The effects of human land development, landscape characteristics, and prey density on the spatial distribution of wolves (*Canis lupus*) on the north shore of Lake Superior

by

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General Abstract

This study investigates the influence of infrastructure (roads, power lines, and railways), landscape parameters (rivers, lakes, clearcuts, and forest cover type), prey densities (moose, Alces alces), and the presence of garbage dumps on habitat use, home range sizes, and travel patterns of wolves (Canis lupus) on the north shore of Lake Superior, Ontario. Wolves neither avoided nor preferred roads but used them according to their availability. Road densities in the core areas of two packs which fed seasonally at a garbage dump exceeded the most commonly reported road density threshold of 0.60 km/km^2. Although roads appear to aid in travel of wolves, they also increased human access and human-caused mortality. Lakes and clearcuts were found not to influence habitat use. Conifer cover type dominated the study area and home ranges of the packs but wolves were located more often in mixed forest cover. Rivers were used by the wolves as travel corridors in winter. Moose densities in the overall study area and in the pack home ranges were near or below 0.20 $moose/km^2$, often considered as the minimum prey density to sustain a viable wolf population. Four of the five packs failed to reproduce during the period of the study, one wolf starved to death, and three died of diseases. These results support the validity of this prey density threshold. The consumption of garbage was observed for two packs during the winter. Wolves that used the garbage dump traveled shorter distances than wolves which fed on moose. The additional food supply of the dump and less energy expended in travel seemed to enhance the reproductive success of one study pack, but also exposed the wolves to higher mortality risks. High wolf mortality, mainly associated with human related activities, in combination with low moose densities and low reproduction are possible factors for the observed wolf decline in the study area.

General Introduction

The need for international efforts for the conservation of large carnivores is recognized by scientists around the world (Primm and Clark 1996, Weber and Rabinowitz 1996). Without question, humans have viewed large carnivores as competitors and have failed to recognize their importance in their respective ecoregions (Primm and Clark 1996, Noss et al. 1996). Extensive habitat requirements of large carnivores often conflict with human activities (Fritts and Carbyn 1995, Primm and Clark 1996) and are often in direct conflict with economic development. Conflicts with humans and insufficient legislation for their protection of such species have contributed to a global decline in large carnivores (Weber and Rabinowitz 1996). Although wolf populations have recovered in certain parts of Europe and the United States (Mech 1995), there is very little legislation in Canada to insure that both wolf populations and their habitat persist unimpaired with an ever increasing demand for natural resources (mining and logging), the building of infrastructure to facilitate such activities, and increases in human population (Clark et al. 1996).

There are several biotic factors which are known to influence the survival of wolves. Prey density has been directly correlated with numbers of wolves (Fuller 1989). Wolves fail to reproduce and even survive when moose densities decline below specific minimum thresholds (Messier and Crete 1985). Apart from the wolves' obligate relationship with their prey, landscape characteristics have been noted to play an important role in the spatial distribution and even survival of wolves (Jensen et al. 1986, Mech 1988, Mladenoff et al. 1996). Unlike other carnivores, the wolf is not a habitat specific species (Fuller 1995, Mladenoff et al. 1995) but occupy a variety of environments (Mech 1995). Human-caused landscape changes such as roads, agriculture, and human settlement have been shown to deter wolves (Thiel 1985, Jensen et al. 1986, Mladenoff et al. 1995) and road traffic can be a direct cause of wolf mortality (DeVos 1949, Mech 1989). Access by roads and other infrastructure into wolf habitat also plays an important role in human-caused wolf mortality (Fuller 1995). Several studies have shown that road density of 0.60 km/km^2 represents a threshold above which wolves are restricted either by direct collision with traffic or by human-caused mortality such as hunting and trapping (Thiel 1985, Jensen et al. 1986, Thurber et al. 1986, Mech et al. 1988, Mech 1989, Mladenoff et al. 1995). Wolf mortality or avoidance of areas with high road densities have both been suggested reasons for slow recolonization of Wisconsin and Michigan in the United States (Jensen et al. 1987, Mladenoff et al. 1995). Such impediments to wolf travel and natural wolf dispersal can affect wolf populations on a large scale (Mladenoff 1995). Wolf dispersal plays a very important role in wolf population dynamics (Fuller 1989, Gese and Mech 1991), gene flow (Lehman et al. 1991), and recolonization of former wolf habitat (Mladenoff 1995). Therefore, travel restriction or even death of dispersing individuals can have detrimental effects on the entire population.

In addition to the building of roads and other landscape alterations, the distribution of and density of humans and their settlement may also deter recolonizing wolves (Mladenoff et al. 1995). While human settlements are generally thought to repel wolves (Mech 1989), the proliferation of garbage dumps and their waste may attract wolves and many other forms of wildlife (Grace 1976, Boitani 1982, Mendelssohn 1982, Afik and Alkon 1983, Mech and Hertel 1983, Salvador and Abad 1987, Blanco et al. 1992, Boitani

1992, Mech 1994). Several studies showed that wolves consume garbage and that such a predictable food source may influence wolf ecology. Wolves which feed at garbage dumps may have smaller home range sizes (Mech and Hertel 1983) and often continue to use garbage despite increases in the density of their natural prey (Salvador and Abad 1987). Because dumps are usually located near human habitation, the use of such sites potentially increases interactions and conflicts between wolves and humans.

The deleterious effect of the industrialized and developed human society on wolves is a historical fact and an ongoing problem in large carnivore conservation. Before species such as wolves can be conserved, the effects of human activities on their survival and distribution need to be fully addressed. This is particularly important in regions where development and large scale habitat alterations are planned or ongoing. In addition, there are regions where wolves are still regarded as pests and not as important links within complex ecosystems.

This study examines several factors which could influence wolf survival and distribution. First, it measures the influences of roads, natural landscape features, and prey densities on the home range sizes and habitat use of five wolf packs on the north shore of Lake Superior, Ontario. Second, the influence of garbage dumps on the spatial use of two wolf packs was measured and compared with the spatial use of a pack which did not have access to such a food source.

The main questions addressed in this study are the following:

1/ Are wolves affected by human-built infrastructure such as roads, power lines, and railways, and do they avoid certain levels of infrastructure density?

2/ Do wolves use the landscape randomly or are some features used more often than others?

3/ Does moose density influence the habitat use of wolves?

4/ Do wolves visit garbage dumps and if so, does this influence their home range sizes and travel patterns?

1. The influence of roads, landscape parameters, and prey densities on habitat use and spatial distribution of wolves (Canis lupus) on the north shore of Lake Superior, Ontario

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1.1 Abstract

This study examines the effect of roads and other types of human-made infrastructure, landscape characteristics, and prey density on the habitat use and home ranges of radio collared wolves (Canis lupus) in five packs. Densities of roads, power lines, and railways did not differ between the general study area and the five pack home ranges. Of all packs studied, those two which seasonally visited a garbage dump had the highest densities of roads in their core areas. This indicates that areas with high road densities are not always avoided, especially when food resources are an attraction. In general, wolves used roads relative to their occurrence within their home ranges and core areas. Wolves also used rivers as travel corridors in the winter. Landscape parameters such as lakes, rivers, clearcuts, and forest cover types were also similar between the general study area and individual home ranges. Although conifer was the most abundant cover type in all areas, all wolves preferred mixed conifer-deciduous forest. Wolf packs with higher moose densities in their home ranges and roads available as travel corridors, had larger home ranges than one pack with a significantly lower moose density and absence of human-made infrastructure. It seems plausible that human-made infrastructure

facilitates wolf travel and, therefore, influences their home range sizes. On the other hand, infrastructure within the study area was associated with high wolf mortality. Both roads, road traffic, and prey densities may be used as indicators of favourable wolf habitat.

1.2 Introduction

Several abiotic and biotic factors have been documented to influence the survival, viability, reproductive success, and spatial distribution of carnivore species world wide. The negative attitude of humans towards wolves (Canis lupus) has played a major role in the global decline of wolf populations (Boitani 1995). Construction of roads and other types of infrastructure (railways, and power-lines) has enabled humans to inhabit new areas and has contributed directly to their widespread distribution. Roads have been used extensively to allow mineral and forestry industries access to remote areas for resource extraction. As a result, habitat loss, forest fragmentation, and human access to wilderness areas have directly impacted wolves and other large carnivores. Landscape alteration by humans and hunting has resulted in changes in prey type and prey density, which may have direct influences on the survival of wolves (Messier and Crete 1985, Messier 1987, Fuller 1989).

Roads and human activities associated with road access affect behaviour and survival of many populations of large mammalian carnivores (Thiel 1985, Jensen et al 1986, Van Dyke et al. 1986, McLellan and Shackleton 1988, Mech et al. 1988, Brody and Pelton 1989, Lavallo and Anderson 1996). Roads increase the degree of landscape fragmentation by dissecting large habitat patches into smaller ones, changing forest interior habitat into edge habitat (Reed et al. 1996). Large carnivores, such as wolves, use the landscape on an enormous scale (Peterson 1987, Noss et al. 1996) and often encounter infrastructure during travel in fragmented and human developed areas (Berg and Kuehn 1982, Mech et al. 1988, Mech 1989, Mech et al. 1994). If wolves are to survive with an ever increasing human population and an emphasis on increased resource extraction, we must understand the thresholds of their tolerance to disturbance by humans.

Human-created infrastructure is a very important source of direct and indirect mortality of large carnivores (Berg and Kuehn 1982, Mech et al. 1988) and numerous ungulate species throughout North America and Europe (Bruinderink and Hazebroek 1996). Some consider that there is little direct effect of vehicles and human activities on wolves, unless they facilitate the killing of wolves by humans (Fuller 1995). However, densities of roads may be related to the spatial distribution of wolves and may be one reason why wolf recolonization has been slow in certain areas (Mladenoff et al. 1995). Some studies indicate that wolves avoid areas with high densities of roads, suggesting that there may be a tolerance threshold for roads above which wolves avoid an area (Thiel 1985, Fuller 1989, Mech 1989, Mladenoff et al. 1995). There are two possible explanations for these findings. First, there might be active avoidance of roads as they reflect human presence (Mladenoff et al. 1995). Second, roads may increase mortality from collisions with vehicles (DeVos 1949) and from increased access by trappers and hunters.

Thiel (1985) showed that the distribution of wolves in parts of Wisconsin was related to the density of roads passable by 2-wheel-drive vehicles. Wolves did not occur in areas where road density exceeded 0.58 km/km^2. Similar thresholds were reported by Jensen et al. (1986), Mech et al. (1988), Fuller (1989), and Thurber et al. (1994). Wolves in Minnesota did not occur in areas with road densities higher than 0.61 km/km^2 (Mech 1988). At higher road densities the risk of human caused mortality increases. In Minnesota, Fuller (1989) reported mean road densities of 0.38 km/km^2, which ranged from 0.15 to 0.72 km/km^2 in wolf pack home ranges. In Ontario and Michigan (Jensen et al. 1986) and in Alaska (Thurber et al. 1994), wolves avoided areas where road densities exceeded 0.6 km/km^2. In Wisconsin, most wolf pack home ranges and core areas had road densities lower than 0.23 km/km^2 (Mladenoff et al. 1995). In Alaska, wolves avoided areas inhabited by humans and heavily used roads, despite low human-caused wolf mortality (Thurber et al. 1994). Wolves were attracted to seasonally closed roads away from human activities which they used as travel corridors. These studies have shown that human-built infrastructure influences the manner in which wolves use habitats, however, there may be geographical differences in the tolerance of roads by wolves. Although there seems to be considerable variation in road density thresholds, the most commonly reported range of road density above which wolf survival is jeopardized is 0.58 to 0.60 km/km^2. There is a need to address this concern within areas of varying road density and traffic to determine how wolves respond to frequency of traffic and what may be the reasons for occasional tolerance of higher road densities. Unused roads, similar to rivers and lakes in the winter (Mech 1970), can serve as travel corridors (Thurber et al. 1994). These roads may represent infrastructure which can be used by wolves without the risk of mortality.

Unlike roads, which at higher densities seem to have a negative effect on wolves, higher prey density has been shown to positively influence wolf presence and survival (Messier and Crete 1985, Fuller 1995). In Quebec, a minimum moose density of 0.20 moose/km^2 was required to sustain a wolf pack (Messier and Crete 1985). Many studies have shown that higher prey biomass supports higher wolf numbers (Packard and Mech 1980, Fuller 1989, Messier 1994). Although wolves show low habitat affinity (Fuller 1995, Mladenoff et al. 1995), landscape parameters such as forest cover type and lake size appear to influence the suitability of wolf habitat (Mladenoff et al. 1995).

The purpose of this study was to investigate the influence of infrastructure and other landscape characteristics on habitat use and home ranges of five wolf packs. The goal was to quantify the possible effects of infrastructure on the distribution and travel habits of wolves. Also, the influence of several abiotic and biotic landscape components, such as river density, lake area, forest cover type, and prey density on the spatial use of wolves was investigated.

1.3 METHODS

Study Area

Wolves were studied from October 1994 to March 1997 on the north shore of Lake Superior (lat. 48° 30' N, long. 86^0 00' W), approximately 300 km east of Thunder Bay, Ontario (Fig. 1). The northern boundary (latitude 48° 55') lies 25 km north of and is parallel to the Trans Canada Highway (Hwy 17). The western and eastern boundaries are Neys Provincial Park and the Town of White River, respectively. The southern boundaries are the shore of Lake Superior and border Pukaskwa National Park (PNP).

The coastal region of the study area is characterized by rugged topography, with elevations ranging from Lake Superior water level (189 m) to 650 m. The landscape is patchy, with numerous river valleys and small lakes. The interior region is a flat plateau characterized by a heavily eroded mountain landscape scoured by continental glaciers (Poitevin et al. 1989). Winter and summer mean temperatures range from -13° C to 14.6° C, respectively, for the coastal area, and -17° C and 15.9° C, respectively, inland (Poitevin et al. 1989). Mean annual precipitation is 737 mm along the coast and 644 mm inland (Poitevin et al. 1989). Snow depth reaches maximum average depth of 100 cm but can range anywhere from 50-150 cm.

The vegetation in both the coastal and the inland regions is predominantly conifer and include species such as balsam fir (Abies balsamea), black spruce (Picea mariana), white spruce (P. glauca), jack pine (Pinus banksiana), with some associations of white birch (Betula papyrifera), and quaking aspen (Populus tremuloides). Dominant species include jack pine, white birch, white spruce, and black spruce in the higher elevations (Poitevin et al. 1989).

Townsites, forest management units, provincial parks and a national park (Fig. 1) represent areas occupied or used by humans for resource extraction and recreation. The southern part of the study area covers PNP, which is abutted by the White River Forest Management Area (WRMA) to the north and both the WRMA and the Wawa Management Area to the east. The Black River Management Area (BRMA), which adjoins the western boundary of the WRMA includes White Lake Provincial Park. The Big Pic River Management Unit (BPRMU) abuts the western boundary of the BRMA.

The west boundary of BPRMU adjoins the Steel River Management Unit and includes Neys Provincial Park.

Mining, timber harvesting, power development, and recreational activities (including trapping, hunting and fishing) occur within the study area, although minimally in PNP. There are many active trap lines in the study area; traplines in PNP are limited to native trappers. Logging of the White River Forest has intensified since the establishment of a new sawmill in 1977. As a result, many roads have been built to facilitate the harvest of timber. Although most of the roads are passable by two wheel drive vehicles, much of the traffic consists of pickup and logging trucks. Logging, mainly by clearcuting, has been active in all the FMA's during and prior to this study.

There are 4 human settlements within the study area. They are: Marathon (5,500 inhabitants), Heron Bay (150 inhabitants), the Pic 50 Ojibway Reserve (400 inhabitants), and White River (2,000 inhabitants).

Potential prey of the wolf in the study area include moose (Alces alces), snowshoe hare (Lepus americanus), beaver (Castor canadensis), and small rodents. Very few caribou (Rangifer tarandus) have been observed in the study area (Moreland 1991, Bergerud 1989, Wade, Ferguson, Thompson pers. com.). White-tailed deer (Odocoileus virginianus) are also rare (Ferguson pers. com.) but they may still serve as potential prey. Other carnivores in the study area include marten (Martes americana), fisher (M. pennanti), mink (Mustela vison), river otter (Lutra canadensis), red fox (Vulpes vulpes), coyote (Canis latrans), black bear (Ursus americanus), weasel (Mustela sp.), and lynx (Felis canadensis).

Wolf capture

I live trapped wolves from five different packs with leg hold traps (modified as described by Kuehn et al. 1986) or by net gun from a helicopter (P. Krizan and Helicopter Wildlife Management, Seattle USA, see Appendix 1). Immobilized wolves were blood sampled, eartagged, weighed, measured, aged (based on tooth ware), and radio collared (Lotec Engineering, Ontario).

Live capture of wolves was approved by the animal care committee of the Ontario Ministry of Natural Resources.

Radio telemetry

All five wolf packs were located with a fixed wing aircraft (Cessna-185, Air Superior, Wawa, Ontario), on average once per week. All locations were recorded with a global positioning system (GPS, Garmen 55®) as Latitude/Longitude (decimal degrees), and converted to a Universal Transverse Mercator Grid System (UTM) with the program GEOCALC (Blue Marble Geographics, Gardiner, Maine). Test radio collars were randomly placed and located during regular telemetry flights to estimate the error of aerial locations. All actual test collar positions were differentially corrected and compared with the observed uncorrected GPS position from the aircraft. The mean error of such locations was 112 m (range = 70.7 - 144.5, n=35).

Home range analysis

Home ranges for each pack were calculated from telemetry locations with the adaptive kernel method (Worton 1987,1989a, 1989b, Kie 1996, Shivik et al. 1996) by the program CALHOME (Calhome®, Kie 1996, Shivik et al. 1996). The adaptive kernel method frees the data from normality assumptions, it is much less sensitive to outliers than other methods of home range estimation, and is not as prone to include unused or untraveled areas (Shivik et al. 1996). Its effectiveness at highlighting areas of concentrated use makes it particularly applicable to studies which compare such areas with areas of general use. Pack home ranges were defined by 95% of pooled locations (White and Garrot 1990) of all radio collared individuals within each pack. Core areas, which represent the area of concentrated use, were delineated by 50% (White and Garrot 1990) of pooled telemetry locations of individuals in a pack. All five pack home ranges and core areas were overlaid on a 1:150,000 digitized map.

Habitat description

Three main characteristics were used to describe the habitats of the overall study area, the home ranges and core areas of the five packs: infrastructure, landscape parameters, and prey density. Each was characterized by several spatial parameters, which were calculated for the entire study area, for individual home ranges, and for corresponding core areas within home ranges, except for prey density, which was only reported for the study area and home ranges.

Total lengths (km) of all linear parameters (roads, power-lines, and railways) in the study area were calculated from vector road maps (1:150,000 digitized maps) using a SPANS

Geographical Information System (GIS, Tydac®) platform. Minimum densities of all linear parameters were calculated as km/km^2.

Roads were defined as any road or highway which are passable by a 2-wheel drive vehicle. Roads were further classified into two groups: 1/ highways: Highway 17 (two to three lane paved highways) and secondary highways 626, 627, and 614 (two lane paved roads, extending from highway 17) and 2/ logging roads (unpaved roads). In winter, highways were plowed. Logging roads were usually unplowed but passable by snow machine. There were separate snow machine trails which included some of the power-lines. These trails were groomed and frequented in the winter but were relatively unused in the summer months. Railways were operational throughout the year. Power-lines (electric and telephone lines) and railways provided possible travel corridors for the wolves and were treated separately from roads.

Traffic on highways is reported as annual average daily traffic (AADT, January 01 to December 31), provided by the Ministry of Transportation (MTO). The frequency of use of logging roads by timber harvest companies was provided by Domtar Forest Products. Additionally, these roads were used periodically by hunters and fishermen.
Frequency of railway use was provided by CP Rail, as average number of trains per day.

To quantify the importance of roads to wolf travel, I measured the relative use of the two classes of roads by wolves within their home ranges and core areas. Relative road use was defined by actual observations and radio telemetry locations of wolves on a road or within a 200 m road buffer (100 m on each side of the road). This minimal buffer was chosen to accommodate telemetry and map error, and to take into account the edge effect created by roads (Reed et al. 1996). All telemetry locations within the 95% probability contour of the home ranges were plotted on 1:16,400 forestry maps (provided by Domtar Forest Products) for the analysis. Road locations were then expressed as percent of all locations for individual wolves.

Forest cover was classified as: conifer (when crown closure > 80% conifer), deciduous (when crown closure > 80% deciduous), and mixed (when crown closure is < 80% for both conifer or deciduous). Areas (km^2) of landscape characteristics (lakes, forest cover type, clearcuts) and densities (rivers) were also calculated from the same source as the linear parameters, except that area and raster files were used. The areas of each class of vegetation were calculated from digitized Land Satellite Image data (1994) in SPANS GIS. Areas of clearcuts were calculated from 1:250,000 digitized maps.
Wolf locations in each forest cover type, in clearcuts, and on or near waterways were recorded during telemetry flights and then expressed as percent of all locations.

To evaluate waterways (lakes, rivers, and creeks) as possible travel routes, locations were divided into summer (waterways without ice cover) and winter (waterways with ice cover, which support wolf travel) periods.

Since moose comprise the main prey in the study area (Krizan this volume), prey density (moose/km^2) was obtained from triannual Ontario Ministry of Natural Resources (OMNR, Bisset, Eason, Ferguson, and Tomson pers. com.) and PNP (Wade pers. com.) moose surveys.

Statistical analysis

Telemetry locations on roads, power-lines, railways, or waterways, and in the different cover types and clearcuts were tested with Wilk-Shapiro test for normality. The same was done for infrastructure and landscape parameters in the home ranges and core areas. Percent values were arcsine transformed before using them in statistical tests (Sokal and Rohlf 1981).

Differences between infrastructure densities (roads, power-lines, and railways) and landscape characteristic densities (rivers) and areas (lakes, forest cover, and clearcuts) between the home ranges and the study area were tested with a modified T-test, which allows to test whether a single parameter sampled at random belongs to a given population (Sokal and Rohlf 1981).

One-way ANOVA and Bonferroni test were used to test for differences in infrastructure and landscape parameters within the packs' home ranges and core areas and among the locations of single wolves. The amount of travel on waterways in winter and summer was also tested with one-way ANOVA. To test for differences in infrastructure and landscape parameters between the home ranges and corresponding core areas, T-test was used. Chi-square test was used to determine whether road locations of the single wolves occurred in proportions to their general occurrence within each home range and core area and in proportion to the traffic on those roads. For the same purpose an ANCOVA was used with road location as the dependent variable and road density as the co-variable. Additionally, a Spearman's rank correlation and a linear regression were performed to test for any association of road density and locations on roads. The Cascade Lake Pack was excluded from infrastructure analysis since the defined infrastructure was absent within their home range.

Moose densities (moose/km^2) within the packs' home ranges and the study area overall (mean density of all FMA) were compared with a modified T-test (Sokal and Rohlf 1981). Moose densities among the pack home ranges were compared with a Chi-square test.

1.4 Results

Study area

The combined Forest Management Areas cover the largest portion (7, 154 km^2, 78%) of the study area. Three parks (Neys Provincial Park, White Lake Provincial Park and Pukaskwa National Park, together covering 1, 922 km^2, 21%) and five towns (Marathon, Pic River First Nation, Heron Bay, Mobert, and White River, together covering 39 km^2, <0.5%) make up the remainder of the 9115 km^2 (Fig. 1). Conifer was the predominant forest cover, followed by mixed and deciduous forest (Table 1). The minimum area of clearcuts covered 3.4% of the overall study area; the 2,865 lakes in the study area covered 5% (Table 1). The calculated river density was 0.54 km/km^2. The total road density in the study area was 0.18 km/km^2, with logging roads predominating over highways (Table 2). The only major highway in the study area, Highway 17, carried on average 1435 vehicles/24 hours. Traffic volumes on secondary highways (highway 614, 626, and 627) were on average 600, 670, and 460 vehicles/24 hours, respectively. Traffic on logging roads consisted mainly of timber harvest trucks (on average 8 vehicles/24 hours) and to a minor degree fishing and hunting activities. The density of power-lines and rail roads was 0.03 and 0.02 km/km^2 (Table 2). Railway traffic was on average 12 trains/24 hours.

The average moose density in the study area was 0.198 moose/km^2 (Table 1) and ranged from 0.097 moose/km^2 in PNP up to 0.278 moose/km^2 in the White River Forest Management Area (WRMA, Eason pers. com.).

Black River Pack (BRP)

Two male wolves, one pup (Sam) and an adult (Aldo), were radio collared in August 1994 (Fig. 3, Table 3). The pack consisted of eight to nine individuals at time of capture; they primarily used the BRMA and occasionally the northwest section of PNP (red dots, Fig. 2) . As a yearling, Sam dispersed from the BRP's home range in July 1995 and was part of a new pack (Neys Pack) from November of the same year. Aldo dispersed from the BRP's home range in November 1995 and was relocated in January 1997, 50 km north of his former home range, where he travelled predominantly alone (Fig. 3).

Neys Pack (NP)

The Neys Pack was formed when Sam dispersed from the BRP and joined two other wolves in November 1995 (Fig. 3). The NP used an area adjacent and west of the BRP (green cross-hatching, Fig. 2). After this pack reproduced successfully it consisted of six individuals after May 1996 (Fig. 3).

Rein Lake Pack (RLP)

An adult female (Cassidy) and one two adult males (Mojo) were captured and radio collared in October 1994 (Fig. 3, Table 3). Cassidy and Mojo were associated with approximately three to four individuals at time of capture. Mojo dispersed in a northerly direction in November 1994. He died in February 1996 of blastomycosis (Campbell pers. com.). An adult male (Star), who was associated with Cassidy from the time of her capture, was radio collared in February 1996 (Fig. 3, Table 3). The RLP used the northern section of PNP and the southern section of the WRMA (blue area, Fig. 2). From December 1994 to February 1997, the RLP consisted of 3 individuals. Cassidy dispersed in a northerly direction in November 1996; she died near a garbage dump in February 1997, probably from mange. Star and the other wolf remained in the RLP's home range after Cassidy's dispersal. Star died in the RLP's home range in February 1997, also from mange.

White River Pack (WRP)

An adult female (Paulina) was captured in September 1994 (Table 3); she was associated with nine other wolves. She dispersed in December 1994 (Fig. 3) and was hit by a train in January 1996, approximately 80 km west of the study area. An adult female (Anna) was captured and radio collared in August 1995 (Table 3). The pack at this time consisted of two individuals. In February 1996, the other wolf of the WARP, also an adult female (Moon), was captured and radio collared (Table 3). The WARP used primarily the MA and overlapped with the home range of the RAP in the southeast (red cross-hatching, Fig. 2). In November 1996, radio collared female Anna was snared and killed by a trapper while dispersing north of her home range. Moon remained in her former home range and was joined by a new individual. After February 1997, Moon was located alone; there was no indication that she was accompanied by another wolf.

Cascade Lake Pack (CAP)

Two adult females (Solitary and Mica) were captured in July 1995 in the southern section of PAP (yellow area, Fig. 2, Fig. 3, Table 3). Mica spent most of the time alone, separate from the rest of the CAP, estimated at 6 to 7 individuals in early winter 1995. Solitary died in December 1995, probably of inter pack aggression. Mica died in February 1996, presumably of starvation (Cappella, pers. communication).

Home ranges of the BURP, MPG, RAP, and WARP overlapped spatially but not temporally (Fig. 2). The core areas (smaller contours within the home ranges, Fig. 2) of the MPG and BRP overlapped graphically (Fig. 2) but the areas of overlap were not used simultaneously by the two packs (pers. obs.). The other wolf packs' core areas did not show any overlap. The NP and the CLP were the only packs which had two core areas within their home ranges.

Home range sizes of individual packs ranged from 170 km^2 in the CLP to 835 km^2 in the RLP (Table 2). Corresponding core areas ranged from 23 km^2 in the CLP (two core areas combined) to 178 km^2 in the RLP (Table 2).

The CLP, which occupied the south section of PNP (Fig. 2), was the only pack which exclusively used an area relatively free of human activity. The other four packs were all exposed to different levels of human activity and human altered landscape (clearcuts, roads, and townships), which are analyzed in the following sections.

Comparison of home range and study area

I. Landscape parameters

The occurrence of landscape parameters (lakes, rivers, forest cover type, and clearcuts) did not differ significantly between the pooled pack home ranges and the general study area (modified T-test, each parameter $P>0.05$, Table 1). Lakes comprised on average 3.9 % (range from 0.2 to 7 %) of the wolf habitat. The river density ranged from 0.13 to

0.92 km/km^2 with an average of 0.47 km/km^2. Clearcuts did not occur in all pack areas, the largest clearcut area was observed in the WRP's core area (8%, Table 1).

Within the home ranges, there were significant differences among the forest cover types (ANOVA; F=26.47, DF=14, P<0.001, Table 1). Conifer forest was most abundant (on average 43%), followed by mixed (19%), and deciduous (8%). The same was true for core areas: conifer (40%), mixed (13%), and deciduous (7%) (ANOVA; F=20.42, DF=20, P<0.001, Table 1).

II. Moose density

Moose density of the pooled pack home ranges did not differ significantly from the moose density in the study area (modified T-test, P>0.05). Moose densities ranged from 0.097 in the CLP's home range to 0.25 moose/km^2 in the area occupied by the WRP (Table 1). The moose density among pack home ranges differed significantly (Chi-square; Chi=45.39, DF=4, P<0.001, Table 1), with the CLP having a significantly lower density than expected from the average moose density in the study area.

III. Infrastructure

There were no significant differences in the occurrence of total infrastructure (highways, logging roads, rail roads, and power-lines combined, P>0.05) between the pooled wolf pack home ranges and the study area. A similar non significant result was observed after splitting infrastructure into single components of roads, power-lines, and rail roads (all P>0.05). The degree of infrastructure density varied among the packs' home ranges and core areas from no infrastructure in the CLP's home range or core area, to most in the home range (0.52 km/km^2) of the NP and core area (1.10 km/km^2) of the BRP (Table 2). Logging roads occurred in four of the five pack areas, while highways were absent in two home ranges and three core areas (Table 2). Also, several pack home ranges and core areas were void of power-lines and rail roads.

Within the packs' home ranges, the average highway density was significantly lower (0.046 km/km^2) than the logging road density (0.155 km/km^2, ANOVA; F=29.32, DF=15, P<0.001, Table 2). On the other hand, the densities of highways and logging roads in the core areas did not differ (0.14 and 0.19 km/km^2, respectively; P=0.52).

Comparison of home ranges and core areas

Differences in infrastructure density and occurrence of landscape characteristics were compared between home ranges (general areas used by the wolf packs) and core areas (areas of concentrated use).

There were no significant differences in the occurrence of landscape parameters (lakes, rivers, forest cover types, and clearcuts, Table 1) between the home ranges and core areas (T-tests, all P> 0.05). These results indicate that the areas of general use and those of concentrated use were similar for the five packs.

Road density (highways and logging roads) did not differ significantly among the core areas and the home ranges (T-test, P=0.16). Separate analyses of each infrastructure parameter (highways, logging roads, power-lines, and rail roads) yielded similar results, they all occurred with similar densities in the home ranges and core areas (T-tests, all P>0.05, Table 2).

Use of infrastructure parameters by wolves

On average, 11% (SE=0.034) of all locations of individual wolves in the core areas occurred on or near roads, compared to 19% (SE=0.022) in the home ranges. This difference was not significant (T-test, P=0.11). This result implies that wolves used roads in the home ranges and core areas with similar frequencies. Although some core areas included highways (Fig. 2, Table 2), wolves were never reported on or near these structures. All road locations in the core areas occurred on or close to logging roads (besides 4 locations of the BRP), contrary to road locations in home ranges where wolves were reported on both types of roads. There was a significant difference in the number of road locations on highways and logging roads (ANOVA; F=86.69, DF=15, P<0.001), with significantly more locations occurring on logging roads (12% and 88%, respectively). This was consistent with the significantly lower highway density in the home ranges as mentioned above. When road density was taken into account and added as a covariable to the dependent variable road location, the difference in the amount of road locations on highways and logging roads for all individual wolves was not significant (ANCOVA, P=0.99). This finding indicates that the wolves used the different road types according to their occurrence in the home ranges. This result was also confirmed by a Spearman's rank correlation of road locations (in core areas and home ranges) on road density (highway, and logging road). There was a significant positive association between the two parameters (r=0.4, N=18, P<0.05). Additionally, a linear regression showed that 20% of the variance in road locations was explained by road density (Fig. 4). The slope (b=0.43) differed significantly from 0 (t=2.99, DF=17, P<0.01).

Comparison of road locations among individual wolves

In home ranges, the number of road locations did not differ among the individual wolves with corresponding road densities (Chi-square, P=0.88, Fig. 5). In the core areas, the percentage of road locations according to road density differed significantly for individual wolves (Chi-square; Chi=11.32, DF=5, P<0.05, Fig. 6). Sam, a male yearling of the Black River Pack, used roads less frequently than expected from the road density in the Black River Pack's core area and compared to Aldo's (an adult male of the same pack) road locations (Fig. 5). Neither Ana or Paulina of the WRP were located on or near a logging road, despite their occurrence in the core area.

When actual road traffic, instead of road density, was taken into account, a Chi-square test showed a highly significant difference in the road use of the individual wolves (Chi=1376.5, DF=7, P<0.001, Fig. 5): Star and Cassidy of the RLP used the roads in their home range significantly more than expected (Fig.6).

Landscape parameter locations

Wolf locations occurred on or near water ways (lakes, rivers, and creeks pooled) significantly more often in the winter (3 % of all locations) than in the summer (1 % of all locations, ANOVA; F=5.43, DF=53, P<0.05), without significant differences among individuals (ANOVA, P=0.50, Table 4). Year round locations did not differ among the waterway types (lakes, rivers, creeks; ANOVA, P=0.51), indicating similar year round use of the single water ways by all wolves. When waterways were analyzed separately, rivers were found to have significantly more locations in the winter (47% of all water way locations) than in the summer (3%, ANOVA; F=8.39, DF=17, P<0.01, Table 4). Lakes and creeks received similar frequencies during both seasons (ANOVA, P=0.23, P=0.57, respectively). Again, all individual wolves were located with similar frequencies during both the winter and summer season on lakes or at the shore (P=0.72), on rivers (P=0.87), and on creeks (P=0.28).

When the locations in the different forest cover types were tested, significant differences were found (ANOVA; F=31.15, DF=17, P<0.001). Most locations occurred in mixed cover type (39%), followed by conifer (25 %) and deciduous cover (3%), despite conifer being most abundant in pack home ranges (Table 1). All wolves showed a similar pattern (ANOVA, P=0.99, Table 4). The results indicate that the wolves used the cover types disproportionately to their occurrence in the home ranges. A Chi-Square test supports this hypothesis: there were significant differences between the proportions of locations amongst the three forest cover types and their occurrence in the home ranges (Chi=13.79, DF=3, P<0.001). Mixed forest cover was used by all wolves significantly more than expected from its abundance in the packs' home ranges. All wolves were rarely located in clearcuts (Table 4), which did not occur frequently in the home ranges as mentioned above (Table 1). A Chi-square test showed that only Sam and Aldo of the BRP were observed more frequently in clearcuts than expected. Their rendezvous site was partially located in these clearcuts. All other wolves either used clearcuts proportionally to their occurrence or less frequently (Chi=19.18, DF=7, $P<0.01$).

1.5 Discussion

Quantifying the relationship between human induced habitat or structural changes and wolf habitat use indicates the potential influence of such factors on wolf distribution and wolf survival. Macrohabitat changes and the building of infrastructure are two factors which seem to be of importance for wolf survival (Thiel 1985, Mech et al. 1988, Mech 1989, Mladenoff et al. 1995). Several studies have shown that wolves either avoid or choose not to inhabit areas with road densities higher than 0.60 km/km^2 (Mladenoff et al. 1995, Mech et al. 1988, Thurber et al. 1994, Jensen et al. 1986). Mladenoff et al. showed that recolonizing wolf pack areas in Wisconsin were not bisected by highways and road densities within these areas rarely exceeded 0.45 km/km^2. Road densities in core areas of their study packs did not exceed 0.23 km/km^2. The results of my study indicate that resident wolves on the north shore of Lake Superior tend to use roads proportionally to their occurrence, reflected in the positive association of road use and road density. The overall road density in the study area was low (0.18 km/km^2), but, in both NP's and BRP's core areas (0.69 and 0.76 km/km^2, respectively) it exceeded the reported road density thresholds reported in other studies (Thiel 1985, Jensen et. al 1986, Mech et al. 1988). This result reflects the wolves' attraction to a garbage dump (Krizan this volume), which was situated within the core areas of both packs. The attraction of this predictable and concentrated food resource probably resulted in a higher tolerance of roads, traffic, and human presence. One limitation of using road densities for evaluating wolf home ranges is the fact that roads are rarely evenly distributed throughout the home ranges. The use of the road density parameter alone can lead to bias results because wolves can use areas without roads more frequently than areas with higher road densities within their home ranges. This problem was overcome in this study by the use of the adaptive kernel method for estimating home ranges (Worton 1989[a]) and by accounting for actual locations of wolves on roads.

In addition to roads, railroad traffic can cause mortality, as shown in the case of one dispersing wolf (Paulina from the WRP). It is therefore important that their effect on wolf travel be considered. Since railways are clear of snow in winter, they may provide potential travel corridors for wolves. Although train traffic in the study area is not as frequent as the road traffic on highways, the fact that they are clear of snow may attract wolves. Power-lines did not receive vehicle traffic, but most of them are regular snow machine routes. Additionally, many trappers use them for trapping. All infrastructure parameters combined (roads, rail roads, power-lines) showed very high densities in the core areas of both packs (1.1 km/km^2 for the BRP, 0.86 km/km^2 for the NP).

During this 3 year study 26 (70%) of 37 individuals in five packs either died or disappeared. The fate of 9 (24%) individuals remains unknown but 17 (46%) mortalities were observed. Road caused mortality from collision and access (due to trapping and hunting) was responsible for the death of 12 individuals from the five study packs, representing 70.6% of the known mortalities. In contrast, natural mortality (starvation and disease, Krizan unpublished data) of five individuals accounted for only 29.4%. Trapping and snaring was the highest cause of mortality (six individuals), followed by road kills (three), shooting (two) and one railway kill. Of the trapped wolves, three were trapped on a logging road, two at a dump, and one on a power-line. One male wolf of the RLP was shot by a trapper during the live capture operation in 1994 and another was shot in a clearcut in fall 1996. Two wolves were killed by vehicles on Hwy 17, within the BRP's home range. Another wolf was hit on Hwy 17 in the home range of the WRP. Paulina, an adult female of the WRP, was killed by a train after she dispersed in December 1994. These minimum accounts of human caused mortality show that infrastructure plays an important role directly (through collisions) and indirectly (by facilitating human access) and should be considered as important factors influencing wolf survival.

Home ranges and core areas of the BRP and the NP overlapped, but the wolves didn't use the area simultaneously. The core areas include two garbage dumps which were visited by both packs during two different years (Krizan this volume). Home ranges of the RLP and the WRP also overlapped spatially. On two occasions, wolves of the two packs were located approximately six km apart. The observed overlap of the home ranges may suggest that wolves do not always respect the boundaries of home ranges or territories as suggested by Peters and Mech (1975). However, the core areas of the packs were strictly separated, indicating the wolves were territorial (Mech 1970, Peters and Mech 1975).

The two core areas observed for each of the NP and the CLP represent differences in spatial travel patterns. For the NP, these two areas represent the den and rendezvous areas and the location of a garbage dump, respectively, both of them visited seasonally (Krizan this volume). One of the CLP core areas represents the travel pattern of an adult female Mika, which travelled predominantly alone but occasionally associated with the rest of the pack. The other core area represents an area believed to be the rendezvous site of the CLP. The RLP, the BRP, and the WRP did not produce offspring during this study, which may be one reason for their single core areas (lack of denning and rendezvous sites).

The CLP had the smallest home range despite the lowest moose density (0.097 moose/km^2). This is contrary to Fuller's (1995) study, where he found that territory size is negatively correlated with prey density. Given the very low reported moose density, and thus longer travel distances to search out vulnerable prey, a larger home range would be expected. However, the lack of roads and other infrastructure such as power-lines, which may have served as travel corridors and facilitated travel for the other four packs, may have restricted the CLP's movements. The rugged topography of the coast with dense old growth forest cover may have also been an impediment to travel. The use of travel corridors by the other four packs may be reflected by their larger home ranges. Although there were relatively few daytime telemetry locations of the wolves directly on power-lines, trapping records, and aerial and ground tracking in winter provided evidence of their use (Krizan, unpublished data), which suggests that wolves used these travel corridors mainly during dark. The results indicate that roads and other infrastructure, such as railways and power-lines are used as travel corridors and may affect the size of wolf pack home ranges.

In addition to road density, vehicle traffic on the roads might influence the wolves' habitat use. In this study, there was a high volume of traffic on Highway 17 and the three secondary highways in the wolves' home ranges. Despite active logging during the study, traffic on logging roads was rather low. Compared to the other wolves, Star and Cassidy from the RLP used roads more than expected, possibly because only logging roads with low daily traffic occurred in the RLP's home range. This suggests that both road density and actual vehicle traffic need to be considered when the quality of wolf habitat is evaluated.

Mladenoff et al. (1995) identified several landscape parameters useful for assessing quality of wolf habitat. They found forest cover type to be an important criterion for wolf presence. The three forest cover types (conifer, deciduous, and mixed) did not differ among the five pack home ranges and between home ranges and the study area. However, wolves were located significantly more often in mixed forest than deciduous and the more abundant conifer. Selection for mixed forest became even more noteworthy, given the significantly higher abundance of conifer forest cover in all pack home ranges and the study area in general. These results concur with those of Mladenoff et al. (1995), and suggest that wolves favour mixed forest types over homogeneous conifer and deciduous forest patches. Although wolves are not habitat specific (Mech 1970, Mladenoff et al. 1995), they do appear to visit areas which are most frequented by their prey. Moose and beaver comprised most of the wolves' diets in this study (Krizan this volume). Since conifer forest cover is generally not favoured by either species (Telfer 1995, Banfield 1974), it could be assumed that the wolves in this study followed their prey and therefore spent significantly more time in mixed forest.

Clearcuts were generally used in proportion to their occurrence, although snow tracking indicated that wolves crossed them to access the next patch of forested area. The wolves Sam and Aldo from the BRP were located more frequently in clearcuts because the location of the their pack's rendezvous site was near a clearcut. In addition, as indicated by a significantly higher percentage of locations on rivers in the winter, wolves frequently used frozen rivers as travel corridors.

Prey density is identified as a primary factor influencing the density (Packard and Mech 1980, Fuller 1989, and Messier 1994), survival, and reproduction (Mech 1977, Messier and Crete 1985) of wolves. Messier and Crete (1985) showed that moose densities must exceed 0.20 moose/km^2 to sustain wolves. Moose densities within the overall study area were slightly below this threshold. However, in three of the study packs' home ranges prey density exceeded 0.20 moose/km^2 minimally. It is plausible that moose densities slightly higher than the reported threshold are not sufficient to sustain a wolf pack, which is supported by the lack of reproduction and low survival of wolves in the study area (Krizan unpublished data). This hypothesis is further supported by Messier (1987), who found that wolves were malnourished when moose densities were below 0.4 moose/km^2. The densities of moose were similar for the home ranges of all packs except for the CLP's home range where moose density was the lowest (0.097 moose/km^2). The only pack known to reproduce during the study was the NP, which fed seasonally at a garbage dump (Krizan this volume). The mortality from diseases and lack of reproduction in the other four packs are consistent with the results of Messier (1987) and imply that wolves which subsisted primarily on moose may have been malnourished and more vulnerable to disease. Mika, an adult female of the CLP, which inhabited the area with the lowest moose density of all study packs, was found dead in February 1996. Necropsy of her carcass showed that she died of starvation (Campbell pers. com.). This observation lends support to the belief that low moose densities within the entire study area cannot sustain a viable wolf population without additional food sources.

Dispersal is an important part of wolf distribution and pack dynamics (Mech 1970). Seven out of ten radio collared wolves dispersed during this study from their original packs. They traveled in a northerly and northwesterly direction, away from or parallel to Lake Superior. Most of the dispersed wolves had to cross logging road complexes and a major highway (Hwy. 17), which further exposed them to traffic and trapping. Seventy one percent of these dispersers died by the end of the study. All ten radio collared study wolves were originally captured in or close to PNP. Low moose densities in and around the park were probably responsible for the observed dispersal and lack of reproduction of the wolves.

The high wolf mortality outside of the park might be due to fragmentation of the landscape surrounding PNP (i.g. clearcutting and road construction). Human activities outside the park have a serious impact on the wolf population inside the park. This study shows that the size of PNP (< 2000 km^2) is not adequate to fully protect or provide the habitat required for a healthy, reproducing wolf population, and likely represents the situation in other national parks in Canada. These impact are likely to be more severe in the future since new plans to clearcut large areas of forest directly adjacent to the park boundaries are in progress. This form of resource extraction will inevitably leave PNP insular, with little natural habitat for wildlife which require large areas for their existence.

This study shows that wolves use roads according to their availability. Although the validity of a the road density threshold model could not be tested for all packs, it is plausible that wolves will use areas with road densities higher than the 0.60 km/km^2 if they are attracted by a food source. The combination of low moose densities and available infrastructural travel corridors is reflected by larger home ranges in the four packs outside of the national park, in contrast to the smaller home range in an area with a significantly lower moose density but lack of infrastructure (CLP). Wolves used roads and other forms of infrastructure when available, but roads were the highest source of direct and indirect human-caused mortality. Contrary to other studies, this study shows that road density alone is not a sufficient indicator of favourable wolf habitat. Rather, the type of use by humans and the frequency of traffic is of equal importance. The combined effect of low moose densities and direct and indirect human-caused mortality facilitated by human-built infrastructure, might have had a negative effect on the packs' reproductive success and survival.

1.6 Tables and Figures

Table 1: Landscape parameters for the study area and the home ranges (H) and core areas (C) of the five packs. Shown are the river density (km/km^2) and the areas (km^2) and percentages (in brackets) covered by lakes, mixed, deciduous, and coniferous forest cover type, clearcuts and the moose densities (moose/ km^2).

Area	Rivers	Lakes	Mixed	Deciduous	Conifer	Clearcut	Moose
Study	0.54	447.6 (5)	1230.6 (14)	733.8 (8)	3444.3 (38)	306.3 (3.4)	0.198
NP, H	0.13	11.79 (3)	111.62 (24)	21.72 (5)	183.53 (40)	30.2 (6.5)	0.225
NP, C_1	0.13	0.66 (2)	8.74 (20)	1.29 (3)	21.44 (50)	——	0.225
NP, C_2	0.66	0.22 (0.5)	11.1 (27)	——	20.44 (50)	——	0.225
BRP, H	0.58	1.34 (0.2)	199.4 (25)	34.08 (4)	435.44 (55)	3.47 (0.4)	0.23
BRP, C	0.17	0.66 (1)	9.95 (19)	2.96 (6)	20.33 (39)	——	0.23
RLP, H	0.58	35.23 (4)	115.7 (14)	60.42 (7)	318.41 (38)	47.14 (6)	0.18
RLP, C	0.54	8.62 (5)	27.42 (15)	0.50 (0.3)	49.61 (28)	11.78 (7)	0.18
WRP,H	0.4	60.32 (7)	168.26 (20)	5.85 (0.4)	370.16 (45)	46.14 (6)	0.25
WRP,C	0.32	10.99 (9)	23.9 (19)	1.02 (0.8)	61.56 (48)	9.83 (8)	0.25
CLP, H	0.71	7.02 (4)	17.59 (10)	36.77 (22)	73.92 (43)	——	0.097
CLP,C_1	0.47	0.89 (7)	——	2.2 (17)	7.76 (60)	——	0.097
CLP,C_2	0.92	0.37 (4)	——	2.48 (25)	2.71 (27)	——	0.097

Table 2: The size of the area (km^2) and densities of total infrastructure (km/km^2), total roads (km/km^2), highways (km/km^2), logging roads (km/km^2), power-lines (km/km^2), and rail roads (km/km^2) for the study area, home ranges (H), and core areas (C) of the five packs.

Area	Size	Infrastr.	Roads	Highways	Log. roads	Power l.	Rail Roads
Study	9115	0.23	0.18	0.02	0.16	0.03	0.02
NP, H	459	0.52	0.25	0.11	0.14	0.16	0.09
NP, C_1	43	0.86	0.69	0.41	0.28	——	0.17
NP, C_2	41	0.45	0.39	0.08	0.30	0.06	——
BRP, H	797	0.23	0.16	0.07	0.09	0.02	0.05
BRP, C	52	1.10	0.76	0.40	0.23	0.35	0.13
RLP, H	835	0.22	0.19	——	0.19	0.03	——
RLP, C	178	0.22	0.22	——	0.22	——	——
WRP,H	824	0.28	0.22	0.04	0.18	0.02	0.04
WRP,C	129	0.08	0.08	——	0.08	——	——
CLP, H	170	——	——	——	——	——	——
CLP,C_1	13	——	——	——	——	——	——
CLP,C_2	10	——	——	——	——	——	——

Table 3: Capture date, sex, weight (kg), estimated age (years), body measurements (all in cm), and colour of the captured and radio collared wolves.

Wolf	Pack	Date	Sex	Weight	Age	Body length	Shoulder height	Tail length	Colour
Aldo	BRP	8/94	M	36.5	3	176	79	50	grey
Ana	WRP	8/95	F	35	5	176.5	76	39.5	grey
Cassidy	RLP	9/94	F	32	5	165	74	47	light grey
Mika	CLP	7/95	F	27	6	162.6	73	42	black
Moon	WRP	2/96	F	37	8	157.5	77	43	white
Paulina	WRP	8/94	F	28	3	160	73	44	brown red
Sam	NP	8/94	M	12.5	0.4	135	60	37	brown grey
Solita	CLP	7/95	F	25	5	149.5	71	42	black
Star	RLP	2/96	M	60	7	187.4	83.9	46	yellow

Table 4: Telemetry locations of the individual wolves on or near roads (total), highways, logging roads, lakes, rivers, creeks, clearcuts, and in the different forest cover types (mixed, deciduous, and conifer) in their home ranges. For all water ways, locations are split in summer (first number) and winter (second number) locations. Shown are percentages of all locations of the individual wolves (N = 528). Locations on highways and logging roads are shown as percentage of all road locations of each wolf.

Wolf	Pack	Road	Highw	Log. rd.	Lake	River	Creek	Clearct	Mixed	Decid	Coni
Sam	NP	18	13.2	86.8	0 / 0	0 / 3	0 / 3	——	46.8	3.2	27.4
Aldo	BRP	32	32.4	67.6	0 / 0	0 / 0	0 / 0	3	32.8	2.7	31.1
Sam	BRP	26	14.8	85.2	0 / 0	0 / 2	2 / 0	2	39.1	1.9	20.4
Cassidy	RLP	11	——	100	0 / 4	0.7 / 2	2 / 0	2	28.0	2.3	28.9
Star	RLP	16	——	100	2 / 4	0 / 11	2 / 0	4	38.3	3.7	28.9
Ana	WRP	20	40	60	9 / 2	0 / 3	7 / 2	9	16.4	3.2	40.9
Paulina	WRP	13	——	100	0 /0	0 / 11	0 / 0	——	56.1	——	21.8
Moon	WRP	17	——	100	11 / 0	0 / 2	2 / 4	7	28.3	2.1	23.0
Mika	CLP	——	——	——	9 / 0	9 / 0	0 / 0	——	43.7	6.2	21.9
Solita	CLP	——	——	——	0 / 4	0 / 4	4 / 0	——	67.8	4.1	8.2

Fig. 1: The general study area between Thunder Bay and Sault Saint Marie on the North Shore of Lake Superior.

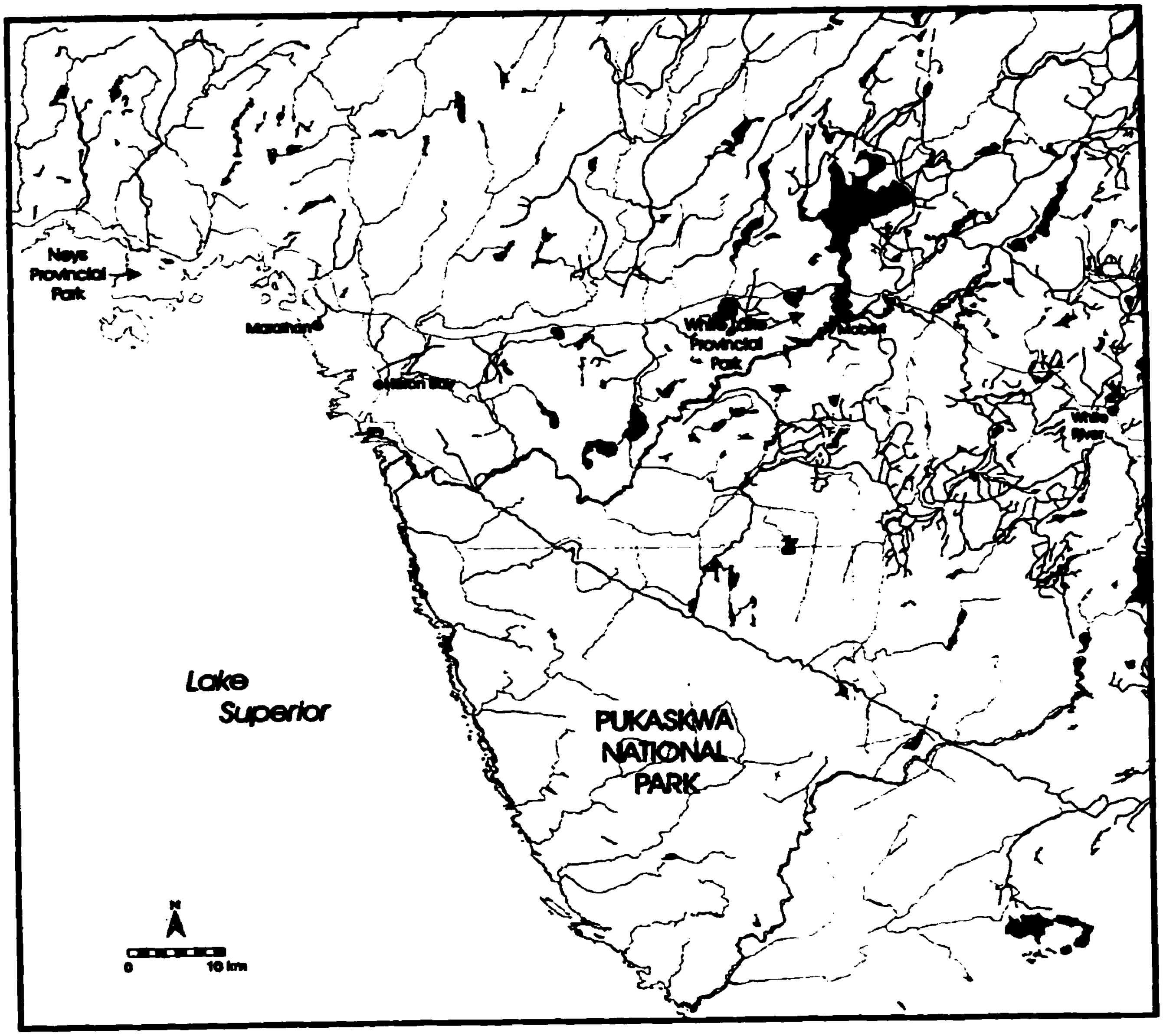


Fig. 2: Home ranges and core areas (represented by the small contours within the home ranges) of the five packs described in this study. For detailed definition see text.

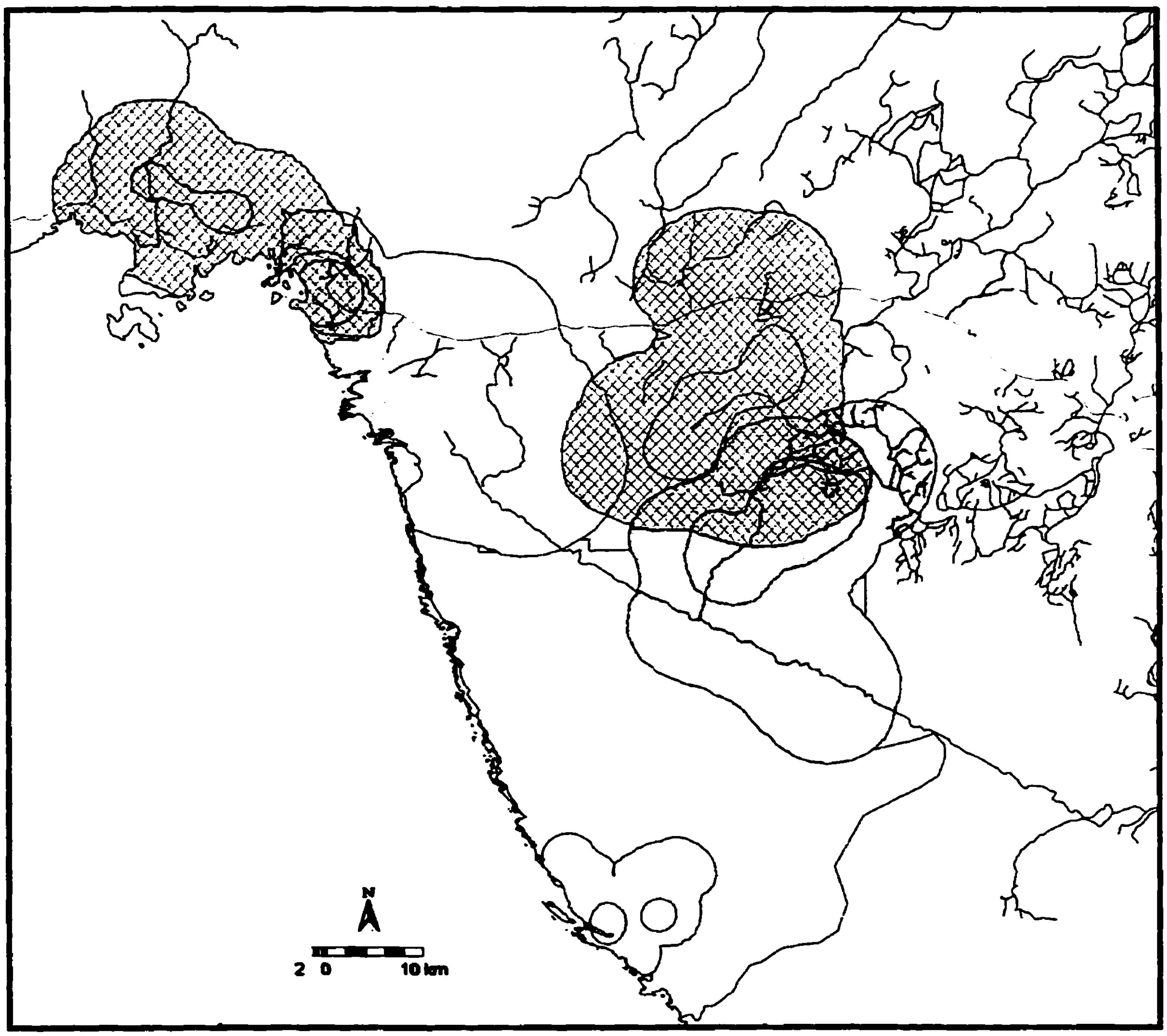


Fig. 3: The history of the wolves of five packs described in this study. Pack and wolf names are shown on the y-axes (including sex). The length of the separate lines indicate the duration of radio telemetry data received from the individual animals.
R = Time of Capture and radio collaring, D = Dispersal, R! = Reproduction, M = Mortality. The numbers shown at the lines indicate the numbers of animals in this pack at the time.

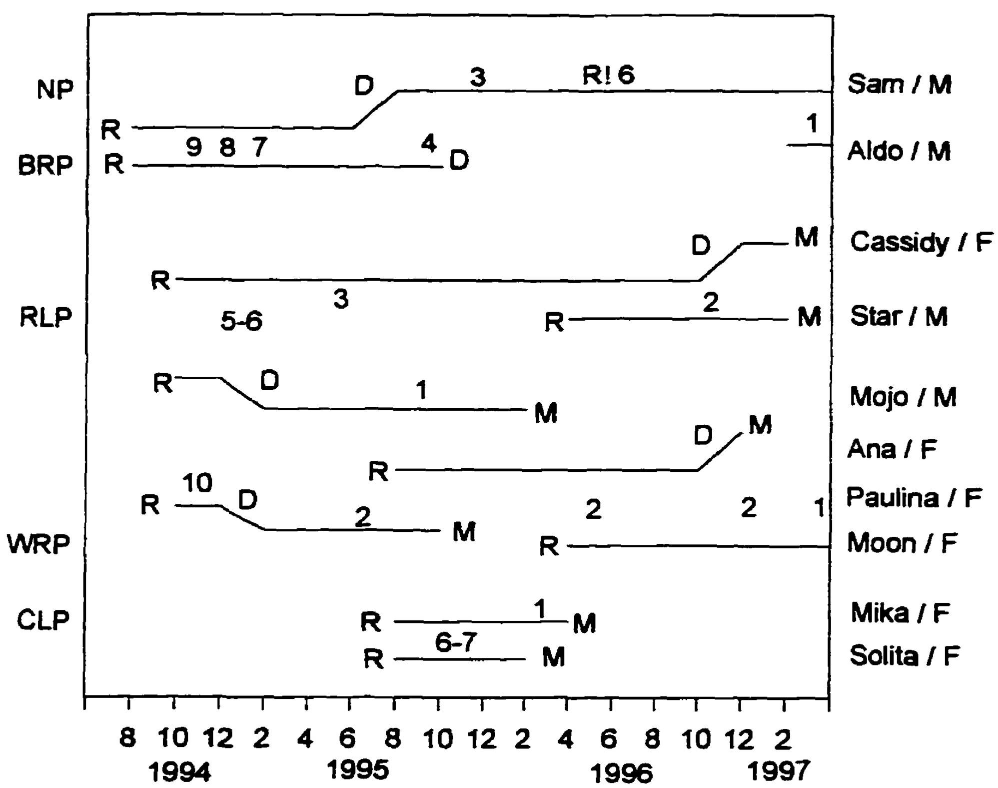


Fig. 4: Average percentage of telemetry locations of the 7 individual wolves (CLP not included) on or near roads in core area and home range and road densities in these areas. Sam appears 3 times, one time for the BRP, the other both times for the NP, which had 2 core areas, therefore N = 18. The line represents the linear regression (b = 43, r_s = 0. 4, $P < 0.05$).

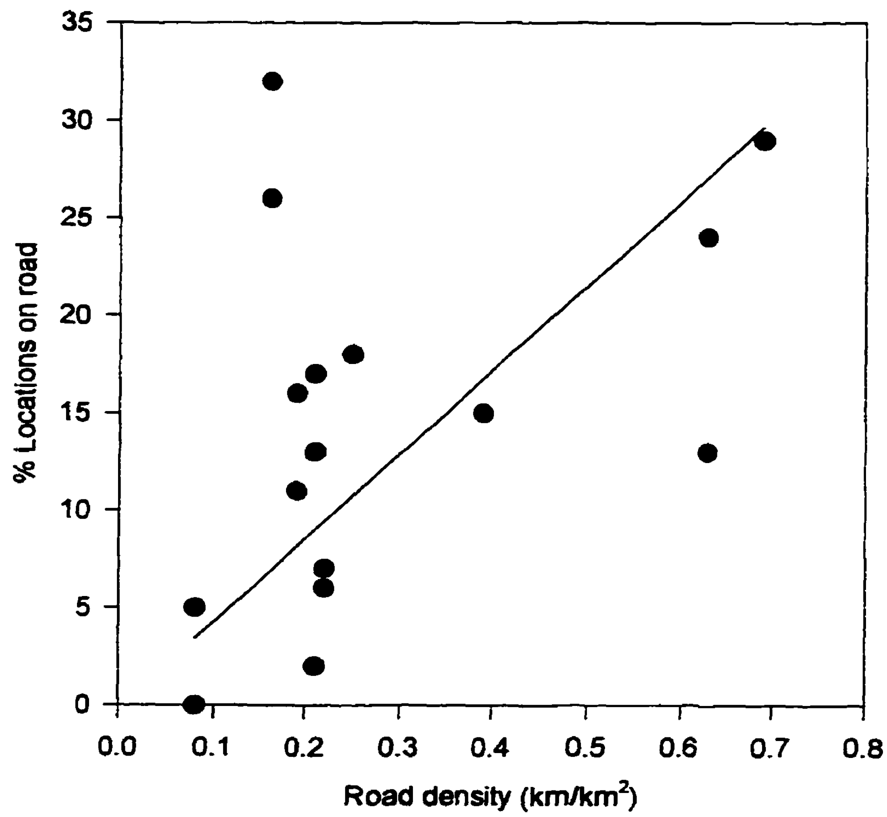


Fig. 5: The densities of roads (highways and logging roads), power-lines, and rail roads (all in km / km^2) in the packs' home ranges and telemetry locations (fraction of all individual locations) of each wolf occuring on these structures. Excluded is the CLP because of the missing infrastructure in their home range. N = 471. The numbers above the road density bars indicate the average daily traffic on the roads in the home ranges.

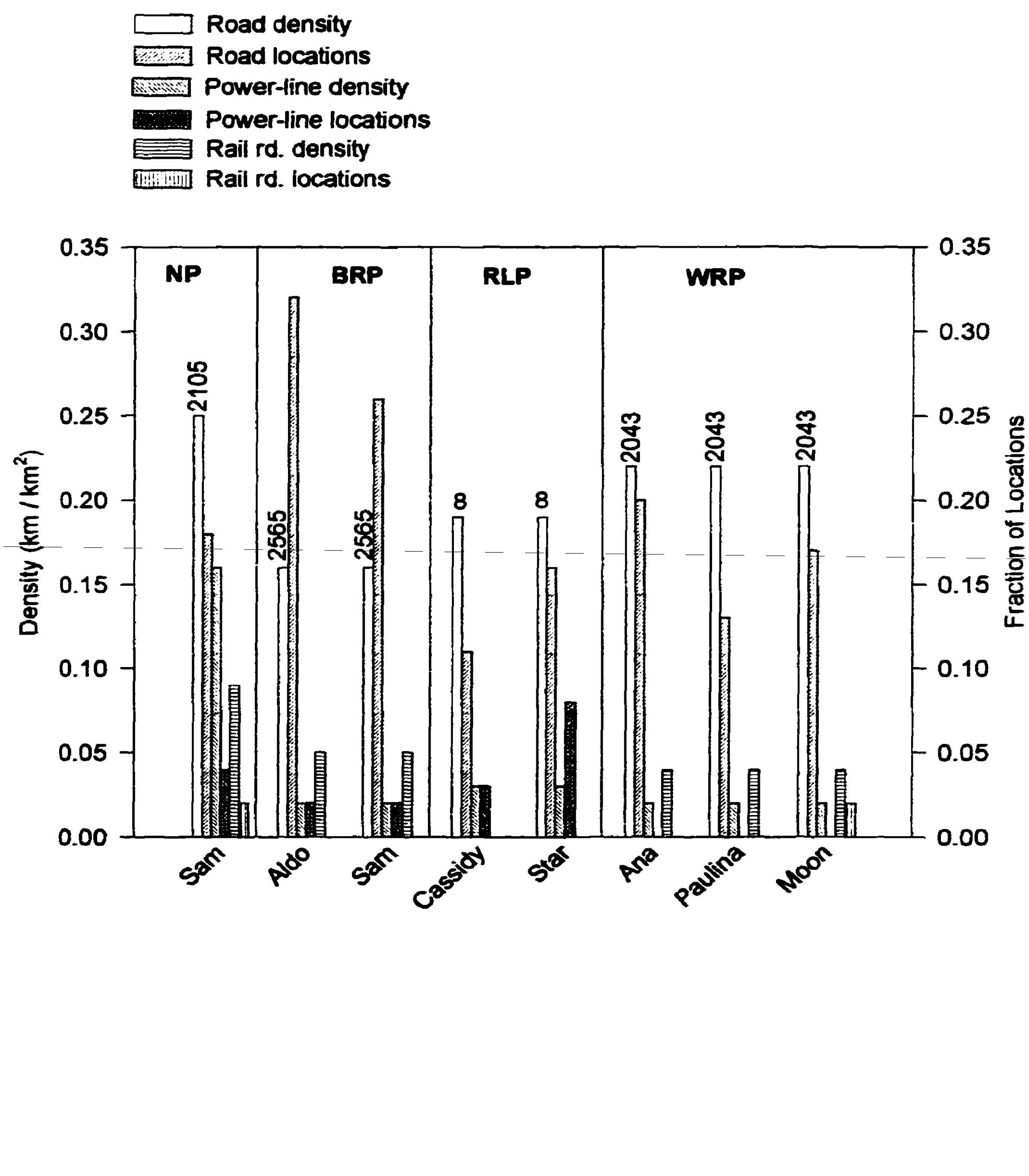
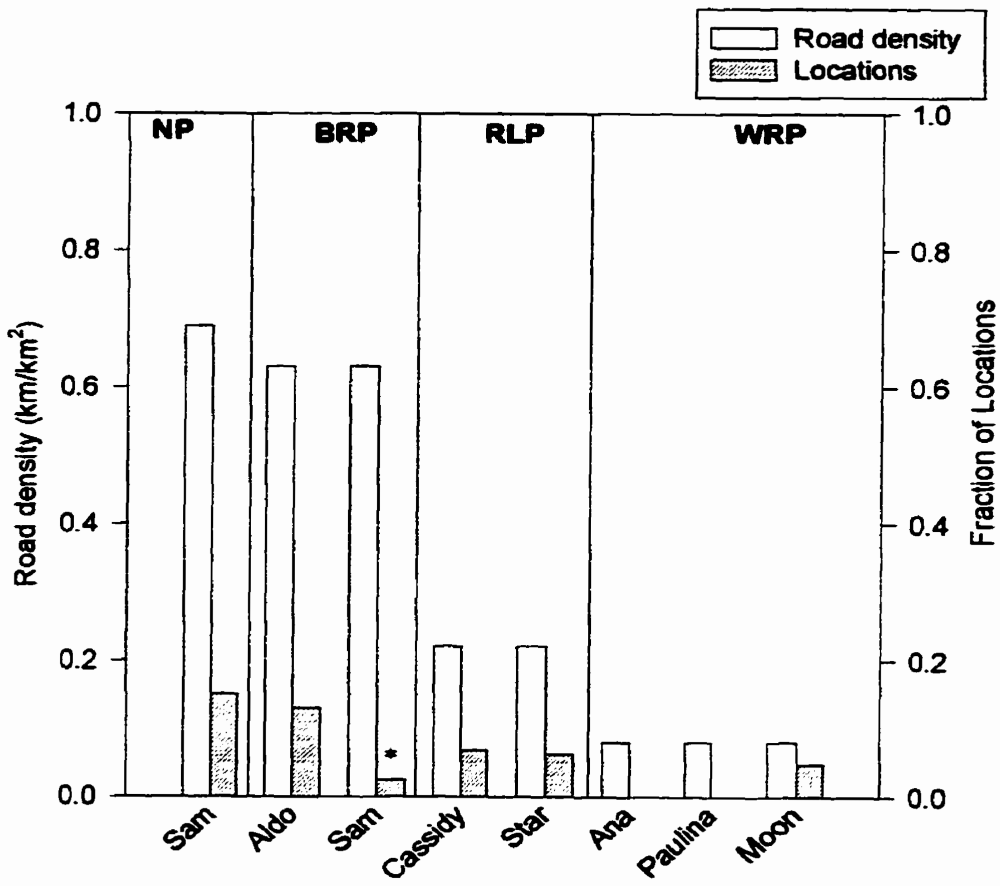


Fig. 6: Road densities (km / km²) in the wolf packs' core areas and corresponding road locations for the individual wolves (as fraction of all individual locations. N=471. * * = significant deviation from the expected value.



2. The influence of garbage dumps on habitat use of wolves (*Canis lupus*) on the north shore of Lake Superior, Ontario

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2.1 Abstract

Three wolf packs were studied from 1994 to 1997 on the north shore of Lake Superior. Two of the packs visited and fed seasonally, mainly from early fall to late February, at a garbage dump. Snow tracking, ground telemetry, and scat collection in all three winters confirmed frequent use of the dump. One of the two packs ceased to use the dump after the first winter. Home ranges and core areas were smaller for the two packs which visited the dump. Accordingly, the distances traveled between subsequent locations were shorter compared to the third pack. The wolves' travel patterns differed seasonally. Distances were shortest during the breeding season, and longest during the period of pup rearing. Although the wolves stayed at the dump during the winter months, they left this location frequently. The average number of consecutive days spent at the dump did not differ from the time the other study wolves spent at a kill site. During summer, wolves did not visit the dumps and scat analysis showed that the diet

was similar for all three packs. While the one pack which fed seasonally at a dump reproduced during this study, the other two did not. The pack's home range which did not contain a dump supported moose densities below the reported threshold required to sustain a viable wolf population. It is probable that the pack which fed at the dump benefited from this food source and was able to successfully reproduce.

2.2 Introduction

The response of wolves (Canis lupus) to the presence of humans is a current topic of interest for understanding the success of existing and recolonizing wolf populations (Mladenoff et. al 1995, Mech 1996, Rasker and Hackman 1996, Noss et al. 1996, Clark et al. 1996). Although wolves are generally thought to avoid areas with human development (Boitani 1992, Mladenoff 1995), they sometimes live in close proximity to human settlements (Boitani 1982, Boitani 1992, Mech 1995a). There is no direct effect of wolf presence on humans (Grace 1976, Rasker and Hackman 1996), yet in Ontario they are commonly regarded as pests. The main conflicts between wolves, as well as other large carnivores, and humans have been due to livestock depredation (Blanco et al. 1992) and mythical beliefs (Mech 1970, Lopez 1975, Kellert et al. 1996). The deleterious effects on wolves by humans is an historical fact, which to this day remains a concern in many parts of the world (Clark et al. 1996). Although wolf populations seem to be recovering in many countries, (Blanco et al. 1992, Mech et al. 1996), a growing global human population is increasing the likelihood of wolf-human conflicts (Mech 1996). Anthropogenic activities such as economic development and habitat degradation affect wolves and other large carnivores in western Canada and the United States (Boyd and Jimenez 1994, Rasker and Hackman 1996). The extent of influence of such activities and thresholds of tolerance are not well understood. There is very little information in North America about how wolves use human inhabited areas and what the effects of such areas are on the ecology of the wolves. Waste disposal or landfill sites, commonly called garbage dumps, are one product of human habitation and when accessible to wolves they are a potential source of food (Fuller 1980, Mech and Hertel 1983).

The use of garbage dumps by wolves and other wildlife has been reported in North America (Grace 1976, Fuller 1980, Eberhardt et. al 1983, Mech and Hertel 1983, Garott et. al 1983, Mech 1994), in Europe (Boitani 1982, Salvador and Abad 1987, Blanco et al. 1992, Boitani 1992), and the near east (Mendelssohn 1982, Afik and Alkon 1983). In Minnesota (USA), a wolf pack which fed at a land fill site in the summer had the smallest territory compared to all the other packs in their study area (Mech and Hertel 1983). In Leon province (Spain), garbage was an important part of the wolves' diet and remained as an important food source independent of the density of other prey species (Salvador and Abad 1987). In Italy, wolves showed affinity to garbage dumps but avoided human contact (Boitani 1992). In several areas, wolves chose den sites and/or rendezvous sites less than two km from garbage dumps (Ciucci and Mech 1992, Mech 1995c). Combined, these studies show that in certain areas where garbage dumps are accessible to wolves: i/ wolves use and feed at garbage dumps; ii/ wolves may locate denning and/or rendezvous sites close to garbage dumps; iii/ wolves may benefit from these human made food depots.

This study compares the spatial use of three wolf packs in different habitats. These differences provided an opportunity to study the potential influence of garbage dumps on the spatial movements of wolves. Three main questions are addressed:

1. Do wolves visit the garbage dumps and do they feed there?
2. Is the use of the garbage dump a seasonal phenomenon?
3. Do the garbage dumps affect home range size and travel patterns of wolves?

2.3 Methods

Study Area

This study was done from October 1994 to March 1997 on the north shore of Lake Superior (48° 30' N, 86° 00' W), Ontario, midway between Thunder Bay and Sault Saint Marie (Fig.1). The entire study area encompasses approximately 9,115 km^2 and includes: Pukaskwa National Park (PNP, 1,878 km^2), the White River Forest Management Area in the northeast, and adjoining Black River and Steel River Forest Management Areas, the later includes Neys Provincial Park to the west (Fig. 1).

The coastal region of the study area is characterized by rugged topography with high rocky elevations ranging up to 650 m from a base level of 189 m at Lake Superior.

Numerous river valleys and small lakes create a naturally patchy environment. The interior region is a flat plateau, characterized by a heavily eroded mountain landscape scoured by continental glaciers (Poitevin et al. 1989). Winter and summer mean temperatures range from -13° C to 14.6° C, respectively, for the coastal area, and -17° C to 15.9° C, respectively, inland (Poitevin et. al 1989). Mean annual precipitation along the coast is 737 mm and 644 mm inland (Poitevin et. al 1989). Snow depth reaches a maximum average depth of 100 cm but can range from 50-150 cm. Ice cover on Lake Superior varies from year to year from 5-100% (Skibicki 1994).

The vegetation in both the coastal and the inland regions consists mainly of coniferous species such as: balsam fir (Abies balsamea), black spruce (Picea mariana), white spruce (P. glauca), jack pine (Pinus banksiana), with some associations with white birch (Betula papyrifera), and quaking aspen (Populus tremuloides) (Poitevin et. al 1989).

Mining, timber harvest, hydro development, recreational activities (including trapping, hunting and fishing), and associated infrastructure occur within the study area, although minimally in PNP. Logging of the White River Forest has intensified since 1977 and has largely concentrated on conifers (jack pine, spruce, balsam fir). As a result, extensive road building has taken place to facilitate the harvest of timber.

Three areas are populated with humans within the focal study area. Marathon, the largest of the three settlements (about 5,500 inhabitants) has its own garbage dump.

The garbage dump is located on a 12.3 hectare site north east of the Town (Fig. 1). It currently handles 3,500 tons of waste each year (D. Brown pers. com.). The site is partially fenced on three sides (two sides adjacent to the town and the other adjacent to a school yard). The total unfenced perimeter area accessible to wildlife exceeds 50%. The waste includes residential and commercial refuse collected twice weekly by the Town of Marathon and depositions by local residents and businesses during scheduled hours. Other materials observed in the dump site include domestic pet carcasses, as well as discarded trapped and other animal carcasses.

The Town of Heron Bay is approximately 9 km south east of Marathon, and has 150 inhabitants. The Pic River First Nation Reserve is 2.5 km south of Heron Bay with a population of 400 residents. There is one shared garbage dump for both settlements, which is also used by Pukaskwa National Park (combined waste generation rate of 200 tons/year). The Heron Bay waste disposal site is 5 km south east of the Marathon dump and is 4 km north of the community of Heron Bay (Fig. 1). This facility has no fencing and it receives similar waste in smaller quantities.

Potential prey species of the wolf in the study area include moose (Alces alces), beaver (Castor canadensis), and snowshoe hare (Lepus americanus). Several small mammals, such as southern red-backed vole (Clethrionomys gapperi), meadow vole (Microtus pennsylvanicus), deer mouse (Peromyscus maniculatus), southern bog lemming (Synaptomys cooperi), and red squirrel (Tamiasciurus hudsonicus) were also present. Very few caribou (Rangifer tarandus) have been observed in the study area (Moreland 1991, Bergerud 1989, Wade 1995). White-tailed deer (Odocoileus virginianus) are even fewer (Ferguson pers.com.) but they are still regarded as potential prey.

Other carnivorous mammals in the study area include marten (Martes americana), fisher (M. pennanti), mink (Mustela vison), river otter (Lutra canadensis), red fox (Vulpes vulpes), coyote (Canis latrans), black bear (Ursus americanus), weasels (Mustela sp.), and lynx (Felis canadensis).

Wolf capture

I live trapped wolves with leghold traps (modified as described by Kuehn et al. 1986) or by net gun from a helicopter (P. Krizan and Helicopter Wildlife Management, Seattle USA, see Appendix 1). Immobilized wolves were blood sampled, eartagged, weighed, measured, aged (based on tooth ware), and radio collared (Lotek Engineering, Ontario). The BRP and later the NP wolves were not trapped by a local trapper from January 1995 to March 1997 as a result of a cooperative agreement between the trapper and the author.

Live capture of all wolves was approved by the animal care committee of the Ontario Ministry of Natural Resources.

Radio telemetry

All radio collared wolves were located with a fixed wing aircraft (Cessna-185) approximately once per week. All aerial locations were recorded with a global positioning system (GPS, Garmen 55®) as Latitude/Longitude (decimal degrees), and translated into a Universal Transverse Mercator Grid System with the program Geographic Calculator (Blue Marble Geographics, Gardiner, Maine USA). Test radio collars of known frequency were randomly placed and located during regular telemetry flights to estimate the error of aerial locations. All actual test collar positions were differentially corrected and compared with the observed uncorrected GPS position from the aircraft. I estimated the mean error of locations (the difference of the actual to the observed location) to be ±112 m (range = 70.7 - 144.5, n=35).

In addition to aerial telemetry, the Black River Pack (BRP), and later the Neys Pack (NP) were located daily by ground telemetry when they used the garbage dump. There are several methods to estimate animal locations from ground telemetry data (White and Garrot 1990), some of which have been found to be unacceptable (Saltz and White 1990, Nams and Boutin 1991, Zimmerman and Powell 1995). In this study, the error polygon method was used to estimate wolf locations. I used two bearings with an angle of intersection between 45° and 135° (Springer 1979). In the vicinity of the garbage dumps, bearings were taken from predetermined and non-predetermined GPS points (stations). Non-predetermined stations were recorded with a hand held GPS (Trimbel Geo-Explorer) and plotted on a 1:50,000 topographic map. The use of non-predetermined points was necessary because access to the proximity of the telemetried wolves was limited, the wolves did not always use the same area, and at times they traveled long distances. The two estimated bearings were taken with a time interval of no more than 15 minutes. Although it is recommended that Lenth's (1981a,b) estimator be used for estimating animal locations (White and Garrot 1990, Saltz and White 1990, Nams and Boutin 1991, Zimmerman and Powell 1995), the time restriction of 15 minutes between bearings and the necessity to take bearings from non-stationary stations prevented my use of this method. The precision and error of estimated locations were determined from randomly placed stationary "test" radio transmitters for predetermined stations and mobile telemetry points. The estimated mean error from the true bearing (i.e. difference between observed and true bearing) for predetermined stations was $\pm 1.9^0$ (SE=0.8, n=35). The estimated mean error from the true bearing for mobile telemetry points was determined to be $\pm 2.2^o$ (SE=1.12, n=35). Reported estimates of error were calculated for bearings taken by the author.

Statistical analysis

Aerial and ground locations for each wolf were analyzed using Chi-square test to test for normal distribution of the data. The program CALHOME was used to calculate home ranges using the adaptive kernel method (Worton 1987,1989, Kie et. al 1996, Shivik et al. 1996). The adaptive kernel method frees the data from normality assumptions, is much less sensitive to outliers than other methods, and is not as prone to include unused or untraveled areas (Shivik et al. 1996). Its effectiveness at highlighting areas of concentrated use make it particularly applicable.

Home ranges and core areas

Spatial use is defined as the home range, "that area traversed by the individual in its normal activities of food gathering, mating and caring for young" (Burt 1943).

Home ranges are specified by 95% of the pooled locations for each pack and were estimated from aerial telemetry for the packs. The 50% utilization distribution (representing 50% of locations for a specified period of time) was selected to represent the core area of use (White and Garrot 1990).

Individual travel distances

Distances between subsequent locations were calculated by Calhome®. When the data were normally distributed (Wilk-Shapiro test) one-way ANOVA was used for analysis, followed by a post-hoc test (Bonferroni). The year was divided into four biological seasons: breeding (01 February to 31 March), denning (01 April to 30 June), pup rearing (01 July to 30 September), and nomadic season (01 October to 31 January). Only aerial locations within the 95% probability of occurrence were used in the analysis of travel distances.

Day time activity

Activities of visually observed wolves during aerial radio telemetry were recorded as: resting, traveling, or feeding. A Chi-square test was used to test the differences in day time activity among the wolves and for each wolf separately.

Intensity of food resource use

The amount of time spent at and the frequency of visits to the garbage dump was assessed by both aerial and ground telemetry. Locations that fell within the dump or in a 2.5 km^2 buffer on the unfenced eastern perimeter were considered to indicate dump use. Percentages of aerial and ground locations within this area were calculated for each month wolves visited the dump. To calculate the average time spent at the food resource (the dump), consecutive days at the dump were counted. As a comparison, for the pack which did not use a garbage dump, the average number of days spent on a killed prey species was calculated. After testing for normality (Wilk-Shapiro test), Mann-Whitney U-test was used to test whether the mean time spent at a food resource differed among the packs.

Additionally, the intensity of habitat use by the pack without a dump was tested by plotting 95% of telemetry locations of the wolves on a stratified moose density plot. The survey area (2775 km^2) was divided into 111 subplots (each 25 km^2) and stratified into high, medium and low moose density strata (Wade 1996 unpublished). The stratified moose density subplots and raw count data (Wade 1996 unpublished) were used to estimate mean moose densities for each stratum: high (0.257 moose/km^2), medium (0.117 moose/km^2) and low (0.04 moose/km^2). A Chi-square test was used to compare the frequencies of the subplots of the three different strata in the entire survey area with their frequencies in the home range. Wolf telemetry locations were compared using Chi-square test to determine whether strata were used at random.

Snow tracking

Investigation of wolf tracks at or in the vicinity of the garbage dumps was done every second to third day from November to March (1994 to 1997). Tracks were reported as present or absent.

Scat Analysis

Scats of each pack were collected from accessible secondary roads, and were dated, labeled and frozen. Only one sample was collected at each wolf kill site to avoid bias in scat analysis. The location of each scat was determined with a handheld GPS, to identify scats in the different home ranges and core areas.

Scats were analyzed as discussed in Adorjan and Kolenosky (1969) and Kennedy and Carbyn (1981). Species of prey were determined from hair, feather, and bone samples. Results were divided into summer (April to September) and winter (October to March) diet and reported as relative percentages of prey found in the scat sample. After arcsine transformation of the percent values (Sokal and Rohlf 1981), the data were tested for normality (Wilk Shapiro test). Differences between the diet components (between seasons and wolf packs) were tested with ANOVA and Bonferroni tests.

2.4 RESULTS

Black River Pack (BRP) and Neys Pack (NP)

The Black River (BRP) and the Neys Packs (NP) used an area in the Black River Management Area which also contained three town sites (Pic River Indian Reserve, Heron Bay, and Marathon), and two garbage dumps (red dots for the NP, green cross-hatchings for the NP, Fig. 2). Two wolves of the Black River Pack (estimated 8 to 9 individuals) were tracked by radio telemetry. Both were captured and radio collared in August 1994 (Fig. 3). Aldo, an adult male, and Sam, a male pup at the time of capture, were closely associated during the following year (Fig. 3). In winter 1994/95, Aldo, Sam and the rest of the pack were frequently located, tracked, and visually observed at two garbage dumps (Heron Bay and Marathon, respectively, Fig. 4). Very few (11% Aldo, 3% Sam) dump locations were at Heron Bay; most occurred at Marathon. In July 1995, Sam left the pack and traveled westward, crossing Hwy. 627 (a previous boundary to his movements), eventually becoming a member of the Neys Pack (approximately 30 km west of Marathon) from November 1995 to the end of this study (February 1997). From November to January the NP consisted of three wolves (Fig. 3). In May 1996, they produced offspring (Krizan unpublished data), and, as in the winter 1995/96, they returned to the dump in the winter of 1996/97 (Fig. 4). Aldo left the Black River Pack's area in November 1995. The last location of Aldo in the BRP's home range was approximately 10 km north of Marathon. In January 1997, Aldo was relocated approximately 50 km north of his former range, and subsequently was located at a new dump 100 km north east of Marathon (not included in the analysis).

Rein Lake Pack (RLP)

The wolves of the Rein Lake Pack used an area with no human settlements within their home range, and, therefore, no garbage dump (Fig. 2, blue area). The home range of this pack includes the northern section of Pukaskwa National Park and the southern section of the White River Forest Management Area (Fig. 2).

In October 1994, 2 adult wolves of the Rein Lake Pack (estimated 5 to 6 individuals, Fig. 3), an adult female (Cassidy) and an adult male (Mojo), were radio collared. Mojo dispersed from the Rein Lake area north of Hwy. 17 in November 1994 (Krizan 1997) and, therefore, was not included in the analysis. After January 1995, two wolves were consistently observed with Cassidy. In February 1996, a male adult (Star) of the same pack was captured and radio collared (Fig. 3); the three wolves stayed closely associated. The pack did not produce viable offspring in 1994, 95, or 96. Both Cassidy and Star died in February 1997, evidently caused by mange.

Home ranges and core areas

During the entire study period, the BRP used an area of 797 km^2 (95% of all locations, Table 1). The area of use for the NP, based on the locations of Sam after he left the BRP, was calculated to be 459 km^2 (Table 1). The RLP used an area of 835 km^2. Since home range sizes describe the general area of use, the intensity of spatial use is better described by the area of concentrated use, the defined core area (50% of the telemetry locations). The RLP had the largest estimated home range, and the largest core area of the 3 packs (Table 1). The Neys Pack used two core areas (Fig. 2), one in the vicinity of the Marathon dump and the other about 35 km north west of the dump where the pack denned and reared pups (Krizan unpublished data). A Chi-square test showed significant differences in the spatial use of home ranges and core areas among the packs (Chi=56.69, DF=2, P<0.001). The BRP used a highly significantly smaller core area than expected, while for the RLP the core area was significantly larger than expected. The NP was the only pack which showed no significant differences in the utilization of the home range and corresponding core area. Differences in the home range/core area relationship were also evident in their ratios (Table 1).

Seasonal travel distances

Individual travel distances between subsequent aerial locations for the four wolves differed significantly among seasons (ANOVA; F=11.98, DF=348, P<0.001, Table 2). The travel distances during the breeding seasons were significantly shorter (4431.3 m) compared with the other three seasons (Table 2). The longest mean distances were observed during the pup rearing seasons, followed by the nomadic and denning seasons (Table 2).

When the four wolves were compared over the entire study period, significant differences in travel distances were found (ANOVA; F=7.58, DF=348, P<0.001, Table 2). Sam (NP) traveled significantly less than the other three wolves (Table 2). Star (RLP) traveled the most, followed by Cassidy and Aldo (Table 2).

Within each of the four seasons, significant differences among individuals were observed only in the breeding season (ANOVA; $F=4.96$, $DF=72$, $P<0.05$). Aldo traveled significantly less, followed by Sam, then by Star. Cassidy traveled significantly more than the three others (Table 2). When each wolf was tested separately by season, significant differences in travel distances were observed for Aldo and Sam ($P<0.05$ each). For both wolves, the smallest distances occurred in the breeding season, followed by the denning, nomadic, and pup rearing seasons (Table 2). Neither Star nor Cassidy showed significant differences in their travel pattern between the seasons.

Day time activity

On average, the study wolves spent 52.2% of all visual observations (N=117) resting and 40.1% traveling. They spent significantly less time feeding (7.7 %, ANOVA; $F=23.51$, $DF=12$, $P<0.001$). Significant differences were observed among the wolves (Chi-square test; Chi=49.44, $DF=6$, $P<0.001$): Sam traveled less than expected (Fig. 5), Aldo traveled and rested more than he fed, and Cassidy fed more than expected. No significant differences were found in day time activities for Star (Fig. 5).

Intensity of food resource use

Black River Pack, Neys Pack

Year round aerial telemetry locations showed that the BRP used the garbage dump seasonally. Of 131 aerial locations during the study period for Sam, 33% fell within the dump buffer, compared to 36% of 74 locations for Aldo. There were three distinct periods when they visited the dump (Fig. 4), generally beginning in fall and continuing through at least the end of February. During these three periods ground and aerial telemetry covered daily accounts of the BRP's and NP's use of the garbage dump (Fig. 4). The longest period of dump use was observed in the 1994/95 period, with the highest number of dump locations in February. The second and third period (only NP) showed a similar seasonal distribution at the dump (October to February), with most locations in December and January (Fig. 4). Although the wolves stayed long periods at the dump, they frequently left this vicinity for some days, after which they returned. This occurred less frequently in February 95 and December/January 96 and 97 than during the remainder of the time (Fig. 4). Outside the three periods reported above, none of the wolves was located at a dump. During the entire study period, Sam was located three times on a moose kill, Aldo only once.

Rein Lake Pack

During the entire study period, Cassidy was located on or near eleven kills (nine moose and two beaver) but only twice at a garbage dump (at the end of the study). After Star was collared, he was present during all but the last two kills (beaver) and two dump visits, where Cassidy was alone. Seven moose kills were reported for Star, which occurred after he was radio collared. Four of these occurred after Cassidy dispersed in November 1996.

To compare the use of the different food resources (dump and kill), consecutive days spent at each food resource were counted for each wolf. An ANOVA showed that there was no significant difference ($P=0.75$) in the number of days each wolf spent at a food resource: Sam stayed on average 5.4 days ± 0.8 (SE), Aldo 7.4 days ±1.6 (SE), Cassidy 6.3 days ± 1.4 (SE), and Star 5.9 days ± 1.2 (SE) at a food resource. Consequently, packs also did not differ in days spent at a food resource (ANOVA, $P=0.97$).

To determine the relationship between moose and wolf distributions, RLP wolf telemetry locations were superimposed on a moose density survey plot consisting of three different moose density strata (high, medium, low). First, a Chi-square test showed that the distribution of high (0.257 moose/km^2, area = 325 km^2), medium (0.117 moose/km^2, area = 1175 km^2), and low (0.04 moose/km^2, area = 1250 km^2) strata in the entire survey area differed significantly from the distribution in the RLP's home range (200, 500, and 125 km^2, respectively; Chi=39.52, DF=2, $P < 0.01$; Fig. 6). The low moose density plots were significantly underrepresented in the RLP's home range, the medium density area was overrepresented (although not significantly). Telemetry locations of the RLP were equally distributed amongst the strata within their home range (Chi-square test, $P= 0.61$). Location points were distributed according to the occurrence of the strata within the home range (Fig. 6). Due to the differences in moose density distribution, the average moose density in the pack's home range (0.18 moose/ km^2) was higher than that in the entire survey area (0.097 moose/ km^2).

Snow tracking

Snow tracking confirmed the periods of absence and presence at the dump shown by radio telemetry (Figure 4). Approximately 25 km of trails were recorded within the dump buffer. Each year, the dump was visited by a single pack. During all 3 periods, the wolves used at least 4 different main trails to access the dump. These trails forked into a complex array of paths and lead to several resting areas recognizable by the presence of beds. These resting areas were always located inside the dump buffer. The presence of tracks and trampled snow indicated where the wolves consumed garbage. Numerous opened garbage bags and chewed debris were evident near the outer periphery of the dump or just inside the tree line. There were very few garbage bags found further than 500 m from the dump site's outer edge. There was no evidence that the wolves dragged garbage to their resting areas. To enter and leave the dump site the wolves had to cross a frequently used snow mobile trail. Tracking directly after snow fall indicated nighttime or early morning visitation of the dump by the wolves. During the day, they were mostly located resting in several resting places in a wooded area free from human access.

Scat analysis

Wolves of the three study packs showed differences in their diet between summer and winter (Fig. 7a and b). In the summer, they fed significantly more on beaver (ANOVA; $F=15.53$, $DF=15$, $P<0.001$), followed by moose, snowshoe hare, garbage, vegetation, rodents and other items(Fig. 7a). Garbage in the scats consisted mainly of plastic, rubber, paper, rope, wood, pieces of metal, tampons, and unidentified matter. Contents were classified as vegetation when berries, leaves, grass, needles or twigs were found. In several cases, the scats contained pebbles, which were not included in the analysis. Rodents were identified from hair or skeletal fragments of squirrels, voles, or deer mice in the scats. The category "other items" included black bear, coyote, caribou, and fish (details are given below). In winter, no significant differences were found among the food components of the scats (ANOVA, $P = 0.199$). The scats contained moose and garbage in similar quantities, followed by beaver, snowshoe hare, vegetation, rodents and other items (Fig. 7b). When the data were pooled for the entire study, beaver and moose comprised the largest part of the wolves' diet (36.2 and 35.3%, respectively; ANOVA; $F=3.6$, $DF=15$, $P < 0.01$), followed by garbage (20.4%), snowshoe hare (4.2%), other items (1.7%), vegetation (1.5%), and rodents (0.6%).

In the following, data from individual packs are analyzed separately for the two seasons.

Black River Pack

The majority of the BRP's diet during the study period consisted of garbage and beaver (Fig. 8). Although the scats contained significantly more beaver during the summer (ANOVA; $F=14.23$, $DF=7$, $P<0.01$), in winter, the wolves of this pack fed significantly more on garbage than on any other food item (Fig. 8). The occurrence of moose did not differ between the seasons and comprised a minor part of the pack's diet. Other items included vegetation (mainly berries in the scats from the dump), a low percentage of snowshoe hare, one summer scat with fish skin and bones, and, interestingly, in one case coyote hair (in winter 94/95 at the dump).

Neys Pack

The scats of the NP did not differ in their prey composition during the study period (ANOVA, $P = 0.35$; Fig. 8). Similar to the BRP but less pronounced, in the summer, they fed mostly on beaver, and in the winter on garbage. The summer scats did not contain any garbage. Moose comprised a higher portion of their diet compared with the BRP. Other items included vegetation, snowshoe hare and very few rodents.

Rein Lake Pack

The scats collected from the RLP's home range contained the highest percentage of moose (Fig. 8). While there was no significant difference between prey species in summer (ANOVA, $P=0.11$), in winter scats contained a significantly higher amount of moose than any other food item (ANOVA; $F=179.25$, $DF=4$, $P < 0.01$). The RLP did not have access to a dump; this was reflected by the lack of garbage in their scats. Other food items comprised a minor part of their diet, including very few snowshoe hare and two interesting prey species: one scat contained 100 % black bear fur and another 100 % caribou. Both scats were collected during the summer.

When the single food items of the three packs' diet were compared, significant differences were found: The RLP showed the highest amount of moose in their winter scats of all packs (ANOVA; $F=1492.64$, $DF=3$, $P < 0.01$). Beaver was found significantly less often in the BRP's winter diet (ANOVA; $F=1233$, $DF=3$, $P < 0.05$) compared to the other packs. In summer, garbage was found only in the BRP's diet, and in the winter it occurred (although not significantly, ANOVA, $P=0.064$) more frequently in the scat's of the BRP than in the NP (Fig. 8).

2.5 DISCUSSION

Long distance travel by wolves has been well documented (Stenlund 1955, Mech 1966, 1970; Mech and Frenzel 1971; Van Camp and Gluckie 1978; Ballard et al. 1983, Mech 1995b), as well as their need for large areas to carry out their biological activities (Mech 1970, Noss et al. 1996). Home ranges of wolves vary throughout North America (Peters and Mech 1975, Fritts and Mech 1981, Fuller 1989, Noss et al. 1996), and their size can be influenced by several factors such as topography (Mech 1970), type of prey and prey density (Fuller 1989). This study shows that wolves visit garbage dumps and feed on refuse. In turn, their travel patterns and size of area used are influenced by such a predictable food source. The data presented show that wolves used the garbage dump seasonally and imply that this behaviour can have both positive and negative implications.

Similar to studies in Europe, where wolves often feed on garbage (Boitani 1982, Salvador and Abad 1987, Boitani 1992, Blanco et al. 1992), the BRP and the NP consumed various items at the dump. Scats collected at times when the BRP and NP were not in the vicinity of either garbage dump contained mainly beaver and moose, and a low percentage of snowshoe hare and rodents (such as squirrels and voles). At this time, their diet was comparable to that of the RLP.

Comparison of areas traveled by the three packs yield different results spatially and temporally. Contrary to Mech and Hertel (1983), but similar to Grace (1976), Fuller (1980), and Boitani (1982), the two packs which used garbage dumps did so in the winter, and only once (1995) in the summer (until July). Both packs showed smaller home ranges and their areas of concentrated use (core area) were smaller than that of the RLP. Although the home ranges and core areas of the BRP and NP appear to overlap (Fig. 2), only one of the packs visited the dump each winter. The NP showed two core areas, which were 35 km apart. One can be explained by the NP's attendance at a den site and consistent returns to pups at rendezvous sites during the summer (pers. obs.) and the other by regular visits to the dump in the winter months. It is interesting that both core areas of the NP combined are still smaller than the core area calculated for the RLP. The RLP had the largest overall home range and the largest core area. The findings have biological importance in that areas of food resources should be used more than areas void of such food resources (Pianka 1994). Since feeding and rearing of pups are two main activities of wolf packs (Mech 1970), and since the food resource in this case was predictable and localized, the two core areas adequately describe these two activities and areas of importance. In contrast, the RLP had no pups to care for and did not have a stationary and dependable food source available to them, resulting in a less concentrated core area. In addition, the ratio of home range to core area emphasizes the need for detailed analysis of spatial use when comparing wolf home ranges, since total home range areas alone can yield misleading results.

Individual travel distances were used to quantify the relative mobility of the wolves in each pack. Significant differences were found in travel distances both seasonally and among individual wolves. The significantly smaller distances traveled by Sam and Aldo in the BRP home range, and Sam in the NP home range, were indicative of the intense use of the Marathon garbage dump by both packs. The shortest distances were traveled by Aldo and Sam during the breeding period (February-March). For the 1995 breeding season, short travel distances resulted from the BRP's continuous presence at the dump. During the 1996 breeding season, Aldo was not present in the study area, and Sam was 35 km north east of Marathon at the den site of the NP. He and the rest of the new pack spent the breeding season close to Little Pic River, near a group of moose (pers. obs.). Early in the 1997 breeding season, the NP left the dump and traveled westward to their old denning area, but the pups remained at the dump (Krizan unpublished data).

Star and Cassidy from the RLP showed no differences in their travel distances among the seasons. This finding further suggests the lack of a den site or rendezvous area and possibly no reproduction in this pack during the time of this study.

A comparison of the available food resources of all three packs, sheds light on the differences in travel distances and size of home ranges. Although wolves are characterized as predators which travel between killed prey (Mech 1970, Kolenosky 1972, Fuller 1980), it is apparent that when given the opportunity to feed from an artificial predictable and localized food source they will do so (Boitani 1982). The smaller distances between locations imply that when at or close to the dump, wolves traveled little and expend less energy on movement. Although staying near the dump potentially exposes the wolves to human encounters, the wolves reduced this risk by staying near the dump in an inaccessible forest patch during times when the dump was open to humans. Similarly to findings of Boitani (1982, 1992), and Afik and Alkon (1983), telemetry locations during the day and snow tracking showed that wolves rested in the same area repeatedly, and that evening locations were closer to the dump. In comparison, Cassidy and Star of the RLP, showed significantly longer travel distances, since they had to seek out vulnerable prey.

The RLP occupied an area with moose densities lower than 0.2 moose/km^2 (average moose density in the pack's home range 0.18 moose/km^2), which has been shown to be the moose density threshold below which a wolf pack could not subsist (Messier and Crete 1985). In the general study area, there seemed to be a clear gradient in moose density, declining from north to south (Eason pers. com.). Moose densities in the north eastern part of the study area were reported as 0.278 moose/km^2. Only 8 % of the RLP's telemetry locations occurred in this area while the majority of the pack's locations were recorded further south in the described moose survey area in and around PNP. The RLP's restriction to move farther north may have been the presence of another pack (White River Pack; Krizan this volume), confirming that at least certain parts of neighbouring wolf pack home ranges are respected by adjacent packs (Peters and Mech 1975). An additional, and perhaps more important factor, which prevented the

RLP from traveling farther north might have been a higher concentration of roads (Krizan this volume, Fig. 1).

The distribution of the three moose density strata differed significantly between survey area and the RLP's home range. The low moose density plots (0.04 moose/km^2) were significantly underrepresented in the home range, the medium density plots (0.117 moose/km^2) showed a trend to be overrepresented, and no difference was found in the relatively rare high moose density plots (0.257 moose/km^2). This different distribution resulted in a higher mean moose density in the pack's home range (0.18 moose/km^2) than in the entire survey area (0.097 moose/km^2). The telemetry locations of the wolves within these three strata in their home range were distributed according to their occurrence, showing that all areas of the estimated home range were used similarly. The low moose densities reported for the RLP's home range may have required longer travel distances for the individual wolves to locate prey, yielding a larger home range and core area than observed for the BRP and NP.

During the entire study period, one kill was recorded for the BRP, three kills for the NP and eleven kills for the RLP. No significant differences were found in the time spent at a food resource (consecutive days at dump or kill site) among the three packs. Interestingly, even the BRP and NP wolves left the dump periodically but returned one to several days later. The reason for this behaviour was unclear and often the wolves did not leave or return together. One explanation could be that certain individuals traveled away from the dump to scent mark other parts of their home range (Peters and Mech 1975). Several times, I observed these wolves following moose, but very few of their pursuits of prey resulted in actual kills. This unwillingness to chase and kill prey could reflect the adequate food supply of the dump, resulting in an overall reduced effort to kill moose.

The observations of different numbers of moose kills for the three packs were also confirmed by scat analysis. The BRP showed the lowest proportion of moose in their diet, followed by the NP, and the RLP which fed predominantly on these ungulates.

Reported day time activities from visual observations (mostly during the winter) of the four study wolves showed that they rested most of the time (52.2%), followed by walking (40.1%), and, in some cases, feeding on a kill (7.7%). Similar results were obtained by Mech (1991) in Minnesota. However, the distribution of the three activities differed significantly among the wolves: Aldo was never observed feeding, Sam spent the most time resting and the least time walking, while the opposite was true for Cassidy. This result exemplifies the different "life styles" of the wolves. Sam and Aldo rested most often during the day time and fed at night. Sam's reported feeding observations occurred at the few reported kills. Cassidy was observed walking most of the time and she rested less. Star showed no differences in the distribution of activities when compared with the other wolves.

Low densities of prey in the RLP's home range were indicated by the dispersal and death of the female Cassidy, and death of Star. Cassidy's dispersal from the pack may also partially reflect her poor social status within the RLP due to her poor physical condition. She traveled north of Hwy. 17 and spent several weeks close to a garbage dump, where she died. The cause of death was most likely mange (pers. obs.). In February 1996, Star was located 32 consecutive days on a kill, was rarely observed feeding, and from visual observation was in very poor condition. He was last located 2.5 km east of the abandoned kill, where he died of mange.

As reported by Grace (1976), the use of the garbage dump by wolves was a seasonal phenomenon, which occurred from October to February for the NP, and November to July for the BRP. Contrary to other studies (Ciucci and Mech 1992, Mech 1995c), which noted that wolves denned or had rendezvous sites within two km of a garbage dump, the den and rendezvous sites of the NP were located 35 km north east of the Marathon. The den of the BRP in 1994 was not found, but the rendezvous site was located about 20 km south east of Marathon. It is interesting that both packs visited the dump but did not den there. Afik and Alkon (1983) showed that radio collared wolves which fed at a garbage dump did not den and failed to reproduce. These findings best describe the fate of the BRP in 1995, which was the only pack to spend the full breeding and denning season (1995) at the dump.

There are several reasons why the NP may have avoided the use of the dump in the summer months. Black bears are common visitors to both the Heron Bay and Marathon dumps in the summer (pers. obs.) and could be potential competitors and a threat for new born pups (Veitch et al. 1993). On several occasions during May to July, I counted more than 10 black bears in one day at the dump. The avoidance of such a concentration of potential competitors and predators of young pups is a logical strategy and thus would explain the distant location of the den and rendezvous site and entailed the renunciation of the stable food source.

Other competitors at the dump were coyotes, which were present year round (Renner pers. com. and pers. obs.). Interactions between these two species were never observed but the finding of coyote hair in one of the wolf scats collected from the dump indicates that they took place and that the wolves might have occasionally killed coyotes. Since the scat was collected in early summer '95, it is unlikely that the wolves consumed a snared animal.

Wolves are known to spend the early part of the summer close to a den site (Mech 1970) and later at rendezvous sites (Harrington and Mech 1982). If both of these areas are not in close proximity to the dump, which was the case for the NP, then their absence from the dump may have spatial and energetic implications. Food obtained from the dump may not be of high enough quality to compensate for the distances traveled, or may be unsuitable for growing pups. It must be mentioned, however, that scats collected from live trapped pups of the BRP at the beginning of this study, in August 1994, contained a certain amount of garbage. Since the pups were trapped at the rendezvous site, 20 km east of the dump, this result implies that some adult animals of this pack traveled to the dump, returned, and regurgitated garbage for the litter.

Significantly longer distances were traveled during the pup rearing season. Sam traveled distances greater than the 35 km to the dump, but he never visited the site, indicating that he avoided the dump at this time. The analysis of scats, collected in the core area around the den and rendezvous sites, confirmed that during the summer month, neither Sam nor the rest of the pack fed on garbage. Main prey species in this time were beaver and moose, similarly to the RLP's diet.

Although the RLP fed predominantly on moose, they enriched their diet by 2 unexpected species. One scat which contained black bear was collected in their home range during summer '95. Since black bears are not hunted at this time of the year, it is possible that the pack actively killed the bear rather than scavenged on a carcass.

Star, the radio collared male of the RLP, visited the northwest coast of the national park three times (not included in the 95% home range analysis) in summer '96. One scat collected in this area contained caribou hair. About a dozen caribou have been estimated to live on the coast of PNP (Wade pers. com.). Holleman and Stephenson (1981) state that caribou are more vulnerable to wolf predation than moose. The moose density inside of PNP during the study period was 0.097 moose/km^2 , which probably resulted in long searches for prey. Star's occasional travels to the coast could therefore be explained by his attempt to find vulnerable prey.

During the entire study period, the BRP and possibly the RLP produced offspring in May 1994, and the NP in May 1996 (Krizan unpublished data). The BRP did not reproduce in 1995; there was no evidence of a den site or pups. The previously breeding female died in October 1994 of unknown causes (Campbell pers. com.), which may be one possible reason for the lack of reproduction in 1995. Aldo and possibly one other adult were observed during the 1995 breeding period. In fall 1995, an adult wolf of unknown sex was hit on the highway within the BRP's home range. A non radio collared but eartagged female wolf, the only female pup in the 1994 litter, was snared in the BRP's home range in December 1996, indicating that she had stayed in the pack's home range. Although females as young as 10 months can reproduce (Medjo and Mech 1978), there was no indication that the young female in the BRP had reproduced in 1995, even though there was no evidence of a breeding female in the pack at the time. From track counts in winters 1996 and 1997, a maximum of four wolves were estimated in the BRP (after Aldo's dispersal). The BRP did not seem to produce any pups in 1996, judging from ground and aerial surveillance of the BRP's former rendezvous sites. Based on ground tracking and aerial observations, the BRP did not revisit the dump in winter 1995/96 and 1996/97, perhaps having been displaced by the NP. The exclusion of this predictable food resource from their home range and therefore a dependence on moose for food may have affected the condition and therefore reproductive capability of the BRP, similarly to the RLP. No pups were observed in this pack during the study, although based on nipple measurements (Mech et al. 1993) at the time of her capture, Cassidy was thought to have produced pups in 1994. Low moose density (Messier and Crete 1985), resulting in greater travel distances, energetic costs and poor physical condition may have had a negative impact on reproduction.

Judging from the lack of reproduction in the other packs, it appears that the NP benefited from the dump. Further, it seems that a more sedentary life style (as shown by the concentrated core areas) can have substantial implications on the energetics, reproductive capabilities, and survival of the entire pack, assuming that the breeding pair survives.

Despite the possible benefits from these human made food depots, evidence shows that the presence of wolves near the towns of Marathon and Heron Bay increases human-wolf conflicts, resulting in predator control. The main conflict results from misunderstanding and fear of wolves (Renner, Dechano pers. com.). Complaints from residents have been answered by snaring at the dump by a local trapper, usually from November to February, which is also the time when the BRP and NP spent time at the dump. As many as 15 wolves have been caught at the Marathon dump in one winter (Renner pers. com.) and trappers in White River reported killing more than 16 wolves in winter 1995. This number of wolves in one area exceeds the number of individuals seen in any pack in the study area from 1994 to 1997. Besides trapping, there is also a risk of mortality associated with crossing of roads and highways (DeVos 1949, Mech 1989), as well as snowmobile tracks and rail roads (Krizan this volume). Therefore, while the wolves in the area may benefit energetically from the constant supply of food from the garbage dump, their survival may be diminished by other factors. Under these circumstances, dumps may be "sinks" to the wolf population. It is likely that through trapping, all but a few wolves of that pack could be killed at the dump. But even if only one of them survives, there is evidence that this wolf will return to the dump in subsequent years with a new pack (Krizan unpublished data). With this process, wolves from a larger area are attracted to this artificial food source, habituate to garbage by not returning to "normal" habitat (Haber 1996), and risk a high probability of mortality.

Interestingly, Aldo was missing until January 1997; he was relocated 50 km north of his former range, and subsequently 100 km north east of Marathon at another dump site. This finding indicates that wolves, once habituated to a dump, might be always attracted by these food sources or, due to very low moose densities (Krizan this volume), may seek out such areas with a predictable food supply.

This study has shown that wolves are attracted to dump sites, which affects their travel patterns and their reproductive potential. Although the extent of this influence on pack social structure and eventual effects on future hunting success of the pack for later generations is not known, habituation to the garbage dump is clearly learned by young from the adults of the pack (Krizan unpublished data). These wolves potentially pass on the tradition of garbage feeding to future litters. Since unfenced garbage dumps affect the survival, ecology, structure and stability of packs (Haber 1996), such sites should be adequately fenced to prevent future habituation. It is obvious that killing habituated wolves is not an effective solution to the "problem". Direct non-lethal action to deter wolves and other wildlife from human produced refuse is a responsibility which humans have to put into practice if coexistence between humans and other species is to persist.

2.6 Tables and Figures

Table 1: Comparison of home range (95% of locations) and core area (50% of locations) and their ratio. The two core areas of the NP are added.

Pack Name	Home range	Core area	Ratio
BRP (Aldo & Sam)	797 km^2	52 km^2	0.07
NP (Sam)	459 km^2	83 km^2	0.18
RLP (Cassidy & Star)	835 km^2	178 km^2	0.21

Table 2: Mean travel distances (±SE;n) traveled by Aldo, Sam, Cassidy, and Star during four seasons (1994-1997). Distances are recorded from subsequent aerial telemetry locations (N=334). * = significant differences in travel distances among wolves during a season (P<0.05). + = significant differences in travel distances among the seasons for this wolf (P<0.05 each).

Season	Aldo [BRP+]	Sam [BRP+]	Cassidy [RLP]	Star [RLP]	Mean††
Breeding [*]	2236.5 m (559.1; 16)	2809.8 m (599.1; 22)	6397.8 m (1149.1; 31)	6069.4 m (2477.8; 6)	4431.3 (511.68)[a]
Denning	8210.2 m (2119.8; 15)	5172 m (1156.5; 20)	9449.5 m (1928.9; 24)	8822.3 m (3601.6; 6)	7789.4 (966.16)[b]
Pup rearing	12760 m (4035.1; 10)	8964.7 m (1373.2; 18)	9680.5 m (2164.6; 20)	9015.4 m (3005.1; 9)	9889.2 (1309.86)[b]
Nomadic	9846.5 m (2461.6; 16)	6276.1 m (878.8; 51)	8350.5 m (1169.3; 51)	11250 m (2580.9; 19)	8154.8 (696.71)[b]
Mean†	7790.3 (1518.7)[b]	5826.1 (1031.9)[a]	8290.5 (738.58)[b]	9605.1 (552.99)[b]	—

† Weighted mean distances (±SE;n) traveled by wolves during the entire study period (1994-1997, seasons are pooled. a and b differ significantly (ANOVA, P<0.01).

†† Weighted mean seasonal travel distances (±SE;n) for the four wolves (pooled). Differences among seasons are significant (a and b, ANOVA, P<0.001)

Fig. 1: The general study area between Thunder Bay and Sault Saint Marie on the North Shore of Lake Superior. X = the Marathon garbage dump and the Heron Bay garbage dump.

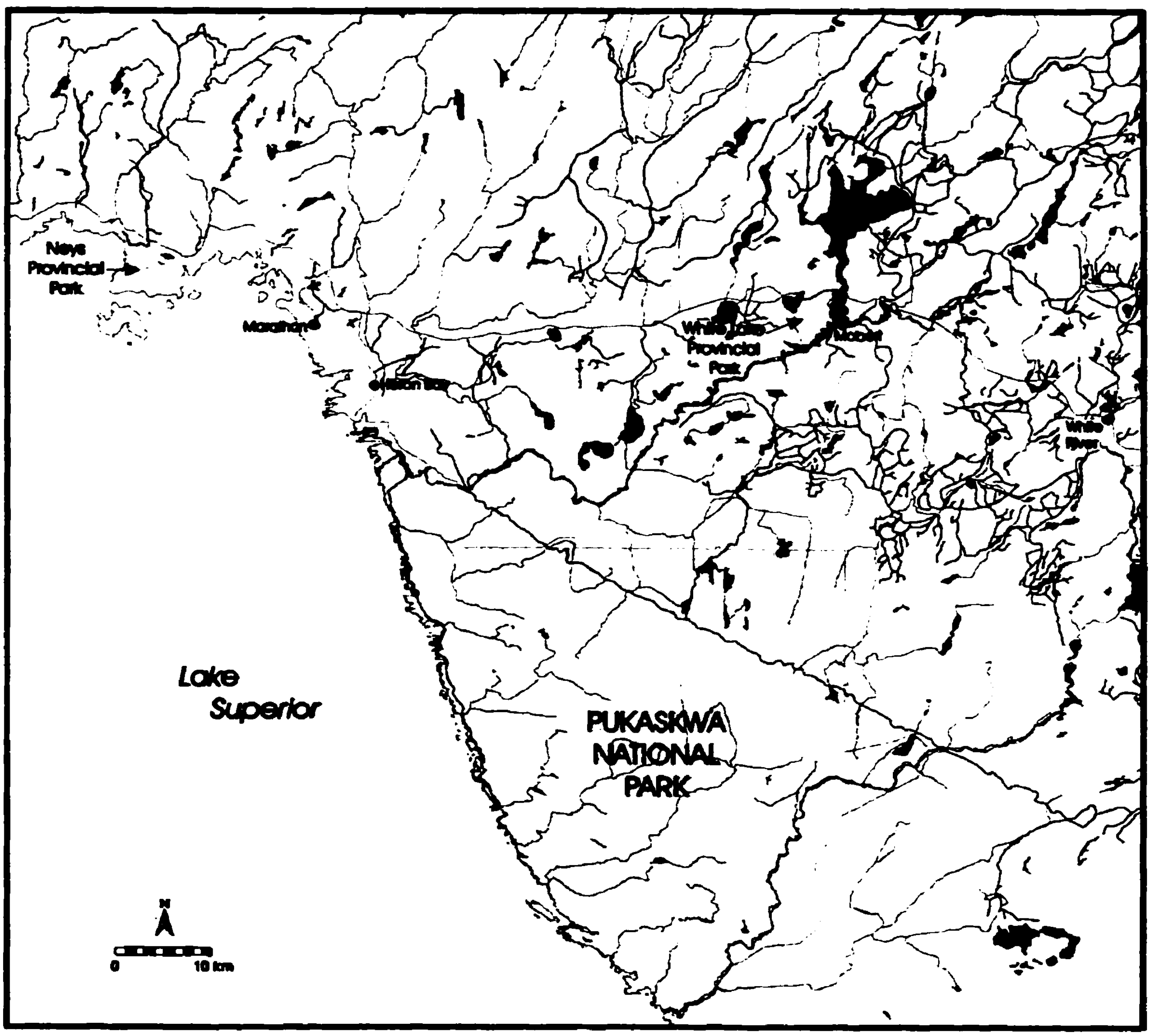


Fig. 2: Home ranges and core areas (represented by the smaller contours within the home ranges) of the three packs described in this study. For detailed definition see text.

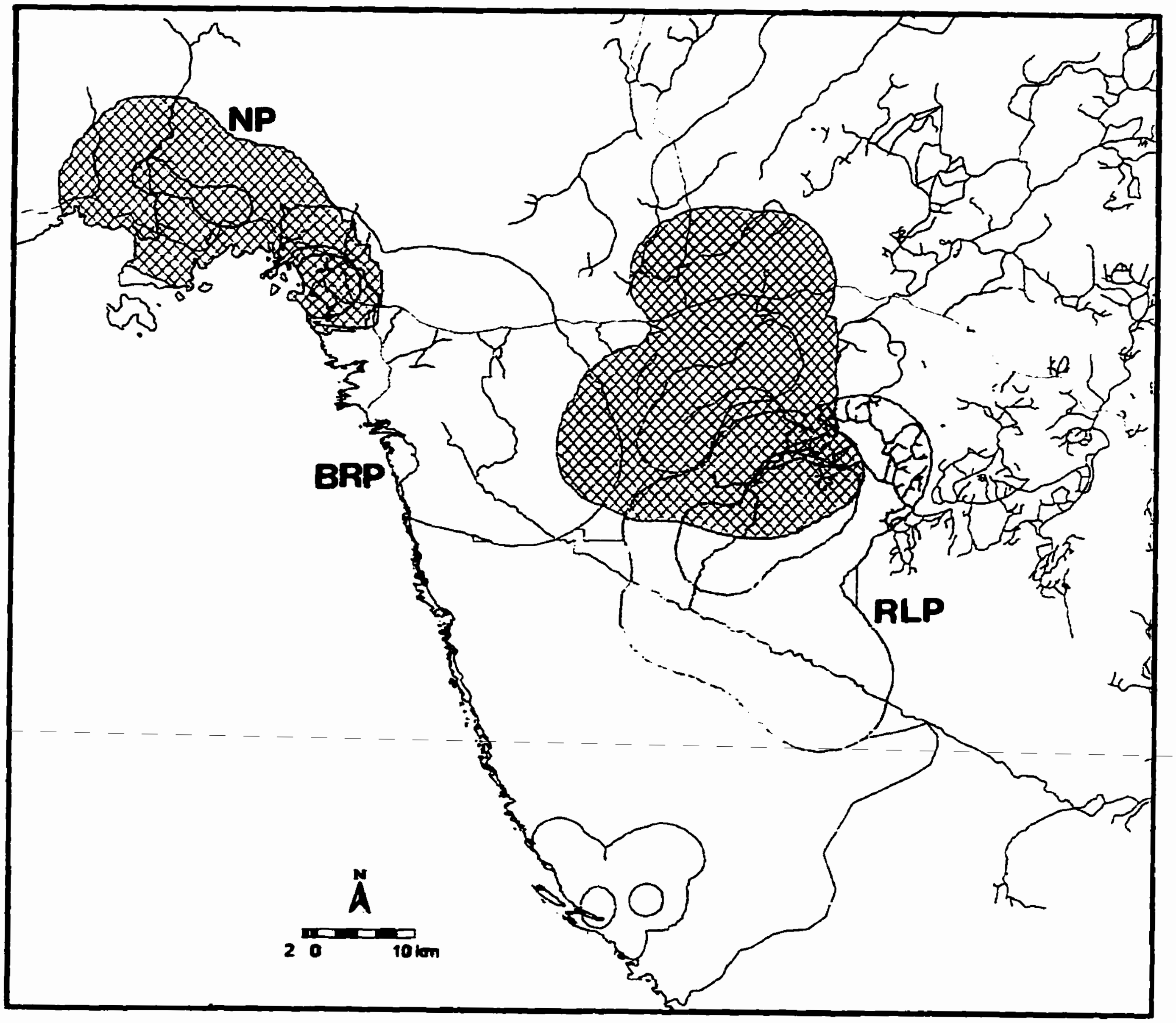


Fig.3: The history of the individual wolves of the three study packs. Pack and wolf names are shown on the y-axes (including sex). The length of each line represents the duration for which radio telemetry data were received from the individual wolves.
R = time of capture and radio collaring, D = Dispersal, M = Mortality, R! = Reproduction. The numbers shown at the lines indicate the numbers of animals in the pack at this time.

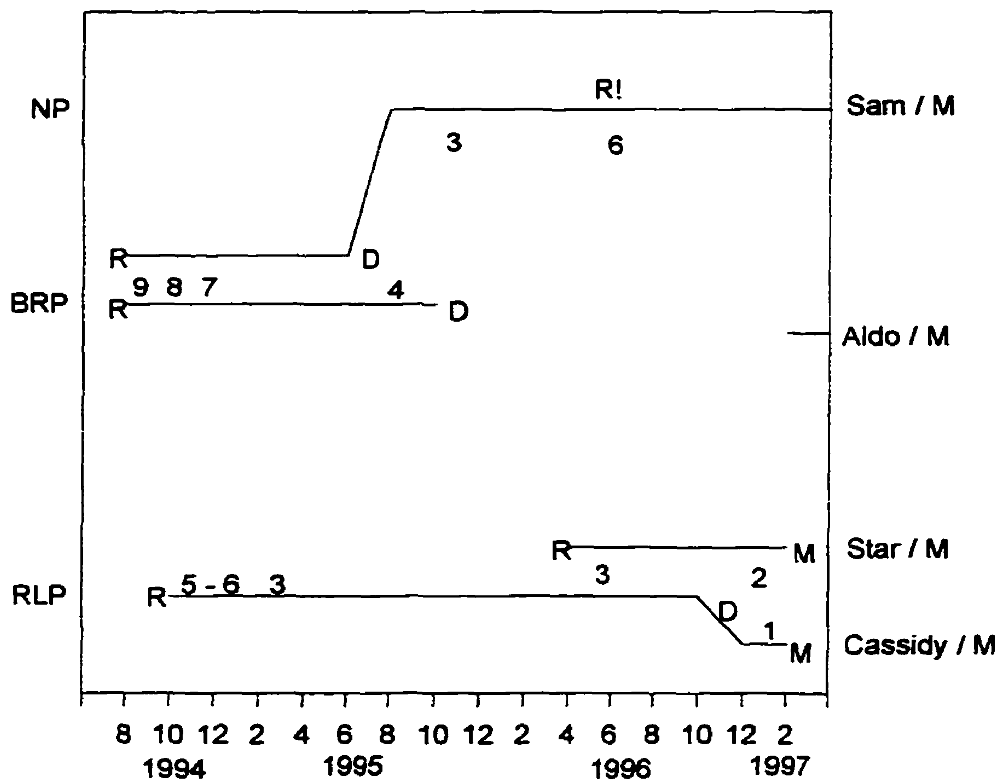


Fig.4: Aerial and ground telemetry locations of the two wolves Sam and Aldo at the dump. Given are percentages of all monthly locations of the individual animals spent at the landfill (N=459). Both wolves only visited the dump at the mentioned time periods.

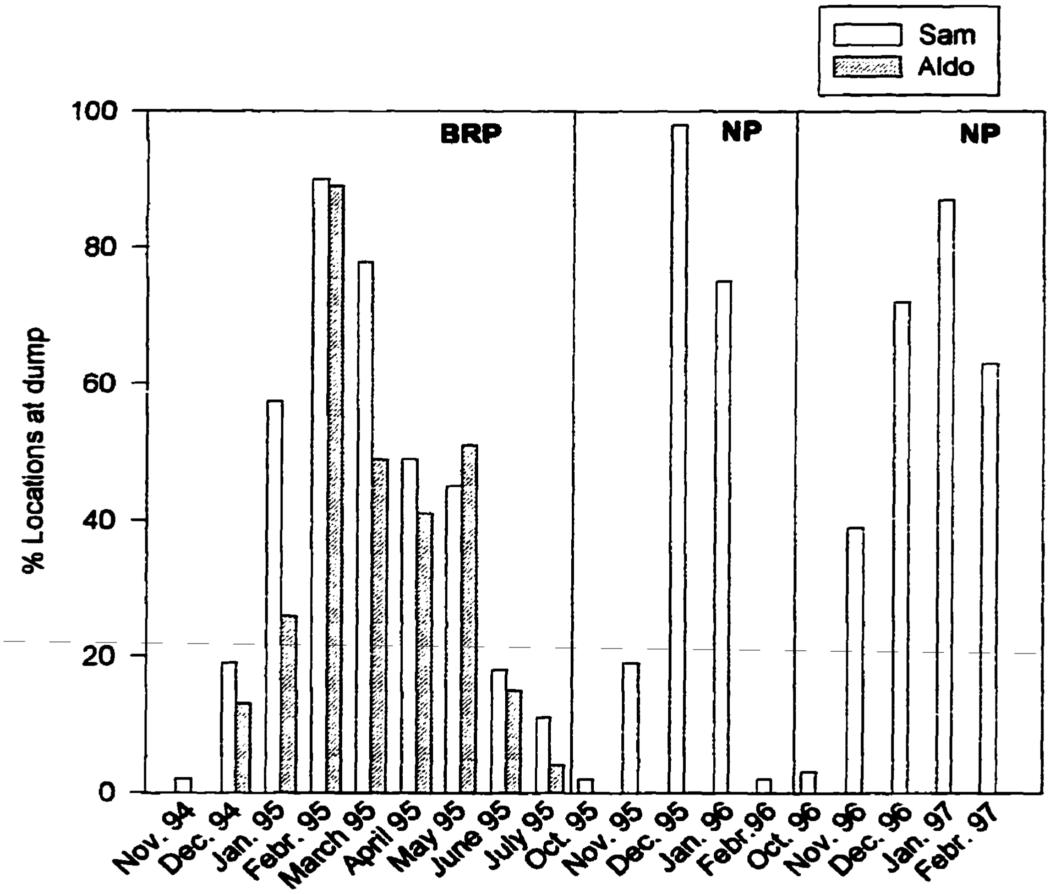


Fig. 5: Daytime activity of the 4 wolves. Shown are the percentages of all visual observations each wolf spent resting, walking, or feeding (N=117). The stars indicate differences from the expected distribution. For details see text.

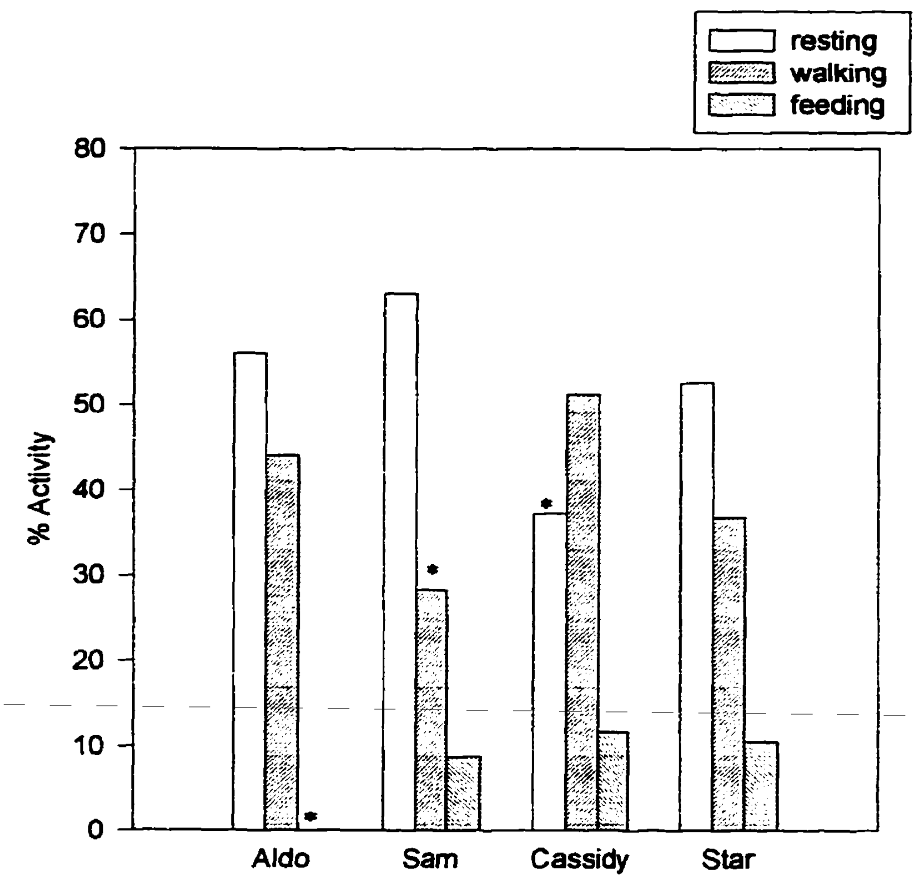


Fig. 6: The distribution of low, medium, and high moose density strata in the survey area (2750 km^2), in the RLP's home range (834 km^2), and actual telemetry locations of the 2 wolves within their home range (N=120). Given are percent values of total areas and locations, respectively. The star indicates a significant deviation from the expected distribution.

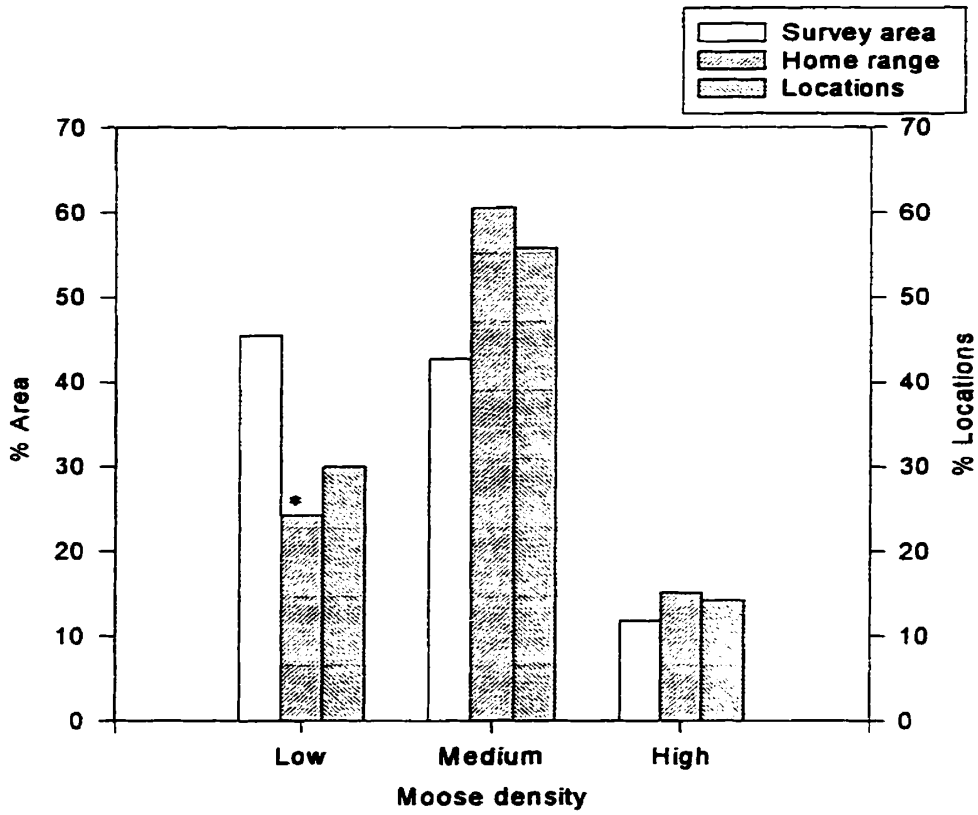
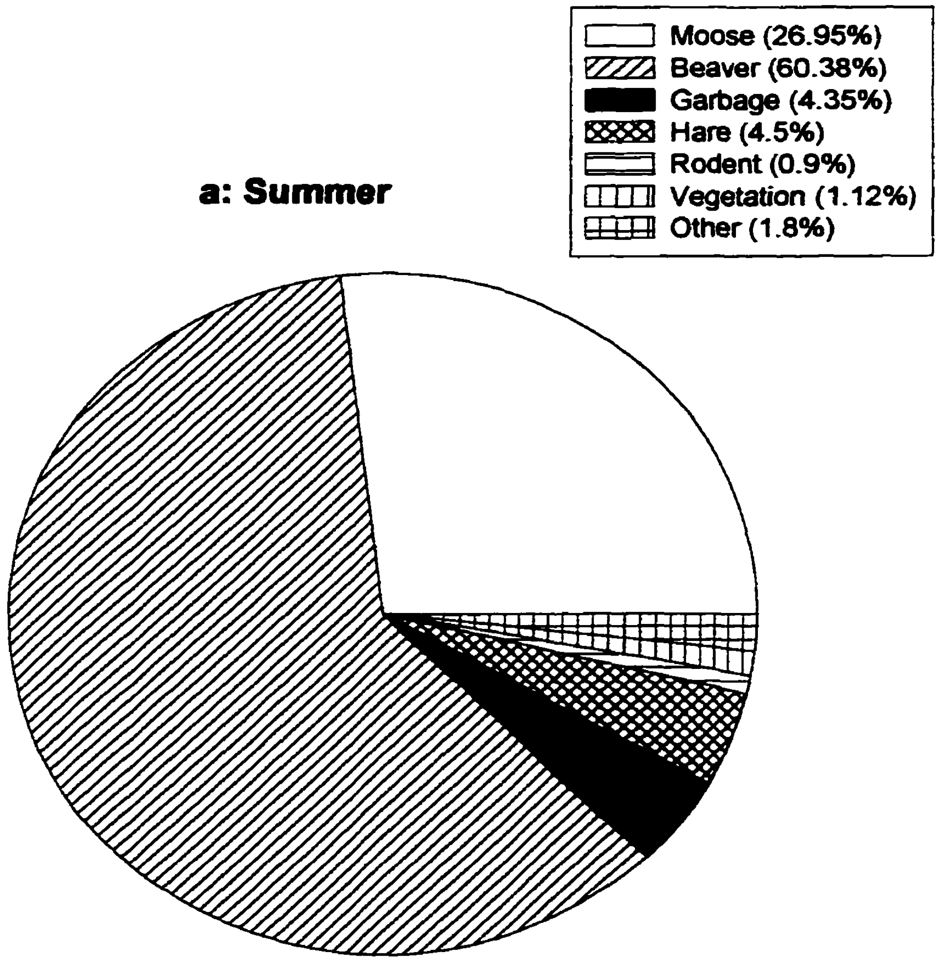
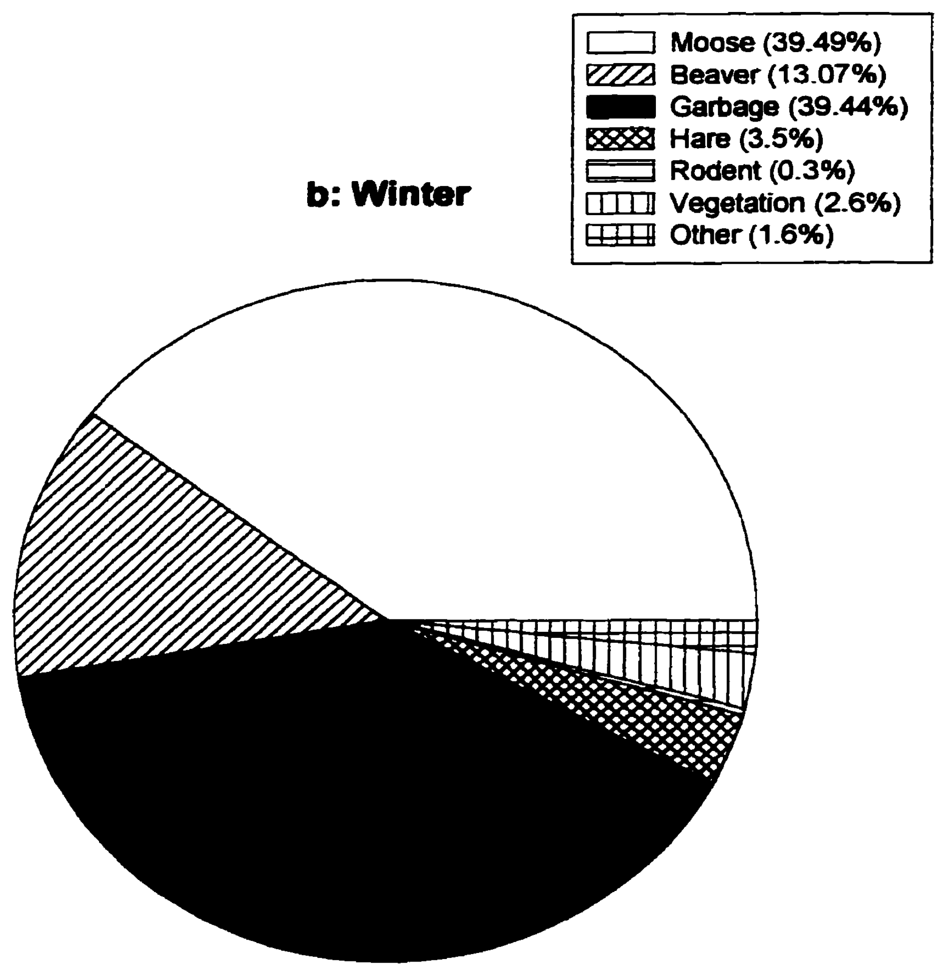


Fig. 7: The percentages of several prey items found in the scats of all 3 study packs (for definition see text). The results are shown separately for the summer, N = 129 (**a**) and for the winter, N = 103 (**b**).




b: Winter
Moose (39.49%)
Beaver (13.07%)
Garbage (39.44%)
Hare (3.5%)
Rodent (0.3%)
Vegetation (2.6%)
Other (1.6%)

General Discussion

Recent research has concentrated efforts to identify factors which may be necessary for wolf survival and to sustain recolonizing and reintroduced wolf populations (Mladenoff et al. 1995). Several biotic and abiotic factors influencing wolf distribution are presented in this study of resident wolves on the north shore of Lake Superior. During this study, wolves which were exposed to roads and other infrastructure used them in proportion to their occurrence. This result implies that wolves did not avoid roaded areas nor did they specifically choose them for travel. Although none of the home ranges had overall road densities above 0.60 km/km^2, two of the packs used core areas with road densities which exceeded this recognized threshold (Thiel 1985, Mech et al. 1988, Thurber et al. 1987, Mladenoff et al. 1995). The presumably high tolerance of such road densities can be attributed partly to the seasonal use of a garbage dump by both packs. It is plausible that the observed road use by wolves influences the sizes of the home ranges. Home ranges of wolves that contained roads and other human-made infrastructure were larger than the home range of a pack that did not have such landscape alterations. In addition, roads that had less traffic were used more by wolves than roads that received considerably more vehicle traffic. This suggests that roads are partially used for travel and that wolves may use roads that receive low vehicle traffic for movement.

Prey density has been shown to be inversely correlated with wolf territory size (Fuller 1989), but in this study, the smallest home range size was observed for a pack with the significantly lowest moose density of all study packs. Moose densities in the overall study area were low in general (<0.20 moose/km^2) and, therefore, large home ranges would be expected. The results imply that the use of roads had a larger effect on home range sizes than did moose density.

Wolves used roads and other human-built infrastructure proportionately to their availability; these travel routes were also the highest sources of mortality. Seventy percent of the known wolf mortalities during the study died due to human caused factors. Both collisions by vehicles and trains and intentional killing of wolves by hunters and trappers were linked to these structures. Similar human-caused mortality rates were reported by other studies (Mech 1977, Fritts and Mech 1981, Berg and Kuehn 1982, Mech 1989, Fuller 1989). In contrast, natural caused mortality among the study packs accounted for 29% of the observed deaths.

Wolf packs in the study area did not show any preferences for the investigated landscape parameters. However, the wolves were located significantly more often in mixed forest cover even though conifer was more abundant. Mixed forest cover was also found to be most prevalent in pack areas in Wisconsin compared to non-pack areas (Mladenoff et al. 1995). Although wolves are not habitat specific (Mech 1970, Mladenoff et al. 1995), they seem to visit areas which are most favourable for their prey. As shown in this study, the main part of the wolves' diet in the study area comprised of moose and beaver. Since conifer forest cover is generally disadvantageous for both species (Banfield 1974, Telfer 1995), it could be assumed that wolves followed their prey and therefore spent significantly more time in mixed forest.

In addition to roads, wolves used rivers as travel routes in the winter and significantly more than lakes and creeks. The results suggest that rivers are important travel routes for wolves (Mech 1970) and may be important in areas of heavy snow fall as suggested by Thurber et al. (1987).

While most wolves live in packs, there are apparent individual behavioural differences among them (shown in Table 4). When observed individual behaviours such as the use of lakes, rivers, and roads are pooled for statistical analysis, these individual differences are lost and as a result are often ignored. This creates some bias in reporting results of habitat use, especially when not all of the individuals of the pack can be accounted for or observed during telemetry sampling. However, since the majority of the packs' activities are synchronized (Mech 1970), pooling of individual behaivours can be justified.

Prey density was found to be similar in most of the investigated home ranges, except for the CLP's home range in Pukaskwa National Park where moose densities were significantly lower. Prey density did not seem to alter habitat use, but packs that hunted predominantly moose traveled longer distances than wolves that fed at a garbage dump. The most striking effects of the reported low moose density in the study area seem to be the high susceptibility to disease and even starvation and the lack of reproduction of all packs except the one that successfully occupied a garbage dump for two winters. This predictable food resource may have decreased the need to travel and seek vulnerable prey and hence decreased unnecessary energy expenditure. It is plausible that the availability and consumption of garbage may have maintained the overall condition of the wolves, reflected by their successful production and upbringing of pups. This result concurs with Messier and Crete (1985) and Messier (1987) in that moose densities below 0.20 moose/km^2 cannot support viable wolf populations, and that wolves that occupy areas with moose densities below 0.40 moose/km^2 were malnourished.

The observed consumption of garbage by wolves is not a unique phenomenon, it occurs world wide (Grace 1976, Boitani 1982, Mendelssohn 1982, Afik and Alkon 1983, Mech and Hertel 1983, Salvador and Abad 1987, Blanco et al. 1992, Boitani 1992). The attraction to such sites exposes them to increased mortality risks. Higher human contact, and highway and road crossing are important factors which have been identified as sources of high wolf mortality (DeVos 1949, Fritts and Mech 1981, Berg and Kuehn 1982, Thiel 1985, Mech et al. 1988, Mech 1989, Fuller 1989). Trapping at dumps is a common practice in the study area, and in the past as many as 15 wolves per dump have been captured at several garbage dumps in one year. This exceeds the maximum number of wolves observed in any pack during this study. Wolves in the study area are commonly trapped for fur, but also as predator control. The latter stems from misconception and a fear of wolves reflecting the poor understanding and low esthetic value of this species. Interestingly, the dump attracted wolves in subsequent years and there is evidence that the habit is passed on from generation to generation (Krizan unpublished data). Because the dump wolves are often seen crossing roads near the town, judgments about the estimated wolf population are usually very misleading. Due to such misconception, wolves are repeatedly killed and the individual turnover within these packs is increased and hence the social structure of packs remains unstable. Clearly, habituation of wolves to dumps can harm the individuals using the site and can affect the population. Effort should be made to deter wolves with non-lethal methods from these human food depots.

The direct effect of garbage dumps on the spatial use of wolves is reflected by the significantly smaller core areas of both packs that used the dump seasonally. Similar results were reported by Mech and Hertel (1983) for a pack of wolves that visited a dump in Minnesota (Mech and Hertel 1983). The only pack that had a comparable core area was the Cascade Lake Pack, which had no human-made infrastructure throughout their home range or core area, and therefore, the wolves were probably restricted in their movements.

Scat analysis showed that both the Black River Pack and the Neys Pack consumed garbage during the winter, and seemed to consume regular prey species during the summer. In comparison, the pack that did not have access to a garbage dump consumed moose and beaver year round.

The den and the rendezvous sites of the BRP and NP were located more than 20 km from the dump, suggesting that the packs avoided the dump during this time. Although both packs visited and remained at or close to the dump for long periods of time in winter, they remained in a small area restricted to human access, suggesting that they avoided human activity. The results of the spatial analysis show the importance of core area analysis as opposed to general home range descriptions of wolf habitat use, especially when parameters such as road density are considered.

In conclusion, the effects of the garbage dumps are three fold. First, the packs that fed at the dump had shorter travel distances compared with a pack that hunted moose, exemplified by the smaller size of the core area. Second, in conjunction with shorter travel distances and a supplemented diet, presumably the wolves expended less energy and, therefore, were in better physical condition, reflected by successful reproduction. Third, visitation of the dump exposed the wolves to mortality risk.

In this study, traffic and human activities on roads, low moose density, and the use of a garbage dump may be responsible for the observed differences in home range sizes, travel distances, and habitat use by the study packs. Consequently, road density in this study area seems to be an insufficient indicator of favourable wolf habitat contrary to previous studies (Thiel 1985, Jensen et al. 1987, Mech 1989, Fuller 1989, Mladenoff et al. 1995). The validity of a road density threshold as a factor influencing wolf presence and survival should not be rejected, but more parameters such as vehicle traffic, the attraction of a food source, and prey density should be considered in future studies.

Appendix I.

Capture dates and fates of each captured wolf from August 1994 to February 1997. Shown are the dates of live capture, the trapper that captured the wolf, the name assigned, sex, ear tag number, fate of the individual (alive, dead, unknown), the date of death, and cause of death.

DATE OF CAPTURE	TRAPPER	NAME	SEX	TAG NUMBER	FATE	DATE OF DEATH	CAUSE OF DEATH
8/20/94	KRIZAN	NELIE	F	269	DEAD	OCT. 94	UK
8/21/94	KRIZAN	LOUIE	M	229	DEAD	DEC. 94	SNARED
8/22/94	KRIZAN	M473	M	473	UK		
8/22/94	KRIZAN	SAM	M	371	ALIVE		
8/25/94	KRZAN	M09	M	9	UK		
8/26/94	KRIZAN	M03	M	3	UK		
8/26/94	KRIZAN	ALDO	M	2	ALIVE		
8/27/94	KRIZAN	F51	F	51	DEAD	DEC. 96	SNARED
9/30/94	NEALE	CASSIDY	F	53	DEAD	FEB. 97	MANGE
10/3/94	KRIZAN	MOJO	M	5	DEAD	FEB. 96	BLASTOMYCOSIS
10/3/94	KRIZAN	ABBEY	M	———	DEAD	OCT 94	SHOT
8/16/94	KRIZAN	PAULINA	F	52	DEAD	DEC. 95	HIT BY TRAIN
6/16/95	KRIZAN	ALDO	M	2	ALIVE		
7/15/95	NEALE	SOLITA	F	76	DEAD	FEB. 96	KILLED BY WOLVES?
7/20/95	KRIZAN	MIKA	F	77	DEAD	DEC. 95	STARVATION
8/29/95	KRIZAN	ANA	F	87	DEAD	NOV. 96	SNARED
2/16/96	HWWM/KRIZAN*	STAR	M	7	DEAD	FEB. 97	MANGE
2/18/96	HWWM/KRIZAN*	MOON	F	54	ALIVE		
7/9/96	KRIZAN	SAM	M	371	ALIVE		
7/12/96	KRIZAN	LEO	M	14	ALIVE		
7/20/96	KRIZAN	SHY	F	71	ALIVE		
7/22/96	KRIZAN	CHARLY	M	23	ALIVE		
7/26/96	KRIZAN	RONJA	F	70	ALIVE		

* Indicates net gunning operation in conjunction with Helicopter Wildlife Management, Krizan handled and radio collared the captured wolves.

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