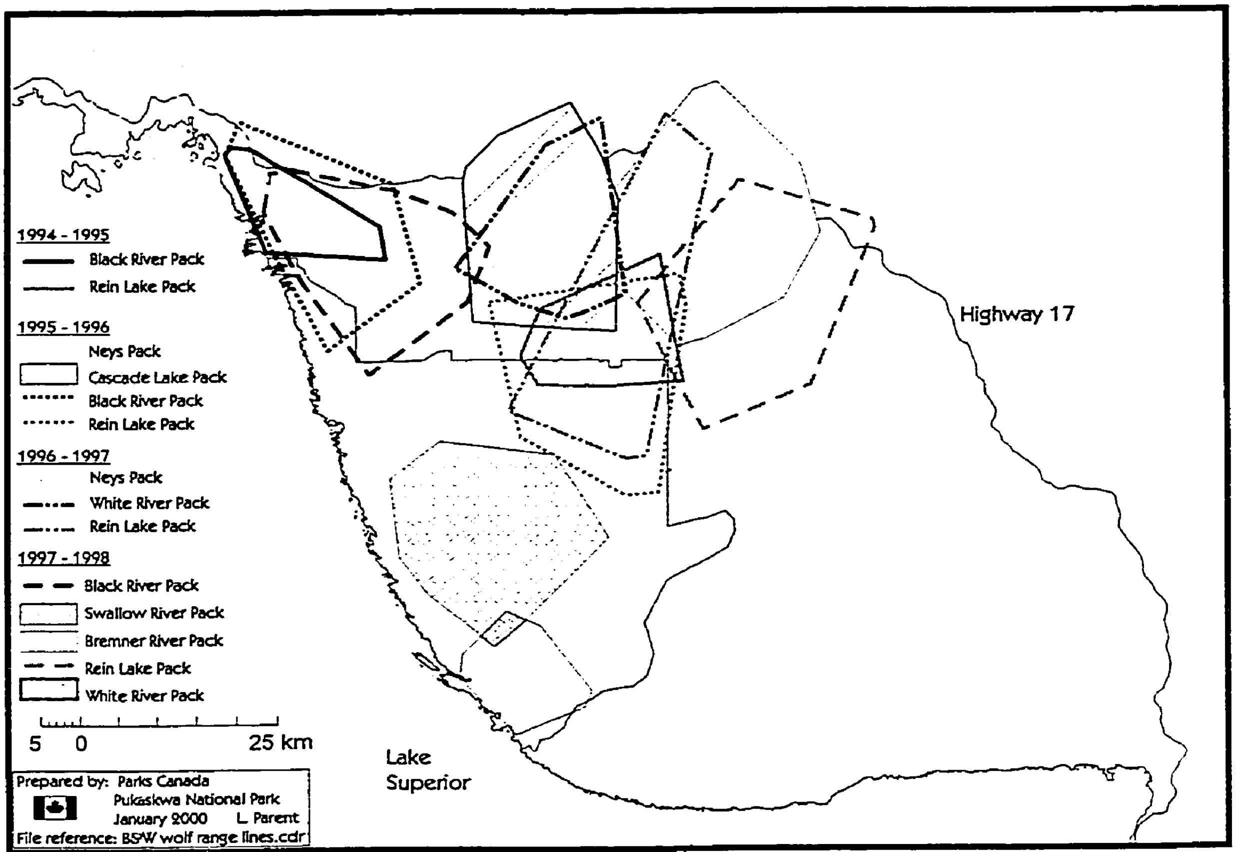


Figure 4-5. Annual (Apr 1 - Mar 31) home ranges of wolves in the study area, 1994 - 1998.

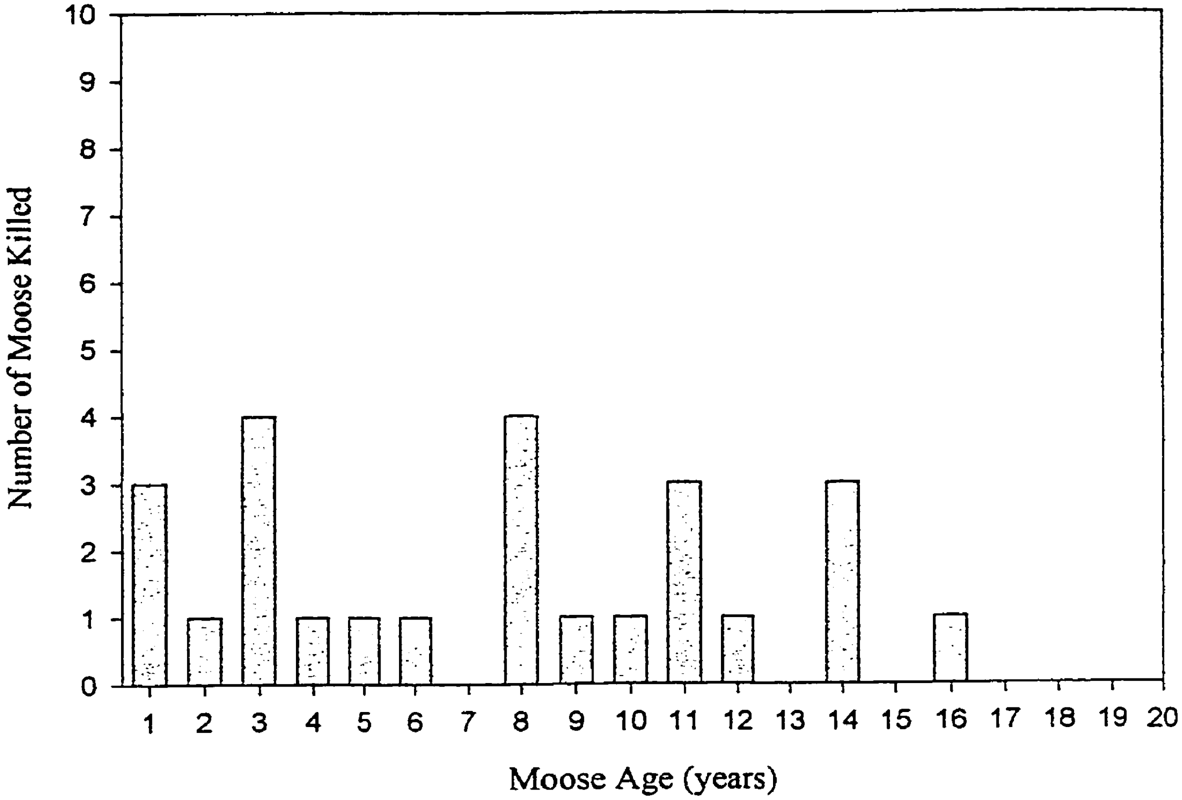


Figure 2-10. Age of 30 moose killed by wolves in the study area, March 1995 - October 1998.

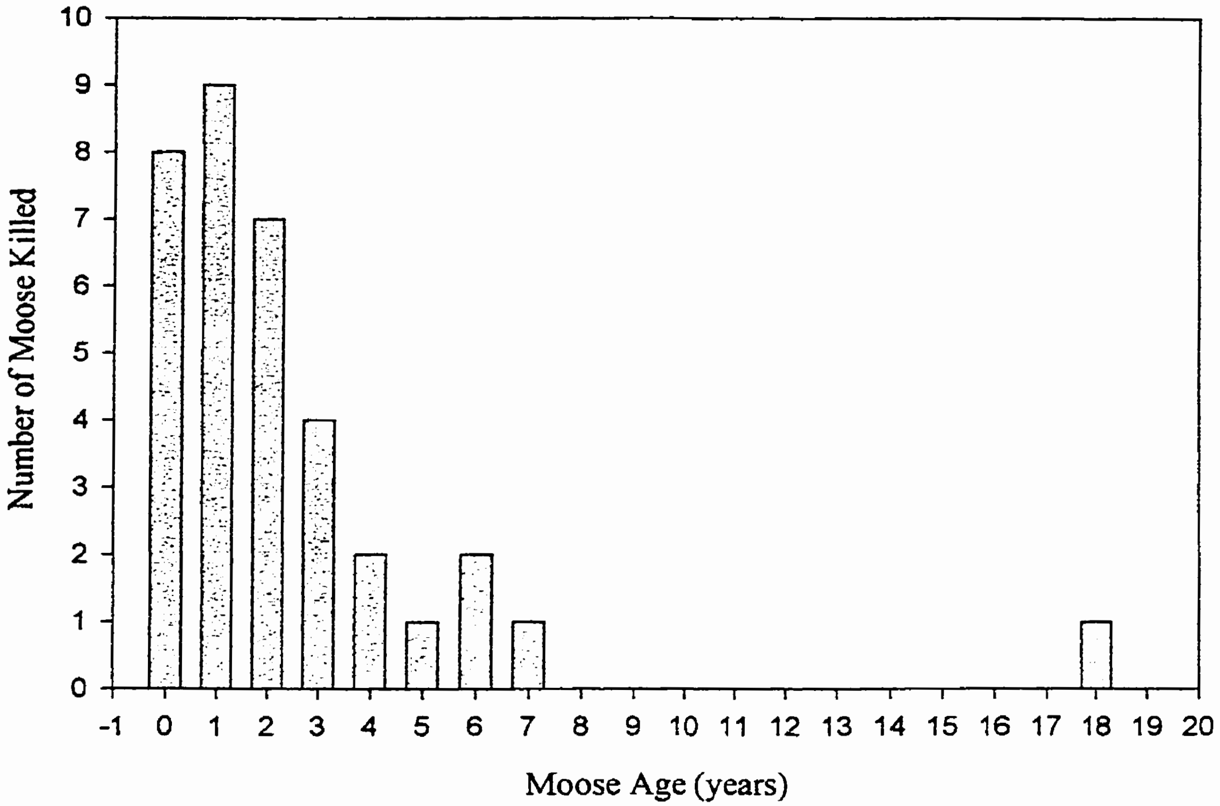


Figure 4-7. Age of 35 moose killed by vehicles, hunters, or moose that died from natural causes in the study area, March 1995 - October 1998.

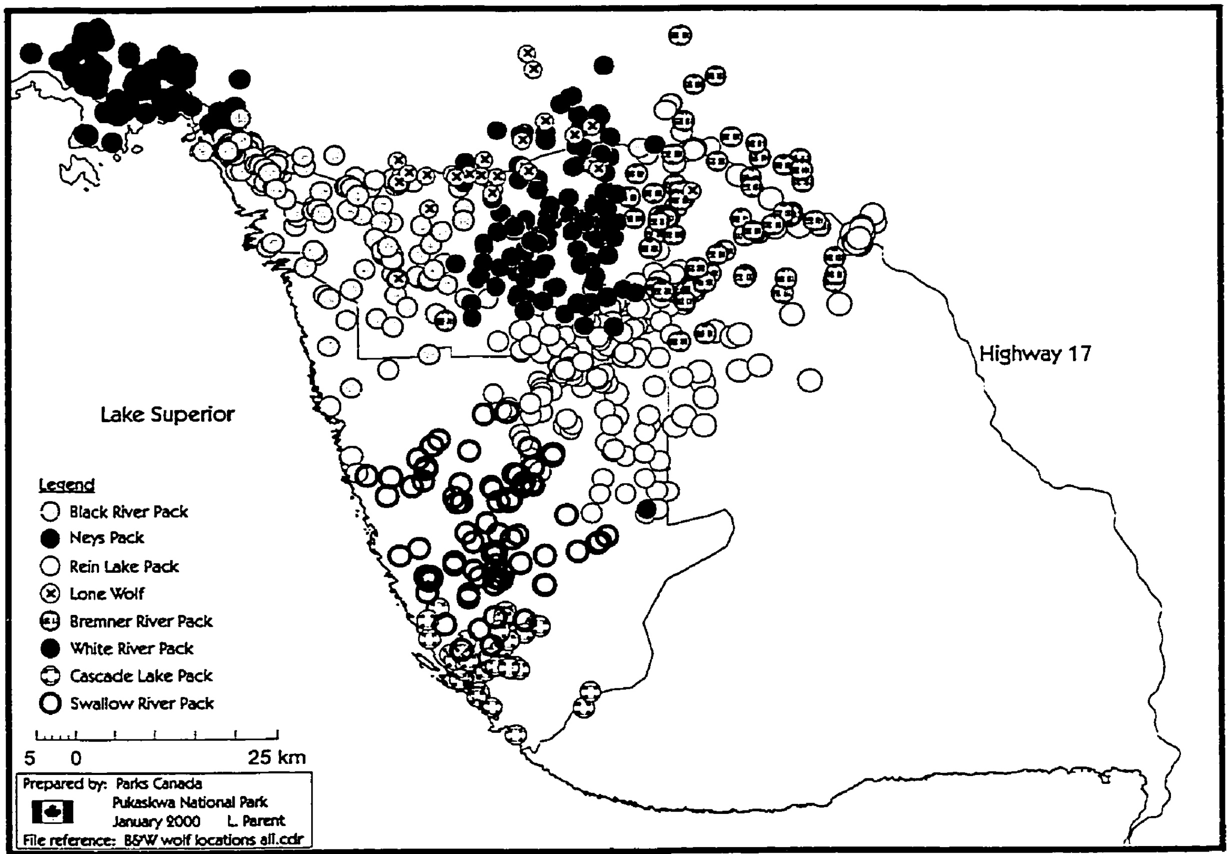


Figure 4-8. Telemetry locations of radio-collared wolves in packs throughout the study area, 1994 - 1998.

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Appendix A. Flight Data Record and Biotelemetry Sheets

Flight Data Record
Pukaskwa National Park

To be completed for each flight.

Date: ____________________

Observer: ________________

Passenger: _______________

Take-Off Time: ______________________________

Landing Time: _____________________________

Total Hours: ______________________________

Total Number of Locations: Moose________ Wolf ________

Minutes per Location: Moose ________ Wolf ________

Comments: ____

____

Bio-Telemetry Data Record
Pukaskwa National Park

Circle choice where appropriate. *areas MUST be recorded.

1. Species: wolf moose caribou	2. Animal Name: ______	*3.Frequency: 15___.____
*4. Observer Frank Anne Keith Gray Other ______	*5.Date dd/mm/yy	
6. Time of Search Start ___:___ hrs	*7. Time of Location ___:___ hrs	8.Total Time (#7 minus#6) ____ minutes
9.Topography: 1.Flat 2.Rolling 3.Hilly 4.Rugged 5.Wetland/lake/river 6. On Lake/River Ice	10.Vegetation Overstory: 1.Conifer >75% 2. Decid >75% 3.Mixed 50/50 4.Cut over 5.Wetland/lake/river 6. Other______	11.Crown Closure: 1.>75% 2.51-75% 3.25-50% 4.<25% 5. Not Applicable
12.Proximity to cut over: 1.<200m 2.200-1000m 3.>1000m	*13. Obtained by: 1. Aerial 2.Railkill 3. Ground 4.Trap/Hunt 5.Capture 6. Report 7.Roadkill 8.Other	14.Activity 1. Standing 5. Unknown 2. Bedded 6. Hunting 3. Moving 7. On kill -ungulate 4. Feeding 8. On kill - other (aquatics,chill) 9.______
15.Aggregation Size ____	16.Photo: 1. Yes 2. No	17. Visual: 1. Yes 2. No
*18.Lat deg/dec min 48°__ __.__ __'	*19. Long deg/dec min 8__°__ __.__ __'	*20. Confidence 1.accurate 2. reasonable 3.questionable 4. No Fix

21. General Location (ie lake/road name, major features - wetland, ridge)

22. UTM E ie. 614000	23. UTM N ie. 5372000	231. No. Of Calves Seen 1.One 2. Two 3. Zero 4. Unkn.
24. Lat dec deg 48°.__ __ __ __	25.Long dec deg 85°.__ __ __ __	

26. Comments (if ground triangulation, record the following:)

Time	Station #	Bearing	Angle of Intersection	Time from 1st to last bearing

Databased By:	Date:

Obs_card.doc April22/97

Appendix B. Pukaskwa National Park Predator Kill Form

Observer(s): ____________________

Sample # : ____________ (year-month-number)

Date Collected: ____________ (d-month-y)

Estimated Date of Death: ____________ (d-month-y)

Est. days at kill: ________

Location (UTMe): ____________

(UTMn): ____________

General Location: ____________________

____

Prey Species: __________

Prey Sex: ________ (M,F,U)

Estimated age of prey: ______
Yoy (<1)
Yly (>=1, <2)
Adult (>2)
Unknown

Marrow Description: ____________

Estimated condition: (Circle one)
Excellent Good Unknown
Fair Poor

Abnormalities??: ____________

Scavengers?? : ____________

Samples Collected: (Circle yes or no)
Hair (include roots, place in a bag) Yes No
Marrow (femur and/or film cannister full) Yes No
Incisor Yes No
Lower Jaw Yes No
Other __________ Yes No
Other __________ Yes No

Predator Species: ______
1=human 2=wolf 3=road 4=rail 5= Other ________

Confidence: ______ 1=high 2=probable 3=unknown

Collared Wolf #1: __________

Collared Wolf #2: __________

Collared Wolf #3: __________

Total Number Wolves: ________

Initial Carcass Use: (Circle one)
1 2 3 4 5
Unknown -1

Final Carcass Use: (Circle one)
1 2 3 4 5
Unknown -1

Chase Length: ________ m

# of Struggles: ________

Wolf Penet. Depth: ________ (cm)

Snow depth: ____________ (cm)

Snow Conditions: (Circle one)
Heavy Crust Light Crust
Fluffy Unknown

Vegetation overstory: ______
1) Conifer > 75%
2) Decid. > 75%
3) Mixed 50/50
4) Cut over
5) Wetland/lake/river
6) Other __________

Vegetation understory: ______
1) >50% Beaked Hazel
2) >50% Mountain Maple
3) >50% Alder
4) > 50% Dogwood
5) Other __________

Comments: ____________________
____
____
____
____
____

Appendix C. Sizes of annual home ranges of 14 wolves in the study area, 1994 – 1998.

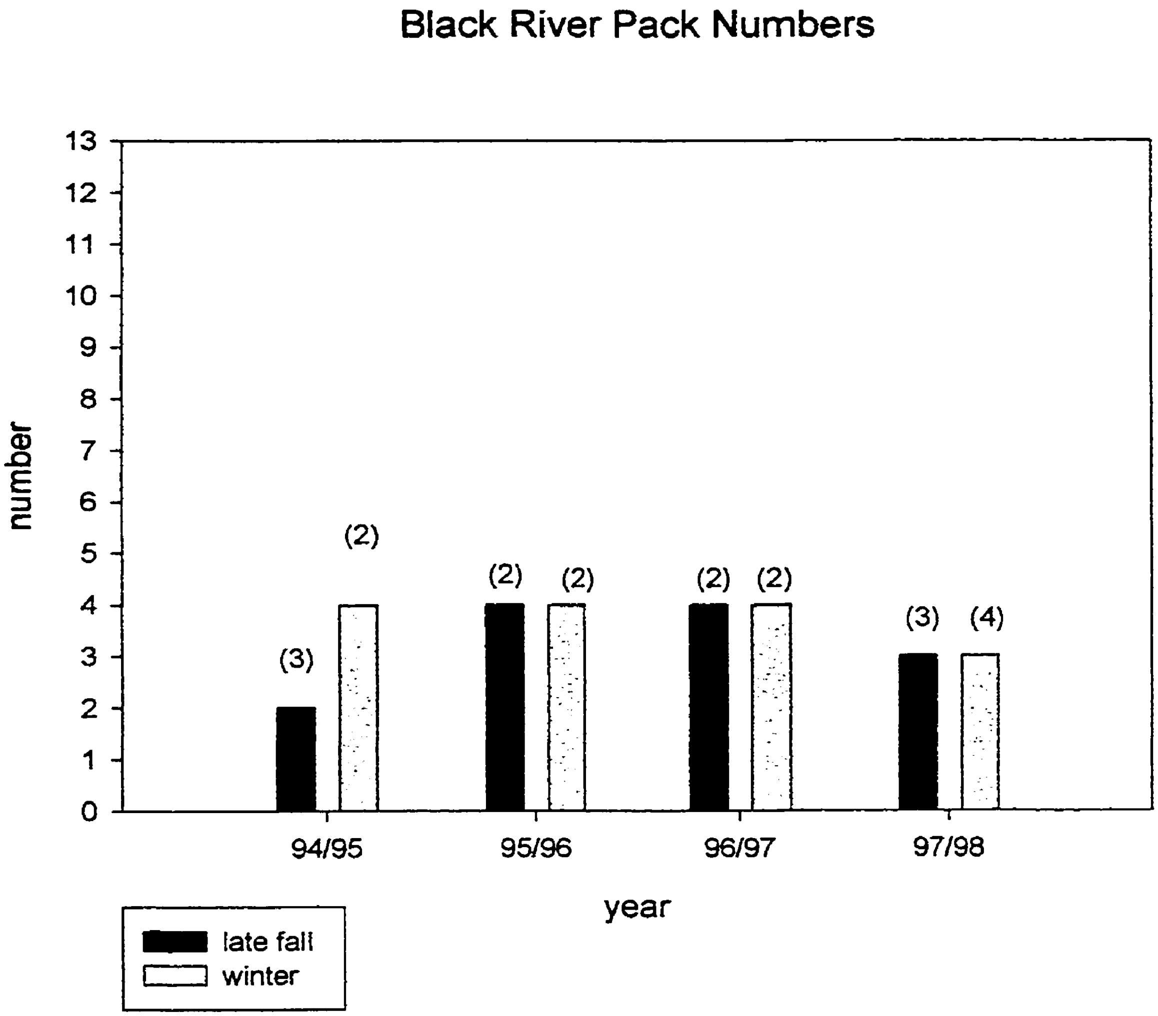
Year	Wolf	Pack	No. of wolves in pack[a]	100%MCP[b] km^2	95%MCP[b] km^2	*n*
1994 - 1995	Sam	Black River	6	283	156	53
	Aldo	Black River	6	282	149	56
	Cassidy	Rein Lake	3	310	249	38
1995 - 1996	Aldo	Black River	4	548	388	55
	Cassidy	Rein Lake	3	600	533	58
	Mika[c]	Cascade River	1	105	92	30
	Solita[c]	Cascade River	1	204	170	26
	Sam	Neys	3			
1996 - 1997	Cassidy	Rein Lake	2	561	557	39
	Star	Rein Lake	2	776	702	37
	Ronja	Neys	6	118	76	77
	Leo	Neys	6	113	101	96
	Charly	Neys	6	98	92	86
	Moon	White River	2	407	345	37
1997 - 1998	Maiingan	Black River	4	468	450	74
	Thunder	Rein Lake	2	692	600	87
	Moon	White River	2	589	498	65
	Bremner	White River	2	609	501	56
	Chaba	Bremner River	6	760	644	92
	Makade	Swallow River	3	567	500	62
	Luz	Swallow River	3	528	483	63

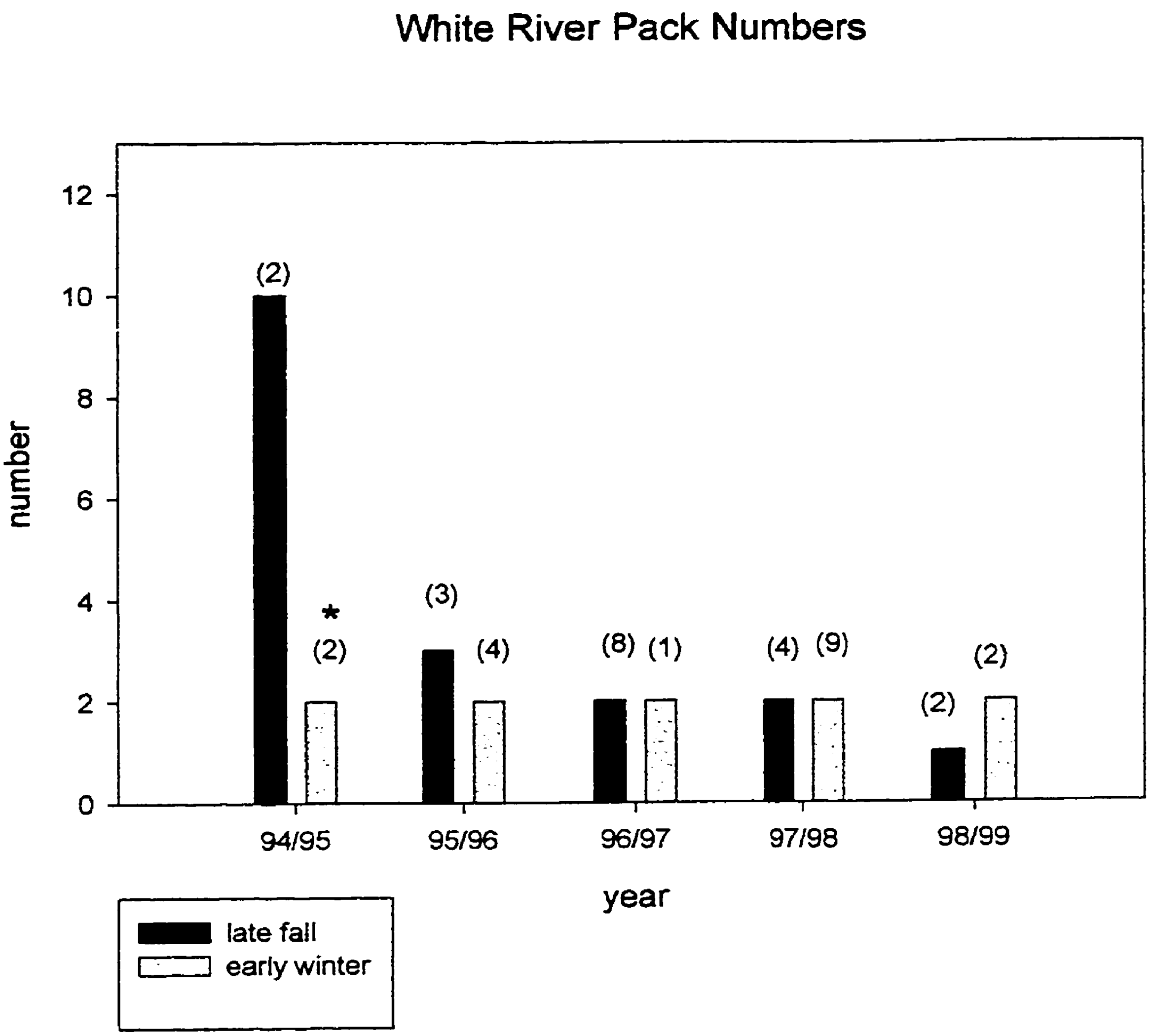
[a] Maximum pack size, January 15 - February 15.

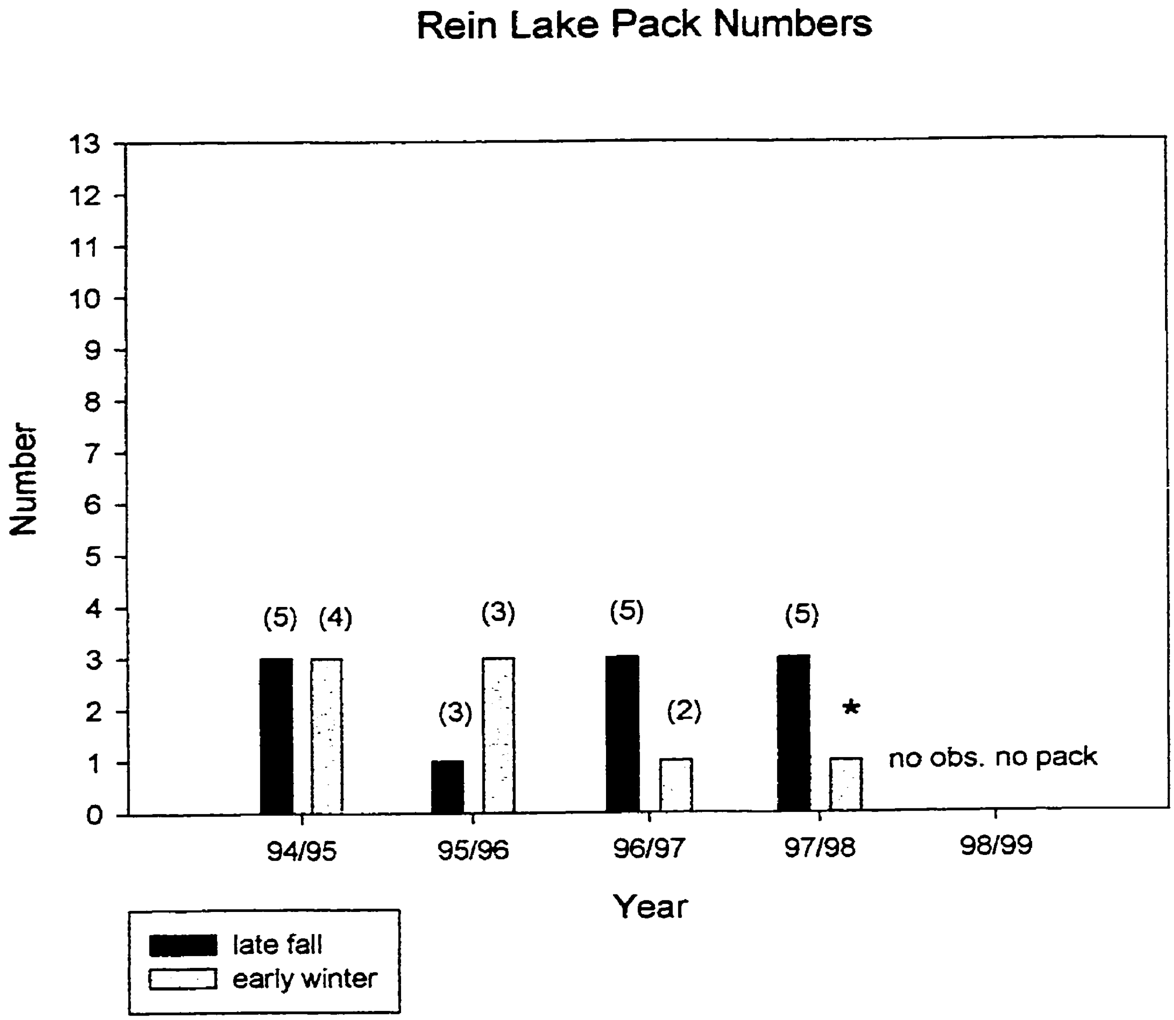
[b] The sizes of home ranges were described using the minimum convex polygon method (MCP) (Mohr 1947).

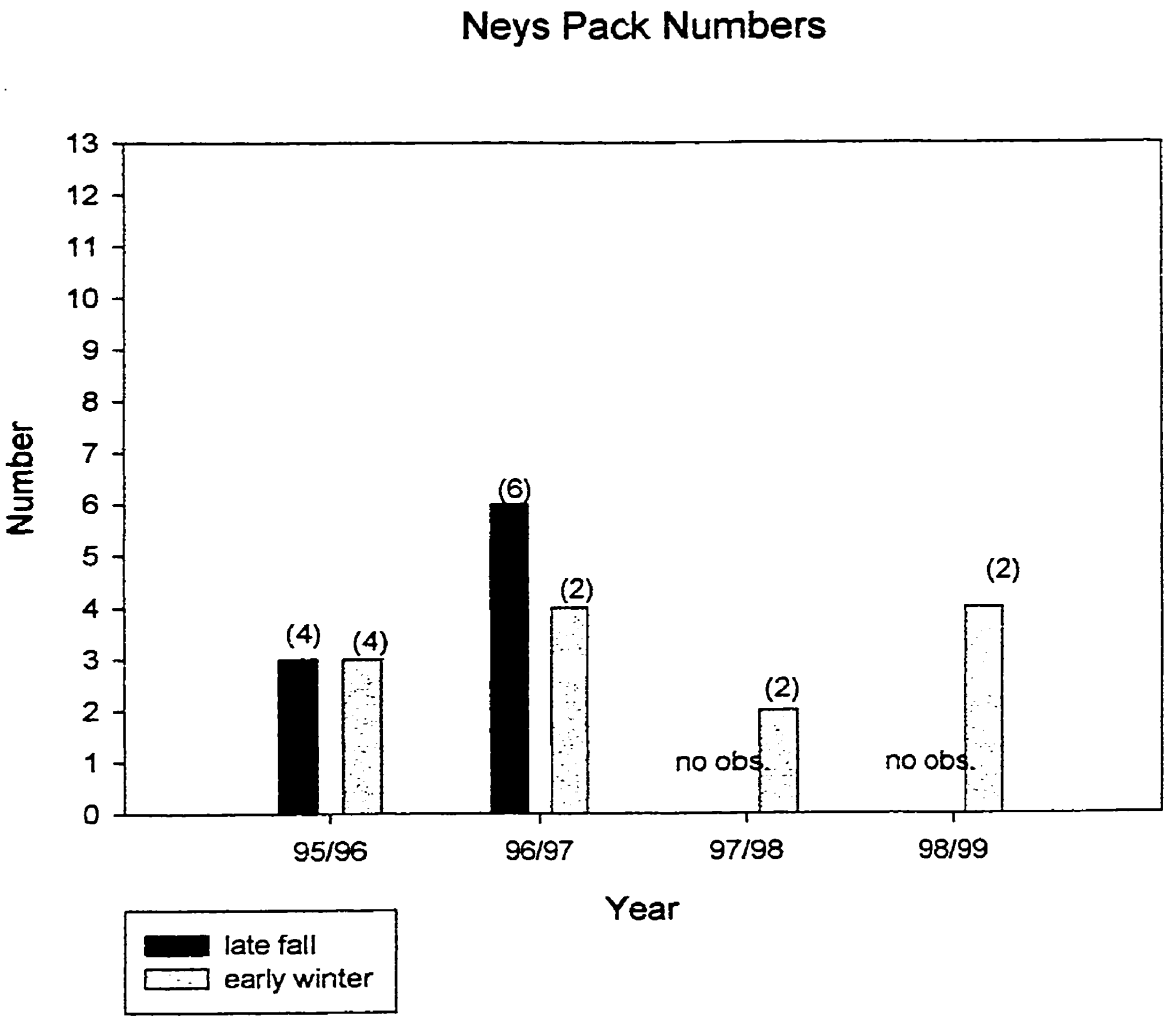
[c] This home range area was not fully defined because wolves were only located between July 1995 and January 1996, instead of the entire season (*e.g.*, April 1 - March 31).

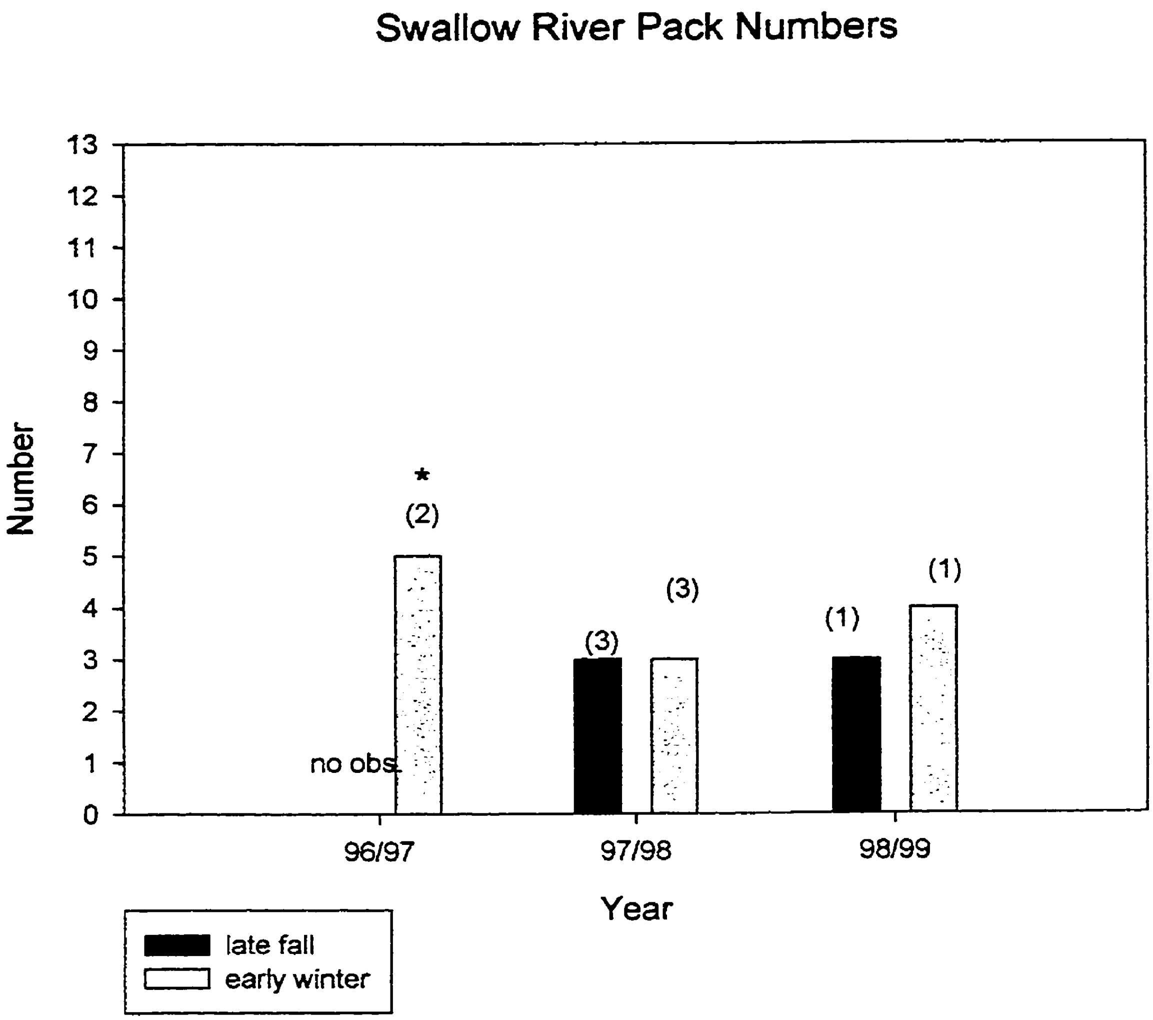
Appendix D. Annual (Apr 1 – Mar 31) late fall (dark; maximum number of wolves observed in Nov - Dec) and late winter (light; maximum number of wolves observed in Mar) wolf numbers in the study area, 1994 – 1999. (#) is the number of pack observations. * includes ground-tracking.

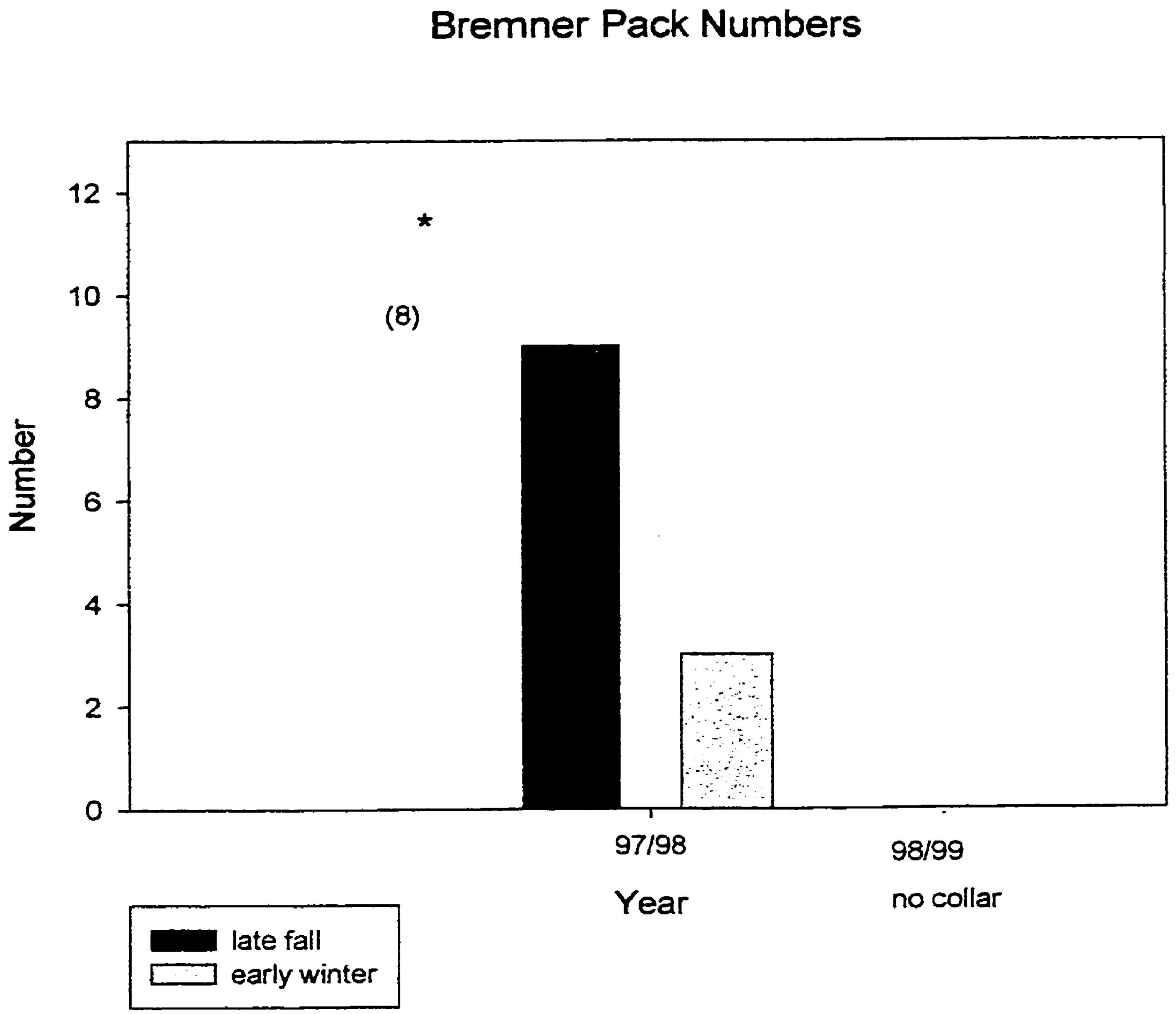



White River Pack Numbers
number
0
2
4
6
8
10
12
(2)
*
(2)
(3)
(4)
(8)
(1)
(4)
(9)
(2)
(2)
94/95
95/96
96/97
97/98
98/99
year
late fall
early winter

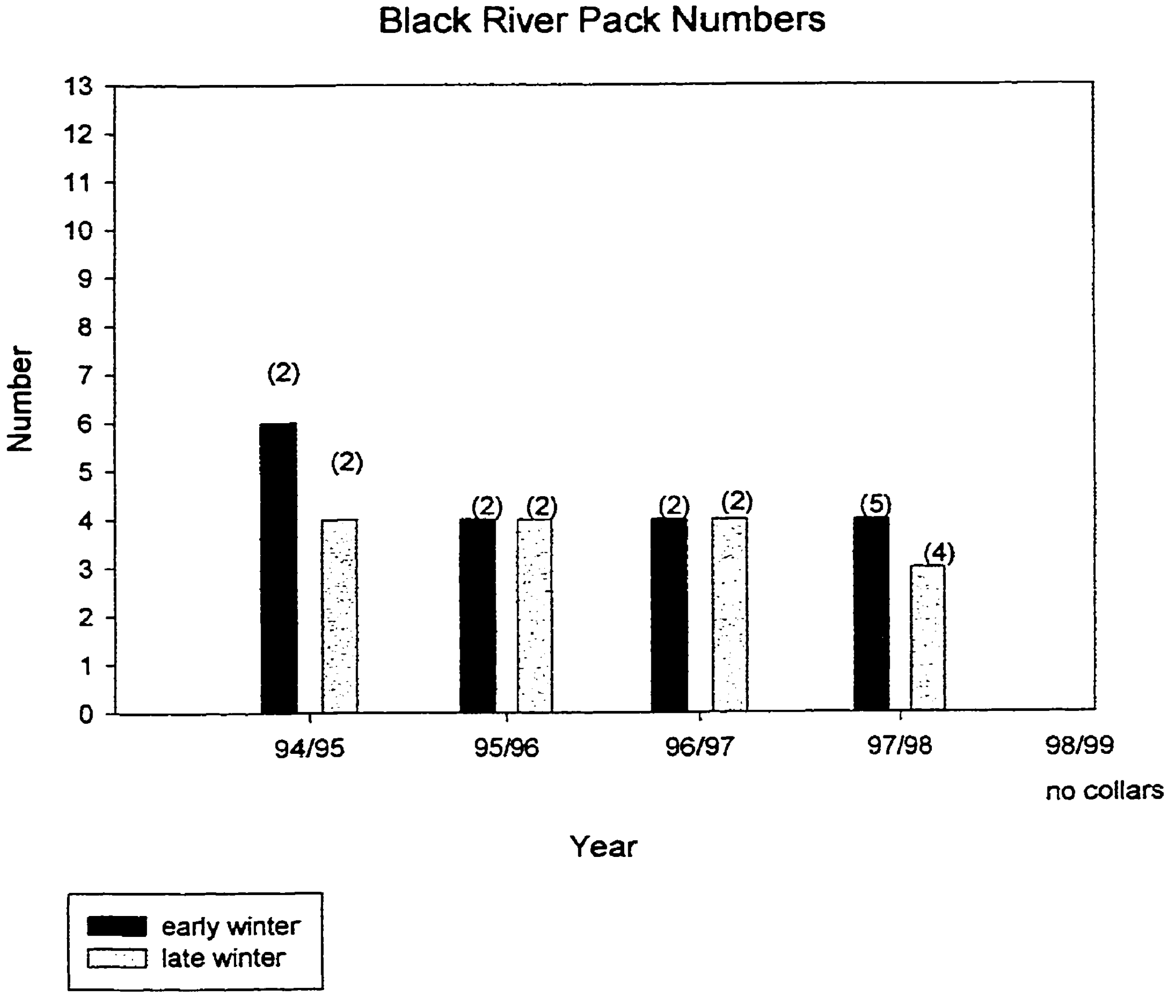

Rein Lake Pack Numbers
Number
13
12
11
10
9
8
7
6
5
4
3
2
1
0
(5)
(4)
(3)
(3)
(5)
(2)
(5)
*
no obs. no pack
94/95
95/96
96/97
97/98
98/99
Year
late fall
early winter

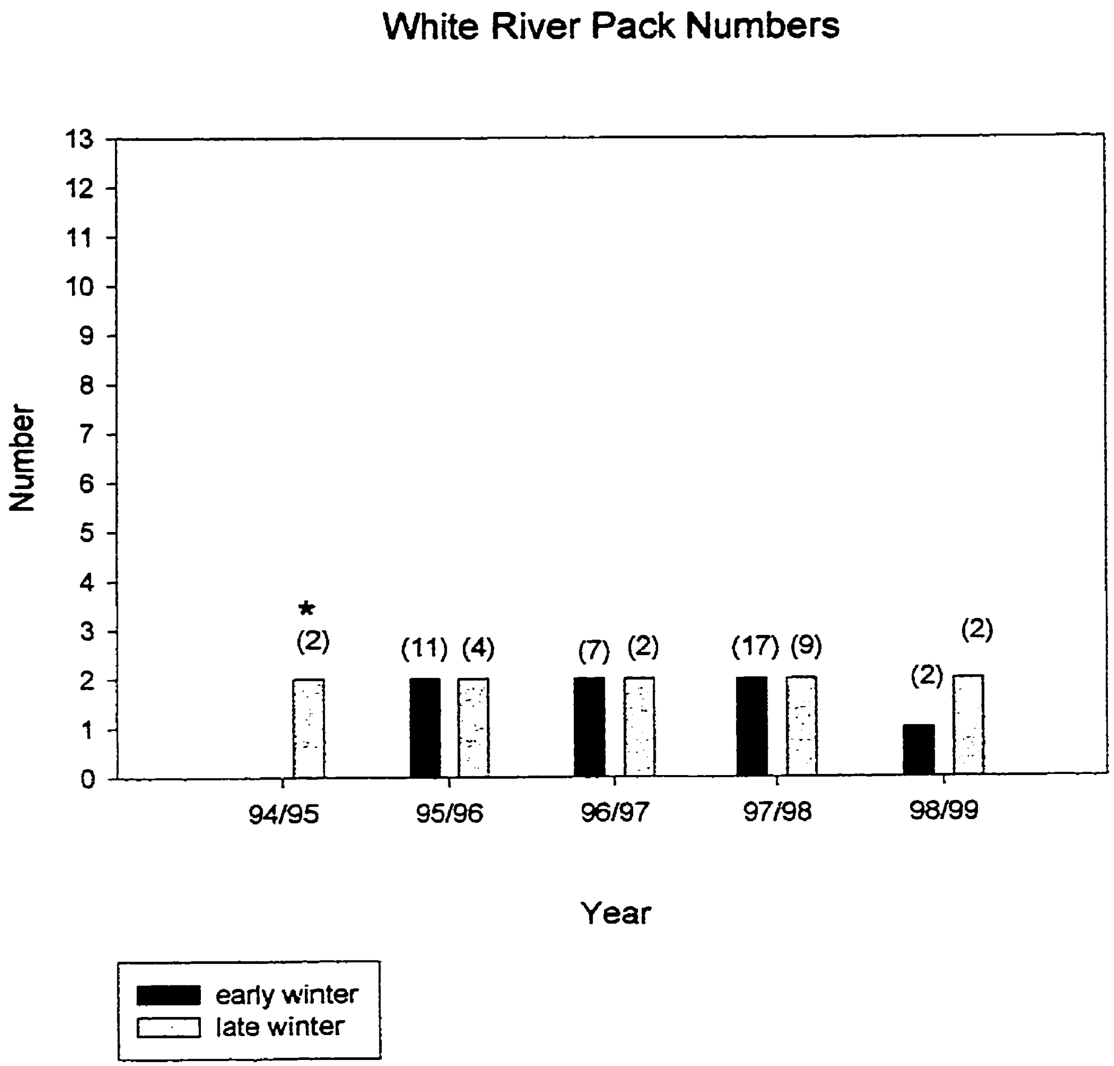

Neys Pack Numbers
Number
13
12
11
10
9
8
7
6
5
4
3
2
1
0
(4)
(4)
(6)
(2)
(2)
(2)
no obs.
no obs.
95/96
96/97
97/98
98/99
Year
late fall
early winter


Swallow River Pack Numbers
Number
13
12
11
10
9
8
7
6
5
4
3
2
1
0
*
(2)
(3)
(3)
(1)
(1)
no obs.
96/97
97/98
98/99
Year
late fall
early winter

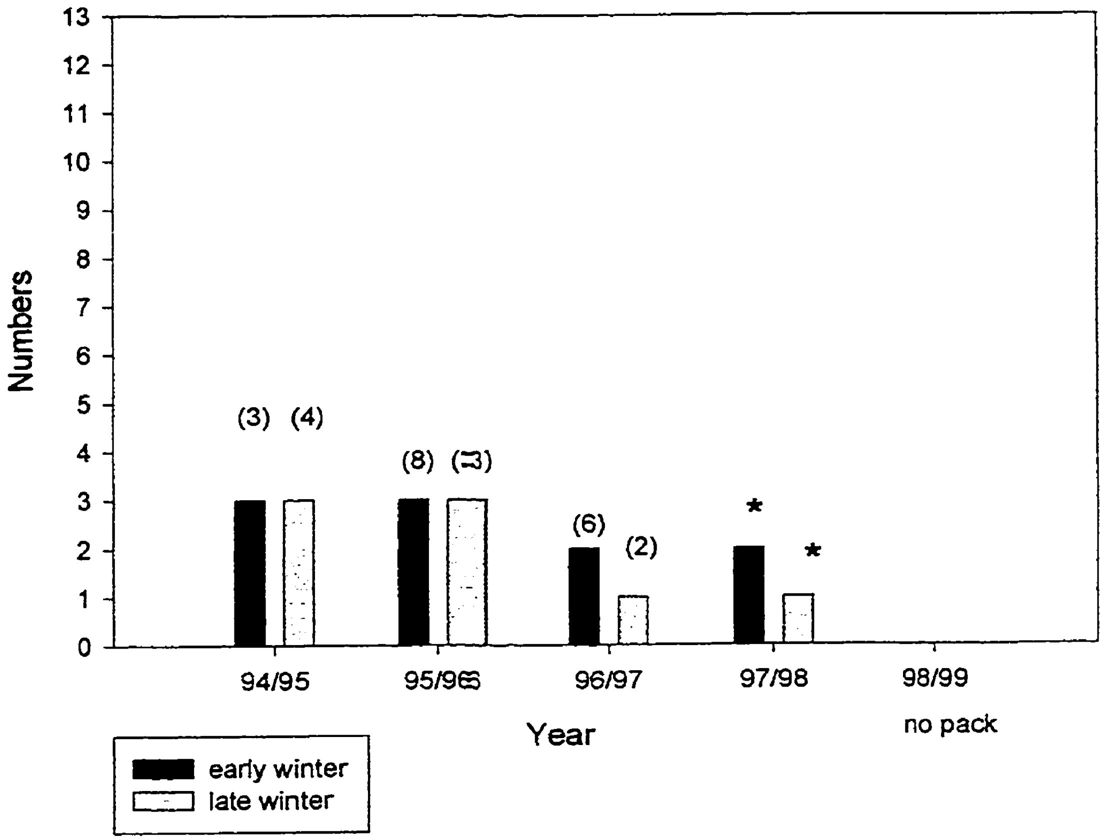

Bremner Pack Numbers
12
10
8
6
4
2
0
Number
*
(8)
97/98
98/99
no collar
Year
late fall
early winter

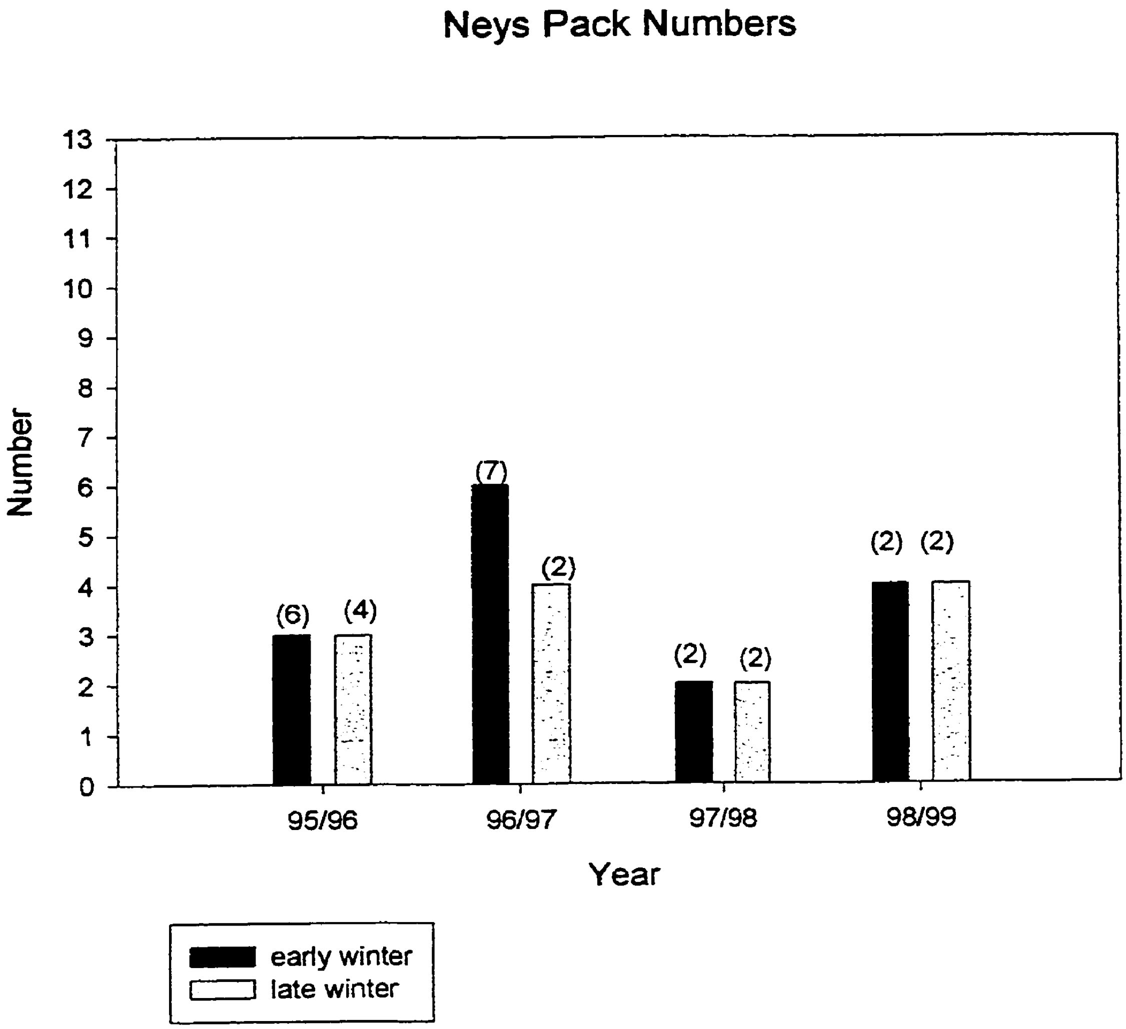
Appendix E. Annual (Apr 1 – Mar 31) early winter (dark; maximum number of wolves observed between Jan 15 – Feb 15) and late winter (light; maximum number of wolves observed in Mar) wolf numbers in the study area, 1994 – 1999. (#) is the number of pack observations. * includes ground-tracking.

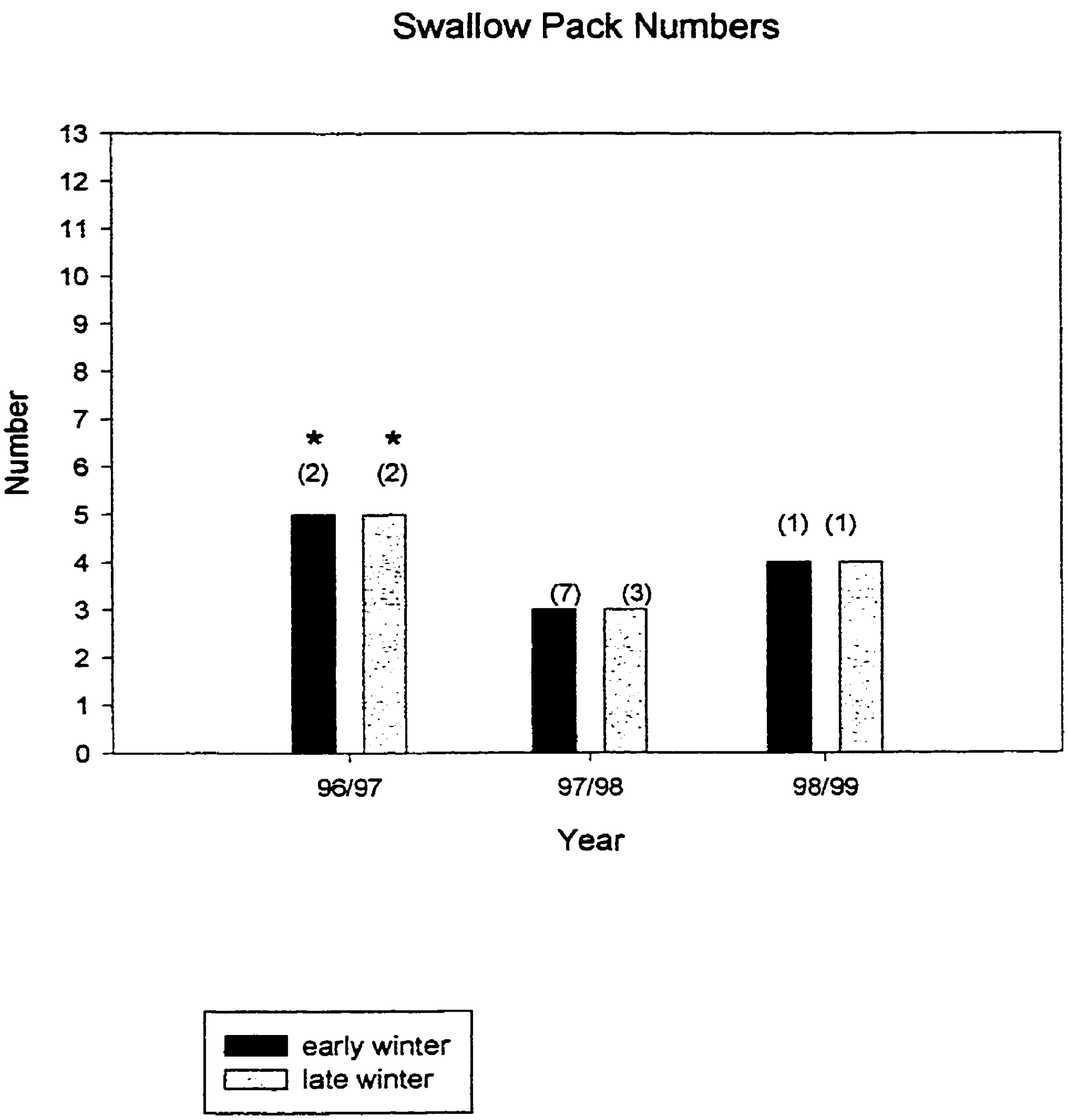


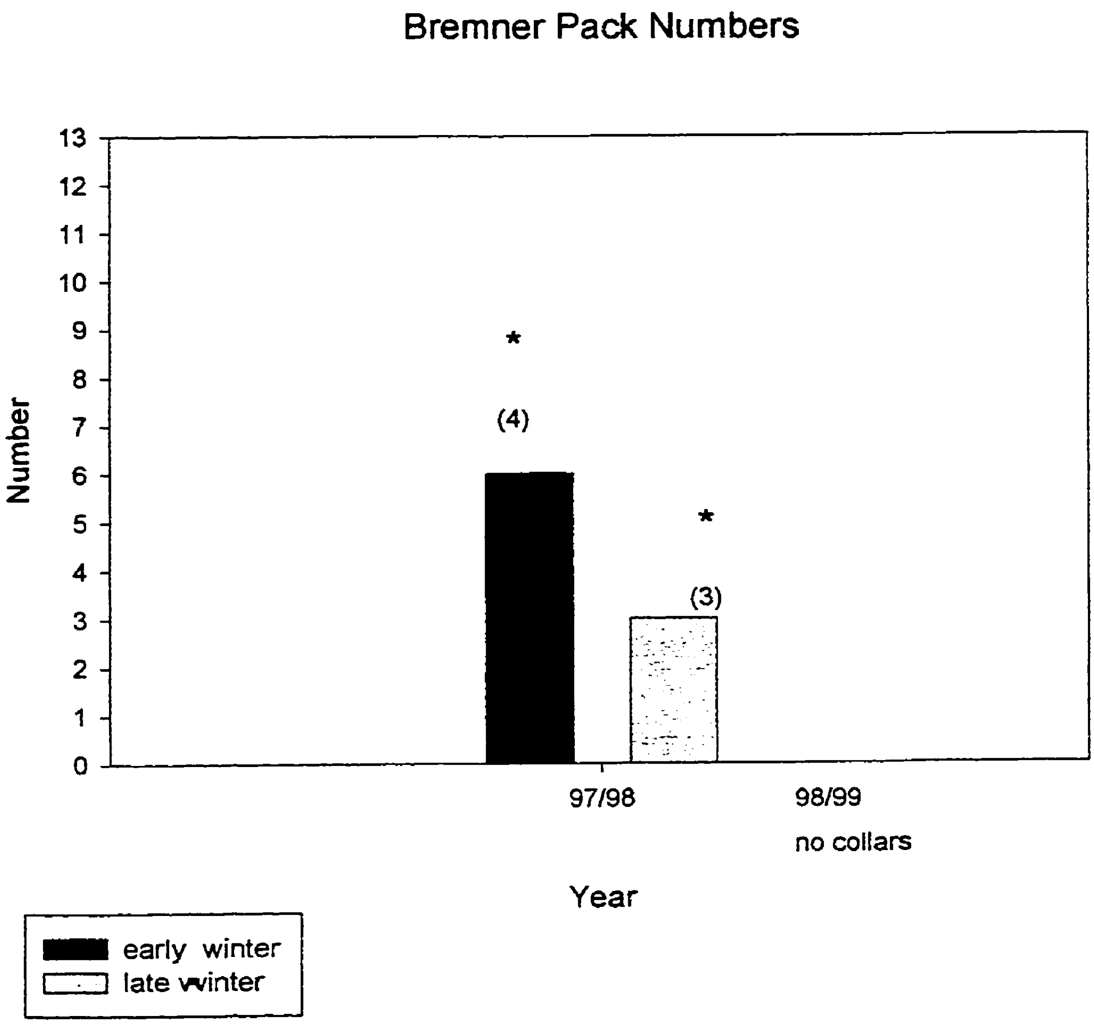

White River Pack Numbers
Number
0
1
2
3
4
5
6
7
8
9
10
11
12
13
*
(2)
(11)
(4)
(7)
(2)
(17)
(9)
(2)
(2)
94/95
95/96
96/97
97/98
98/99
Year
early winter
late winter

Rein: Lake Pack Numbers




Neys Pack Numbers
Number
13
12
11
10
9
8
7
6
5
4
3
2
1
0
(6)
(4)
(7)
(2)
(2)
(2)
(2)
(2)
95/96
96/97
97/98
98/99
Year
early winter
late winter


Swallow Pack Numbers
Number
0
1
2
3
4
5
6
7
8
9
10
11
12
13
*
*
(2)
(2)
(7)
(3)
(1)
(1)
96/97
97/98
98/99
Year
early winter
late winter


Bremner Pack Numbers
Number
0
1
2
3
4
5
6
7
8
9
10
11
12
13
*
(4)
*
(3)
97/98
98/99
no collars
Year
early winter
late winter

Appendix F. Wolves killed on Highway 17 in the study area, October 1995 – August 1998.

Year	Date of death	Location	Age	Sex
1995	Apr 1	Marathon	Adult	M
1995	Oct 1	Marathon	Yoy	F
1996	Mar 1	Marathon	Adult	M
1997	Oct 15	Crocker Lake	Unknown	U
1998	Feb 22	Rouse Lake	Yoy	F
1998	Jun 21	Coldwell Peninsula	Adult	M
1998	Jul 15	White River	Adult	M