NUMERICAL AND FUNCTIONAL RESPONSES OF WOLVES, AND REGULATION OF MOOSE IN THE YUKON

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Robert D. Hayes

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Name: **Robert D. Hayes**

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NUMERICAL AND FUNCTIONAL RESPONSES OF WOLVES, AND REGULATION OF MOOSE IN THE YUKON

Examining Committee:

Chair: Dr. M. Moore, Associate Professor

Dr. A. Harestad, Associate Professor, Senior Supervisor
Department of Biological Sciences, SFU

Dr. R. Ydenberg, Professor
Department of Biological Sciences, SFU

Dr. F. Bunnell, Professor
Department of Forest Sciences, UBC

Dr. E. Cooch, Assistant Professor
Department of Biological Sciences, SFU
Public Examiner

Date Approved 24 August 1995

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NUMERICAL AND FUNCTIONAL RESPONSES OF WOLVES
AND REGULATION OF MOOSE IN THE YUKON

Author:

(signature)

Robert Hayes

(name)

August 22/1995

(date)

Abstract

Numerical and functional responses of wolves (*Canis lupus*) were studied in a 23,000 km^2 area of the east-central Yukon. Populations of wolf, moose (*Alces alces*) and woodland caribou (*Rangifer tarandus caribou*) were increasing following intensive reduction of wolf numbers. Snow-tracking surveys and radiotelemetry studies indicate that the wolf population recovered to pre-reduction densities within 4 years. The area was colonized initially by young wolves that dispersed into vacant territories, and by packs that shifted from the boundaries of the study area. Survival rates of wolves were the highest reported in the published literature. Pack splitting became more common as size of wolf packs increased. Dispersal rates were positively correlated to wolf densities. Wolf numerical response appeared to be tightly regulated by ungulate supply.

Two hundred and ninety-one moose, 30 caribou and 1 mountain sheep (*Ovis dalli*) were found dead during my study. Wolves killed mainly young and old moose and most prey were not nutritionally stressed. Wolf predation was mainly additive mortality to both moose and caribou populations. Killing rates by 21 different wolf packs were studied during 45 periods in late winter. Kill rate of moose by wolves was negatively correlated with wolf pack size but was not correlated with moose density, prey searching rate, snow depth, observation rates, wolf:prey ratios, availability of alternate prey, or snowshoe hare abundance. Also, kill rate of moose calves by wolves was not correlated to wolf pack size, snow depth or calf availability each winter. Wolves in small packs had disproportionately higher kill rates on moose compared to wolves in large packs. Predation by wolves was the main factor limiting recruitment of both moose and caribou, and survival of adult moose.

Wolf functional response was density-independent when moose were between 0.25 and 0.43 moose/km^2. At lower moose densities, a decelerating type II wolf functional response best fit my data, but I could not determine if it is regulatory or anti-regulatory on moose. I combine data from other studies and show that wolf predation could regulate moose to a single low density equilibrium (0.12 moose/km^2) in most wolf:moose systems in North America. My model indicates that bear predation and changes to moose habitat quality have little effect on the stable equilibrium point, where moose are the primary prey of wolves. My model also indicates that no unstable upper density boundary exists beyond which moose could escape the regulating effect of wolf predation. Wildlife managers should not expect permanent benefits for moose from temporary wolf reduction programs in relatively simple wolf:moose systems.

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Introduction

Numerical and functional responses exhibited by wolves (*Canis lupus*) are believed to interact and regulate both the numbers of wolves (Keith 1983) and moose (*Alces alces*) in an area (Messier and Crete 1985, Messier 1994). Wolf density, or numerical response (Solomon 1949), is regulated by the availability of ungulate prey (Packard and Mech 1980, Keith 1983, Messier and Crete 1985, Fuller 1989, Messier 1994). Wolf social behavior determines how tightly wolf numerical response follows changes in food supply (Zimen 1976, Packard and Mech 1980). When prey decline, subsequent declines in wolf numbers lag behind for several years (Mech and Karns 1977, Peterson and Page 1983, Mech 1986), showing that wolf numerical response is relatively loose when ungulate numbers fall. Before my study, data were inadequate to determine how wolves numerically respond when prey are increasing.

Most wolf studies were conducted when prey numbers were stable or declining, or where people caused high wolf mortality (Fritts and Mech 1981, Peterson *et al.* 1984, Ballard *et al.* 1987, Fuller 1989, Hayes *et al.* 1991). Factors that naturally regulate an increasing wolf population were investigated on Isle Royale, Michigan (Peterson and Page 1983, Page 1989). However, Isle Royale is a closed wolf:moose system with limited relevance to open wolf populations elsewhere (Mech 1986).

It is not known how wolves numerically adjust to increasing prey in open systems. If numerical response is loosely regulated by increasing food supply, then wolves could theoretically exceed densities that wolf:prey ratios should stabilize at. A loose lag response could allow wolves to reach higher, unstable densities. Thus, wolves could exert high predation and cause prey to decline back to lower densities through a numerical response alone. If wolf numerical response is sensitive to prey abundance, then wolves should be tightly regulated and stabilize at or below some density that is supported by prey biomass (Pimlott 1967, Keith 1983, Fuller 1989, Messier 1994).

Whether wolf predation has a limiting or a regulatory effect on ungulates is a central debate among wildlife ecologists. Radiotelemetry studies in the 1980s clearly showed wolves are an important limiting factor on ungulates (Fuller and Keith 1980, Keith 1983, Mech 1986, Peterson *et al.* 1984, Gauthier and Theberge 1985, Ballard *et al.* 1987, Fuller 1989, Larsen *et al.* 1989). The evidence is less clear that wolves regulate prey to live within a narrow range of densities (Walters *et al.* 1981, Gasaway *et al.* 1983, Messier and Crete 1985, Sinclair 1989, Messier 1991, Seip 1991a, Seip 1991b, Skogland 1991, Boutin 1992, Gasaway *et al.* 1992, Dale *et al.* 1994, Messier 1994). No study has shown that wolf predation can prevent prey from reaching a higher stable density.

The total wolf predation response is best understood by observing the products of wolf numerical and functional responses across a broad range of prey densities (Theberge 1990, Seip 1991a, Boutin 1992, Dale *et al.* 1994, Messier 1994). The Yukon Fish and Wildlife Branch annually reduced wolf numbers from 1983 to 1989 (Farnell *et al.* unpubl. ms.) to increase woodland caribou (*Rangifer tarandus caribou*) numbers in the Finlayson area. I studied wolf numerical and functional responses from 1990 through 1994, when wolf, moose and caribou numbers were rapidly increasing then all 3 species began to stabilize. The perturbation of the large mammal community provided unique conditions for me to test for the presence of density-dependent processes believed to regulate wolf and prey populations (Keith 1983, Fuller 1989, Gasaway *et al.* 1992, Messier 1994). The reduction of wolves was the first phase of a management experiment that examines specific processes in the long-term dynamics of the wolf/prey community. My thesis describes the second phase, which includes measuring wolf numerical and functional responses after wolf manipulation ended, until wolves began to stabilize. The third phase will examine the large mammal community after wolf and prey populations have stabilized. Two competing wolf-prey models can be compared through this adaptive research approach (Walters and Holling 1990). If wolf predation is density-dependent, then it should eventually regulate prey to live at low density, supporting the Predation Regulation Model (Sinclair 1989, Messier 1994). If wolf predation is density-independent, and prey increase to a higher stable density regulated primarily by food resources, then the Predation-Food Model (Walters *et al.* 1981) is supported; evidence that wolves do not regulate prey to live within a narrow range of densities.

In Chapter 1, I measure wolf numerical response and I assess how tightly an increasing wolf population is regulated by increasing food resources. In Chapter 2, I examine the ecological determinants of kill rate by wolves in winter, and I measure the effect of wolf predation on limiting the size of the Finlayson moose population. In Chapter 3, I examine the contribution of wolf functional response to the regulation of moose at low density.

Study Area

Physiography, Vegetation and Climate

The 23,000 km^2 Finlayson Study Area (FSA) is located in the east-central Yukon (62°N, 128°W), bounded by the home range of the Finlayson caribou herd (Farnell and McDonald 1987). The study area is roughly bordered by the Ross River valley to the west, the Pelly Mountains to the south, and the Logan Mountains to the north and east (Fig. 1).

Oswald and Senyk (1977) described the physiography, vegetation and climate of the region. The Pelly and Logan Mountain ranges are composed of intrusive igneous rock. Most mountains exceed 1,500 m above sea level and peaks commonly rise above 2,000 m. The central study area is part of the Pelly Plateau, a complex of small mountains, forested rolling hills, and plateaus that are separated by broad u-shaped valleys.

Alpine vegetation is dominated by ericaceous shrubs and prostrate willows (*Salix spp.*), except on rocky terrain where lichens are common. Treeline begins at about 1,400 m. Alpine fir (*Abies lasiocarpa*) and white spruce (*Picea glauca*) are the main trees in the subalpine. Lower elevation plateaus are mainly forested by open growing white and black spruce (*Picea mariana*), and lodgepole pine (*Pinus contorta*). Aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) dominate warmer flood plains and exposed slopes. Fruticose lichens are the main ground cover in lower elevation forests, and are the principal winter forage for caribou (Farnell *et al.* unpubl. ms.). In the lowlands, the mean annual temperature ranges from -7 to -4°C. Mean January temperatures range from -35 to -27°C and mean July temperatures range from 13 to 15°C. The large mountain ranges that bound the study area receive the most precipitation. Up to 500 mm of precipitation falls annually in the Pelly Mountains, 750 mm in the Logan Mountains and 250 to 300 mm in lower elevation areas.

Ross River, population 400, is the only human community near the FSA (Fig. 1). Most of my study area is remote wilderness, except along the Robert Campbell Highway

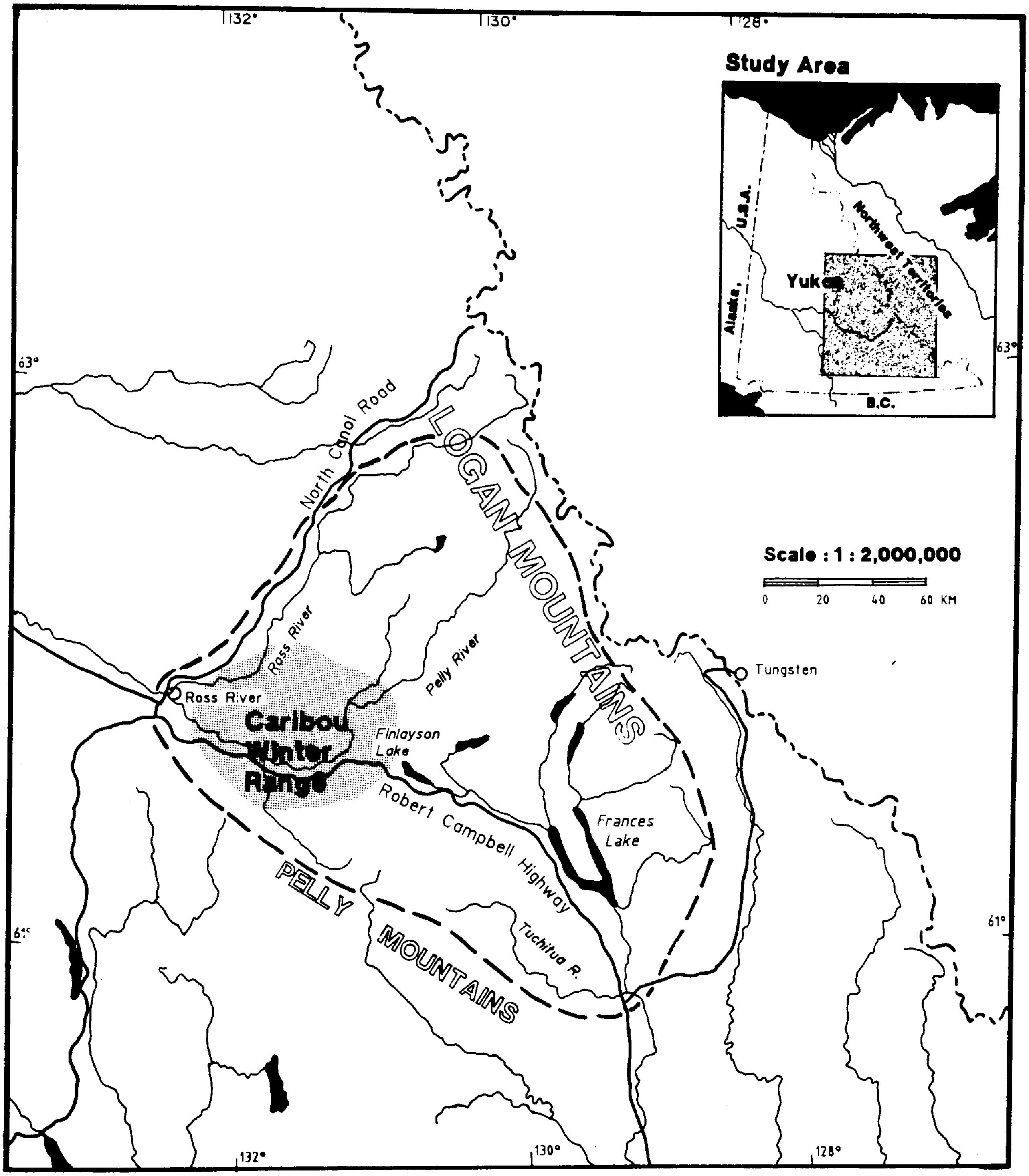


Fig. 1. Location of Finlayson Study Area in the Yukon, Canada.

and North Canol Road. The Robert Campbell Highway bisects the winter range of the Finlayson caribou herd (Fig. 1), and the road is an important winter hunting area for the Ross River First Nation. The North Canol Road is summer-use only and it is an important moose-hunting area in autumn. One big game guide hunts in the southern edge of the FSA. About 10 rural homesteads are scattered throughout the FSA.

Wildlife Populations

From 1983 through 1989, The Yukon Fish and Wildlife Branch annually reduced wolf numbers to less than 20% of their natural density by aerial hunting throughout the range of the Finlayson caribou herd (Farnell *et al.* unpubl. ms.). Before 1983, wolves were lightly harvested (<2% harvested annually). Initially there were 215 wolves in February 1983, for a density of 0.0093 wolves/km^2. Over the next 7 years, wolf density was reduced to 0.0015 wolves/km^2 by 1 April. Wolf density annually recovered to an average of 0.0037 wolves/km^2 by the next February.

The age structure of the wolf population shifted from mostly pups and yearlings in early years of the reduction, to mainly young adult wolves in later years. Reproduction declined from 100% of the packs in 1983 to 42% in later years. At the end of wolf reduction (15 March 1989), 29 known wolves remained in the FSA. My study of the recovery of the wolf population began on 10 January 1990.

The Finlayson caribou herd makes long seasonal movements through the FSA. As winter progresses, the herd moves westward, leaving alpine summering and rutting ranges in the Pelly and Logan Mountains. By late winter, most caribou concentrate in the Pelly River lowlands, where fruticose lichens are abundant and snow fall is the lowest. In April, the herd migrates in a broad arc back into the mountains to calve and spend the summer.

The Finlayson herd is important to the subsistence economy of the Dene people of the Ross River First Nation. In 1982, the herd of about 2,500 caribou was rapidly declining from the combined effects of high hunting mortality and low recruitment (Farnell *et al.* unpubl. ms.).

The herd increased after caribou harvest restrictions and wolf reduction began in 1983. Herd size increased from 3,100 in 1986 to 5,900 in 1990 (Farnell *et al.* unpubl. ms.). Moose are also important subsistence food for people of the region. Jingfors (1988) estimated a density of 0.19 moose/km^2 in the FSA in November 1987, with high calf and yearling recruitment. By November 1991, moose increased to about 0.36/km^2, a mean finite rate of increase of 1.18 per year after 1987 (Larsen and Ward 1995).

Other potential ungulate prey in the area included about 100 Dall sheep (*Ovis dalli dalli*) in the Pelly Mountains and 200 to 300 mountain goats (*Oreamnus americanus*) in the Logan Mountains (Yukon Fish and Wildl. Br. unpubl. data). A small number of mule deer (*Odocoileus hemionus*) live on open slopes along the Pelly River (*pers. observ.*).

Small mammal prey included snowshoe hare (*Lepus americanus*), beaver (*Castor canadensis*) and arctic ground squirrel (*Spermophilus parryi*). Snowshoe hares were abundant from 1989 until 1991 when the hare population crashed (*pers. observ.*). Other carnivores included grizzly bear (*Ursus arctos*), black bear (*Ursus americanus*), wolverine (*Gulo gulo*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and lynx (*Lynx canadensis*). Ravens (*Corvus corax*) were the most important scavengers of wolf kills during winter in my study area (Promberger 1992). Bald eagles (*Haliaeetus leucocephalus*) and golden eagles (*Aquila chrysaetos*) regularly visited wolf kills during March.

Chapter 1

Numerical Response of an Increasing Wolf Population in the Yukon

Introduction

In this chapter, I describe the numerical response of an increasing wolf population after 7 years of intensive reduction. From 1983 through 1989, wolves were annually reduced to below 20% of natural densities in the east central Yukon, as part of a management plan to stop the decline of woodland caribou (Farnell *et al.* unpubl. ms.). After the wolf population was reduced, caribou and moose numbers increased rapidly (Farnell *et al.* unpubl. ms., Jingfors 1988, Larsen and Ward 1995). I report changes to the wolf population within this ecological context.

Wildlife researchers have been concerned about factors that regulate the growth of wolf populations, and the density that wolves stabilize at in relation to prey density. Early wolf researchers (Murie 1944, Cowan 1947, Rausch 1967) found that wolves increased at rates slower than was theoretically possible (Packard and Mech 1980). Pimlott (1967) hypothesized that wolf density was regulated below ungulate food supply through biosocial mechanisms. Early researchers also speculated that wolf populations were limited by various biological and behavioral constraints including: disease, conspecific aggression, social restrictions on breeding, low pup survival, disparate sex ratios, territoriality, surplus of non-breeders and hunting by humans.

A predator population shows tight regulation to fluctuating prey if it quickly returns to a density determined by constant resources, when displaced above or below it (Murdoch 1970). Packard and Mech (1980) proposed that wolves are regulated by a synergistic, two-way feedback with their prey. They argued that changes in food resources ultimately cause changes in wolf social behavior that adjusts wolf reproduction, dispersal and survival rates to eventually balance wolf numbers to food supply. Social factors are thought to influence the lag time, or how tightly wolf numbers adjust to food resources (Packard and Mech 1980). Mech (1986), and Peterson and Page (1983) showed wolf numerical response was loosely regulated by diminishing food resources through a weak negative feedback that caused wolf declines to lag behind prey declines for long periods.

Negative feedback also appears to regulate wolves when prey increase (Pimlott 1967), but there is little information about how tightly wolf numbers are regulated. If feedback is loose then wolves could continue to increase, then temporarily exceed densities that would be predicted by stable food resources (Keith 1983, Fuller 1989). This loose numerical response could then drive prey back to lower density. If feedback is tight, then wolves should theoretically increase, then stabilize in relation to food resources (Keith 1983).

Previous studies (Fritts and Mech 1981, Peterson *et al.* 1984, Ballard *et al.* 1987, Hayes *et al.* 1991) suggest that increasing wolf populations are eventually regulated by ungulate food resources. However, in each study, harvest by humans caused substantial wolf mortality, depressing the wolf numerical response. The only natural study where wolves were responding to increasing prey was on Isle Royale, Michigan (Peterson and Page 1983, 1988; Messier 1991). There, wolf numbers declined as moose density increased (Messier 1991). A subsequent study (Wayne *et al.* 1991) showed that numerical response of wolves on Isle Royale was limited by genetic inbreeding. Depressed numerical response caused by inbreeding has not been observed in other wolf populations.

I studied the natural recovery of wolves in the Finlayson area of the Yukon from 1990 through 1994. During my study, harvest of wolves by humans was very low and had no effect on annual wolf abundance. Low exploitation of wolves by humans allowed me to examine the biosocial mechanisms that naturally regulated wolf density in relation to increasing ungulate populations. My study objectives were to:

1) measure and describe annual changes in wolf population size;
2) describe the annual dynamics of wolf pack formation and development;

3) assess the importance of dispersal, reproduction, survival and natal philopatry to wolf numerical response;
4) identify biosocial factors that regulate increasing wolf numbers; and
5) test my prediction that wolf numerical response is tightly regulated by increasing prey resources.

Methods

Estimating Change in the Abundance of Wolves

I used the finite rate of increase (λ: number of wolves in March of year_{n+1}/number of wolves in March of year_n) to determine annual rates of change in wolf numbers. Winter periods were defined by the last winter month (March). For example, winter 1991 ended 31 March 1991. Biological years for wolves began on 1 May when most pups are born in the central Yukon (*pers. observ.*).

I estimated annual wolf numbers by total counts in February and March 1990 through 1994, using a combination of radiotelemetry (Mech and Karns 1977, Peterson *et al.* 1984, Ballard *et al.* 1987, Messier and Crete 1985, Potvin 1987, Fuller 1989, Hayes *et al.* 1991), aerial snow tracking (Stephenson 1978, Gasaway *et al.* 1983, Hayes *et al.* 1991, Gasaway *et al.* 1992, Farnell *et al.* unpubl. ms.) and ground snow tracking methods (Farnell *et al.* unpubl. ms.).

A total count is suitable for enumerating wolves because most wolves live in packs with minimal spatial overlap (Mech 1970), and they make extensive snow trails that can be followed by trained observers (Stephenson 1978). The 2 requirements of the total count method are: 1) ensuring the complete area is searched, and 2) knowing that groups are not missed or counted twice (Norton-Griffiths 1978). I believe these conditions were met and that annual wolf counts were accurate for the following reasons: 1) study area packs were separated into discrete home ranges; 2) packs traveled in predictable areas (*e.g.*, rivers, creeks, lakes) where prey wintered;

3) wolf trails were extensive, highly visible and easily recognized by experienced observers; 4) wolf habitat was searched between territories until packs were located or observers were confident wolves were not present; and 5) pack duplication was minimal because most FSA packs were radio-tagged each winter, and their locations were known during winter surveys.

Two fixed-wing aircraft crews (PA-18 Supercub and Maule M7) and 1 helicopter crew (Bell 206B) simultaneously flew search routes during wolf censuses. Routes mainly followed water courses and riparian habitats where ungulates wintered, and where wolves were known to travel frequently, based on earlier studies (Farnell *et al.* unpubl. ms.). All alpine areas were searched at least once each winter. In forests, 10-15 km wide transects were flown. Meadows, lake margins and open forests were searched more extensively, where the probability of seeing wolf trails was greatest.

I followed wolf trails until wolves were seen, or until I could estimate the number of wolves by separate track counts. Whenever possible, wolf trails were back-tracked to determine travel routes. Stephenson (1978) found that experienced aerial snow-trackers located 3 times as many wolves as unskilled observers did. I limited observer bias by using the same aircraft crews that conducted 7 years of wolf counts in the FSA during the wolf reduction period. In the core caribou winter range (Fig. 1), I could not rely on aerial snow tracking because wolf trails were usually obscured by the abundance of caribou tracks and feeding craters. To count wolves in caribou range, a field technician traveled by truck and snow machine for up to 15 km along the 160 km stretch of the Robert Campbell Highway between Finlayson Lake and Ross River (Fig. 1). After 1992, most packs in the caribou winter range were radio-tagged, and accurate counts were possible without ground observations.

I estimated wolf density in a 23,000 km^2 area where radio-tagged wolf packs ranged and where wolf trails were regularly observed. Most boundaries followed the center of the Pelly and Logan Mountain ranges where few ungulates wintered and where wolves rarely traveled due to deep snow. Wolves commonly traveled short distances across the study area boundaries along the Ross River and Frances River lowlands.

A wolf pack included groups of 2 or more wolves that traveled together for more than a month (Messier 1994). Single wolves are difficult to count in large areas because it is hard to follow their trails (Mech 1973, Messier 1985a, Fuller 1989). I did not detect changes in the frequency of sightings of single wolves among years. I believe this was because most single wolves paired prior to winter (Fritts and Mech 1981, Fuller 1989), before my annual wolf censuses began. I assumed single wolves represented 10% of the annual winter wolf populations (Mech 1973).

Radiotelemetry and Home Range Use by Wolves

I radio-tagged wolves in all new wolf packs seen during annual censuses in 1990 through 1993. I tried to collar both members of new wolf pairs to monitor their life histories and survival rates for as long as possible. In larger packs, I selected adult wolves for radio-tagging on the basis of their different appearance and behavior compared to subadults (Hayes *et al.* 1991). A helicopter crew immobilized wolves with 2 cc Capchur darts (Palmer Chemical and Equip. Co., Douglasville, GA). Wolves received an average Telazol (A. H. Robins) dosage of 8.0 ± 3.0 (SD) mg/kg (range: 4.4 to 23.4 mg/kg). Wolves were sexed and classified as pup, yearling, 2 or 3 years-old, or older based on tooth coloration and wear, and canine length and eruption patterns (Van Ballenberge *et al.* 1975). Wolves were instrumented with Telonics MOD 500 radio-collars equipped with mortality sensors. Fixed-wing radiotelemetry procedures followed Mech (1974). During my study, 730 fixed-wing hours and 233 helicopter hours were spent capturing, censusing and monitoring wolves.

Home ranges are adequately described when the observation area-curve forms an asymptote. A minimum of 30 to 60 independent radio locations are required to describe most wolf territories (Messier 1985a, Fuller and Snow 1988, Ballard *et al.* 1987). I did not attempt to locate radio-tagged wolves frequently enough to adequately describe annual home ranges. I located wolves a few times in summer and autumn, and I collected nearly all winter locations at daily intervals during predation studies (Chapter 2). I used the 95% area convex polygons (Ackerman *et al.* 1990) to delineate the minimum area used by radio-tagged packs each year, regardless of the number of locations. I combined locations from all years to estimate the total area used by each pack during the entire study period.

Reproduction, Survival, Mortality Causes, and Dispersal of Wolves

I measured reproduction and pup survival during autumn (September to November) and late winter (February through March) each year. I estimated litter size at birth from *corpora lutea* counts of 19 reproducing females killed in 1985 through 1989, during wolf reduction (Farnell *et al.* unpubl. ms.). The same method was used for assessing *in utero* productivity in other wolf studies (Fritts and Mech 1981, Peterson *et al.* 1984, Potvin 1987, Fuller 1989, Boertje and Stephenson 1992). During autumn, I counted wolf pups from the air on the basis of their small size and subordinate behavior (Harrington *et al.* 1983, Peterson and Page 1988). I determined the number of pups that survived from birth to November by comparing pack size in November from pack size the previous March (Harrington *et al.* 1983), then I subtracted the difference from mean litter size. This method was reasonable for estimating pup survival among pairs because I could assume that any increase in pack size the next autumn was from the addition of pups. I did not estimate pup numbers by this method after 2 generations of pups were produced, because I did not know the influence of subadult dispersal on pack size changes.

I estimated annual survival rate of wolves using a Kaplan-Meier (K-M) procedure modified for staggered entry of radio-tagged individuals (Pollock *et al.* 1989a, 1989b). I assumed newly tagged wolves had the same survival probability as previously tagged animals. I calculated bounds on survival estimates by censoring wolves that I lost radio contact with due to either dispersal or transmitter failure. The K-M procedure assumes survival rates of individuals are independent (Pollock *et al.* 1989a, 1989b). My data fails this assumption because of the strong social nature of wolves. For example, the death of a parent wolf should reduce the survival rate of its pups and yearlings. This violation will not cause bias but will produce smaller variances for survival probabilities than are true in nature (Pollock *et al.* 1989a). In addition to FSA packs, survival analyses included 3 radio-tagged wolves from the Lapie River pack located on my study area boundary.

I could not determine most causes of most wolf mortalities because radio-tagged wolves were monitored too infrequently throughout the year. I separated mortalities of radio-tagged wolves into human or natural causes. Hunting and trapping mortalities were voluntarily reported by the public. I assumed that a wolf died from natural causes if it was found a long distance from town or roads.

I indirectly estimated the importance of conspecific mortality by comparing the location of death sites of radio-tagged wolves in relation to their pack territory boundaries. Wolves tend to avoid territorial boundary areas (Taylor and Pekins 1991) where conspecific mortality is highest (Mech 1994), supporting the hypothesis that wolves face higher risks of fatal encounters with other wolves along territorial edges than they do in the center of their territories (Hoskinson and Mech 1976). Because I did not determine annual home ranges, I compared the death site of wolves to the pooled 95% minimum-convex polygon areas for all pack location points during my study. I then measured the distance from the death site to the nearest edge of the polygon edge of the wolf's pack territory (Mech 1994). Intraspecific mortality was assumed if a radio-tagged wolf died within 5 km of its territory boundary. I assumed that a wolf dispersed if it permanently left its original pack and either formed a new pack or joined an existing one (Messier 1985b).

Estimating Changes in Abundance of Caribou and Moose, and Prey Biomass/Wolf Index

I estimated annual rates of increase in ungulate population sizes by interpolation from stratified random censuses. The Finlayson caribou herd was censused in 1986 and 1990

(Farnell *et al.* unpubl. ms.), and moose were censused in 1987 and 1991 (Larsen and Ward 1995). From census interpolations, mean annual mortality rates were derived for adult moose (0.095, Larsen and Ward 1995) and adult caribou (0.110, Farnell *et al.* unpubl. ms.). In later years, no censuses were conducted and I estimated the annual changes in population size of moose and caribou (Appendix A) by subtracting the above adult mortality rates from caribou calf recruitment indices in autumn (Farnell *et al.* unpubl. ms), and from moose calf recruitment indices in March. The percent moose calves in my March counts was modestly higher (mean difference = 3.7 ± 0.6% [SE], t = 2.6, df = 4, P = 0.06) compared to November counts (Jingfors 1988, Larsen and Ward 1995). Calves tend to be underestimated in autumn counts because females with calves occupy more cryptic habitats. Thus, maternal females are more often missed compared to females without calves (Gasaway *et al.* 1986). I believe that moose composition counts in late winter are a reasonable estimate of annual recruitment because moose age and sex classes are well mixed and visible in most habitats, and a large sample of moose can be seen in a short period (R. Florkiewicz, Yukon Fish and Wildl. Br., unpubl. data).

Mean density of moose in 1991 was 0.36 moose/km^2 of habitable moose range (HMR) in the FSA (Larsen and Ward 1995). I estimated the total HMR in the study area by including all areas below 1,500 m (75% of total area), using a digital planimeter on 1:250,000 topographic maps.

The ratio of ungulate biomass:wolf was determined for late winter 1994 (Appendix C) following methods of Fuller (1989). Biomass of prey was weighted as follows: moose (6), caribou (2), mountain sheep, mountain goats and mule deer (1) (Keith 1983, Ballard *et al.* 1987, Fuller 1989).

Results

Radiotelemetry

I radio-tagged 78 wolves (40 F, 38 M; Appendix B) including 75 wolves in packs and 3 single wolves. Of the 75 pack wolves, 57 were tagged once, 16 were tagged twice and 2 wolves were tagged 3 times to maintain radio contact with packs. Radio-tagged wolves included 45 adults (59%), 24 yearlings (32%) and 9 pups (9%) (Fig. 2). No wolves suffered serious injury or died from being captured. I radio-tagged wolves in 26 of the 37 (70%) FSA packs during my study (Table 1, Fig. 3). An average of 71% (range: 46 to 88%) of packs were radio-tagged each winter. I radio-tagged 21 packs in the first year they appeared in the FSA, 4 packs in their second year, and 1 pack in its third year. The monitoring schedule was as follows: 22 tagged wolves in 11 packs in 1990, 38 in 18 packs in 1991, 39 in 22 packs in 1992, 44 in 18 packs in 1993, and 24 in 12 packs in 1994 (Table 1). By 1994, I lost radio contact with 14 of the 26 packs due to wolf deaths, dispersals or transmitter failures.

I located radio-tagged wolves by fixed-wing aircraft 2,017 times from 8 February 1990 to 31 March 1994: 1,723 (85%) locations were made in winter (1 December to 31 March), 164 (8%) in summer (1 June to 31 August), and 130 (6%) in autumn (1 September to 30 November). I made nearly all winter observations during February and March as part of predation studies (Chapter 2). I monitored radio-tagged wolves for a total of 1,374 wolf-months, and I followed individuals for an average of 18.6 ± 1.7 (SE) months (range: 1 to 49 months). I followed packs for an average of 73 ± 7.4 (SE) months and located pack members an average of 13 ± 1.1 (SE) days each year (range: 4 to 19 days); too infrequently to empirically define annual home range sizes.

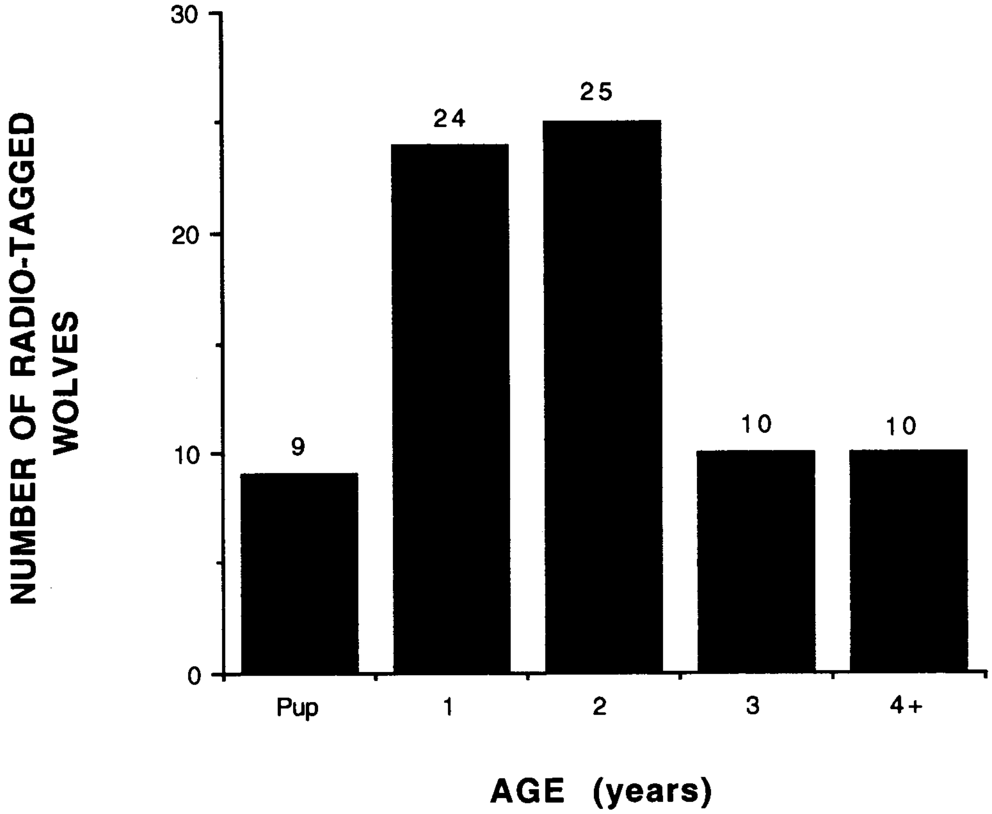


Fig. 2. Ages of wolves when they were radio-tagged in the FSA, 1990 through 1993.

Table 1. Annual size of wolf packs in the FSA, February 1990 to March 1994. Pack numbers refer to home range polygons shown on Figure 8. Numbers in parentheses are radio-collared individuals.

			March Pack Size				
Pack No.	Pack Name	Origin[a]	1990	1991	1992	1993	1994
1	Seven Wolf L.	C	2 (1)	7 (2)	10 (1)	11 (3)	5 (1)
2	Yusezyu R.	C	2 (2)	8 (2)	11 (2)	11 (2)	13 (1)
3	Jackfish L.	C	2 (2)	7 (3)	11 (4)	13 (6)	10 (2)
4	Tyers R.	C	2 (2)	2 (2)	2 (2)	2 (2)	Dead
5	Ketza R.	C	2 (1)	2 (2)	2 (1)	3 (2)	4 (3)
6	Wolverine L.	C	2 (1)	2 (2)	2 (1)	2 (2)	4 (1)
7	Finlayson L.	C	2[t]	2 (2)	2 (2)	Dispersed	
8	Mink L.	C	2[t]	4 (2)	8 (2)	7 (2)	9(3)
9	Woodside R.	R	4 (3)	7 (2)	11 (3)	7 (3)	10[s]
10	Prevost R.	R	6 (2)	11 (3)	10 (2)	11 (1)	6 (1)
11	Tuchitua R.	IS	11 (3)	6 (2)	10 (2)	9 (3)	SO
12	Frances L.	IS	17 (2)	9 (2)	15 (3)	13[t]	15[t]
13	Otter Cr.	C	2[t]	2[t]	2 (2)	2 (2)	6 (2)
14	Weasel L.	R	6 (2)	13 (3)	4 (2)	12[t]	?
15	Upper Pelly R.	C	lone (1)	2 (2)	2 (1)	2 (2)	5 (2)
16	Big Campbell East	C	NP	3[t]	14 (1)	7 (3)	20*(4)
17	Tuchitua R. East	SP	NP	14[t]	Shifted Out		
18	Light Cr.	C	NP	2 (2)	6 (2)	8 (4)	11 (1)
19	McEvoy L.	C	NP	2 (2)	Disintegrated		
20	Ketza R. II	IS	NP	4[t]	6[t]	5[t]	?
21	Gonzo L.	C	NP	3[t]	Disintegrated		
22	One Island L.	C	NP	2 (1)	4 (1)	4[t]	SO
23	East Arm	C	NP	2 (2)	Dispersed		
24	Dragon L.	C	NP	NP	2 (1)	10[t]	8[s]
25	Lobster L.	SP	NP	NP	7 (1)	6 (2)	?
26	Fire Cr.	C	NP	NP	3 (2)	4 (2)	11 (2)

Table 1. (Continued). Annual size of wolf packs in the FSA, February 1990 to March 1994. Pack numbers refer to home range polygons shown on Figure 8. Numbers in parentheses are radio-collared individuals.

			March Pack Size				
Pack No.	Pack	Origin[a]	1990	1991	1992	1993	1994
27	Needle L.	C	NP	NP	2[t]	2[t]	9[s]
28	Nipple Mt.	SP	NP	NP	6[t]	4 (2)	2 (1)
29	Weasel L. II	SP	NP	NP	6 (1)	11	?
30	Hoole R.	C	NP	NP	3 (1)	6[s]	5[s]
31	Big Campell Cr.	SP	NP	NP	NP	10[s]	0*
32	McEvoy L. II	SP	NP	NP	NP	6[t]	7[s]
33	Furniss L.	UNK	NP	NP	NP	NP	6[s]
34	Upper Sheldon L.	IS	NP	NP	NP	NP	5[s]
35	Hegsted	SP	NP	NP	NP	NP	6[s]
36	Whitefish L.	C	NP	NP	NP	NP	2[t]
37	Hyland-Tyers R.	IS	NP	NP	NP	NP	8**
	Totals		62(22)	116(38)	168(39)	188(43)	218(24)

[a] C is colonizing pack, R is resident, IS is in-shifter, SP is pack formed by splitting and UNK is unknown origin.

Dead Both wolves died.

SO Shifted outside my study area.

NP Pack not present.

[t] Pack size estimated from track counts only.

[s] Pack seen during census.

? Pack was not observed in 1994. It was assumed to be present and size was estimated to be 7.8 wolves, based on average size of 19 other packs seen in 1994.

* Big Campbell East and West joined again in 1994, after splitting into 2 packs in 1993.

** Pack was tracked in former range of Tyers R. pack but seen outside FSA boundary.

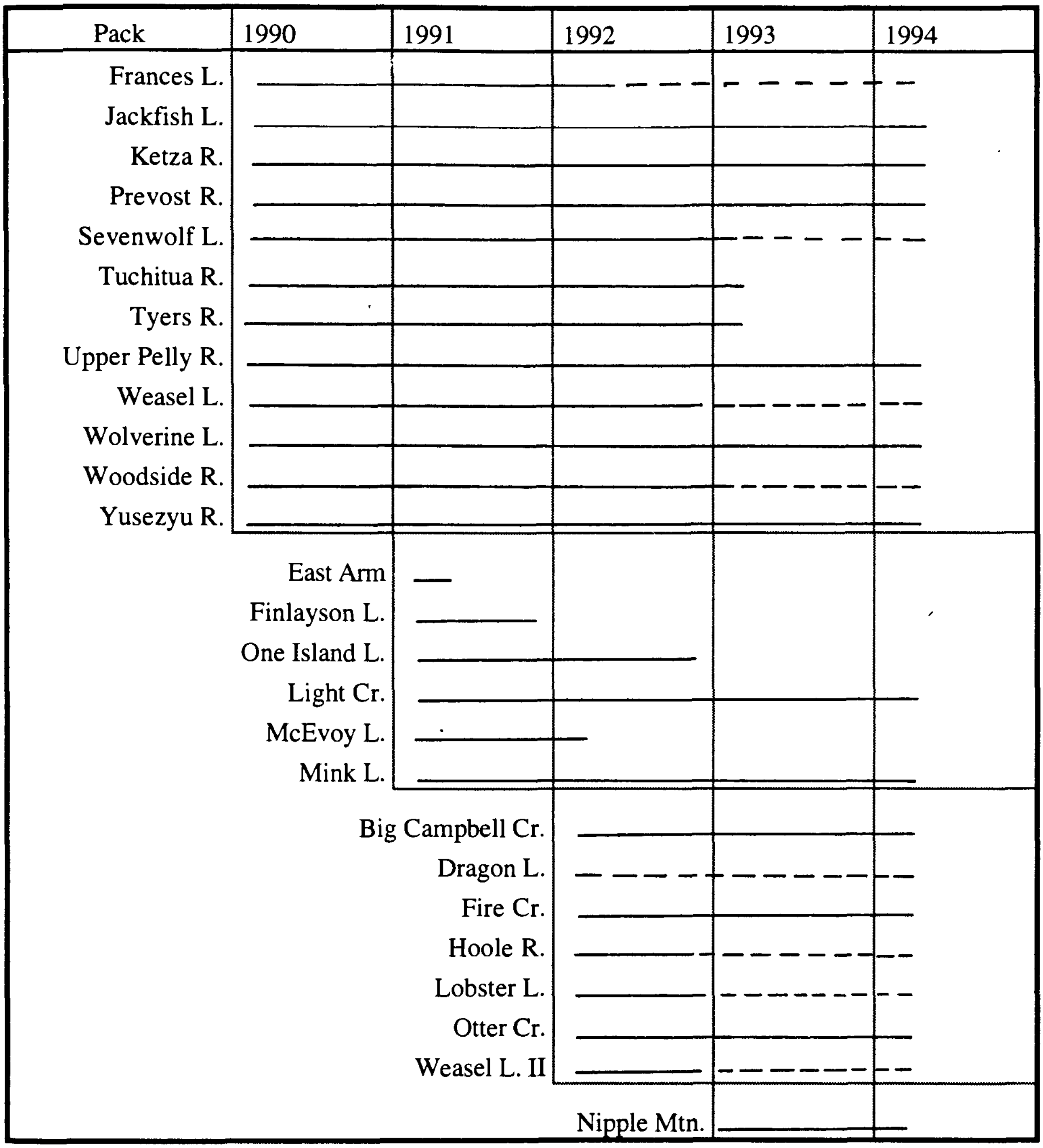


Fig. 3. History of radio contact with 26 wolf packs in the FSA from February 1990 to March 1994. Solid line indicates contact period. Dashed line indicates radio contact was lost, but pack was seen or wolf trails indicated the pack was present.

Annual Changes in Wolf Abundance from 1989 to 1994

Wolf numbers rapidly increased from 29 known survivors at the end of the wolf reduction (15 March 1989) to a high of 240 wolves in March 1994 (Table 2, Fig. 4), 12% greater than the total of 215 wolves found in March 1983 before wolf reduction began (Farnell *et al.* unpubl. ms.). The finite rate of increase (λ) was greatest during the first year of recolonization ($\lambda = 2.38$), then λ declined to 1.12 between 1992 and 1993 (Table 2, Fig. 5). The population continued to increase from 1993 to 1994 ($\lambda = 1.16$) showing wolf numbers probably had not stabilized by the end of my study. Annual rate of increase was negatively correlated to the number of wolf packs in the area ($r^2 = 0.92$, df = 4, $P = 0.01$).

The number of packs increased from 7 at the end of wolf reduction in 1989 (Farnell *et al.* unpubl. ms.) to between 26 and 28 packs after 1991 (Table 2, Fig. 6). Mean pack size increased significantly from 4.4 wolves in 1990 to 7.8 in 1994 (independent t -test, $t = -2.3$, df = 36, $P = 0.025$), increasing at a rate of about 1 wolf year^{-1} (Table 2, Fig. 7). Before wolf reduction began in 1983 there were 25 wolf packs in a 26,000 km^2 area, and mean pack size was 9.6 wolves (Farnell *et al.* unpubl. ms.).

Figure 8 shows the distribution of FSA wolf packs from 1990 through 1994. Home ranges were exclusive in the first 2 years of recovery, but overlaps developed after 1991 as the study area became saturated with wolf packs. Perimeters of some pack territories were unstable from year to year, but activity centers remained generally stable except for the Jackfish Lake, Fire Creek, Finlayson Lake, Wolverine Lake, Tuchitua River and Otter Creek packs. These packs all made substantial home range shifts in some years (Fig. 8). I plotted 95% convex polygon areas for 18 wolf packs that were observed on more than 30 days (range: 38 to 86 days) during my study, to estimate the total area used in all years (Fig. 9). The mean home range area was 1,478 ± 203 (SE) km^2, ranging from 722 km^2 to 3,800 km^2.

Table 2. Annual changes in FSA wolf population, 15 March 1989 through 31 March 1994.

Year	Number of Wolves Alive[a]	Percent of Original[b] Number	Number of Packs	Number of Pairs	Percent Pairs	Percent of Packs with Pups	Mean Pack Size ± SE	Wolf Density no./km^2	Finite Rate of Increase [c]
Reduction [d]									
March 1989	29	13	7	3	43	57		0.0014	na
Recovery									
1990	69	32	14	9	64	35	4.4 ± 1.2	0.003	2.38
1991	128	60	23	10	43	52	5.0 ± 0.8	0.0056	1.85
1992	185	86	26	8	30	71	6.0 ± 0.8	0.008	1.44
1993	207	96	27	5	19	81	7.1 ± 0.7	0.009	1.12
1994	240	112	28	2	7	93	7.8 ± 0.8	0.0104	1.16

[a] Includes total number of wolves in packs plus 10% estimate for single wolves.

[b] Original population size in 1983 was 215 wolves (Farnell *et al.* unpubl. ms.).

[c] Recovery rate = finite rate of increase (number of wolves before March in year$_{n+1}$ ÷ number of wolves in March in year$_n$).

d Data from 1989 is after wolf reduction was completed (Farnell *et al.* unpubl. ms.).

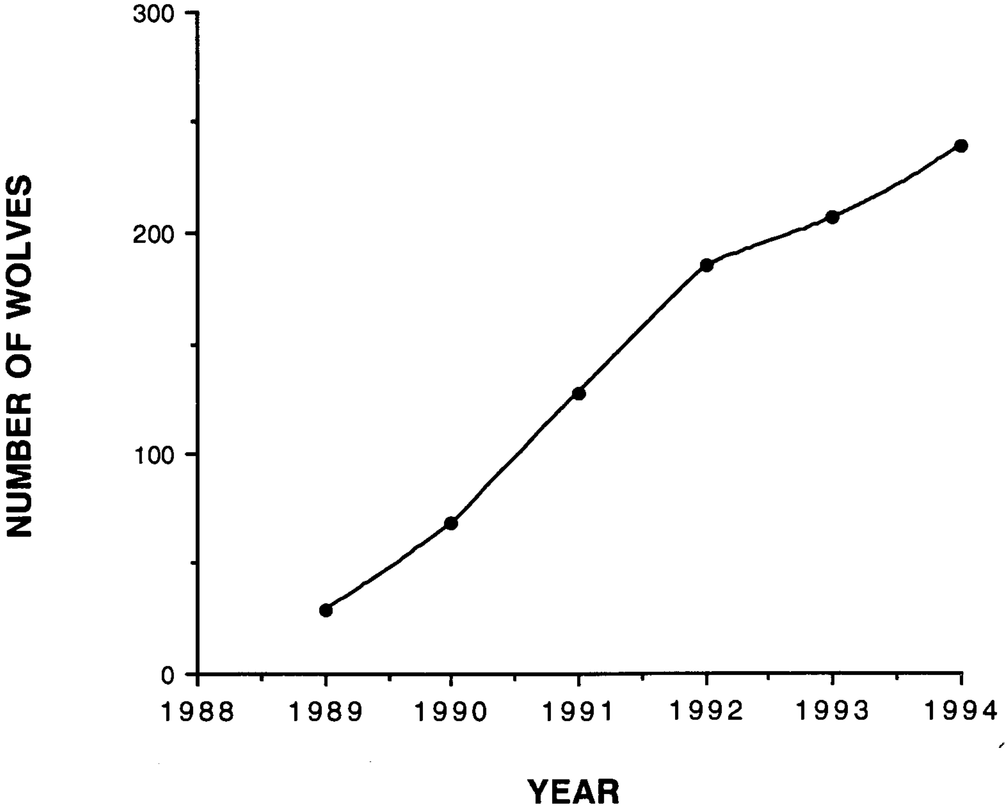


Fig. 4. Wolf population size at the end of March in the FSA, 1989 through 1994.

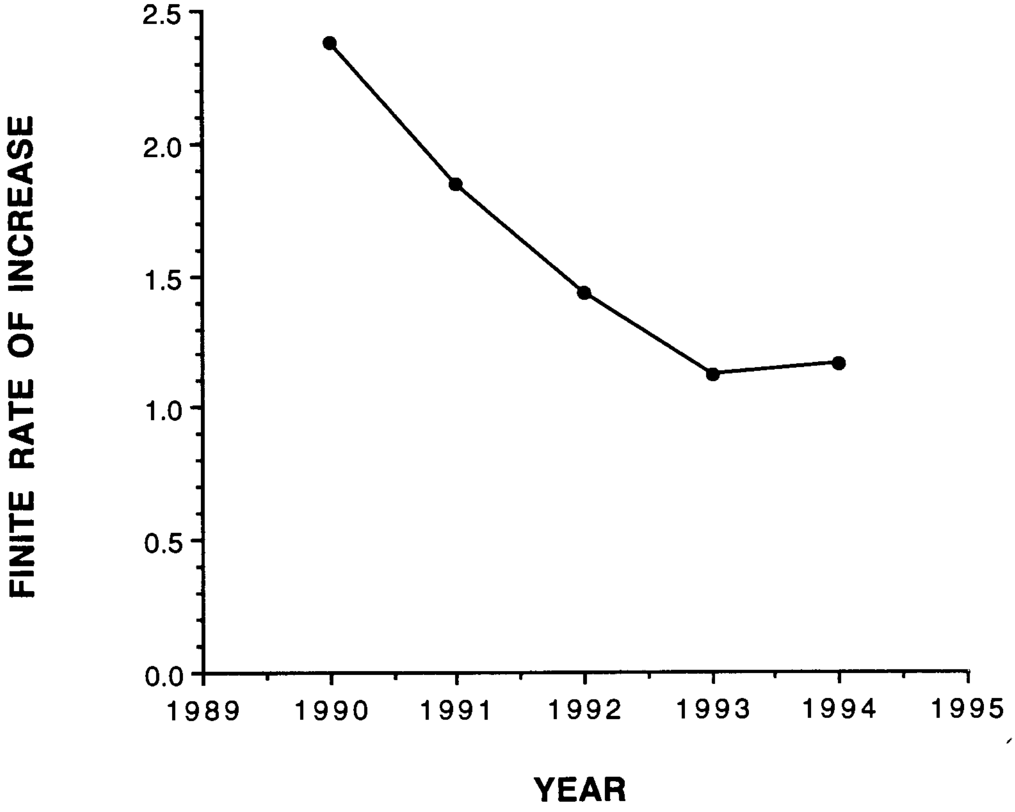


Fig. 5. Annual finite rates of increase of the wolf population in the FSA, 1990 through 1994.

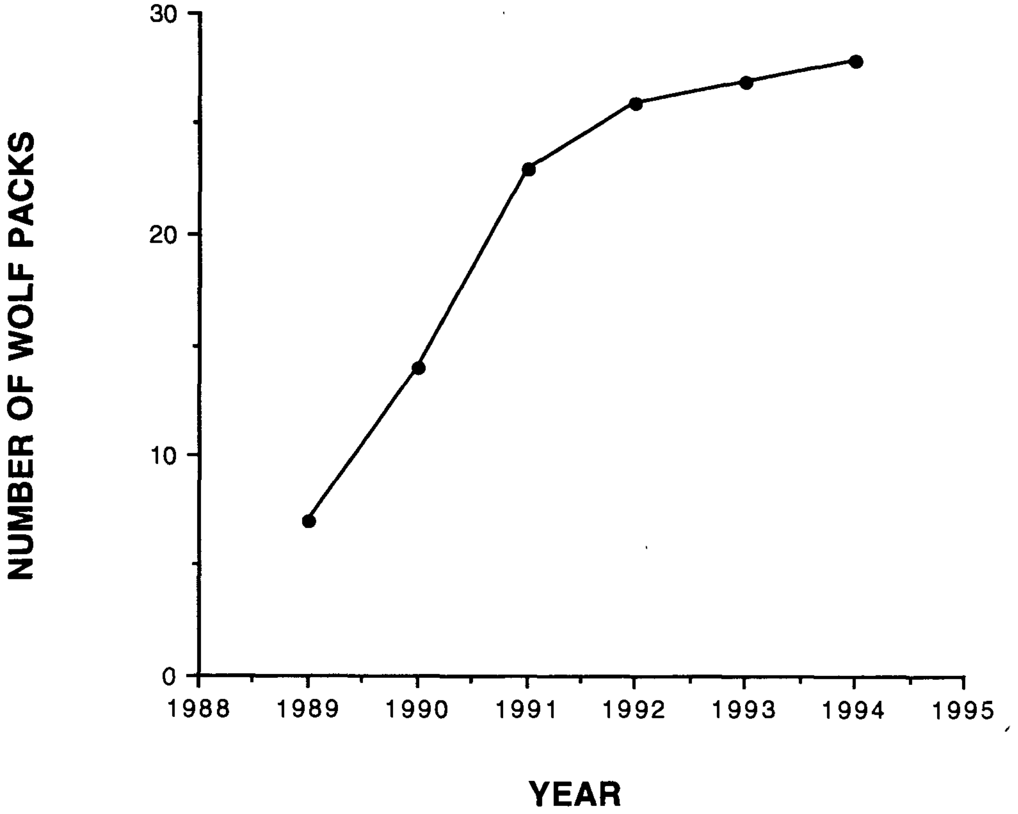


Fig. 6. The number of resident wolf packs during winter in the FSA, 1990 through 1994.

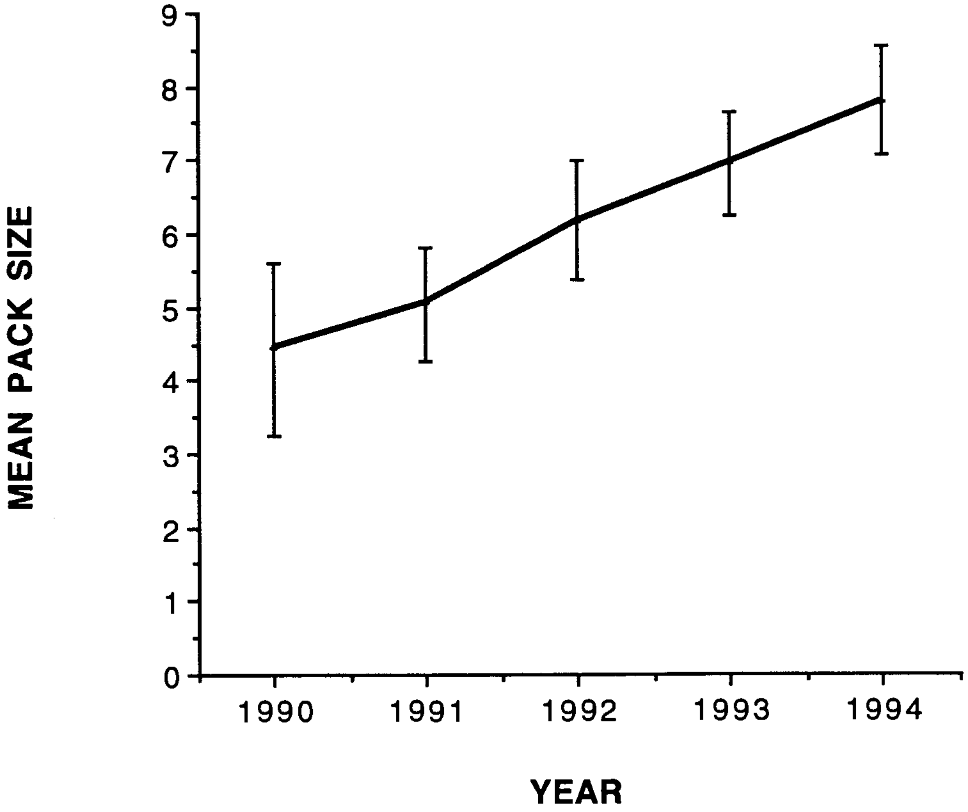


Fig. 7. Mean size of wolf packs in the FSA, 1990 through 1994. Vertical bars show standard error of mean.

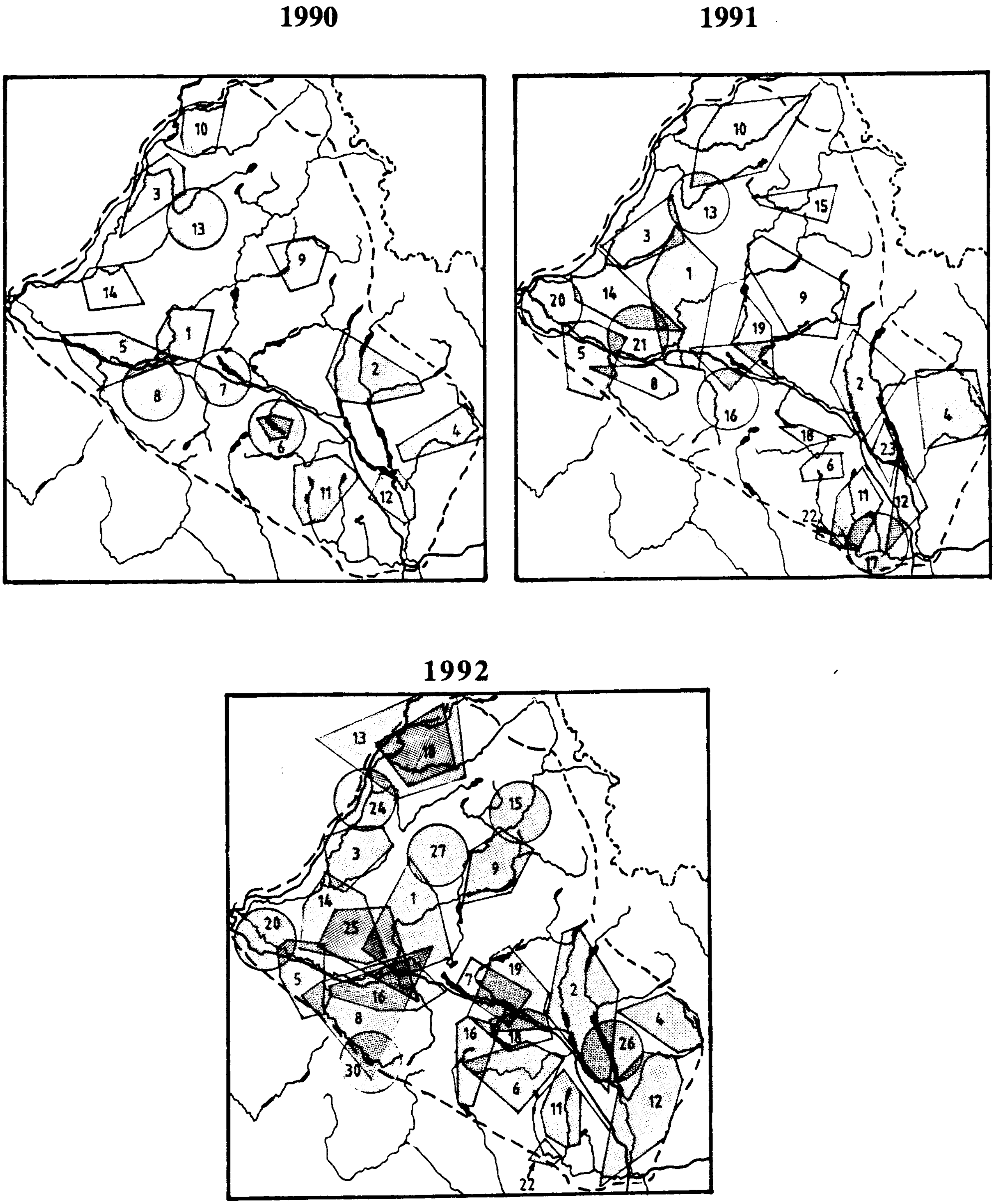
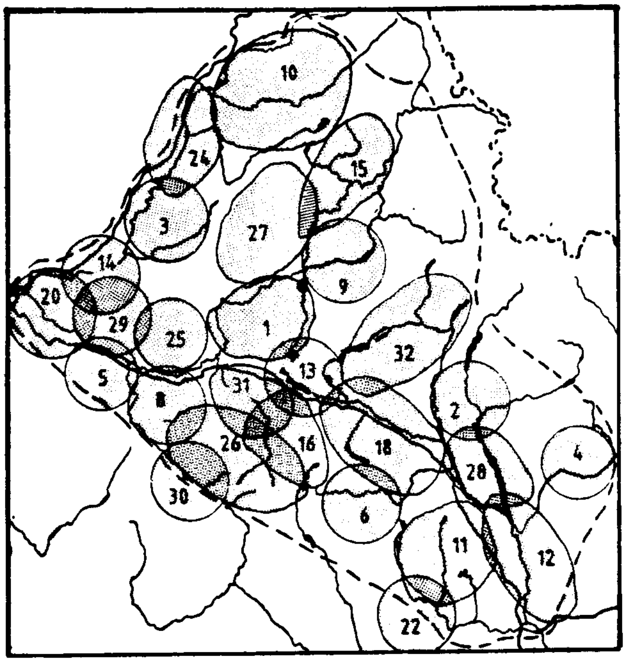


Fig. 8. Annual home ranges of wolf packs in the FSA, 1990 to 1994. Areas shown are 100 percent of convex polygons based on locations for all radio-tagged pack members. Ellipses describe home range areas based on snow trails. Packs are numbered according to Table 1.

1993



1994

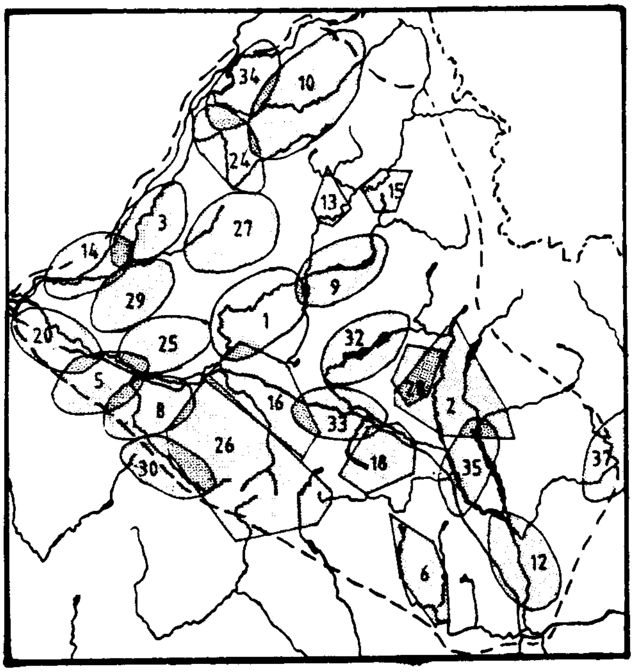


Fig. 8. (Continued). Annual home ranges of wolf packs in the FSA, 1990 to 1994. Areas shown are 100 percent of convex polygons based on locations for all radio-tagged pack members. Ellipses describe home range areas based on snow trails. Packs are numbered according to Table 1.

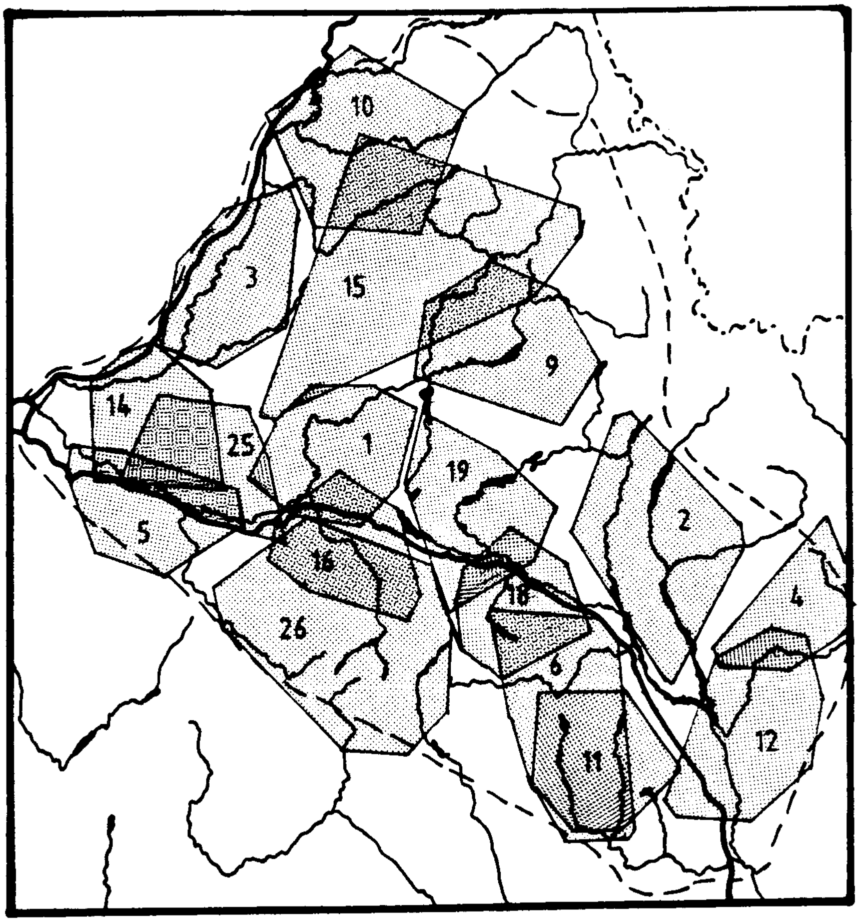


Fig. 9. Total 95% minimum-convex area polygons for 18 wolf packs in the FSA. Packs are numbered according to Table 1. Areas include all locations for all years.

I classified wolf packs as residents, colonizers, in-shifters or splitters, on the basis of their probable origins in the FSA. Three resident packs (Table 1) apparently survived the wolf reduction in 1989, and they accounted for 16 of 62 (26%) wolves in packs in 1990. Eighteen pairs and 3 trios colonized the study area by establishing new territories in vacant wolf range. Six packs shifted home ranges into the FSA from boundary areas. Four packs increased to large sizes then split into 9 packs during the study.

In the first year (1990), repopulation was mainly caused by the dispersal of young adult wolves into vacant wolf territories in the FSA. I did not radio-tag resident survivors in 1989 so I could not directly measure their importance to the recovery. However, the 9 adult pairs found in 1990 could not be explained by the reproduction of surviving resident packs. These colonizing pairs either formed from surviving resident packs or fragments, or they immigrated from outside the FSA. Their young ages suggest that they were dispersers. Wolves dispersing from natal packs are usually less than 3 years-old (Mech 1970, Fritts and Mech 1981, Peterson *et al.* 1984, Ballard *et al.* 1987, Fuller 1989, Gese and Mech 1991, Hayes *et al.* 1991). In 1990, the mean age of 12 wolves in pairs was 3.20 ± 0.38 (SE) years-old; the same mean age for all 28 wolves radio-tagged in pairs during my study.

Wolf pairs accounted for 65% of packs in 1990. Pairs formed the nucleus of the future wolf population, but they contributed to only 29% (18 wolves) of the number of pack wolves in 1990 (Tables 1 and 2). The rest were probably resident survivors (26%, 16 wolves) or members of 2 packs that shifted into the FSA (45%, 28 wolves).

Small packs (2-3 wolves) accounted for 57% of all packs that established home ranges in the FSA during my study. Small packs were most common in the early recovery period (Table 2). Nine new small packs colonized the area in 1990, 7 in 1991, 4 in 1992, none in 1993 and 1 in 1994. The annual number of small packs was negatively correlated with the total number of wolf packs ($r^2 = 0.77$, df = 4, $P = 0.05$). Of the 21 colonizing small packs, 18 were radio-tagged and their pack histories were documented for periods of up to 49 consecutive months (Fig. 10). By the end of my study, 13 colonizing small packs (72%) had

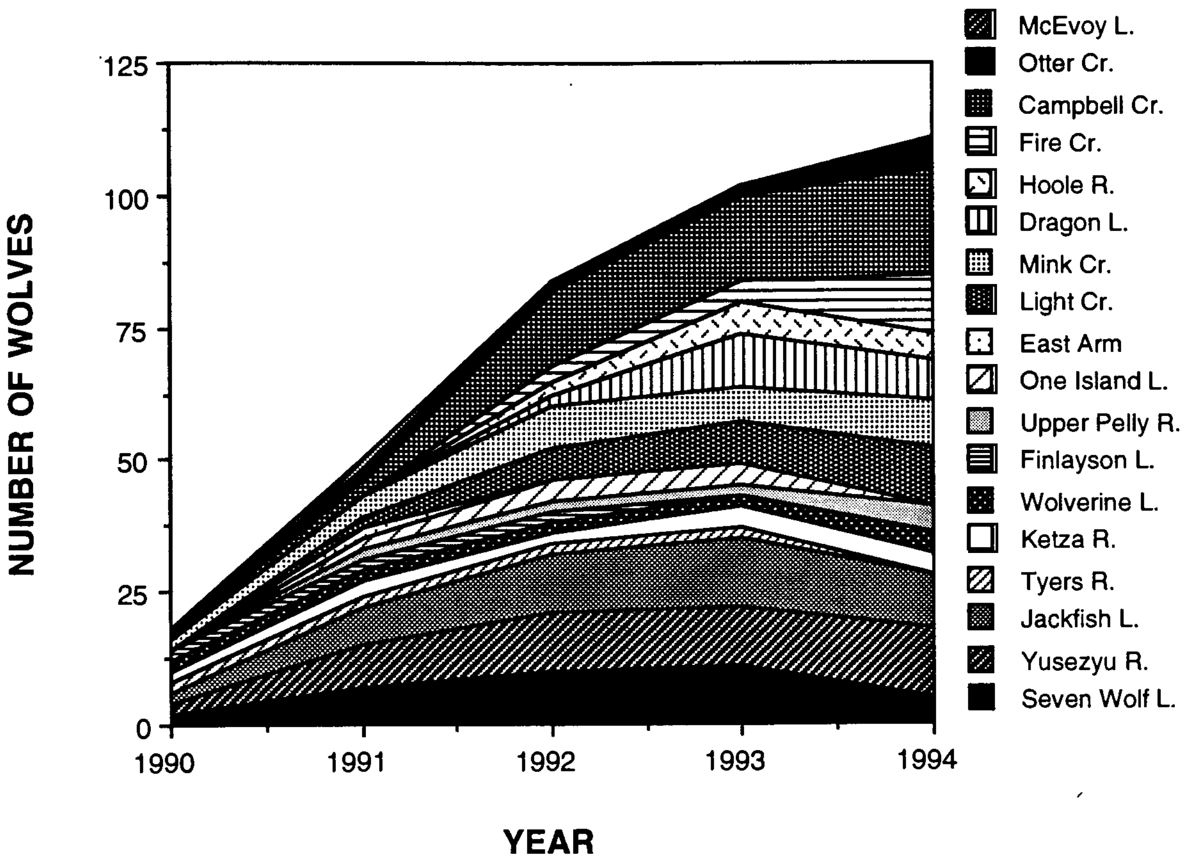


Fig. 10. Annual changes in size of wolf packs that were first radio-tagged as small packs (n = 2 or 3 wolves), March 1990 to March 1994.

successfully bred and remained in the FSA, 1 pair reproduced but shifted outside, 2 pairs dispersed and 2 pairs separated for unknown reasons before reproducing (Table 1). By 1994, members and offspring of the 21 colonizing packs accounted for 122 (56%) of the FSA population of 218 pack wolves.

Four packs shifted from boundary areas and established territories inside the FSA during my study. Pack in-shifting was more important in early years than in later years of the repopulation, because in later years most wolf habitat was occupied and there was no space for boundary packs to shift into. In 1990, 2 packs (Frances River, 17 wolves; Tuchitua R., 11 wolves) shifted into the FSA from boundary areas. The 2 packs accounted for 45% (28 wolves) of all pack wolves in the FSA that winter. Their large pack sizes could not be explained by the reproduction of any known surviving pack in the area in 1989.

Three wolf packs eventually shifted out of the FSA during my study (Table 1), including the Tuchitua River pack that originally shifted into my study area in 1990. These packs all ranged in the southeastern boundary along the Tuchitua and Frances Rivers where moose were relatively abundant.

As pack sizes grew, the frequency of pack splitting increased. Four large packs eventually split and formed new packs in adjacent areas (Table 3). At the time of splitting, these packs averaged 14 ± 1.5 (SE) wolves. Three newly formed packs included radio-tagged wolves. Splitting probably formed 4 other packs because the size of radio-tagged groups sharply declined at the same time a new untagged group appeared nearby. I determined that 9 of 28 (32%) packs present in 1994 were products of packs splitting (Table 3). These 9 packs totaled 84 wolves, 39% of the total number of wolves in packs in 1994.

Reproduction and Survival Rates

I estimated the average wolf litter size at birth was 5.7 ± 0.4 (SE) pups, based on *corpora lutea* counts from earlier years (Farnell *et al.* unpubl. ms.). I did not observe multiple littering among permanent pack members during my study.

Table 3. Chronology of FSA wolf packs that split during 1990 to 1994.

	Year					
Original Pack	1990	1991	1992	1993	1994	Split Packs
				4*	2*	Nipple Mt.
Frances R.	17*	9*	15*	13	15	Frances R.
		12[a]			6	Hegsted
Big Campbell Cr.		3	14*	7* (East) 10 (West)	20*[b]	Big Campbell Cr.
Weasel L.	6*	13*	4*	12	8[c]	Weasel L.
			7*	6*	8[c]	Lobster L.
			6*	11	8[c]	Weasel L. II
Woodside R.	4*	7*	11*	7*	10	Woodside R.
				6	7	MacPherson L.
Total	27	44	57	76	84	

* Radio-collared wolf pack.

[a] Tuchitua R. East pack. Pack shifted out of FSA in 1992.

[b] Big Campbell Cr. East and West packs re-joined in 1994.

[c] Pack not seen but assumed present, and minimum pack size was estimated (see Table 1).

The wolf population increase after 1992 was mainly due to increases in pack size caused by reproduction (Table 2, Fig. 7), not because new packs colonized the area. About 50% of FSA packs had reproduced by 1991, and 90% had reproduced by 1994. The mean rate of increase of all colonizing small packs in their first year of reproduction was 2.40 ± 0.38 (SE), including pairs that did not successfully reproduce. Ten colonizing packs (7 pairs and 3 trios; 53%) raised pups through their first breeding period, 5 (26%) failed to reproduce because a mate died, and 4 (21%) failed for unknown reasons. Among pairs that failed due to mate mortality, 3 females died before giving birth, and 2 females gave birth then died during the summer. Their pups subsequently died before autumn. Mate mortality caused reproductive failure of pairs at least 9 times during my study, and adult mortality was an important factor limiting wolf recruitment in the first 2 years of recovery. I observed reproductive failures for 2 pairs in consecutive years, but I could not determine the reasons. The Tyers River pair remained together in the same territory for 4 years but failed to reproduce, then both were apparently killed by neighboring wolves in 1994. The Otter Creek pair remained together for 3 years (Fig. 8) before successfully raising pups in 1994.

Annual survival rates of all radio-tagged wolves were not different among years (Pearson $\chi^2 = 0.4$, df = 3, $P = 0.94$) and remained high, annually averaging 0.84 ± 0.02 (SE). There was no difference in survival rates (Kaplan-Meier [K-M] log rank, $\chi^2 = 0.08$, df = 1, $P > 0.75$) between early recovery (March 1990 through February 1992) and late recovery years (March 1992 through April 1994) (Table 4). Seasonal survival also did not differ (K-M log rank, $\chi^2 = 0.16$, df = 2, $P > 0.90$) between periods. Cumulative survival probability of radio-tagged wolves declined each year, from 0.79 in 1991 to 0.45 by 1994 (Fig. 11).

I did not radio-tag pups before February (9 months-old) each winter, so I estimated annual pup survival rates by subtracting the number of wolves in packs in autumn from the number seen the previous March. The mean number of pups in autumn (3.7 pups) was not different from that in the previous March (4.3 pups) (independent sample *t*-test, $t = -0.70$, df = 31, $P = 0.49$), and pup survival after December was probably stable, supporting other studies

Table 4. Kaplan-Meier annual survival probabilities for radio-tagged wolves in the FSA, March 1990 to March 1994.

Year*	Number of Wolves at Risk	Number of Deaths	Survival	Number of Wolves Censored	Number of Wolves Added	Variance	95% Confidence Intervals	
							Lower	Upper
1990-1991	24	5	0.79	0	22	0.0054	0.65	0.94
1991-1992	41	7	0.66	6	12	0.0036	0.54	0.77
1992-1993	40	6	0.56	8	17	0.0034	0.44	0.67
1993-1994	43	8	0.45	11	0	0.0026	0.35	0.55

* Annual period began on 1 May.

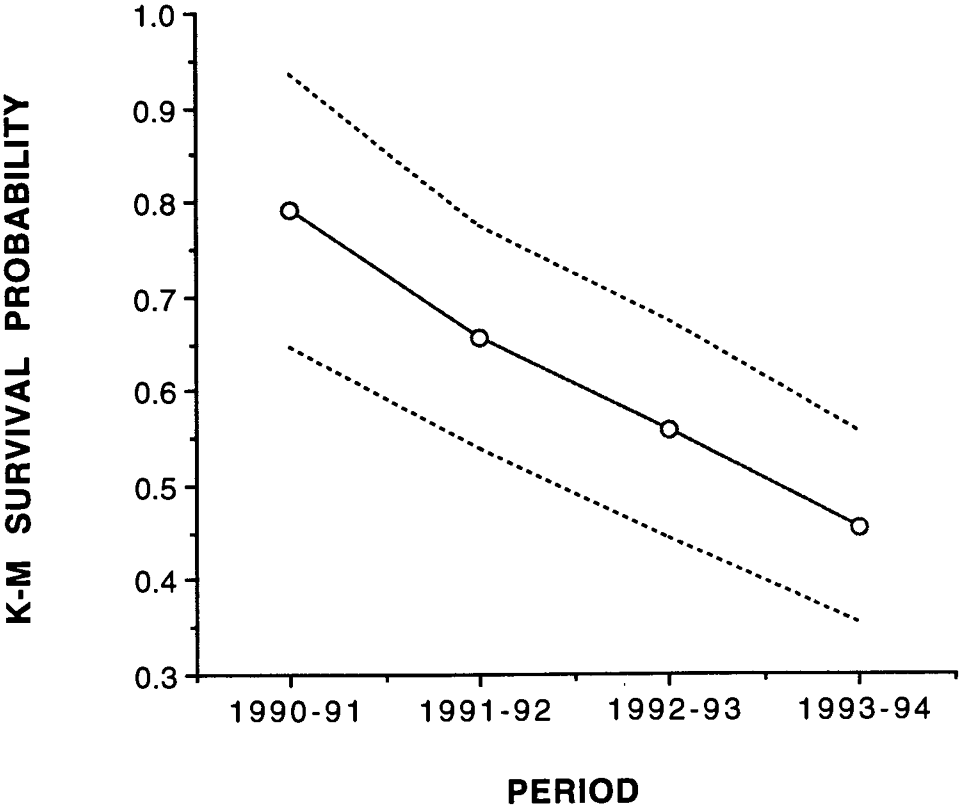


Fig. 11. Kaplan-Meier cumulative survival probabilities for radio-tagged wolves in the FSA, 1990 to 1994. Dashed lines indicates 95% confidence limits.

(Harrington *et al.* 1983, Peterson *et al.* 1984, Fuller 1989). However, the mean number of pups alive in March was significantly smaller (independent sample *t*-test, $t = -2.2$, df = 39, $P = 0.04$) than the mean litter size at birth (5.7 pups). Using this difference, I estimated that pup survival to March was about 0.75 (4.3 ÷ 5.7). From a sample of only 8 radio-tagged pups, I estimated survival from March to May was 0.63 (Table 4), but the sample size was too small to be useful. Also, it is not known if the 3 wolves died as pups before May, or as yearlings in June when the mortalities were detected.

Age-specific survival rates were not different among subadults (pups and yearlings), young adults (2 and 3 years-old) and adjacent age classes of older adults (Pearson $\chi^2 = 1.5$, df = 2, $P = 0.47$). However, wolves < 3 years-old had significantly lower survival rates (Table 5) than did older (≥ 3 years-old) wolves (K-M log rank, $\chi^2 = 4.7$, $P < 0.05$). During my study, mean annual survival rate was 0.81 for yearlings and 0.89 for adult wolves (Table 5).

Causes of Wolf Mortalities

Only a few wolves were trapped or hunted each year in the FSA. Harvest of wolves was limited by the remoteness of most of my study area and a declining interest in trapping throughout Canada due to low world prices for furbearing animals (Hayes and Gunson *in press*). The sex ratio of radio-tagged wolves that died (15 F, 10 M) was not different from the ratio (11 F, 13 M) of radio-tagged wolves that were alive at the end of my study (Pearson $\chi^2 = 0.98$, df = 1, $P = 0.32$). Average age when wolves died was 3.4 ± 0.4 (SE) years-old and was not different between sexes (independent sample *t*-test, $t = -0.13$, df = 23, $P = 0.90$). Most radio-tagged wolves that died were between 1 and 5 years-old (Fig. 12). Twenty-two deaths were probably natural and 3 were human-caused (Appendix B). Only 1 natural death was known; an adult female wolf was killed at her den by a grizzly bear.

Most natural deaths were probably caused by other neighboring wolves, based on where wolves died in relation to their pack territories. Mech (1994) reported a high rate of intraspecific wolf mortality along territorial edges, showing that wolves are more at risk of fatal

Table 5. Kaplan-Meier survival probabilities for different wolf age classes in the FSA, 1990 to 1994.

Age	Number of Wolves at Risk	Number of Deaths	Survival	Variance	95% Confidence Intervals Lower	95% Confidence Intervals Upper
Pup	8	3	0.63	0.0183	0.34	0.89
Yearling*	28	4	0.86	0.0037	0.73	0.98
Yearling**	36	7	0.81	0.0035	0.69	0.92
2	45	8	0.82	0.0027	0.72	0.92
3	32	1	0.97	0.0009	0.91	1.00
4	33	4	0.88	0.0028	0.77	0.98
5 and older	51	6	0.88	0.0018	0.80	0.97

* Assumes 3 pups died before 1 May.

** Assumes 3 pups died as new yearlings between 1 May and 15 June.

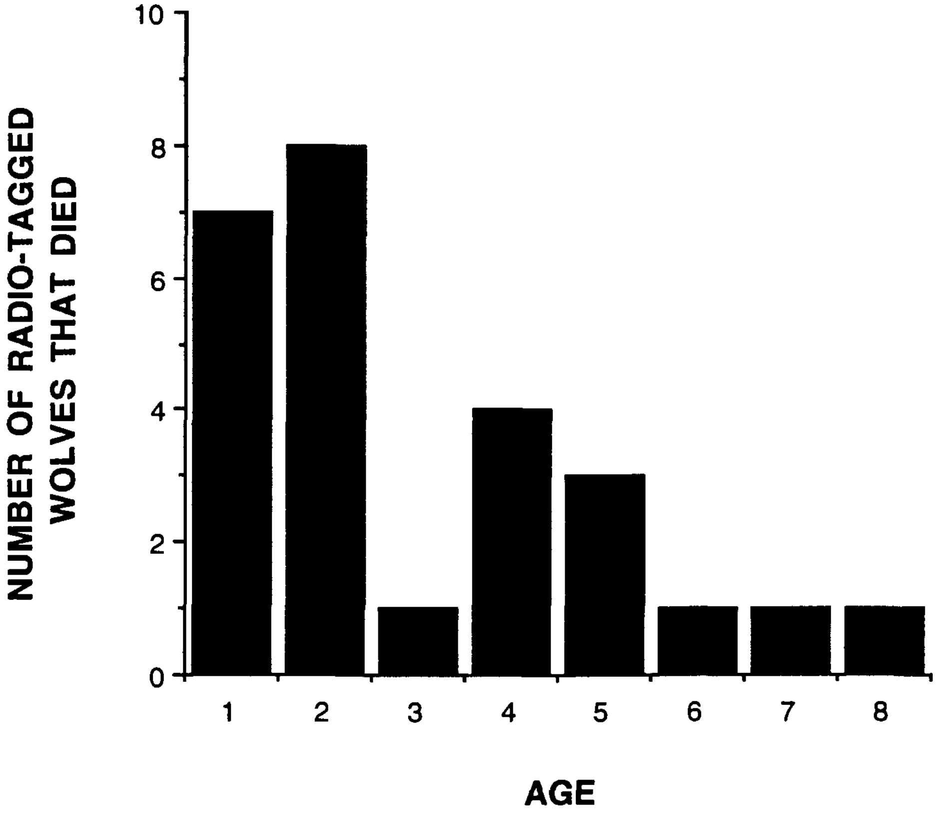


Fig. 12. Numbers of radio-tagged wolves that died as yearlings or older during the study. The seven yearlings include 3 wolves that I assumed died at 12-13 months-old and not 11 months-old (pup).

encounters there than in the centers of their territories. I had adequate data on pack home ranges to calculate distances to boundary edges for 17 wolves that probably died from natural causes. Twenty-four percent died on their territory boundary, 11% were between 0.1 and 2.5 km, 24% were between 2.5 and 5 km, 24% were more than 10 km inside the boundary and 17% were more than 10 km outside the boundary. Overall, 59% were found within 5 km of the edge of their pack territory. Mech (1994) reported that 91% of conspecific mortalities were less than 3.2 km from the boundaries of smaller wolf territories in Minnesota. As young wolves move into unfamiliar territories, they have a greater likelihood of being killed by wolves defending territories (Mech 1970, Peterson *et al.* 1984). Four of the 5 wolves that died more than 10 km outside their pack territories were ≤ 2 years-old, and were likely dispersing when they were killed by other wolves. Six of the 7 adults died within 5 km of their territory boundaries.

I found an association between the ages and the seasons that wolves died, which also implies most were killed by other wolves. All 10 young wolves died between April and November, the period that most young wolves disperse from natal packs in response to intra-pack aggression (Fuller 1989, Gese and Mech 1991). In contrast, 6 of the 7 adult mortalities happened between November and April, when pack territories are more vigorously marked and defended by adults compared to in summer (Mech 1970).

Dispersal

I estimated that 25 (33%) radio-tagged wolves permanently dispersed during my study, including 7 that remained in my study area and 18 censored wolves that probably emigrated (Appendix B). Of the 7 wolves that dispersed into new areas inside the FSA, 4 formed new packs, 1 wolf successfully dispersed into a neighboring pack and 2 older alpha male wolves dispersed from their packs but remained within their territories. I believe that most censored wolves emigrated outside the FSA and were not due to radio-transmitter failures, based on their ages, behavior and censorship schedules. Five censored wolves were alone the last time they were seen in their territories. Pre-dispersing wolves temporarily separate from their packs before permanently leaving their natal territories (Messier 1985b). Two radio-tagged pairs established temporary territories then disappeared. One pair (Finlayson L.) spent the winter of 1991 and 1992 in the centre of the study area without reproducing, then dispersed. The East Arm pair did not appear to have a home range when first contacted in March 1991, then dispersed by the summer. Seventy-seven percent of all dispersed or censored wolves were between 2 and 4 years-old (Fig. 13). The mean age of censored wolves was 3.0 years-old, the same as that for all wolves that colonized new territories in the FSA. I knew the censorship schedule for 10 radio-tagged wolves. Seven were censored during April to June when natal dispersal from wolf packs is the highest (Fuller 1989, Zimen 1976 and 1982, Gese and Mech 1991), supporting my hypothesis that most censored wolves probably dispersed.

To estimate natal dispersal rates, I included only wolves that were born in the area and were members of permanent FSA packs. During my study 18 such wolves dispersed, including 12 males and 6 females. Average age was 2.9 ± 0.3 (SE) years-old and was not different between sexes (Mann-Whitney U-test, $U = 51$, df $=1$, $P = 0.13$). Dispersal rate was 0% in 1991, 17% in 1992, 33% in 1993 and 50% in 1994. Dispersal rate increased (Pearson $\chi^2 = 6.9$, df = 1, $P < 0.01$) in late recovery years (0.45, 1992-1994) compared to earlier years (0.09, 1990-1992). Natal dispersal was positively correlated with annual mean pack size ($r^2 = 0.99$, df = 3, $P < 0.005$). Dispersal was negatively correlated with ungulate biomass/wolf ratio ($r^2 = 0.95$, df = 3, $P < 0.03$).

Changes in the Abundance of Moose and Caribou, and Prey Biomass/Wolf Index

Caribou density increased from 0.23 to 0.35 caribou/km^2 during my study. After 1991, caribou calf survival fell below 32 calves:100 females in autumn (Farnell *et al.* unpubl. ms.). Calf survival rates indicated the Finlayson caribou herd apparently stabilized at about

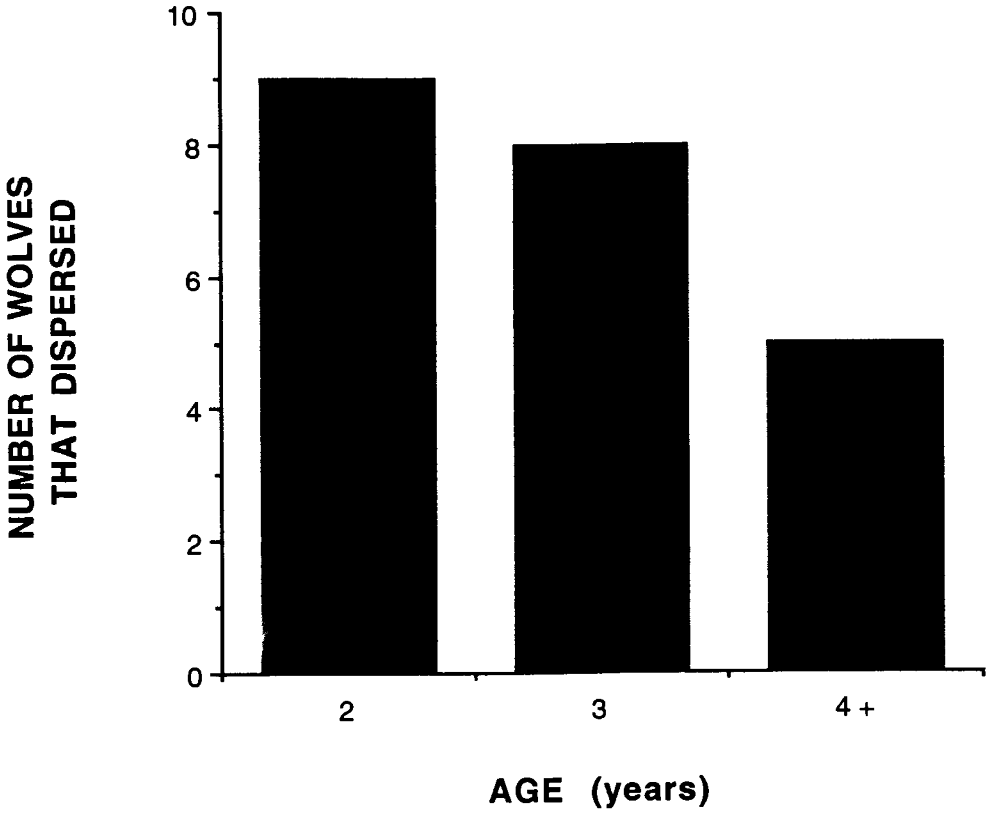


Fig. 13. Ages of radio-tagged wolves that dispersed from packs during the study.

7,500 animals after 1992 (Farnell *et al.* unpubl. ms.). The mean moose density increased from 0.25 moose/km^2 in 1990, to 0.43 moose/km^2 in 1994. During my study, humans annually harvested less than 3% of the caribou (Farnell *et al.* unpubl. ms.) and less than 4% of the moose populations in the FSA (Larsen and Ward 1995).

I estimated the potential wolf density in the FSA during 1994 by the numerical response equation of Fuller (1989), $y = 3.4 + 3.7x$; where y = expected number of wolves (no./km^2) and x = ungulate biomass index/km^2 (Appendix C). On the basis of available prey biomass ($x = 2.63$), potential wolf density was 0.013 wolves/km^2 in 1994. The observed density was 0.0104 wolves/km^2, about 20% lower than that expected from the equation of Fuller (1989).

Discussion

My study provides new information about the dynamics of an increasing wolf population. In other wolf studies, mortality caused by people reduced the rates of increase of wolves (Fritts and Mech 1981, Peterson *et al.* 1984, Ballard *et al.* 1987, Hayes *et al.* 1991), or numerical response was depressed by genetic inbreeding (Isle Royale; Wayne *et al.* 1991). My results support Fritts and Mech (1981) and show numerical response was caused mainly by dispersal of young wolves into new territories, rapid pair bonding, territorial establishment and breeding; and from boundary packs shifting into vacant wolf range. Population growth of wolves was sustained by exceptionally high survival and low dispersal rates, normal reproduction, pack splitting and natal philopatry. Important social factors that limited the rate of increase in later years included: territoriality, exclusive breeding of dominant females, increased dispersal rates of young adults, and intraspecific mortality.

By the end of my study the number of wolf packs had stabilized, but wolf numbers were still increasing as mean pack size continued to rise. The rates of increase of wolves declined annually, and was negatively correlated with both prey biomass:wolf ratios and the number of wolf packs in the area. These correlations suggests that competition for food and space was the main factor regulating the growth of the FSA wolf population. Population growth in later years of recovery (1992 to 1994) was mainly a function of a constant increase in pack size due to high survival rates of young and adult wolves, and low dispersal rates of young wolves.

The highest finite rate of increase was from 1990 to 1991 ($\lambda = 2.38$) when most packs were pairs breeding for the first time. During wolf reduction, Farnell *et al.* (unpubl. ms.) also found high rates of annual increase ($\lambda = 2.06$ to 2.53). They believed that the rapid repopulation each year was due to immigration from naturally regulated wolf packs that surrounded the FSA. Rapid pairing of single wolves was the most important factor in population growth during the early years of wolf recolonization in Minnesota (Fritts and Mech 1981), Alaska (Peterson *et al.* 1984) and southern Yukon (Hayes *et al.* 1991). I observed the same general pattern of population increase in the FSA. In the first year, most packs were young pairs. Wolves usually leave natal packs in spring and summer (Gese and Mech 1991) and pair up before winter (Fritts and Mech 1981, Peterson *et al.* 1984, Ballard *et al.* 1987, Fuller 1989). Their dispersal success ultimately depends on the availability of vacant wolf territories and competition for prey resources (Fritts and Mech 1981, Messier 1985a, Messier 1985b, Fuller 1989, Gese and Mech 1991). In early years, my study area provided a large population sink for young dispersing wolves to colonize. The chances of establishing and defending new territories were high because ungulate prey were increasing, and there was minimal intraspecific competition for space and prey resources.

The rate of wolf pack fragmentation and extraterritorial movements increases when prey abundance is low (Mech 1977, Messier 1985b). In areas adjacent to the FSA in the early recovery years, moose densities were 2 to 3 times lower and wolf densities were 3 times higher than in my study area (Hayes and Bowers 1987, Hayes and Baer 1987), suggesting that surrounding wolves were predisposed to disperse. The low competition for high food resources in the FSA explains the high colonization rate by new pairs, and the tendency of bordering wolf packs to shift from adjacent areas into vacant territories.

After pairs established territories in the FSA, reproduction replaced dispersal in numerical response importance. Most wolf pairs increased to 5-6 wolves after their first breeding season in the FSA. Growth in pack size was a result of normal pup production and low adult and juvenile mortality. The death of breeding mates was the main factor limiting reproduction and reduced the rate of increase of wolves.

Wolf productivity and pup survival rates appear to ultimately depend upon the availability of ungulates (Zimen 1976, Keith 1983, Boertje and Stephenson 1992). Mean litter size in the FSA was similar to other studies where food availability was high (Harrington *et al.* 1983, Fuller 1989, Boertje and Stephenson 1992) indicating that *in utero* production was not different. However, juvenile survival rates in my study were the highest reported in the literature. Harrington *et al.* (1983) found a positive relationship between pack size and pup survival rates and believed that more 'helpers' in a pack increased pup survival. I found no evidence that survival rates of pups increased with increasing pack size. Pup survival did not increase with breeding propensity (*i.e.*, adult experience). First-time breeding pairs were equally capable of raising pups as wolves that had bred before (Peterson *et al.* 1984). I conclude that pack size and breeding propensity had little influence on pup survival in my study because ideal ecological conditions maximized pup survival, even among inexperienced wolf pairs.

Perhaps the survival rates that I observed reflect the maximum possible for wild wolves. Survival rates were lower in 6 other studies where wolf harvest by humans was higher than in the FSA (Fritts and Mech 1981, Peterson *et al.* 1984, Messier 1985a, Ballard *et al.* 1987, Fuller 1989, Hayes *et al.* 1991). Mean pup survival rate among these 6 studies was 27% (0.48) lower than I observed, yearling survival was 20% lower (0.61), and adult survival was 40% lower (0.59). High survival rates in the FSA were elevated by the same low competition conditions that maximized pup production. Despite relatively low competition, intraspecific mortality was still the most important cause of wolf deaths during my study, and was the main factor limiting wolf numerical response of newly formed pairs.

As new pups were annually added to packs, survival rates of yearlings and 2 year-old wolves remained high, and the dispersal rate of juveniles remained low. These conditions caused wolf pack sizes to increase rapidly. Wolf packs have a social capacity limit of about 13 wolves, which seems to be independent of food supply (Mech 1970, Zimen 1976). Large packs split when subordinate wolves disperse as a group in response to social stimuli from dominant members (Zimen 1976). Pack splitting is thought to be a common process of pack formation in increasing wolf populations (Fritts and Mech 1981), but previous studies have not quantified its importance. Pack splitting was especially important in later years of my study when some pack sizes became large. Splitting accounted for about 35% of the wolf packs and 40% of the total number of wolves by the end of my study. The propensity for wolf packs to split can be explained by advantages of philopatric behavior to survival of dispersers. Wolves are strongly philopatric as shown by recent mitochondrial DNA studies (Lehman *et al.* 1992). Colonizing near the edge of a parental territory allows dispersers long-term use of familiar areas, and it minimizes the survival cost of dispersing to a new location where food resources are unknown and the chance of being killed by conspecifics are higher (Cooch *et al.* 1993). Pack splitting in the FSA was adaptive because there was adequate space and ungulate prey in portions of former pack territories for young wolves to establish new territories.

Exclusive breeding was the primary factor limiting reproduction during my study. All FSA wolf packs produced single litters except when a pack permanently split. Although more than 1 female in a pack is physically capable of reproducing, social constraints usually limit breeding to a single dominant female (Medjo and Mech 1976, Zimen 1976). The killing of dominant pack members can lead to instability in breeding by allowing multiple females to be bred (Woolpy 1968). Peterson *et al.* (1984) did not observe multiple litters in a harvest-limited wolf population in the Kenai Peninsula, Alaska. In a more heavily exploited wolf population in Alaska, Ballard *et al.* (1987) found 7 to 10% of wolf packs produced more than 1 litter. They believed multiple littering was a natality strategy that allowed wolves to compensate for low survival rates caused by high harvests. My results disagree, and indicate that multiple litters are probably caused by social disruption related to intensive reduction of wolves, and has little to do with an intrinsic, physiological adaptation by wolves to increase productivity. During the wolf reduction in the FSA most packs were completely removed at the end of the estrous period, restricting the breeding opportunities of subordinate survivors (Farnell *et al.* unpubl. ms.). I conclude that multiple littering is caused by non-selective harvest of wolves that leads to a disruption of wolf pack social structure. This, in turn, allows subordinate females opportunities to breed that would normally be restricted by dominant wolves.

Wolf dispersal rate was positively correlated with the mean number of wolves in packs. Dispersal began to limit the number of wolves in packs by 1994, when I observed the same dispersal rate as that found in a stable wolf population in Minnesota (0.49, Fuller 1989). Messier (1985) and Peterson and Page (1988) showed wolf dispersal rates increased as the prey biomass:wolf ratio declined, implying that intra-pack competition for food determined whether young wolves stayed or were ejected in favor of new pups (Zimen 1976, Harrington *et al.* 1983). Dispersal rates are influenced by the age and social position of wolves, and dispersal rate rapidly increases with the onset of sexual maturity (Packard and Mech 1980, Messier 1985b, Gese and Mech 1991). In a previous section, I showed that early in my study most wolf groups were young pairs that recently dispersed into new territories. These wolves had a propensity not to disperse again, but remained in their territories and reproduced because competition for space was low. As their pack sizes grew with each subsequent breeding and their progeny survived, subadult dispersal rates increased because pack sizes became too large and young adults were forced to find new breeding opportunities outside the pack.

Regulation of Wolves

My results are consistent with the hypothesis that wolf numerical response is, in part, regulated by ungulate prey resources (Zimen 1976, Keith 1983, Packard and Mech 1980, Messier and Crete 1985, Fuller 1989, Dale *et al.* 1994, Messier 1994). A main objective of my study was to determine how closely wolves regulated their densities in relation to prey resources. My results indicate that wolves had not fully recovered from the previous wolf reduction to naturally regulated densities. I conclude that my study was not long enough to determine if wolf numerical response is tightly or loosely regulated when prey increase. However, I found initial evidence that supports the hypothesis that wolves are tightly regulated.

(i) Annual rates of increase, natal dispersal rates and the formation of new pack territories were strongly correlated with the availability of ungulates.

(ii) Although wolves slightly exceeded 1983 pre-reduction densities, biomass:wolf ratios remained 20% below levels that are expected in a stable wolf:prey system. This indicates that wolf densities should continue to increase before stabilizing.

(iii) Wolf territorial establishment was completed after 1991 and the number of wolf packs was slightly more than that before wolf reduction began in 1983 (Farnell *et al.* unpubl. ms.). Space for new wolf territories became saturated early in my study and there was no room for new packs to establish in later years, despite a 3-4 fold increase in prey resources between 1983 and 1994.

(iv) Dispersal rate of wolves increased and was likely limiting pack size by the last year of my study.

(v) In addition to social behavior, various ecological factors also influence pack size, including wolf density and the body size of preferred ungulate prey (Zimen 1976). Most FSA packs hunted moose during my study (Chapter 2) and mean pack size for moose-hunting wolves is <10 wolves (Mech 1970, Zimen 1976). In most Yukon areas, mean size of moose-hunting wolf packs is between 6 and 10 wolves (Hayes and Bowers 1987, Hayes and Baer 1987, Hayes *et al.* 1991, R. Hayes unpubl. data). Mean pack size in my study was 8.5 wolves by 1994. I expect mean pack size to stabilize below 10 wolves. Thus, pack size should increase only slightly during the next few years.

Data Quality

Because of the large scale of this study, there were constraints that reduced the quality of my data. First, because I did not tag resident wolves that survived the wolf reduction phase, I can only indirectly conclude that dispersal from outside the FSA was the key numerical response that initiated the wolf population recovery. Second, because of infrequent monitoring of wolves and the size of my study area I did not know mortality causes of most wolves or the true dispersal rates. Third, although many packs were radio-tagged each winter, I inferred most cases of packs splitting from coincidental declines in the size of a large pack and the presence of a newly formed pack nearby. Fourth, the survival rates of radio-tagged wolves were probably biased during early years of my study. The K-M procedure requires that animals are sampled randomly, but this did not happen in 1990 and 1991 when most (60%) tagged wolves were adults in pairs. These wolves had a clear survival advantage over wolves that entered the study population in later years because they could freely establish new territories and reproduce without competition. Fifth, wolves in the study area experienced large-scale population reductions just before my study began. This confounded my ability to detect true wolf numerical response. For example, by the end of my study wolf density had not reached levels that were predicted by the prey biomass/wolf index. I believe this was due to the low density that wolves were annually reduced to between 1983 and 1989. The numerical responses that I observed may not reflect how a wolf population at naturally low density will react to ungulate prey increases.

Conclusions and Predictions

In this chapter, I provided evidence that the numerical response of an increasing wolf population is probably tightly regulated by ungulate prey through relatively sensitive biosocial feedback. By the end of my study, wolves were still increasing but there were several indicators that the populations of wolves, moose and caribou were all beginning to stabilize.

The convincing test of how tightly or loosely wolves are regulated by prey abundance can happen only after wolf numbers have stabilized. Wolf numerical response will be monitored in 1996 when population censuses of wolves, moose and caribou are planned as part of long term studies in the FSA. On the basis of results from my study of wolf numerical response, I predict that by 1996:

(i) the number of wolf packs in the FSA should not increase substantially;

(ii) wolf survival rates should decline, dispersal rates should remain high and mean pack size should stabilize below 10 wolves, similar to moose-hunting wolves elsewhere;

(iii) wolf density should stabilize at about 0.013 wolves/km^2 based on predictions (i) and (ii), and the wolf:prey biomass ratio in 1994; and

(iv) wolf density should be tightly regulated by ungulate biomass.

Chapter 2

Prey Selection and Kill Rate by Wolves in the Finlayson Study Area, Yukon

Introduction

Why wolves select particular prey, and the rate at which wolves kill different ungulate species are not well understood (Dale *et al.* 1994, Messier 1994), especially in systems where wolves, moose and woodland caribou are sympatric. Wolf predation is a primary factor limiting populations of moose (Mech 1970, Peterson 1977, Gasaway *et al.* 1983, Peterson *et al.* 1984, Ballard *et al.* 1987, Hayes *et al.* 1991, Gasaway *et al.* 1992, Thurber and Peterson 1993) and woodland caribou (Gasaway *et al.* 1983, Gauthier and Theberge 1985, Edmonds 1988, Seip 1991a and 1992). How wolves behave in relation to changing availability of prey can provide insight into the regulatory nature of wolf functional response (Theberge 1990, Seip 1991b, Messier 1991, Dale *et al.* 1994, Messier 1994). To best understand wolf functional response, kill rate by wolves should be measured across a range of prey densities, while assessing other ecological factors that could influence kill rate.

The supply of prey to predators depends on the number of prey and the vulnerability of the prey to being killed (Solomon 1949). The vulnerability of ungulates to wolf predation can depend upon several factors including: 1) density of prey; 2) the age, size and physical condition of prey (*e.g.*, nutrition and disease); 3) the availability of alternate prey; 4) the plasticity of wolf hunting behavior; 5) wolf pack size; and 6) snow depth. Kill rate on moose has been related to wolf pack size (Hayes *et al.* 1991, Thurber and Peterson 1993), moose density (Messier and Crete 1985, Messier 1991 and 1994), moose physical condition (Peterson and Page 1983, Ballard *et al.* 1987), and snow depth (Peterson 1977) .

In this chapter, I describe wolf predation behavior from 1990 through 1994 when wolves, moose and caribou populations were all increasing. I examine whether predation in winter was additive or compensatory mortality for ungulate prey. I also examine the influence of wolf density, wolf pack size, moose density, alternate prey availability, small mammal abundance, and snow depth on prey selection and kill rate by wolves in winter. I estimate the year-round proportion of moose killed by wolves in the FSA, and I assess the importance of wolf predation as a limiting factor on adult and calf moose in the FSA.

From other data on kill rate by wolves (Hayes *et al.* 1991, Thurber and Peterson 1993, Dale *et al. in press*) and predation rates (Messier 1994), and from other studies of wolves in Alaska (Peterson *et al.* 1984, Ballard *et al.* 1987, Gasaway *et al.* 1992) and Yukon (Larsen *et al.* 1989, Hayes *et al.* 1991), I test the following predictions about wolf predation in the FSA:

(i) Wolf predation should be mainly additive mortality on increasing moose and caribou populations;

(ii) Kill rate by wolves should be dependent on prey density, wolf pack size and snow depth;

(iii) Kill rate of moose calves should be related to the percent of calves available each winter;

(iv) Wolves should show a prey switching response away from moose to caribou, as caribou numbers within pack territories increase relative to moose;

(v) Winter predation rate (% moose killed) should depend upon the number of wolves preying upon moose; and

(vi) Wolf predation should be the main factor influencing adult and calf mortality of primary prey.

Methods

I studied wolf predation in a 23,000 km^2 area in the east central Yukon (62°N, 128°W) from February 1990 through March 1994 (see Study Area). I selected this area because the wolf population was reduced until 1989 and both moose and woodland caribou coincidentally increased to higher densities (Farnell *et al.* unpubl. ms.). The manipulation of the wolf/prey system provided a wide range of wolf pack sizes and prey densities to observe changes in kill rates. Moose density increased from 0.248 moose/km^2 (4,300 moose) in November 1990 to 0.434/km^2 (7,500 moose) in 1994. The Finlayson woodland caribou herd increased from

5,900 to 7,500 animals in the same period (Farnell *et al.* unpubl. ms.). Detailed techniques for estimating wolf and prey densities, and wolf radiotelemetry are reported in Methods, Chapter 1.

Observers in PA-18 Supercub and Maule LR-7 aircraft located radio-tagged wolves following methods of Mech (1974). When observers located a radio signal, they circled and counted wolves and searched the area for ungulate carcasses. If most pack members were not seen, aircraft crews followed wolf trails to find missed individuals and locate kills. I classified moose as either calf or adult size by differences in size and body shape (Peterson 1977). I pooled all non-calves as adult-size because I was unable to distinguish between carcasses of adults and yearlings from aircraft.

Causes of ungulate deaths were divided into wolf predation, natural, and human-causes. I assumed wolves killed an animal when there was fresh blood spoor, or snow trails showed the animal was recently attacked by wolves and fed on at the time of death. I assumed wolves were scavenging if a carcass was on its sternum (Stephenson and Sexton 1974, Ballard *et al.* 1987, Hayes *et al.* 1991), there was sign the animal was killed by hunters or sign that other scavengers had fed on the carcass before wolves.

I visited a random sample of *in situ* prey carcasses each winter to determine sex, age and physical condition. Sex of moose was determined by antler pedicels and ilium morphology, and the sex of caribou was determined by the size and shape of antlers. I collected incisor bars from moose kills to determine age (Sergent and Pimlott 1959) and an intact femur or humerus from moose and caribou to assess nutritional condition by marrow fat content (Neiland 1970). I kept bones frozen to minimize dehydration loss (Peterson *et al.* 1982). When moose carcasses were mostly consumed I could still classify them as either calf or adult size, depending on the size and shape of fecal pellets (P. Koser, Ross River, *pers. comm.*).

I defined kill rate as either the number of moose killed wolf^{-1} day^{-1}, or the total biomass (kg) of ungulate prey killed wolf^{-1} day^{-1}. Moose calf kill rate was the number of moose calves killed $wolf^{-1}$ day^{-1}. I studied daily kill rates by locating radio-tagged packs at regular intervals during February and March 1990 and 1992, and during March 1991 and 1994. I defined wolf pack size as the mean number of wolves seen in each pack during each study period, or the traveling pack size (Messier 1994, Dale *et al. in press*). I did not study kill rates of single wolves.

My location intervals varied, depending on the size of the wolf pack and on the composition of ungulate species available within territories. Wolves usually spend more than 48 h handling moose carcasses (Peterson *et al.* 1984, Messier and Crete 1985, Ballard *et al.* 1987, Hayes *et al.* 1991). Caribou are smaller than moose and I expected that caribou would be handled more quickly (Dale *et al. in press,* R. Hayes unpubl. data). If only moose were available in a pack territory, I located the pack every 24 to 48 h. I observed wolf packs in caribou range twice each day, usually between 9:00-11:00 h and 16:00-19:00 h. I compared kill rate to location intervals to test for temporal biases in my ability to detect kills.

In most of my study area, conditions were generally good for observing wolves from the air. The exception was where there were concentrations of caribou trails and feeding craters. If a pack was not seen for 3 consecutive days (72 h), I did not include the missed period in calculations of kill rate because a moose could be completely consumed in that time and not detected by observers (Peterson *et al.* 1984, Hayes *et al.* 1991). I missed one 72 h period in 1992 when a snowstorm prohibited locating all packs. The daily area traveled by radio-tagged packs were estimated by 100% area convex-polygons (Ackerman *et al.* 1990).

The live biomass of ungulate prey was estimated from various sources. I estimated the weight of adult female moose at 375 kg, based on April weights from interior Alaska (Franzmann *et al.* 1978). I assumed that bulls lost 20% of their pre-rut weight during winter (Schwartz *et al.* 1987), and averaged 413 kg in late winter. Adult moose of unknown sex averaged 400 kg, yearlings 250 kg, and calves 150 kg (Ballard *et al.* 1987), adult caribou 152 kg (R. Florkiewicz, Yukon Fish and Wildl. Br., unpubl. data), calf caribou 55 kg (Skoog 1968) and mountain sheep 75 kg (Sumanik 1987, Hayes *et al.* 1991).

Consumable biomass of caribou was 75% of live weight (Ballard *et al.* 1987) and moose was 65%. Previous studies used 75% for moose (Peterson 1977, Carbyn 1983, Messier and Crete 1985, Ballard *et al.* 1987, Sumanik 1987, Hayes *et al.* 1991, Thurber and Peterson 1993, Dale *et al. in press*). I estimated 65% was available to wolves on the basis of differences in live moose weights (see above) and the actual weights of 7 moose carcasses left by wolf packs in 1992. Carcasses were weighed the day that wolf packs abandoned them. Ravens (*Corvus corax*) were important scavengers in the FSA (Promberger 1992). I used Fig. 20 in Promberger (1992) to adjust wolf consumption and account for raven scavenging, depending on wolf pack size.

I defined *predation rate* as the proportion of available prey animals that were killed daily (Oaten and Murdoch 1975, Messier 1991, Dale *et al.* 1994, Messier 1994). I estimated the total winter predation rate by multiplying daily kill rates to 182 day winter periods, then divided the product by the mean annual density of moose. This method does not account for spatial differences in the distribution of prey among pack territories, which could limit the accuracy of predation rate estimates (Dale *et al. in press*). I minimized the influence of heterogeneity of prey by measuring kill rates of many packs in more than 1 year (Table 2). I assumed that rates of change in annual density of moose was constant among all pack territories.

Snow data was annually collected in early March at 7 stations in my study area (G. Ford, Government of Canada Water Resources, unpubl. data). I compared kill rates to the annual snow depth from the station nearest each pack territory.

I used linear regression models to examine relationships between kill rate and several independent variables. The kill rates of some packs were studied in more than 1 winter, disqualifying the assumption of data independence. I tested for pack dependence by comparing the regression equations for all predation periods against the last (or only) kill rate period studied for each pack.

Results

Characteristics of Ungulates Killed by Wolves

I found 326 ungulate carcasses, including 291 moose (89%), 30 caribou, 1 mountain sheep, and 4 unknown ungulates. Three hundred and eleven were found in winter and 297 of these were found by following radio-tagged wolf packs. Causes of death included 300 killed by wolves, 8 shot by humans, 15 by natural causes and 3 by unknown causes. I visited 51 of 300 (17%) wolf kills *in situ*. Scavenging by wolves was uncommon and was not included in my estimates of wolf consumption rates.

Moose calves ($n = 88$) accounted for 31% of wolf-killed moose, annually ranging from 12 to 55% (Table 6). The ratio of killed calves:adults was significantly greater than the live ratio of calves:adults in March 1990, lower than the live ratio in 1994, and not different in the other 3 winters (Table 6). Yearlings were the next most important age class, accounting for 25% ($n = 9$) of the 51 moose visited *in situ*. I assumed that yearlings represented 25% of adult-size moose killed in all winters. Based on this assumption, I estimated that yearlings comprised 11 to 22% and adults comprised 34 to 66% of wolf-killed moose in different winters (Table 6).

The mean age of 21 adult moose was 8.9 ± 0.9 years-old (SE), ranging from 2 to 15 years-old (Fig. 14). Mean age was similar between males and females. Most adults killed by wolves were younger than 4 years-old or older than 10 years-old. Few middle-aged moose were killed by wolves (Fig. 14). Wolves killed 28 female and 18 male moose (≥ 1 year-old), which was not different (Pearson $\chi^2 = 0.06$, df = 1, $P = 0.80$) than the adult sex ratio in the moose population in November 1991 (Larsen and Ward 1995).

Of the 30 caribou killed by wolves, 2 (7%) were calves but I had difficulty separating

Table 6. Numbers and proportions of calf, yearling and adult moose killed by wolves each winter, and live calf and adult moose proportions observed in late winter composition counts. Proportions are in brackets. The chi-square values are differences in proportion of calves in kill sample (observed) versus live calf proportion in winter (expected). Yates corrected chi-square was used for 1991 and 1993 because of small cell sizes for calves in kill sample.

	Wolf-killed Moose (%)				Number of Moose in March			
Year	Calf	Yearling*	Adult	Total	Calf (%)	Adult	χ^2	*P* value
1990	30 (55)	2 (11)	23 (34)	55	42 (27)	114	13.8	<0.01
1991	4 (25)	1 (19)	11 (56)	16	72 (27)	193	<0.01	1.00
1992	35 (26)	5 (19)	95 (55)	135	45 (21)	170	1.2	0.28
1993	4 (12)	1 (22)	28 (66)	33	18 (18)	83	0.6	0.44
1994	15 (32)	0 (17)	32 (51)	47	38 (11)	294	14.3	<0.01
Total	88	9	189	286				

* Yearlings comprised 9 of 36 (25%) adult-size moose inspected on the ground, and I assumed the yearling proportion remained constant each winter.

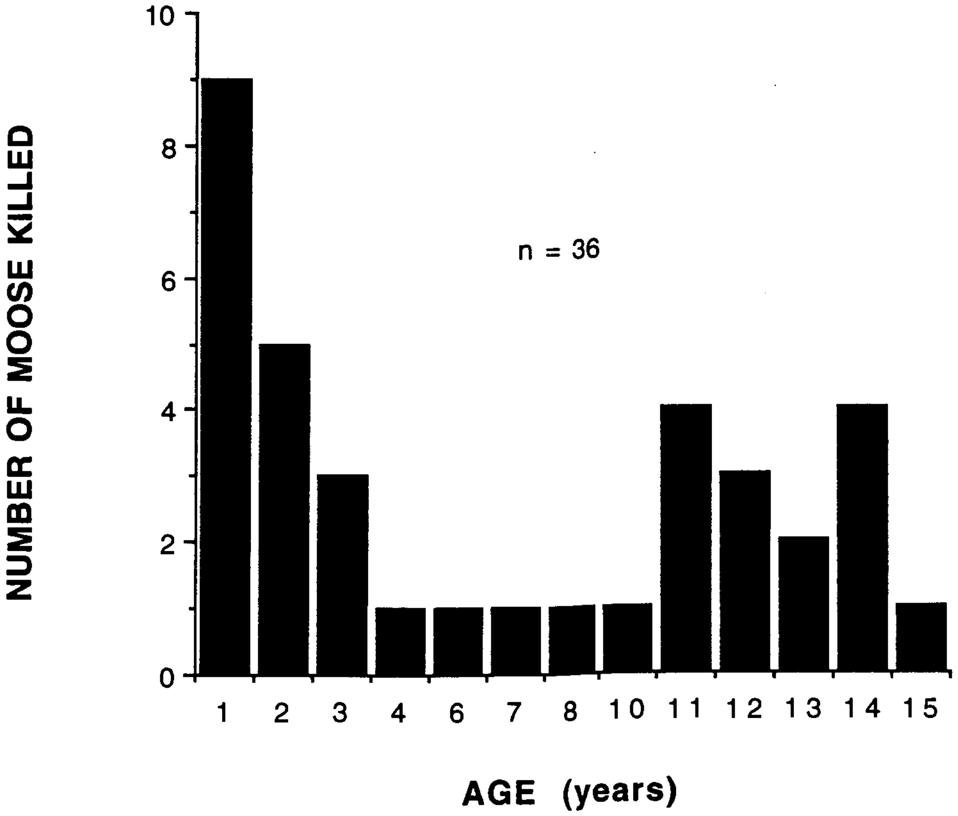


Fig. 14. Ages of moose (excluding calves) killed by wolves during winter in the study area.

caribou age classes from the air. Some large wolf packs completely consumed caribou in a few hours and left few remains for identification. Thus, I collected insufficient data to assess the age and sex of wolf-killed caribou.

Ungulates killed by wolves were not in starved condition at the time of death. Starvation levels for moose calves is ≤10% marrow fat and ≤20% for adults (Peterson *et al.* 1984). Marrow fat of wolf-killed calves ($n = 23$) averaged 34 ± 4% (SE, range: 11 to 78%) (Fig. 15) and adults ($n = 26$) averaged 77 ± 3% (SE, range: 52 to 95%). Adult marrow fat values were significantly higher than that of calves (Mann-Whitney U -test, $U = 565$, df =1, $P < 0.001$). None of these moose were within starvation values, but 8 calves (35%) were between 11 and 20% marrow fat, showing that a high proportion of calves were in low nutritional condition during late winter. Seven adult caribou averaged 66 ± 14% (SE) marrow fat (range: 8 to 95%). One caribou was apparently starved at the time of death.

Killing and Consumption Rates by Wolves

I estimated killing rate by wolves among 21 different packs during a total of 45 periods in 4 winters (Table 7). I studied 12 packs in 1990, 8 in 1991, 17 in 1992 and 8 in 1994. Traveling pack size ranged between 2 and 20 wolves. I measured kill rates by wolves in *small* packs (2-3 wolves) during 18 periods (40% of all periods), *medium* packs (4-9) during 13 periods (29%), and *large* packs (≥ 10) during 14 periods (31%). In total, I studied 283 wolves during 6,153 wolf-days (982 pack-days). The mean study period was 20 ±1.3 days (SE), ranging from 6 to 39 days (Table 7). Packs were located and seen an average of 71 ± 0.9% (SE) of study days, including many packs that were regularly located at 48 hour intervals (Table 7). During the 45 kill rate periods, I found a total of 201 wolf-killed ungulates including 179 moose, 21 caribou and 1 mountain sheep (Table 7). Moose were the main prey comprising 94% (57,764 kg) of all ungulate biomass killed. Mean kill rate was 0.045 ± 0.004 (SE, range: 0.013 to 0.123) moose wolf^{-1} day^{-1} ($n = 44$ periods; 1 period was excluded because wolves only killed caribou). The mean pack kill rate was 0.193 ±0.085 (SE) moose

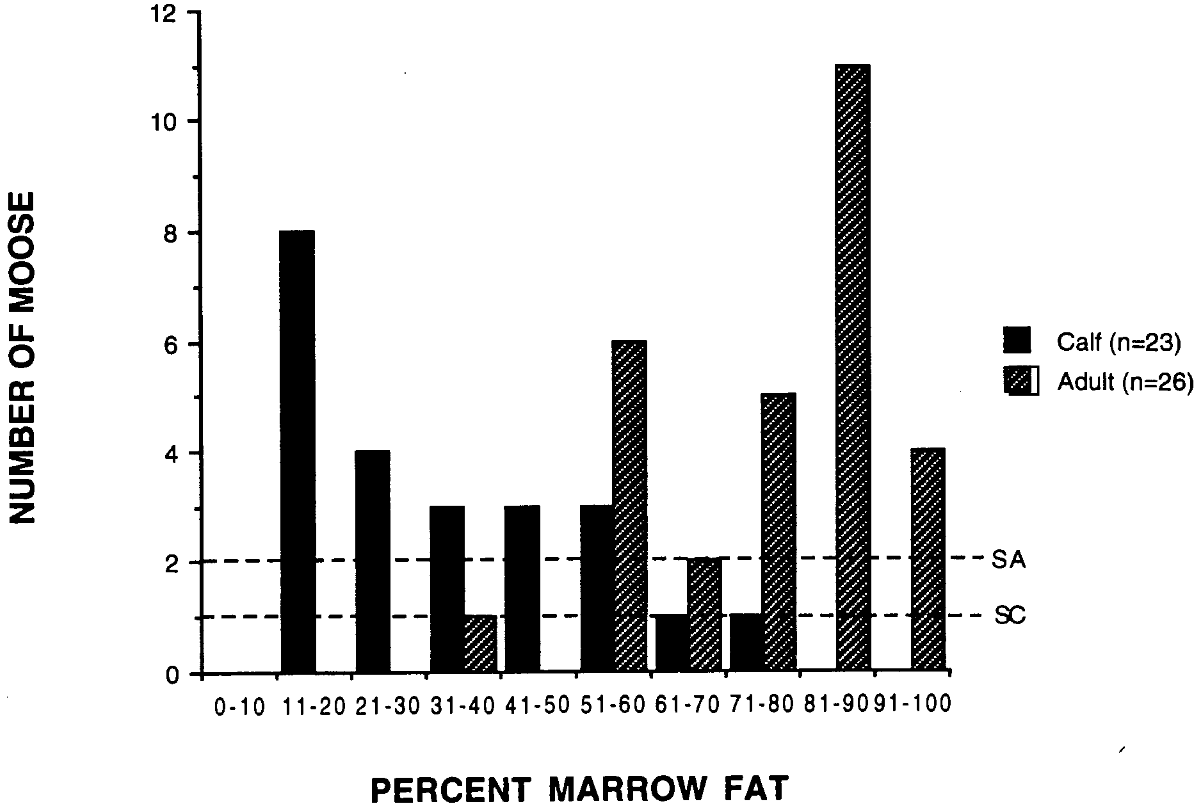


Fig. 15. Marrow fat values for adult and calf moose killed by wolves during winter in the study area. SA is starvation level for adult moose, SC is starvation level for calf moose.

Table 7. Composition of ungulate prey killed and kill rate by wolves among 21 packs monitored during late winter 1990 through 1994 in the FSA.

Year	Pack	Hours Between Locations	Number of Wolves	Number of Days Studied	% Days Observed	No. of Moose Killed	No. of Caribou Killed.	Total Weight[a] (kg) of Prey Killed	Weight (kg) of Prey Wolf^{-1} Day^{-1}
1990	Frances L.	24	17	14	71	6	0	1,850	7.8
	Jackfish L.	24	2	31	84	6	0	1,125	18.1
	Ketza R.	48	2	31	65	3	0	700	11.3
	Lapie R.	48	5	30	53	5	0	1,676[b]	11.2
	Prevost R.	24	6	19	79	4	0	925	8.11
	Seven Wolf L.	24	2	38	89	2	1	452	6.0
	Tyers R.	48	2	20	60	2	0	800	20
	Tuchitua R.	24	11	36	75	5	0	1,725	4.4
	Weasel L.	24	6	16	81	5	0	1,513	15.8
	Woodside R.	24	4	39	77	7	0	2,063	13.2
	Yusezyu R.	24	2	30	87	6	0	1,163	19.4
	Upper Pelly R.	24	2	14	79	3	0	450	16.1
	Total			318		54	1	14,442	
1991	Finlayson L.	6	2	9	100	1	2	205	11.4
	Ketza R.	6	2	12	92	3	0	925	38.5
	Light Cr.	48	2	6	67	1	0	150	12.5
	Mink Cr.	6	4	11	100	1	3	869	19.8
	McEvoy L.	48	2	16	56	1	0	400	12.5
	Woodside R.	48	7	8	50	1	0	150	2.68
	Wolverine L.	24	2	9	78	2	0	813	45.2
	Seven Wolf L.	6	7	13	100	4	1	1,515	16.6
	Total			84		18	5	5,027	
1992	Campbell Cr.	24	14	22	91	6	6	3,112	10.1
	Finlayson L.	24	2	28	57	5	0	1,450	25.9
	Fire Cr.	48	3	24	50	3	0	800	11.1
	Frances L.	48	9	21	81	3	0	1,600	8.5
	Jackfish L.	48	11	23	48	6	0	2,150	8.5
	Ketza R.	48	2	19	63	3	0	1,200	31.6
	Light Cr.	48	6	19	52	4	0	1,588	13.9
	Mink Cr.	48	8	23	48	0	3	456	2.5
	Otter Cr.	48	2	23	52	2	0	800	17.4
	Prevost R.	48	10	10	50	3	0	925	9.3
	Seven Wolf L.	24	10	24	79	5	2	1,817	7.6
	Tuchitua R.	48	10	27	52	5	0	1,225	4.5
	Tyers R.	48	2	19	63	2	0	550	14.5
	Weasel L.	48	10	23	47	5	1	1,877	8.2
	Wolverine L.	48	2	21	52	3	0	950	22.6
	Woodside R.	48	11	24	58	4	0	1,350	5.1
	Yusezyu R.	48	11	33	48	7	0	1,788	4.9
	Total			383		67	12	23,638	

Table 7. (Continued). Composition of ungulate prey killed and kill rate by wolves among 21 wolf packs monitored during late winter 1990 through 1994 in the FSA.

Year	Pack	Hours Between Locations	Number of Wolves	Number of Days Studied	% Days Observed	No. of Moose Killed	No. of Caribou Killed	Total Weight[a] (kg) of Prey Killed	Weight (kg) of Prey Wolf^{-1} Day^{-1}
1994	Campbell Cr.	24	20	27	96	11	2	3,442	6.4
	Mink Cr.	24	11	26	92	4	1	1,752	6.1
	Light Cr.	24	11	26	73	6	0	1,900	6.6
	Nipple Mt.	24	2	24	83	2	0	800	16.7
	Otter Cr.	24	6	21	81	3	0	713	5.7
	Upper Pelly R.	24	5	21	81	3	0	1,200	11.4
	Wolverine L.	24	4	26	73	7	0	2,025	19.5
	Yusezyu R.	24	13	26	81	9	0	2,825	8.4
	Total			197		45	3	14,657	
	Grand Total			982		179	21	57,764	

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[a] Based on the following weights in kg: cow moose 375, bull moose 413, unknown adult moose 400, yearling moose 250, calf moose 150, adult caribou 152, calf caribou 55, and mountain sheep 75 (see Methods, Chapter 1, for sources for weights).

[b] Includes one mountain sheep.

pack^{-1} day^{-1}.

I tested for various factors that could influence kill rate by wolves. I first examined the influence of wolf pack size because other studies showed it strongly affected kill rates (Hayes *et al.* 1991, Thurber and Peterson 1993, Dale *et al.* 1994). The model $y = \log_{10}$ of pack size minimized heteroscedascity for both kg of prey killed wolf^{-1} day^{-1} (KGWD) and the number of moose killed wolf^{-1} day^{-1} (MWD). $\log_{10} y$ = pack size was the best linear model for the period between moose kills (days moose kill^{-1}, DMK). These were the same log transformed models used by Thurber and Peterson (1993) for similar analyses of kill rate by wolves.

Because kill rates of some packs were measured more than once, I first examined the data for dependence. I calculated the regression equation for KGWD and $\log_{10}$ pack size using only data from the last (or only) kill rate period for the 21 different wolf packs ($y = -17.4 - 5.35\log_{10}$ pack size), and compared it to the equation for the 45 pooled periods ($y = -16.8 - 5.4\log_{10}$ pack size). There were no significant differences in the parameters of the 2 models. I conclude that pack dependence had no effect, and I subsequently used all 45 kill rates in regression models. I also tested for any relationship between kill rate and location interval. I found no correlation (Table 8) indicating the rate that I observed wolf packs did not influence my ability to find kills.

Kill rate was significantly correlated only with wolf pack size (Table 8). Kill rate was not related to: 1) daily area (km^2) that wolf packs traveled, 2) the percent of days wolves were observed, 3) the annual ratio of wolves:moose, 4) the number of wolf packs, 5) snow depth, or 6) moose density (see Table 8 for regression values). I also examined the kill rate on moose calves ($\log_{10}$ days calf kill^{-1}) and found it was also not related to any of the above variables, including wolf pack size. Further, moose calf kill rate was not correlated with the ratio of live calves adult moose^{-1} observed in March composition counts (Table 8).

Both KGWD (Fig. 16, $r^2 = 0.40$, df = 44, $P < 0.001$) and MWD (Fig. 17, $r^2 = 0.57$, df = 43, $P < 0.0001$) were inversely related to $\log_{10}$ pack size. The highest kill rates and

Table 8. Linear regression coefficients for kill rate by wolves on ungulates (kg wolf^{-1} day^{-1}), moose (moose wolf^{-1} day^{-1}), and killing intervals on moose ($\log_{10}$ days moose kill^{-1}) and moose calves ($\log_{10}$ days calf kill^{-1}), with independent variables.

Variables				
Dependent	Independent	r^2	*df*	*P* Value
kg wolf^{-1} day^{-1}	km^2 day^{-1}	0.01	44	0.49
	moose density	0.03	44	0.28
	moose:wolf ratio	0.002	44	0.78
	number of packs	0.001	44	0.97
	percent days seen	0.03	44	0.28
	$\log_{10}$ pack size	0.40	44	<0.001
moose wolf^{-1} day^{-1}	$\log_{10}$ pack size	0.57	43	<0.001
$\log_{10}$ days kill^{-1}	km^2 day^{-1}	0.001	43	0.87
	moose density	0.02	43	0.93
	moose wolf^{-1}	0.006	43	0.98
	percent days seen	0.10	43	0.52
	snow depth	0.003	41	0.75
	pack size	0.37	43	<0.001
$\log_{10}$ days calf-kill^{-1}	moose density	0.001	31	0.90
	percent moose calves alive in late winter	0.001	31	0.84
	pack size	0.004	44	0.74
	snow depth	0.008	41	0.58

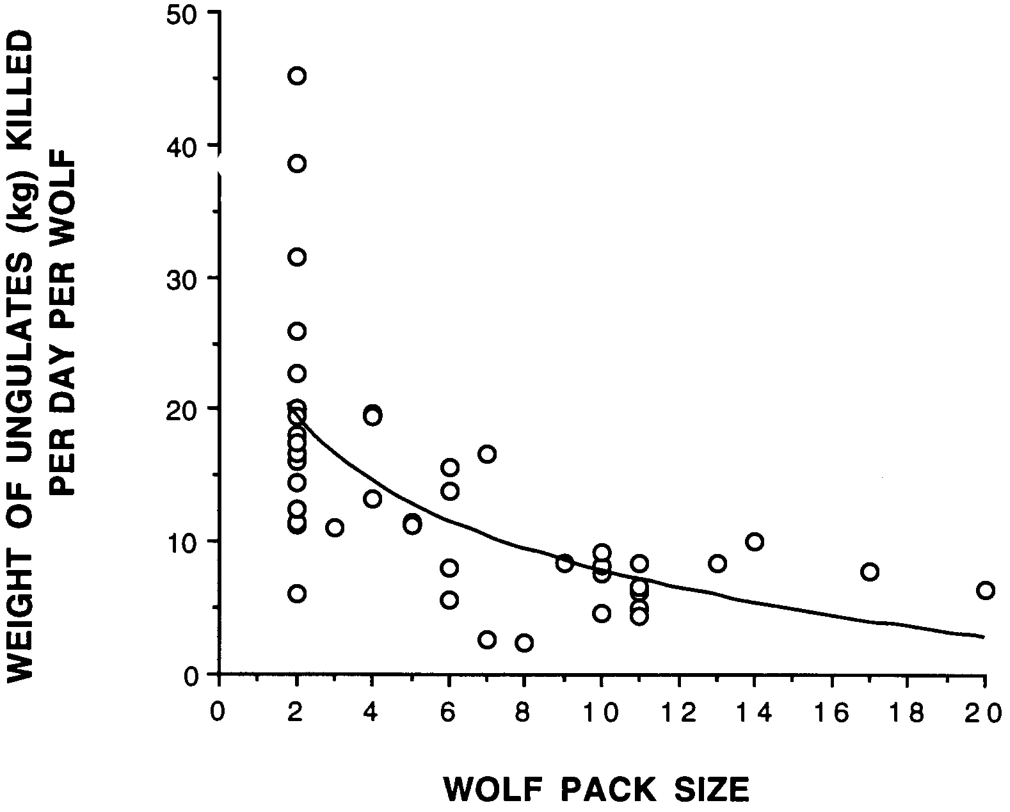


Fig. 16. The estimated weight of prey killed by wolves each day (kg wolf^{-1} day^{-1}) during winter for different size wolf packs in the FSA ($Y = 24.64 - 16.77 \log_{10} X$).

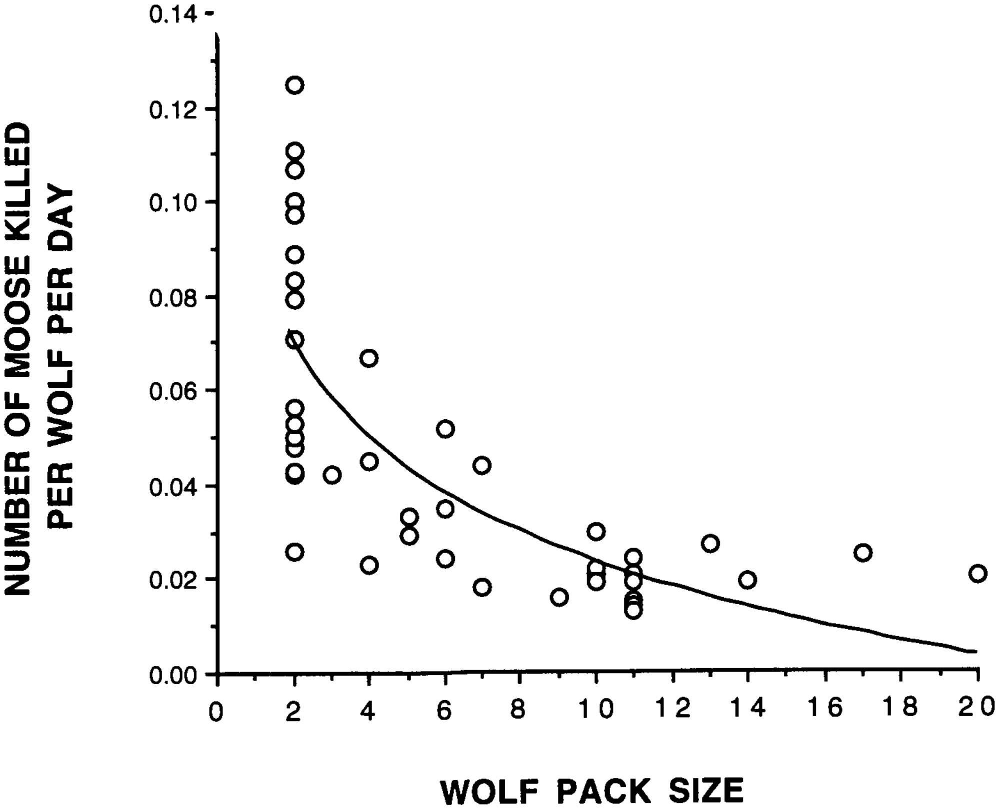


Fig. 17. The moose kill interval (days moose kill^{-1}) during winter for different size wolf packs in the FSA ($\log_{10} Y = 0.93 - 0.03X$).

widest variances were among pairs of wolves. The $\log_{10}$ DMK was inversely related to wolf pack size (Fig. 18, $r^2 = 0.37$, df = 43. $P < 0.001$), with the time between kills decreasing as pack size increased. I excluded small packs to test if kill rates remained significantly correlated with the sizes of larger packs (4 to 20 wolves) (Fig. 19). The variable KGWD remained inversely related to $\log_{10}$ pack size with wolves in medium packs having higher kill rates than wolves in large packs ($r^2 = 0.37$, df = 26, $P = 0.001$). Excluding small packs did not improve the relationship between $\log_{10}$DMK and moose density ($r^2 = 0.007$, df = 25, $P = 0.69$), indicating that food supply did not influence kill rate by wolves in larger packs. Excluding pairs did improve the relationship between the $\log_{10}$ days calf kill^{-1} and the ratio of live calves: adult moose in winter. However, this relationship was insignificant at the 5% level ($r^2 = 0.11$, df = 24, $P = 0.11$).

There was no correlation between the daily area (km^2) traveled (*i.e.*, prey searching rate) and $\log_{10}$ pack size ($r^2 = 0.02$, df = 44, $P = 0.33$). Small packs traveled an average of 23 ± 5 (SE) km^2 day^{-1}. Medium packs traveled 18 ± 5 (SE) km^2 day^{-1} and large packs 28 ± 4 km^2 (SE) day^{-1}. Daily area traveled was also not related to moose density ($r^2 = 0.04$, df =44, P =0.18) or the ratio of moose:wolf each winter ($r^2 = 0.04$, df = 44, $P = 0.17$). These low correlations indicate that wolf competition for food resources did not significantly influence the rate that wolves searched for prey.

I found no significant difference in the handling times (number of days packs spent on kills) between adult moose carcasses ($n = 65$, mean = 2.9 ± 0.17 [SE] days) and calf moose carcasses ($n = 35$, mean = 2.6 ± 0.22 [SE] days). The mean handling time for adult moose was not different (Kruskal-Wallis test, $\chi^2 = 5.4$, $n = 65$, P =0.07) among small (n = 17 kills, mean = 3.3 ± 0.19 [SE] days), medium (n = 19 kills, mean = 3.1 ± 0.5 [SE] days) and large packs (n = 29 kills, mean = 2.6 ± 0.16 [SE] days).

The time that wolves spent handling moose calves differed significantly with pack size (ANOVA, F= 3.9, df =37, $P = 0.03$). Small packs averaged 3.3 ± 0.3 (SE) days (n = 16

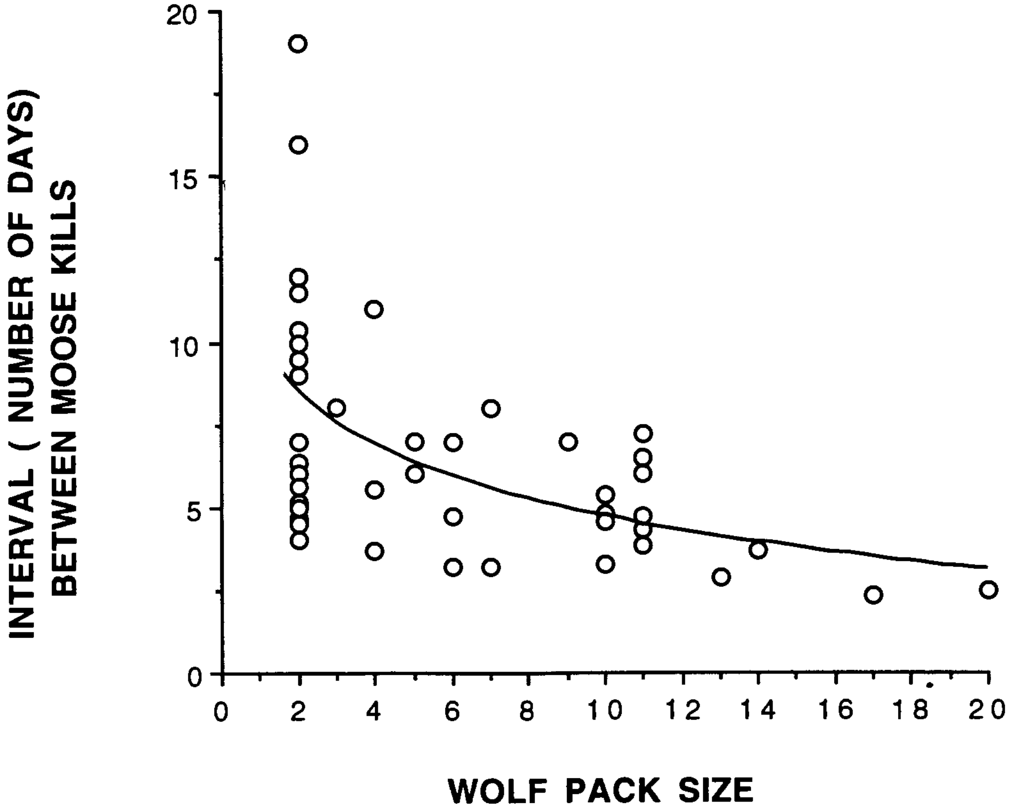


Fig. 18. The moose kill interval (days moose kill^{-1}) during winter for different size wolf packs in the FSA ($\log_{10}Y = 0.93 - 0.03X$).

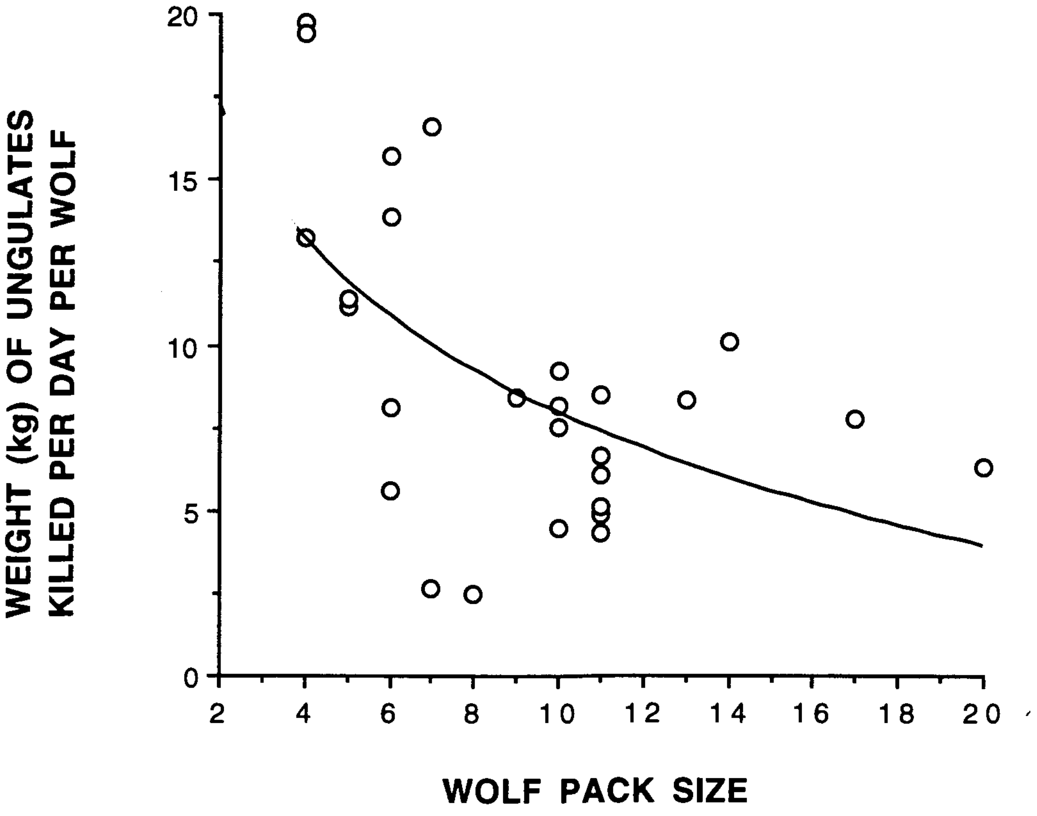


Fig. 19. The estimated weight of prey killed by wolves each day (kg $\text{wolf}^{-1}\ \text{day}^{-1}$) during winter for packs of 4 or more wolves in the FSA ($Y = 23.07 - 15.11 \log_{10} X$).

kills), medium packs averaged 2.5 ± 0.3 days (SE) ($n = 8$ kills) and large packs averaged 2.0 ± 0.3 (SE) days ($n = 29$). All packs spent an average of 1.3 ± 0.1 (SE) days handling caribou kills ($n = 13$). However, large packs consumed caribou carcasses in a few hours, making it difficult to accurately estimate their handling times.

I examined the influence of alternate food availability on prey selection by wolves. Large numbers of wintering caribou were available to 4 packs during 11 kill rate periods (Mink Cr., Seven Wolf L., Campbell Cr., Weasel L.). Caribou greatly outnumbered moose but these packs still killed more moose ($n = 40$) than caribou ($n = 20$). Mean kill rate in these 11 periods was 7.9 ±0.7 (SE) kg moose wolf^{-1} day^{-1} compared to 2.5 ± 0.6 (SE) kg caribou wolf^{-1} day^{-1}.

Snowshoe hare availability did not significantly influence the kill rate by wolves on ungulate prey. Hares were abundant during the winters 1990 and 1991, then the hare population crashed before winter 1992 (*pers. observ.*). I could not use aircraft observations to directly measure the proportion of hares in the wolf diet. Hence, I tested for effects of hare availability by comparing KGWD with $\log_{10}$pack size, nested within the 2 periods of relative snowshoe hare abundance (*i.e.*, present and absent). Kill rate of ungulates was not correlated with the relative availability of snowshoe hares (Nested ANOVA model, F = 0.12, df =1, P =0.91).

I examined the influence of snow depth on kill rate. Both DMK and $\log_{10}$days calf kill^{-1} were not correlated with March snow depth (Table 8). Mean snow depth did not differ significantly among years (ANOVA, F = 0.66, df = 33, $P = 0.63$), ranging from 79 to 94 cm. However, snow depths differed with elevation. There was significantly less snow (71 ± 4 [SE] cm) in lowland forests compare to the mountains (100 ± 3 [SE] cm) (independent t-test, $t = 5.5$, df = 1, $P < 0.001$). Few moose wintered in the mountains, apparently to avoid deeper snow conditions. The vulnerability of moose to predation by wolves usually increases when snow depths exceed 90 cm, especially for calves (Peterson 1977, Peterson *et al.* 1984). Snow depth did not exceed this critical level in most ungulate wintering areas during all years of my study.

I then compared consumption rates of wolves among different size wolf packs. In previous studies, the biomass of prey available to wolves was not adjusted to account for loss due to scavengers, but most authors thought it could be important (Carbyn 1983, Messier and Crete 1985, Ballard *et al.* 1987, Fuller 1989, Hayes *et al.* 1991, Thurber and Peterson 1993, Dale *et al. in press*). Promberger (1992) showed that the ungulate biomass removed by ravens was inversely related to size of a wolf pack. Promberger (1992) estimated that ravens could remove 50% of ungulate biomass from a pair of wolves, 33% from a pack of 6 wolves and 10% from a pack of 10 or more wolves. I calculated wolf consumption rates both with adjustment for raven loss (RA), and without it (NRA) to allow my data to be compared with previous studies. The mean NRA rate was 8.7 ± 0.9 (SE) kg wolf^{-1} day^{-1}, and it was negatively correlated with $\log_{10}$ pack size (Fig. 20, $r^2 = 0.40$, df = 44, $P < 0.0001$). Wolves in small packs apparently consumed 12.7 ± 1.5 (SE) kg wolf^{-1} day^{-1}, medium packs 7.6 ± 1 (SE) kg wolf^{-1} day^{-1}, and large packs 4.6 ± 0.3 (SE) kg wolf^{-1} day^{-1}.

After accounting for biomass lost to ravens, RA consumption rate remained significantly correlated with $\log_{10}$ pack size, but consumption rate differences among pack sizes were reduced (Fig. 21, $r^2 = 0.13$, df = 44, $P = 0.014$). The mean RA consumption rate was 5.5 ± 0.4 (SE) kg wolf^{-1} day^{-1}, down 37% from the NRA mean rate. Ravens had the greatest negative effect on wolf consumption among small packs, reducing the available biomass to 6.4 ± 0.8 (SE) kg wolf^{-1} day^{-1}. Consumption rates declined to 5.7 ± 0.9 (SE) kg wolf^{-1} day^{-1} in medium packs, and to 4.1 ± 0.9 (SE) kg wolf^{-1} day^{-1} in large packs. The RA consumption rate was significantly different among the 3 pack size classes (Kruskal-Wallis test, $\chi^2 = 6.1$, df = 2, $P = 0.04$).

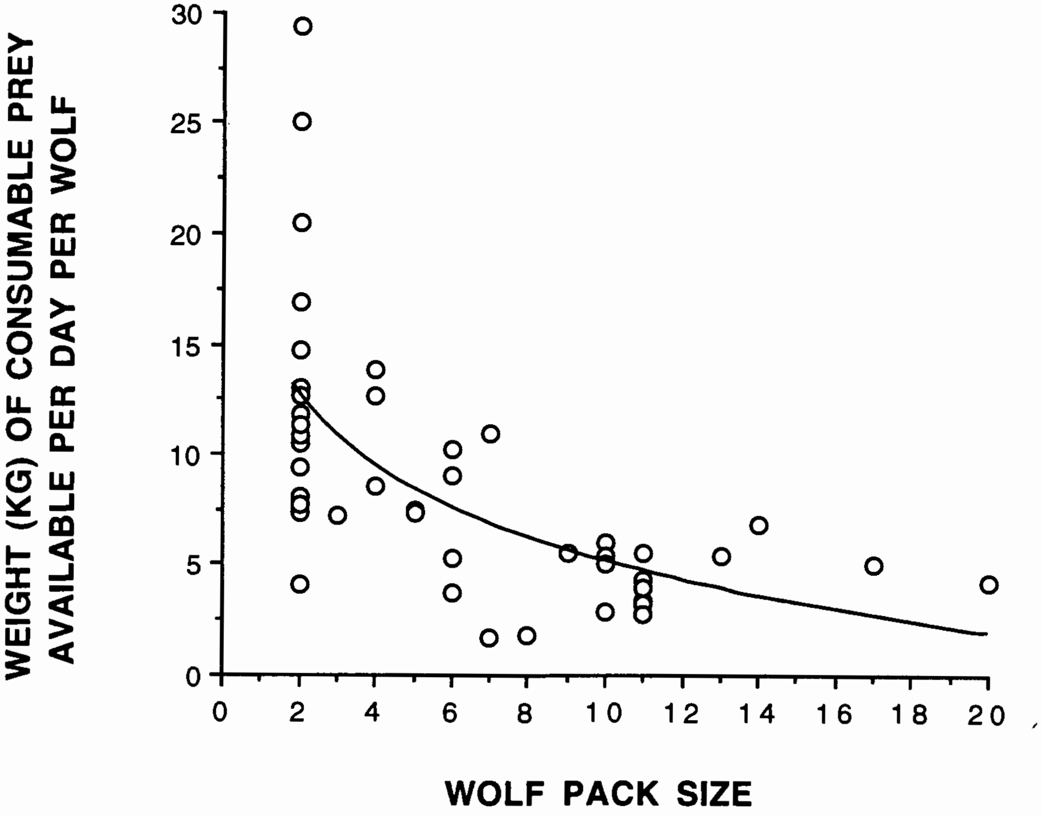


Fig. 20. The estimated weight of prey available to wolves each day (kg consumed wolf^{-1} day^{-1}) during winter for different size wolf packs in the FSA (Y=16.07 - 10.89 log$_{10}X$).

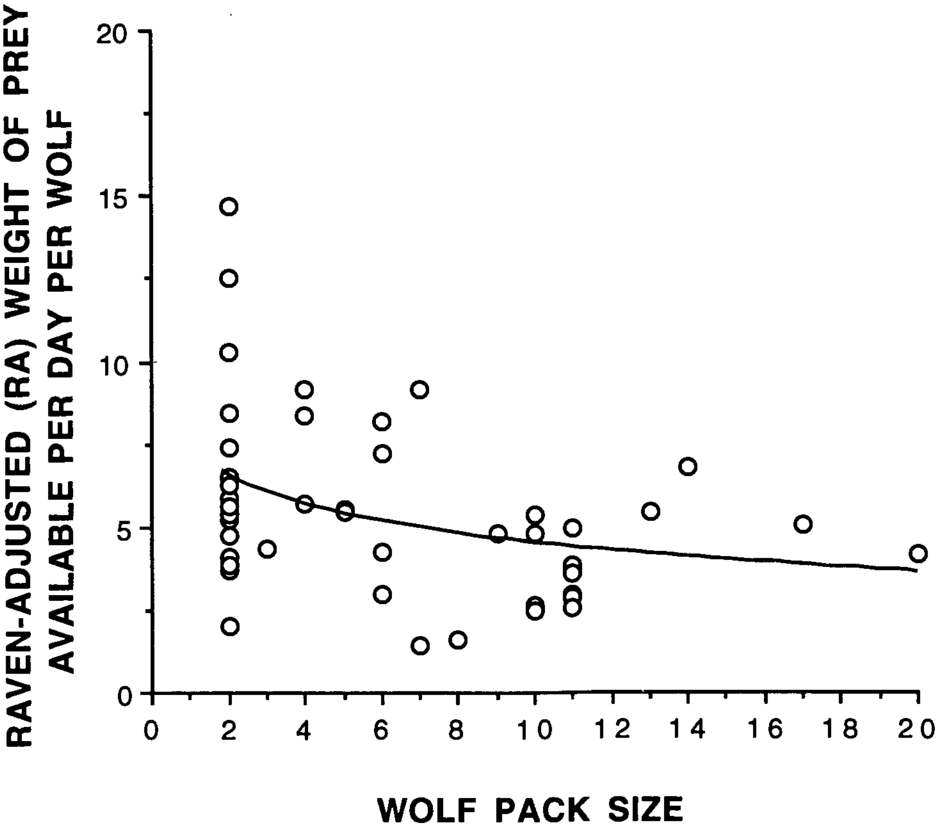


Fig. 21. The estimated weight of prey (raven-adjusted) consumed by wolves each day (kg wolf^{-1} day^{-1}) during winter for different size wolf packs in the FSA ($Y = 7.48 - 2.95 \log_{10} X$).

Wolf Predation Rate on Moose in Winter

The total number of moose killed in winter was positively correlated with $\log_{10}$ pack size (Fig. 22, $r^2 = 0.36$, df = 43, $P < 0.001$). Small packs ($n = 17$) killed an average of 27 ± 2.4 (SE) moose winter^{-1} pack^{-1}, medium packs ($n = 12$) killed 35 ± 3.8 (SE) moose winter^{-1} pack^{-1}, and large packs ($n = 14$) killed 46 ± 3.5 (SE) moose winter^{-1} pack^{-1}. By multiplying these values by the known number of different size packs each winter (Table 2), I estimated that wolves killed about 450 moose in winter 1990. By 1992, wolves killed about 900 moose in winter, then the total number of moose killed leveled off in subsequent winters (Fig. 23). During my study, wolves removed between 7 and 11% of the total moose population in winter (Fig. 24). Wolves killed 4% of the adult moose in winter 1990, increasing their predation rate to 5-7% of adults in subsequent winters (Fig. 24). There was a strong negative relationship between wolf density and the percent moose calves that I observed each March (Fig. 25, $r^2 = 0.86$, df = 4, $P = 0.02$), and the percent caribou calves observed in autumn (Fig. 25, $r^2 = 0.80$, df = 4, $P = 0.04$).

Discussion

My study shows that 1) wolf predation was mainly additive mortality on ungulate prey, and 2) kill rates were dependent on wolf pack size but were not related to other ecological variables that I examined, including prey density. I found wolf predation was mainly additive on ungulates, based on the age and nutritional condition of moose, and from population trends of both species.

Wolf predation should be mainly additive mortality when prey are below the nutrient-climate ceiling (Theberge 1990, Gasaway *et al.* 1992) or when moose are increasing (Gasaway *et al.* 1992). Wolves killed proportionally more calf, yearling and old moose, and fewer

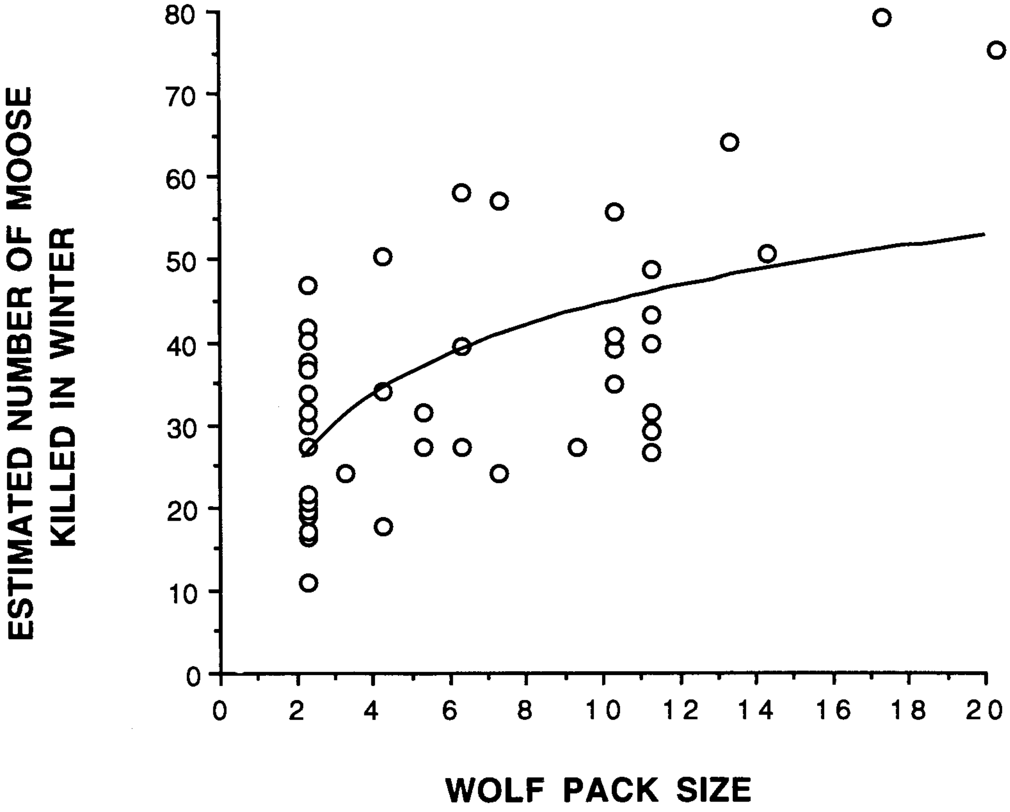


Fig. 22. The estimated number of moose killed wolf^{-1} in 182-day winter periods for different size wolf packs in the FSA ($Y = 15.15 + 28.63 \log_{10} X$).

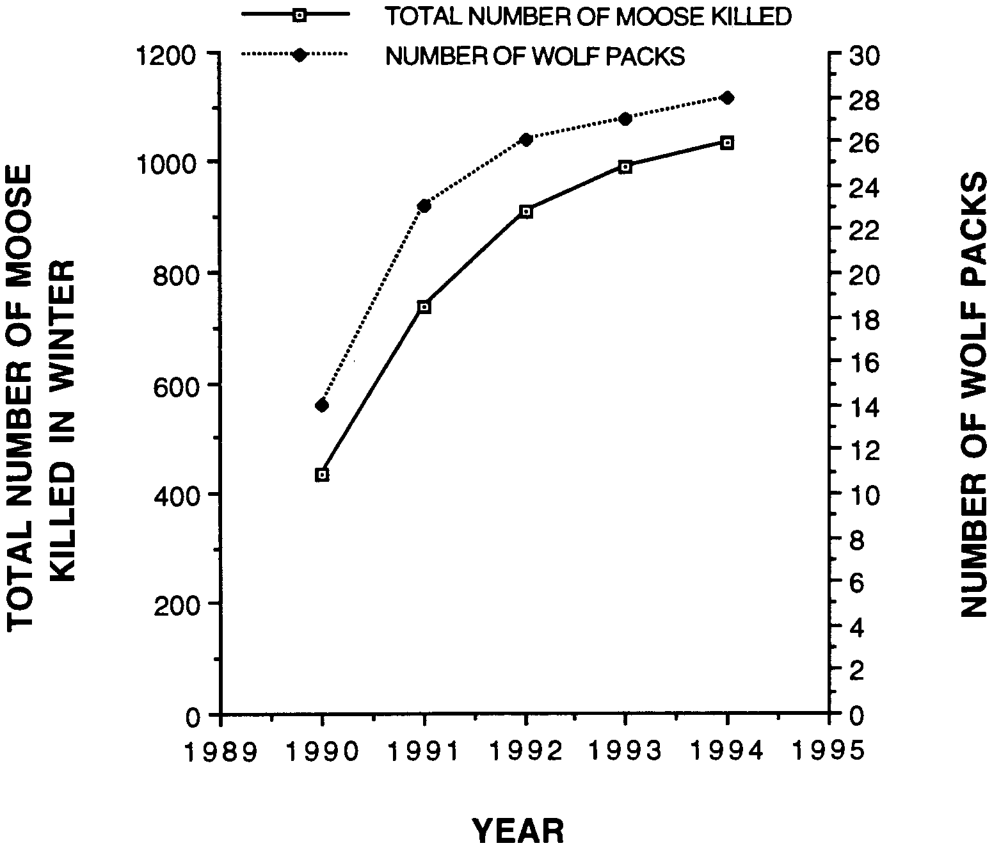


Fig. 23. The total number of moose killed by wolves and the number of wolf packs in the FSA each winter, 1990 to 1994.

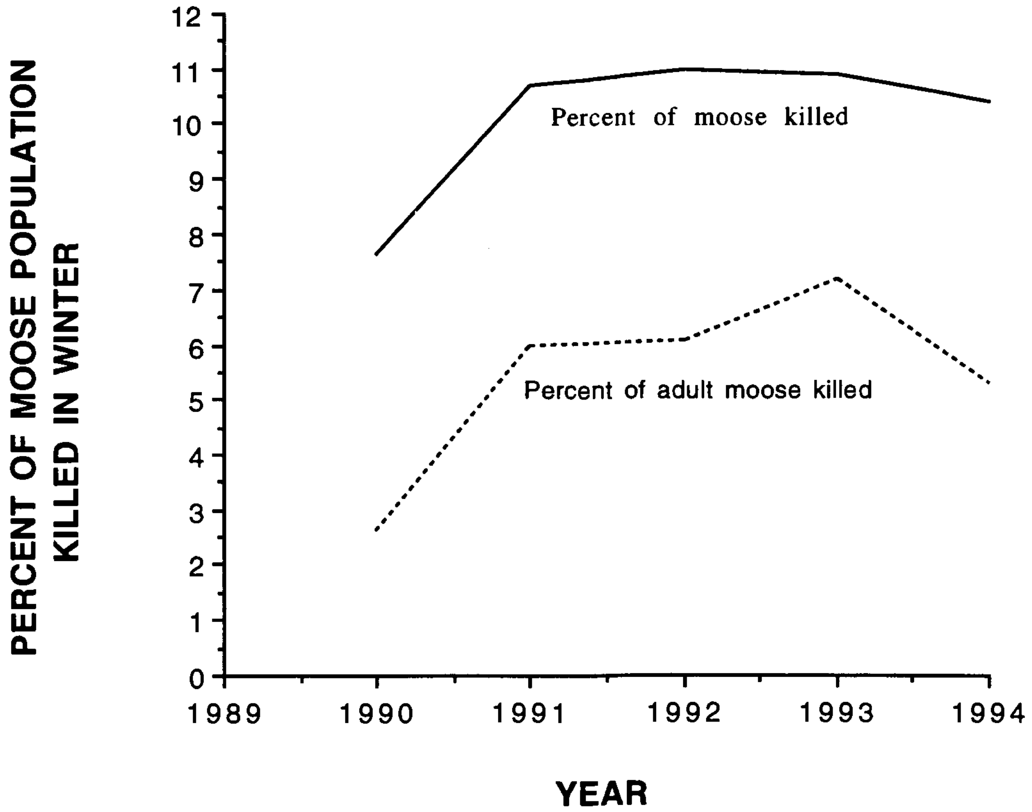


Fig. 24. The estimated percent of the annual moose population (subadults and adults) and adult moose population killed by wolves in the FSA during winter, 1990 to 1994.

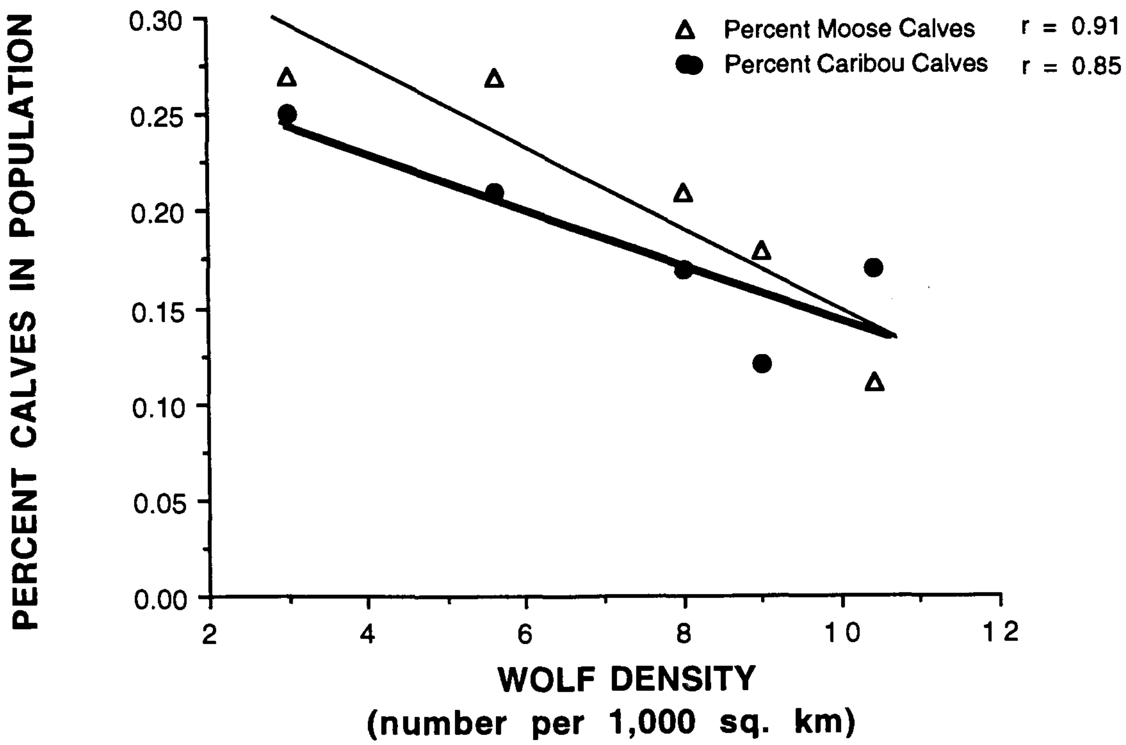


Fig. 25. The relationships between moose and caribou calf survival with wolf density each winter in the FSA. Percent moose calves was estimated from March counts (Appendix A) and percent caribou calves was estimated from October counts (Appendix A). Wide line shows linear relationship for caribou calves, narrow line shows linear relationship for moose calves.

prime-aged animals. This age pattern was similar to other Alaska and Yukon studies (Fig. 26) where moose were below the nutrient-climate ceiling (Peterson *et al.* 1984, Ballard *et al.* 1987, Hayes *et al.* 1991, Gasaway *et al.* 1992). Compared to middle-age moose on Isle Royale, the middle-age moose in Alaska and the Yukon are apparently more resistant to wolf predation due to later onset of disease (*i.e.*, arthritis, Peterson *et al.* 1984).

Gasaway *et al.* (1992) argued moose mortality could be divided into 3 classes: 1) *largely additive* if moose are not severely malnourished (>20% bone marrow fat for adults, >10% for calves) nor very old (bulls <12 and cows <15 years-old); 2) *largely compensatory* if they are very old; and 3) *compensatory* if wolf-killed moose are severely malnourished. I found that neither calf or adult moose were severely malnourished, but a high percent of calves were in low nutritional condition. These lower fat values can be explained by the higher energetic requirements of calves for growth in winter (Peterson *et al.* 1984). Therefore, using calf marrow fat value is not useful to determine the general condition of a moose population. A total of 21 of 27 adults (77%) were in the largely additive age class. The remaining 6 were old adults and thus were largely compensatory mortalities. My nutrition and age data are consistent with the hypothesis that wolf predation on moose is mainly additive when prey are increasing.

Only 1 of 7 adult caribou showed severe nutritional stress. Moreover, caribou in my study area were in good physical condition in winter, based on a sample of 56 animals collected in March 1992 (R. Florkiewicz, Yukon Fish and Wildl. Br., unpubl. data).

Other indicators of healthy prey populations were the high recruitment and population growth rates observed during my study. The percent moose calves in March counts ranged between 18 and 27% until 1993 (Table 6). The mean finite rate of increase of caribou was 1.18 between 1987 and 1992 (Farnell *et al.* unpubl. ms.). High survival rates of juvenile moose and rapidly increasing population trends indicate that moose were well below the nutrient-climate ceiling, indicating that wolf predation was mainly additive.

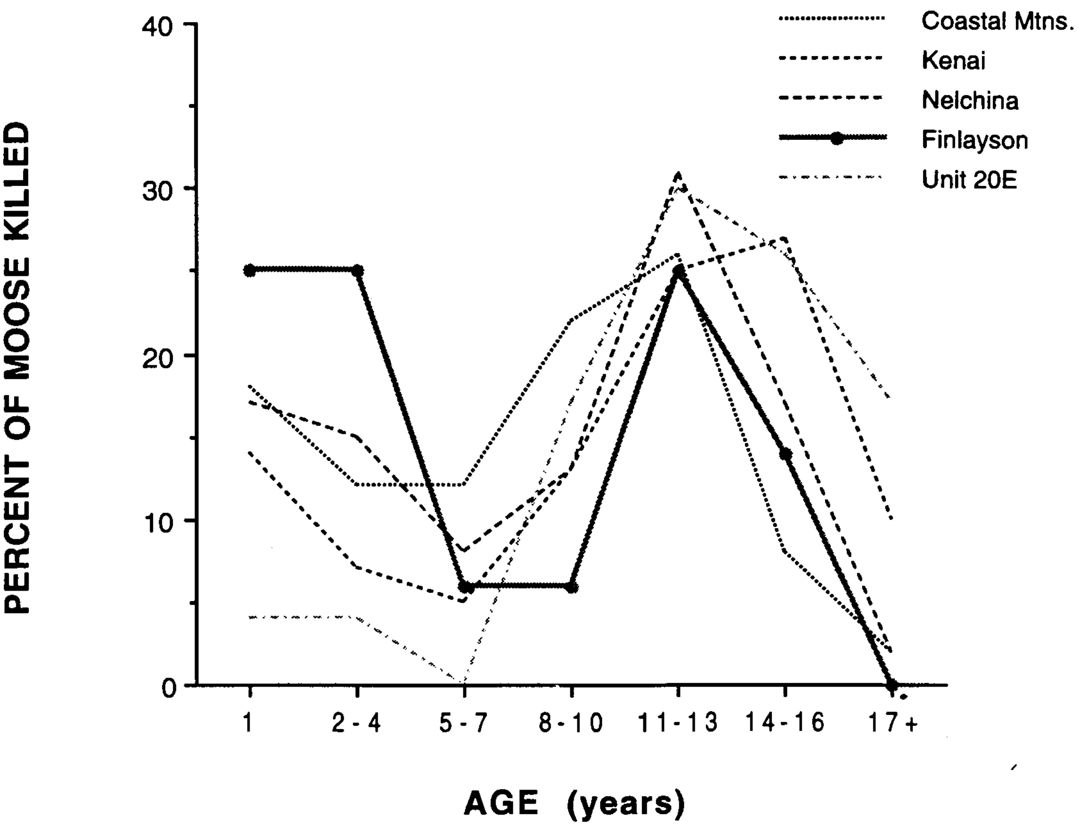


Fig. 26. Ages of moose (excluding calves) killed by wolves in my study and 4 other studies in Alaska and Yukon. Other sources of data were as follows: Kenai Peninsula, Alaska (Peterson *et al.* 1984); Nelchina, Alaska (Ballard *et al.* 1987); Coast Mountains, Yukon (Hayes *et al.* 1991); and Game Management Unit 20E, Alaska (Gasaway *et al.* 1992).

Factors Influencing Killing and Consumption Rates by Wolves

Wolf pack size was the only variable that I found to be correlated with kill rate. Large packs tended to kill prey more often than did small packs, a result consistent with findings of Ballard *et al.* (1987), Hayes *et al.* (1991), Thurber and Peterson (1993) and Dale *et al.* (1994). However, many wolf pairs in my study killed moose as often as larger packs, a result consistent with findings of Hayes *et al.* (1991) and Thurber and Peterson (1993). Most pairs were young adult wolves that dispersed into new territories (Chapter 1). Despite their youth and inexperience in hunting new areas, pairs exhibited exceptionally high kill rates. My results are contrary to the hypothesis that wolves need extensive hunting experience before they become proficient hunters (Packard and Mech 1980). My results suggest that most of these skills are learned by wolves in their natal packs.

Wild wolves require between 1.7 and 4.0 kg food wolf^{-1} day^{-1} to survive (Mech 1977, Thurber and Peterson 1993), and at least 3.2 kg wolf^{-1} day^{-1} to reproduce (Mech 1977). In my study, mean consumption rate (NRA) was 8.7 kg wolf^{-1} day^{-1}, higher than that estimated in previous studies (see Thurber and Peterson 1993). These high consumption rates supported the high juvenile wolf survival rates and rapid population increases of wolves observed during my study (Chapter 1).

I found little difference in the time it took different size wolf packs to handle moose (range: 2.6 to 3.3 days kill^{-1}) among small, medium and large wolf packs. Rapid handling by small packs could be because pairs did not completely consume edible portions of moose carcasses, or because ravens removed proportionally more prey biomass from wolf pairs compared to from larger packs. I found no evidence that supports the hypothesis that small packs abandoned consumable portions more than did larger packs, but the sample of weighed carcasses ($n = 7$) was too small to test for significant differences. In my results, I argue that ravens removed proportionally more food from small packs, substantially reducing the time it took small packs to handle moose kills. I believe that ravens are a major factor influencing wolf predation in the boreal forest, and I have no evidence to reject the hypothesis that raven competition contributed to high kill rates of wolves living in small packs.

Heinrich (1991) showed that juvenile ravens form large cooperative flocks in winter to prevent adult ravens from defending large food sources. In my study area, groups of 20 or more ravens were common at wolf kills. Promberger (1992) found that ravens removed up to 37 kg of food day^{-1} from ungulate carcasses. Raven flocks are especially important competitors with small wolf packs because small packs handle kills less efficiently than do larger packs. The biomass lost to ravens can explain the otherwise unreasonably high consumption rates that I estimated for wolves in the FSA. The largest single meal recorded for wolves was 8.7 kg (Young 1944), about 23% of wolf body weight. The spotted hyaena (*Crocuta crocuta*), another large social carnivore, consumed a maximum of 25% of its body weight in one day (Henschel and Tilson 1988). Wolf pairs in my study would have had to consume an average of 30% (12.7 kg) of their body weight each day of the winter. Adjusting for biomass lost to ravens reduced my estimate of wolf consumption rate to more reasonable amounts (4.1 to 6.4 kg wolf^{-1} day^{-1}), and to within the range of other studies. Recent studies have shown that competition from scavengers can influence the kill rates of other carnivores. In Africa, competition from spotted hyenas forced small groups of lions (*Panthera leo*) to hunt more often (Cooper 1991). Kill rates of maternal cougar (*Felis concolor*) groups were greater in areas where coyotes (*Canis latrans*) scavenged from the cougars' kills (Harrison 1990). I recommend that wherever ravens are common, wolf consumption rates should be adjusted for raven competition to provide more accurate estimates of consumption.

I found that 2 wolves was the optimal foraging group size, similar to other studies (Hayes *et al.* 1991, Thurber and Peterson 1993). Higher kill rates among small packs supports the hypothesis that wolves live in large groups for other reasons than for simply taking large prey (Bertram 1978, Rodman 1981, Thurber and Peterson 1993). Bertram (1978) has proposed that social carnivores evolved to live in groups because individual fitness is greater than if the animals lived alone. Advantages for group living carnivores include: prey locating and capture (*i.e.*, foraging efficiency, Bertram 1978, Nudds 1978), inclusive fitness (Bertram 1978, Rodman 1981), the defense of young (Packer and Ruttan 1988), and the protection of kills from other conspecific groups (Packer *et al.* 1990) and other scavengers (Cooper 1991).

I believe that wolves live in large groups because of advantages imparted for inclusive fitness, not for foraging reasons. Wolf packs are families of closely related individuals (Zimen 1976, Packard and Mech 1980). Wolves are biologically capable of breeding as pups or yearlings, but they rarely reproduce because they are socially immature (Medjo and Mech 1976, Zimen 1982). To be successful group-living animals, wolves must be able to co-exist with their relatives. To develop the necessary complex social skills, wolves need to remain in their natal pack until socially mature at 2 to 3 years-old (L.D. Mech, *pers. comm.*). By deferring breeding, an immature wolf also improves its individual and inclusive fitness because it would otherwise have to compete with its more fit parents or older siblings for a reproductive position in the pack (Packard and Mech 1980). To successfully reproduce, wolf packs then must necessarily increase to sizes for which individual hunting is submaximal (Bertram 1978, Rodman 1981). The declining foraging efficiency is offset by members improving their inclusive fitness because they add close relatives to the population (Rodman 1981).

Snow depth (winter severity) did not influence the rate that wolves killed adult and calf moose. This result was expected because snow depths in ungulate wintering areas were below critical levels in all winters of my study. Huggard (1993) showed that kill rate was correlated with snow depth, and snowfall can add substantial density-independent variation to wolf-prey relationships. In my study, I found no evidence that winter severity predisposed either moose or caribou to predation. Scavenging by wolves was unimportant in all winters of my study, further evidence that snow depth did not substantially decrease ungulate survival (Fuller 1991, Jedrzejewksi *et al.* 1992, Huggard 1993). I conclude that winters were not severe enough to affect wolf predation rate during my study.

In the FSA, the moose calf kill rate by wolves was not related to the number of calves available to wolves in winter, contrary to findings of other studies (Peterson 1977, Peterson *et* *al.* 1984). In most winters, many vulnerable yearlings were also available to wolves (Larsen and Ward 1995), possibly reducing the importance of moose calves in the wolf diet.

The availability of migrant caribou did not cause moose-killing wolves to switch to caribou. Wolves that hunted in caribou winter range killed more moose than caribou; even though caribou greatly outnumbered moose, and caribou apparently pose less of a risk to hunt than do moose (Haugen 1987). I believe there was little switching response because wolves had learned successful hunting strategies for killing moose. Moose were predictable and available year-round to all wolf packs in the study area. Many young, vulnerable moose were available during most winters and they were highly profitable and low risk prey for wolves, especially wolf pairs. Caribou were available to only about 1/4 of wolf packs in late winter.

In some studies, wolves preferred moose over more abundant caribou (Ballard *et al.* 1987, Seip 1992, Hayes *et al.* 1991). In other studies, wolves preferred caribou over more abundant moose (Gasaway *et al.* 1983; Dale *et al. in press*). Dale *et al.* (*in press*) believed that wolves preferred caribou over moose because they found caribou had a stronger influence on wolf numerical response than did total prey biomass (*e.g.*, moose). My results are not consistent with this conclusion, and suggest within the moose densities that I observed, it is non-adaptive for wolves to switch from year-round moose to kill seasonally available woodland caribou. However, my results do not show how wolves might respond when moose are at lower densities, or where migratory barren-ground caribou are available.

My results agree with other studies that show wolves do not readily prey switch in response to changing densities of different ungulate species (Mech 1986, Dale *et al.* 1994). My study, Messier and Crete (1985) and Dale *et al.* (*in press*) found kill rate by wolves is relatively insensitive to the rate that wolves encounter prey. A low switching response can have a potentially strong antiregulatory effect (Mech 1986, Dale *et al. in press*, Chapter 3) because wolves will maintain high kill rates as primary prey decline, to the point at which prey become so rare that wolves cannot kill enough to survive (Mech 1986).

Snowshoe hare abundance did not have any detectable influence on kill rate of ungulates. Wolves will switch to beaver when moose are low (Peterson and Page 1983, Messier and Crete 1985, Potvin *et al.* 1991), but there is no evidence that snowshoe hare is an important prey in winter. Snowshoe hare were available during 1990 and 1991 when moose and caribou were rapidly increasing, competition among wolves for ungulates was lowest, and many vulnerable, young moose and caribou were available. In this ecological context, I believe there were no incentives for wolves to hunt snowshoe hare. Snowshoe hare are unprofitable prey for wolves that have evolved cooperative behavior to kill and share large prey. Snowshoe hare biomass:wolf ratio is only 0.027 kg hare:kg wolf, compared to about 11 kg moose:kg wolf. However, my results do not indicate how wolves will react to differences in snowshoe hare abundance when moose are at lower densities.

The prey searching rate was independent of the supply of prey and the size of wolf packs. My results are consistent with Messier and Crete (1985) and Dale *et al.* (*in press*) who found prey searching rates were similar among packs that were hunting at different prey densities. Perhaps, differences in prey densities in my study were not large enough to be detectable by the daily convex-area polygons traveled by wolves.

Wolf Predation Rate

My results confirm Haber (1977) and Walters *et al.* (1981) who provided theoretical arguments that the number of wolf packs is the best determinant of wolf predation rate. My results also confirm that using the ratio of prey:wolf in an area is a less reliable method (Theberge 1990). The main reason is the strong dependence of kill rates on pack size (Hayes *et al.* 1991, Thurber and Peterson 1993, Dale *et al.* 1994). Higher kill rates of small packs enables them to remove a larger than expected proportion of prey (Hayes *et al.* 1991). This shows there is not a 1:1 relationship between the number of wolves in an area and the number of prey that are killed. For example, I calculated that wolf pairs took over 50% of the moose killed in winter 1990, although pairs comprised only 25% of the total number of wolves. The disproportionately high wolf predation rate in early years of my study was related to the organization of wolves into many small packs, not the total number of wolves in the area each winter. My results show that for ecologists to understand and model the effects of wolf predation, we need to know the frequency of different size wolf packs that comprise the wolf population, and their relative kill rates. I can illustrate this with a simple example. My results show that wolves in pairs killed an average of 13.5 moose wolf^{-1} winter^{-1}, compared to wolves in large packs that killed 4.6 moose wolf^{-1} winter^{-1}. Thus, a single large pack of 10 wolves should kill about 46 (10 X 4.6) moose per winter. If 10 wolves are organized into 5 pairs, then they should collectively kill 135 (10 X 13.5) moose - 3 times as many moose as the single pack of 10. The strong negative correlation of kill rate with wolf pack size contributes important new information for modeling wolf:prey relationships.

My results show that using wolf:prey ratios can be misleading when estimating wolf predation rate, and knowing the number of wolf packs in an area and their sizes provides more relevant information for estimating wolf predation rate than does simply estimating total wolf numbers. This has management implications to wolf population censuses because total counts that miss several small wolf packs will substantially underestimate wolf predation rate.

Another important result from my study is that wolves did not increase their kill rates as prey density increased (Chapter 3). This means that wolf functional response is density-independent when moose were at low (0.25 moose/km^2) to moderate (0.43 moose/km^2) density (Chapter 3), contrary to other studies (Messier and Crete 1985, Messier 1994). This density-independence shows that wolf functional response does not contribute to the regulation of moose at these moose densities (Chapter 3).

Although I found no other ecological determinants of kill rate beside wolf pack size, kill rates could change if a stochastic event (*i.e.*, deep or shallow snow) increases or decreases ungulate vulnerability to predation, or if the species, age and physical condition of prey change with time. Density-invariant response could strongly influence prey selection and wolf functional responses (Huggard 1993), and potential factors besides the effects of prey density should be measured when assessing wolf functional responses.

I estimated year-long predation rate by applying a correction factor of 0.71 to the winter predation rate (Messier and Crete 1985, Messier 1994). Annual wolf predation rate on adult moose increased from 6% in 1990 to 9% or more after 1991. Adult moose mortality rates have ranged between 5 and 9% in other stable and erupting moose populations in Alaska and Yukon (Gasaway *et al.* 1983, Ballard *et al.* 1987, Larsen *et al.* 1989, Gasaway *et al.* 1992). In my study area, Larsen and Ward (1995) estimated annual adult moose mortality was about 10% until 1992. This suggests that wolf predation probably accounted for most of the adult mortality during my study, and it was the principal factor limiting adult moose survival in later years. Wolf predation was possibly the principal factor limiting calf survival of both moose and caribou in later years. Moose and caribou calf survival rates were negatively correlated with wolf density, and there was no evidence that calf survival was linked to abiotic, forage or physiological factors (Farnell *et al.* unpubl. ms.). The exception was in 1992 when caribou calving ranges were covered in deep snow in June, and calf survival rate to autumn was the lowest reported in the area since 1982 (Farnell *et al.* unpubl. ms.).

Data Quality

In the introduction, I outlined various factors that confound our understanding of the ecological factors that influence kill rate by wolves. These factors could limit my ability to extrapolate my results to other times of the year, or to other areas. First, my results may not represent the predation rates in winter or year-round because I collected all my data in a short period in late winter. In early winter, caribou are available to more than 1/2 of the FSA wolf packs and caribou bulls may be killed more frequently because of their stressed physical condition following the rut (T. Meier, National Biol. Sur., *pers. comm.*). Wolf predation on moose calves is also probably higher in early winter because calf body size is smaller and wolves can handle them more quickly than in late winter (Hayes *et al.* 1991, Dale *et al. in* *press*). Second, competition for prey among wolves was relatively low in most study winters except 1994. Kill rates could decline as competition for food resources increases, although I did not detect this. Third, I studied kill rates when moose were at low to moderate densities (0.25 to 0.43 moose/km^2) and when the Finlayson caribou herd size was relatively large. Kill rates on moose cannot be expected to remain the same at some lower moose density (Messier 1994, Chapter 3), or where there are different relative densities of moose and caribou (Dale *et al. in press*).

Test of Predictions

I now compare my results with predictions outlined in the Introduction. Prediction (i) states that wolf predation should be additive mortality as ungulate prey increased. My results show that ungulates that were killed by wolves would not have otherwise died, on the basis of age, physical condition and increasing prey population trends. Thus, the prediction is supported that mortality caused by wolves was mainly additive.

Prediction (ii) states that kill and consumption rates by wolves should depend on wolf pack size and prey density. My results show kill rate by wolves was strongly dependent on pack size but it was not related to moose density.

Prediction (iii) states that the kill rate of moose calves should be related to their availability each winter, and to snow depth. The availability of moose calves each winter did not influence the rate that calves were killed by wolves. Kill rate was not related to winter severity, but snow depths during my study remained below levels that are considered critical for moose.

Prediction (iv) states that wolves should show a strong prey switching response to caribou when caribou numbers increased over moose. Wolves selected moose over more available caribou in late winter and wolves showed a weak prey switching response. Thus, prediction (iv) is not supported.

Prediction (v) states predation rate should depend upon the number of wolves preying upon moose. Results show that wolf predation rate was best determined by the number of wolf packs each winter, and total wolf numbers was an unreliable indicator of predation rate. Thus, prediction (v) is not supported.

Prediction (vi) states that wolf predation should be a principal factor influencing adult and calf mortality of preferred prey, as wolf density increased. My results implied that wolves were the primary cause of adult moose mortality, and were the main mortality cause of both moose and caribou calves. By the end of my study, moose and caribou calf survival rates were below levels that could maintain continued population growth of both ungulates. Thus, prediction (vi) is supported, and wolves were the primary factor limiting ungulate survival by the end of my study.

Conclusions

Wolf predation on moose and caribou was mainly additive mortality during my study. Wolf pack size was the only determinant of kill rate among 10 independent variables that I examined. Wolves in small packs had significantly higher kill rates than did wolves in large packs. Results from my kill rate studies showed that wolf predation was the principal factor limiting adult moose survival, and moose and caribou calf survival rates were negatively correlated to wolf density. The best predictor of annual predation rate on moose was the number of wolf packs, not the total number of wolves in the area. To accurately estimate wolf predation rates on ungulates, wildlife biologists should at least know the frequency of different size wolf packs in an area. Estimating kill rates of different size wolf packs will give the most relevant ecological information for modeling wolf:prey relationships.

Chapter 3

Wolf Functional Response And Regulation of Moose in the Yukon

Introduction

Recent studies of wolves and their prey report conflicting evidence for a density-dependent response that allows wolves to regulate ungulates to a single equilibrium density. Wolf predation regulated some North American moose to low density (Messier and Crete 1985, and Messier 1994); wolves did not regulate moose on Isle Royale, Michigan (Messier 1991); and wolves did not regulate migratory caribou (*Rangifer tarandus groenlandicus*) in Alaska (Dale *et al.* 1994) . To regulate prey, wolf predation must have a density-dependent phase, allowing wolves to remove an increasing proportion as the prey population increases (Solomon 1949, Holling 1959, 1966). Density-dependence is the key element of regulation (Maynard Smith 1974, Murdoch 1994) and wolves must exhibit it to hold prey populations within a narrow range of densities.

Many studies have shown that wolf predation is a major limiting factor for moose (Peterson 1977, Fuller and Keith 1980, Gasaway *et al.* 1983, Peterson *et al.* 1984, Messier and Crete 1985, Ballard *et al.* 1987, Van Ballenberge 1987, Larsen *et al.* 1989, Messier 1991, Hayes *et al.* 1991, Gasaway *et al.* 1992, Thurber and Peterson 1993, Chapter 2). There have been only a few attempts to test for the regulation of moose by wolves (Messier and Crete 1985, Messier 1991, Messier 1994).

Knowing if wolves regulate moose is a central question in wildlife management because it can lead to different decisions (Gasaway *et al.* 1992). If wolf predation eventually regulates moose to low density, regardless of how high moose densities get (*i.e.*, Predation Model, Messier 1994), then releasing moose by reducing wolves will have only temporary benefits (Gasaway *et al.* 1992, Dale *et al.* 1994). If there is a higher threshold moose density where the wolf predation rate falls below the moose rate of increase (*i.e.*, predator pit), then releasing moose should result in a higher stable population that cannot be decreased by wolf predation (*i.e.*, Predation-Food Model, Messier 1994).

In this chapter, I examine wolf functional responses as moose increased from low (0.25 moose/km^2) to moderate density (0.43 moose/km^2) in the Finlayson area of the Yukon. I then determine if wolf functional response contributes to the regulation of low density moose by adding my functional response data to a total wolf predation response model from Messier (1994).

Components of Wolf Predation

There are 2 essential components of predation (Solomon 1949, Holling 1959). The relationship between an individual predator's consumption rate and prey density is known as its *functional response* (Solomon 1949). The functional response plateaus when the predator becomes satiated (Solomon 1949). The *numerical response*, or the change in the number of predators in relation to prey, plateaus when competition for prey restricts the upper predator density. A type II functional response rises at a decelerating rate (Fig. 27, Curve II) and cannot be regulatory without an accompanying density-dependent numerical response (Oaten and Murdoch 1975, Dale *et al.* 1994, Messier 1994). An exponential type III response can regulate prey without a corresponding numerical response because it has a rapidly accelerating phase that allows each wolf to kill an increasing proportion of prey as prey numbers increase (Fig. 27, Curve III).

Wolf Functional Response Models

Dale *et al.* (1994) and Messier (1994) reported type II wolf functional responses. Messier and Crete (1985) and Messier (1991) reported type III responses. Messier (1994) presented the most comprehensive review of wolf predation rates on North American moose.

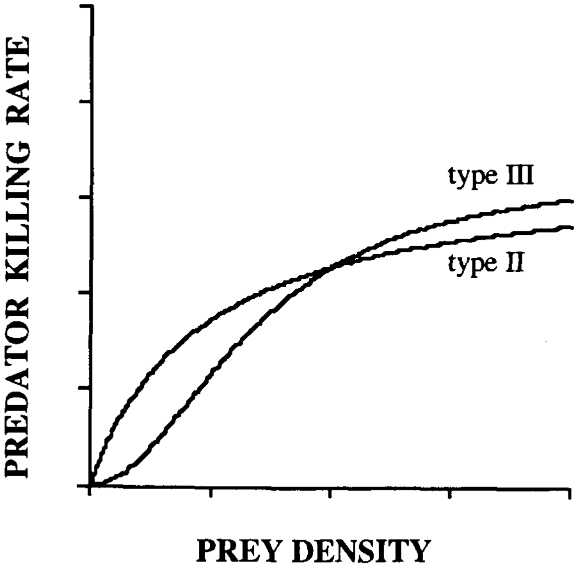


Fig. 27. Two functional responses of predators. Type II is a hyperbolic decelerating response as prey density increases. Type III is an exponentially increasing response that is regulatory.

He found that a type II functional response, combined with a strong numerical response, regulated moose to a stable low equilibrium density between 0.2 and 0.4 moose/km^2. However, his data were sparse below 0.3 moose/km^2. At low moose density, both the shape and elevation of his functional response curve are unconvincing because the curve is loosely fitted through a small number of highly variable kill rates (see Fig. 3, page 482 in Messier 1994).

Experimental Approach and Predictions

From 1983 through 1989, the wolf population in the Finlayson area of the Yukon was annually decreased to about 20% of the natural density. Both moose and caribou populations coincidentally erupted (Farnell *et al.* unpubl. ms.). These experimental field conditions were unique because they allowed me to test the nature of wolf functional responses as moose increased from low to moderate density in the same area. I tested the following predictions from observations of wolf predation in winter:

(i) for wolf functional response to be type II, the kill rate (number of moose killed wolf^{-1} 100 days^{-1}) should increase as moose density increases; and

(ii) for a type III response, the predation rate (percent moose killed wolf^{-1} day^{-1}) should increase faster than the moose rate of increase.

Methods

The 23,000 km^2 study area (62°N, 128°W) is in the east-central Yukon (Fig. 1). Detailed descriptions of the area are provided in the Study Area chapter. Wolf, moose and caribou population dynamics, and methods for estimating kill rate by wolves and prey density are presented in Methods of Chapters 1 and 2. I estimated kill rates on moose among 21 packs during 44 late winter periods (February and March 1990 and 1992, March 1991 and March 1994). Kill rate by wolves was strongly correlated with wolf pack size (Chapter 2), so I separated wolf packs into 3 size classes: small (2-3 wolves), medium (4-9 wolves) and large (10-20 wolves). I then examined linear relationships between kill rates and moose density for the 3 classes of pack size.

I tested for a type II functional response using an equation equivalent to Holling's disc equation (Real 1979, Messier 1994):

$$y = ax/(b + x) \qquad \text{eqn. 1}$$

where y is the kill rate of an individual wolf, x is the annual moose density (moose/km^2), a is the maximum moose killing rate (number of moose killed wolf^{-1} 100 days^{-1}), and b is the moose density at half the maximum kill rate (Messier 1994). Type III models were produced by applying exponents to parameter x (Real 1979, Messier 1994, Dale *et al.* 1994). I used SYSTAT nonlinear regression programs (Wilkinson 1989) to fit equations to the observed responses. The algorithm that I used was the Quasi-Newton estimation (Fletcher 1972). To estimate wolf numerical response I used the equation from Messier (1994):

$$y = a\,(x-c)/(b + (x-c\,)) \qquad \text{eqn. 2}$$

where $a = 58.7$ (maximum wolf density), $b = 0.76$ (moose density at half the maximum kill rate), and $c = 0.03$ (moose density when wolves become absent). As above, x is moose density.

Total wolf response was the product of my observed functional response and wolf numerical response (Seip 1991, Messier 1994). I estimated year-long predation rate (total response ÷ moose density) with the equation used by Messier (1994):

$$y = (fntc)/x \qquad \text{eqn. 3}$$

where f = functional response, n = numerical response, t = constant for year round predation (0.365), x = number of moose/km^2, and c = correction factor (0.71) to scale annual predation rate to include snow-free periods (Messier and Crete 1985, Messier 1994).

Results

In the FSA, wolves killed an average of 6.9 ± 0.7 (SE) moose wolf^{-1} 100 days^{-1} when hunting in small wolf packs (n = 18 pack periods), 3.5 ± 0.4 (SE) moose wolf^{-1} 100 days^{-1} in medium packs (n = 12), and 2.1 ± 0.1 (SE) moose wolf^{-1} 100 days^{-1} in large packs (n = 14) (Table 9). Kill rate was density-independent between 0.25 and 0.43 moose/km^2 for all 3 pack size classes (Fig. 28; small: $r^2 = 0.06$, df = 17, $P = 0.35$; medium: $r^2 = 0.001$, df = 11, $P = 0.91$; large: $r^2 = 0.008$, df = 13, $P = 0.76$). I found no evidence of either a type II or type III functional response. Therefore, I reject both predictions (i) and (ii). I combined kill rate by wolves in medium and large packs (Fig. 28), then calculated mean kill rates at the 4 moose densities to compare with data presented by Messier (1994). I excluded wolves in small packs because their kill rates were higher and more variable than other packs, and because small packs were temporary units (Chapter 1).

Discussion

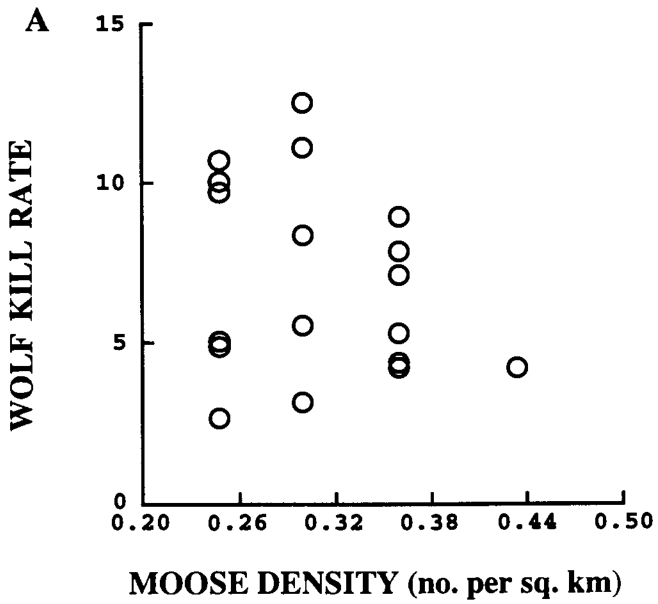
Estimating Wolf Functional Response at Lower Moose Density

I compared my kill rate data with that of Messier (1994) and found new information about the probable shape of wolf functional response at other moose densities. Kill rates in my study were not different (Fig. 29, $r^2 = 0.15$, df =16, $P = 0.13$) from kill rates at similar and at higher moose densities reported in other studies (see Table 2, page 481 in Messier 1994). Kill rates in my study ranged from 2.2 to 3.4 moose wolf^{-1} 100 days^{-1}. The maximum kill rate estimated by Messier (1994) was also 3.4 moose wolf^{-1} 100 days^{-1}.

The consistency in maximum kill rates indicates that kill rates have already peaked when moose are at 0.25 moose/km^2. The asymptote reveals that kill rate by wolves must rapidly increase from some density between 0.0 and 0.25 moose/km^2. There are currently

Table 9. Kill rates by wolves on moose for different size packs, 1990 through 1994. See Table 7 for details on study periods of individual packs.

Period	Moose Density (Moose/km^2)	Traveling Wolf Pack Size	Kill Rate (Moose Wolf^{-1} 100 Days^{-1})
1990 February-March	0.248	17	2.52
		2	9.68
		2	4.84
		5	3.33
		6	3.51
		2	2.63
		2	5.00
		11	1.26
		6	5.21
		4	4.49
		2	10.00
		2	10.71
1991 March	0.299	2	5.56
		2	12.50
		2	8.33
		4	2.27
		2	3.13
		7	1.79
		2	11.12
		7	4.40
1992 February-March	0.360	14	1.95
		2	8.93
		3	4.17
		9	1.59
		11	2.37
		2	7.90
		6	3.51
		2	4.35
		10	3.00
		10	2.08
		10	1.85
		2	5.26
		10	2.17
		2	7.14
		11	1.52
		11	1.93
1994 March	0.434	20	2.04
		11	1.40
		11	2.10
		2	4.17
		6	2.38
		5	2.86
		4	6.73
		13	2.66



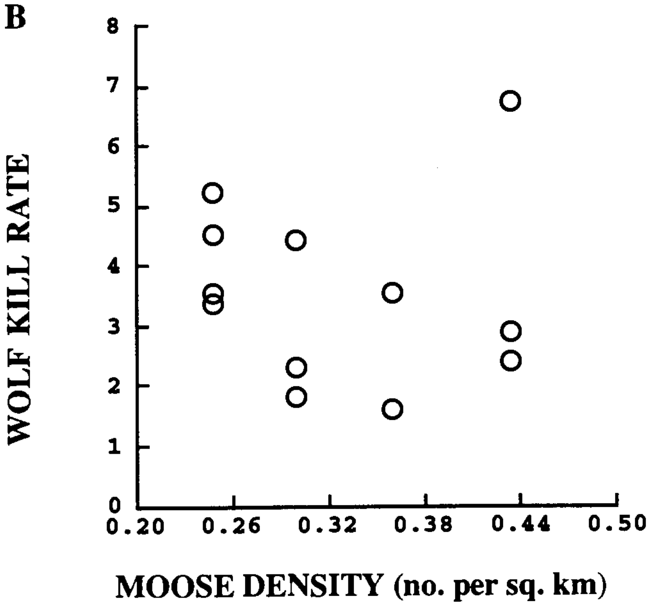
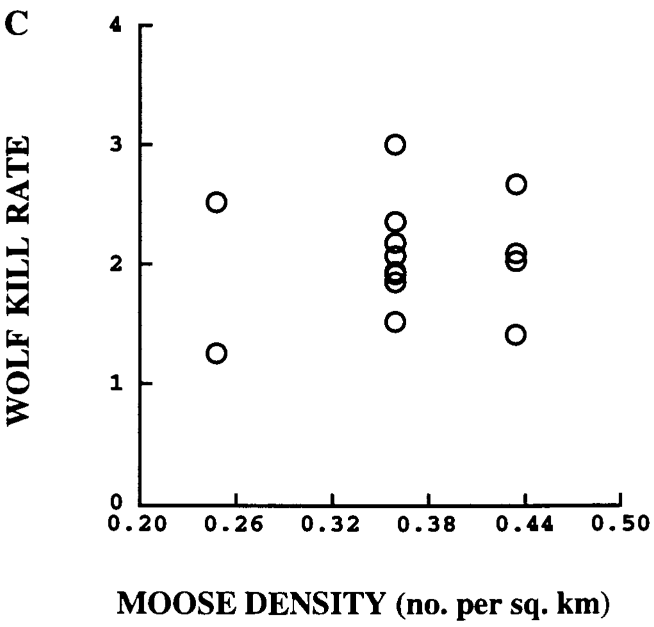


Fig. 28. Kill rate by wolves in small (A), medium (B), large (C) and medium and large packs combined (D). Kill rate is the number of moose killed wolf^{-1} 100 days^{-1}.



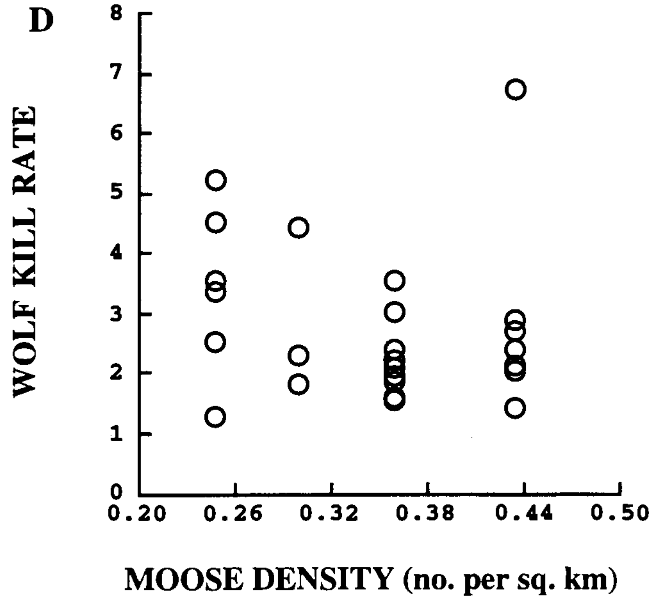


Fig. 28. (Continued). Kill rate by wolves in small (A), medium (B), large (C) and medium and large packs combined (D). Kill rate is the number of moose killed wolf^{-1} 100 days^{-1}.

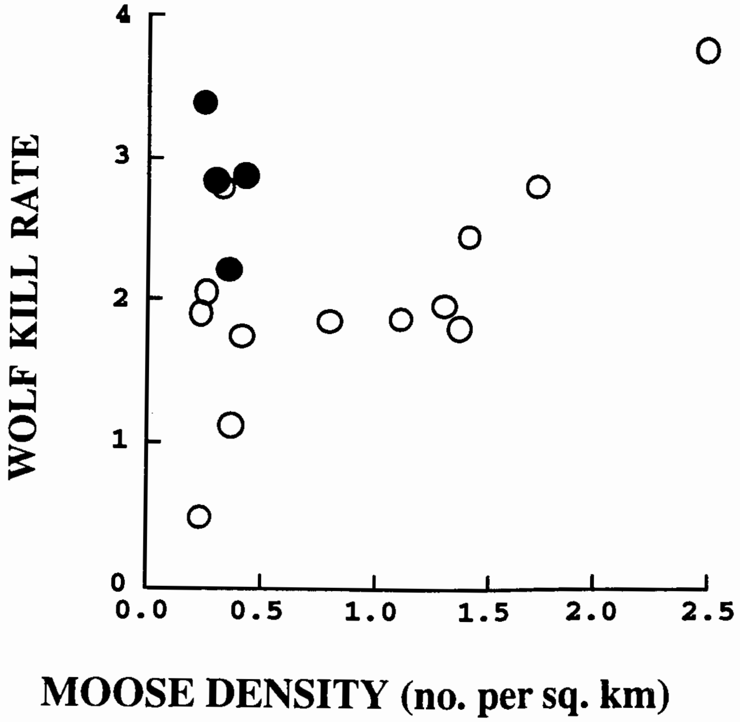


Fig. 29. Kill rate by wolves in my study from my study (●) and from Messier (1994, O), in relation to moose density. Kill rate is the number of moose killed wolf^{-1} 100 days^{-1}.

inadequate data to estimate the shape of the functional curve at moose densities below 0.20 moose/km^2. Thus, I plotted hypothetical curves in this density region by changing parameter b of the functional response model. I set parameter b at different values between 0.0 to 0.2, then I assessed the fit of type II and type III models by comparing the resulting plots (Fig. 30) and the regression coefficients (Table 10). I examined 3 type III models: $x^{2.0}$, $x^{1.5}$ and $x^{1.2}$.

I first set parameter b to 0.0. This allowed kill rate by wolves to remain high until moose theoretically disappeared (Fig. 30). This strong anti-regulatory response causes rapid extinction because wolves sustain a constant kill rate, and kill proportionally more moose as moose density declines (*i.e.*, inverse density-dependence). This anti-regulation model fits the density-invariant response that I observed. There is currently no data on wolf functional response at low moose density to reject this model outcome.

Messier (1994) claimed wolf predation is nil when moose fall below 0.03/km^2 in a simple moose/wolf system. However, when alternate prey are available this may not be true. Caribou can become important prey when primary moose prey is low (Skogland 1991, Gasaway *et al.* 1992, Farnell *et al.* unpubl. ms.). Wolves will normally persist in killing preferred prey even when the prey becomes almost non-existent (Mech 1986, Dale *et al.* 1994). Wolf numerical response is relatively loose and can lag behind prey declines for long periods, increasing wolf predation rates until the wolf population eventually drops (Mech and Karns 1977, Peterson and Page 1983, Mech 1986). Thus, these anti-regulatory responses of wolves theoretically could result in local extinction of preferred prey (*e.g.*, moose).

I found that the 3 type III functional response models ($x^{2.0}$, $x^{1.5}$, $x^{1.2}$) predicted increasing kill rates when moose are between 0.2 and 0.5 moose/km^2, fitting my observations rather poorly (Fig. 30). The type III model with $x^{1.2}$ was best fitting but it still predicted increasing kill rates above 0.25 moose/km^2 (Fig. 30). Thus, I rejected type III models.

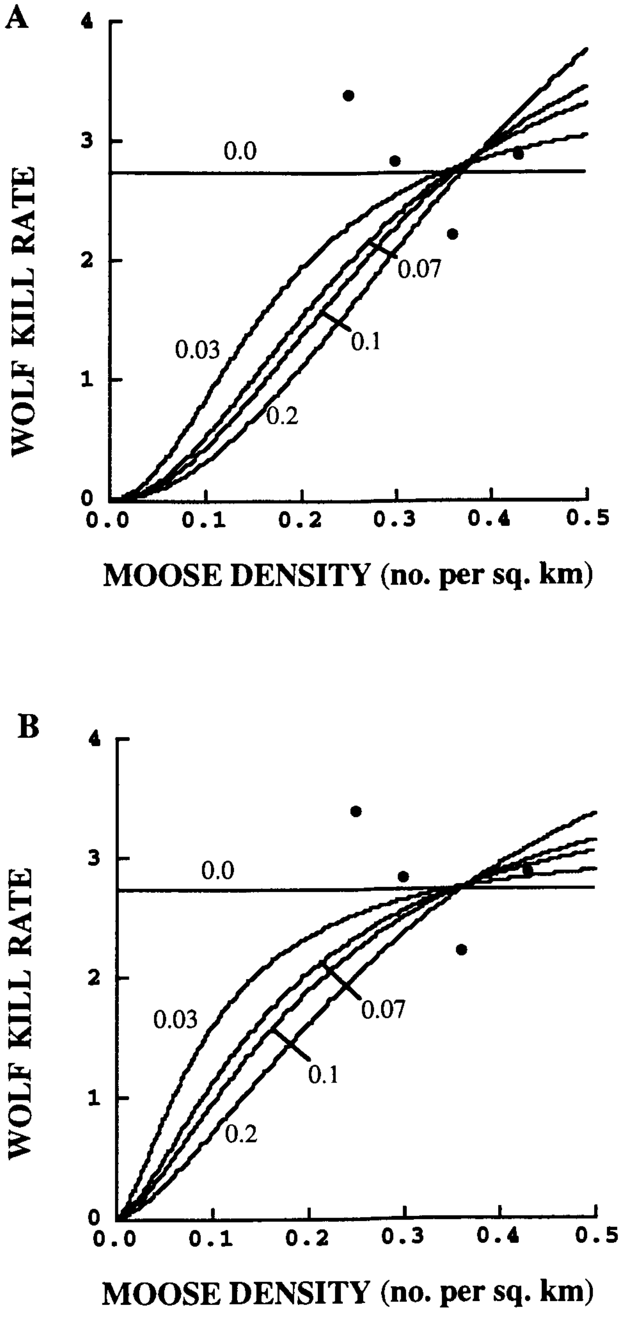


Fig. 30. Hypothetical wolf functional responses estimated by equation: $y = a\, x\, /(b + x)$ (see text for definitions of parameters). Model A is type III response ($x^{2.0}$), B is type III ($x^{1.5}$), C is type III ($x^{1.2}$) and D is type II. Curves estimate responses for different values of b (moose density at half the maximum kill rate). Kill rate is the number of moose killed wolf^{-1} 100 days^{-1}.

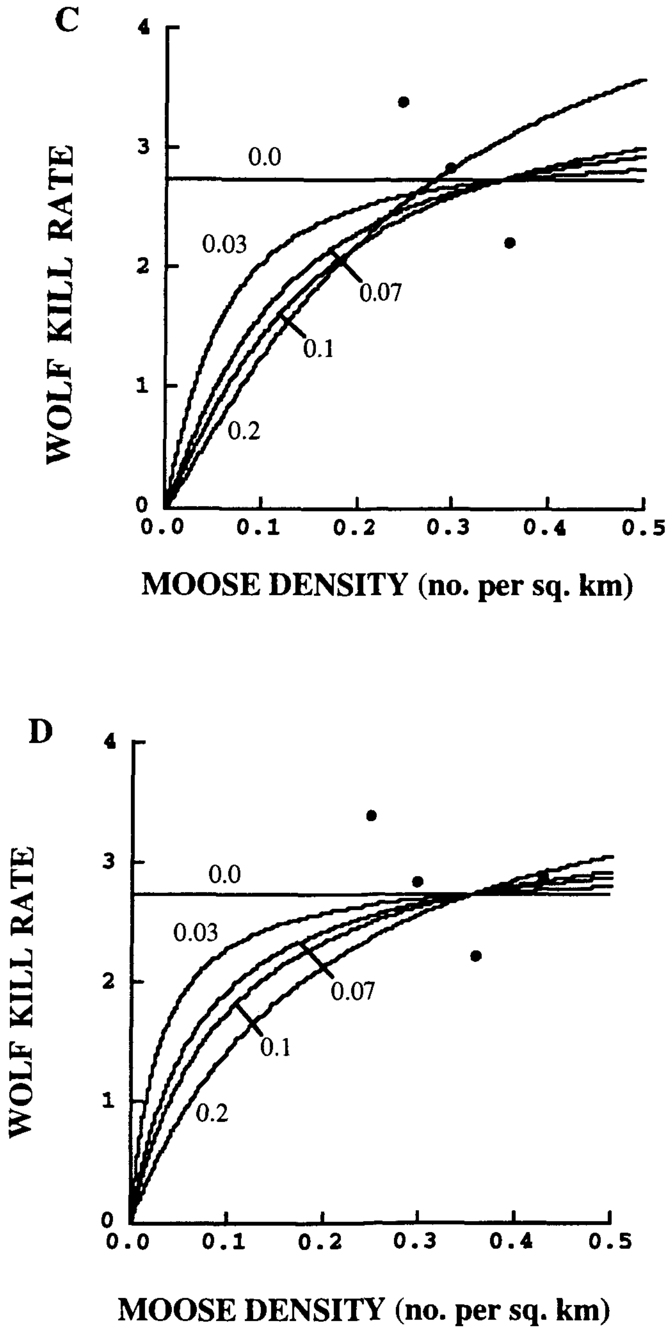


Fig. 30. (Continued). Hypothetical wolf functional responses estimated by equation of Messier (1994), $y = a\,x\,/(b + x)$ (see text for definitions of parameters). Model A is type III response ($x^{2.0}$), B is type III ($x^{1.5}$), C is type III ($x^{1.2}$) and D is type II. Curves estimate responses for different values of b (moose density at half the maximum kill rate). Kill rate is the number of moose killed wolf^{-1} 100 days^{-1}.

Table 10. Regression coefficients for type II and type III functional responses of wolves [$y = ax/(b + x)$]; where y is individual wolf kill rate (number of moose killed wolf^{-1} 100 days^{-1}), x is moose density, a is the maximum moose killing rate and b is moose density at half the maximum kill rate (Messier 1994). To fit the equation, a kill rate of 0.0 was assumed at 0.0 moose/km^2. In all models parameter b is fixed and parameter a is free.

		Parameter *b*				
Model		0.00	0.03	0.07	0.10	0.20
Type III	*a*	2.73	3.41	4.24	4.84	6.77
(x^2)	r^2 *	0.824	0.802	0.780	0.768	0.744
Type III	*a*	2.73	3.14	3.66	4.04	5.28
($x^{1.5}$)	r^2	0.824	0.815	0.805	0.798	0.783
Type III	*a*	2.73	3.02	3.41	3.70	5.24
($x^{1.2}$)	r^2	0.824	0.819	0.813	0.809	0.796
Type II	a	2.73	2.97	3.28	3.51	4.28
(x^1)	r^2	0.824	0.821	0.817	0.814	0.807

* Raw r-squared (1-residual/total)

A type II functional response fits my data better than type III models, and the lower I set *b* the better the model appears to fit (Table 10, Fig. 30d). When *b* is relatively high (0.2), an increasing type II curve persists from 0 to 0.5 moose/km^2. However, on the basis of my data, kill rates were flat above 0.25 moose/km^2 (Fig. 28). Thus, I believe that kill rate by wolves remain high until moose are at a density lower than 0.2 moose/km^2.

At this point, I met an impasse that I could not resolve with current information about kill rate by wolves. Essentially, there are 2 possible outcomes: 1) A high kill rate could persist until moose are extinct, or 2) kill rate could rapidly fall to 0 before moose disappear entirely. The first outcome is an anti-regulatory extinction model and the second is potentially regulatory at some lower moose density. I reviewed the current literature (Gasaway *et al.* 1992, Messier 1994) for evidence of moose extinction where wolves were naturally regulated, but I found no examples. The lowest reported density was 0.04 moose/km^2 (Carmacks, Yukon; Markel and Larsen 1988). However, this could be misleading because moose population estimates are based on relatively large areas, and confidence intervals around density estimates are usually wide (Gasaway *et al.* 1986). 'Patches' or subpopulations of moose could become absent but remain undetected with current moose census methods. For example, wolves in the Carmacks area were at the lowest wolf density in the Yukon (0.003 wolves/km^2: Baer and Hayes 1987), and moose were apparently absent from large areas in winter. However, the absence of moose is most likely due to a combination of moose hunting by people and natural factors. Human hunting confounds the anti-regulation model because wolf predation could decline to 0 before moose disappeared, but continued hunting by people extirpates the remaining small number of moose.

For an extinction model to work at the pack territory scale, wolves must kill all moose within the territory, and there is no evidence in the literature of this happening. In Alaska, wolves that hunt very low moose densities leave territories to follow migratory caribou (R. Boertje, Alaska Dep. of Fish and Game, *pers. comm.*), ensuring low density moose are not completely extirpated. Also, prey refuges in wolf territory interstices (Hoskinson and Mech

1976, Nelson and Mech 1981) should allow some small number of moose to survive before wolves eventually disappear.

I conclude there is no clear evidence that identifies which functional response is more appropriate at low moose densities. On the basis of the above, I chose the following type II equation for the functional response model:

$$y = (2.97x)/(0.03+x) \qquad \text{eqn. 4}$$

This model predicts that kill rate remains high and density-independent until moose fall to low density, but then kill rate drops sharply before moose are extirpated (Fig. 30d). An anti-regulatory model with $b = 0.0$ is also possible, but it does not allow any further examination of regulation outcomes.

Equation 4 predicts a rapidly increasing curve until moose exceed 0.2/km^2, then kill rate plateaus (Curve 1, Fig. 31). Plotting equation 4 shows that Messier (1994) underestimated kill rate at low moose density (Curve 3, Fig. 31). To increase the robustness of the functional response model, I combined my data with Messier (1994) and calculated a new functional response equation:

$$y = (2.56x)/(0.07+x) \qquad \text{eqn. 5}$$

The new curve (Curve 2, Fig. 31) follows the same basic shape as equation 4 (Curve 1, Fig. 31), but its elevation is consistently lower at most moose densities. A strong density-dependent phase is apparent below 0.2 moose/km^2.

Estimating Year-Long Wolf Predation Rate

I calculated year-long wolf predation rate by using equation 5 for the functional response (*f*). I call this new model the HKLD wolf predation model (*i.e.*, high kill rate at low density). The HKLD model (Fig. 32) shows that the predation rate at low moose density is higher, and wolf functional response has a greater proportional effect on predation rate, than that estimated by Messier (1994).

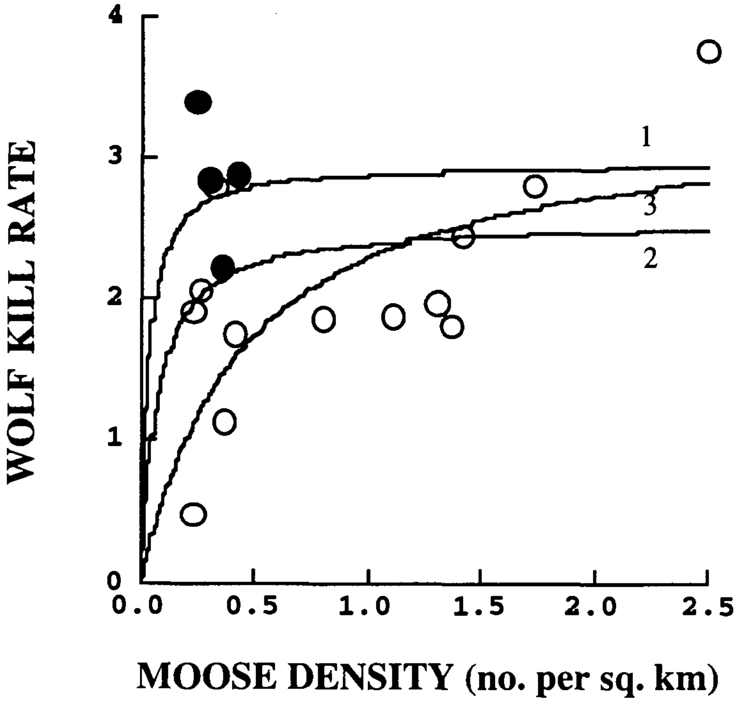


Fig. 31. Wolf functional response to changing moose density based on kill rate data from my study (Curve 1), Messier (1994, Curve 2) and combined data (Curve 3). Mean kill rates are from my study (•) and from Messier (1994, O). Kill rate is the number of moose killed wolf^{-1} 100 days^{-1}.

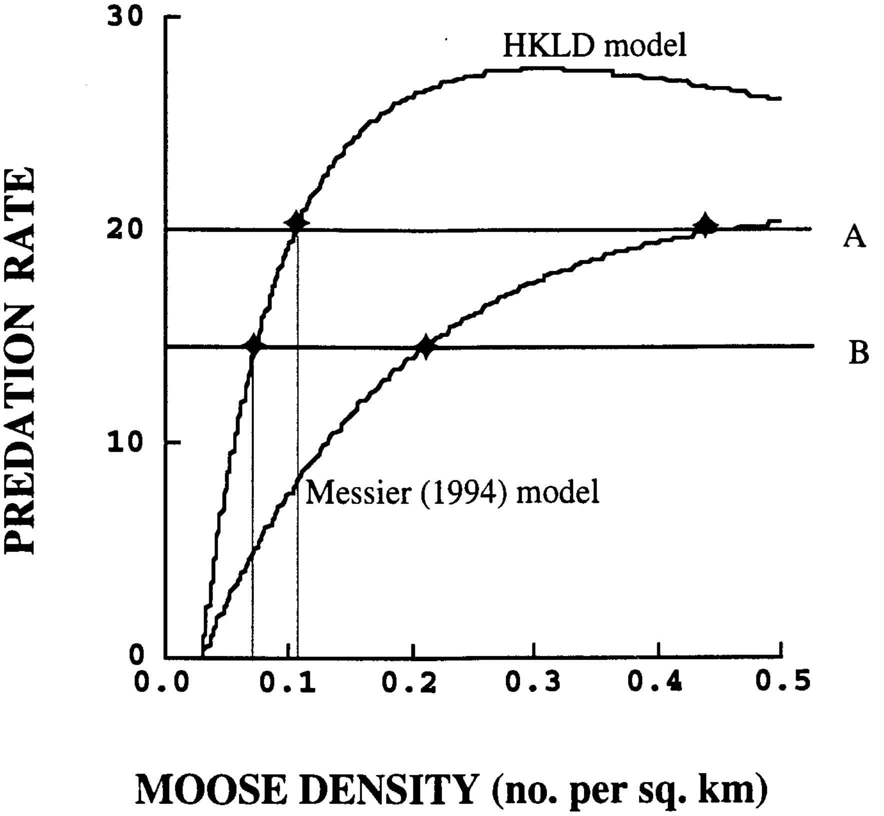


Fig. 32. Changes in wolf predation rate (percent of moose population annually killed by wolves). Messier curve is taken from Messier (1994). HKLD curve includes data from my study and Messier (1994). Possible stable equilibrium conditions are illustrated (◆). Potential rates of increase of moose (A and B) depend on effect of reduced habitat quality and additive bear predation (see Fig. 7, Messier 1994). Narrow vertical lines indicate possible stable equilibrium densities of moose.

To determine if wolves regulate moose to a low density equilibrium, the potential rate of increase of moose (*i.e.*, without wolf predation) must to be compared to the year-long wolf predation rate. Messier (1994) provided a theoretical model for a wolf/moose system where sub-optimal habitat (forage) and density-independent bear predation reduced the potential rate of increase of moose to between 15 and 20% (Fig. 32). This range seems reasonable because moose annually increased by 18% when wolf numbers were annually decreased by 80 to 85% in my study area (Farnell *et al.* unpubl. ms.). The HKLD predation rate model shows a low density equilibrium forms when moose are between 0.07 and 0.12 moose/km^2 (Fig. 32); well below the stable equilibrium range of 0.2 to 0.4 moose/km^2 (Fig. 32) estimated by Messier (1994).

Wolf Functional Response

In my study, wolves were highly efficient predators when moose were at low to moderate densities, and kill rates were similar to those of wolves hunting at higher moose densities (Fig. 29). Predators are more likely to have a type II functional response for preferred prey, and if prey are distributed in patches (Oaten and Murdoch 1975). Moose were the preferred prey in my study, and were distributed in patches in the environment, suggesting a type II response is appropriate. However, there is currently no empirical data on which to base the selection of a type II response over a type III response for wolves.

Combining my results with other wolf/moose studies indicates that kill rate does not increase up to 0.65 moose/km^2 (see Messier 1994). I found a possible leverage problem with the kill rate data at low moose density in the model of Messier (1994; Table 2 on page 481). The 3 lowest kill rates were from 1 study in Quebec (Messier and Crete 1985). These points had strong leverage, and substantially reduced the elevation of Messier's type II curve below 0.4 moose/km^2. This is because his functional response curve passed through the origin. Kill rate by wolves in Quebec were much lower compared to kill rates at similarly low moose densities, including my study. For example, wolves in Quebec killed 0.47 moose wolf^{-1} 100 days^{-1} when moose density was 0.23/km^2. In my study, the mean kill rate was 2.97 moose wolf^{-1} 100 days^{-1} at the same moose density.

Messier (1994) found that wolf pack size did not significantly influence kill rate; however, pack size was the major determinant of kill rate in my study (Chapter 2), and in other recent studies (Hayes *et al.* 1991, Thurber and Peterson 1993, Dale *et al. in press*). My results show that if I had pooled data from different size packs I could have confounded the relationship between kill rates and moose density. This is because wolves in small packs had greater kill rates than wolves in large packs. If I had monitored mostly small packs at moderate moose density, I might have falsely concluded that a density-dependent functional response existed. There is now sufficient data to show that pack size is a primary determinant of kill rate by wolves. I recommend that, in the future, wildlife ecologists do not pool kill rate data from small wolf packs to examine wolf functional responses.

I believe that my results improve our understanding about wolf functional responses at low to moderate density of moose, and lend some insight into the possible shape of the functional response curve at lower moose density range (*i.e.*, 0.0 to 0.25 moose/km^2). Kill rates in my study were reliable because they included replicated observations among various wolf pack sizes and I did not pool different pack size classes in my analyses. My estimates of wolf functional response were also reliable because I made temporal comparisons in the same area. Comparing kill rates among different wolf populations (*i.e.*, Messier 1994) is necessary to compare responses across a wide range of moose densities, but it can be confounded by geographical differences in terrain, weather, vegetation and snow conditions; observation rates; prey size and vulnerability; and the species composition and densities of other predators and prey (Dale *et al.* 1994, Messier 1994). I recognize that stochastic events could produce substantial interannual variation in estimates of kill rates by wolves, but I found no relationships with non-equilibrium factors (*e.g.*, location intervals, snow depth, alternate prey availability). It appears that wolf functional response is density-independent between 0.25 and 2.5 moose/km^2, and that kill rate by wolves must rapidly increase somewhere between 0.0 and 0.25 moose/km^2. However, the shape of the functional response curve remains unknown until data is collected below 0.25 moose/km^2.

Wolf Predation Rate and Regulation of Moose

The HKLD model shows a strong density-dependent effect that could regulate moose at about 0.12 moose/km^2. Gasaway *et al.* (1992) argued that a combination of wolf, grizzly and black bear predation limited moose in interior Alaska and Yukon to a low density equilibrium around 0.15 moose/km^2. Their analyses relied on empirical moose and predator density information across a wide area of Alaska and Yukon. My results indicate that wolf functional response plays a key role in the regulation of moose to low density, and it does not matter whether the shape of the curve is type II or type III.

Observation of moose in the FSA fit the low density regulation model. In 1983, before wolf reduction began, moose were at some density below 0.19 moose/km^2 (Jingfors 1988), and wolves were naturally regulated at a density of 0.009 wolves/km^2 (Farnell *et al.* unpubl. ms.). Moose density was regionally low and was not caused by excessive human hunting or low quality habitat (D. Larsen, pers. *comm.*). The moose population erupted after being released from wolf predation (Jingfors 1988, Larsen and Ward 1995, Farnell *et al.* unpubl. ms.), similar to other moose populations in central Alaska following wolf reductions (Gasaway *et al.* 1983, Ballard *et al.* 1991).

The HKLD predation rate model supports the hypothesis of a single low density equilibrium for moose (Messier and Crete 1985, Van Ballenberge 1987, Gasaway *et al.* 1992, Messier 1994). Year-long predation rate should exceed the moose rate of increase at all densities above 0.12 moose/km^2, despite a strong inverse density-dependence (*i.e.*, declining predation rate) when moose exceed 0.50 moose/km^2 (Fig. 33). The existence of 2 stable equilibria for moose has been a central debate among wildlife ecologists. Haber (1977) and

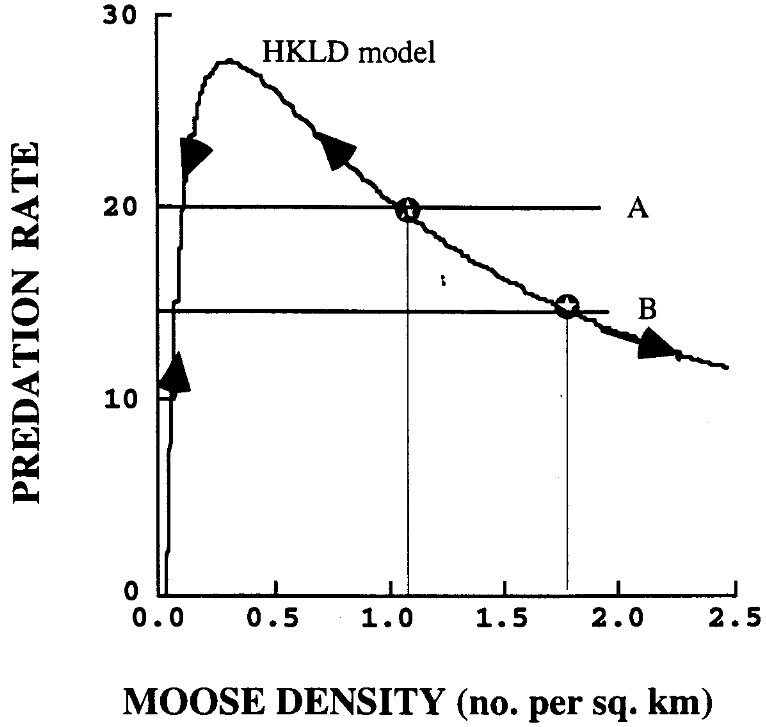


Fig. 33. Empirical model for wolf predation rate on moose (percent of moose population annually killed by wolves). HKLD curve is extrapolated from data collected in my study and from Messier (1994). Potential rates of increase of moose (A and B) depend upon effect of reduced habitat quality and additive bear predation (Messier 1994). Unstable upper boundaries of predator pit are shown for HKLD model (✪), depending on stable rates of increase of moose at high densities. Arrows predict direction of moose population and narrow lines are moose densities where unstable upper boundaries could form.

Walters *et al.* (1981) presented a model showing low and high stable equilibrium points (*i.e.*, Predation-Food Model). The model was later criticized for its lack of supporting quantitative data (Van Ballenberge 1987), and there is still no empirical evidence to support it (Gasaway *et al.* 1992, Messier 1994).

So what do we know about wolf: moose dynamics when moose density is high? Most information about high density moose (>1.0 moose/km^2) is from Isle Royale (Page 1989, Messier 1991, Messier 1994). Moose are not regulated by wolves on Isle Royale (Messier 1991). However, Isle Royale is a 'closed' system and its wolf:moose relationships provide limited insight into the dynamics of 'open' wolf:moose systems elsewhere (Mech 1986). For example, the low wolf predation rate on Isle Royale in recent years is due to a depressed wolf numerical response (Messier 1991), probably caused by genetic inbreeding (Wayne *et al.* 1991). Depressed numerical response caused by inbreeding has not been observed in other wolf populations.

Is there evidence that moose populations in open systems will remain at high density when wolves are allowed to become naturally regulated? In Alaska, moose have remained at over 0.8 moose/km^2 in Game Management Unit 20A (R. Boertje, Alaska Dep. Fish and Game, *pers. comm.*), after being released from low density (0.2 moose/km^2) in the 1970's by a wolf reduction program (Gasaway *et al.* 1983). In 20A, wolves prey heavily on caribou in the winter ((R. Boertje, Alaska Dep. Fish and Game, *pers. comm.*), and high predation rates on caribou appears to limit wolf predation on moose. Where moose are the primary prey of wolves, Messier (1994) speculated that there could be an upper boundary of a shallow predator pit if moose can reach densities greater than 1.0 moose/km^2. If moose could reach this unstable boundary, then they could theoretically escape the regulating effect of predation and live at a higher stable density that is mainly limited by food and space. For the HKLD predation rate model to develop a predator pit, the potential rate of increase of moose should hold at about 20%. A possible unstable equilibrium then forms at about 1.2 moose/km^2 (Fig. 33). If the potential rate of increase of moose is reduced to 15% then the unstable upper boundary of the predator-pit boundary increases to about 1.7 moose/km^2 (Fig. 33). At these high moose densities, the net rate of moose recruitment should follow a n shaped curve due to competition among moose for food resources (Messier 1994). Thus, I agree with Messier (1994) that there is a low likelihood of an unstable boundary forming past 1.2 moose/km^2, especially in northern ecosystems with relatively low productivity.

There is evidence from Alaska that rates of increase of moose can remain high when they are above 1.0 moose/km^2 (see Table 12 in Gasaway *et al.* 1994; Ballard *et al.* 1991; R. Boertje, Alaska Dep. of Fish and Game, *pers. comm.*). However, moose do not appear to remain at high density indefinitely. Hard winters and starvation have caused moose to decline from high density in Alaska (Ballard and Larsen 1987, Gasaway *et al.* 1983, 1992) and on Isle Royale (Peterson and Page 1983, 1988). Wolf predation accelerated the rate of moose decline on Isle Royale, but there is no study that has shown wolf predation has been the ultimate cause of moose falling from high to low density. Regardless, it is not necessary for wolves to initiate declines to regulate prey, because regulation arises as a result of stabilizing density-dependent processes (Murdoch 1994), even when brought about by "non-equilibrium" mechanisms such as severe weather.

How does the HKLD predation rate model behave when other predators of moose are considered? Gasaway *et al.* (1992) believed that a combination of wolf and bear predation is needed to limit moose to low density. Other studies have shown that grizzly bear predation on moose calves in summer can be more important than wolf predation in limiting calf survival (Ballard and Larsen 1987, Larsen *et al.* 1989, Gasaway *et al.* 1992). However, there has been no study that has tested whether reducing bear numbers alone will cause moose density to increase. Ballard and Miller (1990) reduced grizzly bear numbers and observed sharp increases in moose calf survival, but did not report increased moose densities. Wolves in their area were also well below natural densities at the same time (Ballard and Larsen 1987). Figure 32 shows that a strong wolf predation response regulates moose to low density, regardless of the effects of bear predation. My empirical model predicts that, in most cases, wolf predation should compensate for increased survival of moose calves caused by reduced bear densities. The exception would be in systems where moose are not the primary prey of wolves.

Hayes *et al.* (1991) and Messier (1994) suggested that wolf predation has a stronger effect on long-term population dynamics of moose than does bear predation, because moose are preferred prey of wolves all year-round. In my study, moose were available year-round to territorial wolf packs (Chapter 1), they were strongly preferred over migrant caribou (Chapter 2) and they were vulnerable to being killed by wolf packs of all sizes. As wolf density increased, both juvenile and adult moose survival declined significantly. In the last year of my study, both moose and caribou numbers were probably stable (Chapter 2). This could be the first evidence that wolf predation is regulating moose in the FSA from reaching a higher stable equilibrium.

In conclusion, the high kill rate by wolves that I observed had a large effect on elevating the total predation response at low moose density. The potential for regulating moose at low density is determined by this strong functional response combined with a strong numerical response of wolves (Fuller 1989, Messier 1994). It was not important whether the shape of the functional response curve is type II or type III to regulate moose, because the curve is already very high at low density (*i.e.*, 0.25 moose/km^2). It is apparent that wolf functional response must rapidly increase at some lower moose density where kill rate by wolves have not been studied.

Data Quality

Many factors can influence wolf predation rate besides the first-order effects of prey density (see Skogland 1991, Boutin 1992 and Messier 1994). Density-invariant factors that can influence the availability of prey to wolves include: habitat heterogeneity, prey refuges, birth season synchrony, seasonal aggregations of prey, prey size/age vulnerability, primary:alternate prey ratios, bear predation and the effects of other compensatory mortalities (*e.g.*, starvation, disease). Any of these factors can have important effects on the organization of the wolf/prey community for unknown periods, and could compensate for, or exacerbate, the influence of wolf predation.

My functional response model was based on the largest series of kill rates in the literature. Nevertheless, there was inadequate power to test for significant differences in mean kill rate when moose densities were at 0.25-0.30 moose/km^2, compared to 0.36-0.43 moose/km^2. I tested at the 0.10 level of significance, with a 75% chance of detecting a true difference between population means as small as 1.0 moose wolf^{-1} 100 days^{-1}. The within-population variability was 1.59 moose wolf^{-1} 100 days^{-1} based on packs of 4 or more wolves ($n = 26$) . Power and sample size testing for differences between 2 means (Zar 1984, page 135) showed that I needed 20 samples in each density range for one-tailed significance. I had only 9 packs in the lower moose density range and 17 packs in the higher moose density range. However, by only selecting packs with 6 or more wolves, I reduced the variability to 1.02 moose wolf^{-1} 100 days^{-1}. The required sample for minimal power was 9 packs in each moose density range. I had 6 packs with 6 or more wolves in the low density range and 15 packs in the higher density range. For adequate power, I needed an unequal sample of 6 and 18 packs. Thus, I concluded that the data set had inadequate power to test for significant differences. This was mainly because I was unable to combine the 18 data points from small packs in the predation rate calculations, because wolves in small packs had significantly higher kill rates compared to wolves in other packs.

Biases could have also confounded my results. First, kill rates were studied during a rapid recovery phase of wolves. In early study years, wolf density was lowest and the wolves probably did not compete for prey resources. Low wolf competition could have upwardly biased my wolf kill data, especially in 1990 when the fewest packs were present.

Second, year-long predation was calculated using a correction factor (0.71) developed in Quebec to estimate predation during summer periods (Messier and Crete 1985). Wolf predation rate is most difficult to measure during summer because wolves and their kills are hard to see from the air (Hayes *et al.* 1991). Wolf predation in summer probably differs among regions depending on the species composition of prey, or if bear species are sympatric or not (Ballard and Larsen 1987). Thus, the correction factor I used may be inaccurate for my study area. This will not affect the shape of the predation rate curve unless summer predation is density dependent, but the elevation of the curve should change (Messier 1994).

Third, moose densities were estimated by stratified random censuses. Because estimates are bounded by wide confidence intervals, the moose densities that I report here are not precise. Furthermore, after 1992, moose densities were estimated by differences in annual recruitment indices and a constant adult mortality rate. Despite these problems, it is certain that moose were rapidly increasing during my study, on the basis of high proportions of juveniles observed in winter (Gasaway *et al.* 1992), local knowledge and from incidental moose sightings during the study (*pers. observ.*).

Fourth, ungulate prey density nearly doubled in my study, but the change may not have been enough to detect a corresponding change in predation rates. However, because kill rates were similar to wolves hunting moose at higher densities, I believe the density-invariant response was real.

Fifth, average moose density in the Yukon is about 0.13 moose/km^2 (R. Ward, Yukon Fish and Wildl. Br., *pers. comm.*), near the stable equilibrium of 0.12 estimated by the HKLD predation rate model. However, moose densities in the Yukon range from 0.04 to 0.4 moose/km^2. Variations from the equilibrium point should be expected given the many extrinsic factors that can influence moose density or wolf predation rate, including human hunting of moose, weather and regional differences in moose behaviour (R. Florkiewicz, *pers. comm.*).

Despite the data quality limitations above, I found no evidence that my estimates of kill rate were related to other density-invariant factors besides pack size; and I controlled for pack size variability in my analyses. I conclude that the empirical models presented here reasonably reflect the nature of wolf predation rate for most systems where moose are the primary prey.

Wildlife Management Implications

My results have implications for wildlife management policies. Primarily, I found no evidence to support the idea that temporarily releasing moose from wolf predation will produce a permanent, higher stable moose density. The period of higher moose density should depend on the rate of increase of wolves, weather, bear predation and alternate prey availability. As wolves recover to naturally regulated densities, their predation rate should rapidly exceed the potential rate of increase of moose and drive moose back to a low density equilibrium of about 0.12 moose/km^2.

The period of unstable high moose densities appears to depend on the level of alternate prey available to wolves. Where large numbers of alternate prey are available, wolves could switch away from moose, thus allowing the moose population to remain high for a long period. This appears to be the case in Unit 20A in Alaska where many wolves rely on the Delta caribou herd (R. Boertje, Alaska Dep. Fish and Game, *pers. comm.*). Moose declines should be most rapid where moderate numbers of alternate prey are available, but wolves continue to kill moose in a depensatory manner. Thus, anti-regulatory wolf predation could lead to the rapid, local extirpation of 'patches' or subpopulations of moose, because wolf numerical response is sustained by the alternate prey.

Continued harvest by people when moose reach very low densities is probably the primary anti-regulatory mechanism that drives moose from a low density equilibrium, and could lead to extirpation. I recommend that harvest closures be set when moose reach densities below 0.1 moose/km^2 in Yukon and Alaska.

Important management questions are raised including: (1) If wolf numbers are reduced, then how long will moose densities remain temporarily elevated?; (2) At what rate will moose decline back to low density?; (3) Does wolf predation eventually lead to local extirpations of moose?; (4) Will reducing bear numbers slow the rate of decline of moose, and does the stable equilibrium point change with bear predation?; and (5) Is it socially and economically worthwhile reducing wolves to produce temporary benefits to moose?

Answers to questions (1) and (2) ultimately depend on the relative magnitude by which wolf predation exceeds the rate of increase of moose. Moose survival rates are also directly limited by non-equilibrium events (*e.g.*, severe winters) and excessive human hunting (Gasaway *et al.* 1992). If moose vulnerability and human harvest are coincidentally high, then the moose rate of decline will be steepest. If ecological conditions (*i.e.*, low snow) reduce moose vulnerability to wolf predation and harvest by humans is low, then the rate of decline to a lower density should be slow.

For question (3), my data do not reject the hypothesis that wolf predation is strongly anti-regulatory and could cause local extinction of moose. Local extirpation has not been seriously considered in past moose management models, and it deserves research at a moose 'patch' or subpopulation level.

For question (4), reducing bear numbers should make little difference to the density that moose eventually stabilize at, and it makes no sense to only reduce bear numbers to increase moose. The HKLD model implies that bear predation on moose calves is mainly compensatory at low moose density, because high wolf predation rates would still remove most calves by the end of the winter. Reducing wolves in areas where bears are sympatric could have limited benefit to low density moose. This is because depensatory predation by bears could strongly limit the recruitment rate of moose, thus depressing any moose population response to reduced wolf predation. Reducing both bears and wolves should maximize the moose rate of increase (Gasaway *et al.* 1992). The rate of decline to the low density equilibrium should also be slowed by reductions of both predators. However, the HKLD models predicts that the range of equilibrium densities of moose will be narrow (0.07 to 0.12 moose/km^2), regardless of bear predation on moose (Fig. 32), where moose are the primary prey of wolves.

Gasaway *et al.* (1992) attempted to answer question (5). They argued that in order to sustain reasonable levels of human harvest of moose, periodic reductions of wolves need to be used. Large scale killing of wolves to increase ungulates for hunting purposes is a current debate in Canada (Hayes and Gunson *in press*), and it seems improbable that periodic, large scale wolf reductions will remain socially acceptable to most people. North American society's views about wildlife are becoming increasingly polarized between those who regularly use animals for food and those that want to preserve natural wildlife systems, regardless of the utilitarian or economic values of killing wildlife. Gasaway *et al.* (1992) suggested that periodic wolf reduction can be a legitimate conservation tool because it ensures that wildlife values to local people are maximized to counter competing land uses for wildlife habitat. Mech (1995) argued that the recovery of wolves throughout the world is dependent on responsible management plans that include the eventual control of wolves where socio-economic constraints warrant limiting wolf population sizes. My results are consistent with this conclusion, but do little to resolve ethical concerns against temporary wolf reductions to increase ungulate populations for human interests (Mech 1995).

Future Research

Current studies cannot detect whether wolf functional response is type II or type III. Essentially, any steep curve could fit between 0 and 0.25 moose//km^2 and the shape of the curve could be easily changed by extrinsic interactions. However, the actual shape of the response curve appears to be irrelevant to regulating moose because it must be very steep in this density region. Future research on wolf functional response should concentrate at low densities to determine where kill rates lie. The Yukon Fish and Wildlife Branch is currently planning wolf research in an area where moose are at a density of 0.14 moose/km^2.

An equally important problem is determining if there is an upper boundary predator-pit. There are several areas in Alaska where moose density currently exceeds 1.0 moose/km^2 and wolves and bears have been reduced for long periods by the public (Gasaway *et al.* 1992). It is not known whether these high density moose populations are stable (*i.e.*, Predation-Food Model), or unstable and destined to return to low density if wolves become naturally regulated (*i.e.*, Predation Model). To examine the predator pit theory, exploitation on wolves in a high density moose area should be suspended and the wolf population allowed to become naturally regulated. If moose decline to low density due to wolf predation, then the Predation Model would be supported. If moose densities do not decline after wolves stabilize to natural densities, then the Predation-Food Model would be supported.

I recommend that raw kill rate data be re-examined and only packs greater than 4 wolves should be included in predation rate modelling. Furthermore, individual kill rates should be included in the analysis because substantial information about variability is lost by regressing mean kill rates with moose density.

Conclusions

Wolf functional response was density-independent, and kill rates by wolves were high when moose were between 0.25 and 0.43 moose/km^2. Currently, there is inadequate data to determine whether wolf functional response is type II or type III, but the shape of the curve does not appear to be important to regulate moose. Predation rate models imply that wolves could: 1) extirpate moose from local areas, or 2) regulate moose to a single low density equilibrium. My functional response and predation rate models, and empirical moose data from Yukon and interior Alaska are consistent with the single low density equilibrium hypothesis (Messier 1994). Results from my study suggest that the benefits to moose of reducing wolves will not persist indefinitely, and the unstable period of elevated moose numbers will mainly depend on the human harvest levels of moose, wolves and bears.

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Appendices

Appendix A. The percentage of moose and caribou calves, and estimated finite rates of increase each winter in the FSA.

Year	Number of Calves	Number of Adults	Total	Percent Calves	Finite Rate of Increase in November	Density (Moose/km^2)
Moose						
1990	42	114	156	27	1.17[a]	0.248
1991	72	193	265	27	1.17[a]	0.299
1992	45	170	215	21	1.10[b]	0.360
1993	18	83	101	18	1.09[c]	0.399
1994[d]	38	294	332	11	1.02[c]	0.434
Caribou						
1990	313	1176	1489	21	1.17[a]	0.258
1991	234	1170	1404	17	1.07[c]	0.302
1992	180	1314	1494	12	1.00[c]	0.326
1993	213	1036	1249	17	1.07[c]	0.349

[a] Interpolated from stratified moose population counts in 1987 and 1991 (Jingfors 1988, Larsen and Ward 1995) and stratified caribou population counts in 1986 and 1990 (Farnell and McDonald 1987, Farnell *et al.* unpubl. ms.) .

[b] Yearling recruitment rate for FSA was 1.19 in November 1991 (Larsen and Ward 1995). Finite rate of increase was yearling recruitment (1.19) - mean adult mortality rate (0.095) estimated from census interpolation between 1987 and 1991 (Larsen and Ward 1995).

[c] Rate of increase for moose was estimated using difference between percent calves seen in late winter and mean adult mortality rate. Rate of increase for caribou was the difference between percent calves seen in October and annual adult mortality rate (0.11) based on census interpolation (Farnell *et al.* unpubl. ms.).

[d] Late winter moose composition from R. Florkiewicz, Yukon Fish and Wildl. Br., unpubl. data.

Appendix B. Status of radio-tagged wolves in the study area from February 1990 through March 1994.

Pack	Date Radio-tagged	Sex	Age	No. of Months Followed	Period Contact Lost or Death Occurred	Known or Suspected Fate on 31 March 1994
Big Campbell Cr.	25 Feb 92	M	Adult	25		Alive
Big Campbell Cr.	09 Mar 93	F	Yearling	13		Alive
Big Campbell Cr.	09 Mar 93	F	Adult	13		Alive
Big Campbell Cr.	09 Mar 93	M	Yearling	13		Alive
Dragon L.	22 Feb 92	M	Adult	2 days	Feb 92	Unknown
East Arm	08 Feb 91	F	Adult	9	Nov 91	Dispersed
East Arm	08 Feb 91	M	Adult	9	Nov 91	Dispersed
Finlayson L.	07 Feb 91	F	Yearling	14	Apr 92	Dispersed
Finlayson L.	05 Mar 91	M	Adult	13	Apr 92	Dispersed
Fire Cr.	18 Feb 92	F	Adult	26		Alive
Fire Cr.	18 Feb 92	M	Adult	26		Alive
Frances L.	09 Mar 90	M	Yearling	2	May 90	Natural mortality
Frances L.	09 Mar 90	F	Yearling	8	Nov 90	Natural mortality
Frances L.	04 Mar 91	F	Adult	13	Apr 92	Dispersed
Frances L.	04 Mar 91	M	Adult	37		Dispersed-alive
Hoole R.	23 Feb 92	M	Adult	12	Feb 93	Natural mortality
Jackfish L.	19 Feb 90	M	Adult	32	Oct 92	Failed collar
Jackfish L.	19 Feb 90	F	Adult	37	Apr 93	Failed collar
Jackfish L.	11 Feb 91	M	Pup	38		Dispersed-alive
Jackfish L.	12 Mar 92	M	Adult	1	Apr 92	Failed collar
Jackfish L.	20 Mar 93	M	Yearling	13		Dispersed-alive
Jackfish L.	20 Mar 93	F	Yearling	1	Apr 93	Dispersed
Ketza R.	19 Feb 90	M	Adult	37	Mar 93	Failed collar
Ketza R.	10 Feb 91	M	Pup	4	Jun 91	Killed by hunter
Ketza R.	09 Mar 93	F	Yearling	13		Alive
Light Cr.	07 Mar 91	M	Adult	10	Jan 92	Natural mortality
Light Cr.	07 Mar 91	F	Adult	11	Feb 92	Failed collar-alive
Light Cr.	22 Feb 92	F	Pup	4	May 92	Natural mortality
Light Cr. (McEvoy L.)	08 Feb 91	M	Adult	37		Alive
Light Cr.	08 Mar 93	F	Yearling	1	Apr 93	Natural mortality
Light Cr.	08 Mar 93	F	Yearling	1	Apr 93	Natural mortality
Lobster L.	20 Mar 93	F	Pup	1	Apr 93	Dispersed
Lobster L (Weasel L.)	06 Mar 90	M	Pup	36	Mar 93	Natural mortality
McEvoy L.	08 Feb 91	F	Adult	5	Jun 91	Killed by bear
Lobster L.	20 Mar 93	F	Yearling	1	Apr 93	Natural mortality
Mink L.	26 Feb 91	M	Adult	37		Alive
Mink L.	26 Feb 91	F	Adult	37		Alive
Mink L.	08 Mar 93	M	Yearling	14		Dispersed-alive

Appendix B. (Continued). Status of radio-tagged wolves in the study area from February 1990 through March 1994.

Pack	Date Radio-tagged	Sex	Age	No. of Months Followed	Period Contact Lost or Death Occurred	Known or Suspected Fate on 31 March 1994
Nipple Mtn.	10 Mar 93	M	Adult	1	Apr 93	Dispersed
Nipple Mtn.	10 Mar 93	F	Adult	14		Alive
One Island L.	12 Mar 91	M	Adult	13	Mar 92	Natural mortality
Otter Cr.	21 Feb 92	M	Adult	25		Alive
Otter Cr.	21 Feb 92	F	Adult	25		Alive
Prevost R.	04 Mar 90	F	Adult	49		Alive
Prevost R.	04 Mar 90	M	Pup	23	Feb 92	Natural mortality
Prevost R.	08 Mar 91	M	Adult	13	Apr 92	Dispersed
Seven Wolf L.	02 Feb 90	F	Adult	37	Mar 93	Killed by trapper
Seven Wolf L.	06 Feb 91	M	Adult	38		Dispersed-alive
Seven Wolf L.	22 Mar 93	M	Yearling	1	Apr 93	Natural mortality
Seven Wolf L.	22 Mar 93	F	Yearling	1	Apr 93	Dispersed
Tuchitua R.	13 Feb 90	F	Pup	7	Sep 90	Natural mortality
Tuchitua R.	13 Feb 90	F	Adult	38	Apr 93	Dispersed
Tuchitua R.	02 Mar 90	F	Yearling	37	Apr 93	Natural mortality
Tuchitua R.	25 Mar 93	F	Yearling	1	Apr 93	Dispersed
Tuchitua R.	25 Mar 93	F	Yearling	1	Apr 93	Dispersed
Tyers R.	02 Mar 90	M	Yearling	34	Dec 92	Natural mortality
Tyers R.	02 Mar 90	F	Adult	34	Dec 92	Natural mortality
Upper Pelly R.	04 Mar 90	M	Adult	49		Alive
Upper Pelly R.	07 Feb 91	F	Adult	5	Jun 91	Natural mortality
Upper Pelly R.	19 Mar 93	F	Adult	13		Alive
Weasel L.	23 Mar 90	M	Adult	36	Mar 93	Natural mortality
Weasel L.	25 Feb 92	F	Adult	7	Sep 92	Natural mortality
Weasel L. II	11 Feb 91	M	Adult	3	May 91	Dispersed from Weasel L. then dispersed again
Wolverine L.	02 Mar 90	M	Adult	49		Alive
Wolverine L.	09 Feb 91	F	Adult	4	Jun 91	Natural mortality
Wolverine L.	19 Ma r93	F	Adult	13		Alive
Woodside R.	12 Feb 90	F	Yearling	8	Sep 90	Killed by hunter
Woodside R.	12 Feb 90	F	Yearling	38	Mar 93	Natural mortality
Woodside R.	03 Mar 90	F	Adult	38	Mar 93	Failed collar
Woodside R.	10 Mar 92	M	Pup	13	Apr 93	Dispersed
Yusezyu R.	22 Feb 90	F	Yearling	49		Alive
Yusezyu R.	22 Feb 90	M	Adult	37	Mar 93	Failed collar

Appendix B. (Continued). Status of radio-tagged wolves in the FSA from February 1990 through April 1994.

Pack	Date Radio-tagged	Sex	Age	No. of Months Followed	Period Contact Lost or Death Occurred	Known or Suspected Fate on 31 March 1994
Lone wolves						
Wolf Canyon	20 Feb 92	M	Yearling	14	Apr 93	Dispersed
West Arm	06 Mar 91	F	Yearling	1	Apr 91	Dispersed
Cabin Cr.	23 Feb 92	M	Adult	1	Mar 92	Dispersed
Boundary Pack						
Lapie R.*	20 Feb 90	M	Pup	4	Jun 90	Natural mortality
Lapie R.	20 Feb 90	F	Adult	16	Mar 92	Unknown
Lapie R.	10 Feb 91	M	Yearling	12	Mar 92	Killed by hunter

( ) indicates original pack that wolf dispersed from.

* Lapie R. pack ranged along the western boundary of my study area but was not a resident pack.

Appendix C. Ungulate prey biomass in winter 1994 in the FSA.

Prey Species	Number	Weight[a]	Biomass Value
Moose	7,594[b]	6	45,568
Caribou	7,500[c]	2	15,000
Other Ungulates	500[d]	1	500
Total			61,068

[a] Relative biomass from Fuller (1989).

[b] Number of moose in 1994 were estimated using the equation:

$$y = 23\ (0.75)\ 360\ \lambda;$$

where 23 was number of 1,000 km^2 units in FSA; 0.75 is the proportion of habitable moose range; 360 is mean moose density (moose/1,000 km^2) in November 1991; and $\lambda = 1.10$ to 1992, $\lambda = 1.09$ to 1993, and $\lambda = 1.02$ to 1994 (see Appendix A).

[c] Caribou numbers in 1994 were based on known population size in 1990 (6,225: Farnell *et al.* unpubl. ms.) and expected growth to 7,500 caribou by March 1994, based on annual recruitment indices (R. Farnell, unpubl. data).

[d] Dall sheep, mountain goat and mule deer totaled 500 animals (see Study Area).