# A Regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region

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# A Regional Landscape Analysis and Prediction of Favorable Gray Wolf Habitat in the Northern Great Lakes Region

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**Abstract:** *Over the past 15 years the endangered eastern timber wolf (*Canis lupus lycaon*) has been slowly recolonizing northern Wisconsin and, more recently, upper Michigan, largely by dispersing from Minnesota (where it is listed as threatened). We have used geographic information systems (GISs) and spatial radiocollar data on recolonizing wolves in northern Wisconsin to assess the importance of landscape-scale factors in defining favorable wolf habitat. We built a multiple logistic regression model applied to the northern Great Lakes states to estimate the amount and spatial distribution of favorable wolf habitat at the regional landscape scale. Our results suggest that areas with high probability of favorable habitat are more extensive than previously estimated in the northern Great Lake States. Several variables were significant in comparing new pack areas in Wisconsin to nonpack areas, including land ownership class, land cover type, road density, human population, and spatial landscape indices such as fractal dimension (land cover patch boundary complexity), land cover type contagion, landscape diversity, and landscape dominance. Road density and fractal dimension were the most important predictor variables in the logistic regression models. The results indicate that public forest land and private industrial forest land are both important in managing for a broad-ranging animal such as the wolf. Our data portray favorable habitat that is highly fragmented along development corridors in northern Wisconsin, which may be responsible for the slow growth of the wolf population. Upper Michigan, which is just beginning to be colonized by wolves, has very large, contiguous areas of likely habitat approaching the importance of those in northeastern Minnesota. If continuing development or wolf control restrict dispersing wolves from moving from Minnesota to Wisconsin, and Wisconsin habitat becomes more marginal through further fragmentation, Michigan has the potential to maintain a significant wolf population independent of Minnesota and serve as a source population for Wisconsin. However, a simple island/corridor model of wolf habitat in Wisconsin does not seem to apply. Wolves apparently move throughout the landscape, across many unfavorable areas, but establishment success is restricted to higher quality habitat. Source-sink dynamics may be operating here, and they suggest that reduction of the Minnesota population in the near term may affect recovery in Wisconsin and Michigan. Our analysis is an example of use of long-term monitoring data and large-scale cross-boundary regional analysis that must be done to solve complex spatial questions in resource management and conservation.*

Un análisis regional del paisaje y una predicción del hábitat favorable para el lobo gris en la región norte de los Grandes Lagos

**Resumen:** *A lo largo de los últimos 15 años el lobo gris (*Canis lupus lycaon*), en peligro de extinción ha*

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*venido recolonizando lentamente el norte de Wisconsin y más recientemente, el norte de Michigan, principalmente a través de su dispersión desde Minnesota (dónde se encuentra listado como amenazado). En este estudio usamos SIG y datos espaciales de radio-collares, colocados en lobos recolonizadores en el norte de Wisconsin, para evaluar la importancia de los factores de la escala del paisaje en la definición del hábitat favorable para el lobo. Construímos un modelo de regresión logística múltiple aplicado a los Estados del norte de los Grandes Lagos, para estimar la cantidad y distribución espacial del hábitat favorable para el lobo a una escala paisajística regional. Nuestros resultados sugieren que las áreas con una alta probabilidad de poseer un hábitat favorable, son más amplias que lo previamente estimado en los Estados del norte de los Grandes Lagos. Diversas variables fueron significativas en la comparación de nuevas áreas con manadas de lobos en Wisconsin con respecto a áreas sin manadas, incluyendo las clases de tenencia de la tierra, el tipo de cobertura, la densidad de rutas, la población, y los indices espaciales del paisaje tales como la dimension fractal (complejidad de los parches de cobertura), el contagio de los tipos de cobertura, la diversidad del paisaje, y la dominancia del paisaje. La densidad de rutas y la dimensión fractal fueron las variables predictoras mas importantes en el modelo de regresión logística. Los resultados indican que tanto las áreas de bosques públicas, como los bosques privados bajo explotación, son importantes para el manejo de un animal con un amplio rango de distribución, como el lobo. Nuestros datos describen un hábitat favorable que se encuentra altamente fragmentado, a lo largo de corredores de desarrollo en el norte de Wisconsin, esta situación seria responsable del lento crecimiento de la población de lobos. El sector superior de Michigan, que está recién comenzando a ser colonizado por lobos, presenta grandes áreas contiguas de hábitat apropiado, que se acercan en importancia a aquellas del noreste de Minnesota. Si el desarrollo continuado o el control del lobo limita a los lobos dispersantes en su traslado de Minnesota a Wisconsin, y el hábitat de Wisconsin se hace más marginal debido a una mayor fragmentación, Michigan tiene el potencial para mantener a una población de lobos significativa en forma independiente de Minnesota y asi servir como una población fuente para Wisconsin. Sin embargo, un simple modelo de isla/corredor para el hábitat del lobo no parece ser aplicable. Aparentemente, los lobos se mueven a lo largo del paisaje, a través de muchas áreas no favorables, pero el éxito del establecimiento esta restringido a un hábitat de mayor calidad. Una dinámica de fuente-sumidero ("source-sink") podría estar operando en este caso, lo que se sugiere que la reducción de la población de Minnesota en un corto plazo podria afectar la recuperación de Wisconsin y Michigan. Nuestro análisis es un ejemplo del uso de datos de monitoreo a largo plazo y del análisis regional que debe ser llevado a cabo para resolver preguntas espaciales complejas en el manejo de recursos y la conservación.*

## Introduction

The eastern timber wolf (*Canis lupus lycaon*) (Goldman 1944) originally existed throughout most of the eastern United States and southeast Canada. This wolf population was nearly eliminated since the European settlement of eastern North America. The eastern timber wolf was given full protection in 1974 under the Federal Endangered Species Act of 1973, listing all populations of the subspecies in the U.S. as endangered. The Minnesota portion of this wolf population was downlisted to threatened in 1978.

At the time of listing, Minnesota had the only breeding population of gray wolves in the U.S. outside of Alaska and a small population on Isle Royale in Lake Superior (Bailey 1978). Since that time the wolf population in Minnesota has increased from an estimated 500–600 in 1973 to 1500–1750 in 1989 (Mech & Rausch 1976; Fuller et al. 1992). The revised recovery plan for the eastern timber wolf described criteria that must be met for recovery of the species (U.S. Fish and Wildlife Service 1992). These goals include a viable population of 200 animals located over 320 km (200 mi) from the Minnesota population (such as New England or northern New York) or a population of 100 wolves located within 160 km (100 mi) of Minnesota in Wisconsin and upper Michigan (Fig. 1) (U.S. Fish and Wildlife Service 1992).

The purpose of this study is to assess landscape-scale habitat variables and their importance to wolves recolonizing the northern Great Lake States of Wisconsin and upper Michigan and to estimate available habitat. We are interested in using geographic information systems (GISs) to determine if easily available spatial data can successfully describe current wolf habitat and contribute to a predictive spatial model. This is a necessary prelude to estimating potential wolf population size in the region (D. Mladenoff et al. submitted manuscript) and simulating spatial population dynamics and management effects (R. Haight et al. in preparation).

## Background

The wolf once ranged throughout North America and is now endangered and reduced to only 3% of its former range in the U.S. outside Alaska (Bailey 1978; Fuller et al. 1992). Wolves were largely eliminated from the northern Great Lake States and were much reduced where

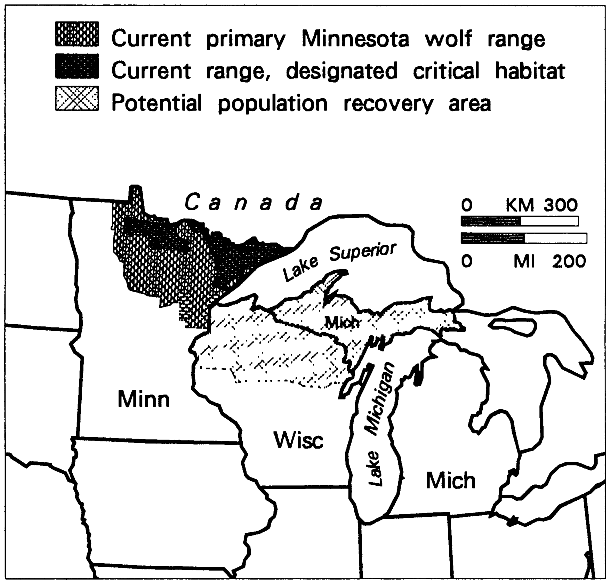

*Figure 1. Current Minnesota wolf management zones (primary range, including designated critical habitat) and potential regions for the gray wolf in northern Wisconsin and upper Michigan (modified from U.S. Fish and Wildlife Service 1992).*

they persisted in northeastern Minnesota by the middle of the century (Fuller et al. 1992; U.S. Fish and Wildlife Service 1992; Wydeven et al. in press). The population decline followed rapid forest logging, land clearing, and settlement during the late 19th and early 20th centuries (Stearns 1990). By the 1950s and 1960s much of the northern portion of Minnesota, Wisconsin, and Michigan had become reforested with early successional forests containing ideal habitat for white-tailed deer (*Odocoileus virginianus*), a preferred prey species of wolves (Mech 1970). Continued forest harvesting of the young second growth forest has maintained high deer levels in many areas (Mladenoff & Pastor 1993; Mladenoff & Stearns 1993; Blouch 1984).

Wolf populations declined rapidly in Wisconsin and Michigan from 1930 through the 1950s and were considered extirpated by 1960 (Schorger 1942; Thiel 1993). Initially, broad recolonization beyond northeastern Minnesota was prevented by a low population, bounties, and negative public attitudes causing continued persecution by humans (Schorger 1942; Mech 1970; U.S. Fish and Wildlife Service 1992; Thiel 1993). Following protection under the Endangered Species Act, wolves have increased beyond their primary range in Minnesota and dispersed and colonized new areas in the three states around Lake Superior (Fuller et al. 1992; U.S. Fish and Wildlife Service 1992).

In the late 1970s, wolves began to reoccur in northern Wisconsin, presumably due to increasing dispersal from the growing Minnesota population (Mech & Nowak 1981; Thiel & Welch 1982). In 1979 the Wisconsin Department of Natural Resources began systematic monitoring of gray wolves in the state (Wydeven et al. in press). Since then the known number of Wisconsin wolves has fluctuated from a low of 15 in 1985 to 40 in 1991 (Wydeven et al. in press). Gradually wolf sitings also began to increase in adjacent upper Michigan (U.S. Fish and Wildlife Service 1992). Knowledge of wolf biology and ecology also expanded greatly during this period through detailed study of captured and radiocollared animals, particularly in Minnesota and Isle Royale National Park, Michigan (Mech 1973; 1986; Fritts & Mech 1981; Berg & Kuehn 1982; Fuller 1989; Fuller et al. 1992; Peterson & Page 1988). Recently, McLaren and Peterson (1994) presented evidence for the role of wolves as an agent in top-down control in a forest ecosystem food chain.

We focused our efforts on patterns at the regional landscape scale. The developing fields of landscape ecology and conservation biology, with tools such as GIS and improved computer modeling (Forman & Godron 1986; Turner & Gardner 1991; Mladenoff & Host 1994), provide opportunities to expand our knowledge of wolves at larger scales. Wolves are an ideal species to study in a landscape context because their social structure results in large-scale territorial behavior. The population structure of wolves may fit the metapopulation model, which describes an interacting set of subpopulations (Levins 1969; Hanski 1991). Wolf packs, the extended family and breeding unit, occupy consistent territories (Mech 1973). These packs are the subpopulation units that can move or become locally extinct, occupying habitat patches within the larger population area. Unlike most other species, wolf populations impose this spatial arrangement at very large regional scales. In Minnesota pack territory size in midwinter averages approximately 166 $km^2$ (Fuller et al. 1992). Wolves dispersing to establish new territories can move over several hundred kilometers. Thus, a wolf population can cover thousands of square kilometers in a predictable fashion, with discrete but interacting breeding units. This large-scale spatial behavior makes wolves amenable to spatial analysis and modeling.

Few studies have examined large-scale spatial factors important to wolves. Thiel (1985) determined road density on a county basis in northern Wisconsin and provided evidence that the historical increase of human influence, as indicated by increasing road density, was correlated with the period of the demise of wolves in Wisconsin (1926–1960). Thiel (1985) similarly showed evidence that newly colonizing wolves were successfully occupying areas of low road density, with a threshold mean road density per pack area of 0.6 $km/km^2$. Similar results were found in areas being colonized in Minnesota and Michigan (Jensen et al. 1986; Mech et al. 1988; Mech 1989). The existence of roads per se is not problematic for wolves. Road densities in these studies serve as an index to human contact, which has historically been the major source of wolf mortality. Human contact has meant high levels of legal, illegal, and accidental killing of wolves. Thiel (1985) pointed out that this relationship may hold particularly for the past when bounties existed and public attitudes resulted in a high level of opportunistic killing of wolves (Kellert 1987; U.S. Fish and Wildlife Service 1992). In Alaska, Thurber et al. (1994) showed that wolves avoided areas near roads with relatively high human use, but favored closed roads for movement lanes.

As the wolf population has recovered in northern Minnesota, areas once thought to be too highly developed are being colonized by wolves (Mech 1993a; Fuller et al. 1992). Wolves are now occupying territory formerly assumed to be marginal in northern Minnesota, with road densities above 0.7 km/km$^2$ (Fuller et al. 1992). Legal protection and changing public attitudes appear to be the critical factors in the wolf population increase. As long as wolves are not killed they appear to have the ability to occupy areas of greater human activity than previously assumed (Mech 1993; Fuller et al. 1992). As a top carnivore wolves are not habitat-specific to certain ecosystems; they were at one time the most widespread large mammal in the world (Mech 1970). Adequate prey density appears to be the main factor limiting wolves where they are present and tolerated by humans (Fuller et al. 1992). At the same time areas with low human contact have been shown to be important in areas with recovering or colonizing wolf populations because much wolf mortality is human-caused, whether intentional, accidental, or indirect through disease (Fuller et al. 1992; Mech & Goyal 1993; Wydeven et al. in press).

Large-scale spatial analysis and modeling using GISs have been applied in studies of a few other species. Much of this work has involved extending habitat suitability models to explicitly spatial contexts, and sometimes at larger scales (Laymon & Barrett 1986; Donovan et al. 1987). The endangered Mt. Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) was studied using GIS and a spatial database covering approximately 6500 ha. A suite of mapped variables was used in a multivariate modeling approach using logistic regression to examine potential habitat loss due to development (Pereira & Itami 1991).

At larger scales Clark et al. (1993) used GIS and a larger-scale multivariate modeling approach in a study of black bear (*Ursus americanus*) habitat, covering an area of 414 km$^2$. Schulz and Joyce (1992) examined the effect of changing scale or grain size of the spatial analysis, in relation to the habitat variables mapped for marten (*Martes americana*). Landscape pattern associations of Northern Spotted Owl (*Strix occidentalis caurina*) home ranges have been analyzed based on detailed habitat maps (Carey et al. 1992; Lehmkuhl & Raphael 1993). California Condor (*Gymnogyps californianus*) sightings were analyzed in relation to mapped habitat variables over a large-scale region using GIS (Stoms et al. 1993). Milne et al. (1989) used a Bayesian statistics approach to develop a predictive model of white-tailed deer habitat.

## Study Region

Our work focused on northern Wisconsin and upper Michigan, one of the primary regions for wolf recovery in the eastern U.S. (U.S. Fish and Wildlife Service 1992). The size of our northern Wisconsin study region is 59,148 km$^2$. Upper Michigan is 41,984 km$^2$, and the northern Minnesota wolf Management zone is over 70,000 km$^2$. The region is transitional between the boreal forests to the north and the largely deciduous forests to the south (Pastor & Mladenoff 1992). Forests have changed from largely mature and old-growth at the time of European settlement in the 19th century (Frelich & Lorimer 1991; White & Mladenoff 1994) to nearly all second growth hardwood and conifer species (Mladenoff & Pastor 1993; Mladenoff et al. 1993). Major forest types include aspen-birch (*Populus tremuloides-Betula papyrifera*); sugar maple (*Acer saccharum*) and other northern hardwood species; upland conifers such as white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), and white pine (*Pinus strobus*); and lowland conifers including spruce-fir and northern white cedar (*Thuja occidentalis*). Northern red oak (*Quercus rubra*), northern pin oak (*Q. ellipsoidalis*), white pine, red pine (*P. resinosa*), and jack pine (*P. banksiana*) are more abundant on progressively well-drained, sandier soil areas. The former dominants of white pine and eastern hemlock (*Tsuga canadensis*), typical of progressively more mesic sites, are reduced to a fraction of their former abundance (Stearns 1990; Mladenoff & Stearns 1993). A great portion of these forests is aspen-birch with conifers, an ideal habitat for white-tailed deer (Thompson 1952; Fuller 1989; Nelson & Mech 1986).

Wolf colonization and movement into Wisconsin and upper Michigan is geographically restricted because of the location of Lake Superior (Fig. 1). Dispersal into this region is only possible from Minnesota to the west or, to a lesser degree, from Canada across the St. Mary's River at the eastern end of upper Michigan (Fuller & Robinson 1982; Jensen et al. 1986).

## Methods

### Wolf Locational Data

Timber wolves recolonizing the study region have been radiocollared and tracked by the Wisconsin Department of Natural Resources since 1979 in an attempt to better understand population growth and dynamics (Wydeven et al. in press). Wolves were caught in foothold traps, fitted with radiocollars, and released at or near the capture site. Using radio telemetry, department personnel located collared wolves once or twice a week throughout the year by aircraft or on the ground and then plotted the locations on 1:24,000 or 1:100,000 topographic maps. Locations were summarized by individual wolf and by season, with summer maps covering April 15–September 14 and winter maps covering September 15–April 14.

Wolves have been captured and radiocollared from 17 of the 21 wolf packs that have existed in Wisconsin between 1979 and mid-1993. Some packs have had only one wolf collared for one season while others have had several collared wolves for multiple years. Fourteen packs had a sufficient number of location points to be included in further analysis. We assumed that pack territory locations that partially overlapped each other but were not continuously occupied by wolves to be separate packs. An individual pack annual home range is defined here as a minimum of 50 points per pack over at least two seasons (Wydeven et al. in press). Fuller and Snow (1988) found that 30–35 telemetry fixes are adequate for defining wolf territories. Radiolocations of collared wolves that dispersed from packs within or outside of the study region were also similarly recorded and digitized. Dispersers are individuals, usually yearlings, that permanently leave their natal pack. These lone wolves may move long distances to find another pack or a mate to establish a new pack (Mech 1970). Monitoring of wolf pack locations and movements over nearly 20 years provides a regional data set useful for analysis and examination with other landscape-scale variables.

Seasonal wolf location data were digitized in Universal Transverse Mercator (UTM) coordinates using the geographic information system PC ARC/INFO 3.4D and combined by wolf pack. Files containing all radiolocation $x$-$y$ coordinates for each pack were exported from PC ARC/INFO and imported into McPAAL 1.2 (M. Stuwe, Conservation and Research Center, Smithsonian Institution), a microcomputer-based home range estimation program. We used the harmonic mean method of home range estimation (Dixon & Chapman 1980), which allows the delineation of home range as concentric percent use contours. Using this technique we generated 20, 40, 60, 80, and 95% use isopleths for each pack territory. We used a companion computer program (provided by E. Anderson, University of Wisconsin-Stevens Point) to calculate the UTM coordinates of the isopleths and export them from McPAAL. The home range coordinates were imported into workstation ARC/INFO and assembled into polygon coverages. We chose the 80% use isopleth to represent home range, as it generally captures most of the data points (>98%) while removing outliers and large areas of possibly unused terrain between them (Spencer & Barrett 1984; Harris et al. 1990).

### Landscape Coverages and Preparation

We compiled five spatial data sets of landscape characteristics or variables describing landscape-scale wolf habitat: human population density, prey (deer) density, road density, land cover, and land ownership. An ARC/INFO data set, or coverage, of human population density was generated by linking 1990 block-group level census data to the census geography in the U.S. Census Bureau TIGER/line files (U.S. Census Bureau 1991). Census blocks in the study region are polygons of relatively homogeneous human density that average 24.4 km$^2$ in size. Population density was calculated for each block group by dividing the total population of each block group by its area. A deer density coverage was produced by linking data on annual deer density, which are compiled by deer management units (DMUs), to a coverage of DMU boundaries provided by the Wisconsin Department of Natural Resources (Creed et al. 1984), and companion data from the Michigan Department of Natural Resources. Deer Management Units are mapped polygons of relatively homogeneous deer density and habitat with mean size in the study region of 681.3 km$^2$. Road density was calculated from an ARC/INFO road coverage extracted from the TIGER/line files. Roads include highways, other paved roads, and improved unsurfaced roads passable by auto, but exclude unimproved forest roads and trails. The road classes used are those indicated by solid lines on USGS 1:100,000 quadrangle maps. Land cover was clipped from 1:250,000 digital USGS Land Use/Land Cover data which is mapped at a 16-ha resolution (Anderson et al. 1976). Land ownership for the Wisconsin study region was digitized from 1:500,000 Land Resources Analysis Program maps (Wisconsin Planning Agency 1974) created at a 16-ha (40-acre) resolution and updated from current county land records. Each wolf pack home range coverage was intersected with the five habitat coverages. Individual pack area values were calculated by proportionally averaging polygons of the given variable in which the pack was located. For deer density this was done for those years that a pack was known to exist.

To provide a range of comparable data for areas not inhabited by wolf packs, we created 14 nonpack areas in ARC/INFO and intersected these with the five habitat coverages. The nonpack areas were randomly located within the study area at least 10 km from known pack territories and were equal to the mean area (80% use area) of the 14 pack areas (153 km$^2$). We assumed these nonpack areas within the general region of probable wolf movement represent less desirable habitat than occupied pack areas. We also excluded from possible nonpack area locations the easternmost third of the northern Wisconsin study region to help assure that nonpack areas were in areas that wolves were likely to have visited.

### Data Summary, Mapping, and Statistical Analysis

We calculated summaries of landscape variables and several descriptive spatial indices based on the land cover data set that were then included as variables in the analyses. Indices were calculated from land cover data within the pack territories and nonpack areas to test for differences in landscape heterogeneity, pattern, and juxtaposition (Mladenoff et al. 1993). These patterns may relate to habitat and landscape spatial relationships that are important to wolves. These indices include 1. land cover mean patch area; 2. total edge between patches (normalized by area), a measure of the amount of juxtaposition between different land cover types; 3. fractal dimension (D), an index of patch boundary complexity in relation to patch size scaled from 1–2 (simple to complex) (Mandelbrodt 1977; Krummel et al. 1987) calculated using the box-counting method (Sugihara & May 1990); 4. two indices based on the Shannon–Wiener information theory index (Shannon & Weaver 1949) landscape diversity ($D_i$) and landscape dominance ($D_o$; O'Neill et al. 1988), with $D_o$ calculated as suggested by Roberts (in press); and 5. landscape contagion (C; O'Neill et al. 1988), an index of aggregation of cover types across a landscape based on the method of Li and Reynolds (1993). Higher values of C indicate landscapes with relatively fewer contiguous patches and reduced joint boundary occurrences between cover types.

We used several univariate and multivariate statistical tests on the data coverage intersections and spatial indices. A modified *t*-test was used to test for differences in means of landscape characteristics between the 14 pack territories and the overall study region (Sokal & Rohlf 1981). We also compared rank differences of these variables and the spatial indices between the pack territories and nonpack areas with the nonparametric Kruskal–Wallis test (Sokal & Rohlf 1981). Differences in the spatial indices between pack territories and nonpack areas were tested with a *t*-test. A correlation matrix was calculated between all independent variables to examine multicollinearity. Finally, all variables for the 28 pack and nonpack areas were simultaneously entered into a stepwise logistic regression analysis (Agresti 1990; SAS Institute 1990) to derive a multivariate model that would predict the presence or absence of wolf packs. Higher samples are desirable, but our analysis avoids the more serious problem of unequal classes of the dependent variables (Agresti 1990). The resulting models were assessed using goodness-of-fit based on maximum likelihood estimates, tests of parameters in the significant models, and classification accuracy of the response variable (wolf presence and absence) from the original data (Agresti 1990; Manly et al. 1993; Trexler & Travis 1993). The model was also tested against a data set of field-mapped wolf territories.

## Results

### Wolf Distribution and Habitat Relations

Spatial locations of known Wisconsin wolf packs are distributed in a pronounced arch across the study region (Fig. 2). The earliest known packs were established before 1980 in two areas, one on the Minnesota border and the other in the south-central part of the study region (Fig. 2). Subsequent packs were established most regularly in the Minnesota border region and only recently in the north-central parts of the region. Wolves have not established in the eastern third of the region or the southwest. Two packs of seven established before 1985 and persisted until 1992. Of the 14 established since 1985 12 remained in 1992 (Fig. 2; Wydeven et al. in press).

Univariate analyses show significant relationships with several landscape-scale variables (Table 1). Wolf pack territories have significantly greater proportions of mixed conifer–hardwood forest and forested wetlands than the nonpack areas. Mixed forest is the most prevalent of all cover types in pack areas (46.7%), but comprises only 18.1% of nonpack areas. Pack areas also have lower amounts of agricultural land, deciduous forest, and large lakes than nonpack areas (Table 1, Fig. 3a). Agriculture is the least common type in pack areas (2.3%), other than lakes, although it comprises 28% of the land cover in random nonpack areas.

Land ownership patterns show two strong relationships (Table 1, Fig. 3b). Pack territories have much greater proportions of public lands than nonpack areas, particularly for county forest land (39.3 vs. 8.4%). Miscellaneous private ownership comprises much lower proportions of pack areas than nonpack areas (20.1 vs. 75.0%). However, private industrial forest was important in some pack areas, though not significant overall (Table 1, Fig. 3b). County forest land and private ownership comprise the largest proportions (12.6 and 65.7%) of the region.

Mean road density ($km/km^2$) is much lower in pack territories (0.23 in 80% use area) than in the random nonpack areas (0.74) or the region overall (0.71) (Table 1, Fig. 3c). Few portions of any pack territory are located in areas of road density $>0.45$ $km/km^2$, and no portion of any pack area is in area of road density $>1.0$ $km/km^2$. Pack core areas defined by the 40% use contour do not exceed 0.23 $km/km^2$. The 40% use contour had the strongest correlation with low road density and

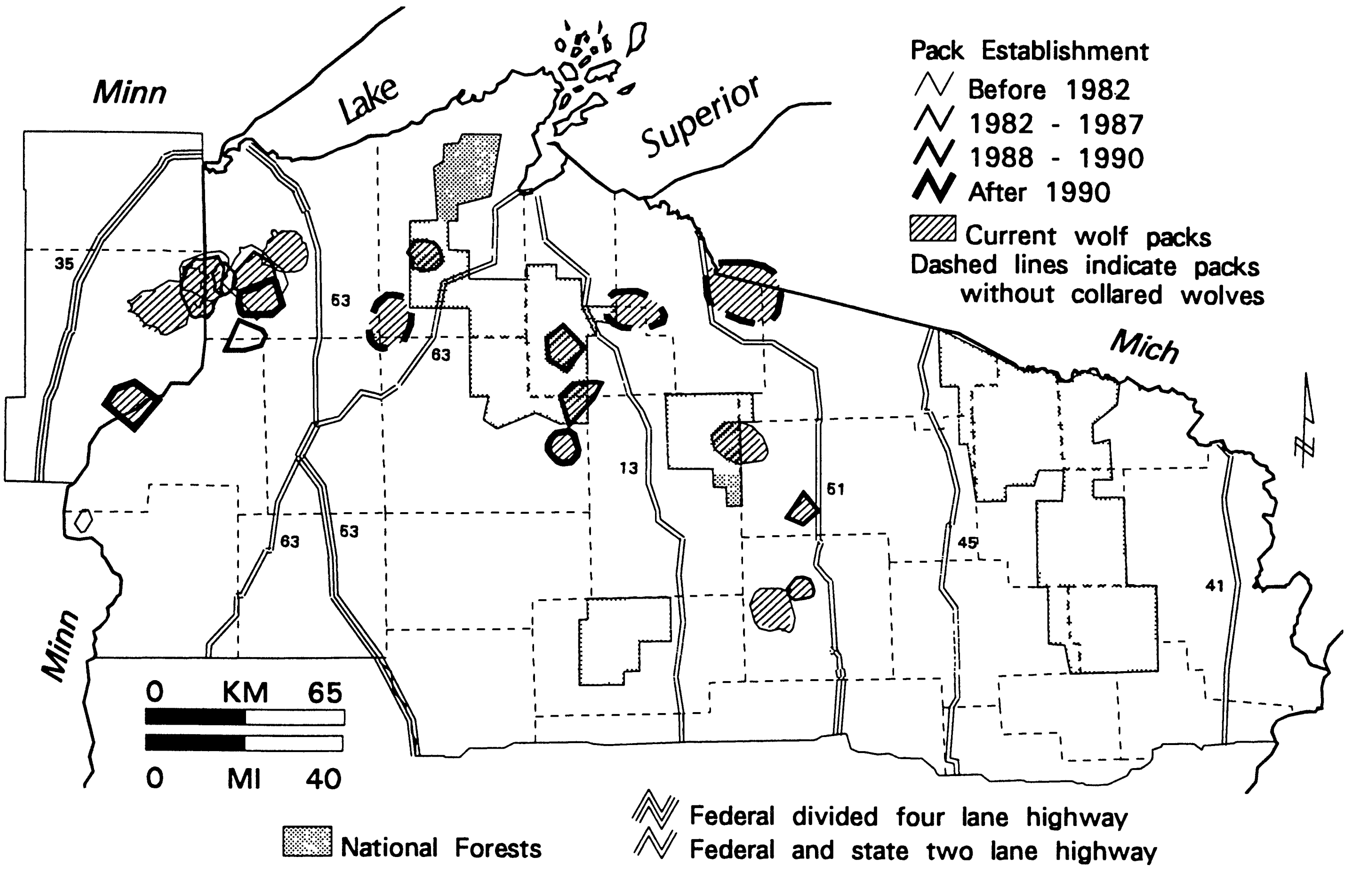

*Figure 2. Known Wisconsin wolf pack territories (1979–1992) and years of establishment. Polygons indicate 80% use areas for territories with radiocollared wolves. Dashed-line polygons are approximate locations of noncollared packs. Overlapping packs did not exist at the same time. Numerals indicate major north–south highway numbers.*

other significant variables; thus, we defined this level as the territory core use area. Also, radiocollared packs are not bisected by any major federal or state highway (Fig. 3c).

No difference was detected between deer densities in pack territories and nonpack areas (Table 1, Fig. 3d). Variation in deer abundance across northern Wisconsin may not affect simple presence/absence of wolves at this time. The relationship between deer and wolves is complex because areas of high deer abundance are often also associated with high road and/or human population density.

The pattern of human population density is very similar to that of road density (Table 1, Fig. 3c). Human population density ($\#/\mathrm{km}^2$) is much lower in the pack territories (1.52) than in the nonpack areas (5.16) or the entire region (7.43).

## Spatial Indices

Four of six indices calculated had values significantly different between pack and nonpack areas (Table 2). Fractal dimension (D) was lower in pack areas, indicating simpler patch shapes than in nonpack areas. Contagion (C) was also lower in pack areas than in nonpack areas, indicating fewer contiguous patches with relatively fewer adjacency relationships than nonpack areas. Landscape diversity ($D_i$) was higher in pack areas and landscape dominance ($D_0$) was lower than corresponding values in nonpack areas. These indices both indicate that pack areas contain more land cover patch types than nonpack areas (Table 2) with this particular scale, land cover classification, and data resolution.

## Logistic Regression

Correlation analysis showed that several variables associated with human land use were highly intercorrelated (private land ownership, road density, deer density, agriculture, and human population; $r > 0.75, p < 0.001$). The variable with the greatest explanatory effect (road density) was retained, and the other correlated variables were deleted during the model building procedure since they did not contribute significantly to the model and could lead to inaccurate model results (Trexler & Travis 1993).

**Table 1. Relationship of landscape variables (means with standard deviations in parentheses) for pack territories ($n$ = 14; 80% use areas described from radiocollar data), randomly chosen nonpack areas ($n$ = 14), and the overall Wisconsin study region.***

| *Variable* | *Pack Territories (%)* | *Nonpack areas (%)* | *Study Area (%)* |
|---|---|---|---|
| Land cover (%) | | | |
| urban | 0.00 (0.00) | 0.18 (0.24) | 0.99 |
| agriculture | 2.34 (4.55)$^{a,b}$ | 27.99 (24.58)$^{a}$ | 20.80$^{b}$ |
| deciduous forest | 15.24 (22.86)$^{a}$ | 30.81 (25.77)$^{a}$ | 19.47 |
| coniferous forest | 4.82 (12.75) | 2.17 (4.24) | 4.28 |
| mixed forest | 47.69 (24.45)$^{a}$ | 18.09 (16.99)$^{a}$ | 35.50 |
| water | 0.94 (0.96)$^{a}$ | 6.49 (8.99)$^{a}$ | 3.51 |
| forested wetlands | 24.67 (9.51)$^{a}$ | 11.93 (14.22)$^{a}$ | 13.69 |
| nonforested wetlands | 4.28 (4.75) | 1.85 (4.56) | 1.75 |
| Land ownership (%) | | | |
| state | 20.27 (28.20) | 9.05 (18.64) | 5.00 |
| county | 39.25 (37.13)$^{a}$ | 8.40 (11.65)$^{a}$ | 12.65 |
| national forest | 10.04 (27.37) | 6.49 (20.39) | 9.31 |
| private | 20.68 (17.61)$^{a,b}$ | 75.07 (28.41)$^{a}$ | 65.70$^{b}$ |
| private industrial forest | 9.60 (20.98) | 0.98 (2.55) | 4.78 |
| Density** | | | |
| road (km/km$^2$) | 0.23 (0.18)$^{a,b}$ | 0.74 (0.26)$^{a}$ | 0.71$^{b}$ |
| human (no./km$^2$) | 1.52 (1.61)$^{a,b}$ | 5.16 (3.48)$^{a}$ | 7.43$^{b}$ |
| deer (no./km$^2$) | 8.58 (2.82) | 8.38 (2.58) | 8.22 |

* *Superscripts indicate differences for (a) Kruskal–Wallis test between wolf pack areas and randomly located nonpack areas, and (b) modified t test between pack areas and the overall northern Wisconsin study region, which includes the small portion of Minnesota included in Fig. 2. Significance levels: $p < 0.05$ for comparisons of road density and human population density in pack areas vs. overall study area; and $p < 0.01$ for all others.*

** *Densities are per km$^2$ of pack territory.*

The stepwise logistic regression analysis converged on two significant models. A model of two noncorrelated variables based on the function

$$\text{logit}\,(p) = -49.550 + 19.854R + 26.861D, \quad (1)$$

where $p$ is the probability of occurrence of a wolf pack, $R$ is road density, and $D$ is the fractal dimension index value scaled from 1–2. A second model was based on the constant relation and one variable with the function

$$\text{logit}(p) = -6.5988 + 14.6189R, \quad (2)$$

where $p$ is the probability of occurrence of a wolf pack and $R$ is road density. Goodness-of-fit was assessed by log likelihood chi-square ($-2\ln$ [likelihood ratio]), or deviance, for the improvement of the two models over the simplest possible model containing only a constant. Goodness-of-fit improvement over the constant-only model was significant for both the roads + fractal model ($\chi^2 = 31.05$, 1 df, $p = 0.0001$) and the roads model ($\chi^2 = 25.20$, 1 df, $p = 0.0001$), with the two-variable model test indicating slightly better fit. The parameter tests based on analysis of maximum likelihood estimates showed, however, that the roads variable was somewhat more significant in the single-variable model ($\chi^2 = 5.534$, $p = 0.018$; versus the parameters in the two-variable model (roads $\chi^2 = 3.33$ $p = 0.068$; fractal $\chi^2 = 2.73$, $p = 0.098$)).

Probability values for occurrence of the response variable (wolf presence) can be calculated based on equations (1) or (2) by

$$p = 1/1 + e^{\text{logit}\,(p)}, \quad (3)$$

where $e$ is the natural exponent.

Classification accuracy of pack and nonpack areas was high based on both models. Probability ($p$) cut levels were assessed that produced the least misclassification error for both models, balancing the classification of the response variable (wolf presence and absence). At the $p > 0.5$ cut level the roads + fractal model correctly classified 13 of 14 pack areas and 12 of 14 nonpack areas, and the roads model correctly classified 12 of 14 pack areas and 12 of 14 nonpack areas. For independent validation both models were applied to seven pack areas of noncollared wolves that had been mapped in the field and reserved from the analysis. In this test, six of the seven pack areas were correctly classified by both models. Model fit and classification accuracy are high, despite being built with a sample of $n = 28$. This may partly be because in this spatial analysis each sample (wolf territory) is not based on a single observation point but an aggragation of 50–120 points.

## Favorable Habitat Prediction and Land Ownership

We mapped the amount and distribution of favorable wolf habitat in the three-state region by applying the regression model at various probability levels to the

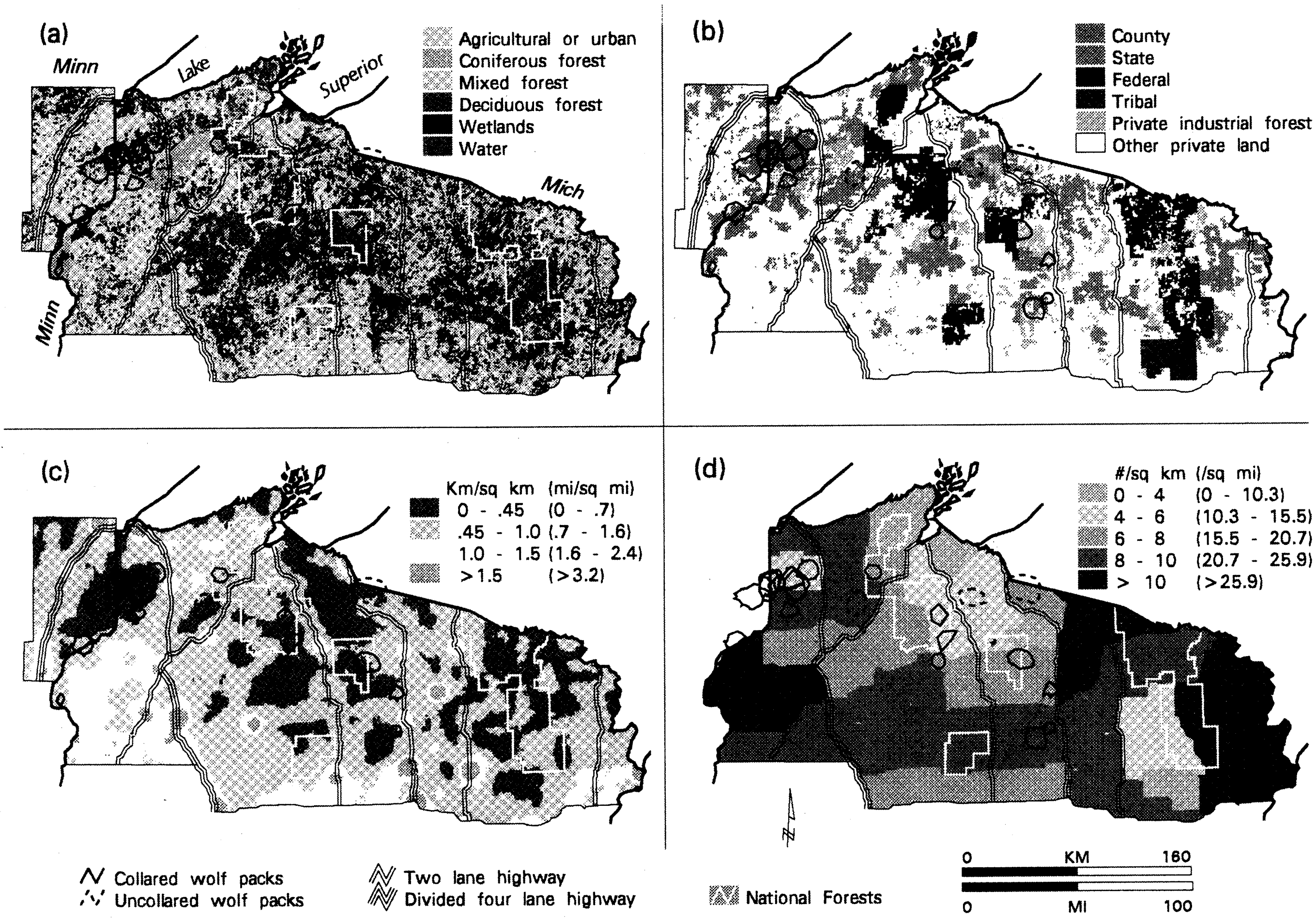

*Figure 3.*

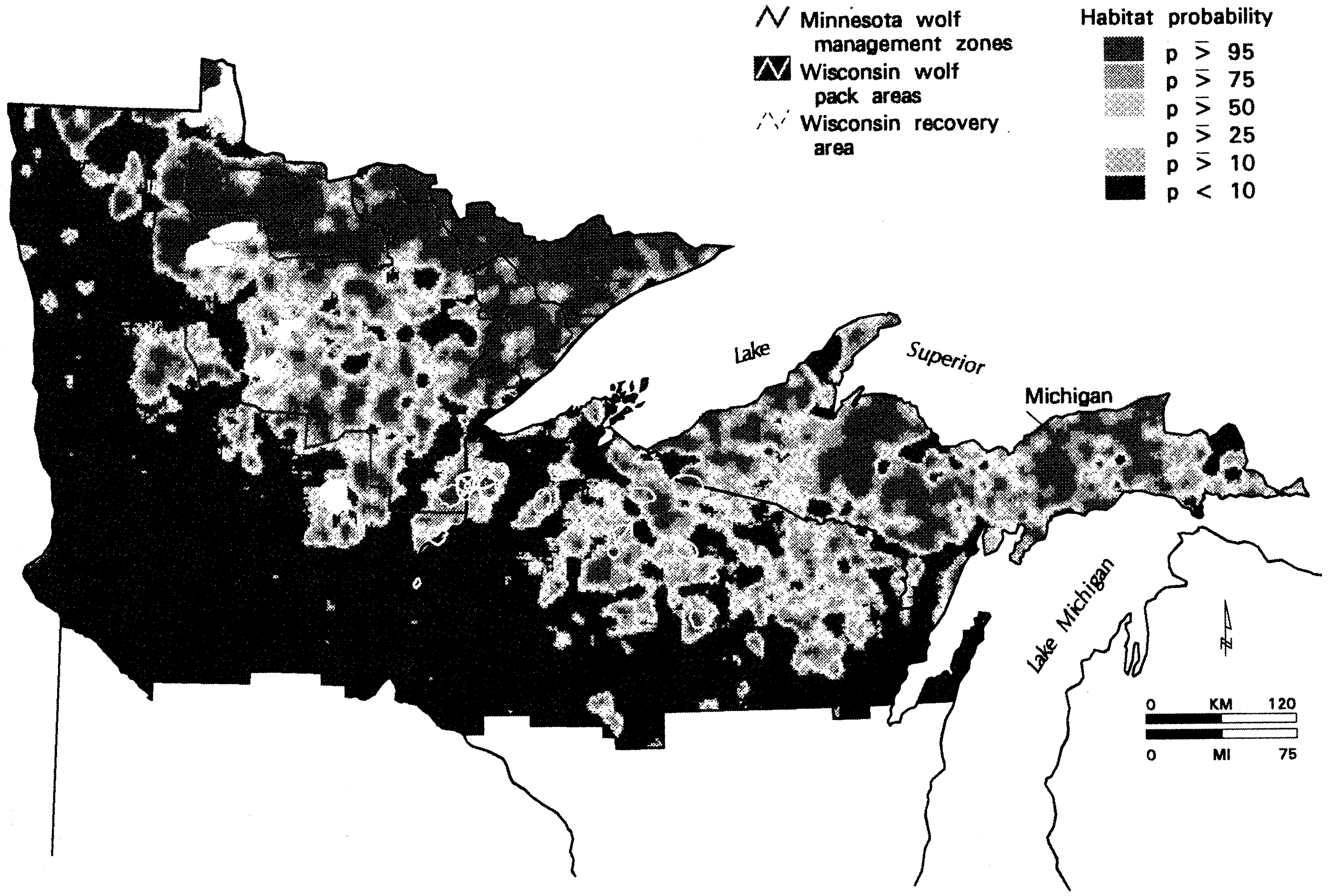

*Figure 4.*

**Table 2. Relationship of spatial landscape indices and wolf pack territories (80% use areas).**[a]

| *Variable* | *Pack Areas (n = 14)* $\bar{x}$ *(sd)* | *Nonpack Areas (n = 14)* $\bar{x}$ *(sd)* |
|---|---|---|
| Patch area | 4.23 (1.76) | 3.29 (1.21) |
| Total edge | 1.40 (0.29) | 1.51 (0.33) |
| Fractal *d* | 1.47 (0.08)[a] | 1.55 (0.07) |
| Diversity | 1.57 (0.25)[b] | 1.41 (0.17) |
| Dominance | 0.99 (0.27)[c] | 1.16 (0.18) |
| Contagion | 0.49 (0.10)[a] | 0.60 (0.08) |
| Number of cover types | 5.86 (1.61) | 7.29 (2.02) |

[a] *Differences between pack and nonpack areas are significant ($p <$ 0.01; 2-tailed t-test).*
[b] *$p = 0.054$*
[c] *$p = 0.057$.*

mapped variables (Fig. 4). We used probability values calculated from the single parameter roads model for further analysis because of the better fit of the parameters in the roads model vs. the roads + fractal model, nearly equivalent classification accuracy, and because it was not computationally possible to calculate the fractal dimension values for the entire study region.

Total favorable habitat area differs markedly among the three states both as total area and habitat distribution (Figs. 4 and 5; Table 3). Favorable habitat as described by the model for areas of probability $>0.5$ is 3.5 times more abundant in Minnesota than Wisconsin (50,168 vs. 14,864 km$^2$) or 1.65 times that of upper Michigan (29,348 km$^2$) (Fig. 5). Of the most favorable ($p > 0.95$) habitat, Minnesota has nearly 15 times as much habitat as Wisconsin (30,088 vs. 2120 km$^2$) and more than twice that of Michigan (13,032 km$^2$). Whereas most of the Wisconsin landscape is in least favorable classes, Michigan has habitat classes in similar proportions to Minnesota, although only half the total area of favorable habitat as Minnesota (Figs. 4 and 5, Table 3).

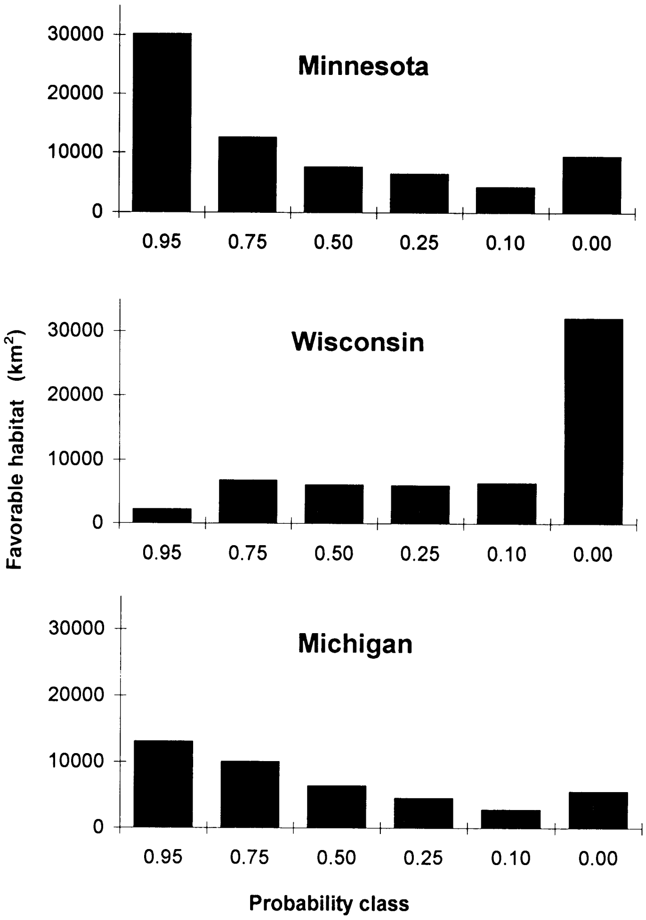

*Figure 5. Favorable habitat area comparison of Minnesota, northern Wisconsin, and upper Michigan, based on probability levels from the logistic regression model (single variable roads model depicted spatially in Fig. 4).*

Public land ownership patterns in Wisconsin are strongly related to habitat favorability (Figs. 6 and 7, Table 1). Wisconsin county forest lands in particular are important at the higher habitat probability levels followed by national forests and private industrial forest (Fig. 7). The largest areas of unoccupied favorable habitat are in north central county forests and the Nicolet National Forest and Menominee Tribal Lands in northeastern Wisconsin (Figs. 6 and 7). Both of these areas also form linkages with adjacent large habitat areas in upper Michigan (Fig. 4). Spatially, each of these ownership categories is important because they correspond to a pattern of alternating favorable habitat patches of dif-

*Figure 3. Major landscape-scale habitat variables for the northern Wisconsin study region: land cover classes from USGS Land Use/Land Cover data (a) major land ownership classes (b), road density categories (c), and estimated mean deer density for the period 1979–1992 (d). Wolf pack territories (80% use areas) existing from 1979–1992 are shown on each map (black outlined ovoid polygons). White outlined polygons on a, c, and d are national forest boundaries from b. Double and triple black lines indicate major north–south two and four lane highways, respectively. Note maps a, b, and c contain a small portion of eastern Minnesota.*

*Figure 4. Probability of favorable wolf habitat for Minnesota, northern Wisconsin, and upper Michigan based on the logistic model of landscape characteristics. These results are based on single variable roads model. Road density is the predictor variable for this simpler model. Wisconsin wolf pack locations are shown. Blue-lined Minnesota wolf management units indicate primary wolf range and designated critical habitat for the wolf. White inclusions in Minnesota are large inland lakes.*

**Table 3. Area of habitat probability classes for the three-state region (northern Minnesota, northern Wisconsin, upper Michigan) from the logistic regression model and Fig. 1 and corresponding road density for each class.**

| *Probability Class (p)* | *Road Density (km/km²)* | *Minnesota* | | *Wisconsin* | | *Michigan* | |
|---|---|---|---|---|---|---|---|
| | | *Area (km²)* | *(%)* | *Area (km²)* | *(%)* | *Area (km²)* | *(%)* |
| ≥0.95 | 0–0.25 | 30,132 | 43.0 | 2120 | 3.6 | 13,032 | 31.0 |
| 0.75–0.94 | 0.25–0.38 | 12,552 | 17.9 | 6716 | 11.4 | 9972 | 23.8 |
| 0.50–0.74 | 0.38–0.45 | 7516 | 10.7 | 6028 | 10.2 | 6344 | 10.6 |
| 0.25–0.49 | 0.45–0.53 | 6384 | 9.1 | 5920 | 10.0 | 4448 | 10.6 |
| 0.10–0.24 | 0.53–0.60 | 4228 | 6.0 | 6264 | 10.6 | 2712 | 6.5 |
| <0.10 | >0.60 | 9328 | 13.3 | 32,100 | 54.3 | 5476 | 13.0 |

fering ownership from west to east across the state (Fig. 6).

## Discussion

### Wolf Population Dynamics

Deriving estimates of favorable habitat in a region being recolonized by the gray wolf poses particular difficulties. As a top predator, wolves are not habitat-specific and are limited by human-caused mortality, intraspecific strife, disease, starvation, and prey abundance (Mech 1970; Mech 1977; Keith 1983; Fuller 1989). Also, it cannot be completely assumed that unoccupied areas have been rejected by the species in a region still being colonized. We have found, however, that several landscape-scale characteristics appear to be good predictors of preferred habitat, areas that wolves appear to be occupying over others in the unsaturated landscape of northern Wisconsin. Both wolf packs and dispersing wolves occupy a similar arch-shaped portion of northern Wisconsin (Figs. 2 and 3). Our analysis suggests that wolves are selecting heavily those areas that are most remote from human influence, as defined largely by low road density. Landscape fractal dimension (*D*), an index of land cover patch boundary complexity, was also significantly lower in pack areas and was the only additional variable that improved the logistic model. This metric indicates that overall land cover patches within pack territories have simpler shapes than patches in nonpack areas. This may be an indicator of lower human presence and less landscape fragmentation. Many other significant variables relate to areas of low human contact or prey habitat (Table 1). Recently, radiocollared wolves have been shown to be moving from far northeastern Minnesota to upper Michigan and south central Wisconsin only to be killed by auto traffic (Mech et al. 1995). These are distances of hundreds of kilometers through unfavorable habitat, suggesting that although wolves are dispersing through such areas mortality is high.

Expansion of the Minnesota wolf population in the 1970s following legal protection was also largely limited to the lowest road and human density areas. However, recent evidence shows that wolves are now colonizing areas formerly thought to be unsuitable by these criteria

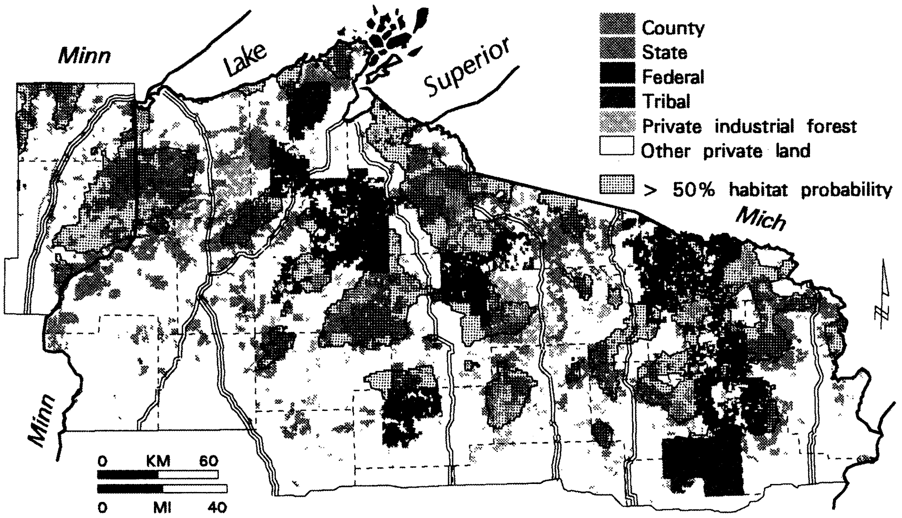

*Figure 6. Land management responsibility and favorable wolf habitat (p > 0.5 probability level from the single variable roads logistic model) for northern Wisconsin.*

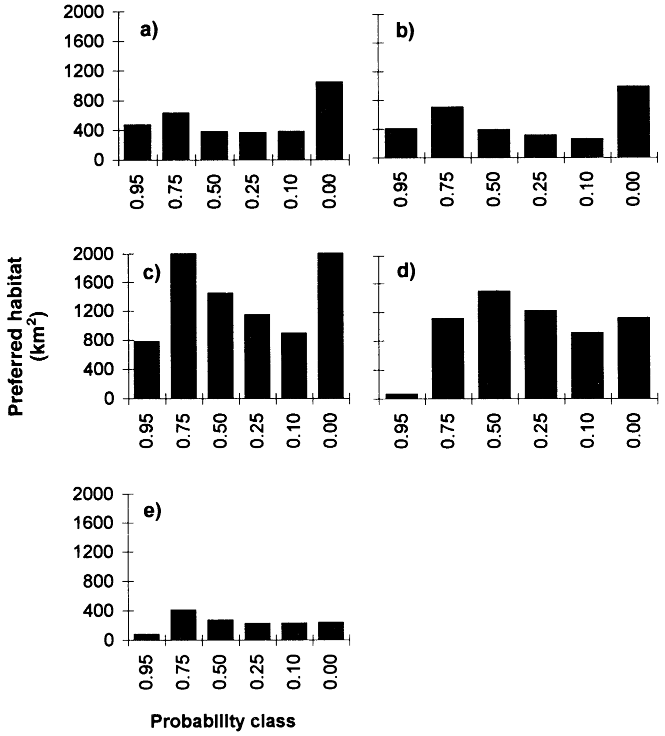

*Figure 7. Area of preferred habitat at various probability levels by major land ownership classes in northern Wisconsin state (a), private industrial forest (b), county (c), national forest (d), and tribal (e).*

(Fuller et al. 1992) both in Minnesota and elsewhere (Mech 1993*a*). If this is generally characteristic of colonizing and saturated wolf populations, our favorable habitat projections may be conservative. However, we believe several factors warrant consideration before assuming that northern Wisconsin wolves will follow the pattern of population growth that has occurred in Minnesota.

Prevailing conceptual population models apply imperfectly to species such as wolves. Wolves have a complex social structure and behaviors, and populations interact at large spatial scales (thousands of square kilometers). Only a dominant pair of family unit (pack) generally breeds (Mech 1970), making application of simple quantitative models for population viability analysis difficult (R. Haight, unpublished manuscript). Also, because they are a top carnivore, wolves are not habitat-specific to a vegetation or ecosystem type in the sense of sensitivity to a particular habitat structure. This is born out in our logistic model, where road density and not typical habitat variables such as forest type was the major predictor of wolf pack locations. Because of these factors, we are deliberate in describing the habitat areas generated by the model as favorable habitat, which implies a continuous gradient, rather than suitable habitat, which suggests an absolute class or binary map. In addition, habitat favorability is also a complex sum of selection, avoidance, and indirect effects (Y. Haila et al. unpublished manuscript).

Similarly, our habitat favorability map suggests an interpretation based on concepts of habitat fragmentation, but this too is based on a binary conception of suitable or unsuitable habitat. Although all habitat is heterogeneous at some scale (Haila et al. 1993), habitat for species such as the wolf is poorly described by traditional models of population patch dynamics (Johnson et al. 1992); this is true particularly at the spatial scale of wolf populations. At the local regional scale a wolf population appears to fit the metapopulation model as described earlier, where a number of breeding units (packs) interact. But at a larger scale wolf populations may in fact be better described by a source-sink model (Pulliam 1988; Hanski 1991). This may be particularly true when real landscapes, especially those under strong human influence, are considered (Pulliam et al. 1992).

For example, during 20 years of growth, the nearly saturated wolf population in Minnesota has been adjacent to the large wilderness area of northern Minnesota and Ontario, Canada. Further, our results show that the landscape distribution of favorable habitat in the Minnesota wolf region itself differs both in quantity and distribution from that in Wisconsin (Fig. 5). There is much more favorable habitat in Minnesota; spatially it forms the landscape matrix (Forman & Godron 1986) and has less favorable habitat interspersed usually along the margins of the region. In northern Wisconsin there is much less favorable habitat, and non-favorable areas form the matrix (Fig. 5). Wolves may now be able to colonize these less favorable areas in Minnesota and disperse into Wisconsin because of the saturated population and the source-sink dynamics, i.e., repeated dispersers are being produced, making successful colonization and maintenance more likely in less favorable areas despite a high cost (mortality). Recent reports of long distance dispersers from highly favorable habitat to unfavorable areas (Mech et al. 1995) also suggest that wolves from a larger portion of the Minnesota range, beyond the Minnesota-Wisconsin border region, are important in colonizing Wisconsin and Michigan.

## Regional Landscape Characteristics

Wolves moving further east into Wisconsin encounter less and more fragmented favorable habitat and a series of semipermeable barriers to movement in the form of development corridors along major north–south highways (Fig. 3c). The lack of established wolf packs in eastern Wisconsin, despite preferred habitat equal to the rest of the state, is consistent with this interpretation. Human-caused mortality operates in several ways, some of which are more direct and changeable than others. In areas of high human contact public attitudes are important and relate directly to deliberate, illegal killing of wolves (Thiel 1993). As wolves colonize regions of more fragmented wild areas, such as Wisconsin, conflicts such as livestock depredation may be higher than in Minnesota, prompting renewed negative human attitudes and a need for active wolf population control (Fritts et al. 1992). Unintentional killing such as vehicle collisions is more difficult to change and may increase with further highway development across northern Wisconsin. Indirect human-caused mortality may occur due to diseases, such as parvovirus that may enter the population from high populations of domestic pets (Mech & Goyal 1993; Wydeven et al. in press) or competition and/or diseases due to higher populations of species favored by more developed landscapes, such as coyote or fox.

Direct killing of wolves by humans is a large source of mortality for older wolves in regions of high human contact; however, disease and parasites, which can be higher in more developed landscapes, are a greater threat to reproductive ability and pup survival (Mech & Goyal 1993; Wydeven et al. in press). These factors combined, in a less-favorable landscape structure such as Wisconsin (a sink region), may mean that continued colonization or population maintenance is dependent on a high level of migration from a source population, in this case largely Minnesota. Under this scenario continued development and habitat loss in Wisconsin and further development along highway corridors may cause wolf population declines in the future, particularly if dispersal into the state decreases.

However, the landscape characteristics of upper Michigan and growing evidence of wolf movement into that area have the potential to eventually modify the scenario described above. Our analysis shows that upper Michigan has a much more favorable habitat than Wisconsin, and this favorable habitat constitutes the landscape matrix much like northern Minnesota (Fig. 5). Until recently, movement of wolves through Wisconsin into Michigan has been slow. Current evidence, however, suggests that this rate has been increasing as the Wisconsin wolf population grows (Hammill 1993). This is important for several reasons. If movement of wolves east from Minnesota declines, available habitat suggests that an established Michigan population can be large enough to act as a source for less favorable areas in Wisconsin. We suggest that Michigan wolves will be the more likely successful dispersers into currently unoccupied habitat in eastern Wisconsin (Fig. 4). However, our results and evidence of wolf behavior suggest that the population in the three-state region must be considered as a whole. Recent evidence of wolf movement over long distances from northern areas to central Wisconsin and upper Michigan (Mech et al. 1995) implies that the nearly saturated Minnesota population remains an important source of dispersers, a high proportion of which are unsuccessful. The regional habitat configuration and source-sink dynamics suggest that a reduction in the source population may leave some areas now occupied unsuitable. In the near term reduction of the Minnesota population too quickly could jeopardize recovery in Wisconsin and Michigan.

Similarly, our results and recent dispersal evidence suggest that a simple island/corridor habitat model applies poorly to the wolf, a species with low habitat affinity. Wolves readily move through a variable complex of habitat favorability where differential selection, avoidance, and mortality occur. These patterns may result in high mortality, but even a highly fragmented landscape is well explored by a growing wolf population. Wolf pack biology and behavior constantly produce new dispersers (Mech 1970). Favorable areas are found and rapid population growth is therefore possible even in fragmented landscapes, as long as the source population remains high and a constant source of colonizers is available.

The importance of landscape indices as significant descriptors of wolf habitat merits further attention (Table 2), as does the importance of fractal dimension ($D$) as an important variable in the predictive model. These indices are scale-dependent and must be interpreted in the context of the resolution and classification specificity of the land cover data from which they are derived. Because these indices appear to be useful in describing preferred habitat, this avenue should be pursued with finer level land cover data (Wolter et al. in press). These indices have the potential to be useful as easily obtained monitoring indicators of regional landscape change over time. If further work can interpret them more precisely in relation to wolf success, repeatable data sources such as satellite imagery could be used to monitor habitat quality over large areas. These data sources are generally available and landscape indices could be compared as predictors in different regions, such as the western U.S. Finally, this would provide spatial input data into simulation models of landscape change (Mladenoff et al. in press) that could be linked with a spatial metapopulation model to examine the consequences of land use and management changes for the wolf.

### Landscape-Scale Cooperative Management

We believe that human-caused mortality, either direct or indirect, will remain critical to the Wisconsin population for some time because it is a colonizing population in a matrix of less-than-favorable habitat. Continued development and habitat loss in a fragmented region such as Wisconsin could reverse current trends in population recovery. Road density will remain an important index of wolf success in this context. Currently, wolves in Wisconsin are limited to areas with overall pack area mean road density of 0.45 km/km$^2$. Pack core areas, which typically contain sensitive den and rendezvous sites, are located in areas that individually do not exceed a road density of 0.23 km/km$^2$. Basing a road density standard on the mean of overall pack areas may not always provide the security needed in smaller portions of the pack territory. Such remote core areas may be important for the success of a population attempting to colonize marginal habitat where an abundant, nearby source of dispersers is not available.

The largely habitat-independent nature and large-scale dynamics of wolf populations strongly suggest that cross-boundary, multiagency coordination can be important for successful wolf management, as for other aspects of landscape-scale management (Schonewald-Cox et al. 1992; Harris & Eisenberg 1989; Noss 1983). The evolving ecosystem management approach to biodiversity and sustainability directly highlights the perspective necessary for long-term management at regional scales for species such as the gray wolf (Salwasser et al. 1987; Overbay 1992; Crow et al. 1993; Noss 1993). Recent evidence for wolves as a controlling factor in forest food chains underscores the potential functional importance in ecosystems of species that have been eliminated by past human activity (McLaren & Peterson 1994). In regions of fragmented habitat such as Wisconsin, coordination will be required to balance control of the wolf population as well as protection (Mech 1993*b*, 1995). Spatial information such as we have developed in this study can identify priorities for multi-ownership, active management, and also indicate those areas of low-priority for the target species (Figs. 6 and 7). This work is an example of the use of long-term monitoring data and large-scale cross-boundary analysis. Such approaches are of crucial importance where many resource demands must be integrated in a regional context.

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