Gray Wolves in and Adjacent to Voyageurs National Park, Minnesota
Research and Synthesis 1987–1991

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ABOVE
A biologist inspects the teeth of
an instrumented wolf.
NPS Photo

ON THE COVER
Gray wolf, northern Minnesota.
NPS photo by W. Route

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Abstract

We investigated the status of wolves *(Canis lupus)* in and adjacent to Voyageurs National Park (VNP), Minnesota, from September 1987 through September 1991. Thirteen wolf packs were followed by radiotelemetry (13 males, 18 females were radio-marked) for 6 to 48 months. Six packs had territories exclusively or partially within VNP. Radiotelemetry data gathered during winter daylight hours indicated that wolves within VNP avoided the frozen surfaces and shorelines of larger lakes during that time period. In contrast, snow tracking revealed that wolves regularly traversed frozen surfaces and shorelines after dark. Our howling surveys averaged detection near 50% of the wolf packs known to exist in the study area. Pack territories ranged from 48 km^2 to 296 km^2 with a mean of 152 km^2. Overall, mean mid-winter pack size was 5.5 wolves with a high of 6.3 in 1988–1989 and a low of 4.5 in 1989–1990. Non-territorial wolves made up 9.5% of the population. Overall, mean wolf density was 33/1,000 km^2 with an annual range of 24 to 42/1,000 km^2. We detected nine dispersals among 20 radio-marked wolves more than eight months old. All dispersals occurred in winter. Dispersing wolves averaged 2.1 pre-dispersal movements beyond their home territory. Ages of dispersing wolves ranged from 1.5 to 7.5 years. Natural causes of mortality among radio-marked wolves included intraspecific strife (*n* = 4) and starvation (*n* = 2). Confirmed human-induced causes of mortality among radio-marked wolves included shooting (*n* = 2), trapping or snaring (*n* = 2), and unknown method (*n* = 2). Natural causes of mortality among non-radio-marked wolves included intraspecific strife (*n* = 1) and starvation (*n* = 1). Confirmed human-induced causes of mortality among non-radio-marked wolves included automobile collisions (*n* = 3), shooting (*n* = 3), and trapping or snaring (*n* = 2). All mortalities within the boundaries of VNP were attributed to natural causes. Six of eight confirmed mortalities among instrumented wolves and eight deaths of non-instrumented wolves beyond the boundaries of VNP were human caused. Two additional instrumented wolves disappeared at the onset of the Minnesota deer rifle season, but their fate was not confirmed. Twenty remains were necropsied, but no mortalities were attributable to diseases or parasites. The annual survival rate of adult wolves was 0.75. Season, and then age, were the most important parameters in explaining survival of all instrumented wolves. Instrumented wolves with territories exclusively within the boundaries of VNP had higher survival than those whose territories straddled or were beyond the park boundaries. The annual wolf diet consisted of 80% white-tailed deer *(Odocoileus virginianus)* and 15% beaver *(Castor canadensis)*, as determined by scat analysis. Deer made up 56% of the spring and 91% of the winter diet while beaver made up 35% of the spring and 7% of the winter diet. The overall sex ratio of adult deer killed by wolves in winter did not differ from 50:50. However, the sex ratio of wolf-killed adult deer was skewed toward males in the winter of 1987–1988 and toward females in 1988–1989. The median age of deer killed by wolves in winter was 6.5 and 7 years for females and males, respectively.

Key Words: *Canis lupus,* abundance, density, diseases and parasites, dispersal, feeding ecology, gray wolf, howling surveys, mortality, radiotelemetry, snow tracking, survival rates, pack size, territory size, Voyageurs National Park, Minnesota.

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Introduction

Gray wolves once occupied much of North America (Nowak 1995), but were extirpated from most of their range south of Canada by the mid-1960s (Thiel and Ream 1995). In 1963, the estimated 350–700 wolves in extreme northeastern Minnesota (Stenlund 1955, Fuller et al. 1992) likely constituted the only viable population of gray wolves in the contiguous United States other than those at Isle Royale National Park (IRNP), Michigan. In Minnesota, a statewide wolf bounty system was in effect between 1849 and 1965 (Minnesota Department of Natural Resources [MnDNR] unpublished data). In addition, the state of Minnesota administered a Directed Predator Control Program until 1974. Aerial gunning was a component of these control programs from 1948 to 1956. The first significant protection for wolves in Minnesota came in 1970 when Superior National Forest (SNF) was closed to the taking of wolves. In 1972, an estimated 500 to 1,000 wolves occupied 30,720 km² of wolf habitat in northeastern and north-central Minnesota (MnDNR unpublished data). The creation of VNP from public and private lands in 1975 provided additional protection for wolves and their habitat.

Wolves became federally protected throughout their historic range in the contiguous United States in 1974 when they were listed as endangered under the Endangered Species Act (ESA) of 1973 (U.S. Fish and Wildlife Service [USFWS] 1992). By 1978, wolf numbers had increased in Minnesota so that the species was reclassified as threatened under the ESA (USFWS 1992). Currently, wolves are expanding their range south and west across Minnesota (Berg and Benson 1998) and have reoccupied portions of Wisconsin (Wydeven et al. 1995) and the Upper Peninsula of Michigan (Hammill 1997).

In the mid-1980s, VNP was one of only three national parks (Isle Royale, Glacier) in the contiguous United States known to support gray wolves year-round. Results of winter ground tracking efforts in VNP from winter 1976–1977 through 1985–1986 suggested wolf numbers declined (Cole 1987). This trend paralleled a decade-long decline in wolf numbers in the central SNF ending in winter 1983–1984 (Mech 1986b). In both cases, the wolf population declines were attributed to a decline in the abundance of the primary ungulate prey species, white-tailed deer (Mech 1986b, Cole 1987). A review of historical data suggested that the ungulate prey base for wolves at VNP might have been more diverse prior to the 1920s (Cole 1987). In response to the observed decline in wolf abundance and to examine the potential for reintroducing extirpated woodland caribou *(Rangifer tarandus)* (Gogan et al. 1990, Gogan and Cochrane 1993), we conducted a study of wolves in and adjacent to VNP from 1987 through 1991. Voyageurs National Park served as the focus of this study of wolves. However, it became clear early in the study that wolves utilizing VNP ranged extensively beyond the park boundaries. We therefore opted to define VNP as the core study area but annually defined a survey area that included territories of all instrumented wolves in and adjacent to VNP.

Our goals were to assess the ability of VNP to support long-term resident and "across-boundary" packs of wolves and to identify human activities within and adjacent to the park likely to affect their long-term viability. Specific objectives were to (1) determine the number of wolf packs using VNP and adjacent lands; (2) estimate the approximate size and location of pack territories; (3) estimate wolf density, including the number of resident pack wolves and lone wolves; (4) calculate the percentage of wolves leaving packs; (5) determine causes and timing of mortality; (6) calculate survival rates of select cohorts of wolves; (7) identify diseases and parasites of wolves; (8) examine wolf population genetics; (9) determine wolf food habits; and (10) evaluate the utility of howling surveys for assessing the presence or absence of wolf packs in the park.

Study Area

Voyageurs National Park covers an area of 882 km² of forest and lakes atop the Canadian Shield along the United States–Canada boundary between northern Minnesota and northwestern Ontario. The park's northern boundary extends from 20 to 70 km east of the communities of International Falls, Minnesota, and Fort Frances, Ontario. The park is part of a relatively unsettled region that includes the larger than 4,850 km² Boundary Waters Canoe Area Wilderness of the 8,500 km² SNF, Minnesota, and the 4,450 km² Quetico Provincial Park, Ontario (figure 1).

Voyageurs National Park includes a central landmass of the Kabetogama Peninsula and its adjacent islands (330 km²), a separate southeastern landmass (210 km²), and 4 large lakes comprising an area of 342 km². The landmasses contain 26 small lakes, ranging from 13 to 305 ha in size. As of 1986, beaver im-

poundments covered 13% of the Kabetogama Peninsula (Broschart et al. 1989). Maximum topographic relief is 80 to 90 m. The park lies within the Border Lakes subsection of the Laurentian Mixed Forest Province (McNab and Avers 1994) and along the boundary between the southern boreal and northern hardwood forest types (Pastor and Mladenoff 1992). Vegetation in the southern boreal type is mostly a secondary-growth mosaic of jack pine *(Pinus banksiana)*, quaking aspen *(Populus tremuloides)*, paper birch *(Betula papyrifera)*, white spruce *(Picea glauca)*, and balsam fir *(Abies balsamea)* (Kurmis et al. 1986). The northern hardwood forest type is characterized by red pine *(Pinus resinosa)*, white pine *(Pinus strobus)*, red maple *(Acer rubrum)*, and green ash *(Fraxinus pennsylvanica)* (Kurmis et al. 1986). Extensive wildfires in the 1920s and 1930s (Crowley 1995) shaped current forest vegetative cover. Forests within the present

Figure 1. Location of Voyageurs National Park, northern Minnesota.
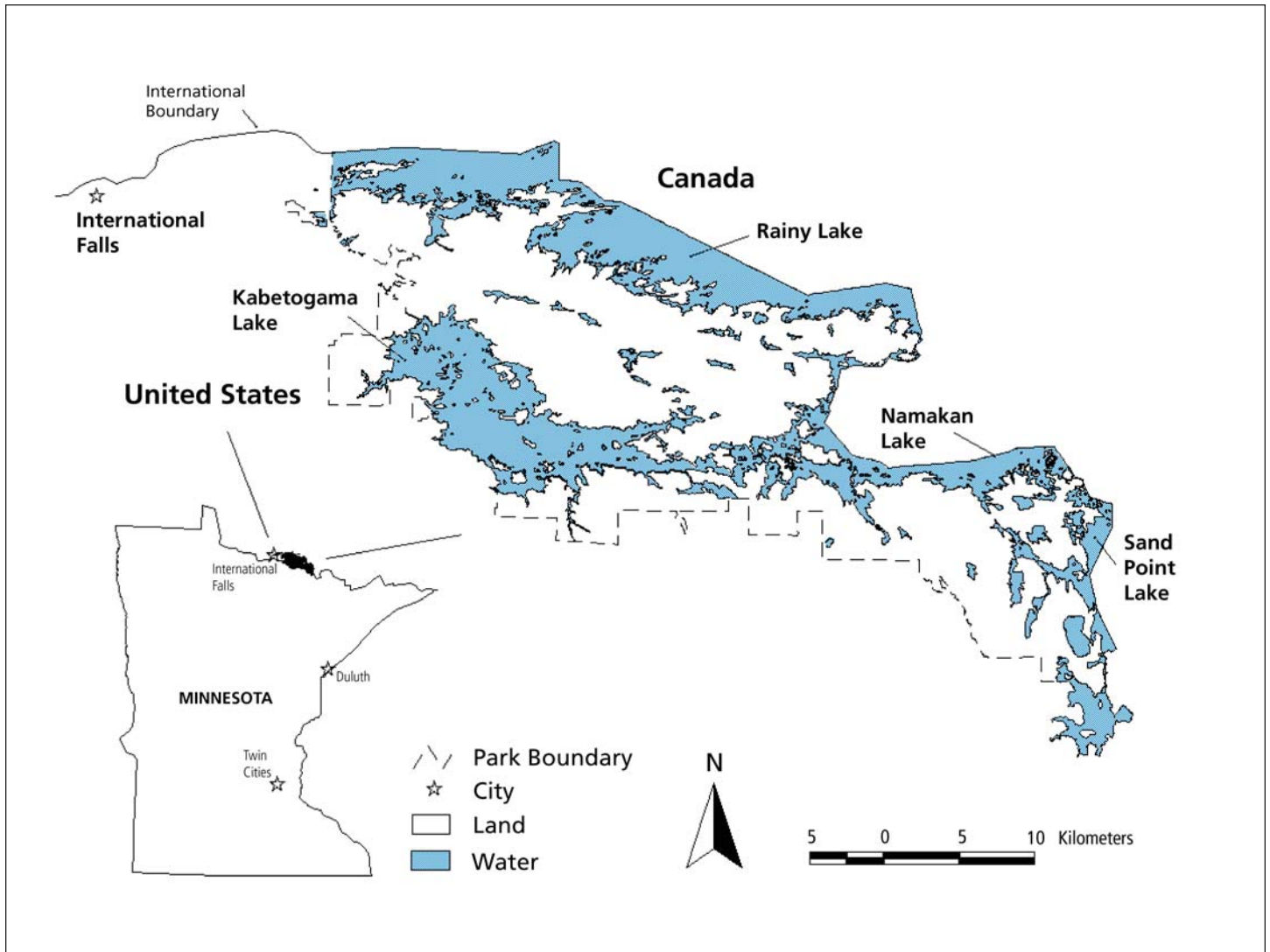
Figure 2. Winter Severity Index (WSI) for International Falls, Minnesota, for winter 1984–1985 through winter 1994–1995. The WSI is calculated as the number of days below -17.7° C or with more than 45.7 cm snow covering the ground. Winter Severity Index values greater than 100 are considered severe. Data provided by F. Swendsen, Minnesota Department of Natural Resources, International Falls, Minnesota.
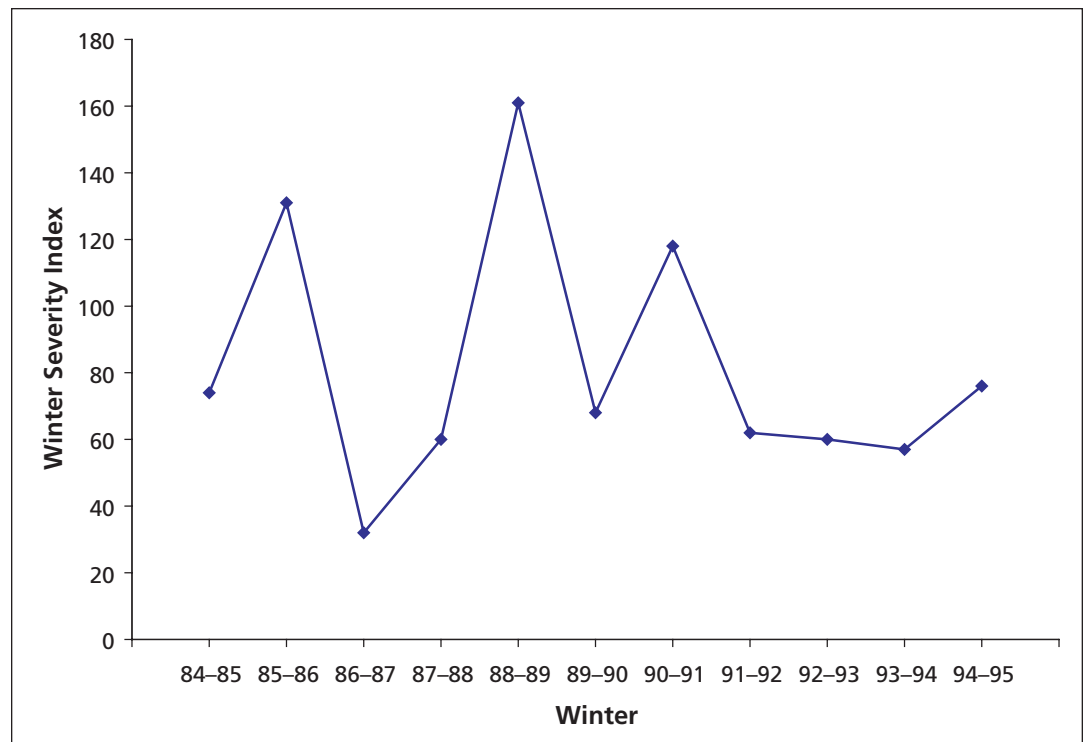
VNP were extensively logged between 1910 and 1930 (Crowley 1995), and approximately 25% of the Kabetogama Peninsula was logged post-1940 (J. Pastor, University of Minnesota, personal communication). Natural fires have been suppressed and logging prohibited since the establishment of VNP in 1975. Most lands adjacent to the park on both sides of the international border are managed for timber production.

Temperatures average 18.6° C in July and −6.1° C in January, but extremes vary from 36.6° C to −43° C (National Weather Service, International Falls, MN). Lakes in the area are usually ice-covered by the third week in November, and spring break-up occurs about 1 May (Kallemeyn 1987). A winter severity index for International Falls, Minnesota, shows that the winters of 1988−1989 and 1990−1991 were particularly severe (figure 2) (F. Swendsen, Minnesota DNR, personal communication).

As of 1985, wolves occurred throughout much of the Laurentian Mixed Forest Province of Minnesota and adjacent Ontario (figure 3) (Mech et al. 1988). The U.S. Department of Interior's recovery plan for the eastern timber wolf identified four management zones for wolves in Minnesota (USFWS 1992). Voyageurs National Park lies at the extreme northwest corner of the 11,423-km² zone one of primary wolf range (figure 3). The park's western and southern boundaries are coincident with the boundary between primary range zones one and three (USFWS 1992). Both zones are identified as critical habitat for wolves (USFWS 1992). Wolves were harvested legally in Ontario adjacent to VNP throughout the life of this study. Some 75 wolves were trapped in the 23,595-km² Fort Frances District during winter 1987−1988 but less than 20 were trapped in the latter three years of our study (appendix 1).

Moose *(Alces alces)* and woodland caribou were likely the most common ungulates in terms of numbers and biomass in pre-European times (Cole 1987). Caribou were extirpated from the region by the 1940s. Moose densities within VNP were estimated at 0.23/km² in 1992 (Gogan et al. 1997a). White-tailed deer expanded northward with logging of the mature pine forest; they became common by the 1920s (Petraborg and Burcalow 1965). From 1975 through 1992, estimates of deer density in and directly adjacent to VNP ranged from 1.5 to 11.5/km² (Peterson 1976, Whitlaw and Lankester 1994, Gogan et al. 1997a). Densities of deer in the areas south of VNP ranged from 4.2 to 5.2/km² between 1985 and 1995 (M. Lenarz, Minnesota Department of Natural Resources, personal communication). Density of beaver colonies on the Kabetogama Peninsula increased continuously from the mid-1930s through 1986 (J. C. Schneeweis, Minnesota Department of Natural Resources, personal communication). Beaver density on the Kabetogama Peninsula was estimated at 5.8 to 6.6/km² in the mid-1980s (Smith

Figure 3. Continuous distribution of wolves in Minnesota in 1988–1989 (left panel) (Fuller et al. 1992) and wolf management zones in Minnesota identified in the 1992 wolf recovery plan (right panel) (USFWS 1992).
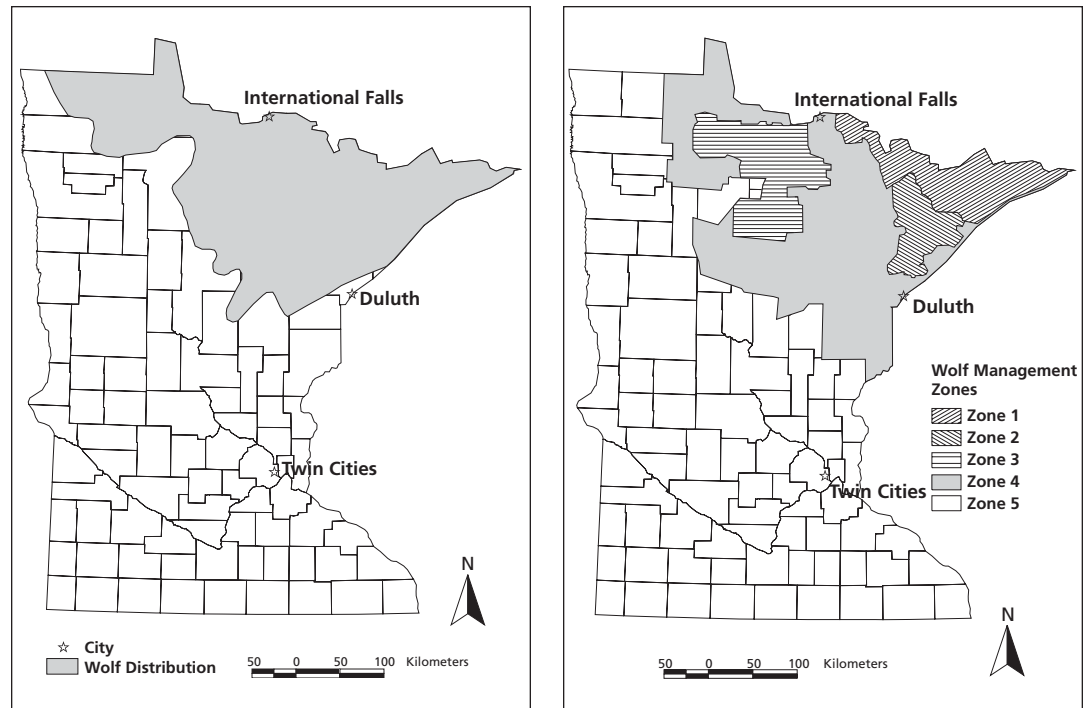
and Peterson 1988) and 9.7/km² in the early 1990s (Smith 1997). Statewide, snowshoe hare *(Lepus americanus)* numbers exhibited a low-amplitude high, rising from 0.5/km² in 1987 to 2.7/km² in 1989 before declining to initial densities. Hare density in 1989 was only one-seventh that of the late 1970s (Dexter 1998: 49). Black bear *(Ursus americanus)* densities in nearby portions of SNF ranged from 0.16 to 0.24/km² from 1969 to 1985 (Rogers 1987). Lynx *(Felis lynx)* and cougar *(F. concolor)* may occur at low numbers in the region (Gerson 1988). Based upon our observations, coyote *(Canis latrans)* are uncommon, and red fox *(Vulpes vulpes)* are common within VNP.

Human recreational activities tend to be distributed on the water and along the shorelines of the region's lakes during summer. The freeze-up of the larger lakes in late November enables a proliferation of "ice houses" or fishing shacks on the frozen lake surfaces of the four major lakes (Kabetogama, Rainy, Namakan, and Sand Point) within VNP. The structures on the west end of Rainy Lake are accessed by automobile via a plowed road over the frozen lake surface. Similarly, the onset of snow permits extensive use of snowmobiles on both the land surfaces and across the frozen lake surfaces. Snowmobile users tend to remain on groomed trails while traversing land but become more dispersed while crossing frozen lake surfaces, except where unsafe ice or portages funnel them into more restricted areas. Logging beyond the park boundaries is limited to uplands in the warmer

months, while lowland forests are logged in winter when the frozen ground permits access by heavy equipment.

Annual visitor use of VNP rose from approximately 210,000 in 1985 to more than 270,000 in 1991 (figure 4, page 6). Monthly visitation is more than 40,000 from June through August, approximately 25,000 during the "shoulder" months of May and September, and ranges from 1,500 to 12,000 during winter months (figure 4, page 6) (J. Schaberl, National Park Service, personal communication). Most winter visitation is snowmobile use.

Figure 4. Annual (upper panel) and monthly (lower panel) visitation patterns for Voyageurs National Park, Minnesota, 1985–1995. Vertical bars are 95% confidence intervals.
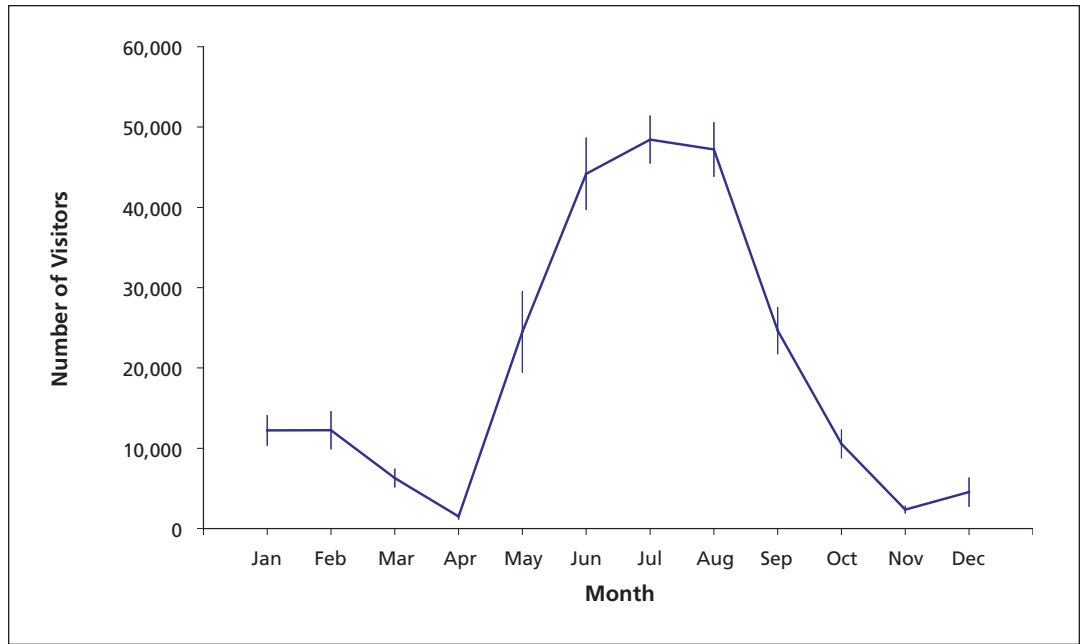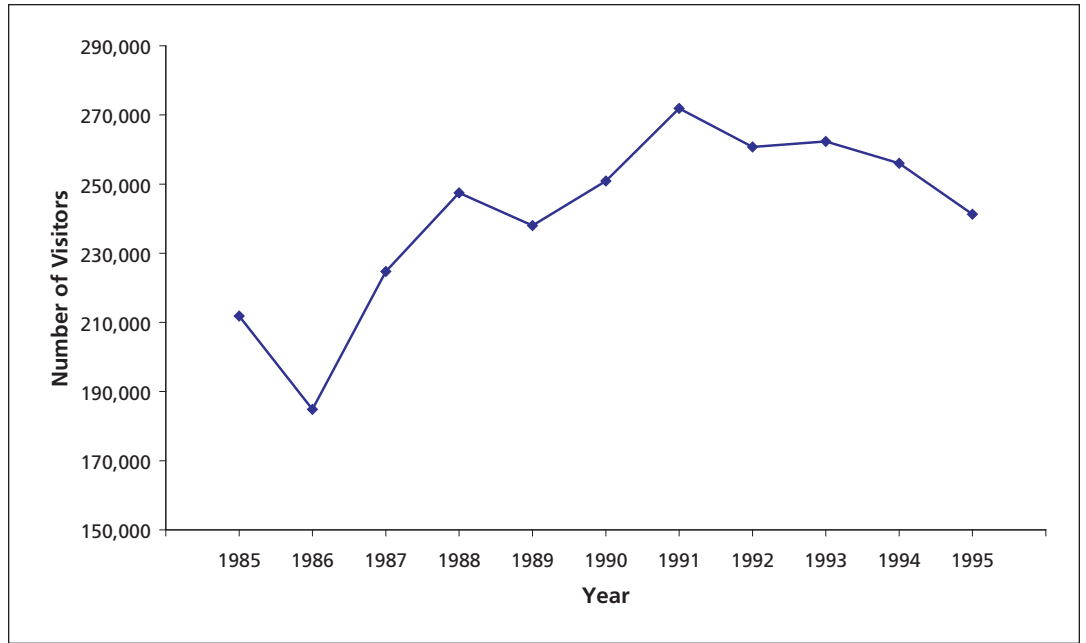
Methods

Capture and radiotelemetry

Wolves were captured during approximately 21-day trapping periods between 25 April and 15 May, and from 15 August to 15 September, from fall 1987 to fall 1990. A single wolf was trapped during summer 1989 (June 6 to August 18). Wolves were captured with #14 Newhouse foothold traps (Kuehn et al. 1986) and immobilized using a pole-mounted syringe with a mixture of xylazine hydrochloride, ketamine hydrochloride, and atropine sulphate (Fuller and Kuehn 1983). Captured wolves were fitted with mortality-sensing radio collars (164−166 MHz; Telonics, Inc., Mesa, Arizona). The ages of wolves were estimated at capture as either pup (less than eight months old) or adult (more than one year old). Collars were loosely fitted on pups (less than eight months old) and were padded with foam to allow for growth. Captured wolves were eartagged with 3.5×1-cm aluminum tags issued by the Minnesota Department of Natural Resources, sexed, weighed, and given penicillin as an antibiotic (Fuller and Kuehn 1983). Up to 20 ml of blood were collected from each wolf to evaluate for diseases and endoparasites (Zarnke and Ballard 1987, Peterson et al. 1998), and for genetic studies (Lehman et al. 1991). When available, fecal material and ectoparasites were also collected for disease evaluation and parasite identification (Ash and Orihel 1987). In 1987 and 1988, we captured wolves in VNP and within 16 km of the south boundary to ensure transboundary packs were instrumented. In 1989 and 1990, we restricted trapping to within and immediately adjacent to the park boundaries to focus our efforts on wolves ranging into the park.

Radio-marked wolves were located at approximately weekly intervals ($\bar{x}$ = 6.9 days, range (0−57 days) using standard aerial radiotelemetry techniques (Mech 1986a, Mech et al. 1998) from a Piper PA-18 SuperCub or occasionally a Cessna 180. When possible, radio-marked wolves and their pack members were observed and counted. Wolf locations were obtained with an onboard LORAN-C positioning device and 1:24,000-scale topographic maps and recorded as Universal Transverse Mercator (UTM) coordinates. Some LORAN-C locations differed from mapped locations during a portion of the study. Subsequently, we incorporated a combination of LORAN-C and map coordinates to determine a relative directional bias in locations of 187 m at 108°, (appendix 2). A directional bias in locations based on LORAN-C alone was 565 m at 104.2° (appendix 2). We concluded that, given the wide ranging habits of wolves, these mean levels of bias were acceptable for assessing territory, movements, and pack affiliations.

Noninvasive population sampling

Snow tracking—We tracked wolves from the ground in snow from approximately mid-December through March 1987−1988 and 1988−1989 to augment telemetry data on pack size and movements, and to verify the existence of packs with no radio-marked wolves. Most tracking was conducted on the surfaces of the four large lakes within VNP. Tracks were plotted on 1:50,000-scale topographic maps. We estimated the age of tracks, the minimum and maximum number of wolves, and noted evidence of predation and prey consumption. We did not use snow tracks in 1989−1990 or 1990−1991 when most packs in the study area contained radio-marked wolves. Data from snow tracking were not used to calculate average territory size but were used to delineate the total annual survey area and to estimate winter pack size.

Howling surveys—Wolves respond to simulated howling (D. H. Pimlott, University of Toronto, unpublished report), and standardized howling surveys can be used to follow trends in wolf populations (Harrington and Mech 1982, Fuller and Sampson 1988). We established a simulated wolf howling survey (Harrington and Mech 1982, Fuller and Sampson 1988) in VNP. Twenty-four sampling stations were distributed approximately 6 km straight-line distance apart along the shorelines of the four large lakes. This placed sampling stations within 3 km of most of the park's landmass. Sampling (simulated howling) was conducted at each station during late July and early August from 1988 through 1991. Stations were sampled three nights consecutively using three trials of three howls each, with two minutes between trials (Fuller and Sampson 1988). Pups were distinguished from older animals in the responses by their distinctive yips (Harrington and Mech 1982). The location, number, and estimated age (adult or pup) of wolves returning howls were recorded at each station. We classified elicited howls from more than two wolves as a pack response and elicited howls of a single wolf as a lone wolf response.

Wolves were captured during approximately 21-day trapping periods between 25 April and 15 May, and from 15 August to 15 September, from fall 1987 to fall 1990.

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Incidental observations—We recorded all wolf sightings and non-elicited howling detected in the course of our field activities. These incidental observations augmented radiotelemetry locations, snow tracking surveys, and howling surveys.

Pack territory size

Territory size was estimated for radio-marked packs that were relocated more than 30 times (Fuller and Snow 1988, Fuller 1989) in a biological year, beginning 1 May and continuing through 30 April of the following year (Mech 1970). Territories were delineated using the minimum convex polygon (MCP) method (Mohr 1947, Odum and Kuenzler 1955). We excluded locations of wolves beyond the delineated territories or that entered adjacent pack territories (Fuller 1989). Unmarked packs and those with less than 30 telemetry locations were not used in territory area calculations. However, for density calculations, the territory boundaries of these packs were estimated using available radio locations, snow tracks, fall howling surveys, incidental observations, and landscape features such as large lakes and human developments.

Pack size and density estimates

We estimated minimum pack size (more than two wolves) between November and February each winter. For radio-marked packs that were counted more than five times during telemetry flights, the estimate was the maximum number of wolves observed. For unmarked packs and those counted less than five times during telemetry flights, we estimated the minimum pack size as the maximum number determined from aerial observations, snow tracks, and incidental observations. We defined a *lone wolf* as a wolf not located with other wolves during more than 30 telemetry locations and less than 15 visual observations of a specific individual.

The number of non-territorial wolves is often ignored in population estimates. Capture and sightability biases make estimating non-territorial wolves difficult (Fuller 1989). We calculated the percent of non-territorial wolves from telemetry data each year during the census period; however, because of low sample size and the potential for capture and sightability biases, we assumed that 15% of the population comprised non-territorial wolves when estimating population density (Fuller et al. 1992). The use of 15% is comparable with recent population estimates for Minnesota (Fuller 1989, Fuller et al. 1992, Berg and Benson 1998).

We calculated wolf density each winter over a survey area defined as the area encompassed by all adjoining wolf packs of known size. This area included unoccupied space between territories. The total number of pack wolves, as estimated from snow tracking and visual observations, was divided by 0.85 to compensate for non-territorial wolves in the population (Fuller 1989, Fuller et al. 1992, Berg and Benson 1998). This quotient was then divided by the survey area for an annual estimate of density (Fuller 1989).

Dispersal events

We defined *dispersal event* as movement more than 5 km from the instrumented wolf's original territory, or into another territory, and with the wolf not returning to its original territory (Fuller 1989:10). A wolf must have been located within its home pack territory more than five times before being classified as dispersing. Dispersal distance was measured from the most distant radio location to the nearest edge of the original territory (Fuller 1989:10, Messier 1985). Dispersal date was inferred as the mid-date between the last telemetry location within and first location beyond the original territory (Fuller 1989:10). Age at dispersal was inferred from estimated birth date. We assumed the loss of a radio signal was indicative of dispersal when signal loss was immediately preceded by dispersal-like movements (Messier 1985, Fuller 1989).

Timing and causes of mortality

We investigated mortality signals from transmitters to recover carcasses of study animals and examined unmarked wolves that were found dead. All carcasses and sites were evaluated for cause of death. We removed a tooth from each dead wolf for aging by dental cementum annuli (Goodwin and Ballard 1985, Ballard et al. 1995) and submitted 23 carcasses to the National Wildlife Health Center (NWHC), Madison, Wisconsin, for necropsy. Causes of mortality were classified as intraspecific strife, starvation, vehicle collision, gunshot, trapped, snared, unknown human-related, or unknown. Mortality sites were classified as in or outside of VNP. Furthermore, we assumed human-induced mortality in two instances in which instrumented wolves disappeared at the onset of the Minnesota deer rifle season (Fuller 1989). However, these latter two mortalities were excluded from calculations of survival rates (see following).

Survival rates

We used "Known Fates" models in program MARK (White 1998) (appendix 3) to estimate wolf survival. To meet assumptions of Known Fates survival analysis, we used only information on mortalities that was confirmed via radiotelemetry and on-ground inspection of each location. We created seasonal encounter histories from radiotelemetry records and assessed the potential influences of (1) age, (2) sex, (3) territory location relative to VNP, and (4) time of year on survival of marked wolves (appendix 3). Specific hypotheses were:

H_{01}: Survival is constant between pups and adults
H_{A1}: Survival varies between pups and adults

H_{02}: Survival is constant between males and females
H_{A2}: Survival varies between males and females

H_{03}: Survival is constant among wolves utilizing territories that are contained within VNP, border VNP, and are outside VNP
H_{A3}: Survival varies among wolves utilizing territories that are contained within VNP, border VNP, and are outside VNP

H_{04}: Survival is constant over time of year
H_{A4}: Survival varies by time of year

To facilitate comparisons with other North American wolf populations, we assessed overall annual survival over a biological year, from 1 May through 30 April of the following year. A biological year was divided into four biological seasons (Mech 1970): pup rearing (1 May–30 June), early rendezvous (1 July–30 September), late rendezvous or winter freeze-up (1 October–31 November), and winter post-iceup (1 December–30 April). The late rendezvous period included the northern Minnesota deer rifle-hunting season.

To address the hypothesis of differing survival by age, we included relocation data for all instrumented wolves. Within a given biological year, each animal was classified as a pup or an adult. Survival probabilities were calculated for each classification only for the nine-month period from 1 August–30 April. The pup-rearing season and first month of the early rendezvous season were excluded from analysis because we did not radio-mark pups during these months. To address hypotheses two through four regarding survival by sex and territory location, we included relocation data for only instrumented adults for the entire biological year. Pups were excluded from analysis because they were not sampled for an entire biological year. Within a given biological year, each adult was coded as male or female and as to territory location relative to VNP. We addressed hypothesis four regarding survival over time, i.e., biological season, in the context of the previous three hypotheses. That is, we assessed survival over time in conjunction with examination of survival by age, sex, and territory location.

Diseases and parasites

Necropsies, including gross and microscopic examination, were performed on intact and partial carcasses of instrumented and non-instrumented wolves collected in and adjacent to VNP. This included some wolves that were trapped legally in adjacent Ontario. Laboratory tests in bacteriology, virology, and parasitology were used to determine causes of death and to identify incidental abnormalities.

Blood, ectoparasites, and feces were collected from captured wolves, and additional fecal samples were collected opportunistically along trails. Tests for serum antibodies to *Borrelia burgdorferi*, canine parvovirus (CPV-2), canine distemper, infectious canine hepatitis, rabies, *Brucella canis, Leptospira interrogans,* and blastomycosis were identical to procedures detailed in Peterson et al. (1998). Serology to detect canine heartworm (dirofilariasis) was done at Colorado State University (Ft. Collins, Colorado). Knott's test was used to detect microfilaria in blood, and fecal flotation or sedimentation and direct-smear examination were used to survey for internal parasites (Ash and Orihel 1987). Feces from captured wolves, trails, and carcasses were screened for CPV-2 with a test kit for canine-parvovirus antigen (Peterson et al. 1998).

Population genetics

Blood and tissue samples obtained from 19 wolves during trapping or at time of death were sent to the Department of Biology, University of California, Los Angeles, for analysis. Researchers there pooled our samples with wolf and coyote samples from across North America and mitochondrial DNA (mtDNA) genotypes were determined using restriction fragment length polymorphisms (Lehman et al. 1991).

Feeding ecology

We collected wolf scats from January 1987 through September 1989. Each scat was referenced with date of collection, approximate time of deposition, and location. Scats were air dried and autoclaved prior to examination

Laboratory tests in bacteriology, virology, and parasitology were used to determine causes of death and to identify incidental abnormalities.

with a dissecting microscope to identify prey (Adorjan and Kolenosky 1969, Schmidt 1990). Occurrence of each prey species was tallied by month and season. Vegetation was tallied if it comprised more than 50% of the scat by volume.

We estimated the relative biomass of each prey species consumed by wolves using correction factors for prey size.

Small mammals have a relatively large ratio of indigestible hair to digestible meat, so may be over-represented in frequency of occurrence data (Mech 1970, Floyd et al. 1978, Fritts and Mech 1981, Weaver 1993). To rectify this, we estimated the relative biomass of each prey species consumed by wolves using correction factors for prey size (Weaver 1993). We reasoned that each scat was representative of a meal and that each prey species in that scat had equal weight in that meal. Thus, we assigned a value of 0.5 for each prey in the 10% of scats that contained two prey items. We did not find more than two prey represented in any scat. We used data from this study and other nearby studies to estimate aver-age weight of prey consumed in each season (Fritts and Mech 1981).

We examined the remains of wolf-killed deer and other prey to assess their age, sex, and nutritional status. A tooth was collected for age determination by dental annuli (Larson and Taber 1980). When teeth were not available, remains were classified as either fawn (less than one year old) or adult (more than one year old) based upon skeletal measurements (Fuller et al. 1989). Sex was determined by examination of soft tissues or by the presence or absence of antler pedicels. We collected deer leg bones in the following order of preference: femur, humerus, tibia, radius, metacarpal, and metatarsus. Bones were submitted to the MnDNR Grand Rapids, Minnesota, for analysis of percent marrow fat to provide an index to physical condition of prey. When femurs were not available, femur percent marrow fat was calculated from other limb bones following the procedures of Fuller et al. (1989).

Results and Discussion

Capture and radiotelemetry

Thirty-one wolves, 13 males and 18 females, were radio-marked in and adjacent to VNP between August 1987 and May 1991. The mean weight of male wolves one or more year old was 32.7 kg while that of females one or more year old was 30.8 kg (table 1). The difference was non-significant ($t = -0.869$, df = 16.3, $P = 0.397$). One of 23 adult wolves died because of our trapping and handling procedures. Three of eight radio-marked pups lost their collars within 10 days (two collars slipped off, and pack mates chewed off one).

The remaining 27 instrumented wolves were relocated 1,174 times (appendix 4): 15 (54%) were followed for two months to one year, nine (32%) for one to two years, and four (14%) for more than two years for a total of 307 transmitter exposure months. We radio-tracked an average of three adult males (range 1–6), seven adult females (6–9), one male pup, and one female pup (0–3) associated with from 1 to 10 ($\bar{x} = 6$) packs each year between 1987 and 1991 (figure 5). We identified 13 packs (figure 5, page12), but four study wolves were solitary or left the area before pack affiliation was deter-

mined. One pack of three wolves abandoned their territory and became nomadic.

Noninvasive population sampling

Snow tracking—We snow-tracked wolves on 29 and 28 days during winter 1987−1988 and 1988−1989, respectively. Wolf tracks were encountered 152 times during the two winters. The exact number of wolves in a group was determined with confidence on 74 (49%) track encounters (table 2): 41% were single wolves, 35% were pairs, 19% were of three to five, and 5% ranged from six to nine wolves. There was a significant difference ($\chi^2 = 6.30$, df = 1, $P = 0.012$) in the occurrence of lone wolves and wolf packs (more than two wolves) in the winters of 1987−1988 and 1988−1989 (table 2). A possible cause for the high proportion of single wolves in winter 1987−1988 was food stress, although we collected no data on kill rates. Both the winters of 1986−1987 and 1987−1988 were relatively mild (figure 2). Ungulate prey is less vulnerable during mild winters (Mech 1970), and wolf pack cohesiveness declines when food resources are limited (Mech 1970). In contrast, we detected an increase in the number of packs during the severe winter of 1988−1989. Overall,

Table 1. Weight by age class and sex of 30 wolves captured, radio-marked, and released for study in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Age[a]	Sex	n[b]	$\bar{x}$ (kg)	SD	Range
≥1 yr	M	9	32.7	4.4	29.0–43.1
	F	13	30.8	3.4	25.0–35.5
<1 yr	M	3	17.3	7.2	10.9–25.0
	F	5	15.2	4.1	11.0–20.9

[a]Estimated age at time of capture.

[b]One adult male was not weighed.

Table 2. Frequency of wolf group sizes encountered during snow tracking in and adjacent to Voyageurs National Park, Minnesota, winter 1987–1988 and 1988–1989.

Group Size	1987–1988 Frequency	%	1988–1989 Frequency	%	Total Frequency	%
1	22	55.0	8	23.5	30	40.5
2	12	30.0	14	41.2	26	35.1
3	2	5.0	4	11.8	6	8.1
4	1	2.5	2	5.9	3	4.1
5	2	5.0	3	8.8	5	6.8
6	0	0.0	1	2.9	1	1.4
7	0	0.0	0	0.0	0	0.0
8	1	2.5	1	2.9	2	2.7
9	0	0.0	1	2.9	1	1.4
Total	40	100.0	34	100.0	74	100.0

Figure 5. History of radio contact with 31 radio-marked wolves in and adjacent to Voyageurs National Park, Minnesota. Black bars represent contact with wolves associated with packs or groups. Gray bars represent contact with wolves not associated with packs or groups or with wolves dispersing from packs or groups. Two wolves that dispersed from their original packs and joined other packs and one wolf that dispersed from a pack and joined a wandering group are represented twice.

Levels of human use of the frozen lake surfaces are less at night than in daylight and wolves may move more freely under the cover of darkness.
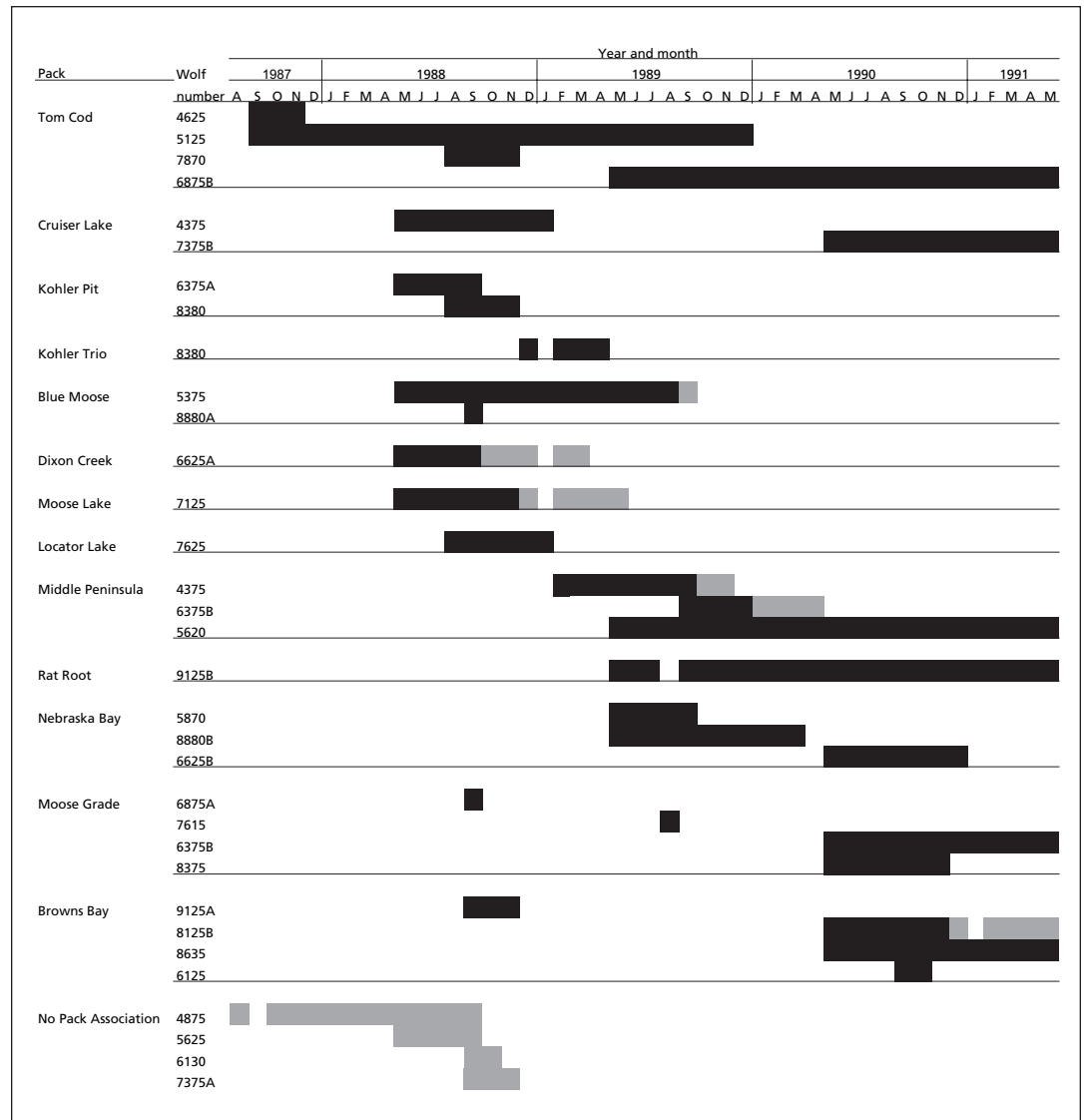
larger groups were encountered with decreasing frequency ($r = -0.81$, $P = 0.009$) (figure 6). Similar findings were presented by Mech et al. (1998:108).

The number of wolves identified as traveling together from snow tracks (table 2) does not always equal pack size because pack members often separate and rejoin (Mech et al. 1998). However, repeated snow track observations provide reliable estimates of pack size similar to multiple observations from telemetry (Stenlund 1955, Fuller et al. 1992, Wydeven et al. 1995, Berg and Benson 1998). Snow tracks were the sole data to estimate the presence and size of 5 of 6 known packs (83%) in 1987−1988 and 4 of 11 (36%) in 1988−1989 (appendix 4). We used a combination of both methods in 1988−1989. Estimates of pack size derived from snow tracks were identical to estimates derived from telemetry for all five packs where both data types were available (appendix 4). This finding supports snow

tracking as an appropriate method to determine the presence or absence of packs and to estimate pack size.

Snow tracking during winter 1987−1988 and 1988−1989 showed that wolves traversed the shorelines and crossed the frozen surfaces, especially at narrow areas, of larger lakes such as Rainy, Kabetogama, and Namakan (figure 7). However, our radiotelemetry data, collected only during daylight hours, did not detect wolves in these same areas (see Fox et al. 1999). Presumably, the tracks reflect use of these areas at night. Levels of human use of the frozen lake surfaces are less at night than in daylight and wolves may move more freely under the cover of darkness. In contrast, winter daylight movements of wolves at the largely uninhabited Isle Royale included regular travel along the island's shoreline, crossing large frozen embayments, and ranging out onto the open ice of Lake Superior (Peterson 1995). Similarly, wolves in the Boundary Waters

Figure 6. Percent of encounters with different wolf group sizes during snow tracking in and adjacent to Voyageurs National Park, Minnesota, winter 1987–1988 and 1988–1989.
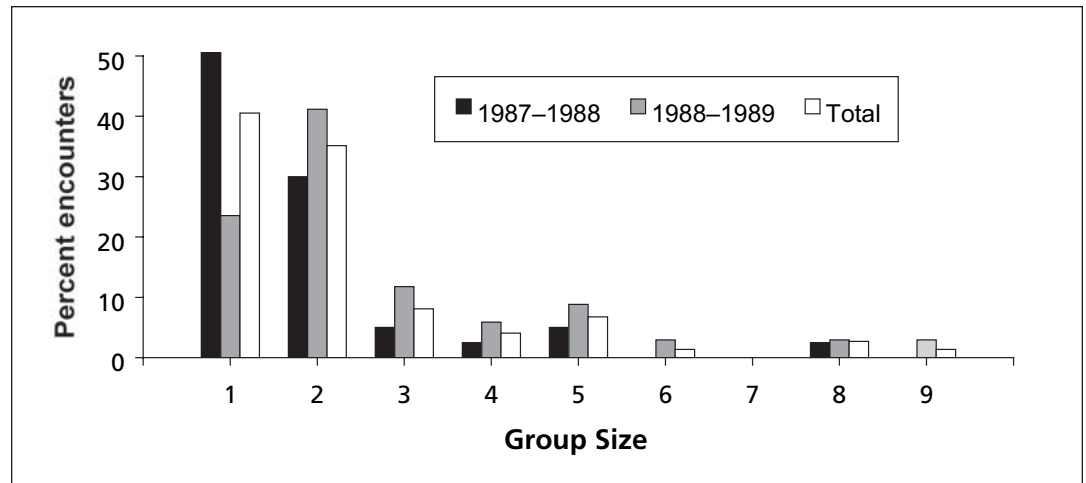
Figure 7. Location of tracks of all wolves encountered (upper left) and groups of two or more wolves encountered (upper right) in winter 1987–1988 and all wolves encountered (lower left) and groups of two or more (lower right) encountered in winter 1988–1989 in and adjacent to Voyageurs National Park, Minnesota.

a. All Tracks, 1987–1988

b. Pack Tracks, 1987–1988

c. All Tracks, 1988–1989

d. Pack Tracks, 1988–1989
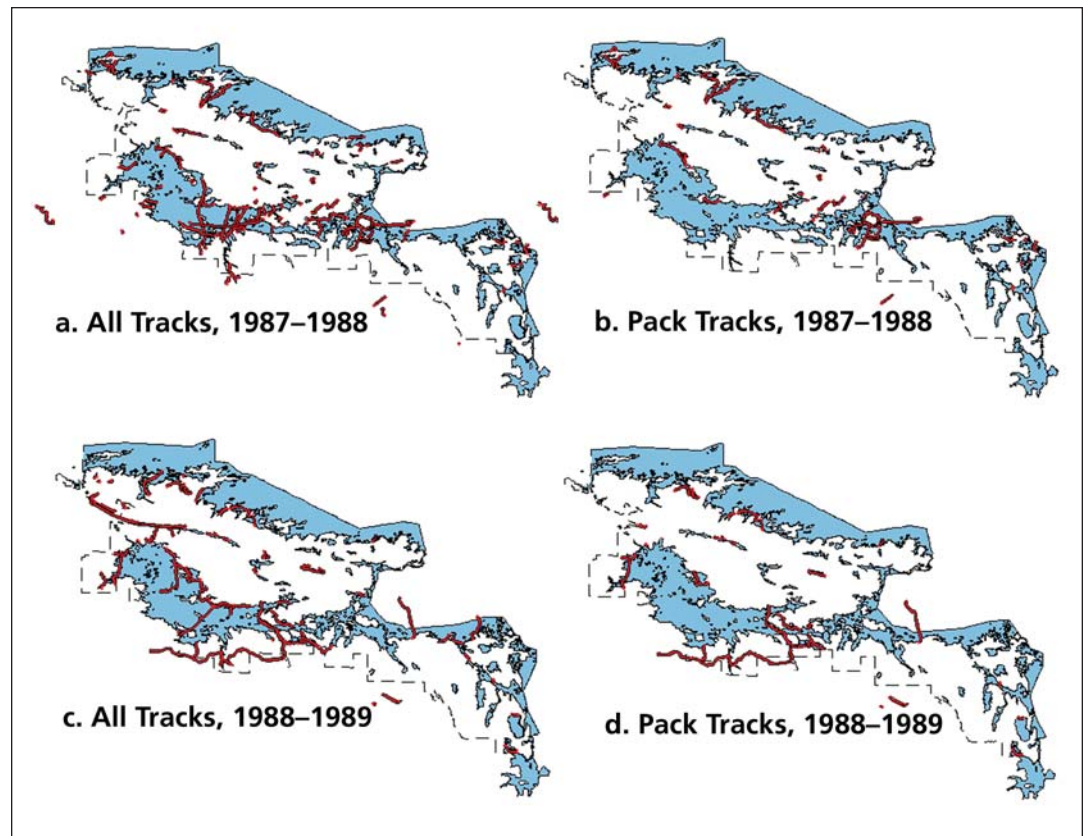
Females in estrous were identified by the presence of blood in the urine....

Canoe Area Wilderness are seen regularly in daylight hours along the shorelines and frozen surfaces of lakes (M. E. Nelson, U.S. Geological Survey [USGS], personal communication).

While snow tracking between late January and late February of 1988 and 1989, females in estrous were identified by the presence of blood in the urine in five packs. Howling surveys confirmed that three of these packs bore pups, and live capture of a pup confirmed the fourth. Insufficient data were collected to evaluate the birth rates for packs in the study area.

Howling surveys—We conducted howling surveys at 24 water-based sites throughout

VNP each July and August from 1988 through 1991 (figure 8, page 14). Adults and pup wolves responded to simulated howls in all years. Wolf packs responded to simulated howls at a high of 16.7% of howling sites in 1989 to a low of 8.3% in 1990 (table 3, page 15). The percent of responding packs that contained pups varied from 100% in 1988 and 1991 to a low of 50% in 1990. Often, the responses of packs and lone wolves were elicited at the same sample site. The greatest number ($n = 8$) of responses of single wolves was in 1991.

We evaluated the utility of our howling surveys to monitor for the presence of wolf packs by comparing howling responses at survey

Figure 8. Location of howling survey sites with an estimated perimeter of audibility of 2.5 km (upper left) and responses by wolves to simulated howling for 1988 (upper right), 1989 (lower left), and 1990 (lower right), Voyageurs National Park, Minnesota.
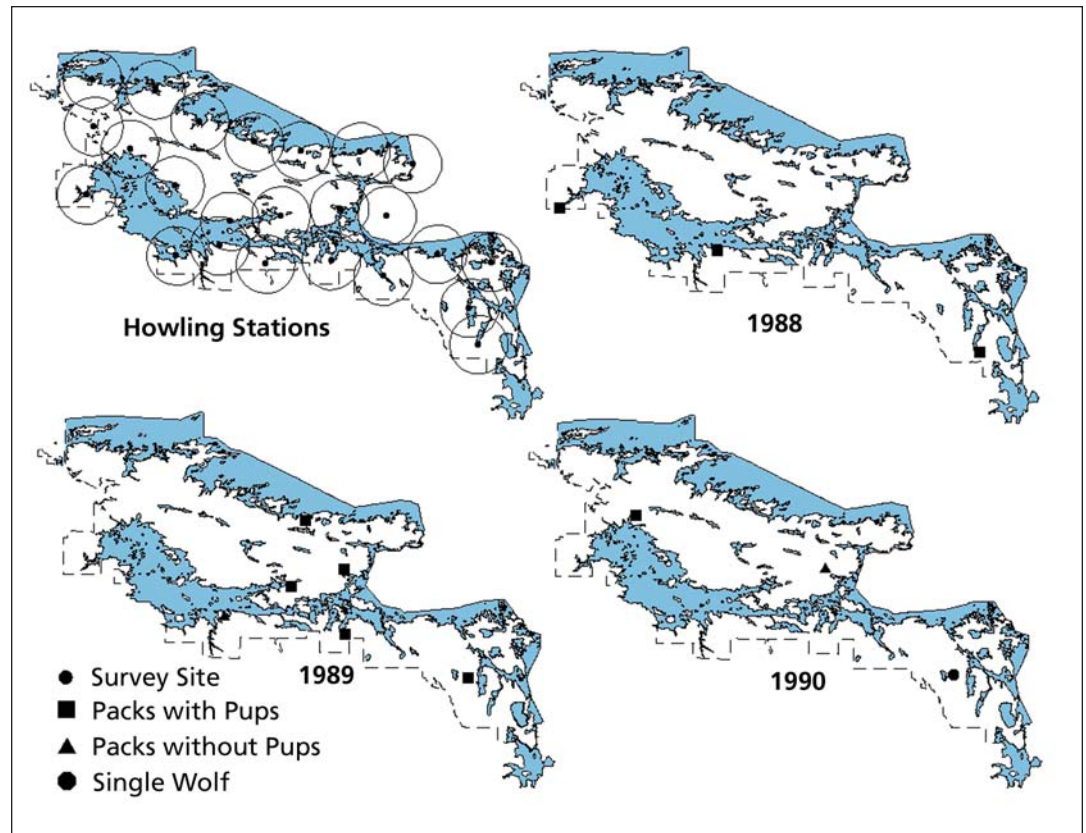
The detectability of packs that were known to exist the following winter … averaged 56% [over three years].

locations within known wolf territories. Detectability of packs known to exist the winter prior to the howling survey ranged from 40% to 67% and averaged 52% (table 4, page 16). The detectability of packs that were known to exist the following winter ranged from 33% to 83% over three years and averaged 56% (table 4). Detectability varied by pack with one pack (LLP) never being detected. Our ability to elicit responses from known packs may have been limited by the difficulty of projecting simulated howls over the entire landmass from the shoreline (figure 8). For example, our failure to elicit responses from two known packs (the LLP and CLP) in 1988 was likely because both packs were beyond the audible range of the simulated howls. Fuller and Sampson (1988) found that human observers detected 80% of simulated howls between 0.3 and 1.5 km from sampling stations and no simulated howls at more than 2.5 km from sample stations.

Limitations of howling surveys were detailed by Harrington and Mech (1982): (1) response rates vary and may be biased towards detecting larger packs, (2) the method does not indicate the number of wolves present because individual animals can seldom be distinguished during a pack response, (3) pack territories cannot be determined, and (4) response rates may be low relative to the work effort to complete the survey because coverage

of the entire survey area cannot be guaranteed and not all packs will respond. We add to this list that in VNP accessing sampling stations by boat at night poses numerous safety hazards. We reduced the possible bias of detecting larger packs by using a single stimulus, i.e., only one person howled during each trial, and we surveyed during late summer and early fall when packs are less cohesive but pups are more vocal. Others have judged elicited howling surveys as an unsatisfactory index of wolf density (Crête and Messier 1987). However, the sample stations may be used to determine the presence or absence of reproductively successful wolf packs—although with the relatively low annual response rates, it will be necessary to pool data from a number of years before any trend is detected. Cumulative effects modeling shows that pup recruitment is a critical population parameter in assessing the long-term sustainability of wolves within VNP (Cochrane 2000). In spite of the shortcomings, fall howling surveys may be one of the most effective nonintrusive means of detecting pups within the Voyageurs region wolf populations. A revised fall howling survey, perhaps land based, should be considered as a monitoring tool.

Snow tracking and howling as monitoring tools—Snow tracking was essential to estimate the number of wolves in packs containing no radio-marked animals. Estimates of pack sizes

Table 3. Results of human-elicited wolf howling surveys at 24 sites in Voyageurs National Park, Minnesota, 1988–1991.

Lake/Sample Site[b]	Sample Period[a]			
	1988	1989	1990	1991
Kabetogama				
K1	n/s	x	x	x
K2	p(w)	p(wo)	x	x
K3	x	x	x	x
K4	p(w), l(1)	x	x	x
K5	x	x	p(w), p(wo)	x
K6	x	x	x	x
K7	x	x	x	x
K8	x	p(w), l(2)	x	l(1)
Pack response (%)	28.6	25.0	12.5	0.0
Total response (%)	28.6	25.0	12.5	12.5
Namakan/Sand Point				
N1	x	x	x	p(w)
N2	x	x	x	x
N3	x	x	x	x
N4	x	x	x	x
N5	x	p(w), l(1)	l(1)	x
N6	p(w)	x	x	p(w)
N7	x	x	x	x
N8	x	x	p(wo)	x
Pack response (%)	12.5	12.5	12.5	25.0
Total response (%)	12.5	12.5	25.0	25.0
Rainy				
R1	x	x	x	l(1)
R2	x	x	x	l(2)
R3	x	x	x	x
R4	x	x	x	l(1)
R5	x	x	x	l(1)
R6	x	p(w)	x	l(2)
R7	x	x	x	x
R8	x	x	x	p(w)
Pack response (%)	0.0	12.5	0.0	12.5
Total response (%)	0.0	12.5	0.0	75.0
Total				
Sites sampled	23	24	24	24
Sites with packs (%)	13.0	16.7	8.3	12.5
Sites with responses (%)	13.0	16.7	12.5	37.5

Note: n/s = not surveyed; x = surveyed but no response; p = pack responded; (w) = with pups; (wo) = without pups; l = lone wolf responded; (#) = number of lone wolves responding from different locations.

[a]Surveys conducted between late July and early August each year (see text).

[b]For location of sampling sites see figure 8.

ing wolf abundance and movements (Mech 1966, Berg and Benson 1998, Wydeven et al. 1995). However, the accuracy of snow tracking is difficult to substantiate, and the methodology is subject to observer bias. Repeated sampling efforts are often necessary to deduce pack size, and teasing apart the presence of adjacent packs can be problematic. Furthermore, the methodology is of limited utility in determining the numbers of pups within a pack (two occurrences out of 19 track encounters with packs in our study). Nevertheless, done repeatedly by experienced observers, snow tracking provides reasonably reliable estimates of wolf numbers. Snow tracking provides insights into differences in day and night movement patterns of wolves and, in some cases, helps elucidate pack territory boundaries. In addition, we found evidence of female reproductive activity via snow tracking. Finally, snow tracking led us to wolf kill sites where we were able to obtain information on prey species age, sex, and condition, and to scats from which we obtained information on food habits.

In contrast, howling surveys verified the existence of only about 50% of the wolf packs we determined to occur within the Voyageurs region via radiotelemetry and snow tracking. Wolf abundance and pack territorial limits cannot be determined from howling surveys. Pack response rates vary with the pack's distance from simulated howls and the presence or absence of pups. Packs that include pups may respond more frequently than packs without pups because pups readily respond to simulated howls. Howling surveys may provide an index of wolf reproductive success while snow tracking may provide an index to wolf abundance.

Incidental observations—Forty-three sightings of 106 wolves (range 1 to 11 wolves) were made without the aid of radiotelemetry, and 11 occurrences of packs or single wolves were determined from unelicited howls (as opposed to those elicited during howling surveys). Of these, 17 incidental sightings and five unelicited howlings were used to support the existence and size of study packs (appendix 4). Other incidental observations provided evidence of movements of single wolves and the probable presence of unmarked packs.

Pack numbers, territories, and wolf density

Thirteen wolf packs were followed by radiotelemetry for six months to four years (figure 9, page 17). Six packs (TCP, LLP [replaced later

obtained by snow tracking were identical to those derived from telemetry in all five cases where we obtained both data types in winter 1988−1989. This finding supports snow tracking as an appropriate method to determine the presence or absence of packs and to estimate pack size (see *Pack numbers,* territories, and wolf density). Other investigators have used snow tracks as the primary means of estimat-

Table 4. Detectability of known wolf packs by human-elicited howling surveys in Voyageurs National Park, Minnesota, 1988–1991.

Pack[b]	1988 P	1988 D	1989 P	1989 D	1990 P	1990 D	1991 P	1991 D	Detection Rate by Pack (%)
Detectability of packs known to exist the winter prior to howling surveys									
Tom Cod	yes	yes	yes	no	yes	yes	yes	no	50
Locator Lake	yes	no	yes	no					0
Middle Peninsula					yes	no	yes	no	0
Cruiser Lake	yes	no	yes	yes	yes	yes	yes	yes	75
Browns Bay	yes	yes	yes	yes			yes	yes	100
Moose Grade	yes	no	yes	yes	yes	no	yes	yes	50
Nebraska Bay	yes	yes	yes	yes	yes	no	yes	no	50
Subtotal	6	3	6	4	5	2	6	3	
Detection rate (%)	50		67		40		50		
$\bar{x}$ (%)	52								
Detectability of packs known to exist the winter following howling surveys									
Tom Cod	yes	yes	yes	no	yes	yes			67
Locator Lake	yes	no							0
Middle Peninsula			yes	yes	yes	no			50
Cruiser Lake	yes	no	yes	yes	yes	yes			67
Browns Bay	yes	yes	yes	yes	yes	no			67
Moose Grade	yes	no	yes	yes	yes	no			33
Nebraska Bay	yes	yes	yes	yes	yes	no			67
Subtotal	6	3	6	5	6	2			
Detection rate (%)	50		83		33				
$\bar{x}$ (%)	56								

Note: Pack presence (P) and its territory were determined by radiotelemetry, snow tracking, and incidental observations during the winter preceding and following the howling survey. Pack detection (D) was affirmative if ≥1 howling response was heard from a pack (≥2 wolves) within its known territory.

[a]Surveys conducted between late July and early August each year (see text).

[b]See figure 9 for pack territories.

Table 5. Minimum territory size for radio-marked wolf packs where 30 or more radiotelemetry locations were obtained in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Pack Year[a]	No. of Packs	No. of Locations $\bar{x}$	No. of Locations Range	Territory Size (km²) $\bar{x}$	Territory Size (km²) Range	Pack Size $\bar{x}$	Pack Size Range
1987–1988	1	59	—	122	n/a	5	—
1988–1989	5	41	32–65	120	48–232	4.8	2–8
1989–1990	3	66	62–82	216	145–296	5	4–6
1990–1991	7	70	41–100	148	70–289	5	2–9
$\bar{x}$	4	58	30–100	152	48–296	5	2–9

[a]Pack year defined as May 1 through April 30.

by MPP], CLP, MGP, BBP, and NBP) used the park each year, and two to three of these packs occupied portions of the Kabetogama Peninsula each year (figure 9). The large lakes, notably Rainy Lake and to a lesser extent Kabetogama, Namakan, and Sand Point, appeared to be effective obstacles to movement, even when frozen, and served as boundaries to territories, as did the open water and thin ice of the narrow channel at the east end of the Kabetogama Peninsula. After May 1989, we ceased efforts to capture and instrument wolves in five packs (KPP, BMP, DCP, MLP, and RRP) that ranged primarily beyond the boundaries of VNP. However, we did continue to relocate instrumented wolves from these packs for the life of the study. One pack (KTP) dispersed from the area, and one pack (LLP) apparently dissolved after a territorial dispute (see *Dispersal events*, appendix 5). The 13 packs were relocated a mean of 58 times per wolf year (range 30–100), and mean territory size was 152 km² (range 48 km² to 296 km²) based on 16 annual pack territories ($\bar{x} = 4$
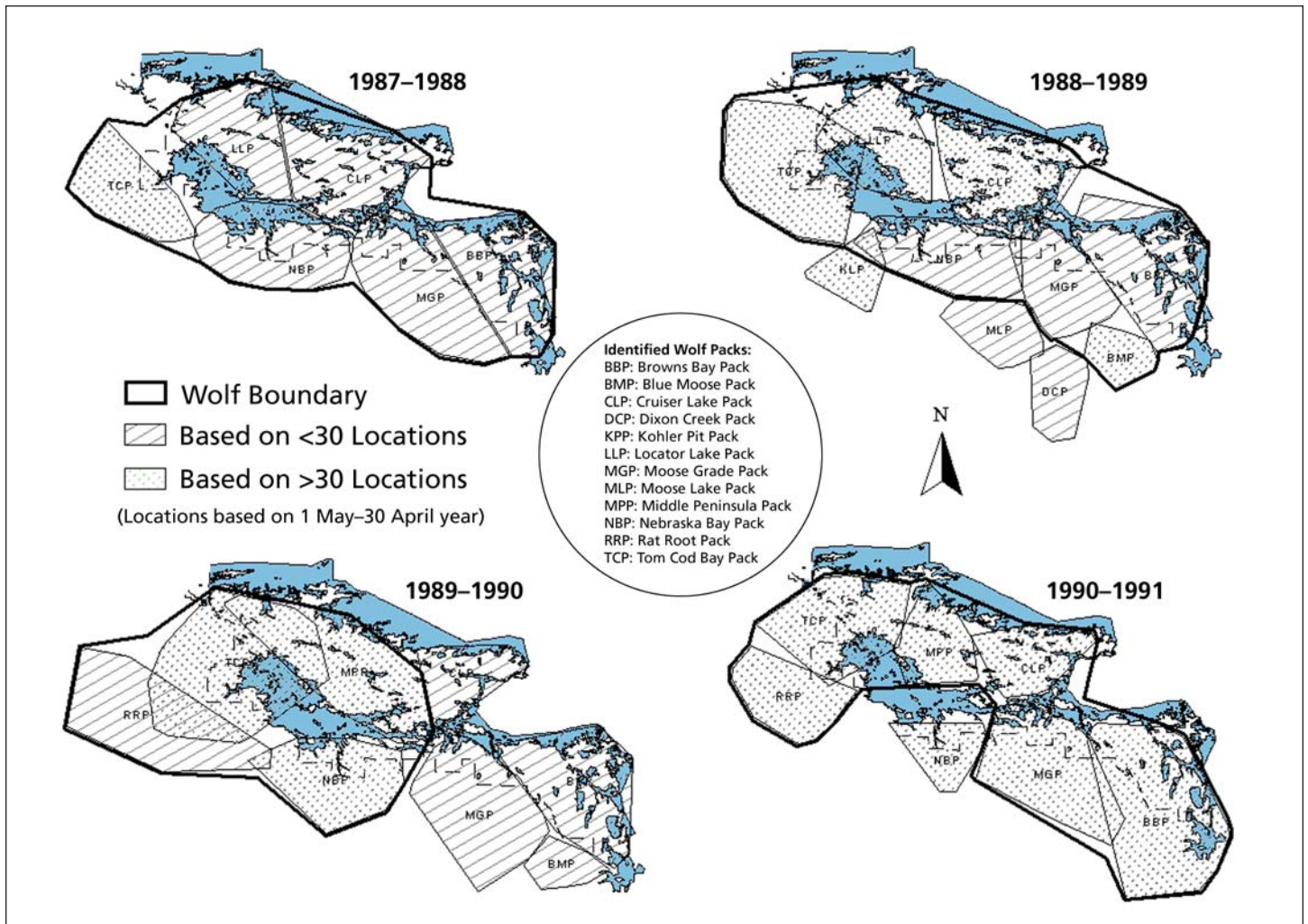
Figure 9. Locations of wolf packs within and adjacent to Voyageurs National Park, Minnesota, by year, 1987 through 1991. Three-letter abbreviations correspond with pack names in table 6. Stippled polygons indicate pack territories determined by 30 or more radiotelemetry locations. Other polygons were estimated from less than 30 radiotelemetry locations, snow tracking, howling surveys, incidental observations, terrain, and human developments. Area estimates are for areas within the bold line.

packs per year) determined by 30 or more locations (table 5). We combined our observations during winter telemetry flights with snow tracking and incidental sightings (appendix 4) to estimate the numbers of wolves in nine packs at least once during the study for a total of 23 pack years (table 6, page 18). Packs ranged in size from 2 to 11 wolves. We adjusted the number of pack wolves upward by 15% to estimate winter densities of wolves in the Voyageurs region (table 6). Territory sizes for wolves in the Voyageurs region were within the range of other wolf populations that exist on a white-tailed deer economy (table 7, page 19).

The mean mid-winter pack size was 5.5 wolves, ranging from 6.3 during 1988−1989 to 4.5 during 1989−1990 and did not differ significantly ($P > 0.05$) from those in other studies of wolves preying primarily on white-tailed deer ($n = 12$, unweighted $\bar{x} = 5.6$; table 7). Excluding newly forming packs or expanding populations (table 7), the mean pack size for Voyageurs region wolves falls at the lower range of estimated pack sizes for wolves on a white-tailed deer economy (5.3 to 8.0), but the

means did not differ significantly (two-tailed t-test; $P > 0.05$).

Pack sizes were smallest in the winter of 1989−1990. However, our estimate of mean pack size that winter is likely low; we did no snow tracking that winter, and our efforts the previous two trapping periods to capture and radio-mark wolves in three of the largest packs within the park were unsuccessful.

Four of 31 (13%) captured wolves were lone wolves (figure 5). In three of the four years, we detected only one solitary and non-territorial wolf. A subadult female wolf trapped in 1987 in the territory of the CLP was radio-located 56 times and observed 14 times from August 1987 to September 1988. She was solitary on all occasions and ranged over an area larger than 6,000 km². This wolf was classified as solitary (Fuller 1989). In 1988−1989, two single wolves and a trio of wolves (KTP) were non-territorial. Other studies suggest that the number of single, non-resident wolves varies from 2 to 29% of the population (Pimlott et al. 1969; Mech 1966, 1973; Fuller and Keith 1980;

Table 6. Minimum estimates of pack size (E) and wolf density for nine packs, as estimated from track counts (T), incidental observations (I), and direct counts with the aid of radiotelemetry (R), in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

	Census Period[a]															
	1987–1988				1988–1989				1989–1990				1990–1991			
Pack	T	I	R	E	T	I	R	E	T	I	R	E	T	I	R	E
Tom Cod (TCP)	5	5	5	5	5		5	5			5	5			2	2
Locator Lake (LLP)	4	3		3	7		7	7								
Middle Peninsula (MPP)											4	4			9	9
Cruiser Lake (CLP)	8			8	8	8	8	8							6	6
Browns Bay (BBP)	7			7	9			9							9	9
Moose Grade (MGP)	9	11		11	8	8		8							3	3
Blue Moose (BMP)					2	2	2									
Nebraska Bay (NBP)	2			2	5			5			6	6				
Rat Root (RRP)											3	3			2	2
Total packs enumerated				6				7				4				6
$\bar{x}$ pack size				6.0				6.3				4.5				5.2
Range of pack sizes				2–11				2–9				3–6				2–9
Estimated no. pack wolves				36				44				18				31
Estimated no. single wolves[b]				6				8				3				5
Total wolves				42				52				21				36
Survey area (km²)[c]				1,190				1,242				866				1, 150
Density (wolves/1,000 km²)				36				42				24				32

Note: Final estimates (E) take into account the reliability, frequency, and type of observations.
[a]Census period defined as November through February of each winter.
[b]Calculated as 15% of the total population (Fuller et al. 1992, Berg and Benson 1998).

Peterson and Page 1988). Fuller (1989) noted that estimates of non-territorial wolves from radiotelemetry data alone could be biased because non-territorial wolves are more difficult to observe and because researchers tend to focus trapping efforts within known pack territories. Because of this, Fuller (1989) used 16%, the midpoint in the range of estimates from the literature, to estimate the number of non-resident single or paired wolves. Subsequently, Fuller et al. (1992) and Berg and Benson (1998) used 15% single non-resident wolves to calculate the total wolf numbers in Minnesota. Given our small sample of captured wolves and the potential for observability and sampling bias, we assumed 15% of wolves in the study area were solitary and non-territorial (table 6).

Wolf densities averaged 33/1,000 km² over the four years and ranged from a high of 42/1,000 km² in 1988−1989 to 24/1,000 km² in 1989−1990 (table 6). Mean wolf density in the Voyageurs region did not differ significantly ($P > 0.05$) from other locations either when including ($\bar{x}$ = 30 wolves/1,000 km²) or excluding ($\bar{x}$ = 33 wolves/1,000 km²) newly forming packs or expanding wolf populations (table 8, page 20). The estimated low density of wolves for the winter of 1989−1990 was likely due to a lack of information on three large packs during that winter (see earlier discussion).

Dispersal

Eight (29%) of 20 instrumented adult wolves with known pack affiliation dispersed and one dispersed twice for a total of nine dispersal events (table 9, page 20). These nine included four wolves dispersing beyond the study area, two disappearing, one being killed by wolves after dispersing, and two joining or forming neighboring packs. Two incidents of dispersal involved three to five wolves in "pack-splitting" events (Mech et al. 1998) (see following discussion). Animals less than two years old dispersed in December and January while those more than two years old dispersed in October, December, and March. The timing of dispersal from late fall through early spring is consistent with timing of dispersal in north-central Minnesota (Fuller 1989) and elsewhere in North America (Messier 1985). The mean dispersal distance was 33 km (0.9−83.7) (table 9). Both instances of dispersal where we determined that a pack was joined or formed were within 2 km of VNP. However, three solitary wolves dispersed more than 50 km. All except one dispersal were to the south or west, suggesting that even when the area's large lakes were frozen in winter, they were partial barriers to dispersal. The mean age of dispersing wolves was four years (1.5−7.5 years). Three of the dispersing wolves were yearlings while three additional dispersing wolves were more

than seven years old (table 9). The mean age of dispersing wolves excluding the three oldest animals was 2.3 years (table 9). The proportion of wolves more than two years old and the incidence of wolves more than seven years old dispersing from the Voyageurs region is exceptional. More than 75% of dispersing wolves in SNF were pups or one-year-olds (Gese and Mech 1991). The oldest known aged dispersing wolf was five years (Gese and Mech 1991). Eleven of 18 dispersing wolves on the Kenai Peninsula, Alaska, were yearlings or two-year-olds (Peterson et al. 1984). The mean annual dispersal rate in the Voyageurs region from 1987 through 1991 of 0.37 (table 10, page 21) is one of the highest reported (Mech et al. 1998, Fuller 1989). We cannot explain the high rate of dispersal in the Voyageurs region.

Dispersing wolves in the Voyageurs region made an average minimum of 2.1 pre-dispersal movements (range 0−5) (table 11, page 21). Similarly, Messier (1985) reported an average minimum of 2.1 pre-dispersal movements, and Fuller (1989) reported wolves made from one to six pre-dispersal movements (mean minimum of 0.9). The mean distances between consecutive locations within new territories were greater than in the original territory ($P < 0.008$, t-test) indicating that wolves occupying new areas expended greater effort (travel distance), presumably to explore, mark, and defend their new territory.

The observed incidents of pack splitting (Mech et al. 1998) or of a dwindling pack dispersing from its home territory deserve additional discussion.

Cruiser Lake Pack split—In fall and early winter 1988, radio tracking of instrumented wolves of the LLP (seven wolves) and CLP (eight wolves) packs indicated non-overlapping territories (figure 9). On 20 January 1989 all eight members of the CLP were located in the LLP territory, and the single radio-marked LLP wolf and an unmarked wolf had been killed by wolves (appendix 5). Visual inspection of the site where the LLP pack members were killed confirmed that the packs had encountered one another. Because all eight CLP wolves were located alive after this date, we believe the dead unmarked wolf was also from the LLP. Thus, two of the seven LLP members were likely killed. We were unable to determine the size or fate of the LLP after the death of the instrumented wolf. However, the instrumented CLP wolf and at least four others occupied the LLP area after this dispute.

The previously instrumented CLP wolf along with two newly radio-marked wolves and one

Table 7. Mean territory size and pack size for wolf populations on a white-tailed deer economy.

Location	No. of Packs	Territory Size (km²)		Pack Size		Reference
		$\overline{x}$	Range	$\overline{x}$	Range	
Northeast Minnesota	5	110	52–145	8.0	5–10	Van Ballenberghe et al. 1975
East-central Ontario	1	224	—	8.0	—	Kolenosky 1972
Northeast Minnesota	11	243	—	7.0	3–11	Mech 1973
East-central Ontario	4	175	—	7.0	—	Pimlott et al. 1969
North-central Minnesota	5	215	161–272	6.6	5–8	Berg and Kuehn 1980, 1982
North-central Minnesota	33	116	51–223	5.7	2–12	Fuller 1989
Southern Quebec	21	199	85–325	5.6	—	Potvin 1988
Northern Minnesota	16	152	48–296	5.5		This study
Northeast Minnesota	9	183	59–323	5.3	4–7	Mech 1986b
Northwest Minnesota[a]	22	260	77–664	4.6	2–9	Fritts and Mech 1981
Northern Wisconsin[a]	72	137	47–287	3.9	—	Wydevan et al. 1995
North-central Minnesota[a]	3	87	40–135	2.7	2–4	Fuller 1989
Wisconsin-Minnesota border[a]	5	196	67–310	2.6	2–4	R. Thiel, *in* Fuller et al. 1992
$\overline{x}$ with[b]	$n = 12$[c]	179		5.6		
Median with[b]	$n = 12$[c]	190		5.7		
$\overline{x}$ without[b]	$n = 8$[c]	183		6.7		
Median without[b]	$n = 8$[c]	191		6.8		

Note: Adapted from Fuller (1989) and Fuller et al. (1992).

[a]Newly forming packs or expanding population.

[b]With or without studies of newly forming packs or expanding populations.

[c]Number of studies excluding this study.

Table 8. Density of wolves that exist primarily on a white-tailed deer economy.

Location	Wolf Density/1,000 km² of Habitat	Reference
Northwest Minnesota[a]	17	Fritts and Mech 1981
Northern Wisconsin[a]	19	Wydevan et al. 1995
Northeast Minnesota	23	Stenlund 1955
Northeast Minnesota	25	Mech 1986b, Nelson and Mech 1986a,b, MDNR files
North-central Minnesota	28	Berg and Kuehn 1980
Southern Quebec	28	Potvin 1988
Northern Minnesota	33	This study
East-central Ontario	36	Pimlott et al. 1969, Kolenosky 1972
East-central Ontario	38	Pimlott et al. 1969
North-central Minnesota	39	Fuller 1989
Northeast Minnesota	40	Mech et al. 1971, Peek et al. 1976, Nelson and Mech 1986a
Northeast Minnesota	42	Van Ballenberghe et al. 1975
$\bar{x}$ with[b]	30	
Median with[b]	28	
$\bar{x}$ without[b]	33	
Median without[b]	36	

Note: After Fuller 1989.
[a]Newly forming packs or expanding population.
[b]With or without studies of newly forming packs or expanding populations.

Table 9. Sex, pack affiliations, age, and dates of nine dispersals for eight different wolves radio-marked in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Wolf Number	Sex	Pack Affiliations: Original/After Dispersal	Dispersal Age (yrs)	Date	Location and Status	Distance (km)	Direction	In/Out of Study Area
4375	M	Cruiser Lake Pack (CLP)/Middle Peninsula Pack (MPP)	1.5	01/29/89	Split from CLP with 4 others to form MPP after taking over LLP territory. Dispersed again later (see below).	0.9	west	in
4375	M	Middle Peninsula Pack (MPP)	2.5	10/26/89	Likely killed by deer hunter Nov. 1989.	17.0	west	in
5375	F	Blue Moose Pack (BMP)	3.5	10/12/89	Likely killed by deer hunter Nov. 1989.	23.4	west	in
7125	F	Moose Lake Pack (MLP)	7.5	12/03/88	Dispersed to Nett Lake area; found dead by hunter in Fall 1992 near Big Fork.	83.7	south-west	out
8380	M	Kohler Trio Pack (KTP)	7.5	12/10/88	Began to settle near Black Bay with 2 other wolves then killed by other wolves (likely MPP) in April 1989.	26.3	north	in
6375B	F	Middle Peninsula Pack (MPP)/ Moose Grade Pack (MGP)	1.5	01/12/89	Joined/formed MGP, still transmitting when study ended in April 1991.	1.8	south-east	in
6625A	M	Dixon Creek Pack (DCP)	7.5	10/09/88	Dispersed to Chub Lake area; illegally snared March 1989.	24.5	south	out
8125B	F	Browns Bay Pack (BBP)	1.5	12/01/90	Moved near Vermilion Lake, then returned near home territory ($n = 1$ location), then missing.	60.8	south	out
8880B	F	Nebraska Bay Pack (NBP)	3.0	03/31/90	Remains found by hunter in Nov. 1990 west of Cook.	59.5	south	out
Totals 9		$\bar{x}$	4.0		$\bar{x}$	33.1		
M 4		SD	2.7		SD	28.5		
F 5		$\bar{x}$ excluding 3 older wolves	2.3		$\bar{x}$ without 2 dispersing to adjacent packs	42.2		

Table 10. Estimated annual dispersal rates for wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Year	Wolves Collared	Wolf-Years[a]	Total Dispersers No. Wolves	Total Dispersers Rate	Left Study Area No. Wolves	Left Study Area Rate
1987–1988	3	1.34	0	0.00	0	0.00
1988–1989	15	7.35	5	0.68	2	0.27
1989–1990	10	7.30	3	0.41	1	0.14
1990–1991	10	8.14	1	0.12	1	0.12
Total		24.13	9	0.37	4	0.17

[a]A wolf-year is 1 wolf (>5 months old) radio-tracked for 12 months.

Table 11. Mean straight-line distance between consecutive locations and number of pre-dispersal movements for dispersing wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Wolf Number	Pre-dispersal Mean Distance Between Locations	Pre-dispersal Total Locations	Pre-dispersal No. Extra-territorial Locations	Post-dispersal Mean Distance Between Locations	Post-dispersal Total Locations
4375[a]	4.97	40	1	8.10	37
4375	8.10	37	3	11.03	2
5375	3.26	63	0	14.46	4
7125	5.28	32	4	15.22	11
8380	4.70	12	2	9.86	11
6375B[a]	8.08	16	5	7.92	8
6625A	4.88	26	2	3.89	6
8125B	6.15	41	2	21.63	8
8880B	5.00	45	0		
$\bar{x}$	5.60	35	2.1	11.51	11
SD	1.60	16	1.7	5.48	11

[a]Dispersed to occupy a nearby pack territory.

Modeling highlights the importance of adjacent wolf populations in maintaining a viable wolf population within VNP.

unmarked adult wolf (four total) continued to occupy the original LLP territory during winter 1989–1990 (figure 9). This group was subsequently named the Middle Peninsula Pack (MPP). Responses to simulated howls (see *Howling surveys,* tables 3 and 4) indicate the MPP included pups during spring 1989 and that an unmarked pack within the original CLP territory also had pups. From these observations, we speculate that the CLP split during winter 1988–1989 with five members taking over the LLP territory and forming the MPP and that three other CLP members remained in the eastern portion of the original CLP territory. Indeed, in the spring of 1990 we captured and radio-marked an adult male wolf that, with five other wolves, occupied a portion of the original CLP territory (figure 9).

Kohler Pit Pack split—The second case involved the Kohler Pit Pack (KPP), which contained more than five wolves (two adults and more than three pups) in summer 1989 (appendix 5). By fall, one pup had been killed and

the alpha female injured in separate vehicle collisions. The injured alpha female survived, but we lost contact with her in early October when other pack members chewed off her collar. In late November 1989, an instrumented adult male wolf left the pack with at least two other wolves. This group of more than three wolves, designated the Kohler Trio Pack (KTP), roamed northwest into Canada more than 16 km from the original pack territory. This wandering pack then returned south and began localizing in the Black Bay area. However, the single instrumented wolf was killed by other wolves in early April 1990 before we could determine whether the pack had established a territory.

We may have detected a wolf immigrating into the study area to form or join the Rat Root Pack (RRP) in 1989–1990. A newly instrumented wolf made erratic movements ($n = 12$) before localizing in the RRP territory (figure 9) with two other wolves in 1989–1990 and with a single wolf in 1990–1991 (table 9). Detection of wolves immigrating into a study area was difficult due to the lack of capture effort beyond the study area boundaries. Thus, other immigration may have been undetected. Cumulative effects modeling suggested that immigration was important in determining whether wolves in the Voyageurs region will decline to low numbers or go to extinction within the next 100 years (Cochrane 2000). Current rates of non-territorial wolves passing through more than one wolf pack territory in the Voyageurs region are estimated at 50/year (L. D. Mech, USGS, personal communication in Cochrane 2000). This rate of immigration is sufficient for predicted long-term persistence of wolves in the Voyageurs region (Cochrane 2000). The modeling highlights the importance of adjacent wolf populations in maintaining a viable wolf population within VNP.

Timing and causes of mortality

We recovered 12 radio collars transmitting mortality signals, and two instrumented wolves disappeared within the study area. An additional two instrumented wolves classified as dispersers were found dead beyond the boundaries of our study area more than one year after we lost radio contact and are not considered further. Study animals that died ranged from 0.5 to 8 years of age. Mortalities occurred between September and May for all years combined (figure 10, page 22). Six instrumented wolves died of natural causes: four from intraspecific strife and two from starvation (table 12, page 22). The four mortalities

Table 12. Cause, residency, and location of death for known deaths of 14 radio-marked wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Cause	Total Mortalities	Status Within Population[a]		Location of Death[b]	
		Resident	Non-resident	In Park	Out of Park
Gunshot, by deer hunter	1	1	0	0	1
Gunshot, other than deer hunter	1	1	0	0	1
Trapped or snared[c]	2	0	1	0	2
Human, method unknown	2	1	1	0	2
Intraspecific strife	4	3	1	2	2
Starvation	2	2	0	2	0
Presumed human cause[d]	2	2	0	0	2
Total	14	10	3	4	10

Note: One study-related mortality is excluded.

[a]Considered resident if within 5 km of its territory and nonresident if beyond. Residency unknown for 1 wolf.

[b]Considers the actual location where death occurred in relation to park boundaries.

[c]Residency status unknown for 1 wolf in this category.

[d]These met Fuller's (1989) criteria to be assumed killed by humans during the Minnesota deer rifle season or land trapping season.
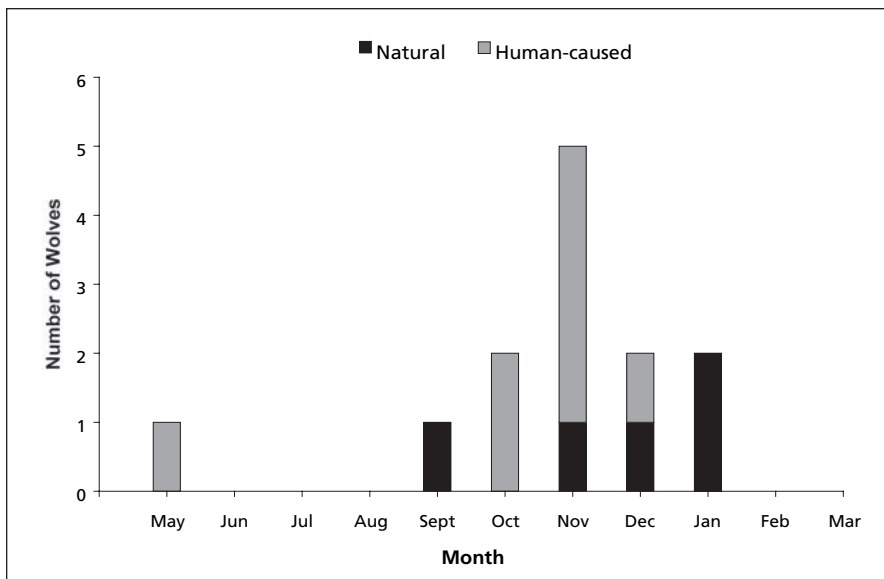
Figure 10. Number of mortalities by month of instrumented wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

within VNP's boundaries were attributed to natural causes (table 12). By contrast, six of eight confirmed mortalities outside of VNP's boundaries were human induced while two were from natural causes (table 13). Six human-induced mortalities beyond the boundaries of VNP included two killed by gunshot, two trapped or snared, and two by unknown cause yet human involvement was certain, i.e., the radio collars were recovered from a river bottom with collar belting cut with a knife and at a garbage dumpster site, respectively. An additional two instrumented wolves disappeared during or immediately prior to the Minnesota deer rifle hunting season. Both had been followed consistently by telemetry for more than one year and were adult members of territorial packs. We were unable to locate either of these wolves by telemetry again. We feel justified in presuming the disappearance of both

wolves was the result of mortalities caused by deer hunters (Fuller 1989). However, to be conservative, the fates of these two wolves were classified as unknown in our analysis of survival with program MARK (see *Survival rates*).

The same general pattern of mortality was evident for 10 non-radio-marked wolves found within 10 km of the territories of instrumented wolves (table 13). Two non-radio-marked wolves found dead within VNP died of natural causes (one pup died from starvation and one adult from intraspecific strife) and eight found beyond VNP were attributed to human-induced mortality. Notably, 3 of the 10 non-radio-marked wolves were killed by vehicle collisions whereas none of our instrumented wolves was killed by vehicles. However, we did document an instrumented wolf being struck and injured by a vehicle, and one of her non-radio-marked pups was killed in a separate automobile accident. We suggest that the higher number of automobile-induced mortalities among non-radio-marked wolves is attributable to the greater probability of locating carcasses along roadways. Conversely, most of our instrumented wolves occupied lightly roaded areas within a national park and national forest.

The high proportion of illegally killed wolves in our study (43% of deaths) is consistent with findings from other studies in Minnesota. Fuller (1989) found that in north-central Minnesota, 80% of wolf mortality was human-caused. Further, he found that 26% of all wolf mortality was attributable to shootings by deer hunters during northern Minnesota's 16-day

Table 13. Cause and location of death for 10 unmarked wolves found less than 10 km from study wolf pack territories in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Cause	Total Mortalities	Location of Death[a]		Relationship to Park Wolf Population
		In Park	Out of Park	
Accidental vehicle collision[b]	3	0	3	Includes 1 pup from KPP and 2 adults of unknown pack affiliation.
Illegally shot[c]	3	0	3	Pack associations and affiliation with park wolves unknown.
Illegally trapped	2	0	2	One adult known to be member of TCP, other unknown.
Intraspecific strife	1	1	0	Pup, likely a member of NBP.
Starvation	1	1	0	Adult, likely a member of LLP and died in CLP territory.
Total	10	2	8	

[a]Considers the actual location where death occurred in relation to park boundaries.

[b]Another uncollared wolf was observed hit by a vehicle and presumed killed, although a follow-up search (<24 hr) revealed no carcass.

[c]One shot from the air in Ontario <2 km from the international border.

The high proportion of illegally killed wolves in our study (43% of deaths) is consistent with findings from other studies in Minnesota.

rifle season in November and an additional 27% were shot, snared, or killed by vehicles during other times of the year. These findings are consistent with a survey of Minnesotan's attitudes toward wolves that found that 30% of white-tailed deer hunters would shoot any wolf during the northern Minnesota deer season in November (Kellert 1986). This represents 5,000–6,000 hunters in wildlife management units adjacent to VNP (J. Schneeweis, Minnesota Department of Natural Resources, personal communication). Moreover, 17% of trappers in northern Minnesota admitted to capturing or killing wolves (Kellert 1986). The lower percentage of human-induced mortalities in our study relative to Fuller (1989) likely reflects the considerable portion of our study area within the boundaries of VNP that is closed to hunting and trapping.

Survival rates

Of the 14 mortalities identified, only those with fates confirmed as mortalities via radio-telemetry and subsequent physical evidence ($n = 12$) were so classified in our survival analysis. Thus, the two instrumented wolves that disappeared during Minnesota deer rifle season were classified as missing rather than mortalities for the purposes of this survival analysis. While categorizing the latter two as "presumed killed by hunters" permits comparisons between this and other studies in Minnesota (Fuller 1989), classification as "missing" is more appropriate for an analysis of survival rates with a Known Fates model.

Known Fates survival models were particularly suited for analysis of these radiotelemetry data because sampling occasions documented both live and dead relocations. These procedures provided maximum likelihood estimates

of survival and a rigorous means for model comparison (Lebreton et al. 1992). Differences in survival models were assessed via Akaike's Information Criterion corrected for small sample sizes (AIC_c) and Likelihood Ratio (LR) tests (Burnham and Anderson 1998). All information criteria are constructed as $-2 * (\log - \text{likelihood}) + (\text{an adjustment})$. The adjustment for AIC is $2 * p$ where p = the number of parameters included in the error variance). The model with the lowest value for the information criterion is selected as the best supported model. Differences in information criterion values of ≥ 2 are generally considered to indicate that models are statistically distinguishable (Sakamoto et al. 1986). Additionally, program MARK provides AIC weights that permit objectively comparing each model relative to other models run in a suite from the same data set. An LR test provides p-values indicating whether addition of a term to a base model significantly improves fit. Because of low sample sizes when testing for differences in survival among groups of wolves, we considered p-values significant when less than <0.10.

Survival by age—We developed an overall nine-month survival model for 30 instrumented wolves meeting Known Fates criteria. The probability of a wolf surviving nine months was 0.67 for this constant-survival model {S(.)} (table 14, page 24). We then tested for differences in nine-month survival between pups and adults. Adults had a nine-month survival rate of 0.73, 1.9 times higher than pups. AIC_c values showed a model allowing survival to vary by age {S(age)} to be more parsimonious than {S(.)} (table 14). AIC weights suggested that the age-varying model was 1.3 times as well supported as the constant-survival model. However, an LR test indicated that addition of

Table 14. Effects of age and time of year on Known Fates survival estimates from 30 radio-marked gray wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Model	AIC_c	AIC_c Weight	Likelihood Ratio Test. Model Versus S(.)	9-month Survival Estimate	95% Confidence Interval	Number of Wolves[a]
S(.)	74.1	0.13863	n/a	0.667	0.501–0.799	30
S(age)	73.5	0.18462	$\chi^2 = 2.66, P = 0.103$	0.394 pups 0.729 adults	0.126–0.747 0.545–0.858	8 23
S(season)	70.9	0.67675	$\chi^2 = 7.39, P = 0.025$	0.624	0.445–0.774	30

Note: Survival estimates based on 9-month period from August–April.

[a]Total number of wolves <pups + adults because 1 wolf was both a pup and an adult during the study.

Table 15. Effects of sex and time of year on Known Fates survival estimates from 23 radio-marked adult gray wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Model	AIC_c	AIC_c Weight	Likelihood Ratio Test. Model Versus S(.)	12-month Survival Estimate	95% Confidence Interval	Number of Wolves
S(.)	59.8	0.01403	n/a	0.745	0.568–0.867	23
S(sex)	54.5	0.20590	$\chi^2 = 7.45, P = 0.006$	0.456 males 0.903 females	0.212–0.729 0.683–0.975	9 14
S(season)	51.8	0.78007	$\chi^2 = 14.37, P = 0.002$	0.694	0.495–0.839	23

Note: Survival estimates based on 12-month period from May–April.

> *There was evidence that adult survival differed based on territory location.*

an age term to the constant-survival model did not significantly improve fit (table 14). Thus, we found weak evidence that survival was different between ages possibly because the LR test result is influenced by our relatively small sample sizes, giving little power to identify differences in survival between adults and pups.

Survival by sex—We first developed an overall 12-month survival model for all 23 adults. The probability of an adult surviving 12 months was 0.75 {S(.)} (table 15). Next, we tested for differences in 12-month adult survival between males and females. For this sample, females had a 12-month survival rate of 0.90, two times higher than males. AIC_c values showed a model allowing survival to vary by sex {S(sex)} to be more parsimonious than {S(.)} (table 15). AIC weights suggested that the sex-varying model was 14.7 times as well supported as the constant-survival model. An LR test indicated that addition of a sex term to the constant-survival model improved fit (table 15). Thus, there was evidence that adult female survival was higher than that of adult males.

Survival by territory location—We began with the overall 12-month survival model {S(.)} for all 23 adults, showing adult survival at 0.75 (table 16), and tested for differences in 12-month adult survival among territory locations. Wolves with territories within VNP had a calculated survival rate of 1.0 and those

with territories straddling the boundaries of VNP had the lowest survival rate (table 16). The calculated survival rate of 1.0 for adult wolves with territories exclusively within the park boundaries reflects that no radio-collared wolves in this category died during the study. Those wolves with territories beyond the boundaries of VNP were intermediate in survival rate. AIC_c values showed a model allowing survival to vary by territory location {S(territory)} to be slightly more parsimonious than {S(.)} (table 16). AIC weights suggested that the territory location-varying model was two times as well supported as the constant-survival model. An LR test also indicated that addition of a territory location term to the constant-survival model marginally improved fit (table 16). Thus, there was evidence that adult survival differed based on territory location.

Survival by time of year—To assess the effects that time of year had on survival of pup and adult wolves combined, we first tested to see if nine-month survival varied by biological season for all wolves. Mean seasonal survival estimates were 0.97, 0.82, and 0.78 for a two-month rendezvous period, a two-month winter pre-iceup period, and a five-month winter post-iceup period, respectively. Monthly survival rates within the three seasons were 0.99, 0.91, and 0.95, respectively. AIC_c values showed {S(.)} to be less parsimonious than a model allowing survival to vary by season

Table 16. Effects of territory location and time of year on Known Fates survival estimates from 23 radio-marked adult gray wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Model	AIC_c	AIC_c Weight	Likelihood Ratio Test. Model Versus S(.)	12-month Survival Estimate	95% Confidence Interval	Number of Wolves[a]
S(.)	59.8	0.01708	n/a	0.745	0.568–0.867	23
S(territory)	58.5	0.03372	$X^2 = 5.55$, $P = 0.063$	1.000 in / 0.614 border / 0.873 out	1.000–1.000 / 0.384–0.802 / 0.458–0.982	4 / 16 / 7
S(season)	51.8	0.94920	$X^2 = 14.37$, $P = 0.002$	0.694	0.495–0.839	23

Note: Survival estimates based on a 12-month period from May–April.

[a]Total number of wolves < in + border + out because 4 wolves had range locations that changed during the study.

The lowest survival rates occurred in the two-month pre-iceup period, which coincides with the Minnesota deer rifle-hunting season....

Season had the greatest influence on overall wolf survival. Season and sex had the greatest influence on adult wolf survival.

{S(season)} (table 16). AIC weights suggested that the season-varying model was 4.9 times as well supported as the constant-survival model. An LR test indicated that addition of a season term to the constant-survival model improved fit (table 16). Thus, there was evidence that pup and adult survival varied among seasons, and that the lowest survival rates occurred in the two-month pre-iceup period, which coincides with the Minnesota deer rifle-hunting season.

To assess the effects of time on survival of wolves more than one year old only, we tested to see if 12-month survival varied by biological season. In each suite of models, AIC_c values showed {S(.)} to be less parsimonious than {S(season)} (tables 14−16). AIC weights suggested that a season-varying model was 55.6 times as well supported as a constant-survival model. An LR test indicated that addition of a season term to the constant-survival model improved fit (tables 14−16). Mean seasonal adult survival estimates were 1.000, 1.000, 0.86, and 0.81 for pup-rearing, rendezvous, winter pre-iceup, and winter post-iceup periods, respectively. This converted to monthly survival estimates of 1.000, 1.000, 0.93, and 0.96 within the respective seasons. Thus, there was strong evidence that survival of wolves more than one year old differed among seasons and evidence that survival was lowest in the two-month pre-iceup period.

Survival summary—The order in which models best explained survival for all wolves including pups, based on AIC_c values, was (1) season, (2) age, and (3) constant survival. The order in which models best explained survival for adult wolves, based on AIC_c values, was (1) season, (2) sex, (3) territory location, and (4) constant survival. Season had the greatest influence on overall wolf survival. Season and sex had the greatest influence on adult wolf survival.

The findings from our analysis with program MARK are largely consistent with a preliminary survival analysis (Gogan et al. 1997b) undertaken with Kaplan-Meier survival estimates and log rank tests for differences between groups of wolves (Pollock et al. 1989). However, the preliminary analysis indicated that survival was lowest for wolves occupying territories beyond the park boundaries whereas this latter analysis shows survival to be lowest in wolves occupying territories that overlap the park boundaries. The preliminary analysis found that wolves occupying territories overlapping the park boundaries were intermediate in survival between those occupying territories exclusively within the VNP boundaries (highest survival) or exclusively beyond VNP boundaries (lowest) (Gogan et al. 1997b). The following differences in classification of causes of mortality among instrumented wolves (as a result of more detailed evaluation of available data under more rigorous criteria) contributed to differences in the survival estimates from the Kaplan-Meier and program MARK analyses include (1) two wolves initially presumed to have been killed by hunters at the onset of the Minnesota deer rifle-hunting season but whose collars were never found were reclassified as unknown fate, (2) a wolf pup identified as hunter-killed in the Kaplan-Meier analysis was reclassified as having lost its collar, (3) a second wolf pup was reclassified from a research-induced mortality to a natural mortality due to starvation, and (4) an adult wolf initially classified as shot was reclassified as being killed by wolves. Furthermore, the territorial boundaries of instrumented wolves utilized for the analysis with program MARK were re-evaluated through a more complete analysis of our radiotelemetry data. The analysis presented herein is more complete and accurate than the preliminary analysis (Gogan et al. 1997b) and represents our final assessment of survival rates for wolves in the Voyageurs region.

Table 17. Parasites and diseases found in live and dead wolves in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Parasites and Diseases	Sample Type	Cases Positive	Cases Negative
Disease Screening (whole blood, serum, feces)			
Blastomyces dermatitidis (blastomycosis)	Serum		6
Borrelia burgdorferi (lyme disease)	Serum	3	
Brucella canis (brucellosis)	Serum		6
Canine distemper	Serum	0	18
Canine parvovirus (CPV-2)	Serum	11	13
Canine parvovirus (CPV-2)	Feces		28
Canine parvovirus (CPV-2)	Scats from trails		47
Dirofilaria immitis (canine heartworm)	Serum	5	1
Dirofilaria immitis microfilaria (Knott's test)	Whole blood		18
Infectious canine hepatitis (ICH)	Serum	5	1
Leptospira pomona (leptospirosis)	Serum		6
L. icterohemorrhagica	Serum		6
L. hardjo	Serum		6
L. grippotyphosa	Serum		6
L. canicola	Serum		6
Rabies	Serum		6
Examination of Carcasses, Feces, and Pelage			
Alaria sp.	Small intestine, feces	6	
Ancylostoma caninum (hookworm), adult, eggs	Intestine, feces	5	
Baylisascaris egg	Feces (probably from prey)	1	
Borrelia burgdorferi (lyme disease)	Joint tissue	1	
Cestode sp., adults, larvae, eggs	Duodenum, jejunum	9	
Dermacentor sp. (ticks)	Pelage	13	
Dioctophyma renale (giant kidney worm)	Abdominal cavity	1	
Echinococcus granulosus	Small intestine	1	
Echinococcus multilocularis	Small intestine	1	
Echinococcus sp.	Intestine, duodenum	1	
Filaroides (Oslerus) osleri	Trachea and bronchi	7	
Filaroides sp.	Trachea and bronchi	1	
Moraxella phenylpyruvica	Fistula (bite wound)	1	
Moraxella sp.	Abcess	1	
Sarcocystis spp. (coccidiosis)	Intestine, feces	7	
Staphylococcus sp.	Abcess	2	
Streptococcus equisimilis	Abcess, fistula	2	
Strigeid eggs (probably *Alaria*)	Fecal	12	
Taenia sp., adults, larvae, eggs	Intestine, feces	12	
Toxocara sp.	Intestine	2	
Trematode eggs	Feces	2	
Trichodectes canis (dog louse)	Pelage	9	
Unicinaria sp. (hookworm)	Intestine	3	
No parasites detected	Feces		6
No parasites detected	Fecal swab		2

No disease fatalities were identified in this study.

Diseases and parasites

Diseases and parasites were identified in live-captured wolves via disease screening tests and in moribund wolves at necropsy (table 17). No disease fatalities were identified in this study. Localized abscesses or fistulas were incidental to other causes of death and probably arose from wounds or embedded plant material.

Borrelia burgdorferi, the spirochete that causes Lyme disease in humans, was found in the shoulder joint of a wolf killed by a gunshot. No abnormalities were present in that joint so the significance of the Lyme disease organism is uncertain. Kazmierczak et al. (1988) demonstrated that wolves inoculated with *B. burgdorferi* exhibit lymph node enlargement and develop antibodies to the disease. Antibodies

against Lyme disease were found in 43% of the wolves we tested, much higher than reported for wolves in other parts of Minnesota and Wisconsin (3%) (Kazmierczak et al. 1988: 525). In domestic dogs, Lyme disease has been shown to cause arthralgia, fever, inappetence, arthritis, and glomerulonephritis (Kornblatt et al. 1985), and in coyotes the agent is known to be transmitted across the placenta (Burgess and Windberg 1989). The upper Midwest is an epicenter of this disease of public health concern. The primary vector in the Midwest is believed to be the deer tick *(Ixodes damini)*; however, Lyme disease has been isolated from other ticks including the winter tick *(Dermacenter albipictus)* that infests moose (Anderson and Magnarelli 1984, Magnarelli et al. 1986). Ticks of the genus *Dermacenter* were common on the pelage of wolves examined in this study (table 17). White-footed mice *(Peromyscus* spp.) and white-tailed deer are the principal reservoirs for *B. burgdorferi* (Bosler et al. 1984).

Parasites were varied and infections were small to moderate in number. Overall, parasitism was an incidental finding. The giant kidney worm *(Dioctophyma renale)* has not been found in wolves in Wisconsin or IRNP, Michigan, and could be acquired by eating an intermediate form associated with crustaceans, fish, or possibly when drinking fresh water. The tracheal worm *(Filaroides osleri),* found in seven of the Voyageurs region wolves, is uncommon in IRNP or Wisconsin wolves; heavy infections may cause respiratory difficulty or bronchopneumonia in dogs. The cestodes *Echinococcus granulosus* and *E. multilocularis*, found in two Voyageurs region wolves, are benign in wolves but cause hydatid disease in humans by encysting in internal organs. The hookworms *(Ancylostoma* and *Uncinaria)* and the trematode *(Alaria* sp.) were common in wolves at necropsy and in fecal samples taken from live-captured wolves or collected feces. These parasites could be debilitating in neonatal pups if infection rates are high; they can cause infections at a very young and vulnerable age by passage through the mammary gland.

Forty-six percent of the Voyageurs region wolves tested had been exposed to canine parvovirus (CPV); this frequency is similar in other wolf populations in North America (Zarnke and Ballard 1987). In addition to serologic tests for exposure, samples of feces from live-captured wolves or feces collected in the field were tested for the presence of CPV, and no virus was found in any sample. These results indicate that though a large propor-

tion of the wolves had contacted CPV at some time, current infections were uncommon. Evidence has linked CPV, a disease transmitted through the feces of domestic dogs or wolves, to a major decline in the population of wolves in IRNP in 1980–1982 (Peterson et al. 1998), and to low wolf and coyote pup survival when introduced into canid populations (Mech and Goyal 1993, 1995; Thomas et al. 1984; Johnson et al. 1994; Windberg 1995). Cumulative effects modeling suggests that pup mortality related to diseases is a critical factor in determining whether wolves within VNP maintain high population densities (Cochrane 2000). Given the high rates of immigration of wolves into the Voyageurs region, estimated at 50 wolves/year traveling through more than one Voyageurs region wolf pack territory (L. D. Mech USGS, personal communication in Cochrane 2000) and the proximity of VNP wolves to domestic dogs, the potential transmission of diseases to Voyageurs region wolves must be considered high.

Antibodies against infectious canine hepatitis virus were found in most (83%) wolves tested, similar to Alaskan and IRNP wolves (Zarnke and Ballard 1987, Peterson et al. 1998). The significance of these results is unclear for wolves in the Voyageurs region and elsewhere because no evidence of detrimental consequences of this disease has been found.

Five of six wolves that were tested had low concentrations of antibodies to canine heartworm, but no larval heartworms were found in blood tests of live-captured wolves, and no adult heartworms were found at necropsy of dead wolves (table 17). The antibodies detected in Voyageurs region wolves may have been formed to a parasite that resembles canine heartworm but resides elsewhere because there is no confirmed evidence of canine heartworm in the Voyageurs region wolf population.

There was no evidence of Voyageurs region wolf exposure to canine distemper virus, rabies virus, blastomycosis (fungal disease), brucellosis, or several forms of leptospirosis (bacterial diseases) (table 17).

Population genetics
Of 13 wolf and 4 wolf-coyote hybrid genotypes identified across North America, Voyageurs region wolves were classified as belonging to a single wolf genotype (W1) (*n* = 11) and 2 of the wolf-coyote hybrid genotypes (W7, W9) (*n* = 8) (Lehman et al. 1991). Both
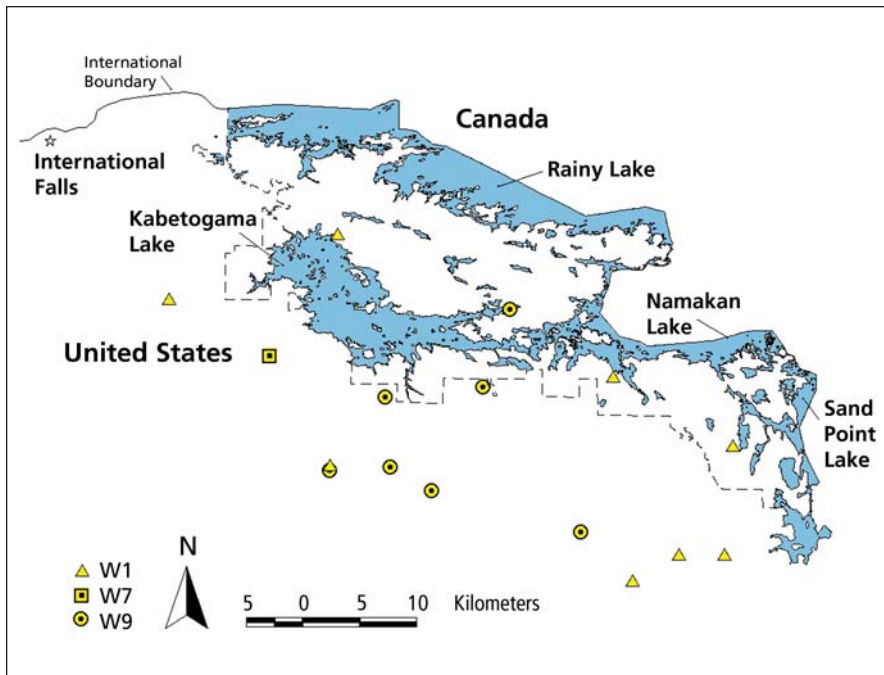
Figure 11. Capture sites of wolves with a common wolf genome (W1) or with two distinct wolf-coyote genomes (W7, W9) in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Opportunities for wolf-coyote breeding may increase when wolves move beyond the park boundaries into areas occupied by coyotes during the breeding season or when coyote-like canids move into the park.

ing into the wolf population (Lehman et al. 1991). Opportunities for wolf-coyote breeding may increase when wolves move beyond the park boundaries into areas occupied by coyotes during the breeding season or when coyote-like canids move into the park. At Algonquin Provincial Park, Ontario, the latter is thought to be more likely to occur when wolf packs have been eliminated from an area or when the wolf social order has been disrupted through high mortality (Theberge and Theberge 1998).

Feeding ecology
The 220 wolf scats examined contained 243 items of nine prey types (table 18) (Schmidt 1990). White-tailed deer comprised 186 (77%) occurrences of which 91% were adult and 9% were fawn. Fawn deer hair was identifiable in scats from May through August but was then indistinguishable from that of adults. Beaver occurred in 42 scats, accounting for 17% of occurrences. In combination, deer and beaver made up 94% of the annual wolf diet (table 18). The occurrence of deer remains (both adult and fawn) in scats increased from 56% in spring to 91% in winter while beaver decreased from 35% to 7% (figure 12). Moose was found in 4 of the 220 scats, 2% of total occurrences. Other prey consumed by wolves included muskrat (2% of occurrences), snowshoe hare

wolf and wolf-coyote hybrid genotypes occurred throughout the Voyageurs region (figure 11). The single wolf genotype is relatively common throughout Minnesota and northwestern Ontario (Lehman et al. 1991, Wayne et al. 1991). Hybridization is likely the result of introgression of coyote mtDNA into wolves via male wolves breeding with female coyotes and the resulting offspring backcross-

Table 18. Number of occurrences and percent occurrence of prey by season for 220 wolf scats collected in and adjacent to Voyageurs National Park, Minnesota, 1988–1989.

Prey[b]	Spring (64) Occ.[c]	Spring (64) %[d]	Summer (32) Occ.	Summer (32) %	Fall (27) Occ.	Fall (27) %	Winter (97) Occ.	Winter (97) %	Total (220) Occ.	Total (220) %
Adult deer[e]	42	54	10	28	24	89	93	91	169	70
Fawn deer[e]	2	3	15	42	0	0	0	0	17	7
Subtotal deer	44	56	25	69	24	89	93	91	186	77
Beaver	27	35	5	14	3	11	7	7	42	17
Muskrat	4	5	0	0	0	0	0	0	4	2
Moose	0	0	2	6	0	0	2	2	4	2
Mice	2	3	0	0	0	0	0	0	2	1
Hare	0	0	2	6	0	0	0	0	2	1
Livestock[f]	1	1	0	0	0	0	0	0	1	0
Grouse	0	0	1	3	0	0	0	0	1	0
Bird unknown	0	0	1	3	0	0	0	0	1	0
Total	78	100	36	100	27	100	102	100	243	100

Note: Sample size for each season shown in parentheses.

[a]Spring = April, May; summer = June, July, August; fall = September, October, November; winter = December, January, February, March.

[b]Does not include occurrences of dirt (*n* = 29), vegetation (*n* = 27), rope (*n* = 3), pieces of plastic bag (*n* = 1), and insects (*n* = 1).

[c]Number of times this prey item was identified in scats during this time period.

[d]Percent of total occurrences this time period.

[e]The remains of fawn deer could be distinguished from adult deer only during spring and summer seasons.

[f]A single scat containing cattle hair was found on the southern boundary of the study area.

Deer **Beaver**

Percent Wolf Diet

100
90
80
70
60
50
40
30
20
10
0

Spring Summer Fall Winter

Season

Occurrence **Biomass**

Percent Wolf Diet

70
60
50
40
30
20
10
0

Deer (adult) Beaver Deer (fawn) Moose Other

Prey Item

Figure 12. Percent occurrence of white-tailed deer and beaver in the wolf diet (upper panel) and relationship between occurrence and estimated biomass of prey species in the wolf diet (lower panel) in and adjacent to Voyageurs National Park, Minnesota, 1988 and 1989.

of prey represented in non-winter (appendix 6; table 19, page 30) and winter scats (appendix 7; table 20, page 30). Biomass estimates, when compared against occurrence data, underscored further the prevalence of deer in the diet of wolves in the Voyageurs region (figure 12). Moose, owing to their large size, increased slightly in prevalence while smaller prey (beaver, fawn deer, other) declined in prevalence relative to the percent occurrence data (figure 12, table 19, and table 20).

Deer remains were located on the frozen surfaces of the large lakes (60%) and inland (40%) during systematic winter track surveys by snowmobile and opportunistically during other fieldwork (figure 13, page 32). The cause of death of 80% of all deer year-round was attributed to wolf predation with adults of both sexes making up approximately 60% of the wolf-killed deer (table 21, page 31). The age and sex classification of 65 deer killed by wolves during three winters was 14 (22%) fawns, 2 (3%) yearlings, 36 (55%) adults, and 13 (20%) unknown (table 22). There was no difference in the sex ratio of adult deer killed by wolves over the three winters combined ($\chi^2 = 0.257$, $P = 0.612$, $n = 1$). However, there was a significant difference in the age and sex composition of wolf-killed deer between the winter 1987−1988 and winter 1988−1989 ($\chi^2 = 19.632$, $P = 0.0001$, $n = 2$) with more males and fewer adult females and fawns taken by wolves during the winter of 1987−1988 than the winter of 1988−1989. We can offer no definite reason for the observed differences between winters. However, the 1987−1988 winter was far less severe than the 1988−1989 winter (figure 2). It may be that adult female and fawn white-tailed deer are less vulnerable than adult males to wolf predation during mild winters. Fuller (1989) reported that in north-central Minnesota 54% of instances of winter wolf predation on deer was of fawns, and 60% of predation on deer more than one year old was of females. We speculate that such differences between our work and his study may be due to a higher proportion of males and a lower proportion of fawns in the unhunted herd of deer within VNP.

The age and sex classification of 24 deer killed by wolves in summer was 8 (33%) fawn, 2 (8%) yearling and 14 (58%) adult (table 23).

Of the 89 wolf-killed deer, age was determined for 50 (65%) by dental annuli and an additional 8 by foreleg length (figure 14, page 32). Males ranged in age from less than 1 to 12 years with a median age of 7 years. Females ranged in age

(1%), mice (1%), livestock (<1%), grouse (<1%), and unknown bird (<1%). Insects occurred in one scat in small numbers, and they were not included in the scat analysis. However, such low frequency items may increase dietary variety: the stomach of a wolf necropsied in July 1989 contained 0.38 kg of grasshoppers, eight juvenile mice, and blueberries (*Vaccinium* sp.). The scat containing livestock hair came from the southernmost area of the Voyageurs region where wolf depredation on livestock has been documented (Fritts 1982).

Small mammals have a relatively large ratio of indigestible hair to digestible meat so biomass may be overestimated in frequency of occurrence data (Mech 1970, Floyd et al. 1978, Fritts and Mech 1981, Weaver 1993). To correct for this we estimated the relative biomass

Table 19. Percent of total meals and relative biomass of prey consumed during spring, summer, and fall by wolves in and adjacent to Voyageurs National Park, Minnesota, 1988 and 1989.

Prey[a]	Estimated Live Weight of Prey (kg)[b]	No. of Meals[c]	% of Total Meals	Estimated Biomass Consumed (kg)[d]	% Relative Biomass
Adult deer[e]	62.9	68.5	55.7	64.57	66.8
Fawn deer[e]	7.1	16.0	13.0	7.93	8.2
Subtotal deer		84.5	68.7	72.5	75.0
Beaver	13.3	29.0	23.6	15.82	16.4
Moose	247.5	2.0	1.6	4.84	5.0
Muskrat	1.2	2.5	2.0	1.12	1.2
Hare	1.3	1.5	1.2	0.67	0.7
Other[f]	0.1	2.0	1.6	0.88	0.9
Livestock[g]	25.0	1.0	0.8	0.64	0.7
Grouse	0.7	0.5	0.4	0.22	0.2
Total		123.0	100.0	96.7	100.0

Note: *n* = 123 scats.

[a]Non-prey items found: 4 unknowns, 29 scats with dirt, 21 with vegetation, and 1 with insects.

[b]Weight calculations are provided in appendix 6.

[c]In scats with 2 prey types (14.5%), each was assigned an occurrence of 0.5 meal (see text; appendix 5).

[d]Estimated kg of prey biomass consumed: $Y = 0.439 + 0.008 X$ (Weaver 1993) multiplied by number of occurrences, where X = estimated live weight of prey.

[e]The remains of fawn deer could be distinguished from adult deer through summer.

[f]Includes 2 occurrences of microtine rodents and 1 unknown bird.

[g]Includes 1 scat containing cattle hair found on the southern edge of the study area.

Table 20. Percent of total meals and relative biomass of prey consumed during winter by wolves in and adjacent to Voyageurs National Park, Minnesota, 1988 and 1989.

Prey[a]	Est. live wt. of prey (kg)[b]	No. of meals[c]	% of total meals	Est. biomass consumed (kg)[d]	% Relative biomass
Deer[e]	58.6	90.5	93.3	82.13	90.4
Beaver	15.7	4.5	4.6	2.54	2.8
Moose	330.0	2.0	2.1	6.16	6.8
Total		97.0	100.0	90.8	100.0

Note: *n* = 97 scats.

[a]Non-prey items: 3 scats with rope, 1 with plastic bag, and 6 with vegetation.

[b]Weight calculations are provided in appendix 6.

[c]In scats with 2 prey types (5%), each was assigned an occurrence of 0.5 meal (see text; appendix 2).

[d]Estimated kg of prey biomass consumed: $Y = 0.439 + 0.008 X$ (Weaver 1993) multiplied by number of occurrences, where X = estimated live weight of prey.

[e]The remains of fawn deer and adult deer could not be distinguished from one another in winter scats.

from less than 1 to 14 years with a median age of 6.5 years. Mech et al. (1971) reported wolves in SNF killed deer of both sexes ranging from less than 1 to more than 14 years. Fuller (1989) reported the median age for 9 adult male and 13 adult female deer killed by wolves to be 3.3 years and 9.5 years, respectively, in an area of north-central Minnesota where deer were subjected to intensive sport hunting. We attribute the younger age of wolf-killed deer in Fuller's (1988) study to the impact of sport hunting on deer age structure (Fuller 1989).

Wolf predation has been identified as an important cause of mortality among white-tailed deer where both species coexist (Kolenosky 1972, Fuller 1989) but its role in regulating deer numbers is less clear. The numerical and functional responses of wolves to prey abundance are mediated by winter severity (Messier 1991). In SNF, wolf density negatively impacts deer

Table 21. Cause of mortality by sex and age class of 111 dead white-tailed deer found year-round in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Cause	Fawn			Yearling			Adult			Unknown	Totals	% of Total
	M	F	Unknown	M	F	Unknown	M	F	Unknown	Unknown		
Killed by wolves	3	2	17	3	1	0	16	22	11	14	89	80.2
Accident[a]	4	0	0	0	0	0	4	2	0	0	10	9.0
Unknown	0	0	0	1	0	0	2	0	2	0	5	4.5
Starvation[b]	1	1	0	0	0	0	1	1	0	0	4	3.6
Human[c]	0	0	0	0	0	0	2	1	0	0	3	2.7
Total	8	3	17	4	1	0	25	26	13	14	111	
% of Total	7.2	2.7	15.3	3.6	0.9	0.0	22.5	23.4	11.7	12.6		

[a]Three drowned after falling through thin ice and 7 died of exposure or were euthanized after being stranded on glare ice.

[b]All occurred in late winter 1989; the adults were 9 years of age.

[c]Believed killed illegally as evidenced by wounds and vehicle tracks near remains.

Table 22. Age and sex of wolf-killed white-tailed deer in and adjacent to Voyageurs National Park, Minnesota, during winter 1987–1991.

Year/Sex	Age Class				Total
	Fawn	Yearling	Adult	Age Unknown	
1987–1988					
Female	0	0	4	0	4
Male	0	0	11	0	11
Sex unknown	3	0	4	7	14
Subtotal	3	0	19	7	29
1988–1989					
Female	2	1	11	0	14
Male	2	1	3	0	6
Sex unknown	6	0	0	5	11
Subtotal	10	2	14	5	31
1989–1990					
Female	0	0	1	0	1
Male	0	0	0	0	0
Sex unknown	1	0	2	1	4
Subtotal	1	0	3	1	5
Total	14	2	36	13	65

Note: Wolf kills were found on the surface of the large lakes (60%) and inland (40%) during systematic track surveys and opportunistically during other fieldwork.

Table 23. Age and sex of white-tailed deer killed by wolves in and adjacent to Voyageurs National Park, Minnesota, during summer 1988 and 1989.

Sex	Age Class				Total
	Fawn	Yearling	Adult	Age Unknown	
Female	0	0	6	0	6
Male	1	2	2	0	5
Sex unknown	7	0	6	0	13
Total	8	2	14	0	24

Note: One male fawn and 1 male adult were examined in 1988; all others were sampled in 1989.

Figure 13. Number of deer found dead as a result of wolf predation and other causes in and adjacent to Voyageurs National Park, Minnesota, December 1987 through May 1990.
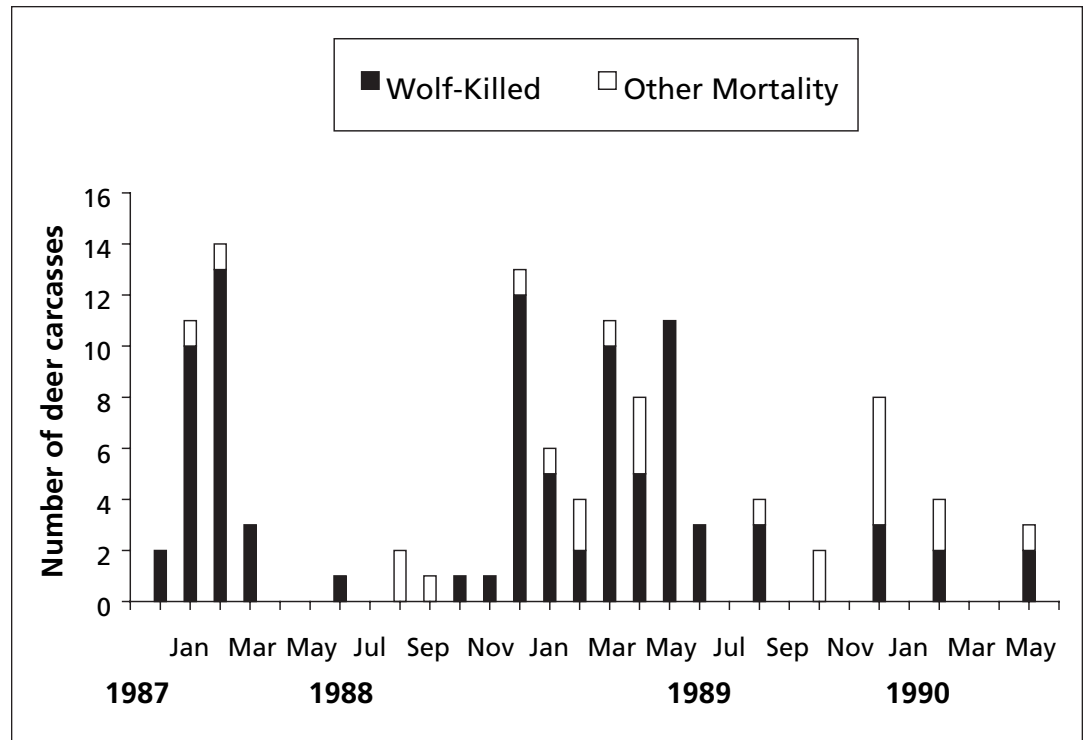
Figure 14. Age and sex structure of deer killed by wolves in and adjacent to Voyageurs National Park, Minnesota, December 1987 through May 1990.
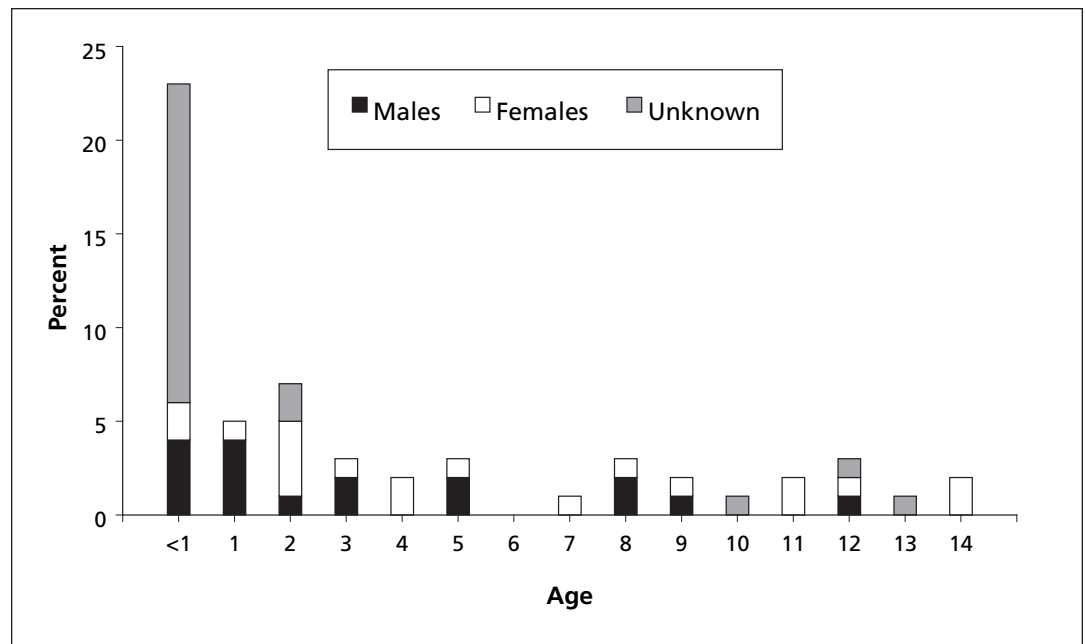
The numerical and functional responses of wolves to prey abundance are mediated by winter severity.

population growth rates (Messier 1991). Yet, white-tailed deer herds in northern Minnesota respond to winter severity with time lags influenced by both wolf predation and negative-density dependent factors (Post and Stenseth 1998). This combination of factors is of particular importance in our study given the mild winters of 1986–1987 and 1987–1988 and harsh winters of 1988–1989 and 1990–1991 as measured by an index of winter severity (figure 2). Wolves are more successful in killing deer in winters of greater snow depth (Nelson and Mech 1986b).

Conclusions

The relatively high density of wolves (33/1,000 km²) in and adjacent to VNP, Minnesota, was supported by high densities of white-tailed deer and beaver. The mean pack size of 5.5 in mid-winter and mean pack territory size of 152 km² for wolves in the Voyageurs region were consistent with wolves elsewhere dependent on white-tailed deer (Mech 1986b, Potvin 1988, Fuller 1989). Territories of the two to three wolf packs on the Kabetogama Peninsula were entirely within the boundaries of VNP. The territories of wolf packs utilizing VNP's southern landmass ranged beyond the park boundaries, although two packs ranged almost entirely within VNP. We found no evidence of wolf packs with territories straddling the international border between Canada and the United States.

Snow tracking revealed a different pattern of use of frozen lake surfaces and shorelines than did daytime aerial radiotelemetry. Presumably, much of this difference is attributable to wolves using such areas at night when we did not conduct telemetry flights. Such use patterns may reflect a response to diurnal human activities within VNP (Fox et al. 1999).

Howling surveys provided a means of determining the presence or absence of reproductively successful wolf packs within VNP. However, averages of only 52−56% of known packs were detected by solicited howling. The method required nighttime access to many locations. This created hazardous working conditions for sampling crews because access to many sampling stations was by small boat only. The low rate of wolf responses coupled with the hazards of sampling renders howling surveys a poor technique for monitoring population trends within VNP.

We documented nine dispersals among 20 instrumented wolves. One of the instrumented wolves dispersed twice. Permanent dispersal was preceded by a mean of 2.1 pre-dispersal movements. Two dispersals resulted in wolves joining neighboring packs while two others involved pack splitting. Ages of dispersing wolves ranged from 1.5 to 7.5 years. The rate of dispersal was high relative to other wolf populations.

Causes of mortality in wolves differed by location. The four mortalities of instrumented wolves within VNP were all attributed to natural causes. Only 2 of 10 mortalities beyond the boundaries of VNP were attributed to natural causes while 8 were attributed to human activities. Similarly, two non-instrumented wolves found dead within VNP died of natural causes while eight non-instrumented wolves found beyond the boundaries of VNP died as the result of human activities. All dead instrumented wolves and only one of the dead non-instrumented wolves were found in Minnesota. The carcass of a single non-instrumented wolf was found on a frozen lake surface immediately north of the international border. However, information suggested that the wolf had been killed by aerial gunning in Minnesota and the carcass abandoned in Ontario. The high rate of human-induced mortality indicates that the federal Endangered Species Act and other federal and state regulations provided only limited protection to wolves in non-park areas in northern Minnesota. The lack of human-induced mortality within VNP underscores the effectiveness of national parks and other lightly roaded areas in protecting wolves.

The nine-month survival rate for pup and adult wolves combined was 0.73. We found little evidence of a significant difference in survival between pups and adults, although our small sample sizes undoubtedly limited the power of our statistical tests. The annual survival rate for adult wolves was 0.75. Annual survival differed between the sexes with females surviving at a rate twice that of males. Adult wolves with territories entirely within the boundaries of VNP survived at higher rates than did those with territories crossing or beyond the park boundary. Survival of all instrumented wolves and adult wolves varied by season with the lowest survival rates in the two-month pre-ice-up period in winter, which included the Minnesota rifle-hunting season for deer.

Wolves have been exposed to a number of diseases and parasites, including Lyme disease and infectious canine hepatitis, but the significance of these findings is unclear. Approximately half the wolves had been exposed to CPV, but actual infections were uncommon at the time of the study. Parasitism was an incidental finding. No fatalities were attributable to diseases or parasites.

Wolves of the Voyageurs region belong to a single common wolf genotype and two wolf-coyote genotypes. Such wolf-coyote hybrids have backcrossed into the wolf population.

White-tailed deer provided the majority of the wolf diet, and combined with deer and beaver made up approximately 95% of the annual wolf diet. Ages of wolf-killed deer ranged from less than 1 to 14 years.

Management Implications

Voyageurs National Park should begin to monitor trends in land use practices along its boundaries.

The National Park Service is committed to "manage the natural resources of the national park system to maintain, rehabilitate, and perpetuate their inherent integrity" (National Park Service 1988). Maintaining a viable population of wolves at VNP in the future could be a challenge. Wolves within the Voyageurs region presently occur at a high density, and those within park boundaries are largely protected from illegal take. However, wolves in areas of Minnesota adjacent to VNP are subjected to illegal killing, and wolves are taken legally in adjacent Ontario. Voyageurs National Park is not of adequate size to support a self-sustaining wolf population. A population of wolves completely isolated within VNP might be expected to experience the population viability difficulties exhibited recently by wolves at IRNP (Peterson 1999). Isolation of wolves at VNP may result from changes in land use on both sides of the international border—both increased logging (timber harvest and associated roads) and other development, or increased harvest of wolves beyond the park boundaries. Fortunately, there are a number of large protected, mostly roadless areas, close to VNP, including the SNF's Boundary Waters Canoe Area Wilderness, Minnesota, and Quetico Provincial Park, Ontario. Successful conservation of wolves will require management agencies to identify and maintain potential wolf movement corridors between these protected areas. Such an effort will involve cooperation with multiple agencies at the international level. In addition, VNP should begin to monitor trends in land use practices along its boundaries.

Changes in prey density resulting from natural vegetative succession or consecutive harsh winters could impact wolf density.

Our radiotelemetry data and that of others (Fox et al. 1999) show wolves making relatively little use of the shorelines of larger lakes and frozen lake surfaces during the day, especially in comparison to wolves at IRNP. The implication is that human winter activities at VNP could be impacting wolf behavior patterns. The issue begs further resolution. At present, wolves are abundant in VNP, and there is no evidence that the current types and levels of human activities are depressing wolf numbers. However, the potential effects of increasing levels of human activity, especially snowmobiling, and the take of wolves beyond the park that could reduce immigration necessitate continuous data gathering and evaluation by the National Park Service.

Wolves at VNP are currently dependent on a high-density prey base of deer and beaver. Changes in prey density resulting from natural vegetative succession or consecutive harsh winters could impact wolf density. Applications of models predicting plant succession for northern Minnesota (Tester et al. 1997) and linked estimates of the ecological carrying capacity of deer and beaver would provide insights of the likelihood of VNP continuing to support wolves. Such insight could provide direction to the use of prescribed burning and response to wildfires in and out of VNP.

Wolves at VNP have been exposed to Lyme disease and CPV with no detectable impact on survival of individuals or measurable population parameters. However, these instances highlight the vulnerability of wolves to the introduction of other diseases and parasites. The potential establishment of additional diseases and parasites requires careful monitoring.

Similarly, the evidence of past hybridization with coyotes in VNP wolves underscores the threat of such events in the future, particularly as the postulated scenario of pioneering wolves breeding with coyotes exists across a broad front as wolves expand into southern Minnesota, Wisconsin, and Michigan.

Appendix 1. Number of wolves harvested in the Fort Frances District, Ontario, 1948–1998

Annual Timber Wolf Harvest (1948–1998) Fort Frances District

Bar chart. Y-axis: "Number of Animals Harvested by Trappers" (0–140). X-axis: trapping seasons from 48/49 to 96/97. Legend: blue bars = "Study Years".

* NOTE: Harvest data for 1970/71 trapping season is estimate only
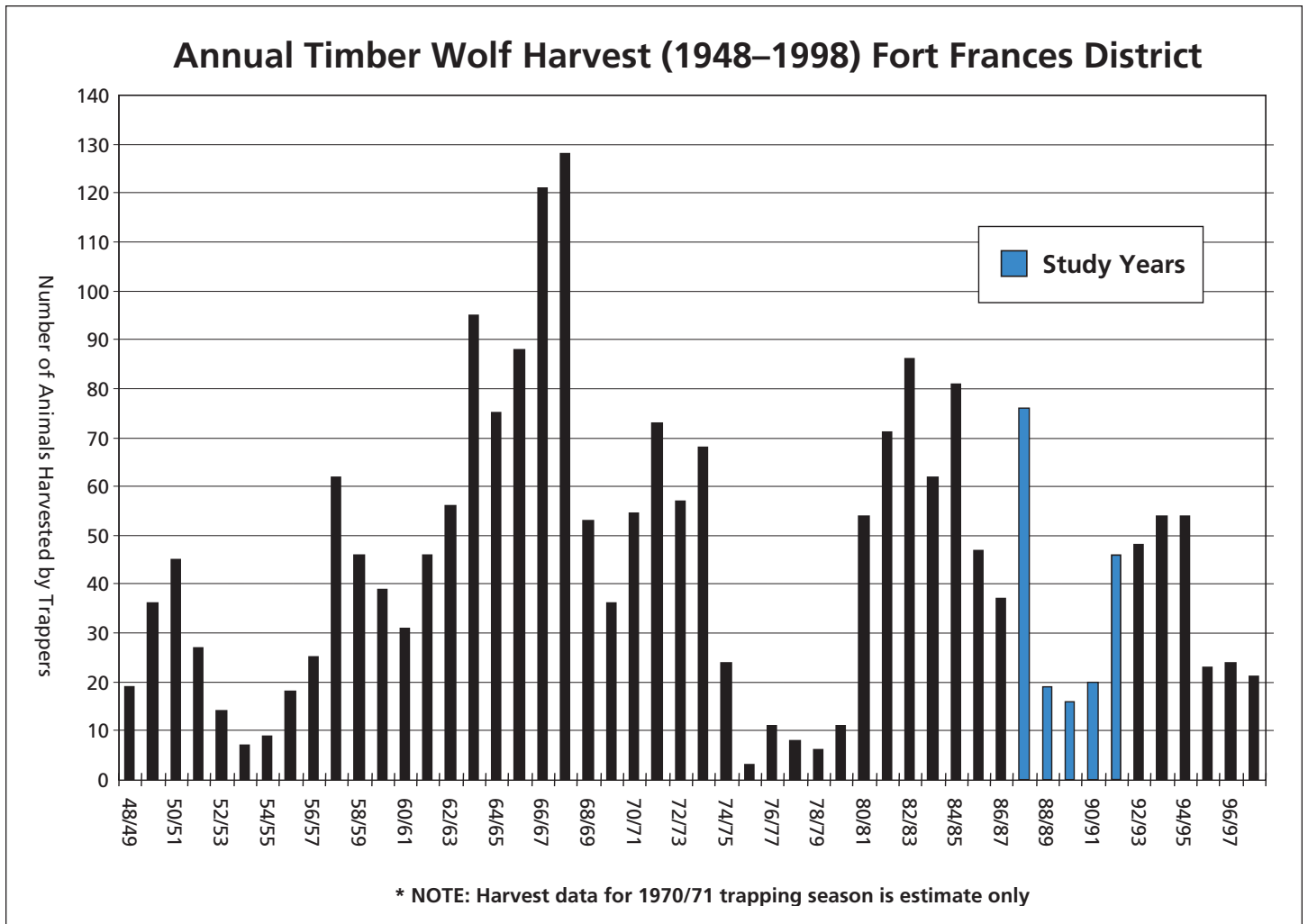
Appendix 2. Accuracy of aerial-telemetry location estimates for gray wolves in and adjacent to Voyageurs National Park, Minnesota, 1989–1991.

Background

From August 1987 to May 1991, 31 wolves were captured within and up to 16 km south of VNP. Each animal was fitted with a radio collar and monitored every 2–10 days throughout the year until (1) a mortality sensor on the radio transmitter indicated that the animal had died, (2) the individual dispersed from the study area, or (3) the radio transmitter failed. Wolves were relocated from fixed-wing aircraft and location x-y coordinates were recorded based on LORAN-C fixes and visual estimates marked on 1:50,000-scale topographic maps (topographic mapping).

A total of 1,174 location estimates was recorded for wolves in and near VNP during the study. Prior to mid-December 1989, 544 location estimates consisted solely of x-y coordinates read from an onboard LORAN-C positioning device. Bias and precision of LORAN-C location estimates during this early period were unknown. After mid-December 1989, 630 location estimate "final calls" consisted of x-y coordinates read from an onboard LORAN-C positioning device, x-y coordinates estimated off topographic maps via a graduated grid overlay (topographic mapping), or a combination of LORAN-C and topographic mapping (e.g., LORAN-C northing and topographic-mapped easting). As with the early period, bias and precision of "final call" location estimates during this later period were unknown. Potential errors affecting bias and precision existed for all location methods (i.e., LORAN-C, topographic mapping, and combination).

Most error associated with topographic mapping likely can be attributed to human error.

Most error associated with LORAN-C is likely due to inherent system error. Precision and bias of LORAN-C location estimates can be affected by the geographic arrangement of transmitting towers, proximity of receiver to transmitting tower(s), elevation of aircraft, terrain/topography, proximity to power lines, location relative to mineral deposits, and weather (IIMorrow 1989, Rhoades et al. 1990, Anonymous 1991, Keating 1994, Leptich et al. 1994). Additionally, equipment malfunction may lead to erroneous coordinates. For example, tower(s) within a LORAN-C transmitter chain may become temporarily inoperable,

changing their geographic configuration, or a LORAN-C receiver may malfunction. Finally, human error may lead to erroneous coordinates; LORAN-C coordinates may be misread off the receiver or misentered onto data sheets. Previous studies have reported on both precision and bias associated with LORAN-C location estimates. LORAN-C location estimates have differed from actual locations by mean distances of 20−97 m for land-borne receivers (Patric et al. 1988, Rhoades et al. 1990), 200−386 m for airborne receivers (Boer et al. 1989, Brown 1992, Leptich et al. 1994, Carrell et al 1997), and 128−328 m for airborne receivers after bias adjustment (Jaeger et al. 1993, Carrell et al. 1997). Locational bias is a known issue for inland LORAN-C locations and can vary from study area to study area (Jaeger et al. 1993, Leptich et al. 1994). Reported locational bias has ranged from 99−265 m in a north-south direction and from 163−484 m in an east-west direction (Jaeger et al. 1993, Carrell et al. 1997).

Most error associated with topographic mapping likely can be attributed to human error. Mapped coordinates may be placed in wrong positions on the topographic map, interpolation from a coarse-scale grid overlay may provide incorrect or non-precise coordinates, and mapped coordinates may be misread or misentered. Previous studies have reported on the precision associated with topographic mapping location estimates. Topographic mapping location estimates have differed from actual locations by mean distances of 77−1,414 m (Krausman et al. 1984, Garrott et al. 1987, Walsh et al. 1992, Carrell et al. 1997). No study has reported a directional bias associated with topographic mapping.

Error associated with combination coordinates can be ascribed to the above sources for LORAN-C and for topographic mapping. However, another source of error is also introduced. The decision to choose a LORAN-C fix or topographic mapping coordinate may be incorrect (e.g., map coordinate was chosen yet LORAN-C fix for that location was more correct). This final source of error may be inflated if no set criteria are followed consistently throughout a study by all observers. Arbitrary

Digital mapping removed the error associated with interpolation from a course grid overlay and misread or misentered data from topographic mapping.

decisions on whether to use a LORAN-C fix or topographic mapping coordinate could lead to discrepancies that cannot easily be adjusted.

To fully describe the accuracy (i.e., precision and bias) of "final call" location estimates and LORAN-C location estimates, optimally we would compare their estimated coordinates to known true coordinates. However, we did not know the true locations of the wolves and could not quantify the precision of the location estimates. Yet we can potentially report locational bias. Bias can be calculated for "final call" or LORAN-C coordinates if their coordinates are compared to those of another method that is not biased. We can then remove bias post hoc as suggested by Carrell et al. (1997).

We determined the relative directional bias of "final call" x-y coordinates and LORAN-C coordinates collected for wolf aerial locations in and adjacent to VNP from 1989 to 1991. This provided an objective means of correcting for potential locational errors based on LORAN-C prior to mid-December 1989 and correcting for potential locational errors based on "final calls" after mid-December 1989. We also provide recommendations regarding the utility of various x-y coordinate sources (e.g., LORAN-C, topographic mapping) for home range analysis.

Methods

To quantify potential biases of various location estimates, we used data available from 16 December 1989 to 16 May 1991 (i.e., the period when both LORAN-C and topographic mapping were employed). The first coordinate data set consisted of the potentially biased "final call" x-y coordinates (i.e., the wolf location estimates used in subsequent movement analysis). These coordinates were coded as LORAN-C estimates, topographic mapping estimates, or combination estimates. LORAN-C estimates were those with both x and y coordinates originating from a LORAN-C positioning device. LORAN-C x-y coordinates read off the positioning device as longitude and latitude were converted to Universal Transverse Mercator (UTM) coordinates (zone 15, datum NAD27) using the coordinate conversion program Tralaine (Mentor Software Inc., Thornton, Colorado, USA). LORAN-C was not calibrated to the study area as suggested by Jaeger et al. (1993). Topographic mapping estimates were those with both x and y coordinates originating from a graduated

grid overlay placed over a topographic map. Coordinates were read as longitude and latitude and were converted to UTM coordinates (zone 15, datum NAD27) using the coordinate conversion program Tralaine. Combination estimates were those with x and y coordinates originating from LORAN-C or topographic mapping. The second coordinate data set consisted of the potentially biased LORAN-C x-y coordinates collected for all of the above location estimates. The final coordinate data set consisted of x-y coordinates taken from a digital topographic map for those "X"s plotted directly onto study-area maps (digital mapping). We obtained precise x-y coordinates (UTM zone 15, datum NAD27) for the plotted locations using DLG Viewer (USGS, Mid-Continent Mapping Center, Rolla, Missouri). A mouse cursor placed on a digital topographic map at the exact position where the center of the "X" plotted on the paper map fell provided appropriate coordinates. For all plotted "X"s, digital mapping provided x-y coordinates with sub-meter precision (relative to where the "X" was placed, not relative to the true location). Digital mapping removed the error associated with interpolation from a course grid overlay and misread or misentered data from topographic mapping.

To calculate locational bias, we compared "final call" coordinates and LORAN-C coordinates (the biased estimates) to coordinates generated from an unbiased estimate. By subtracting the estimated "final call" or LORAN-C location coordinates from coordinates obtained from the unbiased method, the resulting discrepancies were used to calculate a mean vector whose coordinates could be used to adjust the original x-y coordinate values. The new adjusted coordinates should then be unbiased. Precision would still be unknown (assumed to be ~200 m from literature). Although we did not know the precision of digitally mapped coordinates, we assumed those mapped coordinates to be unbiased and used them to detect and adjust for bias.

Results

Of 630 "final call" location estimates collected from 16 December 1989 to 16 May 1991, 598 (95%) had LORAN-C x-y coordinates *and* topographic mapping "X" s plotted on paper maps. We calculated x-y coordinates for mapped "X"s via digital mapping. We acknowledge that plotted map coordinates may only have had a precision of approximately 100–1,000 m, however, it has been demonstrated that plotted coordinates are at least un-

biased. The bias of reported "final calls" and LORAN-C location estimates was then calculated by subtracting those x and y coordinates from unbiased x and y coordinates provided by digital mapping.

When we compared coordinates reported as final wolf locations to the unbiased estimate (digitally mapped coordinates minus "final call" coordinates) we got a distribution of discrepancies (figure 1). The "final call" estimates were, on average, 177.5 m west and 58.0 m north of the digitally mapped coordinates. This translated to a mean vector distance of 186.7 m at an angle of 108° from the arithmetic center of the digitally mapped coordinates. The coordinate errors do not appear to come from a bivariate normal distribution and it would be difficult if not impossible to compute a single adjustment factor to transform the final calls to unbiased estimates.

Upon closer examination, it was apparent that the distribution of x-y discrepancies actually consisted of three separate distributions (figure 2). These three distributions were the coordinate differences between LORAN-C and digital mapping, topographic mapping and digital mapping, and combination coordinates and digital mapping.

"Final call" coordinates estimated from a paper topographic map via grid overlay differed by as much as approximately 2,000 m from digitally mapped coordinate estimates (figure 2). These large errors likely were the result of reading coordinates incorrectly off the grid or transcription error. The "final call" estimates based on topographic mapping were, on average, 21.1 m west and 39.3 m south of the digitally mapped coordinates. This translated to a mean vector distance of 44.6 m at an angle of 28.2° from the arithmetic center of the digitally mapped coordinates. Most points were very close to the digitized points and showed no significant bias (Hotelling's $T^2_{2,55} = 2.02$, $P = 0.143$). The 95% confidence ellipse encompassed the origin also indicating no difference from digital mapping estimates (figure 3, page 49). Thus, "final call" estimates based on topographic mapping coordinates did not require a post hoc adjustment to correct for bias.

"Final call" coordinates estimated from LORAN-C differed by as much as approximately 5,000 m from digitally mapped coordinate estimates (figure 2). Errors of this magnitude may have been caused by problems in the LORAN-C transmitter chain (these larger errors only occurred on two days). The "final call" estimates based on LORAN-C were, on average, 437.2 m west and 98.2 m north of the digitally mapped coordinates. This translated to a mean vector distance of 448.1 m at an angle of 102.7° from the arithmetic center of the digitally mapped coordinates. LORAN-C coordinates differed significantly from digitally estimated coordinates and showed significant bias (Hotelling's $T^2_{2,232} = 372.91$, $P < 0.001$). The 95% confidence ellipse did not encompass the origin also indicating a difference from digital mapping estimates (figure 3). Thus, "final call" estimates based on LORAN-C coordinates required a post hoc adjustment to correct for bias.

Because most "final call" coordinates were a combination of LORAN-C northing and mapped easting, the differences from digitally mapped coordinates showed some easting error with more dispersed northing errors (figure 2). The "final call" estimates based on combination coordinates were, on average, 9.97 m west and 45.3 m north of the digitally mapped coordinates. This translated to a mean vector distance of 46.3 m at an angle of 167.6° from the arithmetic center of the digitally mapped coordinates. Location estimates with coordinates consisting of a combination of mapped coordinates and LORAN-C coordinates also differed significantly from digitally estimated coordinates (Hotelling's $T^2_{2,308} = 7.77$, $P = 0.001$). The 95% confidence ellipse did not encompass the origin also indicating a difference from digital mapping estimates (figure 3, page 43). Thus, "final call" estimates based on combination coordinates required a post hoc adjustment to correct for bias (likely, the LORAN-C portion of the combination coordinates created most of the detected bias).

We adjusted individual location estimates by the mean vector coordinates for the two cases that produced significantly different means than digital coordinates (figure 4, page 43). The adjusted "final call" estimates were, on average, 2.0 m west and 3.7 m south of the digitally mapped coordinates. This translated to a mean vector distance of 4.2 m at an angle of 28.2° from the arithmetic center of the digitally mapped coordinates. The new adjusted final coordinates produced errors that were unbiased and were not significantly different from the origin (Hotelling's $T^2_{2,597} = 0.11$, $P = 0.895$). A 95% confidence ellipse (not shown) also encompassed the origin indicating no differ-

Figure 1. Locational discrepancies (m) between "final call" x-y co-ordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting "final call" coordinates from unbiased, digitally mapped coordinates.

Figure 2a. Discrepancies (m) between paper-mapped "final call" x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting topographic mapping and combination "final call" coordinates from unbiased, digitally mapped coordinates.

Figure 2b. Discrepancies (m) between LORAN-C–only based "final call" x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting LORAN-C and combination "final call" coordinates from unbiased, digitally mapped coordinates.

Figure 2c. Discrepancies (m) between combined coordinate-based "final call" x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting combination "final call" coordinates from unbiased, digitally mapped coordinates.

Figure 3. Ninety-five percent confidence ellipses for locational discrepancies (m) between "final call" x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting LORAN-C, topographic mapping, and combination "final call" coordinates from unbiased, digitally mapped coordinates.

Figure 4. Locational discrepancies (m) between adjusted "final call" x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting adjusted LORAN-C, raw topographic mapping, and adjusted combination "final call" coordinates from unbiased, digitally mapped coordinates.

ence from digital mapping estimates. However, the distribution of x-y deviations still did not appear to show a classic bivariate normal shape. There still appeared to be an unnatural compression of points on either side of the y-axis for part of the data (i.e., the adjusted combination coordinates). An additional and more serious problem exists because to correct for biases in wolf locations, two separate corrections were required, one for LORAN-C and one for combination coordinates (if paper map coordinates would have been significantly different from digital coordinates, three adjustments would have been required). A final serious problem with the separate adjustments was that no set criteria were followed to determine when to use LORAN-C or paper map coordinates. The corrections developed could only be used for this sample.

Coordinates estimated via LORAN-C differed by as much as approximately 6,000 m from digitally mapped coordinate estimates (figure 5). As with "final call" LORAN-C discrepancies, the extreme large differences are likely the result of two days with different transmitting tower configurations (i.e., there were consistent biases for each of the two days). Estimates based on LORAN-C were, on average, 547.8 m west and 138.3 m north of the digitally mapped coordinates. This translated to a mean vector distance of 564.9 m at an angle of 104.2° from the arithmetic center of the digitally mapped coordinates. LORAN-C coordinates differed significantly from digitally estimated coordinates and showed significant bias (Hotelling's $T^2_{2,597} = 941.90$, $P < 0.001$). The 95% confidence ellipse did not encompass the origin, which also indicates a difference from digital estimates (figure 6). Telemetry data gathered during these two days were not used in our assessments of wolf territory sizes or movements.

Discussion and recommendations

For the purposes of the VNP wolf study, "final call" estimates are likely accurate enough to meet the needs of home range and movement analysis. In many cases "final call" coordinates may be more accurate than either LORAN-C or topographic mapping. However, locations based on several different types of "final call" x-y coordinates (LORAN-C, topographic mapping, and combination) will be difficult to defend under stringent peer review. Without a strict protocol for basing "final call" estimates on LORAN-C, topographic mapping, or combination coordinates, the resulting error distribution is unpredictable and makes meet-

ing statistical assumptions difficult if not impossible. It would be more appropriate to use only topographic mapping *or* bias-adjusted LORAN-C x-y coordinates whose resulting error distributions show a typical bivariate normal shape. We recommend not using combination coordinates to describe wolf locations.

Topographic mapping has the advantage of producing unbiased estimates without adjustment. Also, topographic mapping coordinates can be more precise than LORAN-C (see Carrell et al. 1997), especially in heterogeneous environments or varied terrain. But both topographic mapping and LORAN-C precision vary by area. Since we do not know the true locations we cannot assume that precision is better with topographic mapping in the VNP region.

Due to limited precision, Jaeger et al. (1993) were critical of the use of LORAN-C in aerial-telemetry studies, and suggested locations from which they were based had limited utility. Rhoades et al. (1990) indicated that the type of analysis LORAN-C location estimates could provide would be scale dependent. However, LORAN-C has advantages over topographic mapping. LORAN-C can provide location estimates in flat or featureless terrain or habitats that would otherwise preclude accurate topographic mapping; it also is less labor intensive and time consuming, reduces costs and increases efficiency, and gives the ability of different work crews to achieve similar results (Patric et al. 1988, Boer et al. 1989). Carrell et al. (1997) maintain that LORAN-C location estimates should provide adequate accuracy for home range studies.

With regard to VNP wolf data, we recommend that bias-adjusted LORAN-C coordinates be used to describe wolf locations for the first portion of the study when only LORAN-C was employed. When both topographic mapping and LORAN-C were employed in the latter part of the study, we recommend either using all topographic mapping coordinates or using all bias-adjusted LORAN-C coordinates to describe wolf locations. We cannot recommend using both coordinate types for the latter period of the study. For this latter period, topographic mapping likely provided more precise and unbiased estimates than LORAN-C. Thus, we recommend using topographic mapping if accurate locations are the main concern. But, using bias-adjusted LORAN-C will provide a single, consistent adjustment for the entire period of study with less effort. If

Figure 5. Locational discrepancies (m) between LORAN-C x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting LORAN-C coordinates from unbiased, digitally mapped coordinates.
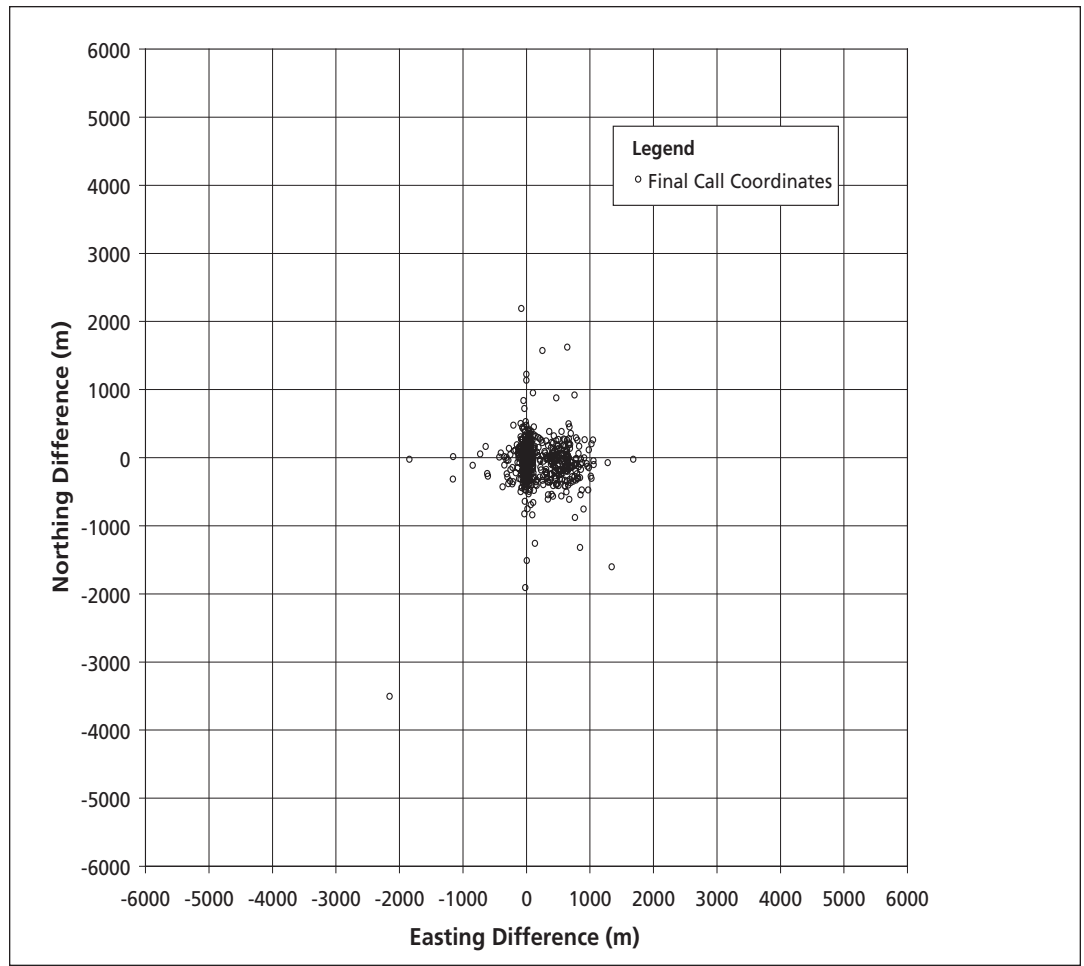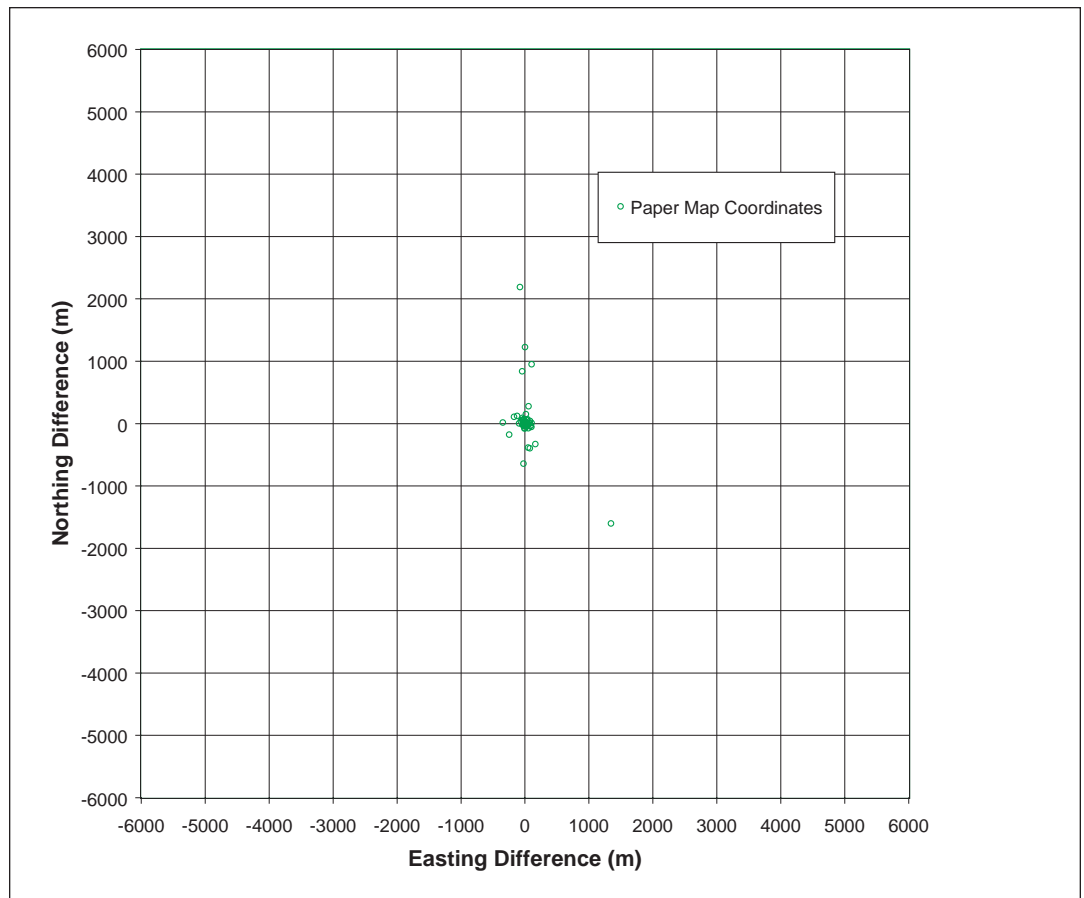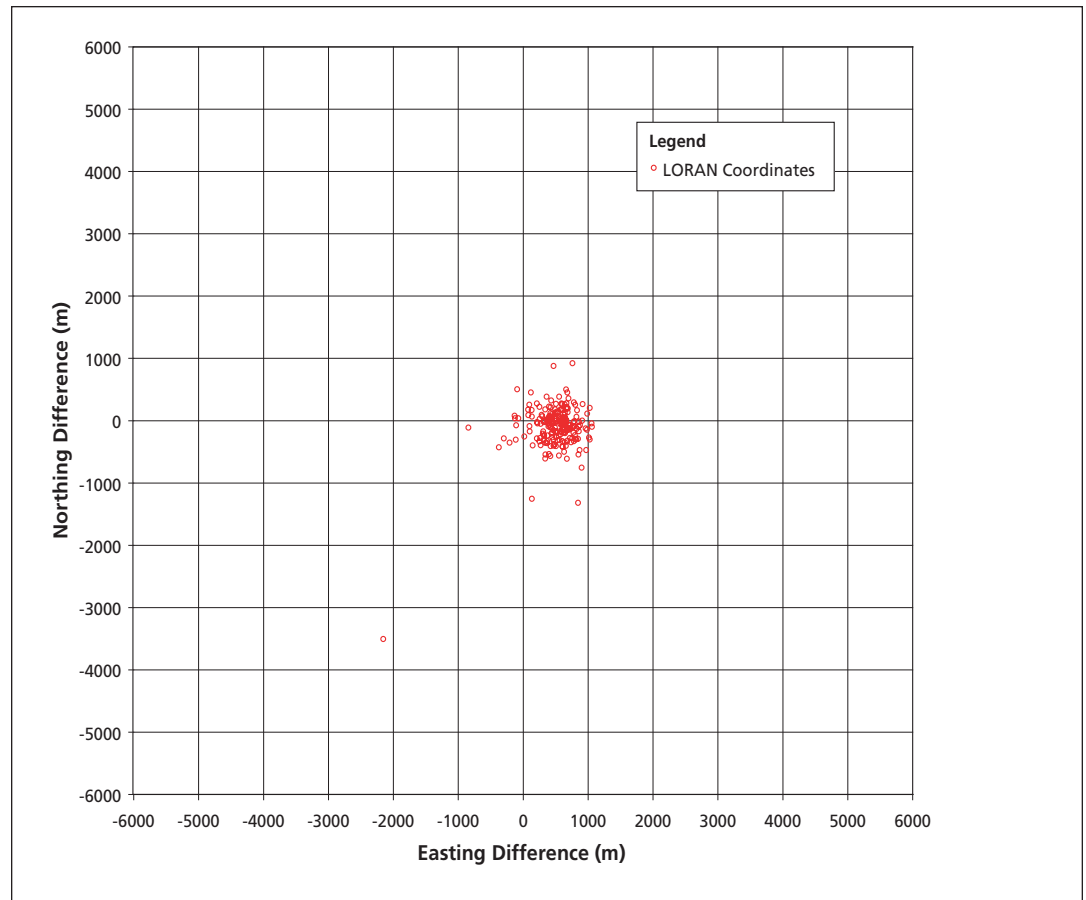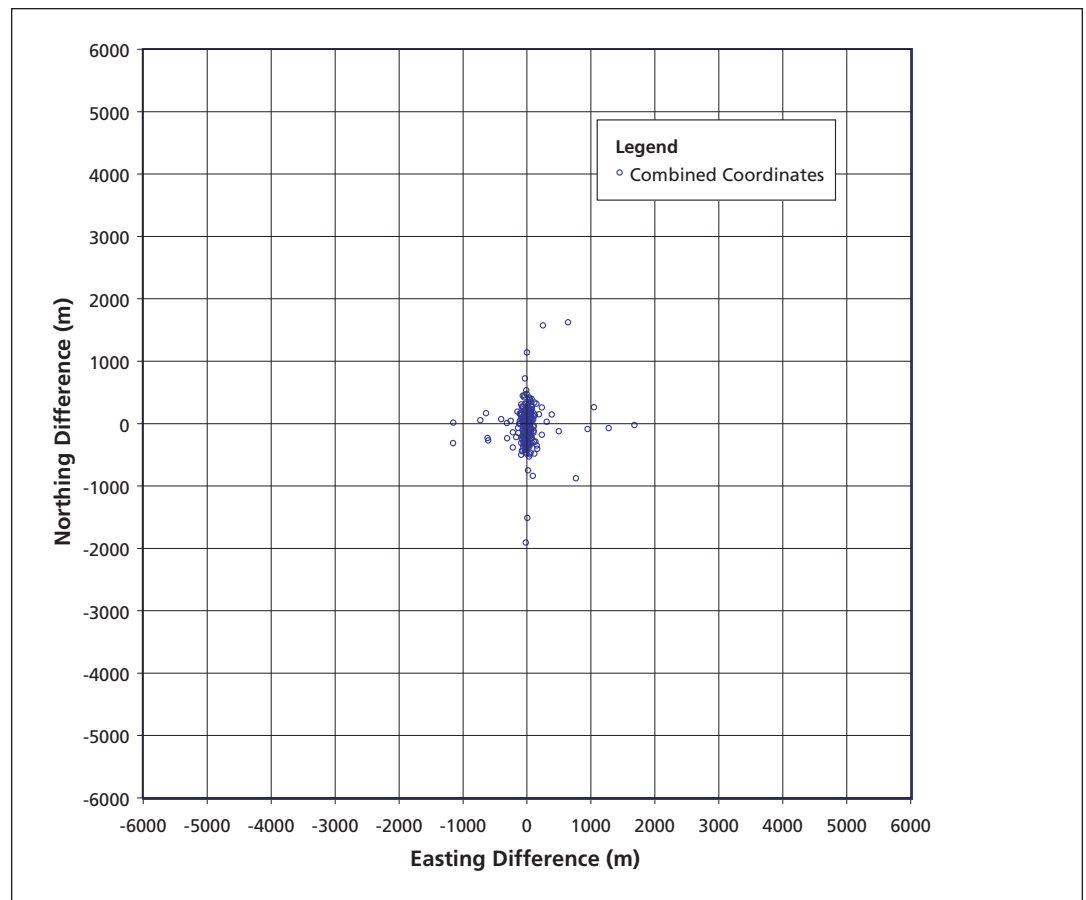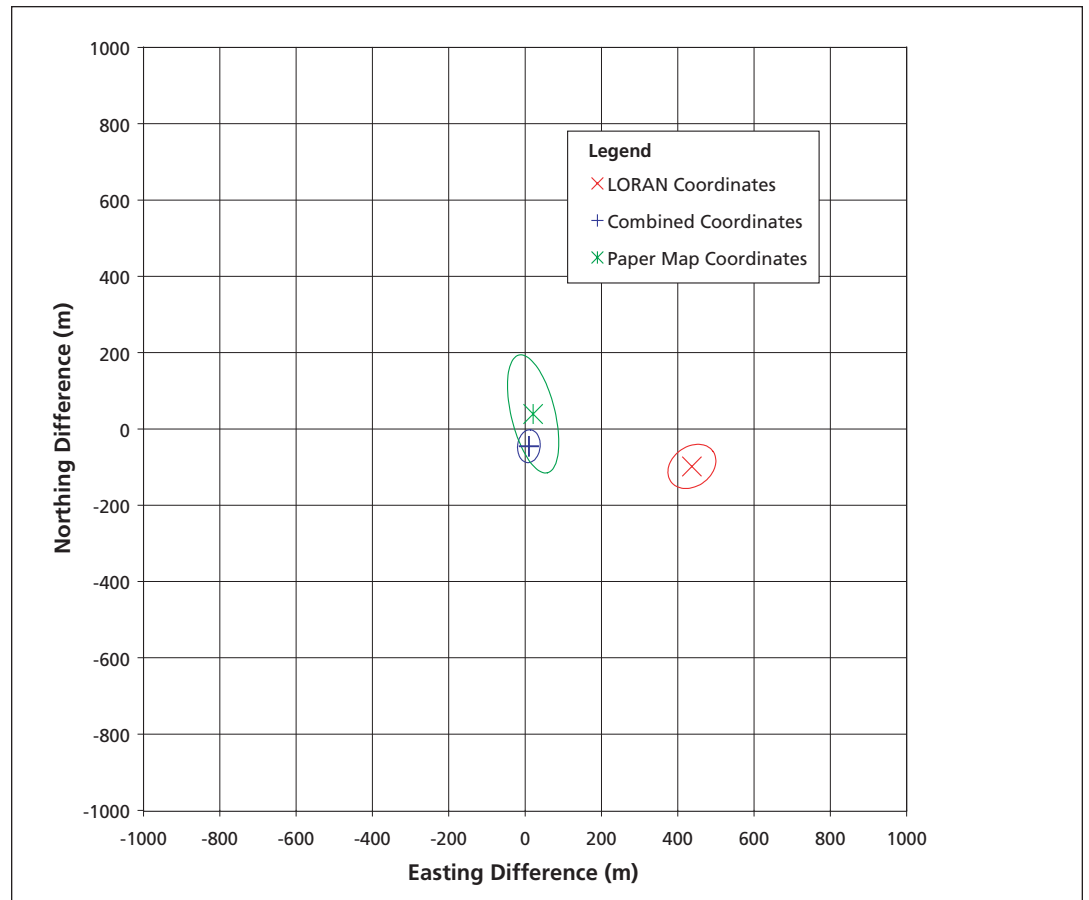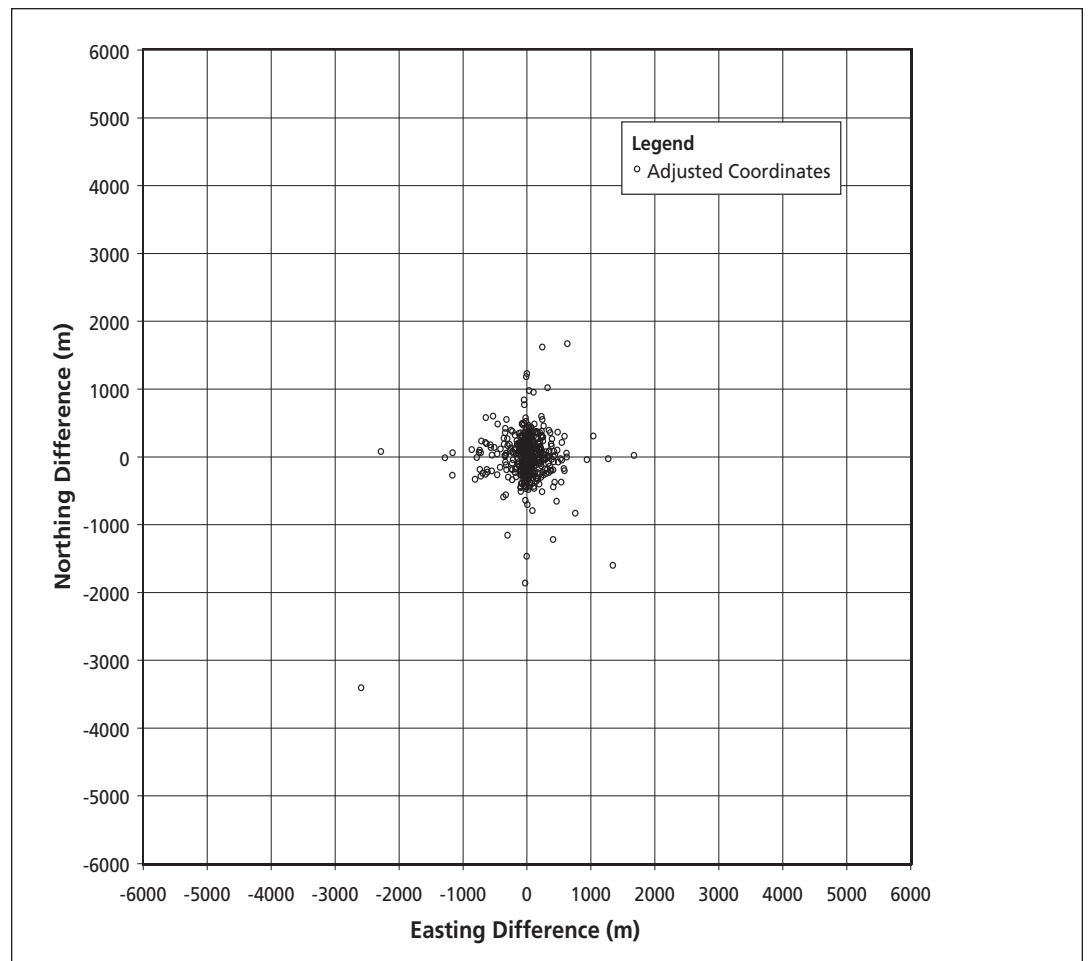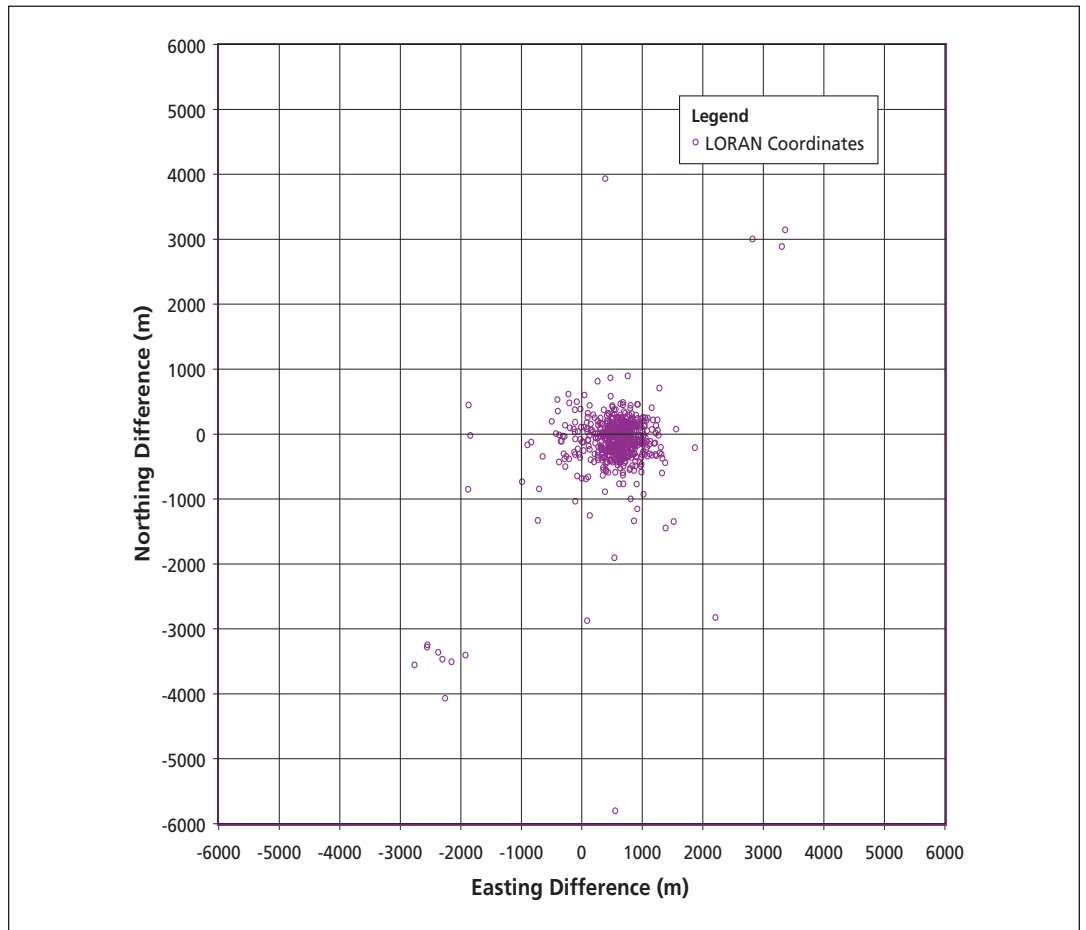

Figure 6. Ninety-five percent confidence ellipse for locational discrepancies (m) between LORAN-C x-y coordinates and digitally mapped coordinates for aerial-telemetry locations of wolves in the Voyageurs National Park region, Minnesota, 1989–1991. Differences were calculated by subtracting LORAN-C coordinates from unbiased, digitally mapped coordinates.
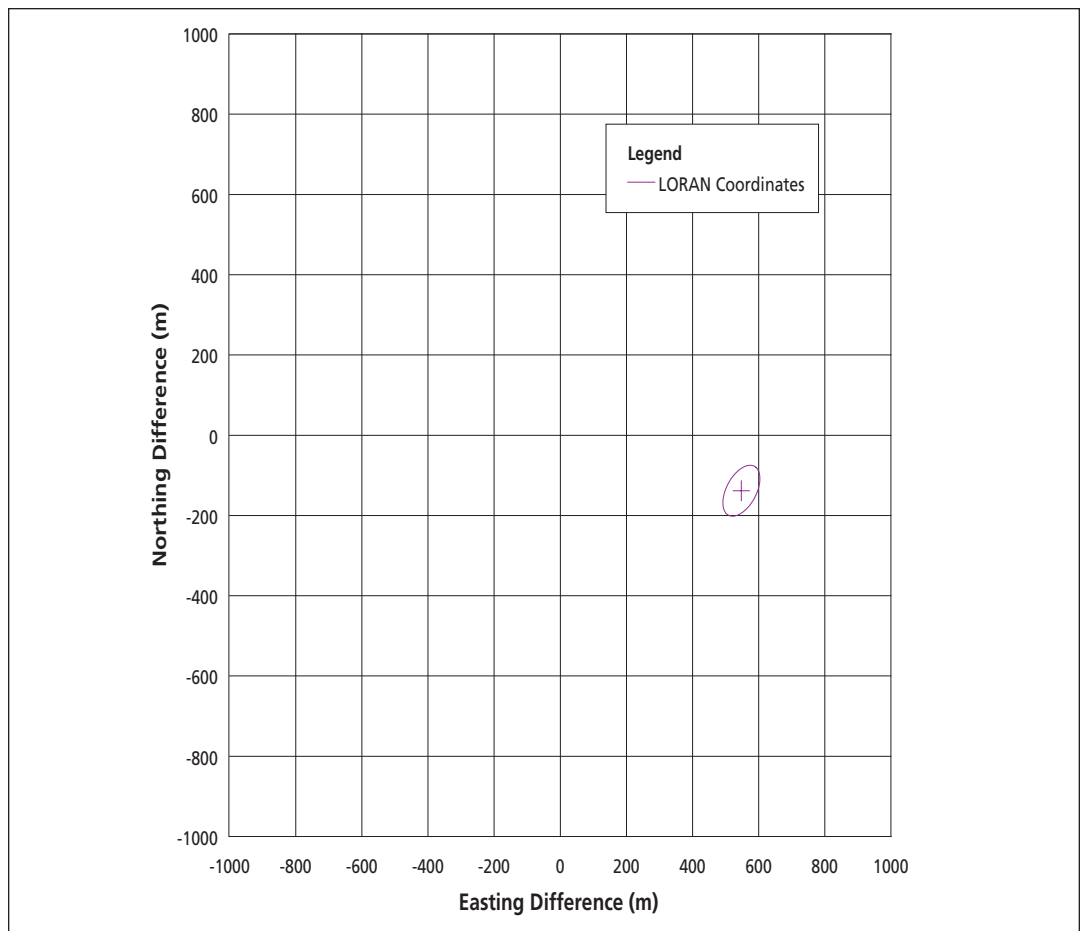
These results provided an example of how it may be possible to correct previously unreported or uncorrected bias.

the level of accuracy provided by bias-adjusted LORAN-C is sufficient for study objectives, we recommend using bias-adjusted LORAN-C. Regardless of the location estimate method chosen, a more objective means of excluding potentially low-quality location data may be developed following Keating (1994).

Global positioning systems (GPS) technology has essentially replaced LORAN-C in recent years because of low cost and increased precision (Leptich et al. 1994, Carrell et al. 1997). However, location data may exist based on previously gathered LORAN-C results. Therefore these results provided an example of how it may be possible to correct previously unreported or uncorrected bias. In the case of other studies conducted in the same study area during the same period (e.g., white-tailed deer and moose), adjustments based on wolf location discrepancies may be used to correct these locations.

Appendix 3. Examples of use of Program Mark in analysis of survival of instrumented wolves in and adjacent to Voyageurs National Park, Minnesota.

Example of Known Fates model data entry in program MARK

Encounter histories files included seasonal records for radio-marked gray wolves and facilitated Known Fates models in program MARK. Known Fates models were able to document both live and dead captures or relocations. Data were coded in the encounter histories file with a series of "1"s or "0"s, entered in pairs, to represent either live or dead encounters via radiotelemetry.

Examples of encounters included:

"10" = live on encounter occasion (includes initial capture occasion and subsequent relocations)
"11" = dead on encounter occasion

Consider the following excerpt from an encounter histories file:

```
/* 4.6375B     89−90   pack   A F P I   */   00 10 10 00   0 1;
/* 4.6375B     89−90   disp   A F N B   */   00 00 00 10   0 1;
/* 4.6375B     90−91   pack   A F P B   */   10 10 10 10   0 1;
/* 4.6375B     91−92   pack   A F P B   */   10 00 00 00   0 1;
```

Known Fates models were able to document both live and dead captures or relocations.

Data within the "/*   */" are comments and are used to break down the data into appropriate periods. Thus, the same animal can be coded several ways, even in a given year. All four lines are for animal 4.6375. The first two lines represent the biological year 1989−1990, the third line represents the biological year 1990−1991, and the fourth line represents the biological year 1991−1992. This animal was an adult during each year (A). It was a female (F). For seasons two and three of year 1989−1990, immediately after being trapped, it belonged to packs (P) whose home ranges were in VNP (I). It dispersed from the pack and was a non-pack member (N) during season four in 1989−1990. During this period its range bordered VNP. From the first season in 1990−1991 to the end of the study it belonged to a new pack. This pack's home range bordered VNP every biological year. In this excerpt, the code at the end of each line first includes data on survival for the given periods. There are four sets of two numbers representing each of the four seasons of the biological year. Survival codes for each season include "10" (found alive) or "11" (found dead). This animal did not die during the study period so there was never a "11" in the data string. In this example, the last two single numbers in each line represent a pack animal "1 0" or a non-pack animal "0 1". This code changes for the particular model that was run depending on the research hypothesis being investigated (e.g., age, sex, pack status, home range location).

(Continued)

Survival by age and time of year
/*

Comments (/*   */) included in each row:

   Wolf ID
   Wolf year
   Age class—pup, adult
   Sex—male, female
   Pack status—pack member, non-pack animal (disperser, loner, unknown)
   Location of pack home range (pack members) or individual home range (non-pack members) relative to VNP—in VNP, bordering VNP, out of VNP

Encounter histories entered seasonally within wolf years, August–April 1987–1991:

   10 = confirmed alive via radiotelemetry within season,
   11 = confirmed dead via radiotelemetry within season

Data codes:

   1 0 = adults,
   0 1 = pups
*/

```
/*  4.4375      88–89   pack   A M P I   */   10 10 10   1 0;
/*  4.4375      89–90   pack   A M P I   */   10 00 00   1 0;
/*  4.4375      89–90   disp   A M N B   */   00 10 00   1 0;

/*  4.4625      87–88   pack   P M P B   */   10 11 00   0 1;

/*  4.4875      87–88   none   A F N B   */   10 10 10   1 0;
/*  4.4875      88–89   none   A F N B   */   10 00 00   1 0;

/*  4.5125      87–88   pack   P F P B   */   10 10 10   0 1;
/*  4.5125      88–89   pack   A F P B   */   10 10 10   1 0;
/*  4.5125      89–90   pack   A F P B   */   10 10 11   1 0;

/*  4.5375      88–89   pack   A F P O   */   10 10 10   1 0;
/*  4.5375      89–90   pack   A F P O   */   10 00 00   1 0;
/*  4.5375      89–90   disp   A F N B   */   00 10 00   1 0;

/*  4.5620      89–90   pack   A F P I   */   10 10 10   1 0;
/*  4.5620      90–91   pack   A F P I   */   10 10 10   1 0;

/*  4.5625      88–89   none   A M N B   */   10 11 00   1 0;

/*  4.5870      89–90   pack   A F P B   */   10 00 00   1 0;

/*  4.6125      90–91   pack   P M P B   */   10 10 00   0 1;

/*  4.6130      88–89   unkn   A F N O   */   10 10 00   1 0;

/*  4.6375A     88–89   pack   A F P O   */   10 00 00   1 0;

/*  4.6375B     89–90   pack   A F P I   */   10 10 00   1 0;
/*  4.6375B     89–90   disp   A F N B   */   00 00 10   1 0;
/*  4.6375B     90–91   pack   A F P B   */   10 10 10   1 0;
```

```
/* 4.6625A     88–89   pack   A MP O    */   10 00 00   1 0;
/* 4.6625A     88–89   disp   A M N O   */   00 10 11   1 0;

/* 4.6625B     89–90   pack   A F P B   */   10 10 11   1 0;

/* 4.6875A     89–90   pack   P F P B   */   11 00 00   0 1;

/* 4.6875B     89–90   pack   A F P B   */   10 10 10   1 0;
/* 4.6875B     90–91   pack   A F P B   */   10 10 10   1 0;

/* 4.7125      88–89   pack   A F P O   */   10 10 00   1 0;
/* 4.7125      88–89   disp   A F N O   */   00 00 10   1 0;

/* 4.7615      89–90   pack   P MB P    */   10 00 00   0 1;

/* 6.7375A     88–89   unkn   A MN B    */   10 11 00   1 0;

/* 6.7375B     90–91   pack   A MP I    */   10 10 10   1 0;

/* 6.7625      88–89   pack   P MB I    */   10 10 11   0 1;

/* 6.7870      88–89   pack   A MP B    */   10 11 00   1 0;

/* 6.8125B     90–91   pack   A F P B   */   10 10 00   1 0;
/* 6.8125B     90–91   disp   A F N B   */   00 00 10   1 0;

/* 6.8375      90–91   pack   A MP B    */   10 11 00   1 0;

/* 6.8380      88–89   pack   A MP O    */   10 10 00   1 0;
/* 6.8380      88–89   disp   A MN B    */   00 00 11   1 0;

/* 6.8635      90–91   pack   A MP B    */   10 10 10   1 0;

/* 6.8880A     88–89   pack   P F P O   */   10 00 00   0 1;

/* 6.8880B     89–90   pack   A F P B   */   10 10 10   1 0;

/* 6.9125A     88–89   pack   P F P B   */   10 11 00   0 1;

/* 6.9125B     89–90   pack   A F P O*  /    10 10 10   1 0;
/* 6.9125B     90–91   pack   A F P O   */   10 10 10   1 0;
```

Adult survival by sex and time of year
/*

Comments (/*   */) included in each row:

    Wolf ID
    Wolf year
    Age class—pup, adult
    Sex—male, female
    Pack status—pack member, non-pack animal (disperser, loner, unknown)
    Location of pack home range (pack members) or individual home range (non-pack
    members) relative to VNP—in VNP, bordering VNP, out of VNP

Encounter histories entered seasonally within wolf years, August–April 1987–1991:

    10 = confirmed alive via radiotelemetry within season,
    11 = confirmed dead via radiotelemetry within season

Data codes:

    1 0 = males,
    0 1 = females
*/

```
/*  4.4375      88–89    pack    A M P I    */   10 10 10 10    1 0;
/*  4.4375      89–90    pack    A M P I    */   10 10 00 00    1 0;
/*  4.4375      89–90    disp    A M N B    */   00 00 10 00    1 0;

/*  4.4875      87–88    none    A F N B    */   00 10 10 10    0 1;
/*  4.4875      88–89    none    A F N B    */   10 10 00 00    0 1;

/*  4.5125      88–89    pack    A F P B    */   10 10 10 10    0 1;
/*  4.5125      89–90    pack    A F P B    */   10 10 10 11    0 1;

/*  4.5375      88–89    pack    A F P O    */   10 10 10 10    0 1;
/*  4.5375      89–90    pack    A F P O    */   10 10 00 00    0 1;
/*  4.5375      89–90    disp    A F N B    */   00 00 10 00    0 1;

/*  4.5620      89–90    pack    A F P I    */   10 10 10 10    0 1;
/*  4.5620      90–91    pack    A F P I    */   10 10 10 10    0 1;
/*  4.5620      91–92    pack    A F P I    */   10 00 00 00    0 1;

/*  4.5625      88–89    none    A M N B    */   10 10 11 00    1 0;

/*  4.5870      89–90    pack    A F P B    */   10 10 00 00    0 1;

/*  4.6130      88–89    unkn    A F N O    */   00 10 10 00    0 1;

/*  4.6375A     88–89    pack    A F P O    */   10 10 00 00    0 1;

/*  4.6375B     89–90    pack    A F P I    */   00 10 10 00    0 1;
/*  4.6375B     89–90    disp    A F N B    */   00 00 00 10    0 1;
/*  4.6375B     90–91    pack    A F P B    */   10 10 10 10    0 1;
/*  4.6375B     91–92    pack    A F P B    */   10 00 00 00    0 1;

/*  4.6625A     88–89    pack    A M P O    */   10 10 00 00    1 0;
/*  4.6625A     88–89    disp    A M N O    */   00 00 10 11    1 0;

/*  4.6625B     89–90    pack    A F P B    */   10 10 10 11    0 1;
```

```
/*  4.6875B    89–90   pack   A F P B   */   10 10 10 10   0 1;
/*  4.6875B    90–91   pack   A F P B   */   10 10 10 10   0 1;
/*  4.6875B    91–92   pack   A F P B   */   10 00 00 00   0 1;

/*  4.7125     88–89   pack   A F P O   */   10 10 10 00   0 1;
/*  4.7125     88–89   disp   A F N O   */   00 00 00 10   0 1;
/*  4.7125     89–90   disp   A F N O   */   10 00 00 00   0 1;

/*  6.7375A    88–89   unkn   A MN B    */   00 10 11 00   1 0;

/*  6.7375B    90–91   pack   A MP I    */   10 10 10 10   1 0;
/*  6.7375B    91–92   pack   A MP I    */   10 00 00 00   1 0;

/*  6.7870     88–89   pack   A MP B    */   00 10 11 00   1 0;

/*  6.8125B    90–91   pack   A F P B   */   10 10 10 00   0 1;
/*  6.8125B    90–91   disp   A F N B   */   00 00 00 10   0 1;
/*  6.8125B    91–92   disp   A F N B   */   10 00 00 00   0 1;

/*  6.8375     90–91   pack   A MP B    */   10 10 11 00   1 0;

/*  6.8380     88–89   pack   A MP O    */   00 10 10 00   1 0;
/*  6.8380     88–89   disp   A MN B    */   00 00 00 11   1 0;

/*  6.8635     90–91   pack   A MP B    */   10 10 10 10   1 0;
/*  6.8635     91–92   pack   A MP B    */   10 00 00 00   1 0;

/*  6.8880B    89–90   pack   A F P B   */   10 10 10 10   0 1;

/*  6.9125B    89–90   pack   A F P O   */   10 10 10 10   0 1;
/*  6.9125B    90–91   pack   A F P O   */   10 10 10 10   0 1;
/*  6.9125B    91–92   pack   A F P O   */   10 00 00 00   0 1;
```

Adult survival by home range location and time of year
/*

Comments (/*   */) included in each row:

    Wolf ID
    Wolf year
    Age class—pup, adult
    Sex—male, female
    Pack status—pack member, non-pack animal (disperser, loner, unknown)
    Location of pack home range (pack members) or individual home range (non-pack members) relative to VNP—in VNP, bordering VNP, out of VNP

Encounter histories entered seasonally within wolf years, August–April 1987–1991:

    10 = confirmed alive via radiotelemetry within season,
    11 = confirmed dead via radiotelemetry within season

Data codes:

    1 0 0 = in VNP,
    0 1 0 = bordering VNP,
    0 0 1 = out of VNP
*/

```
/* 4.4375      88–89   pack   A MP I   */   10 10 10 10   1 0 0;
/* 4.4375      89–90   pack   A MP I   */   10 10 00 00   0 1 0;
/* 4.4375      89–90   disp   A MN B   */   00 00 10 00   0 1 0;

/* 4.4875      87–88   none   A F N B  */   00 10 10 10   0 1 0;
/* 4.4875      88–89   none   A F N B  */   10 10 00 00   0 1 0;

/* 4.5125      88–89   pack   A F P B  */   10 10 10 10   0 1 0;
/* 4.5125      89–90   pack   A F P B  */   10 10 10 11   0 1 0;

/* 4.5375      88–89   pack   A F P O  */   10 10 10 10   0 0 1;
/* 4.5375      89–90   pack   A F P O  */   10 10 00 00   0 0 1;
/* 4.5375      89–90   disp   A F N B  */   00 00 10 00   0 1 0;

/* 4.5620      89–90   pack   A F P I  */   10 10 10 10   1 0 0;
/* 4.5620      90–91   pack   A F P I  */   10 10 10 10   1 0 0;
/* 4.5620      91–92   pack   A F P I  */   10 00 00 00   1 0 0;

/* 4.5625      88–89   none   A MN B   */   10 10 11 00   0 1 0;

/* 4.5870      89–90   pack   A F P B  */   10 10 00 00   0 1 0;

/* 4.6130      88–89   unkn   A F N O  */   00 10 10 00   0 0 1;

/* 4.6375A     88–89   pack   A F P O  */   10 10 00 00   0 0 1;

/* 4.6375B     89–90   pack   A F P I  */   00 10 10 00   1 0 0;
/* 4.6375B     89–90   disp   A F N B  */   00 00 00 10   0 1 0;
/* 4.6375B     90–91   pack   A F P B  */   10 10 10 10   0 1 0;
/* 4.6375B     91–92   pack   A F P B  */   10 00 00 00   0 1 0;

/* 4.6625A     88–89   pack   A MP O   */   10 10 00 00   0 0 1;
/* 4.6625A     88–89   disp   A M N O  */   00 00 10 11   0 0 1;
```

```
/*  4.6625B        89–90    pack     A F P B    */   10 10 10 11    0 1 0;

/*  4.6875B        89–90    pack     A F P B    */   10 10 10 10    0 1 0;
/*  4.6875B        90–91    pack     A F P B    */   10 10 10 10    0 1 0;
/*  4.6875B        91–92    pack     A F P B    */   10 00 00 00    0 1 0;

/*  4.7125         88–89    pack     A F P O    */   10 10 10 00    0 0 1;
/*  4.7125         88–89    disp     A F N O    */   00 00 00 10    0 0 1;
/*  4.7125         89–90    disp     A F N O    */   10 00 00 00    0 0 1;

/*  6.7375A        88–89    unkn     A M N B    */   00 10 11 00    0 1 0;

/*  6.7375B        90–91    pack     A M P I    */   10 10 10 10    1 0 0;
/*  6.7375B        91–92    pack     A M P I    */   10 00 00 00    1 0 0;

/*  6.7870         88–89    pack     A M P B    */   00 10 11 00    0 1 0;

/*  6.8125B        90–91    pack     A F P B    */   10 10 10 00    0 1 0;
/*  6.8125B        90–91    disp     A F N B    */   00 00 00 10    0 1 0;
/*  6.8125B        91–92    disp     A F N B    */   10 00 00 00    0 1 0;

/*  6.8375         90–91    pack     A M P B    */   10 10 11 00    0 1 0;

/*  6.8380         88–89    pack     A M P O    */   00 10 10 00    0 0 1;
/*  6.8380         88–89    disp     A M N B    */   00 00 00 11    0 1 0;

/*  6.8635         90–91    pack     A M P B    */   10 10 10 10    0 1 0;
/*  6.8635         91–92    pack     A M P B    */   10 00 00 00    0 1 0;

/*  6.8880B        89–90    pack     A F P B    */   10 10 10 10    0 1 0;

/*  6.9125B        89–90    pack     A F P O    */   10 10 10 10    0 0 1;
/*  6.9125B        90–91    pack     A F P O    */   10 10 10 10    0 0 1;
/*  6.9125B        91–92    pack     A F P O    */   10 00 00 00    0 0 1;
```

Appendix 4. Number of track encounters, incidental observations, howling responses, radiotelemetry locations and counts during flights for wolf packs studied in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.

Pack Year[a]	Pack	Track Encounters[b]	Incidental Visuals[c]	Howling Responses[d]	Radio-telemetry Locations[e]	Radio-telemetry Counts[f]
1987–1988	Cruiser Lake (CLP)	15	1			
	Browns Bay (BBP)	6				
	Locator Lake (LLP)	16	4			
	Moose Grade (MGP)	4	1			
	Nebraska Bay (NBP)	7				
	Tom Cod (TCP)	5			59	15
	Subtotal	53	6		59	15
	x	9	2		59	15
1988–1989	Blue Moose (BMP)	1			48	7
	Cruiser Lake (CLP)	14	4	w	60	18
	Dixon Creek (DCP)	0			32	0
	Browns Bay (BBP)	7		w	8	0
	Kohler Pit[g] (KPP)	0	4	w	34	0
	Kohler Trio[g] (KTP)	0			14	5
	Locator Lake (LLP)	19	1	w	18	3
	Moose Grade (MGP)	5	1		3	0
	Moose Lake (MLP)	0			32	0
	Nebraska Bay (NBP)	9		w	0	0
	Tom Cod (TCP)	4	1	w	65	11
	Subtotal	59	11	6	314	44
	x	5	2	n/a	29	4
1989–1990	Blue Moose (BMP)				22	0
	Cruiser Lake (CLP)			w		
	Browns Bay (BBP)			w, wo		
	Middle Peninsula (MPP)			w	82	19
	Moose Grade (MGP)			w, w	11	4
	Nebraska Bay (NBP)			wo	62	11
	Rat Root (RRP)				25	9
	Tom Cod (TCP)				78	12
	Subtotal	0	0	5	280	55
	x	n/a	n/a	n/a	47	9
1990–1991	Cruiser Lake (CLP)			wo	63	10
	Browns Bay (BBP)				115	10
	Middle Peninsula (MPP)				66	17
	Moose Grade (MGP)				104	10
	Nebraska Bay (NBP)				41	3
	Rat Root (RRP)				66	9
	Tom Cod (TCP)			w	66	8
	Subtotal	0	0	2	521	67
	$\overline{x}$	n/a	n/a	n/a	74	10
	Total	112	17	13	1,174	181

[a]Pack year defined as May 1 through April 30.
[b]Tracks that could be attributed to a known pack (>2 wolves); winters of 1987–1988 and 1988–1989 only.
[c]Visual counts of pack (>2 wolves) other than during radio-telemetry flights.
[d]Pack (>2 wolves) heard howling; w = with pups, wo = without pups; underlined letters denote incidentals, see text.
[e]Cumulative number of locations for all collared wolves in the pack this period.
[f]Visual count of pack (>2 wolves) during telemetry relocation flight.
[g]KPP either dispersed as the KTP or divided into two groups; see text.

Appendix 5. Histories of radio-marked wolves and wolf packs studied in and adjacent to Voyageurs National Park, Minnesota, 1987–1991.[1]

Tom Cod Bay Pack (TCP)

198 7–1988: This was the first pack radio-marked during the study and the only pack radio-marked for the first eight months. During the fall of 1987, male pup 4625 and female pup 5125 were captured and radio-marked along old logging roads south of Tom Cod Bay off park lands. The male pup was shot illegally in early November 1987 during the small-game hunting season. The female continued to associate with the TCP for more than two years until she died from undetermined causes in December 1989. After observing five wolves consistently during telemetry flights the winter of 1987−1988, the pack was observed on 2 March as four animals. The pack was subsequently tracked on the ground on 5 March to a site where one wolf was illegally trapped and killed as evidenced by blood, wolf hair, wolf scat, and tracks, which showed five wolves came to the site and only four wolves left. The wolves had been following a snowmobile trail southwest of Tom Cod Bay. The mid-winter estimate of pack size was five wolves. From visual counts and trapping histories, this pack was at least six wolves in fall 1987. Two wolves (33%) were illegally killed by humans between fall 1987 and the end of March 1988.

1988−1989: Female pup 5125 from the previous year was still with the TCP, now as a yearling. Adult male 7870 was captured in August 1988, but was illegally shot in early November. Adults and pups responded to simulated howls during the 1988 fall survey. From sightings during winter telemetry flights we estimate the mid-winter pack size was five wolves. The TCP territory was primarily south of Black Bay in 1988−1989. Of 65 telemetry locations, the pack was only located on the Kabetogama Peninsula twice (3%).

1989−1990: Female 5125 continued to associate with the pack, but died from undetermined causes in December 1989. In May, adult female 6875B was captured and this wolf remained with the pack for the rest of the study. The pack did not respond to simulated howls the fall of 1989. No tracking was

conducted the winter of 1989−1990, but from sightings during telemetry flights the mid-winter pack size was again five wolves. In 1989−1990 the TCP began ranging farther north and west onto the Kabetogama Peninsula. Along with this change in territory came an extensive overlap with the newly formed MPP who we believe split from the CLP and displaced the LLP (see LLP, MPP, and CLP histories).

1990−1991: Adult female 6875B continued to occupy a territory that included the western one-third of the Kabetogama Peninsula, and she was now the only radio-marked wolf in the TCP. The pack did not respond to simulated howls during the fall 1990 survey, and during winter telemetry flights 6875B was observed with only one other wolf. This pair used a well-delineated territory, about half of which now included the Kabetogama Peninsula.

Locator Lake Pack (LLP)

1987−88: This pack was not radio-marked in 1987−1988, but from repeated track encounters and incidental visual counts the mid-winter pack size was estimated as three wolves. However, tracks suggest a fourth wolf accompanied them occasionally or scavenged from their kills. For example, on 19 February 1988 I jumped a wolf off Sugarbush Island while investigating a kill made by three wolves on the island. This wolf could have been one of the three wolves returning for a meal; however, repeated observations of a single wolf track disassociated from tracks of three suggest a fourth animal.

1988−1989: In fall 1988 male pup 7625 was radio-marked in the LLP. The pack did not respond to simulated howls during the routine fall survey, but unsolicited howls were heard from a pack northwest of Locator Lake in early October. During early winter telemetry flights, the pack was counted once as seven wolves. Until late January 1989 the LLP territory was non-overlapping with the adjacent CLP, which was also radio-marked and with eight wolves (see also CLP history). On 20 January all eight members of the CLP were located well within the known territory of LLP and 7625 (LLP pup) was located in mortality

mode. We subsequently found 7625 and one other wolf dead from wolf-inflicted wounds. Previous radio locations for both packs were on 28 December, but based on sign (snow tracks and the lack of scavenging) we estimate the two packs collided sometime between 12 and 19 January. All eight members of CLP were located on 20 January, so the unmarked dead wolf was also from the LLP. After losing radio contact with LLP we were unable to confirm their existence, though tracks suggest that two to four wolves persisted in the area in addition to at least five members of the CLP who ranged widely throughout LLP's territory and the entire Kabetogama Peninsula.

Middle Peninsula Pack (MPP)
1989–1990: During the winter of 1989–1990 a pack of five wolves, including male 4375, originally of CLP, and newly radio-marked adult females 5620 and 6375B, continued to roam across most of the Kabetogama Peninsula. Three factors indicate that this pack of five originated from CLP to form the MPP pack. First, all eight CLP wolves were observed together within days of the territorial dispute with LLP during winter 1988–1989, yet on 12 subsequent observations CLP male 4375 was never observed with more than four other wolves and that group roamed widely into LLP territory. Pack size was four or five on six (50%) of the observations and one to two on six (50%) of the observations. We could not account for the remaining three CLP wolves that winter. Second, during howling surveys in fall 1989, packs with pups responded to simulated howls at three howling sites within the original (1988–1989) CLP territory. These sites were separated by more than 12 km and, while wolves will easily cover this distance in a day, male 4375 and females 5620 and 6375B were associated with only one of the howling sites (K8). And though they could not be excluded from having been at the second site (R6), they were never located near the third site (N8) and were 30 km away the day of the howling response at R6. Finally, 4375, 5620, and 6375B spent very little time on the eastern end of the peninsula in 1989–1990, and by 1990–1991 female 5620 (the other two had dispersed by this time) was consistently in the central portion of the peninsula between the TCP and a newly radio-marked pack on the east end of the peninsula. This newly radio-marked pack now occupied a somewhat smaller version of the original 1988–1989 CLP territory.

Two of the MPP wolves began making forays off the peninsula in 1989–1990 and later dis-

persed or disappeared. Male 4375 made forays to the southwest in late October 1989. He was located four times off the Kabetogama peninsula deep into TCP territory, and on 21 October he was located in close proximity to TCP female 5125. Male 4375 was last located on 3 November, 27 km southwest of Black Bay. His disappearance was preceded by dispersal-type movements, but with the deer hunting season beginning about the time of his disappearance, human involvement could not be ruled out. The wolf was officially listed as "missing." Female 6375B was located directly south along the Moose River corridor on more than 14 occasions. By 30 April 1990 she had dispersed from the MPP and had joined with two other wolves to occupy the MGP territory (see MGP history starting 1990–1991).

1990–1991: By the winter of 1990–1991 the MPP numbered nine wolves, including adult female 5620. The pack consistently occupied the center of the Kabetogama Peninsula. MPP's territory was well defined between TCP and CLP in contrast to the wide-ranging and extensively overlapping situation the previous year. Whatever social disruption occurred during winter 1989–1990, pack territories were well sorted by the winter of 1990–1991.

Cruiser Lake Pack (CLP)
1987–1988: The CLP was not radio-marked in 1987, but from snow tracks the pack was estimated at eight wolves during winter 1987–1988, and they occupied the eastern portion of the Kabetogama Peninsula.

1988–1989: In May, 1988 adult male 4375 was radio-marked and in September adult alpha female 8125A was radio-marked. The alpha female was lactating, and pups were heard yipping around the trap site as she was being fitted with a radio collar before release. This female was found dead from malnutrition 20 days later. Necropsy at the USFWS lab in Madison, Wisconsin, revealed that a stick was wedged between her upper carnasial teeth on the pallet of her mouth, which likely inhibited proper feeding. It probably became wedged in her mouth when she bit down on sticks and saplings at the capture site. Meanwhile, male 4375 continued to occupy the eastern end of the Kabetogama Peninsula. The death of 8125A, the alpha female of CLP, may have lead to the territorial dispute with the LLP followed by a splitting of CLP and subsequent formation of the MPP.

We received no howling response within CLP territory during howling surveys in fall 1988, but unsolicited howls were heard from a pack with pups just north of Ek Lake in CLP territory. Early winter telemetry flights verified there were eight wolves in the CLP, and they occupied the eastern half of the Kabetogama Peninsula. Between radio locations on 28 December and 20 January, however, the CLP began moving west into LLP's territory. On 20 January the LLP pup (7625) was located in mortality mode and the CLP, consisting of eight wolves, was located on the boundary of LLP and CLP territories. We recovered the carcass of the LLP pup within 24 hours of the last location, and at the site we found another unmarked wolf, both dead from wolf-inflicted wounds. From the profusion of wolf tracks, blood, wounds on the carcasses, and the lack of scavenging, we surmised that the two packs had collided sometime during the week preceding 20 January and that two LLP wolves (all eight CLP wolves were observed on 20 January) were killed in the ensuing fight. Thereafter, at least five members of the CLP pack continued to roam across the peninsula and were often located in LLP's territory. As evidenced from telemetry the following year, we believe five wolves from the original CLP of eight split off and took over the LLP territory. In 1989−1990 these five wolves became the MPP (see LLP and MPP descriptions). Whether the remaining three CLP animals continued to occupy the Cruiser Lake area is not known (but see below).

1989−1990: The CLP likely existed at the far eastern end of the Kabetogama Peninsula, but the pack was not radio-marked and snow tracking was not done during this winter. The newly formed MPP, including male 4375 who originated from the CLP, roamed across the Kabetogama Peninsula, but they were located only occasionally on the far eastern end. During howling surveys in fall 1989, packs with pups responded to simulated howls from three sites within the original (1988−1989) CLP territory. At least one and possibly two of these sites were associated with the MPP, but the response from site N8 was likely the CLP. The wolves were heard on the evening of 9 October, and on 8 October the MPP was radio-located 30 km away at the far western end of the peninsula. The MPP could have easily covered that distance in the elapsed time, but MPP continued to be located on the western end of the peninsula the rest of October, and at no time were they located within 3.5 km of this howling site.

1990−1991: Adult male 7375B was radio-marked in CLP territory in May 1990 and was consistently located on the east end of the Kabetogama Peninsula with five other wolves. The territorial boundary between MPP and CLP was well delineated. A pack (no pups were heard) responded to simulated howls during the fall 1990 howling survey. They howled from the same location as the previous fall survey (N8), providing further evidence that a third pack existed on the Kabetogama Peninsula in 1989−1990. These wolves may have originated from three wolves that remained in the CLP territory after the LLP and CLP clashed in January 1989.

Moose River Grade Pack (MGP)
1987−1988: No wolves were radio-marked in the MGP territory in 1987−1988, but a large pack was snow tracked on four occasions. Twice tracks of between 9 and 11 wolves were encountered and tracks on 23 January indicated at least four were pups. Blood was observed in scent marks (urine) of one adult wolf suggesting the pack contained a female in estrous. On 9 March during a telemetry flight for other radio-marked wolves, a pack of 11 wolves, believed to be the MGP, was observed and photographed on the ice of Little Johnson Lake.

1988−1989: In September, 1988, female pup 6875A was radio-marked west of Junction Bay, but this pup died from undetermined causes within four days. No wolves responded to simulated howls in fall 1988. From snow tracks and one incidental observation of eight wolves on Franklin Lake (22 November), this pack was estimated at eight wolves during winter 1988−1989.

1989−1990: In August 1989, male pup 7615 was radio-marked, but this pup dropped its collar within nine days. During the fall 1989 howling survey, a pack with pups responded to simulated howls from southeast of Hoist Bay. With no wolves radio-marked and no snow tracking, no estimate on pack size was available.

By January 1990, radio-marked adult female 6375B was making dispersal-type movements from the MPP south along the Moose and Ash Rivers which was considered the western boundary of the MGP territory. This wolf later settled in to the MGP territory (see following).

1990−1991: Adult female 6375B dispersed from the MPP and occupied the MGP terri-

tory by May 1990. However, she returned to the peninsula occasionally as evidenced by five telemetry locations in her original MPP territory. In May, adult male 8375 was radio-marked and, along with 6375B and one unmarked wolf, comprised the MGP and occupied a well-delineated territory between BBP to the east and NBP to the west.

Browns Bay Pack (BBP)
1987–1988: A large pack of four to seven wolves was snow tracked in the Browns Bay area and on 29 February tracks of seven wolves were followed from Hammer Bay to Grassy Bay, a distance of approximately 11 km over numerous islands, peninsulas, and lake ice. It was previously reported that 11 wolves observed on Little Johnson Lake were the BBP; however, we now believe these were the MGP (see MGP history) and from snow tracks we estimate the minimum size of BBP was seven this winter.

1988–1989: Female pup 9125A was radio-marked southwest of Browns Bay in September 1988, but was later found dead from starvation. A pack with pups responded to simulated howls from southeast of Staege Bay during the fall 1988 howling survey. Snow tracks provided a minimum estimated nine wolves in the BBP this winter.

1989–1990: No wolves were radio-marked during this census period, and tracking was not conducted in winter 1989–1990; however, a pack with pups responded to simulated howls west of Browns Bay during fall 1989. A pack with pups also responded to simulated howls south of Hoist Bay within MGP territory, further supporting our belief that there were two packs between Moose River and Crane Lake (see also MGP history). Unfortunately, there are no data available to estimate pack size for BBP during this period.

1990–1991: In May 1990, two adult wolves, female 8125B and male 8635, were finally radio-marked from the BBP. A pup was also radio-marked in September, but the radio collar dropped off. Only a lone wolf responded to simulated howls from west of Browns Bay in fall 1990. From direct visual counts during telemetry flights, minimum pack size was estimated as nine wolves during the winter of 1990–1991 and the territory was well defined.

Nebraska Bay Pack (NBP)
1987–1988: From snow tracks it was estimated a minimum of two wolves used the Nebraska Bay area this winter. However, a pack of six wolves traveled from Nebraska Bay north to the Kabetogama Peninsula on 22 March. Possibly these were tracks of a portion of the CL (eight wolves). Yet a larger pack has existed in the Nebraska Bay area in the recent past. Unsolicited pack howls were heard by one of the authors (Route) from east of Daley Bay during fall 1986, and Minnesota Conservation Officer Lloyd Steen observed and counted five wolves in winter 1986–1987 on the Meadwood Road.

1988–1989: A pack with pups responded to simulated howls in fall 1988 from south and east of Nebraska Bay, and from snow tracks the NBP was estimated at five wolves in 1988–1989. The territory was delineated by howls, tracks, and from knowledge of adjacent territories (see KPP and MGP).

1989–1990: In May 1989, adult females 5870 and 8880B were captured and radio-marked in the NBP, and during the fall howling survey a pack (adults only) responded to simulated howls from south of Nebraska Bay. The two radio-marked wolves provided the first telemetry-aided glimpse of the NBP territory; however, 5870 disappeared after she was located on 29 September and 8880B died of unknown causes. Her radio collar and skeletal remains were found in November 1990 about 64 km southwest of Nebraska Bay. The mid winter estimate of pack size was six based on visual counts. At least seven wolves were present in fall (5870 disappeared in September). By spring the pack had dropped to at least five with the loss of 8880B and may have dropped as low as two based on visuals, though sample size was too low to be certain ($n = 2$ visuals after February). Sufficient telemetry data existed to get a good estimate of territory size even with the loss of both radio-marked wolves.

1990–1991: Adult female 6625B was captured in May 1990 and remained in the NBP territory until at least 19 November when she was last located. Her radio collar was detected in mortality mode on 13 December about 21 km south of the NBP territory. She was killed by other wolves. This wolf provided a reasonable delineation of pack territory through mid-November, but with minimal visual counts, the pack size estimate of three must be considered a minimum.

Kohler Pit (KPP) and Kohler Trio (KTP) Packs
In April 1988, project personnel were informed that a couple living near the corner of Highway 53 and the Ash River Trail were feed-

ing wolves. We visited the couple and found that they had been feeding meat scraps and dog food to wolves for several months. The couple said they began feeding a coyote who came around their house, but later this coyote was displaced by wolves. They were placing food at the edge of their yard about 30 m from their home. They had named the wolf that consistently came to the food pile, and they observed other less bold wolves further back in the woods. They had Polaroid photographs, taken from their kitchen window, of an adult wolf at the edge of their yard as evidence. Reportedly, the man was eventually able to stand outside his door near the house while the wolf grabbed food off the food pile. We told the couple that feeding wildlife was not a good idea, but clearly this was a highlight of their evenings and they were not going to give it up easily.

We explained that their feeding likely contributed to her being hit since she had to cross a major highway to get to the food.

On 11 May a lactating adult female (6375A) was captured and radio-marked along the Kohler Pit Road. She was subsequently found to occupy an area centered to the south of Highway 53, but she was often located near the corner of Highway 53 and the Ash River Trail. The couple that was feeding wolves subsequently reported "their" wolf was limping slightly. We informed them we may have trapped and radio-marked the wolf. They later confirmed they could see the collar. On 11 June this female was accidentally hit at night on highway 53 by a vehicle driven by a VNP employee. A telemetry location the following day found her near an uprooted tree south and west of where she was hit. She was found at the same location four days later, but during the next flight, eight days after the accident, she had moved. The couple later reported she had returned to feed at their home. We explained that their feeding likely contributed to her being hit since she had to cross a major highway to get to the food. However, they now wanted to feed her all the more, believing the food would get her and her pups through this injury.

On 25 July a park employee reported that at ~10:15 p.m. five to seven wolves, "several" believed to be pups, were playing on the Ash River Trail near the corner of Highway 53. This pack responded to simulated howls (not as a part of a survey) on several occasions in late July and early August. Again on 11 and 12 August, two different park employees reported observing three pups on the Ash River Trail near the corner of Highway 53. One observer was able to stop her vehicle, get out, and take several steps towards the pups before they ran off the road. She described being able to see the yellow eyes.

On 29 August a wolf pup was found dead from a vehicle collision on Highway 53 about 400 m southeast of the corner of Ash River Trail. The couple finally stopped feeding the wolves after being told of this pup's death. The radio-marked female continued to be located in her territory, but on 6 October her radio was detected in mortality mode. The radio collar was found later that day with the collar-belting and antennae cable chewed completely through. We presume her pups or other wolves had chewed the collar off during routine social activities of the pack.

On 25 September adult male 8380 was captured and radio-marked. This male was located near the alpha female of the KPP (6375A) on one occasion before she lost her collar. He continued to occupy the same territory delineated from locations of the alpha female. We presume this male was a member of the KPP, and from the above incidental observations this pack went into winter with at least two adults and two pups (three observed but one later killed, see above). By late November this male had dispersed northwest and was observed twice with two other wolves. Several locations of this pack of three were centered west of the TCP territory south of Black Bay, but on 15 March all three were observed northeast of Brule Narrows in Canada more than 16 km from the KPP territory. This pack of wandering wolves was named the Kohler Trio Pack (KTP). Wolf 8380 was located south of Black Bay again, but was found dead in April from injuries inflicted by other wolves. Likely these three wandering wolves met up with the TCP. Except for this wandering pack of three wolves, the disposition of the KPP was unknown during winter 1988–1989. Because it was at the edge of the study area, the pack was not trapped in the remaining years of the study.

Blue Moose Pack (BMP)
1988–1989: A lactating adult female wolf (5375) was captured and radio-marked off logging roads south of VNP in May 1988, and her pup, female 8880A, was radio-marked that September. The pup provided little data on movements because her collar dropped off 15 days after capture. The female provided sufficient data to delineate the BMP territory. The female was observed with one adult wolf in winter 1988–1989, but the pup was not observed.

1989–1990: Female 5375 continued to occupy the BMP territory until mid-October 1989 when she dispersed north then west from her territory. She was last located on 30 October more than 8 km from the center of her territory. The cause of her disappearance was never determined, and no effort was expended to radio-mark this pack again. Very little snow tracking and no howling was done in this area.

Dixon Creek Pack (DCP)
1988–1989: Adult male 6625A was captured and radio-marked in May 1988 and provided some information on the location of this pack until early October when he dispersed southwest to the Chub Lake area. This male was located in mortality mode and later found dead from a wire snare on 15 March 1989. This pack territory was not trapped for study purposes again because it was outside of the study area. No snow tracking and no howling was done in this area.

Moose Lake Pack (MLP)
1988–1990: Adult female 7125 was captured and radio-marked in May 1988. She provided a reasonable estimate of a territory boundary, but dispersed west to the Nett Lake area in late November. She was never observed while in the Moose Lake area and was observed only once, alone, while in the Nett Lake area. She was last located on 17 February 1990 while we flew at a search altitude of 1,525 m south of Nett Lake. No snow tracking and no howling was done in this area.

Appendix 6. Calculations for estimating biomass and number of prey represented in 123 scats collected during summer 1987 and 1988 in and adjacent to Voyageurs National Park, Minnesota.

Prey	Estimated Prey Biomass (kg)	Prey Biomass (kg)/scat	No. of Scats With Prey Item	Prey Biomass (kg) Consumed	Ratio of Biomass Consumed to Adult Deer	No. of Individuals Eaten (Prey Biomass/ Biomass Consumed)	Ratios of Individuals Eaten to Adult Deer
Adult deer[b]	62.9	0.94	68.5	64.57	1.000	1.0	1.00
Beaver[c]	13.3	0.55	29.0	15.82	0.24	1.2	1.1
Moose[d]	247.5	2.42	2.0	4.84	0.07	0.02	0.0
Fawn deer[e]	7.1	0.50	16.0	7.93	0.12	1.1	0.4
Livestock[f]	25.0	0.64	1.0	0.64	0.01	0.03	0.0
Muskrat[g]	1.2	0.45	2.5	1.12	0.007	0.9	0.2
Snowshoe hare[h]	1.3	0.45	1.5	0.67	0.004	0.5	0.2
Other[i]	0.1	0.44	2.0	0.88	0.005	10.1	2.7
Grouse[j]	0.68	0.44	0.5	0.29	0.001	0.3	0.1

Note: Calculations for biomass follow Weaver (1993) where Y = 0.439 + 0.008 X and Y= kg of prey biomass consumed/scat and X = estimated weight of prey animals.

[a]In scats with 2 prey types (14.5%), each was assigned an occurrence of 0.5 for biomass calculations.

[b]Adult deer = Based on an observed summer kill ratio of 2 yearlings to 15 "adults" with assumed even-sex ratios for yearlings and an observed sex ratio of 6 females to 3 males for adults. Estimated yearling weights = 48.8 kg (Sauer 1984) adult does = 57.7 kg (Kunkel and Mech 1994) and adult bucks = 79.1 kg (M. Nelson unpublished data).

[c]Beaver = Based on an assumed kill ratio of 1 kit to 2 yearlings to 1 adult and weights of 6.3 kg, 13.5 kg, and 20 kg, respectively (D. Smith unpublished data).

[d]Moose = Based on an assumed kill of 1 calf (June) to 1 adult (July) and weights of 14.5 kg and 480 kg, respectively (Bubenik 1998).

[e]Fawn deer = Based on 2 occurrences in May, 2 in June, 8 in July, and 5 in August with mid-month calf weights estimated using Y = 2.74 + 0.075 X where X = days since birth (Kunkel and Mech 1994).

[f]Livestock = Based on 1 occurrence assumed to be a calf with estimated weight of 25 kg (Spector 1956; cited in Fritts and Mech 1981).

[g]Muskrat = Assumed weight of 1.2 kg (Perry 1982).

[h]Snowshoe hare = Assumed weight of 1.3 kg (Bittner and Rongstad 1982).

[i]Other = Based on 1 occurrence of an unknown bird and 2 occurrences of small rodents assumed to be microtines with estimated weights of 20 g (Terres 1991) and 3 g (Johnson and Johnson 1982), respectively.

[j]Grouse = Assumed weight of 68 g (Terres 1991).

Appendix 7. Calculations for estimating biomass and number of prey represented in 97 scats collected during winter 1987 and 1988 in and adjacent to Voyageurs National Park, Minnesota.

Prey	Estimated Prey Biomass (kg)[a]	Prey Biomass (kg)/Scat	No. of Scats With Prey Item[a]	Prey Biomass (kg) Consumed	Ratios of Biomass Consumed to Deer	No. of Individuals Eaten	Ratio of Individuals Eaten
Deer	58.6	0.91	90.5	82.13	1.000	1.4	1.00
Beaver	15.7	0.56	4.5	2.54	0.015	0.2	0.06
Moose	330.0	3.08	2.0	6.16	0.037	0.02	0.01

Note: Calculations follow Weaver (1993) where $Y = 0.439 + 0.008 X$ and Y = kg of prey biomass consumed/scat and X = estimated weight of prey animals.

[a]In scats with 2 prey types (5%), each was assigned an occurrence of 0.5 for biomass calculations.

[b]Based on an observed winter kill ratio of 13 fawns to 4 yearlings to 33 "adults" with observed even-sex ratios for fawns, assumed even-sex ratios for yearlings, and an observed even-sex ratio for adults. Estimated fawn weight = 36.6 kg (M. Nelson unpublished data), yearling weight = 48.8 kg (Sauer 1984), adult doe weight = 57.7 kg (Kunkel and Mech 1994), and adult buck weight = 79.1 kg (M. Nelson unpublished data).

[c]Based on an assumed kill ratio of 2 yearlings to 1 adult with respective weights of 13.5 g and 20 kg (D. Smith unpublished data).

[d]Based on an assumed kill of 1 calf to 1 adult and weights of 180 kg (Coady 1982) and 480 kg (Bubenik 1998).

Literature Cited

Adorjan, A. S., and G. B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Ontario Department of Lands and Forest Research Report Wildlife 90. Maple, Ontario.

Anderson, J. F., and L. A. Magnarelli. 1984. Avian and mammalian hosts for spirochete-infected ticks and insects in a Lyme disease focus in Connecticut. Yale Journal of Biology and Medicine 57:627–641.

Anonymous. 1991. Wonder nav for the 90's? Plane and Pilot January:22–26.

Ash, L. H., and T. C. Orihel. 1987. Parasites: A guide to laboratory procedures and identification. American Society of Clinical Pathologists, Chicago, Illinois.

Ballard, W. B., G. M. Mattson, and P. R. Krausman. 1995. Comparison of two methods to age gray wolf *(Canis lupus)*. Pages 455–459 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Occasional Publication 35. Canadian Circumpolar Institute, Edmonton, Alberta.

Berg, W. E., and S. Benson. 1998. Updated wolf population estimate for Minnesota, 1997–1998. Pages 85–98 in B. Joselyn, editor. Summaries of wildlife research findings. Minnesota Department of Natural Resources, St. Paul, Minnesota.

Berg, W. E., and D. W. Kuehn. 1980. A study of the timber wolf population on the Chippewa National Forest. Minnesota Wildlife Research Quarterly 40:1–16.

Berg, W. E., and D. W. Kuehn. 1982. Ecology of wolves in north-central Minnesota. Pages 4–11 in F. H. Harrington and P. C. Paquet, editors. Wolves: A worldwide perspective on their behavior, ecology, and conservation. Noyes Publishing, Park Ridge, New Jersey.

Bittner, S. L., and O. J. Rongstad. 1982. Snowshoe hare and allies. Pages 146–166 in J. A. Chapman and G. A. Feldhamer, editors. Wild Mammals of North America. The Johns Hopkins University Press, Baltimore, Maryland.

Boer, A. H, G. Redmond, and T. J. Pettigrew. 1989. LORAN-C: a navigation aid for aerial surveys. Journal of Wildlife Management 53:228–230.

Bosler, E. M., B. G. Ormiston, J. L. Coleman, J. P. Hanrahan, and J. L. Benach. 1984. Prevalence of the Lyme disease spirochete in populations of white-tailed deer and white-footed mice. Yale Journal of Biology and Medicine 57:651–659.

Broschart, M. R., C. A. Johnston, and R. J. Naiman. 1989. Predicting beaver colony density in boreal landscapes. Journal of Wildlife Management 53:929–934.

Brown, C. G. 1992. Movement and migration patterns of mule deer in southeastern Idaho. Journal of Wildlife Management 56:246–253.

Bubenik, A. T. 1998. Evolution, taxonomy, and morphophysiology. Pages 77–123 in A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of North American moose. Smithsonian Institution Press, Washington, D. C.

Burgess, E. C., and L. A. Windberg. 1989. *Borrelia* sp. infection in coyotes, black-tailed jack rabbits, and desert cottontails in southern Texas. Journal of Wildlife Diseases 25:47–51.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: A practical information theoretic approach. Springer-Verlag, New York, New York.

Carrell, W. K., R. A. Ockenfels, J. A. Wennerlund, and J. C. Devos, Jr. 1997. Topographic mapping, LORAN-C, and GPS accuracy for aerial telemetry locations. Journal of Wildlife Management 61:1406–1412.

Coady, J. W. 1982. Moose. Pages 902–922 in J. A. Chapman and G. A. Feldhamer, editors. Wild Mammals of North America. The Johns Hopkins University Press, Baltimore, Maryland.

Cochrane, J. F. 2000. Gray wolves in a small park: Analyzing cumulative effects through simulation. Dissertation. University of Minnesota, St. Paul, Minnesota.

Cole, G. F. 1987. Changes in interacting species with disturbance. Environmental Management 11:257–264.

Crête, M., and F. Messier. 1987. Evaluation of indices of gray wolf, *Canis lupus,* density in hardwood-conifer forests of southwestern Québec. Canadian Field-Naturalist 101: 147–152.

Crowley, K. F. 1995. Patterns of temporal and spatial change in the vegetation of Voyageurs National Park. Thesis. University of Minnesota, St. Paul, Minnesota.

Dexter, M. H. 1998. Status of wildlife populations, fall 1998. Unpublished Report, Section of Wildlife, Minnesota Department of Natural Resources, St. Paul, Minnesota.

Floyd, T. J., L. D. Mech, and P. A. Jordan. 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management 42:528–532.

Fox, J. E., R. O. Peterson, T. D. Drummer, P. J. Gogan, and J. Schaberl. 1999. Do wolves in winter avoid large lakes with snowmobile use? Poster presentation in D. Harmon, editor. On the frontiers of conservation: Proceedings of the tenth conference on research and resource management in parks and on public lands. The George Wright Society, Hancock, Michigan.

Fritts, S. H. 1982. Wolf depredation on livestock in Minnesota. U. S. Fish and Wildlife Service, Resource Publication 145, Washington, D. C.

Fritts, S. H., and L. D. Mech. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monograph 80.

Fuller, T. K. 1988. Hunter harvest of white-tailed deer in the Bearville Study Area, north-central Minnesota. Minnesota Wildlife Report 6. Minnesota Department of Natural Resources, St. Paul, Minnesota.

Fuller, T. K. 1989. Population dynamics of wolves in north-central Minnesota. Wildlife Monograph 105.

Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and G. B. Joslyn. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Society Bulletin 20:42–55.

Fuller, T. K., and L. B. Keith. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. Journal of Mammalogy 62:403–405.

Fuller, T. K., and D. W. Kuehn. 1983. Immobilization of wolves using ketamine in combination with xylazine and promazine. Journal of Wildlife Diseases 19:96–72.

Fuller, T. K., R. M. Pace III, J. A. Markl, and P. L. Coy. 1989. Morphometrics of white-tailed deer from north-central Minnesota. Journal of Mammalogy 70:184–188.

Fuller, T. K., and B. A. Sampson. 1988. Evaluation of a simulated howling survey for wolves. Journal of Wildlife Management 52: 60–63.

Fuller, T. K., and W. J. Snow. 1988. Estimating wolf densities from radiotelemetry data. Wildlife Society Bulletin 16:367–370.

Garrott, R. A., G. C. White, R. M. Bartmann, L. H. Carpenter, and A. W. Alldredge. 1987. Movements of female mule deer in northwest Colorado. Journal of Wildlife Management 51:634–643.

Gerson, H. B. 1988. Cougar, *Felis concolor,* sightings in Ontario. Canadian Field-Naturalist 102:419–424.

Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves *(Canis lupus)* in northeastern Minnesota, 1969–1989. Canadian Journal of Zoology 69:2946–2955.

Gogan, P. J. P., and J. F. Cochrane. 1993. Restoration of woodland caribou to the Lake Superior Region. Pages 219–242 in M. L. Bowles and C. J. Whelan, editors. Restoration of endangered species: Conceptual issues, planning, and implementation. Cambridge University Press, Cambridge, England.

Gogan, P. J. P., J. F. Cochrane, and E. M. Olexa. 1997b. Home ranges and survival of gray wolves in and adjacent to Voyageurs National Park, Minnesota. Pages 171–179 in D. Harmon, editor. Making protection work: Proceedings of the ninth conference on research and resource management in parks and on public lands. The George Wright Society, Hancock, Michigan.

Gogan, P. J. P., P. A. Jordan, and J. L. Nelson. 1990. Planning to reintroduce woodland caribou in Minnesota. Transactions of the North American wildlife and natural resources conference 55:599–608.

Gogan, P. J. P., K. D. Kozie, E. M. Olexa, and N. S. Duncan. 1997a. Ecological status of moose and white-tailed deer at Voyageurs National Park, Minnesota. Alces 33: 187–201.

Goodwin, E. A., and W. B. Ballard. 1985. Use of tooth cementum for age determination of gray wolves. Journal of Wildlife Management 49:313–316.

Hammill, J. 1997. Wolf recovery in Michigan. Pages 22–23 in Wolves around the world 1997 update. International Wolf Center Publication No. IWC-96–902, Ely, Minnesota.

Harrington, F. H., and L. D. Mech. 1982. An analysis of howling response parameters useful for wolf pack censusing. Journal of Wildlife Management 46:686–693.

IIMorrow. 1989. Pilot's operating handbook, Apollo Model 604 LORAN-C receiver. IIMorrow, Salem, Oregon.

Jaeger, J. R., J. D. Wehausen, V. C. Bleich, and C. L. Douglas. 1993. Limits in the resolution of LORAN-C for aerial telemetry studies. Desert Bighorn Council Transactions 37:20–23.

Johnson, M., D. H. Pletscher, and D. K. Boyd. 1994. Serologic investigations of canine parvovirus and canine distemper in relation to wolf *(Canis lupus)* pup mortalities. Journal of Wildlife Diseases 30:270–273.

Johnson, M. L., and S. Johnson. 1982. Voles. Pages 326–354 in J. A. Chapman and G. A. Feldhamer, editors. Wild Mammals of North America. The Johns Hopkins University Press, Baltimore, Maryland.

Kallemeyn, L. 1987. Effects of regulated lake levels on northern pike spawning habitat and reproductive success in Namakan Reservoir, Voyageurs National Park. Resources Management Report MWR-8. Midwest Regional Office, National Park Service, Omaha, Nebraska.

Kazmierczak, J. J., E. C. Burgess, and T. E. Amundson. 1988. Susceptibility of the gray wolf *(Canis lupus)* to infection with the lyme disease agent *Borrelia burgdorferi*. Journal of Wildlife Diseases 24:522–527.

Keating, K. A. 1994. An alternative index of satellite telemetry location error. Journal of Wildlife Management 58:414–421.

Kellert, S. R. 1986. The public and the timber wolf in Minnesota. Transactions of the North American Wildlife and Natural Resources Conference 51:193–200.

Kolenosky, G. B. 1972. Wolf predation on wintering deer in east-central Ontario. Journal of Wildlife Management 36:357–369.

Kornblatt, A. N., P. H. Urband, and A. C. Steere. 1985. Arthritis caused by *Borrelia burgdorferi* in dogs. Journal of the American Veterinary Medical Association 186: 960–964.

Krausman, P. R., J. J. Hervert, and L. L. Ordway. 1984. Radio tracking desert mule deer and bighorn sheep with light aircraft. Pages 115–118 in P. R. Krausman and N. S. Smith, editors. Deer in the Southwest: a workshop. Arizona Cooperative Wildlife Research Unit and School of Renewable Natural Resources, University of Arizona, Tucson, Arizona.

Kuehn, D. W., T. K. Fuller, L. D. Mech, W. J. Paul, S. H. Fritts, and W. E. Berg. 1986. Trap-related injuries to wolves in Minnesota. Journal of Wildlife Management 50: 90–91.

Kunkel, K. E., and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology 72:1557–1565.

Kurmis, V., S. L. Webb, and L. C. Merriam, Jr. 1986. Plant communities of Voyageurs National Park, Minnesota, U.S.A. Canadian Journal of Botany 64:531–540.

Larson, J. S., and R. D. Taber. 1980. Criteria of age and sex. Pages 143–202 in S. D. Schemnitz, editor. Wildlife Techniques Manual. Fourth edition. The Wildlife Society, Washington, D. C.

Lebreton, J. D., K. P. Burnham, J. Colbert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. Ecological Monographs 62: 67–118.

Lehman, N., A. Eisenhawer, K. Hansen, L. D. Mech, R. O. Peterson, P. J. P. Gogan, and R. K. Wayne. 1991. Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. Evolution 45:104–119.

Leptich, D. J., D. G. Beck, and D. E. Beaver. 1994. Aircraft-based LORAN-C and GPS accuracy for wildlife research on inland study sites. Wildlife Society Bulletin 22: 561–565.

Magnarelli, L. A., J. F. Anderson, C. S. Apperson, D. Fish, R. C. Johnson, and W. A. Chappell. 1986. Spirochetes in ticks and antibodies to *Borrelia burgdorferi* in white-tailed deer from Connecticut, New York State and North Carolina. Journal of Wildlife Diseases 22:178–188.

McNab, W. H., and P. E. Avers, compilers. 1994. Ecological subregions of the United States: Section descriptions. Administrative Publication WO-WSA-5. U.S. Department of Agriculture, Forest Service, Washington, D.C.

Mech, L. D. 1966. The wolves of Isle Royale. U.S. National Park Service Fauna Series 7. Washington, D.C.

Mech, L. D. 1970. The wolf: The ecology and behavior of an endangered species. The Natural History Press. Garden City, New York.

Mech, L. D. 1973. Wolf numbers in the Superior National Forest of Minnesota. U.S. Forest Service report NC-97. St. Paul, Minnesota.

Mech, L. D. 1986a. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, Minnesota.

Mech, L. D. 1986b. Wolf populations in the central Superior National Forest, 1967–1985. U. S. Forest Service Research Paper NC-270. St. Paul, Minnesota.

Mech, L. D., L. G. Adams, T. J. Meier, J. W. Burch, and B. W. Dale. 1998. The wolves of Denali. University of Minnesota Press, Minneapolis, Minnesota.

Mech, L. D., L. D. Frenzel. Jr., R. R. Ream, and J. W. Winship. 1971. Movements, behavior, and ecology of timber wolves in northeastern Minnesota. Pages 1–34 in L. D. Mech and L. D. Frenzel Jr., editors. Ecological studies of the timber wolf in northeastern Minnesota. U.S. Forest Service Research Paper NC-52. St. Paul, Minnesota.

Mech, L. D., S. H. Fritts, G. Radde, and W. J. Paul. 1988. Wolf Distribution in Minnesota relative to road density. Wildlife Society Bulletin 16:85–87.

Mech, L. D., and S. M. Goyal. 1993. Canine parvovirus effect on wolf population change and pup survival. Journal of Wildlife Diseases 29:330–333.

Mech, L. D., and S. M. Goyal. 1995. Effects of canine parvovirus on gray wolves in Minnesota. Journal of Wildlife Management 59: 565–570.

Messier, F. 1985. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. Canadian Journal of Zoology. 63:239–245.

Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. Journal of Animal Ecology 60:377–393.

Mohr, C. O. 1947. Table of equivalent animal populations of North American small mammals. American Midland Naturalist 37: 233–249.

National Park Service. 1988. Management policies. U.S. Department of Interior, National Park Service, Washington, D.C.

Nelson, M. E., and L. D. Mech 1986a. Deer population in the central Superior National Forest, 1967–1985. U.S. Forest Service Research Paper NC-271.

Nelson, M. E., and L. D. Mech 1986b. Relationship between snow depth and gray wolf predation on white-tailed deer. Journal of Wildlife Management 50:471–474.

Nowak, R. M. 1995. Another look at wolf taxonomy. Pages 375–398 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Occasional Publication 35. Canadian Circumpolar Institute, Edmonton, Alberta.

Odum, E. P., and E. J. Kuenzler. 1955. Measurements of territory and home range size in birds. Auk 72:128–137.

Pastor, J., and D. J. Mladenoff. 1992. The southern boreal–northern hardwood forest border. Pages 216–229 in H. H. Shugart, R. Leemans, and G. B. Bonan, editors. A system analysis of the global boreal forest. Cambridge University Press, New York., New York.

Patric, E. F., T. P. Husband, C. G. McKiel, and W. M. Sullivan. 1988. Potential of LORAN-C for wildlife research along coastal landscapes. Journal of Wildlife Management 52: 162–164.

Peek, J. M., D. L. Urich, and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildlife Monograph 48.

Perry, H. R. 1982. Muskrats. Pages 282–325 in J. A. Chapman and G. A. Feldhamer, editors. Wild Mammals of North America. The Johns Hopkins University Press, Baltimore, Maryland.

Peterson, R. O. 1976. Wolf survey in Voyageurs National Park. Final contract report to the National Park Service. Voyageurs National Park files, International Falls, Minnesota.

Peterson, R. O. 1995. The wolves of Isle Royale: A broken balance. Willow Creek Press, Minocqua, Wisconsin.

Peterson, R. O. 1999. Wolf–moose interaction on Isle Royale: The end of natural regulation? Ecological Applications 9:10–16.

Peterson, R. O., and R. E. Page. 1988. The rise and fall of Isle Royale wolves, 1975–1986. Journal of Mammalogy 69:89–99.

Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy 79:828–841.

Peterson, R. O., J. D. Woollington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monograph 88.Petraborg, W. H., and D. W. Burcalow. 1965. The white-tailed deer in Minnesota. Pages 11–48 in J. B. Moyle, editor. Big game in Minnesota. Technical Bulletin 9. Minnesota Department of Conservation, St. Paul, Minnesota.

Pimlott, D. H. 1960. The use of tape-recorded wolf howls to locate timber wolves. Twenty-second Midwest Wildlife Conference. Unpublished report (typewritten). University of Toronto, Ontario. 15 pp.

Pimlott, D. H., J. A. Shannon, and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department of Lands and Forests Resource Report Wildlife 87. Maple, Oregon.

Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: The staggered entry design. Journal of Wildlife Management. 53: 7–15.

Post, E., and N. C. Stenseth. 1998. Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer. Journal of Animal Ecology 67:537–543.

Potvin, F. 1988. Wolf movements and population dynamics in Papineau-Labelle reserve, Quebec. Canadian Journal of Zoology 66: 1266–1273.

Rhoades, J. D., S. M. Lesch, P. J. Shouse, and W. J. Alves. 1990. Locating sampling sites for salinity mapping. Soil Science Society of America Journal 54:1799–1803.

Rogers, L. L. 1987. Effects of food supply and kinship on social behavior, movements and population growth of black bears in northeastern Minnesota. Wildlife Monograph 97.

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criterion statistics. KTK Scientific, Tokyo.

Sauer, P. 1984. Physical characteristics. Pages 73–90 in L. K. Halls, editor. White-tailed deer ecology and management. Stackpole books, Harrisburg, Pennsylvania.

Schmidt, J. A. 1990. Food habits of the timber wolf in Voyageurs National Park. Thesis. St. Cloud State University, St. Cloud, Minnesota.

Smith, D. 1997. Dispersal strategies and cooperative breeding in beavers. Dissertation. University of Nevada, Reno, Nevada.

Smith, D., and R. O. Peterson. 1988. The effects of regulated lake levels on beaver in Voyageurs National Park, Minnesota. Research/Resource Management Report MWR-11. Midwest Regional Office, National Park Service, Omaha, Nebraska.

Stenlund, M. H. 1955. A field study of the timber wolf *(Canis lupus)* on the Superior National Forest, Minnesota. Minnesota Department of Conservation Technical Bulletin 4, St. Paul, Minnesota.

Terres, J. K. 1991. The Audubon Society Encyclopedia of North American Birds. Wings Books, New York, New York.

Tester, J. R., A. M. Starfield, and L. E. Frelich. 1997. Modeling for ecosystem management in Minnesota pine forests. Biological Conservation 80:313–324.

Theberge, J. B., and M. T. Theberge. 1998. Wolf country: Eleven years of tracking the Algonquin wolves. McClelland and Stewart, Toronto, Ontario.

Thiel, R. P., and R. R. Ream. 1995. Status of the gray wolf in the lower 48 United States to 1992. Pages 59–62 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Occasional Publication 35. Canadian Circumpolar Institute, Edmonton, Alberta.

Thomas, N. J., W. J. Foreyt, J. F. Evermann, L. A. Windberg, and F. F. Knowlton. 1984. Seroprevalence of canine parvovirus in wild coyotes from Texas, Utah, and Idaho (1972–1983). Journal of American Veterinary Medical Association 185:1283–1287.

U. S. Fish and Wildlife Service. 1992. Recovery plan for the eastern timber wolf. Twin Cities, Minnesota.

Van Ballenberghe, V. A., W. Erickson, and D. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. Wildlife Monograph 43.

Walsh, N. E., S. G. Fancy, T. R. McCabe, and L. F. Pank. 1992. Habitat use by the porcupine caribou herd during predicted insect harassment. Journal of Wildlife Management 56:465–473.

Wayne, R. K., D. A. Gilbert, D. Lehman, K. Hansen, A. Eisenhawer, D. Girman, L. D. Mech, R. O. Peterson, P. J. P. Gogan, U. S. Seal, and R. J. Krumenaker. 1991. Conservation genetics of the endangered Isle Royale gray wolf. Conservation Biology 5:41–51.

Weaver, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57:534–538.

Windberg, L. A. 1995. Demography of a high-density coyote population. Canadian Journal of Zoology 73:942–954.

White, G. C. 1998. Program MARK version 1.0: mark and recapture survival rate estimation. Colorado State University, Fort Collins, Colorado.

Whitlaw, H. A., and M. W. Lankester. 1994. The co-occurrence of moose, white-tailed deer, and *Parelaphostrongylus tenuis* in Ontario. Canadian Journal of Zoology 72: 819–825.

Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring of a gray wolf *(Canis lupus)* population in Wisconsin, 1979–1991. Pages 147–156 in L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of wolves in a changing world. Occasional Publication 35. Canadian Circumpolar Institute, Edmonton, Alberta.

Zarnke, R. L., and W. B. Ballard. 1987. Serological survey for selected microbial pathogens of wolves in Alaska. Journal of Wildlife Diseases 23:77–85.