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Resource Selection of Recolonizing
Gray Wolves in Northwest Wisconsin

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Paul W. Keenlance

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PH.D. degree in Fisheries & Wildlife

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# RESOURCE SELECTION OF RECOLONIZING GRAY WOLVES IN NORTHWEST WISCONSIN

By

Paul W. Keenlance

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Fisheries and Wildlife

2002

UMI Number: 3075028



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## ABSTRACT

RESOURCE SELECTION OF RECOLONIZING
WOLVES IN NORTHWEST WISCONSIN

By

Paul W. Keenlance

The gray wolf *(Canis lupus)* has expanded numerically and geographically in eastern Minnesota and northwest Wisconsin since the late 1970s. Based on data collected from 40 wolves in 15 resident packs during 1992-2001, I examined resource selection by wolves at the following scales: territory selection on the landscape, resource selection within territories, and den placement. Road density within pack territories increased from a mean of 0.35 $km/km^2$ in packs established in 1992 to 1.09 $km/km^2$ in packs established in 1999. Mean road density in pack territories was lower (0.70 $km/km^2$) than in unused areas (1.43 $km/km^2$, $p < 0.001$). Forested wetland (14%), lowland shrub (13%), and aspen (P*opulus spp.*) (22%) were all more prevalent ($p < 0.10$ in all cases) in wolf pack territories than in unused areas (7%, 6%, and 9% respectively). County owned land comprised larger proportions ($p < 0.001$) of pack territories (61%) than unused areas (15%), while privately owned land were less prevalent ($p < 0.001$) in territories (19%) than unused areas (56%). A logistic regression-based habitat model including terms for road density, proportion of county and national forest land, and proportion of forested wetland in the area of interest correctly classified 14 of 15 pack territories and 13 of 15 unused areas outside of the area where the data used to develop the model was collected.

A compositional analysis indicated that forested wetland, lowland shrub, and aspen were the 3 most selected land cover categories at the landscape level of selection

while forested wetland, aspen, and oak were the 3 most selected land cover categories within territories. The proportion of wolf telemetry locations in buffers of 25 - 250 m around roads was lower ($p < 0.10$ in all cases) than the proportion of territories occupied by these same buffers. Wolf dens fell within an arbitrarily defined territory core occupying the inner 25% of the territory more often (78%) ($p = 0.002$) than random sites (35%). Roads occurred within 1212m of fewer ($p < 0.029$) dens (50%) than random points. This distance represented the average distance from a den that an alpha female was located during the study. Pine (8%) and shrub (6%) comprised higher proportions ($p < 0.10$ in both cases) of buffers around dens than random sites (3%, and 4% respectively), while lowland shrub comprised a lower proportion ($p = 0.068$) of buffers around dens (16%) than random sites (10%). A compositional analysis indicated that deciduous forest, aspen, and lowland shrub were the 3 most selected land cover categories at wolf den sites. Logistic regression indicated that location within the 25% inner core of a territory was the measured variable contributing the most to classification accuracy of a model delineating den sites versus random sites.

As the wolf population in Wisconsin continues to increase, wolves are establishing territories in areas with road densities that are both increasing and higher than past paradigms of wolf habitat suitability would predict. In spite of this, wolves are still establishing territories in areas with lower road density than unoccupied areas, and at least during daylight, are avoiding roads within territories. Wolves appear to select land cover and ownership category based on the avoidance of human disturbance and prey availability. Wolves also select den sites that tend to be centered in their territories.

# ACKNOWLEDGEMENTS

By the time that any of us reaches the end of a doctoral program, we owe a great deal to a great many individuals and organizations. Though I am sure that I will miss many whom I should be thanking, I need to express my heartfelt thanks to the following (in no particular order):

Funding for this project and my involvement in it was provided by the Wisconsin Department of Natural Resources Bureaus of Integrated Science Services and Endangered Resources, the Wisconsin Department of Transportation, The Michigan State University Fisheries and Wildlife Department, Biological Sciences and Integrated Studies in Biology programs, and the students of the Manawa, Wisconsin School district.

I would like to thank the members of my Doctoral committee for their enthusiastic contributions to this project, their time and their guidance: Thank you Drs. Gary Roloff, Michael Jones, Kay Holekamp, and David Lusch. I owe a special debt of gratitude to my major professor, Dr. Kelly Millenbah. Thank you for your guidance, your advice, your incredible level of commitment to all your students, the example you set as an educator and most of all, your patience. I could not have asked for a better advisor.

I must thank Dr. Eric Anderson and his graduate students, Dr. Tom Gehring, Doug Shelley, and Jacqui Friar. This project would not have been possible without the enormous amount of work they expended during their M.S. projects in the early stages of the H53 study. A special thanks to Dave Unger who contributed not only through his M.S. work on the H53 study, but who served as an invaluable field assistant during the last 2 ½ summers of my doctoral research. The aid provided by his knowledge of wolf ecology, the H53SA, and his skills as a biologist were exceeded only by the value of his friendship throughout my M.S. and my Doctoral degrees….I owe you buddy.

The personnel of the WDNR Gordon Ranger station and Douglas county forestry departments were unfailingly supportive of this project and aided greatly in its completion. The pilots of the WDNR Siren and Gordon hangers saved us countless hours of ground telemetry and kept me in contact with the wolves during the time each year when I was back in East Lansing. Thank you all very much for your efforts.

Thank you Drs. Daniel Trainer and Dave Staszak for the gentle nudge on a trip to Australia that got me started on the road to where I am now.

Heartfelt thanks to the ladies of team Millenbah for the humor, the unswerving support, the insight into the mysterious psyche of "the collective", and most importantly, for putting up with me with unwavering good humor. I could not have asked for better labmates.

Thank you Bruce (B. Eric) Kohn. From start to finish, you were the heart and soul of the H53 study. I can never put into words the level of gratitude I feel to you or the amount of respect I hold for you. I think that we all look for mentors in our lives. The first summer that we worked together I found mine. I have never met anyone who I respect more as a person and as a professional. Eternal thanks.

Nearly lastly, I must thank my family. They have been there for me in every segment of my life and though I am sure that they did not always understand why I was taking as long as I did to finally get out of school, my Doctoral program was no exception. I could not have done it without your love and support. No matter where I go

or what I do, you are the basis of all things good in my life. Mom, Dad, and Laura, thank you for who I am. I love you all.

And now, finally, though it may be a bit clichéd, and potentially not even overly professional, I thank the wolves of the H53SA for allowing the long ago dreams of a little boy to come true. If only I could have learned all that you had to teach.

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# CHAPTER 1

# INTRODUCTION AND DISSERTATION STRUCTURE

## INTRODUCTION

The gray wolf (*Canis lupus*) was listed as an endangered species in 1974 under the Endangered Species Act (ESA). Prior to 1974, the wolf was extirpated from its historical range in the lower 48 states with the exceptions of northeast Minnesota and Isle Royale in Lake Superior (Bailey 1978). At the time of listing, 550 - 650 individuals represented the entire United States population outside of Alaska (Mech 1970, Peterson and Page 1988, Fuller et al. 1992). Much of the reduction in wolf populations was due to human activities, which historically have been the major source of wolf mortality (Mech 1970).

With a reduction in human induced mortality due to the species listing under the ESA and an increasingly favorable public attitude toward wolves, the Minnesota wolf population steadily increased during the mid-1970s and 1980s (Fuller et al. 1992). With this increase in the number of individuals, dispersing wolves began to recolonize northwest Wisconsin in the late-1970s (Mech and Nowak 1981, Thiel and Welch 1982). At this time northwest Wisconsin offered an abundant prey base and large contiguous tracts of land unoccupied by wolves. Exploitation of these factors by wolves has led to a steady expansion of the wolf population both numerically and geographically over the past 25 years. In 2002, the Wisconsin population was estimated at approximately 270 individuals (A. P. Wydeven, Wisconsin Department of Natural Resources (WDNR), pers. comm.).

During this period of wolf population growth, wolves in the Great Lakes region have dispersed into a wide variety of habitats outside of traditional wilderness areas (Mech 1995). Expansion into these areas has increased the need for research examining wolf ecology in human dominated, non-wilderness or semi-wild landscapes. Past research in these areas has focused on relating wolf resource selection to landscape features including land cover, road density, prey base, and land ownership patterns (Mladenoff et al. 1995, 1999).

**The importance of examining resource selection at differing scales**

Mladenoff et al. (1995) examined resource selection at the landscape level (within a 171,000 $km^2$ study area) using the geographic information system (GIS) ARC/INFO to compare the landscape attributes of Wisconsin wolf pack territories to similarly sized unused areas. This study found that road density was the best predictor of wolf territory placement (Mladenoff et al 1995). Wolf pack territories were also found to contain higher percentages of publicly owned land, mixed conifer-hardwood forest, and forested wetlands than unused areas (Mladenoff et al. 1995). Human population density was also found to be lower in pack territories than in unused areas (Mladenoff et al. 1995).

Though the studies by Mladenoff et al. (1995, 1999) provide useful information about wolf habitat use in a semi-wild landscape, they examined resource selection at only one scale. Mladenoff et al. (1995, 1999) examined resource selection at the level of territory placement on the landscape (i.e., where territories occur and why). Resource selection occurs hierarchically from the geographic range of a species, to individual home ranges within this geographic range, to use of general features within the home range, to the selection of particular elements within the general features (Manly et al. 1993). This hierarchy for wolves proceeds from selection of territories, to the use of particular habitat types within territories, to the selection of specific locations such as den sites within habitat types or portions of the territory. The criteria for resource selection may differ at each level (Johnson 1980, Weins 1981). It has been suggested that as a general rule, researchers should consider studying selection at more than one scale (Manly et al. 1993). Thus, management guidelines based on research conducted at one scale of resource selection may be inadequate. By examining resource selection at multiple scales based on the organism's biology, a more complete understanding of a species' resource requirements can be gained.

The establishment and location of wolf pack territories across a landscape results from the cumulative effects of factors often beyond the control of individual land managers. However, the activities of individual land mangers undoubtedly influence the landscape's potential to support wolves. These activities typically involve the manipulation of habitat and or human activity at a scale corresponding to individual territories. Thus, analyses of resource selection at multiple scales (i.e., selection of territory within the landscape, differential use of habitat within the territory, and (den) site selection within the territory) is necessary.

To facilitate these types of analyses, land cover maps with a resolution that corresponds to the finest scale of analysis must be used. For example, Mladenoff et al. (1995) evaluated the regional placement of pack territories using a land cover map based on a 16 ha resolution satellite image. This resolution was sufficient for the coarse analysis of territory placement. In contrast, for the evaluation of habitat use and den site placement within individual territories, a finer resolution is required. Mladenoff et al.

(1995) acknowledged this and state "indices of landscape characteristics...must be interpreted in the context of the resolution and classification specificity of the land cover data from which they are derived."

**Changes in resource selection as population density increases**

Two assumptions of resource selection theory are that a species will select resources that best satisfy its life requirements and that higher quality resources will be selected first (Manly et al. 1993). If these assumptions are valid, the first pack territories established in an area will contain the highest quality habitat and subsequent territories will contain lower quality habitat. This process appears to be occurring in northwest Wisconsin where local wolf populations have been intensively monitored since 1992 (Kohn et al. 1997). The number of packs in this area has increased from 3 in 1992 to 15 in 2001.

Since the mid-1980's road density has been the most commonly used measure of habitat quality for wolves, with higher road densities associated with lower quality habitat (Mech 1995). Several of the pack territories within northwest Wisconsin are in areas with road densities identified as unsuitable in past studies (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Mladenoff et al. 1995). Also, in contrast to the findings of Mladenoff et al. (1995), where no pack territories were bisected by major federal or state highways, 3 pack territories in this area are bisected by U. S. Highway 53 (H53). The establishment of territories (if persistent and productive) in areas of what is generally considered marginal or unsuitable habitat (e.g., higher road densities, more human activity, more open land cover), may indicate that our perceptions of suitable habitat within the Great Lakes region need to be revised.

In the past decade, wolves have been documented in a variety of non-traditional settings. For example, wolves in Spain have persisted in predominantly agricultural areas with human densities of up to 200 people/km$^2$ (Vila et al. 1993). Fuller et al. (1992) found that wolves are occupying areas of higher road densities than any previously reported in Minnesota. Mech (1995) also reported that the range of wolves in the Great Lakes region continues to include new areas that are "much more open, accessible, and heavily populated."

Although recent research has provided valuable insight into wolf habitat associations at the landscape level, including a density-dependent component in this analysis can increase our understanding. An improved understanding of changes in wolf resource selection as the population in the Great Lakes region continues to expand is important for several reasons. If wolves are adapting to successfully use areas that have been regarded as marginal quality or unsuitable habitat (e.g., higher road densities, more human activity, differing land covers), present estimates of carrying capacity (Mladenoff and et al. 1997) in Wisconsin (380) may need to be updated. With state management agencies in the Great Lakes region striving to develop wolf management guidelines and population goals for the time period after delisting from the ESA, accurate estimates of biological carrying capacity are increasingly more important. Another need to accurately quantify and map wolf habitat relates to the potential for increasing conflicts between wolves and human activities as the number of wolves in the area continues to grow. Though wolves may be successfully colonizing areas that in the past would have been viewed as unsuitable, the higher level of human activity in many of these areas increases the likelihood of conflict between wolves and humans.

This study examined changes in resource selection over a 9-year period (1992-2001) encompassing a period of recolonization and geographic expansion by gray wolves in a semi-wild landscape. Resource selection was examined at the following scales: territory selection on the landscape, within the territory, and at den sites.

The information gained from this study will increase our understanding of gray wolf ecology in semi-wild landscapes and provide several benefits to resource professionals managing areas within current or future wolf range. It will aid in more accurately estimating biological carrying capacity within a given region. Appropriate population objectives cannot be set by management agencies without reasonable estimates of biological carrying capacity. Also, a greater understanding of resource use in this region will allow us to more accurately predict areas of potential conflict between wolves and humans as wolves expand into more developed areas. Results of this study may also be useful for assessment of wolf habitat potential in the northeastern United States. This area is generally regarded as the next potential area for gray wolf recolonization or reintroduction. The northeastern United States has ecosystems, land use, and amounts of favorable habitat more similar to the Great Lakes region than to areas examined in most past studies dealing with gray wolf ecology (Mladenoff and Sickley 1998). These similarities indicate that the findings from this study should be more useful in the delineation of wolf habitat (and resultant management decisions) in the northeast United States than the results of past studies in other portions of gray wolf range.

**DISSERTATION STRUCTURE**

This Dissertation is divided into five chapters:

**Chapter 1**: Introduction and Dissertation Structure

**Chapter 2:** Pack Territory Placement and Habitat Characteristics of a Recolonizing Population of Gray Wolves in Northern Wisconsin

**Chapter 3:** Cover Type and Land Ownership Selection of Recolonizing Gray Wolves in Northwest Wisconsin

**Chapter 4:** Gray Wolf Den Site Characteristics in Northwest Wisconsin: Additional Data

**Chapter 5:** Synthesis and Future Research Direction

Note: Images in this dissertation are presented in color.

## STUDY AREA

This research was conducted in the U. S. Highway 53 study area (H53SA) in portions of Douglas, Washburn, Burnett, Bayfield, and Sawyer counties in northwest Wisconsin and Pine county in east-central Minnesota (Figure 1). This study area was established by the WDNR in response to a project to expand H53 from 2 lanes to 4 lanes in 1992. This expansion took place along a 44-mile section of the highway from Trego in the south to Hawthorne in the north. The final 6-mile section of this expansion was completed in the summer of 1999. This stretch of highway passes through established wolf territories and bisects the primary wolf dispersal corridor from Minnesota into Wisconsin (Kohn et al. 1997). This prompted the Wisconsin Department of Transportation (WDOT) to contract with the WDNR to conduct a study examining the effects of the expansion on wolves in the area.

The landscape in the H53SA is primarily a mixture of upland mixed deciduous forest (*Acer rubrum, Quercus rubra, Q. alba, Betula papyrifera*), aspen (*Populus tremuloides, P. grandidentata*), grasslands (*Pteridium aquilinum, Hieracium aurantiacum, Phleum pratense, Poa compressa, P. pretensis*, Curtis 1992), idle pasture, mixed upland deciduous/coniferous forest (*Acer rubrum, Quercus rubra, Q. alba, Betula papyrifera, Pinus banksiana, Pinus strobus, Picea glauca*), wetland deciduous shrubs (*Alnus rugosa*, immature *Fraxinus pennsylvanica*), wetland forest (*Thuja occidentalis, Picea mariana, Fraxinus nigra, Ulmus rubra*), emergent/wet meadow and bogs (*Scirpus spp., Sphagnum spp*; Curtis 1992) and agricultural lands. The topography in this area is that of a rolling plain (Curtis 1992).

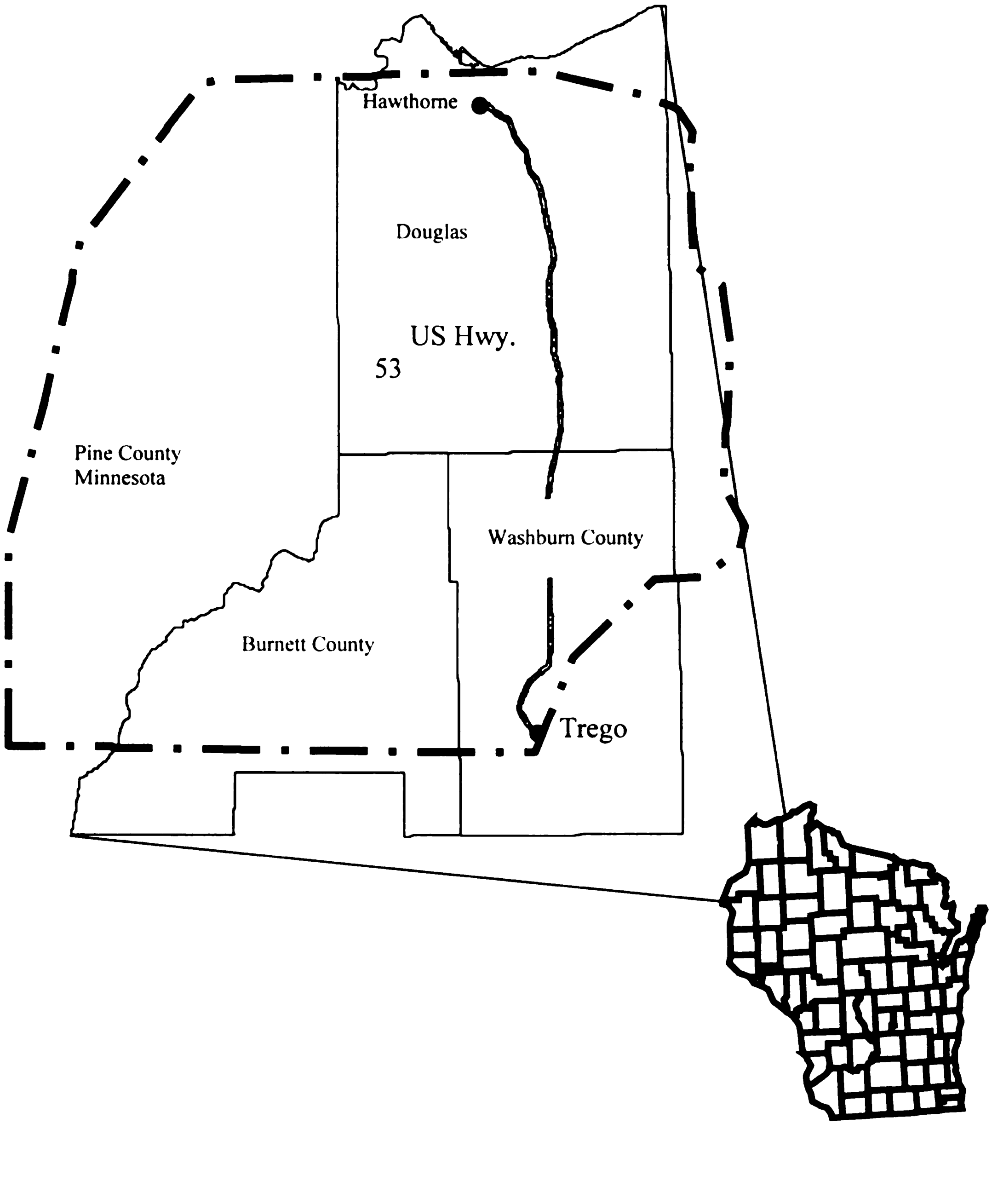


Figure 1. The Highway 53 Study Area (H53SA) in northwest Wisconsin and east-central Minnesota.

Available prey within the H53SA consists largely of white-tailed deer (*Odocoileus virginianus*) and beaver (*Castor canadensis*), both of which have been shown to be primary food sources for wolves in the Great Lakes region (Mandernack 1983, Fuller 1989). Estimates of deer densities within the H53SA have ranged from 9.7 deer/km$^2$ to 13.5 deer/km$^2$ (mean = 11.68 deer/km$^2$,) since 1995 (B. E. Kohn,WDNR, pers. commun.). Beaver are also common in the H53SA, with 1998 helicopter surveys in northwest Wisconsin estimating densities at 0.61 active beaver colonies/km$^2$ (B. E. Kohn, pers. commun.).

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# CHAPTER 2

# PACK TERRITORY PLACEMENT AND HABITAT CHARACTERISTICS OF A RECOLONIZING POPULATION OF GRAY WOLVES IN NORTHERN WISCONSIN

## INTRODUCTION

Two major assumptions of resource selection theory are that a species will select resources that will best satisfy its life requirements and that higher quality resources will be selected first (Manly et al. 1993). If these assumptions are valid for wolves, the first pack territories established in an area will contain the highest quality habitat and subsequent territories will contain lower quality habitat. This process may be occurring in northwest Wisconsin where local wolf populations have been intensively monitored since 1992 (Kohn et al. 1997). The number of packs in this part of the state has increased from 3 in 1992 to 15 in 2001 and the habitat characteristics of pack territories established early in this period appear to differ from those of territories established later in the recolonization (B. E. Kohn, pers. commun.).

Although the estimated number of wolf packs in Wisconsin has varied greatly since their recolonization of the state (2 in 1979, 52 in 2001, A. P. Wydeven, pers. commun.), no examination of density-dependent changes in resource selection has been conducted. Due to the strong territorial behavior of wolves, previously established packs will limit the choice of potential territory locations for additional packs within an area (Mech 1970). Thus, only the first pack to establish a territory in Wisconsin was unlimited (in relation to intraspecies strife) in its choice of territory location. This limitation affects wolf pack territory placement and our perceptions of habitat selection and suitability. An examination of the characteristics of pack territories established sequentially throughout recolonization will provide insight into whether the attributes of areas being colonized by wolves are changing as the wolf population and pack density increase.

Past research in the Wisconsin has focused on relating wolf resource selection to landscape features including land cover, road density, prey base, and land ownership patterns (Mladenoff et al. 1995). Mladenoff et al. (1995) examined resource selection at the landscape level (within a 171,000 $km^2$ study area) using the geographic information system (GIS) ARC/INFO to compare the landscape attributes of Wisconsin wolf pack territories to similarly sized unused areas. This study found that road density was the best predictor of wolf territory placement (Mladenoff et al. 1995). Wolf pack territories were also found to contain higher percentages of publicly owned land, mixed conifer-hardwood forest, and forested wetlands than unused areas (Mladenoff et al. 1995). Human population density was also found to be lower in pack territories than in unused areas (Mladenoff et al. 1995).

Although past research has provided valuable insight into wolf habitat associations at the landscape level, our understanding can be increased by examining changes in resource use and selection as wolf populations and pack density increase. An improved understanding of changes in wolf resource selection as the population in the Great Lakes region continues to expand is important for several reasons. If wolves are adapting to successfully use areas that have been regarded as marginal quality or unsuitable habitat [e.g., higher road densities (Merril 2000), more human activity (Vila et al. 1993), differing land covers (Mech 1995)], present estimates of carrying capacity

(Mladenoff and Sickley 1998) in the region may be low. With state management agencies in the Great Lakes region striving to develop wolf management guidelines and population goals for the time period after delisting, accurate estimates of biological carrying capacity are increasingly important. Another need to accurately quantify and map wolf habitat relates to the potential for increasing conflicts between wolves and human activities as the number of wolves continues to increase. Although wolves may be successfully colonizing areas that in the past would have been viewed as unsuitable, the higher level of human activity in many of these areas increases the likelihood of conflict between wolves and humans.

I conducted an analysis of the characteristics (land cover category, road density, land ownership category, and landscape pattern) of wolf pack territories established between 1992 and 1999 in northwest Wisconsin. My first objective was to examine whether the characteristics of pack territories changed based on the year of pack initiation (and the related difference in the number of packs in the study area). The assumption underlying this analysis was that packs establishing territories later in the study would be more limited in where they could place territories and might be forced to establish territories in lower quality habitat. This analysis provides insight into whether pack territory characteristics are changing as the wolf population and resultant wolf pack density increases. My second objective was to examine differences in the characteristics of wolf pack territories compared to corresponding unused areas. This examination provides information on what habitat factors are influencing the placement of wolf pack territories. My final objective was to use the data from the comparison of territories and unused areas to develop a logistic regression-based GIS model to predict the occurrence and spatial pattern of suitable wolf habitat and resulting wolf pack territory placement. This model, while developed from data collected only in the H53SA, allowed me to generate a habitat-based carrying capacity for wolves in the entire area I judged to be primary wolf range (PWR) [(zone 1 in Wisconsin wolf management plan (WIDNR 1999)] (Figure 2.1) in Wisconsin.

## METHODS

### Capture, Handling, and Radiotelemetry

Wolves were trapped by WDNR personnel using modified #14 Newhouse leg-hold traps (Schultz et al. 1996) May-August 1992-2000. Captured wolves were immobilized using a mixture of ketamine hydrochloride/xylazine hydrochloride administered with a jabstick. Any trap-related injuries were treated, blood samples were taken, an injection of antibiotics was administered, and animals were weighed. Animals > 15kg were also fitted with radio collars (Telonics Inc., Mesa, Arizona) and uniquely numbered ear tags. Yohimbine was administered as a reversal agent for the xylazine hyrdrochloride and wolves were monitored until they could move away from the trap site under their own power.

Radio-collared animals were located 1-5 times per week using telemetry from fixed-wing aircraft (Ballard and Dau 1983, Fuller 1989) or a vehicle-mounted 5-element Yagi directional antenna until radio failure, death of the animal, or a permanent movement out of the study area. Locations were collected from January 1992 – April 2001. The majority (>95%) of locations were collected during daylight hours and a minimum of 3 bearings were collected for each location. Triangulations for locations collected on the ground where solved using a Lenth estimator (Lenth 1981) in the

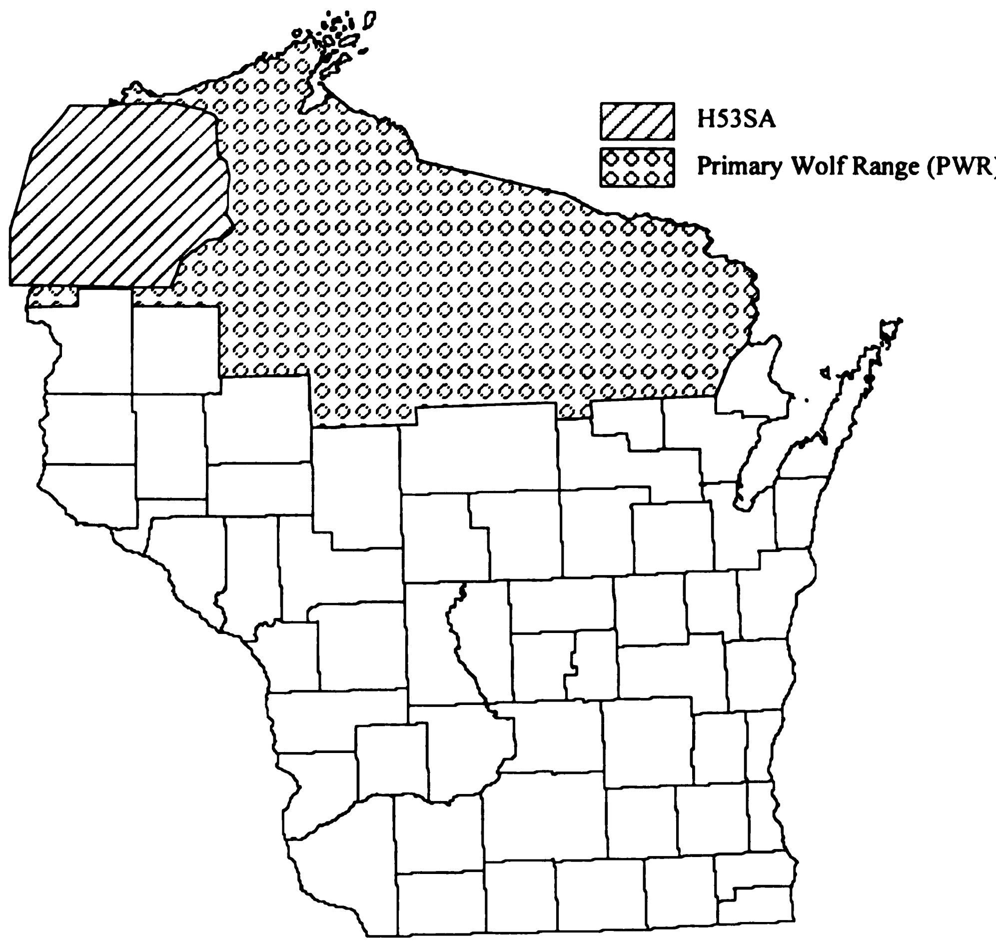


Fig 2.1 Location of the Highway 53 Study Area (H53SA) within primary wolf range (PWR) in Wisconsin.

program Locate II (Pacer, Turo Nova Scotia, Canada). Shelly and Anderson (1995) found no significant difference between the accuracy of aerial and ground locations in the study area using the same telemetry techniques and equipment, so locations were pooled for territory estimation and resource selection analyses. Locations obtained for an individual wolf were at least 4 hours apart to maintain independence (Reynolds and Laundre 1990). Date, time, Universal Transverse Mercator (UTM) coordinates, ear tag number, and pack were recorded for each telemetry location. Animals were classified as belonging to individual packs based on trapping location and movement patterns after release.

Extensive track surveys were conducted each winter throughout the study area to estimate the number of individuals in each pack and to locate any newly formed packs. This effort as well as additional track searching and howling surveys each summer allowed for the identification and monitoring of all resident pup producing packs within the study area throughout the study. Knowing where all pack territories in the H53SA were was crucial in the analysis or territories versus unused areas. Efforts were also made to maintain at least one radio collared animal in each pack at all times, although there were periods when this was not possible.

**Territory Boundary Estimation**

Pack territory boundaries were estimated using a fixed kernel method (Worton 1989) based on an 80% isopleth using the animal movement analysis extension (Hooge and Eichenlaub 1997) in ArcView [Environmental Systems Research Inc. (ESRI), Redlands CA]. A minimum of 30 locations (Fuller and Snow 1988, Seaman et al. 1999) was used in estimating territory boundaries. Only territories of packs which had been monitored for at least one year and which had produced pups were included in the analysis. All locations from all radio-marked animals within a pack during the course of the study were used in territory boundary estimation.

**Evaluation of Changes in Territory Characteristics With Increasing Population and Territory Density**

Variables potentially affecting wolf habitat suitability based on my understanding of current paradigms of wolf habitat use and personal experience were determined for each pack territory and corresponding unused area. These variables were: road density, the proportion of each pack territory classified as forested wetland, aspen, lowland shrub, shrub, and agricultural; the proportion of each pack territory under private, county, state, and industrial forest ownership; and 5 measures of landscape pattern [weighted mean fractal dimension (Mandelbrodt 1977), mean patch edge, mean patch area, edge density, and Shannon's diversity index (Shannon and Weaver 1949)].

Road density was calculated using a line coverage based on U. S. Geologic Survey 1:100,000 scale Digital Line Graphs in ArcView. Two measures of road density were calculated. The first was based on all roads and trails in the area (hereafter roads and trails). The H53SA contains an extensive system of trails that are heavily traveled by all-terrain vehicles during the summer and snowmobiles during the winter. The current paradigm is that increased human access provided by higher road density into an area is the mechanism that causes road density to be a useful indicator of wolf habitat suitability (Fuller et al. 1992, Mladenoff et al. 1995). It is probable that the system of trails in the H53SA provides additional access into otherwise roadless areas and I chose to include trails in this measure of analysis. The second measure of road density included all parts of the road network other than trails, hereafter referred to as "roads only". This coverage may have included more unimproved forest roads than the one used by Mladenoff et al. (1995, 1999) in the region, but I judged it to be an equally appropriate metric for two reasons. This measure of road density is easily derived from existing GIS data layers and this widespread availability increases its utility to resource managers. Road density for both measures of roads was determined by intersecting a roads coverage with the 80% use isopleths representing wolf pack territories and calculating the straight-line road distance and area of the pack territory. All road densities were calculated as $km/km^2$.

The proportion of each pack territory classified as forested wetland, aspen, lowland shrub, agricultural, and shrub within the WDNR's GIS WISCLAND land cover classification system (http://www.dnr.state.wi.us/org/at/et/geo/data/wlc.htm) was also calculated. These proportions were determined by intersecting the WISCLAND land cover layer with territory isopleths to calculate the area of each territory in a land cover category divided by the total area of the territory. Mladenoff et al. (1995) identified forested wetland as compromising a higher proportion of wolf pack territories than corresponding unused areas and agricultural lands as comprising lower proportions of pack territories than unused areas. I found that both forested wetland and aspen were highly selected by wolves at both the landscape and within-territory level of analysis (Chapter 3 this document). This examination also revealed that lowland shrubland was selected and that agricultural lands and shrub were avoided by wolves at the landscape level of analysis. Based on these findings, I believed that these cover types could serve as reasonable measures of habitat suitability and as metrics to differentiate between wolf pack territories and unused areas.

I also examined the proportions of county owned, privately owned, state owned, and industrial forest land in pack territories. Privately owned land comprised a lower proportion and county owned land comprised a higher proportion of pack territories than corresponding unused areas in the study by Mladenoff et al. (1995). Other publicly owned lands including state owned were also found to be important to wolves by Mladenoff et al. (1995). Industrial forest land was found to be important in some pack territories by Mladenoff et al. (1995) and was also observed to comprise large portions of some pack territories the H53SA (Chapter 3 this document). Based on these findings, I believed that the four land ownership categories that I included in this analysis would serve as useful indicators of wolf habitat suitability.

It has been suggested that landscape indices may be useful as descriptors of wolf habitat (Mladenoff et al. 1995), therefore the following measures of landscape pattern where also included in the analysis: 1) weighted mean fractal dimension, an index (scaled 1-2) of patch boundary complexity related to patch size (Mandelbrodt 1977), 2) mean patch edge, 3) mean patch area, 4) edge density, and 5) Shannon's diversity index (Shannon and Weaver 1949). These spatial indices were generated using the Patch Analyst extension (Elkie et al. 1999) within ArcView.

Mean values of measured landscape variables were generated for each pack territory. Pack territories were grouped based on the year of pack establishment. Packs present in the study area before 1992 were classified as having been established in 1992. The means for each variable were grouped by year of territory initiation and analyzed with a one-way ANOVA (Zar 1999) ($\forall = 0.10$) to determine if pack territory composition changed as decreasing amounts of the H53SA were available for colonization by new packs. A number of unused areas equal to the number of pack territories were generated for each year of the analysis to allow comparisons between habitat characteristics in areas occupied by wolves and areas that were not occupied by wolves. For example, there were 3 pack territories established in 1999, so 3 corresponding unused areas were generated and included in the analysis for 1999. These areas were the same size as the average size of pack territories in the year of interest and where randomly located within the H53SA with the restriction that no part of the random area could intersect a pack territory. These areas were generated using the pixel aggregation process described by Roloff and Haufler (1997) and each was iterated 5 times to avoid potential bias due to the shape or position of the random area. Calculated values for measured variables were averaged across all 5 iterations of a random site before comparison with used sites. The same landscape variables measured in pack territories were also measured in corresponding random areas and means for each variable were derived. The means of pack territories and unused areas were compared using a Wilcoxon rank-sum test ($\alpha = 0.10$) (Zar 1999).

**Development of Landscape Level Habitat Suitability Model**

All variables examined in the year of initiation analysis were considered for inclusion in a logistic regression analysis (Zar 1999) differentiating between pack territories and unused areas. All variables considered for inclusion in the analysis were checked for colinearity using a Pearson correlation analysis before they were entered into the model. The final choice of which variables to include in the logistic model was based on observed differences in mean values between pack and unused territories, a forward selection procedure, and knowledge of wolf ecology gleaned from relevant literature and personal experience. Proportions of area within pack territory or unused area classified as forested wetland and county owned lands as well as the road density (km/km$^2$) of the roads only coverage were selected for inclusion in the logistic model.

One adjustment was made to the land ownership category values input into the logistic model. There is no national forest land in the H53SA, but based on past predictions of wolf habitat suitability in Wisconsin (Mladenoff et al. 1995, 1999) I believed that national forest land would contribute to quality habitat for wolves. Since I planned on testing the logistic model in portions of the state that included national forest, I needed to assign a value for national forest land within the model. The best method of selecting a value for national forest land was to assign it the same value as the most similar land ownership category that was present in the H53SA that had been assigned a value by the logistic regression procedure. The land ownership category present in the H53SA with the most similar management regime and structure to national forest was county owned. Based on this, I assigned the same logistic-based value (coefficient) to national forest land as was assigned to county owned lands by the logistic regression procedure.

Logistic models including all possible combinations of proportion of forested wetland, proportion of county owned land and road density were compared using maximum likelihood goodness-of-fit and classification accuracy. The classification accuracy of the final logistic model was also tested against 15 pack territories and 15 unused areas outside of the H53SA, which had not been used in developing the logistic model.

Once the final model had been selected it was programmed into ARC/INFO and tested by comparing areas predicted as being favorable wolf habitat with known wolf pack territories in PWR in Wisconsin. This was accomplished by creating coverages of both forested wetland and county owned lands (grouped with national forest land) in ARC/INFO and calculating the proportion of these two variables across the landscape. This same process was used to determine road density across the landscape.

The resulting values for each 30 m pixel across the landscape were entered into the logistic regression model within the Grid module in ARC/INFO. This process yielded an output GIS coverage with "habitat values" between 0 and 1 for each 30 m pixel across the landscape (0 = the lowest quality wolf habitat and 1 = the highest quality habitat). These values were converted to 0 – 100 to facilitate running the pixel aggregation procedure described by Roloff and Haufler (1997). This process simulated the placement of wolf pack territories across PWR in Wisconsin based on both the quality of habitat as predicted by the logistic model and the spatial arrangement of that habitat. This process randomly assigned seeds or starting pixels across PWR. It subsequently aggregated pixels until the area being selected equaled the average size of wolf pack territories analyzed in the H53SA (119 $km^2$). A minimum habitat value for inclusion in an area being selected is set within this process. Pixels with habitat values below this lower limit may be included in simulated territories, but these pixels will not contribute toward the preset target size (average wolf pack territory size in this case). This acknowledges the fact that while low quality habitat may be included in a territory, it will contribute little to the value of the territory, and therefore territories comprised of low quality habitat will generally be larger than territories comprised of high quality habitat.

The following guidelines were incorporated into this process. Seeds were not placed in pixels with habitat values less than 10 to recognize that there is some lower bound of habitat quality below which wolves would not attempt to establish a territory. The process was set to generate 50 pack territories since this is the approximate number of wolf pack territories estimated in PWR in the state. I set a lower habitat value limit of 30 for a pixel to contribute to the size of the area aggregated by the procedure. The level of this lower limit was developed by calculating the average habitat value for pixels within actual wolf pack territories as plotted by the WDNR (68.3) and subtracting one standard deviation (38.7) from this value. I hypothesized that wolves would expand into lower quality habitat as the population and pack density increased and the minimum habitat value for this analysis should be set lower than means within currently occurring pack territories.

The pixel aggregation process was iterated 10 times and the number of times each pixel across PWR was included in a simulated pack territory was calculated. This created a frequency distribution with values ranging from 0-10. This coverage was used to compare the probability of areas occupied by wolves being selected by the pixel aggregation procedure to the probability of areas not occupied by wolves being selected. The mean and frequency distributions of the pixel values (from the 0-10 distribution output by the pixel aggregation procedure) of areas occupied by wolves and areas not occupied by wolves were compared using a Wilcoxon rank-sum test and a Kolmogorov-Smirnov test ($\alpha = 0.10$). These tests were conducted to determine if the combination of the logistic regression model and the pixel aggregation technique were actually differentiating between favorable and unfavorable wolf habitat in a non-random manner.

I assumed that if the pixel aggregation procedure was working correctly, the likelihood of a pixel being selected (mean pixel value from the 0-10 frequency distribution) within actual wolf pack territories should be higher than in areas that wolves are not using and that the frequency distribution of individual pixel values should also be different.

The areas selected by the pixel aggregation technique were also converted into a GIS coverage and used to clip the original coverage of habitat values derived from the logistic regression model. The pixel values from this coverage were compared to the pixel values from a coverage created by clipping the same logistic-generated habitat value coverage with a coverage of actual wolf pack territories using a 2 sample t-test (∀ = 0.10). This was done to determine if the combination of the logistic regression model and the pixel aggregation technique was selecting areas that are actually being used by wolves. I assumed that if this combination was working as planned, the habitat values in pixels within areas selected by the pixel aggregation procedure should not be different than those in areas actually occupied by wolves.

The final step in this analysis was to run the pixel aggregation technique across PWR with an initial number of seeds set to 500 and set to aggregate pixels to the average size of wolf pack territories observed in the H53SA. This process saturated the landscape with simulated territories and provided an estimate of the maximum number of wolf pack territories possible within PWR based on the logistic model developed from my data in the H53SA. This estimated maximum number of packs was combined with the average pack size of wolves in Wisconsin (4.3 individuals, Wydeven and Cervantes 1997) to estimate a carrying capacity for PWR. Past estimates of habitat-based carrying capacity (Fuller et al. 1992, Mladenoff and Sickley 1998) have been developed by estimating the total area of suitable or favorable habitat and dividing that by the average size of wolf pack territories and interstices. This approach fails to take into account the spatial arrangement of favorable habitat and may over estimate carrying capacity. For example, if there is enough favorable habitat for 10 territories in an area but it is broken up into 20 patches, there will almost certainly be less than 10 territories established in the area. Including the spatial pattern of favorable habitat when estimating carrying capacity yields a more accurate estimate.

**RESULTS**

During the course of the study, 8,303 telemetry locations from 40 wolves in 15 packs were collected and analyzed. Three packs were present in the H53SA when the study began in 1992. Additional packs were detected in 1993 (2), 1995 (4), 1997 (3), and 1999 (3). This led to 5 distinct years of pack initiation, which were used in analysis of changes in pack territory characteristics with increasing territory density across time. There was a general trend of packs established earlier in the study being located further west in the study area (nearer the core Minnesota wolf population). Packs established later in the study tended to be located further east (Figure 2.2). Average pack territory size based on the 80% use isopleth was 119.1 $km^2$ (range 9.5- 347.1 $km^2$).

**Evaluation of Changes in Territory Characteristics With Increasing Population and Territory Density**

Pack territories established later in the study had higher road density than those established early in the study (Table 2.1, Figure 2.3). Mean road densities calculated using roads and trails ranged from 0.67 $km/km^2$ in packs established in 1992 to 1.37 $km/km^2$ in packs established in 1999. Mean road densities calculated excluding trails

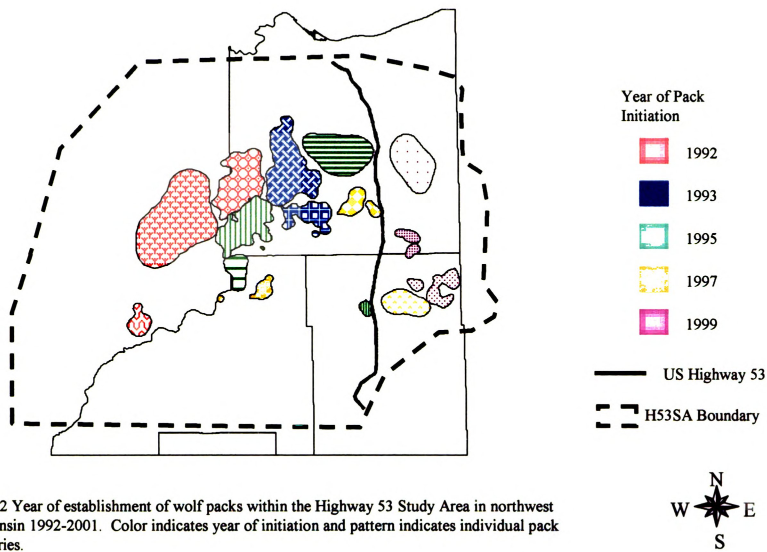


Fig. 2.2 Year of establishment of wolf packs within the Highway 53 Study Area in northwest Wisconsin 1992-2001. Color indicates year of initiation and pattern indicates individual pack territories.

Table 2.1 Mean road density within wolf pack territories established in different years calculated from coverages using roads and trails and roads only in the Highway 53 Study Area in northwest WI 1992-2001.

| | roads and trails density (km/km$^2$) | | roads only density (km/km$^2$) | |
|---|---|---|---|---|
| Year of Establishment (n) | $\bar{x}$ | (SE) | $\bar{x}$ | (SE) |
| 1992 (3) | 0.67 | (0.12) | 0.35 | (0.17) |
| 1993 (2) | 0.99 | (0.15) | 0.54 | (0.21) |
| 1995 (4) | 0.90 | (0.11) | 0.67 | (0.15) |
| 1997 (3) | 1.15 | (0.12) | 1.01 | (0.17) |
| 1999 (3) | 1.37 | (0.12) | 1.09 | (0.18) |
| All packs (13) | 1.09 | (0.11) | 0.70 | (0.13) |

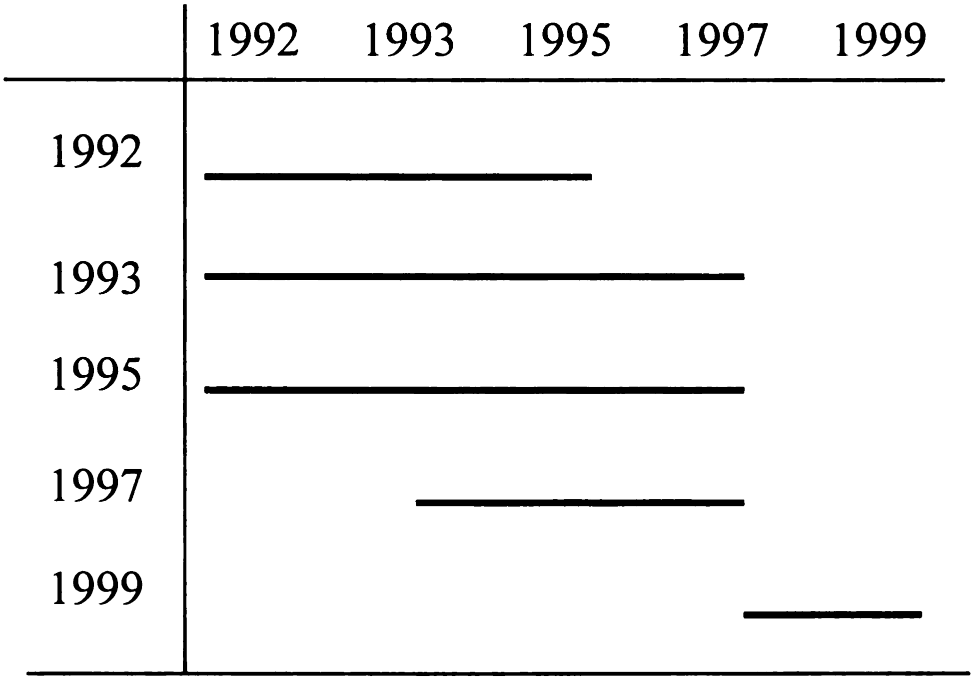


Fig. 2.3. Differences in road density within wolf pack territories established in Different years in the Highway 53 Study Area in northwest Wisconsin 1992-2001. Mean road density calculated using roads and trails was not different within pack territories established in year groups connected by a line ($p > 0.10$ from Fisher LSD multiple comparison test). Groupings were the same when road density was calculated using roads only ($p > 0.10$ from Fisher LSD multiple comparison test).

from the analysis ranged from 0.35 km/km$^2$ in packs established in 1992 to 1.09 km/km$^2$ in packs established in 1999 (Table 2.1).

State owned land comprised a higher proportion ($p < 0.001$) of territories established in 1992 (49%) than in territories established in all other years of the study ($\alpha = 0.10$ for Fisher LSD multiple comparison test). No other differences ($p > 0.10$) in land ownership composition or land cover category based on year of territory establishment were detected (Tables 2.2 and 2.3)

**Differences in Measured Habitat Variables Between Pack Territories And Random Unused Areas**

Mean road density within pack territories was lower than in unused areas for roads and trails ($p < 0.001$, 1.06 and 1.57 km/km$^2$, respectively) and roads only ($p < 0.001$, 0.70 and 1.43 km/km$^2$, respectively) measures of road density (Table 2.4). County owned land comprised a higher proportion ($p < 0.001$) of wolf territories (61%) than unused areas (15%) (Table 2.4), while private lands comprised a lower proportion ($p < 0.001$; 19%) of territories than of unused areas (56%) (Table 2.4). Lowland shrub ($p = 0.005$), forested wetland ($p = 0.005$), and aspen ($p = 0.073$) cover types were all more prevalent in wolf territories than in unused areas (Table 2.4). No other measured variables were different between territories and unused areas ($p > 0.10$).

**Landscape Level Habitat Suitability Model**

A Pearson correlation analysis of all variables considered for inclusion in the logistic regression analysis indicated that the roads only and roads and trails measures of road density were correlated ($r = 0.89$, $p < 0.001$). Based on this result, the forward step

Table 2.2 Land ownership category composition [proportions (SE)] of gray wolf pack territories grouped by year of territory establishment in the Highway 53 Study Area in northwest Wisconsin 1992-2000.

| | 1992 | 1993 | 1995 | 1997 | 1997 | $p^{A}$ |
|---|---|---|---|---|---|---|
| State | 0.49 (0.07) | 0.0 | 0.0 | 0.10 (0.07) | 0.01 (0.01) | <0.001 |
| County | 0.28 (0.18) | 0.91 (0.22) | 0.67 (0.15) | 0.45 (0.18) | 0.80 (0.18) | 0.19 |
| Private | 0.21 (0.09) | 0.08 (0.01) | 0.24 (0.08) | 0.20 (0.09) | 0.18 (0.09) | 0.81 |
| Industrial Forest | 0.0 | 0.0 | 0.09 (0.07) | 0.25 (0.08) | 0.0 | 0.22 |

[A] *p* value reported from ANOVA examining differences among years of establishment.

Table 2.2 Land ownership category composition [proportions (SE)] of gray wolf pack territories grouped by year of territory establishment in the Highway 53 Study Area in northwest Wisconsin 1992-2000.

| | 1992 | 1993 | 1995 | 1997 | 1997 | $p^A$ |
|---|---|---|---|---|---|---|
| State | 0.49 (0.07) | 0.0 | 0.0 | 0.10 (0.07) | 0.01 (0.01) | <0.001 |
| County | 0.28 (0.18) | 0.91 (0.22) | 0.67 (0.15) | 0.45 (0.18) | 0.80 (0.18) | 0.19 |
| Private | 0.21 (0.09) | 0.08 (0.01) | 0.24 (0.08) | 0.20 (0.09) | 0.18 (0.09) | 0.81 |
| Industrial Forest | 0.0 | 0.0 | 0.09 (0.07) | 0.25 (0.08) | 0.0 | 0.22 |

[A] *p* value reported from ANOVA examining differences among years of establishment.

Table 2.4 Mean (SE) of habitat variables in wolf pack territories and corresponding random unused areas in the Highway 53 Study Area in northwest Wisconsin 1992-2001.

| | Territory | | Unused | | |
|---|---|---|---|---|---|
| Variable | $\bar{x}$ | SE[A] | $\bar{x}$ | SE[A] | $p$[B] |
| Roads and trails (km/km$^2$) | 1.06 | 0.01 | 1.57 | 0.11 | <0.001 |
| Roads only (km/km$^2$) | 0.70 | 0.11 | 1.43 | 0.12 | <0.001 |
| County ownership[C] | 0.61 | 0.01 | 0.15 | 0.01 | <0.001 |
| Private ownership[C] | 0.19 | 0.01 | 0.56 | 0.01 | <0.001 |
| Lowland shrub[C] | 0.13 | 0.02 | 0.06 | 0.02 | 0.005 |
| Forested wetland[C] | 0.14 | 0.01 | 0.07 | 0.01 | 0.005 |
| Aspen[C] | 0.22 | 0.15 | 0.09 | 0.11 | 0.073 |
| Shrubland[C] | 0.04 | 0.01 | 0.01 | 0.01 | 0.321 |
| Agriculture[C] | 0.02 | 0.03 | 0.02 | 0.02 | 0.396 |
| Mean Fractal Dimension | 1.39 | 0.01 | 1.38 | 0.01 | 0.203 |
| Edge Density[D] | 316.41 | 40.96 | 309.73 | 28.63 | 0.253 |
| Mean Patch Area[E] | 2.44 | 0.32 | 2.46 | 0.48 | 0.533 |
| Mean Patch Edge [F] | 767.73 | 111.12 | 744.97 | 115.74 | 0.309 |
| Shannon's Diversity Index | 2.38 | 0.17 | 2.42 | 0.21 | 0.719 |

[A] Values < 0.01 rounded to 0.01.

[B] Wilcoxon Rank-Sum test of medians.

[C] Values reported as the proportion of the total territory or random unused area classified in this category.

[D] Meters/Hectare.

[E] Hectares.

[F] Meters/Patch.

logistic regression analysis was performed twice, once including the roads only density and once including the roads and trails density. In both cases, the stepwise procedure converged on a model including the proportions of forested wetland, proportions of county owned land, and the measure of road density.

Log likelihood $\chi^2$ (-2ln [likelihood ratio]) tests indicated that both models improved significantly over a model including only the logistic generated constant ($\chi^2 = 28.12$, 3df, $p < 0.001$ roads and trails, $\chi^2 = 29.57$, 3 df, $p < 0.001$ no trails). Both of these models correctly classified 93% of the sampled sites as wolf pack territories (14 of 15) or unused areas (14 of 15) (observations with $p < 0.50$ classified as unused by the model, those with $p > 0.50$ are classified as a territory for purposes of testing classification accuracy). Based on the log likelihood tests, I used the logistic model incorporating the roads only measure of road density. The logistic equation for this model was:

$$\frac{e - 1.455 - 3.643(R) + 4.691(C) + 36.623(F)}{1 + e - 1.455 - 3.643(R) + 4.691(C) + 36.623(F)}$$

with a logit of: p = $1.455 - 3.643(R) + 4.691(C) + 36.623(F)$ where R is the density of roads in km/km$^2$, C is the proportion of county owned land, and F is the proportion of forested wetland in the area of interest. This model correctly classified 14 of the 15 pack territories and 13 of the 15 unused areas outside of the H53SA. When this model was incorporated into a GIS, it delineated 22,694 km$^2$ of favorable wolf habitat [$p > 0.5$ from the logistic model (Mladenoff et al. 1995)].

The comparison of the probability of areas known to be occupied by wolves to those not occupied by wolves being selected by the pixel aggregation procedure indicated that areas occupied by wolves had a higher probability of being selected as suitable habitat than areas which are not occupied by wolves ($p$ <0.001, mean probability from 0 – 10 range, 1.6 for pack territories and 0.62 for unused areas). This indicated that the pixel aggregation technique was selecting pixels in a non-random manner and that it was more likely to select areas being occupied by wolves.

The comparison of the habitat values generated by the logistic model in actual wolf pack territories to areas that the pixel aggregation technique selected as suitable habitat indicated that the aggregation technique was selecting habitat similar to what wolves are selecting. The mean habitat value (0-100 range) for pixels in actual wolf pack territories was 74.8 (SE = 36.14). The mean pixel value in areas selected as suitable habitat by the pixel aggregation procedure was 59.36 (SE = 29.18). This difference was not statistically different, ($p$ = 0.32) indicating that the pixel aggregation worked as intended. The distribution of habitat values generated by the logistic model compared to wolf pack territories in PWR delineated by the WDNR from radio telemetry locations is presented in Fig 2.4.

When the pixel aggregation technique was run to saturate PWR with simulated territories, it selected 66 areas as being suitable for wolf pack territories. Combining this with the estimate of a mean pack size of 4.3 wolves, PWR in Wisconsin can support approximately 284 wolves in resident packs.

**DISCUSSION**

The mean road density observed within wolf pack territories increased throughout the course of this study and was higher overall than that reported by Mladenoff et al. (1995, 1999) in Wisconsin. There are several possible explanations for this relating to differing methodology. The first is a difference in the definitions

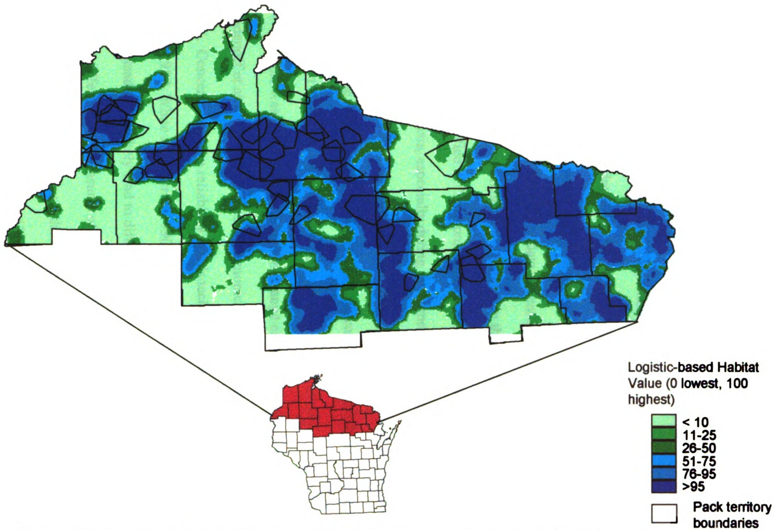


Fig. 2.4 Predicted wolf habitat quality within zone 1 (primary wolf habitat) on a scale of 0-100 using a logistic regression model developed from data collected in the Highway 53 Study Area in the northwest Wisconsin 1992- 2001 compared to documented wolf pack territories.

of the term "road." Mladenoff et al. (1995, 1999) used a more conservative definition based on features represented by solid lines on USGS 1:100,000 scale quadrangles and that did not include "unimproved forest roads." I reported values for my measure of roads only density using any road feature that was not classified as a trail in a GIS coverage developed within the WISCLAND data. This coverage was also developed from USGS 1:100,000 quadrangles, but likely included some features that would have been classified as unimproved by Mladenoff et al. (1995, 1999). I chose this measure for two reasons. First, these data are easily attainable by WDNR land managers. Second, from personal observations in the H53SA, road features that would likely be classified as "unimproved" are used to access otherwise roadless areas on a regular basis, especially during the summer tourist and fall hunting seasons. The benefits of using this measure of road density balanced the loss of ability to make direct comparisons between the measures of road density presented by Mladenoff et al. (1995, 1999) and my own.

There was also a difference in home range estimation technique used. Mladenoff et al. (1995, 1999) used a Harmonic Mean estimator (Dixon and Chapman 1980). Concerns over the reliability of this technique have been raised (Worton 1987, Worton 1989, White and Garrott 1990) and I chose to use a fixed kernel (Worton 1989) instead. This likely lead to different definitions of territory boundaries and resultant differences in measures of road density and other measured variables.

The final difference in methodology was related to the resolution of land cover data used. Mladenoff et al. (1995, 1999) used a land cover data set with a 16 ha resolution. I chose to use land cover data with a 30 m resolution. This difference could have contributed to observed differences in wolf land cover category usage between studies. The impacts on calculated landscape pattern metrics due to different resolution land cover data could also have led to the difference in the importance of fractal dimension to the logistic models developed in both studies. These differences in methodology should be kept in mind when viewing differences in the reported results of this study and Mladenoff et al. (1995, 1999).

**Changes in Territory Characteristics With Increasing Population and Territory Density**

The mean road density observed for this study within pack territories was higher than any in the Great Lakes region other than that reported by Merrill (2000) (1.42 $km/km^2$) from Camp Ripley military reservation in central Minnesota. Merrill (2000) proposed that the persistent occupation of this area of higher than normal road density was possibly due to lower than normal speed limits and generally favorable human attitudes toward wolves. It seems likely that wolf occupation of Camp Ripley and areas of similarly high road densities in the H53SA is due not only to favorable human attitudes toward wolves, but also to increasing tolerance of roads by wolves. Due to their territorial nature dispersing wolves are constantly exploring areas unoccupied by resident packs. As the landscape fills up with resident packs, the unoccupied areas available for colonization by newly forming packs become less preferred. In spite of the generally higher road densities and resultant higher levels of human activity in many of these recently colonized areas, with the current level of human tolerance and legal protection wolves appear to be establishing territories and persisting in them. While wolves seem to prefer areas with low road densities and low levels of human contact to establish territories, they will establish territories in areas of higher road density and human activity if these are the only areas available to them. The currently high levels of human tolerance and legal protection seem to allow wolves to survive in these areas, which in the past would have been viewed as marginal or unsuitable as wolf habitat. The increasing road densities within pack territories established later in the study as the wolf population increased and the high overall mean road density within territories indicate that the use of areas previously viewed as unsuitable or unfavorable is occurring in the H53SA. Even several authors who identified road density as the most important measure of wolf habitat suitability (Mech 1995, Mladenoff et al. 1995, 1999) acknowledge that wolves are expanding into more human dominated areas and that this may require the revision of our perceptions of what is suitable wolf habitat.

Our understanding of wolf habitat suitability since the mid 1980s has largely been based on two conflicting paradigms. The first is based on the widespread distribution of wolves in North America before European settlement and their habitat generalist and highly adaptable nature (Mech 1970, 1995). The other has been the paradigm that road density is the best measure of habitat suitability for wolves, with higher road density indicating lower habitat quality and probability of occupation by wolves (Thiel 1985, Jensen et al. 1986, Mech 1995, Mladenoff et al. 1995, 1999). The factor that allows both of these contradictory paradigms to be valid is the effect of human activity on wolf populations. While wolves are very adaptable in their habitat requirements, they generally do not inhabit areas of high road density due to potential conflicts with humans. Mladenoff et al. (1995) and Mladenoff and Sickley

(1998) proposed that "roads per se are not avoided by wolves but serve as indicators of human contact and thus the likelihood of deliberate or accidental human caused mortality." Fuller et al. (1992) proposed that where humans tolerate wolves, prey density is likely the main limiting factor in wolf populations. This again indicates that human activity is the main limiting factor on wolf populations, but without this limitation, wolves are very adaptable in their habitat use.

It seems likely that past views of wolves as a wilderness species which needs large roadless areas to survive are due to data on wolf distributions being gathered in periods when human tolerance of wolves was low or in the period when wolves were recolonizing formerly occupied areas as human tolerance increased. In short, wolves were found only in wilderness areas because they were extripated in areas more accessible to humans before public attitudes toward wolves began to improve in the 1970s (Mech 1995).

The increase in mean road density within pack territories established later in this study is likely due to wolves taking advantage of the present relatively high level of human tolerance of wolves by moving into areas with high levels of human activity. High levels of human tolerance allow wolves to express their highly adaptable nature and colonize areas with a high probability of human contact, but which provide otherwise high quality habitat (e.g., high prey density, good denning habitat). The higher mean road density in all pack territories within this study compared to those observed by Mladenoff et al. (1995, 1999) in Wisconsin is likely due to this same trend of wolves continuing to move into more human dominated areas as the wolf population increases.

**Differences in Measured Habitat Variables Between Pack Territories and Random Unused Areas**

The higher proportions of forested wetland observed in pack territories compared to unused areas supports past findings in the area by Mladenoff et al. (1995). It also supports the results of a compositional analysis (Aebischer et al. 1993) conducted in the study area (Chapter 3, this document) that found forested wetland was highly selected by wolves at both the landscape and within-territory levels of analysis. The importance of forested wetland to wolves is likely related to both the avoidance of human disturbance and the value of this cover type to white-tailed deer (*Odocoileus virginianus*), which is the preferred prey item of wolves in Wisconsin throughout the year (Mandernack 1983).

Areas of forested wetland are generally not hospitable to human activity that requires movement away from roads due to difficulty in walking, high populations of biting insects in the summer, and the general lack of human development. Wolves are likely selecting forested wetland both when establishing territories and when pursuing life needs within territories at least in part due to relatively low levels of human activity. As wolves colonize more human dominated areas, tracts of forested wetland may serve as refuges of low human activity compared to the territory as a whole. Areas classified as lowland shrub also comprised a greater proportion of territories than unused areas. The apparent importance of these areas to wolves is also likely due to low levels of human access and activity in them.

Lowland conifer stands (classified within the forested wetland category in this study) are an important component of deer habitat, especially during severe winters, providing thermal cover and lower snow depths than surrounding areas (Verme 1965, Blouch 1984). The high use of these areas by white-tailed deer likely leads to increased use by wolves and the resulting importance of forested wetlands areas to wolves.

The higher proportion of aspen in pack territories than in unused areas is also likely tied to white tail-deer habitat use. Aspen has been identified as the most favorable forest type for deer production in the northern Great Lakes (Byelich et al. 1972). It is also a preferred habitat of Wisconsin deer (Habeck and Curtis 1959) and was identified as dominating the diet of deer in northern Wisconsin during the early and late summer by McCaffrey et al. (1974). This preference for aspen as a food source likely leads to the high level of deer use observed by McCaffrey and Creed (1969) during the summer when deer trails and tracks were 2-5 times more abundant in aspen than in northern hardwood habitat types. The high use of aspen by deer, therefore, leads to high levels of hunting by wolves in aspen areas and the resulting importance of aspen in wolf territories.

County owned lands were more common in pack territories than in unused areas, which supports the findings of Mladenoff et al. (1995) in northern Wisconsin. They found that 39.3% of pack territories and 8.4% of unused areas were county owned and that areas under county ownership contributed highly to favorable wolf habitat rankings. The majority of county owned lands in the H53SA are managed as commercial forest. This leads to the maintenance of early succesional forests on large portions of county owned lands. These early serial stage forests provide high quality habitat for deer, which likely increases their attractiveness to wolves. County ownership of an area generally precludes human development of the area, which also likely increases the habitat quality of county owned land to wolves.

In contrast to county owned land, lands under miscellaneous private ownership comprised lower proportions of wolf pack territories than unused areas. This finding also supports Maldenoff et al. (1995) who reported 20.1% of pack territories and 75.0% of unused areas were privately owned. Privately owned land was highly correlated with road density and human population density by Mladenoff et al. (1995). It, therefore, seems likely that the comparatively low use of privately owned land is due to avoidance of human activity by wolves.

**Landscape Level Habitat Suitability Model**

The logistic based GIS model predicting suitable wolf habitat indicates that there is still suitable wolf habitat that is unoccupied. This unoccupied habitat is primarily in northeastern Wisconsin and was also identified by Mladenoff et al. (1995). This indicates that there is the potential for the wolf population in the state to continue to expand toward the target population of 350 individuals (WIDNR 1998).

The habitat suitability predictions created using this model and the pixel aggregation procedure described by Roloff and Haufler (1997) provide managers with a tool that allows the prediction of wolf occurrence based not only on habitat quality but also on habitat juxtaposition. This predictive capability will prove useful not only in managing habitat, but also in avoiding human/wolf conflict, and potentially targeting areas for wolf harvest when a public harvest is conducted.

The importance of including the juxtaposition of habitat, as well as habitat quality when estimating carrying capacity is illustrated by my data and predictions of suitable wolf habitat in PWR. Average observed pack territory size in the H53SA was 119 km$^2$. The logistic based model that I developed classified roughly 23,000 km$^2$ of favorable habitat in PWR. This means that based solely on predicted habitat quality, there is enough favorable habitat in PWR to support 193 packs. When the juxtaposition of habitat (and the territorial nature of wolves) is included in this calculation by incorporating the pixel aggregation procedure, only 66 areas where classified as being suitable to support pack territories. This type of a difference can have significant implications for population management, especially when estimating carrying capacity for threatened or endangered species.

**SUMMARY AND MANAGEMENT IMPLICATIONS**

Evidence that at current levels of human tolerance/legal protection wolves are successfully colonizing areas that are more human dominated and which have higher road densities is growing (Fuller et al. 1992, Mech 1995, Merrill 2000, this study). Wolf populations in these non-wilderness or semi-wild areas appear to be stable or growing. This suggests that some areas that would have in the past been considered as unsuitable wolf habitat (based primarily on road density) are in fact suitable. This does not mean that road density is no longer a useful measure of wolf habitat suitability. There is undoubtedly some level of road density (and the resultant level of human activity/contact) above which wolves will generally not attempt to establish territories or will not be able establish sustainable territories. With the wolf population in the Great Lakes region continuing to increase, we likely have yet to discover this upper limit of road density. Lacking a definitive upper road density value for wolf colonization, I suggest that resource managers consider areas with less

1.5km\km$^2$ as potential suitable wolf habitat given current levels of human tolerance/legal protection. This figure is based on the highest mean road density observed for a year of establishment group in this study (1.37 km/ km$^2$ for packs established in 1999). Packs established in 1999 have consistently produced pups and appear viable 3 years after establishment. I saw no evidence that the packs established in 1999 were encountering conditions which would likely lead to the territories failing to persist or act as population sinks. While these packs were monitored for less than two years after they were established, all 3 produced pups both years and one of the three included the largest number of individuals of any pack in the study area at the conclusion of the study. After only two years of monitoring, the perception that these packs are experiencing no greater stress due to road density than any other packs in the study area is preliminary. Nonetheless, I observed no evidence that the road density within these packs was the maximum level tolerated by wolves to establish sustainable territories.

Setting an upper road density limit for potential wolf habitat will aid managers in two ways. It will help to avoid expending resources on wolf management in areas that are likely not quality habitat. It will also aid in delineating areas of high potential risk of human/wolf conflict. For example, if wolves move into an area with a road density above the upper limit and a high likelihood of human contact and human/wolf conflict, this area would be a good candidate for wolf population control if and when it needs to be implemented. Since the WDNR wolf population target was set at 350 at least in part in an attempt to maintain the state's wolf population at or below human social carrying capacity, the need to control the population seems likely at some point in the future. If this becomes necessary, being able to select areas to target for wolf removal will be necessary. Areas, which wolves have colonized, and which have higher than acceptable road densities seem like good regions to target for population control measures, whether they are conducted by resource management agencies or are some type of a public harvest.

Forested wetlands are an important component of wolf territories in the H53SA. This cover type comprised larger portions of pack territories than unused areas and was also the most selected cover type by wolves at the landscape and within-territory level (Chapter 3, this document). This selection is probably due to the relatively low levels of human activity in most forested wetland areas and the importance of forested wetland to white tailed deer as winter yarding areas. Forested wetlands are areas that managers should consider protecting if they are attempting to maintain high quality wolf habitat.

Aspen was also highly selected by wolves at the landscape and within-territory levels (Chapter 3, this document) as well as comprising higher proportions of pack territories than unused areas. This indicates that aspen also has value to wolves (likely due to its importance to white-tailed deer) and management for high quality wolf habitat should include maintaining aspen as a component of the area. This is especially important considering the maturation of the state's aspen stands since the mid-1980s. The percentage of forested stands in the state classified as aspen-birch dropped from 67% in 1983 to 57% in 1996 (Schmidt 1996). Thus, by the late 1990s over 40% of the state's aspen was in stands that were dominated by other forest types and were in the final stages of converting to these other forest types due to succession.

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# CHAPTER 3

# COVER TYPE AND LAND OWNERSHIP SELECTION OF RECOLONIZING GRAY WOLVES IN NORTHWEST WISCONSIN

## INTRODUCTION

Past research on wolves has focused on relating resource selection to features including land cover, road density, prey base, and land ownership patterns (Mladenoff et al. 1995) at the landscape level. Likely due the wide range of habitats originally occupied by wolves and their overall generalist nature (Mech 1995), little research has been conducted on cover type selection by wolves within territories. Although the habitat generalist nature of wolves allows them to successfully utilize various cover types, differences in cover type composition across a landscape do influence where wolves establish territories (Mladenoff et al. 1995). Therefore, information about cover type selection is important for this generalist species more as a tool in predicting where wolves will occur in the future than as a tool in protecting or providing suitable habitat. This is especially important in semi-wild landscapes due to the high potential for conflicts with humans as wolves continue to expand their range. An increased ability to predict areas of future occupation within these areas allows for a more accurate assessment of the potential for human/wolf conflicts in semi-wild landscapes.

Another measurement of habitat quality that needs more investigation in semi-wild landscapes is road density. Since the mid-1980s road density has been the most commonly used measure of habitat quality for wolves, with higher road densities associated with lower quality habitat (Mech 1995). It is generally accepted (Mladenoff et al. 1995, Mladenoff and Sickley 1998) that while wolf mortalities do occur on and along roads, increased human access into wolf occupied habitat and the resulting increased direct killing of wolves by humans and potential for disease and parasite occurrence (Mech and Goyal 1993), rather than vehicle caused mortality is the mechanism responsible for the negative influence of increasing road density on wolf habitat suitability. Wolf use of roads and trails as travel and hunting corridors has also been documented (Thompson 1952, Mech 1970, Gehring 1995) indicating that roads may have value to wolves. Based on past research there are still questions regarding whether roads are actually being avoided or whether they have value to wolves and the avoidance observed is actually of human activity promoted by roads.

This study examined selection of 14 land cover and 5 ownership categories by gray wolves. It also examined the use of areas in proximity to roads by wolves during daylight hours. The goal of these analyses was three-fold. My first objective was to examine and quantify year-long selection of land cover and ownership categories by recolonizing gray wolves in the H53SA at the landscape (placement of territories within the H53SA) and within-territory levels. The second objective was to identify land cover categories that were being highly selected by wolves. These cover types are presumably of importance to wolves and identifying them should allow resource managers to identify key wolf habitat areas. Since wolves are using these areas heavily, identifying them will also identify areas that have high probabilities of human/wolf conflict. A third objective was to examine whether wolves use areas in proximity to roads in proportion to availability, indicating selection or avoidance. This information can prove useful in further understanding the actual mechanism that drives the documented negative effects of road density on wolf habitat quality (Mladenoff et al. 1995, 1999).

## METHODS

### Capture, Handling, and Radiotelemetry

Wolves were trapped by WDNR personnel using modified #14 Newhouse leg-hold traps (Schultz et al. 1996) during May-August in 1995-2000. Captured wolves were immobilized using a mixture of ketamine/xylazine administered with a jabstick. Any trap-related injuries were treated, blood samples were taken, an injection of antibiotics was administered, and animals were weighed. Animals > 15kg were also fitted with radio collars (Telonics Inc., Mesa, Arizona) and uniquely numbered ear tags. Yohimbine was administered as a reversal agent for the xylazine and the animals were monitored until they could move away from the trap site under their own power.

Radio-collared animals were located 1-5 times per week during 1995-2001using telemetry from fixed-wing aircraft (Ballard and Dau 1983, Fuller 1989) or a vehicle-mounted 5-element Yagi directional antenna until radio failure, death of the animal, or a permanent movement out of the study area. The majority (>95%) of locations were collected during daylight hours and a minimum of 3 bearings were collected for each location. Triangulations for locations collected on the ground where solved using a Lenth estimator (Lenth 1981) in the program Locate II (Pacer, Turvo Nova Scotia, Canada). Ground locations were collected during the course of data collection for this study and two other graduate projects conducted within the H53SA during 1995-1997. The accuracy of telemetry locations I collected was tested as described by White and Garrot (1990). In addition to average error ellipse (3.8 ha), I also calculated the average error in straight line distance from the actual location of the test transmitters to the estimated locations (123 m). No estimates of telemetry accuracy were reported for the locations collected in 1995-1997. Since Shelly and Anderson (1995) found no significant difference between the accuracy of aerial and ground locations in the study area using the same telemetry techniques and equipment, locations were pooled for territory estimation and resource selection analyses. Locations obtained for an individual wolf were at least 4 hours apart to maintain independence (Reynolds and Laundre 1990). Date, time, Universal Transverse Mercator (UTM) coordinates, ear tag number, and pack were recorded for each telemetry location. Animals were classified as belonging to individual packs based on trapping location and movement patterns.

**Territory Boundary Estimation**

Pack territory boundaries were estimated using a fixed kernel method (Worton 1989) based on an 80% isopleth using the animal movement analysis extension (Hooge and Eichenlaub 1997) in ArcView (Environmental Systems Research Institute, Redlands, CA). A minimum of 30 locations (Fuller and Snow 1988, Seaman et al. 1999) was used in estimating territory boundaries. Only territories of packs which had been monitored for at least 6 months and which had produced pups were included in the analysis. Locations from all radio-marked animals within a pack during the course of the study were used in territory boundary estimation.

**Determination of Territory Land Cover and Land Ownership Composition**

Territory boundaries were overlaid on a 30 m resolution LANDSAT land cover data layer created in 1992 from Thematic Mapper imagery and a land ownership data layer provided by D. Mladenoff and T. Sickley (University of Wisconsin Dept. of Forestry) in ArcView. The land cover layer was provided by the WDNR and categories had been classified within the WISCLAND land cover scheme (http://www.dnr.state.wi.us/org/at/et/geo/data/wlc.htm). The original 28 land cover categories present within the H53SA in this layer were consolidated into 14 categories (Appendix A) to lessen the occurrence of cover categories with small values for use and availability. This consolidation was conducted based on the following 3 criteria. Any cover type that represented less than 0.1% of both territories and the total study area and which was present in less than 4 pack territories was excluded from analysis. Any cover type category which, based on traditional paradigms of wolf ecology would not be used by wolves (i.e., open water and urban) was excluded from the analysis. Similar cover types that represented little variability in resources to wolves were combined (i.e., red oak *Quercus rubra* and northern pin oak *Quercus ellipsoidalis* were combined).

The area of each territory and proportion of the total area of the territory within each land cover and ownership category were calculated from the consolidated land cover and ownership categories. The resulting land cover and ownership proportions were used in a Compositional Analysis (CA) (Aebischer et al. 1993) to analyze year-long landscape level and within-territory land cover and ownership selection. The calculations for CA were conducted using ReSelect software (http://ces.iisc.ernet.in/hpg/envis/resdoc1120.html). CA was also used to analyze within-territory land cover selection during "summer" and "winter" seasonal periods. CA involves a use vs. availability approach to delineate and quantify selection, while avoiding the problem of non-independence of proportions calculated for use and availability in many habitat selection techniques (Aebischer et al. 1993).

At the landscape level of analysis, the proportion of the study area within each land cover or ownership category represented availability while the proportion of each land cover or ownership category within territories represented use. At the within-territory level of analysis, the proportion of a territory within each land cover or ownership category represented availability while use was represented by the proportion of the total number of wolf telemetry locations within each land cover or ownership category. Use for the within-territory analyses was calculated for entire year, as well as "summer" (15 April-14 September) and "winter" (15 September-14 April) seasonal periods to facilitate analysis of potential differences in selection due to seasonal changes in behavior. These periods were defined by Fuller (1989) corresponding to changes in pack cohesiveness related to denning in northcentral Minnesota and corresponded well with observed wolf behavior in the H53SA.

My use of CA varied in one way from that described by Aebischer et al. (1993). They suggested using individual radio-marked animals as the sample unit when conducting CA. Due to the territorial nature of wolves and the resultant restrictions on movement, independence of telemetry locations, and habitat use, I used a territory (all marked animals in a pack) as the experimental unit for these analyses. Alpha levels for both overall tests of selection and pair-wise comparisons of land cover categories within compositional analysis were 0.10.

The examination of wolf use of areas in proximity to roads was based on comparisons of used areas to their relative availability. To accomplish this, roads within territories were buffered at arbitrarily set distances of 25, 50, 100, and 250 m. The proportions of the area of territories within these road buffers were calculated. The mean proportion of territories within these buffers was compared to the mean proportion of the number of telemetry locations falling within buffers in each territory using a Mann-

Whitney U test (Zar 1999) ($\alpha = 0.10$) to provide an indication of the selection or avoidance of areas near roads. There is an extensive system of trails in the H53SA used for both forestry harvest and recreation. This trail system allows access to otherwise roadless areas and is used heavily during the summer by all terrain vehicle riders and during the winter by snowmobile users. Since increasing human access to wolf habitat is generally regarded as a negative influence for wolf sustainability, I included this trail system in my definition of roads for this analysis. With this addition, all features identified as any class of road or trail was included in the analysis.

## RESULTS

### Selection of Land Cover Category

Five-thousand one-hundred and two telemetry locations, from 40 wolves in 14 packs (Figure 3.1), were analyzed. CA indicated that there was differential selection of land cover types occurring at both the landscape ($p < 0.001$) and within-territory ($p < 0.001$) levels when telemetry locations (use) were considered as one year-long set of data with no allowance for seasonal changes. The three cover types that comprised the largest proportions of the study area were aspen, mixed/other broad-leaved deciduous, and lowland shrub (21.5%, 14.1%, and 10.8% of the study area respectively) (Table 3.1). Not only were these the three most common cover types in the study area, but they were also three of the top four most selected cover types at the landscape level (Table 3.2). Jack pine (*Pinus banksiana*), shrubland, and agricultural were the three least selected of the three least common cover types within territories (1.8% and 1.3%) (Table 3.2). While there were some differences between landscape and within-territory selection rankings, forested wetland and aspen were two of the top three most selected cover types at both

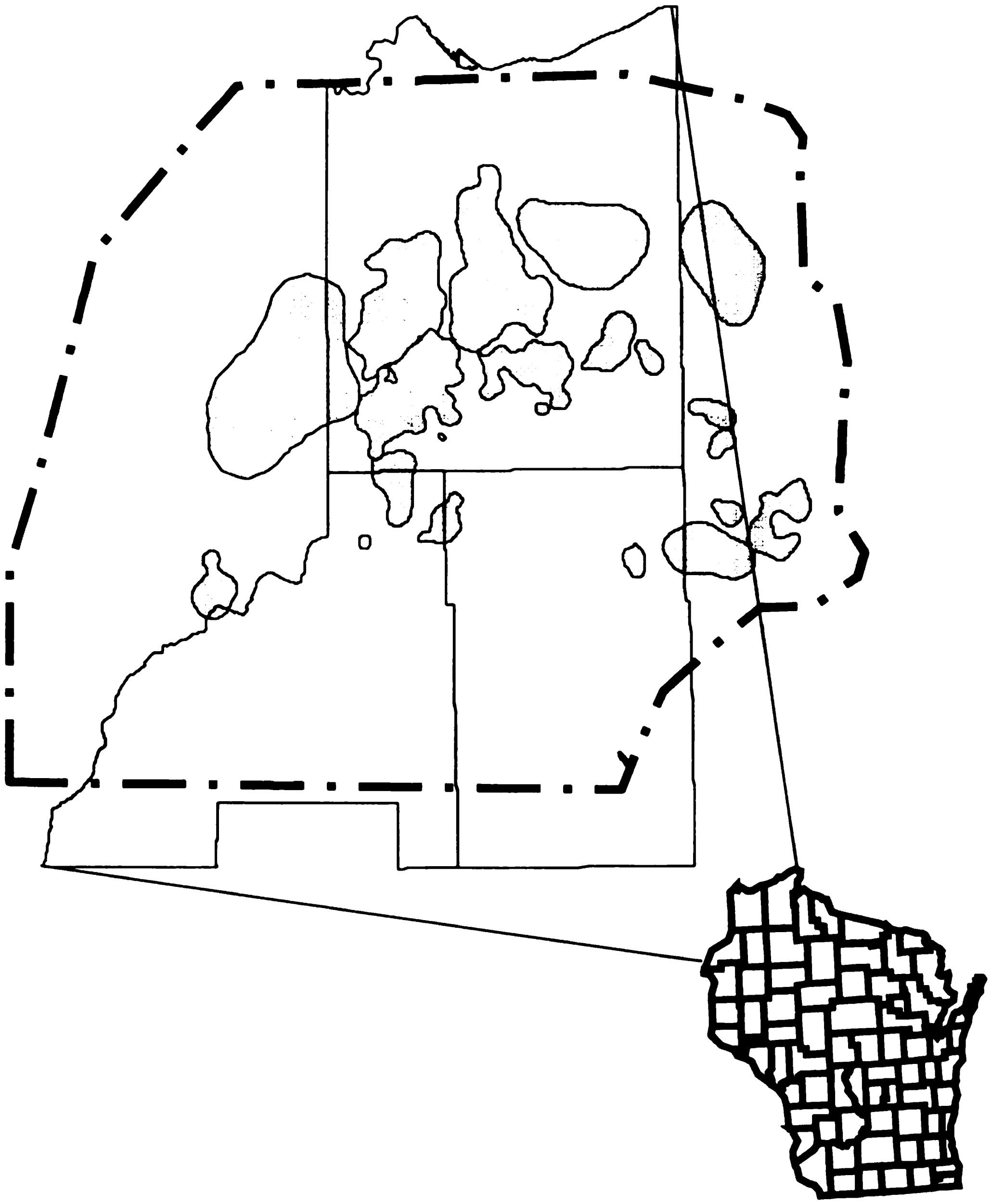

Fig. 3.1 Wolf pack territories in the Highway 53 Study Area in northwest Wisconsin and adjacent Minnesota 1995-2001

Table 3.1. Mean percent land cover category composition in the Highway 53 Study Area and within wolf pack territories and the percentage of telemetry locations within the 14 cover types used in a compositional analysis of land cover type selection in northwest Wisconsin 1995-2001.

| Land cover category | % telemetry locations in cover type within territories [A] | | % territory composition [B] | | % study area composition [C] |
|---|---|---|---|---|---|
| | $\bar{x}$ | SE | $\bar{x}$ | SE | |
| Forested wetland | 21.9 | 2.78 | 12.8 | 1.44 | 8.3 |
| Aspen | 21.2 | 2.37 | 22.4 | 2.18 | 21.5 |
| Lowland shrub | 14.7 | 2.41 | 14.1 | 1.76 | 10.8 |
| Mixed/other broad-leaved deciduous | 12.5 | 3.22 | 17.0 | 3.41 | 14.1 |
| Emergent wet meadow | 1.9 | 0.29 | 2.5 | 1.76 | 3.0 |
| Mixed deciduous/coniferous | 7.0 | 1.91 | 6.0 | 1.54 | 6.4 |
| Red Pine | 1.9 | 0.69 | 2.2 | 0.64 | 2.8 |
| Grassland | 3.3 | 0.78 | 5.5 | 0.83 | 9.9 |
| Oak | 2.6 | 1.02 | 2.3 | 0.70 | 2.9 |
| Mixed/other coniferous | 1.3 | 0.42 | 1.3 | 0.30 | 1.5 |
| Maple | 3.7 | 2.04 | 1.8 | 0.30 | 1.4 |
| Jack pine | 1.5 | 6.92 | 4.0 | 1.73 | 4.6 |
| Shrubland | 1.7 | 0.87 | 4.4 | 1.86 | 3.7 |
| Agricultural | 1.7 | 0.78 | 2.1 | 1.12 | 4.6 |

[A] Percent of the number of telemetry locations located in each land cover type was the measure of use in compositional analysis at the within-territory level.

[B] Percent of the area within all territories in each land cover type was the measure of use in compositional analysis at the landscape level. It was also the measure of availability in compositional analysis at the within-territory level.

[C] Percent of the total study area within each land use category was the measure of availability in compositional analysis at the landscape level.

Table 3.2. Consolidated thematic mapper based WISCLAND land cover categories used in the compositional analysis of landscape level and within-territory selection and corresponding selection ranks for both levels of analysis based on year-long use data for gray wolves in the Highway 53 Study Area in northwest Wisconsin 1995-2001.

| Land cover category | Landscape level rank[A] | Within-territory rank[B] | Ranking average |
|---|---|---|---|
| Forested wetland | 1 | 1 | 1 |
| Lowland shrub | 2 | 6 | 4 |
| Aspen | 3 | 2 | 2.5 |
| Mixed/other broad-leaved deciduous | 4 | 9 | 6.5 |
| Emergent wet meadow | 5 | 8 | 6.5 |
| Mixed/other coniferous | 6 | 14 | 10 |
| Maple | 7 | 12 | 9.5 |
| Grassland | 8 | 13 | 10.5 |
| Mixed deciduous/coniferous | 9 | 5 | 7 |
| Red pine | 10 | 7 | 8.5 |
| Oak | 11 | 3 | 7 |
| Jack pine | 12 | 10 | 11 |
| Shrubland | 13 | 11 | 12 |
| Agricultural | 14 | 4 | 9 |

[A] $\chi^2$(13 df = 58.59 $P < 0.001$) for overall test of nonrandom use of habitat.

[B] $\chi^2$(13 df = 39.09$P < 0.001$) for overall test of nonrandom use of habitat.

levels (Table 3.2).

The analysis of seasonal land cover selection also indicated that cover type use was not random ($p < 0.001$ for both "winter" and "summer" periods). Several differences in selection rankings between "summer" and "winter" periods (i.e., oak, lowland shrub) as well as between seasonal periods and the entire year (oak) were also detected (Table 3.3, Appendix D, Appendix E). Forested wetland and aspen, which where the two most selected cover types in the year-long analysis, where also in the top 4 in both "summer" and "winter" (Table 3.3). In contrast, oak was the third most selected cover type in the year-long analysis and the most selected type in the "summer" analysis, but dropped to twelfth out of 14 in the "winter" period. The selection of lowland shrub was also different among "winter", "summer" and the year-long period. It was the second most selected cover type during "winter", but the eighth most selected during "summer" and the sixth most selected during the entire year. Grassland and maple where ranked among the 4 least selected cover categories in all 3 seasonal periods.

**Selection of Land Ownership Category**

Compositional analysis indicated that the use of land ownership classifications was not different from random at either the landscape ($p = 0.118$) or within-territory ($p = 0.508$) levels (Table 3.4). The H53SA was primarily privately (61%) or county (21%) owned. While the majority of the area within territories was also within these two categories, county-owned lands (53%) were more prevalent than privately owned lands (28%). A similar trend was evident with telemetry locations; 61% of locations occurred on county-owned land and 21% occurred on privately owned-land (Table 3.4).

Table 3.3. Compositional analysis selection rankings of consolidated WISCLAND based land cover types for year-long and seasonal periods at the within-territory level of analysis for gray wolves in the Highway 53 Study Area in northwest Wisconsin 1995-2001.

| Land cover category | Year-long rank | Winter rank[A] | Summer rank[B] |
|---|---|---|---|
| Forested wetland | 1 | 1 | 2 |
| Aspen | 2 | 3 | 4 |
| Oak | 3 | 12 | 1 |
| Agricultural | 4 | 5 | 3 |
| Mixed deciduous/coniferous | 5 | 9 | 6 |
| Lowland shrub | 6 | 2 | 8 |
| Red pine | 7 | 14 | 10 |
| Emergent wet meadow | 8 | 7 | 7 |
| Mixed/other broad-leaved deciduous | 9 | 4 | 5 |
| Jack pine | 10 | 8 | 11 |
| Shrubland | 11 | 6 | 14 |
| Maple | 12 | 13 | 9 |
| Grassland | 13 | 10 | 13 |
| Mixed/other coniferous | 14 | 11 | 12 |

[A] Winter = 15 September- 14 April.

[B] Summer = 15 April-14 September.

Table 3.4 Land ownership category composition within the Highway 53 Study Area and wolf pack territories and the percent of telemetry locations within each category in northwest Wisconsin, 1995-2001.

| Ownership Category | % study area composition | % territory composition | | % of total telemetry locations in land cover category | |
|---|---|---|---|---|---|
| | $\bar{X}$ | $\bar{X}$ | SE | $\bar{X}$ | SE |
| County | 21.6 | 53.6 | 8.10 | 61.2 | 8.61 |
| National Park | 0.5 | 0.3 | 0.15 | 0.9 | 0.46 |
| Private | 61.6 | 27.2 | 4.71 | 21.5 | 4.91 |
| State | 11.7 | 10.5 | 4.67 | 12.3 | 5.96 |
| Industrial Forest | 5.0 | 8.4 | 3.63 | 3.7 | 2.01 |

### Use of Buffers Around Roads

Approximately 4 -33% of the area within wolf pack territories and 2–28% of telemetry locations were within the buffers around roads and trails (Table 3.5). The percent of telemetry locations within buffers of 25, 50, 100, and 250 m around roads and trails was lower ($p$ = 0.002, 0.067, 0.040, 0.032 respectively) than the percent of the total area of territories within these buffers (Table 3.5).

## DISCUSSION

It is generally accepted that wolves are habitat generalists (Mech 1970), originally occupying every habitat in the northern hemisphere where large ungulates were present (Mech 1995). It has also been documented that road density (as a measure of increased human access and activity) is a useful measure of wolf habitat suitability (Mladenoff et al. 1995, 1999) and that even in legally protected populations human activity is generally the leading cause of death for adult wolves (Fuller 1989, Wydeven et al. 1995). In areas where human tolerance for wolves is high and human caused mortality is low, the density of large ungulate prey is the primary limiting factor on wolf populations (Fuller et al. 1992). Therefore, it seems reasonable that any analysis of habitat (cover type) use and preference must consider both the potential impacts of cover type on the level of human activity and on major prey species usage. Discussion of the selection or avoidance of individual cover types by wolves will relate how a given cover type affects either or both of these factors and wolf use of the cover type.

### Selection of Land Cover Category

Wolf pack territories have been shown to be positively correlated with

Table 3.5. Percent of the Highway 53 Study Area and mean percent of territories within buffers of varying distances around roads and trails compared to percent of telemetry locations within these same buffers in northwest Wisconsin 1995-2001.

| Road Buffer Distance | % of H53SA within road buffer | % of territories within road buffers (Available) | | % of wolf telemetry locations within road buffers (Used) | | |
|---|---|---|---|---|---|---|
| | | $\bar{X}$ | SE | $\bar{X}$ | SE | P[A] |
| 25m | 4.95 | 3.69 | 0.30 | 2.23 | 0.52 | 0.002 |
| 50m | 9.72 | 6.74 | 0.76 | 5.38 | 0.80 | 0.067 |
| 100m | 18.55 | 13.08 | 1.45 | 10.02 | 1.53 | 0.040 |
| 250m | 41.15 | 32.63 | 2.67 | 27.52 | 4.49 | 0.032 |

[A] Mean available values for all road buffer categories were greater than mean used values for all buffer categories when analyzed in a Mann-Whitney U test ∀ = 0.10, $H_0$: Available > Used.

forested wetland in the northern Great Lakes with territories containing higher proportions of forested wetland than areas unoccupied by wolves (Mladenoff et al. 1995). The results of the CA that I conducted confirm this finding. Forested wetland was the most selected cover type at both the landscape and within-territory level when examined with no allowance for seasonal differences. It was also the most selected cover type during the winter seasonal period and the second most selected during the summer seasonal period. This affinity for forested wetland areas is likely as much a product of the lack of human access and activity in these areas as it is to the actual vegetation composition of the area.

Road density has been recognized as an important measurement of wolf habitat suitability since the mid 1980s with higher road density indicating lower wolf habitat suitability (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Mladenoff et al. 1995). It has been stated "roads per se are not avoided by wolves but serve as indicators of human contact and thus the likelihood of deliberate or accidental human caused mortality" (Mladenoff et al. 1995, Mladenoff and Sickley 1998). It has been shown that wolves may use roads and trails as travel corridors under certain conditions (Pimlott et al. 1969, Thurber et al. 1994, Gehring 1995). While this indicates that roads may have value to wolves, Thurber et al. (1994) found that wolves avoided roads with relatively high human use, opting to use closed roads as travel corridors. Thus, human activity and not road density, per se, is likely what wolves are avoiding. While forested wetland areas within the H53SA had higher densities of roads and trails (2.48 km/km$^2$) than the entire study area (0.99 km/km$^2$), actual human activity in these areas is possibly lower than in areas dominated by other cover types due to the difficulties of movement away from roads.

Forested wetland was also consistently highly selected across seasonal periods. This was probably due to a combination of low human activity in these areas and secondary factors including the importance of this cover type to prey species especially white-tailed deer (*Odocoileus virginianus*). In the H53SA, white-tailed deer are the preferred prey item throughout the year (Mandernack 1983). Lowland conifer stands (classified within the forested wetland category in this study) are an important component of deer habitat during severe winters, providing thermal cover and lower snow depths than surrounding areas (Verme 1965, Blouch 1984). It has also been suggested that yarding behavior in deer may be an anti-predator strategy (Nelson and Mech 1981) evolved to compensate for the increased vulnerability to wolves during the winter months. In either case, the increased use of these swamp conifer areas by white-tailed deer may lead to increased use by wolves and an increased selection of the forested wetland cover type.

Aspen was highly selected by wolves at both the landscape and within-territory levels. It was also highly selected across all seasonal periods. The high use of aspen areas is also likely tied to the white-tailed deer population. Aspen has been identified as the northern Great Lakes' leading deer producing forest type (Byelich et al. 1972). It is also a preferred habitat of Wisconsin deer (Habeck and Curtis 1959) and was identified as dominating the diet of deer in northern Wisconsin during the early and late summer by McCaffrey et al. (1974). This preference for aspen as a food source likely leads to the high level of deer use observed by McCaffrey and Creed (1969) during the summer when deer trails and tracks were 2-5 times more abundant in aspen than in northern hardwood habitat types. The high use of aspen by deer likely leads to high levels of hunting by wolves in aspen areas and the resulting high cover type selection ranking.

The one cover type that showed a large difference in selection ranking between the landscape and within-territory levels of selection was agricultural. At the landscape level agricultural lands were the least selected of all cover types. In contrast, agricultural lands were the fourth most highly selected within-territories. The avoidance of agricultural areas at the landscape level (territory placement) is consistent with the findings of Mladenoff et al. (1995, 1999). They found that wolf pack territories contained lower proportions of agricultural land than corresponding unoccupied areas. This avoidance is possibly due to the relatively high levels of human activity in agricultural areas. The higher selection of agricultural areas within territories is likely related to prey activity patterns. Agriculture in the H53SA is generally practiced on relatively small parcels of land ($\bar{x}$ = 3.7 ha). It also tends to be interspersed with forested lands that are frequently harvested. This mixture often leads to high populations of preferred prey species, including white-tailed deer. Agricultural practices maintain edge and open areas providing favorable wildlife habitat in close proximity to cover for forest wildlife. While wolves tend to avoid areas with high proportions of agricultural land when establishing territories, once a territory is established, the relatively small proportions of agricultural lands within the territory are used presumably due to high use of these areas by prey species.

There were two cover type categories that showed large differences in selection rankings between "summer" and "winter" periods. The biggest difference in selection rankings between seasonal periods was observed for oak. It was the highest ranked cover type during "summer" and the twelfth most selected during "winter". The low ranking of oak during the "winter" is likely related to the relatively low use of these areas by deer during the winter months. Areas of oak provide little thermal cover during the winter in comparison to the conifer-dominated lowland areas where deer tend to yard. Non-conifer areas, including areas of oak also tend to have deeper snow depths than areas used as deeryards due to a much more open overstory during the winter (Verme 1965, Ozoga 1968, Moen 1976). These factors lead to low quality winter cover in areas dominated by oak and deer avoid areas of poor cover during the winter even if these areas provide plentiful browse (Verme 1965). The relatively low use of oak areas by deer during the winter (i.e. lower prey densities for wolves) likely leads to corresponding lower use by wolves. The movement of deer out of deeryards and back into more upland areas in spring likely raises the prey density in oak areas during the summer. The use of oak areas by deer may be related to mast production during the later portions of the "summer" period (as defined in this study). This may influence wolves to use oak areas more heavily during the summer than during the winter. Another factor that may be partly responsible for the high selection ranking of oak during the "summer" period is the use of these areas as denning sites. Oak in the H53SA tends to be associated with upland areas having light, more sandy soil types. Wolves in the H53SA dig dens in these lighter soils (Unger 1998) and may be spending more time in areas of oak during the summer due to denning behavior.

**Selection of Land Ownership Category**

The failure of the CA to identify any selection of land ownership category is not surprising. While some trends relating land ownership to biotic characteristics do seem apparent, (e.g., county owned lands tend to be more forested than privately owned lands) the correlations between land ownership and other biotic factors including land cover category are apparently not strong enough to effect selection of ownership category by wolves. The lack of consistent fine scale links between land ownership category and biotic factors affecting wolf use limits the usefulness of land ownership category as a predictor of wolf use of an area.

While CA indicated that the selection of ownership category was not different from random at either the landscape or within-territory levels of selection, the raw data did support past findings in the area. Both Mladenoff et al. (1995) and I found that county owned lands were the most common ownership category within wolf pack territories and that the percentage of county owned lands was higher in pack territories than in the entire study area. The reverse was true in both studies with private lands comprising higher proportions of the study areas than pack territories. These results are likely due to the low human development of and activity within county owned lands in comparison to privately owned lands.

**Use of Buffers Around Roads**

My examination of wolf use of areas around roads was limited by the lack of telemetry locations during periods of darkness, but it does seem to indicate that wolves are avoiding areas within 250 m of roads during periods of daylight. Vehicular traffic and other activities along roads and trails are generally heavier during daylight periods and the avoidance of these areas during the day is not surprising. While most use of roads and trails by wolves likely takes place between sunset and sunrise, the avoidance of roads during the day could potentially limit wolf habitat use and movements if the proportion of the landscape in proximity to roads and trails becomes too high. Over 40% (418,764 of 1,017,528 ha) of the H53SA is within 250 m of a road or a trail; wolves are avoiding nearly one half of the area during daylight periods.

While wolves are most active during the night in the summer, they travel and hunt extensively during the day in the winter (Mech 1970). The avoidance of roads and trails could particularly constrain wolf activities in areas of high road densities during the winter. The avoidance of roads during daylight may be one of the underlying reasons that past authors (Thiel 1985, Jensen et al. 1986, Mech et al. 1988, Mladenoff et al. 1995) have found an upper limit to road density in areas occupied by wolves. If wolves are avoiding areas around roads during daylight hours and much of normal wolf activity during the winter takes place during daylight, there is likely a level of road density that will not allow enough freedom of movement for wolves to satisfy their life needs during winter. This may be a specific example of the type of mechanism that leads to the avoidance of areas of high road density when wolves are establishing territories. The avoidance of areas around roads and trails does not seem to be limiting the wolf population in the H53SA, but it is likely that some level of road density would cause this avoidance to limit the population.

## SUMMARY AND MANAGEMENT IMPLICATIONS

The status of any wolf population is dependant on two primary factors (Fuller 1989). These are: 1) the level of human tolerance of and or legal protection of wolves and 2) given human tolerance, the density of large ungulate prey species, which in Wisconsin primarily consist of white-tailed deer. Any discussion of management issues for wolves must focus on these two factors at least as heavily as any more habitat specific issues.

The gray wolf population in Wisconsin will be reclassified under the ESA within the foreseeable future. This will lead to lower levels of legal protection and eventually to the total removal of legal protection. Human tolerance of wolves will become even more important in maintaining viable wolf populations after legal protection for them is removed. While the need to maintain a minimum biologically viable population should set a lower limit for a target population, social carrying capacity must also be considered when setting population goals.

Current forestry harvest practices are maintaining quality white-tailed deer habitat throughout much of wolf range within Wisconsin (Mladenoff et al. 1997). Deer prefer early succesional forests with ample openings (Fuller et al. 1992, Mladenoff and Stearns 1993, Fuller 1995). The abundance of this type of habitat maintained by current forest harvest practices promotes a high density of white-tailed deer, which in turn supports growing populations of wolves. Thus, where wolves are tolerated by humans and or legally protected, maintaining current forestry harvesting practices constitutes productive habitat management for wolves. While maintaining high populations of deer is almost inarguably good for wolf populations it is not, as discussed by Mladenoff et al. (1997) good for some other components of the ecosystem including regeneration of vegetation species highly preferred by deer as browse (Anderson and Loucks 1979, Verme and Johnson 1986, Alverson et. al. 1988, Tilghman 1989, Pregitzer, 1990).

The apparent connection between the avoidance of humans and the habitat use of prey species and the cover type selection of wolves observed in this study, support the paradigm that “wolves are habitat generalists that are not habitat specific to a vegetation or ecosystem type in the sense of sensitivity to a particular habitat structure” (Mladenoff et al. 1995). Since wolf management does not need to focus on habitat creation or preservation in a conventional sense, management efforts should focus on maintaining high levels of public tolerance for wolves and quality habitat for prey species, especially white-tailed deer.

While recent literature indicates that wolves are successfully colonizing areas with road densities higher than past perceptions would have regarded as suitable habitat (Merrill 2000, Chapter 2 this document), my findings on the avoidance of areas within 250m of roads suggest that road density may still be a limiting factor in wolf habitat suitability. If wolves are avoiding areas near roads, there is likely a level of road density which will place too much of a potential territory within the area being avoided for the territory to be viable. If a primary management goal is maintaining quality wolf habitat, it may become necessary to set upper limits on road density to avoid this situation. Average road density within pack territories in the H53SA during 1992-2001 was 1.09 km/km$^2$ (Chapter 2, this document). Territories established in 1999 had an average road density of 1.37 km/km$^2$ (Chapter 2, this document). Packs in territories with both these levels of road density appear to be viable and therefore, at least in northern Wisconsin, there seems to be no need to limit road densities to levels below 1.09-1.37 km/km$^2$. While I observed no signs that a road density of 1.37 km/km$^2$ was approaching the upper limit of road density for a viable pack territory, areas with road density greater than this may prove to be unsuitable.

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Appendix A. Original and consolidated land cover categories within the Highway 53 Study Area in northwest Wisconsin.

| WISCLAND code | Description | Consolidated code |
|---|---|---|
| 100 | URBAN/DEVELOPED | 100 |
| | High Intensity | |
| 104 | Low Intensity | |
| 110 | AGRICULTURE | 110 |
| 113 | Corn | |
| 118 | Other row crops | |
| 124 | Forage crops | |
| 150 | GRASSLAND | 150 |
| 162 | JACK PINE (*Pinus banksiana*) | 162 |
| 163 | RED PINE (*P. resinosa*) | 163 |
| 166 | WHITE SPRUCE (*Picea glauca*) | Excluded from analysis |
| 173 | MIXED/OTHER CONIFEROUS | 173 |
| 176 | ASPEN (*Populus spp.*) | 176 |
| 177 | OAK (*Quercus spp.*) | 177 |
| 179 | Northern pin oak (*Q. palustris*) | |
| 180 | Red oak (*Q. rubra*) | |
| 183 | MAPLE (*Acer spp.*) | 183 |
| 185 | Sugar Maple (*Acer saccharum*) | |
| 187 | MIXED/OTHER BROAD LEAVED DECIDUOUS | 187 |
| 190 | MIXED DECIDUOUS/CONIFEROUS | 190 |
| 200 | OPEN WATER | Excluded from analysis |
| 211 | EMERGENT/WET MEADOW | 211 |
| 212 | Floating aquatic vegetation | |
| 217 | LOWLAND SHRUB | 217 |
| 218 | Broad-leaved deciduous | |
| 219 | Broad-leaved evergreen | |
| 220 | Needle-leaved | |
| 222 | FORESTED WETLAND | 222 |
| 223 | Broad-leaved deciduous | |
| 229 | Coniferous | |
| 234 | Mixed deciduous/coniferous | |
| 240 | BARREN | Excluded from analysis |
| 250 | SHRUBLAND | 250 |

Appendix B. Compositional analysis based pair-wise comparisons of landscape level land cover category selection by gray wolves in the Highway 53 Study Area of northwest Wisconsin 1995-2001[A].

| Land cover[B] category | 110 | 150 | 162 | 163 | 173 | 176 | 177 | 183 | 187 | 190 | 211 | 217 | 222 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 150 | +* | | | | | | | | | | | | |
| 162 | + | - | | | | | | | | | | | |
| 163 | +* | - | +* | | | | | | | | | | |
| 173 | +* | + | +* | + | | | | | | | | | |
| 176 | +* | +* | +* | +* | + | | | | | | | | |
| 177 | +* | - | + | - | - | -* | | | | | | | |
| 183 | +* | + | + | + | - | - | + | | | | | | |
| 187 | +* | +* | +* | + | + | - | + | + | | | | | |
| 190 | +* | - | + | + | - | - | + | - | - | | | | |
| 211 | +* | +* | +* | + | + | - | + | + | - | + | | | |
| 217 | +* | +* | +* | + | + | + | +* | + | + | + | +* | | |
| 222 | +* | +* | +* | +* | +* | + | +* | +* | + | +* | +* | + | |
| 250 | + | -* | - | -* | -* | -* | - | - | -* | - | -* | -* | -* |

[A] + indicates category in left column was preferred over category in top row.
- indicates category in top row was preferred over category in the left column.
* indicates preference was significant based on a *t* distribution at $\alpha = 0.05$.

[B] Definitions of WISCLAND land cover category codes:

110 Agricultural
150 Grassland
162 Jack Pine
163 Red pine
173 Mixed/other coniferous
176 Aspen
177 Oak
183 Maple
187 Mixed/other broad-leaved deciduous
190 Mixed/deciduous coniferous
211 Emergent/wet meadow
217 Lowland shrub
222 Forested wetland
250 Shrubland

Appendix C. Compositional analysis based pair-wise comparisons of within-territory land cover selection by gray wolves in the Highway 53 Study Area of northwest Wisconsin 1995-2001[A].

| Land cover[B] category | 110 | 150 | 162 | 163 | 173 | 176 | 177 | 183 | 187 | 190 | 211 | 217 | 222 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 150 | - | | | | | | | | | | | | |
| 162 | - | + | | | | | | | | | | | |
| 163 | - | + | + | | | | | | | | | | |
| 173 | - | - | - | - | | | | | | | | | |
| 176 | +* | +* | + | + | + | | | | | | | | |
| 177 | +* | + | + | - | + | - | | | | | | | |
| 183 | - | + | - | - | + | - | - | | | | | | |
| 187 | - | + | + | - | + | - | - | + | | | | | |
| 190 | - | + | + | + | + | - | - | + | + | | | | |
| 211 | - | + | + | - | + | - | - | + | + | - | | | |
| 217 | - | +* | + | + | + | - | - | + | + | - | + | | |
| 222 | +* | +* | +* | +* | *+ | +* | + | +* | + | + | +* | + | |
| 250 | - | + | - | - | + | - | - | + | - | - | - | - | - |

[A] + indicates category in left column was preferred over category in top row.
- indicates category in top row was preferred over category in the left column.
* indicates preference was a significant based on a $t$ distribution at $\alpha = 0.05$.

[B] Definitions of WISCLAND land cover category codes:

110 Agricultural
150 Grassland
162 Jack Pine
163 Red pine
173 Mixed/other coniferous
176 Aspen
177 Oak
183 Maple
187 Mixed/other broad-leaved deciduous
190 Mixed/deciduous coniferous
211 Emergent/wet meadow
217 Lowland shrub
222 Forested wetland
250 Shrubland

Appendix D. Compositional analysis based pair-wise comparisons of within-territory land cover selection by gray wolves in the Highway 53 Study Area of northwest Wisconsin during "summer" seasonal periods (15 April-14 September) 1995-2001[A].

| Land cover[B] category | 110 | 150 | 162 | 163 | 173 | 176 | 177 | 183 | 187 | 190 | 211 | 217 | 222 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 150 | -* | | | | | | | | | | | | |
| 162 | - | + | | | | | | | | | | | |
| 163 | - | + | + | | | | | | | | | | |
| 173 | - | + | - | - | | | | | | | | | |
| 176 | - | +* | +* | + | +* | | | | | | | | |
| 180 | + | + | + | + | + | + | | | | | | | |
| 183 | - | + | + | + | + | - | - | | | | | | |
| 187 | - | + | + | + | + | - | - | + | | | | | |
| 190 | - | + | + | + | + | - | - | + | - | | | | |
| 211 | - | + | + | + | + | - | - | + | - | - | | | |
| 217 | - | + | + | + | + | - | - | + | - | - | - | | |
| 222 | + | +* | + | + | + | + | - | + | + | + | + | + | |
| 250 | -* | - | - | - | - | -* | -* | -* | -* | -* | -* | -* | -* |

[A] + indicates category in left column was preferred over category in top row.
- indicates category in top row was preferred over category in the left column.
* indicates preference was a significant based on a *t* distribution at $\alpha = 0.05$.

[C] Definitions of WISCLAND land cover category codes:

110 Agricultural
150 Grassland
162 Jack Pine
163 Red pine
173 Mixed/other coniferous
176 Aspen
177 Oak
183 Maple
187 Mixed/other broad-leaved deciduous
190 Mixed/deciduous coniferous
211 Emergent/wet meadow
217 Lowland shrub
222 Forested wetland
250 Shrubland

Appendix E. Compositional analysis based pair-wise comparisons of within-territory land cover selection by gray wolves in the Highway 53 Study Area of northwest Wisconsin during "winter" seasonal periods (15 September – 14 April) 1995-2001[A].

| Land cover[B] category | 110 | 150 | 162 | 163 | 173 | 176 | 177 | 183 | 187 | 190 | 211 | 217 | 222 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 150 | - | | | | | | | | | | | | |
| 162 | - | + | | | | | | | | | | | |
| 163 | - | - | - | | | | | | | | | | |
| 173 | - | + | - | + | | | | | | | | | |
| 176 | + | + | + | + | + | | | | | | | | |
| 177 | - | - | - | + | - | - | | | | | | | |
| 183 | - | - | - | + | - | - | - | | | | | | |
| 187 | + | + | + | + | + | - | + | + | | | | | |
| 190 | - | + | - | + | + | - | + | + | - | | | | |
| 211 | - | + | - | + | + | - | + | + | - | + | | | |
| 217 | + | +* | + | + | + | + | + | +* | + | + | + | | |
| 222 | +* | +* | +* | +* | +* | +* | +* | +* | +* | +* | +* | + | |
| 250 | - | + | - | - | + | - | - | + | - | + | - | - | -* |

[A] + indicates category in left column was preferred over category in top row.
- indicates category in top row was preferred over category in the left column.
* indicates preference was based on a $t$ distribution at $\alpha = 0.05$.

[B] Definitions of WISCLAND land cover category codes:

110 Agricultural
150 Grassland
162 Jack Pine
163 Red pine
173 Mixed/other coniferous
176 Aspen
177 Oak
183 Maple
187 Mixed/other broad-leaved deciduous
190 Mixed/deciduous coniferous
211 Emergent/wet meadow
217 Lowland shrub
222 Forested wetland
250 Shrubland

# CHAPTER 4

# GRAY WOLF DEN SITE SELECTION IN NORTHWEST WISCONSIN: ADDITIONAL DATA

## INTRODUCTION

Much effort has been focused on investigating biotic and abiotic attributes of gray wolf (*Canis lupus*) dens and den site selection (Joslin 1966, Joslin 1967, Mech 1970, Peterson 1977, Ballard and Dau 1983, Unger 1998). This is likely due to the importance of den sites to overall wolf ecology and population dynamics. The location of den sites may determine the reproductive success of each wolf pack (Harrington and Mech 1982) and have a direct influence on overall population dynamics of the wolf population in an area.

Investigations have examined both pack-level and micro-scale selection of den sites. Ballard and Dau (1983), Gehring (1995), and Unger (1998) reported that den sites tended to be located in the approximate center of territories. Stephenson and Johnson (1973) and Ballard and Dau (1983) examined the distance between the dens of adjacent packs and reported that the average distance between dens was approximately 40 - 45 km. Mech (1970) and Fuller (1983) noted that den sites appeared to be selected based on slope, sandy soil, and aspect. Lawhead (1983) also examined micro-scale selection and reported that depth to permafrost, active soil layer thickness, and drainage were important attributes influencing den site location.

The importance of den success and den site placement led the WDNR to investigate den site characteristics and placement (Unger 1998) as a component of the overall H53 Expansion Project (Kohn et al. 2000). The study by Unger (1998) used a geographic information system (GIS) to analyze den site locations within annual territories in relation to 1) an arbitrarily defined inner core of the territory, 2) roads, and 3) land cover categories. He also conducted a logistic regression analysis on the variables collected at dens and corresponding random sites to determine which variables most influenced den site selection. Unger (1998) found that wolves were selecting a central core of a territory for dens. This inner core was centered in the territory and was the same shape as the territory boundary, but encompassed only 25% of the territory's area. Unger (1998) hypothesized that the prevention of interpack strife and optimal foraging behavior might explain this behavior. He also reported that at the microscale level, wolves selected for areas of sandy soil and steeper slope, possibly for ease of digging and drainage purposes.

While providing useful insight into wolf den site placement and characteristics, Unger's (1998) investigation was conducted on a relatively small number of dens (n = 13) due to the relatively small number of den sites across any landscape and the difficulty in locating them. When research examining other aspects of wolf ecology (Chapters 2 and 3, this document) in the H53SA began, the WDNR requested that effort be directed at locating and delineating additional den sites as part of the continuing wolf population monitoring program. With this request in mind, I attempted to locate wolf den sites during the summers of 1998-2000 and to investigate den site location and characteristics in a manner similar to that used by Unger (1998).

The objectives of this study were to: 1) locate and delineate gray wolf den sites within the H53SA, 2) determine which landscape level factors (placement within territory central core, presence/absence of and density of roads near dens) most influence wolf den site selection, and 3) determine if wolves are selecting land cover categories in a non-random manner when establishing dens.

## METHODS

### Capture, Handling, and Radiotelemetry

All methods follow those used by Unger (1998) unless noted. Wolves were trapped by WDNR personnel using modified #14 Newhouse leg-hold traps (Schultz et al. 1996) during May-August in 1997-2000. Captured wolves were immobilized using a mixture of ketamine hydrochloride/xylazine hydrochloride administered with a jabstick. Any trap-related injuries were treated, blood samples were taken, an injection of antibiotics was administered, and animals were weighed. Animals > 15kg were also fitted with radio collars (Telonics Inc., Mesa, Arizona) and uniquely numbered ear tags. Yohimbine was administered as reversal agent for the xylazine and the animals were monitored until they could move away from the trap site under their own power.

Radio-collared animals were located 1-5 times per week during 1997-2000 using telemetry from fixed-wing aircraft (Ballard and Dau 1983, Fuller 1989) or a vehicle-mounted 5-element Yagi directional antenna until radio failure, death of the animal, or a permanent movement out of the study area. The majority (>90%) of locations were collected during daylight hours and a minimum of 3 bearings were collected for each location. Triangulations for locations collected on the ground where solved using a Lenth estimator (Lenth 1981) in the program Locate II (Pacer, Turo Nova Scotia, Canada). Date, time, Universal Transverse Mercator (UTM) coordinates, ear tag number, and pack were recorded for each telemetry location. Animals were classified as belonging to individual packs based on trapping location and movement patterns.

## Den Site Location and Delineation

Areas that showed a tight cluster of telemetry locations (generally >3 locations in a 1 $km^2$ area) between February and April were searched for dens between July and September of the same year. The locations of dens were recorded using a hand-held global positioning system (GPS) (Garmin International, Lenexa, Kansas) and mapped using ArcView (Environmental Systems Research Incorporated, Redlands, CA).

Annual territory boundaries were estimated using the 95% minimum convex polygon method (MCP) (Mohr 1947) in the animal movement analysis extension in ArcView (Hooge and Eichenlaub 1997). The MCP estimation technique was used instead of the fixed kernel used in chapters 2 and 3 to avoid the potential bias caused by examining telemetry locations centered on the den. Due to the algorithms used in a kernel technique, the clusters of locations around dens would have made it more likely that dens were located in the center of estimated territories. A 95% MCP was used to maximize the distribution of wolf locations while allowing outliers to be eliminated. Unger (1998) used a 99% MCP, but with territory estimation generally based on less than 100 telemetry locations, I believed that a 99% MCP allowed for the removal of an unacceptably small number of potential outlier points.

Territories were required to have at least 30 locations (Fuller and Snow 1988) obtained in at least 6 different months of the year to be included in analysis. Territories were estimated based on yearly telemetry locations. A year was defined as 1 June to 30 May. This led to the calculation of territory boundaries based on telemetry locations from approximately the time of den site abandonment the previous year through the denning period the year of analysis.

Random sites corresponding to each den site were generated within territories based on 1 random site per 4,000 ha of territory (Unger 1998). All variables examined at den sites were also analyzed at random sites.

**Analysis of Variables Influencing Den Site Selection**

To examine whether wolves were placing dens near the center of their territories as observed by Ballard and Dau (1983), Gehring (1995), and Unger (1998), I generated an area the same shape as the estimated territory boundary, but occupying 25% of the area of the entire territory and centered in the territory; hereafter referred to as core areas. Core areas were created in ArcView by calculating the size of an area encompassing 25% of the total area of territories. Territory boundaries were negatively buffered (buffers were inside the boundary, not outside) at a distance that resulted in a polygon that encompassed 25% of the area of the territory. Location of dens and random points were recorded as occurring within this core area or outside of it. This technique was used by Unger (1998) and the selection of a core encompassing 25% of the area of a territory was an arbitrary choice.

When examining the affect of roads on den placement, Unger (1998) created a 1000 m radius buffer zone around the den or random point and overlaid these sites with a roads coverage in ArcView. I chose instead to base the size of this buffer on the average distance from the den an alpha female would travel (1212 m) during the denning period (1 April – 1 July) based on radio telemetry locations. This distance was based on the one confirmed alpha female monitored during the study. While this technique relied on data from only one individual, I believed that it was more tightly tied to the biology of the species and equally as valid as any arbitrarily set distance. The roads coverage used in this analysis was based on U. S. Geologic Survey 1:100,000 scale Digital Line Graphs and included all road features that were not classified as trails. Presence or absence of roads within buffers around dens or random points was recorded. Road density ($km/km^2$) was also calculated by determining the straight-line distance of all road segments within a territory in ArcView and dividing by the area of the territory.

A Fisher's Exact test ($\alpha = 0.10$) was used to test for differences in the frequency of den or random site location within the 25% inner core of territories. This test ($\alpha = 0.10$) was also used to examine differences in the occurrence of roads within the buffer around dens and random sites. A two sample T-test ($\alpha = 0.10$) was used to test for differences in road densities within buffers around dens and random sites.

When analyzing the selection of land cover type category around den and random sites, Unger (1998) created an arbitrarily defined 400 ha plot centered on the den or random site. He judged this area to represent the area that wolves would most likely use during the denning period. I chose instead to base the size of this buffer on the average distance from the den an alpha female would travel (1212 m) during the denning period (1 April – 1 July) based on radio telemetry locations. Buffers of this size were created around each den and random point in ArcView.

The proportions of buffers around each den and random point classified as grassland, pine, mixed/other conifer, aspen, oak, maple, mixed/other broad leaved deciduous, mixed deciduous/coniferous, emergent wet meadow, lowland shrub, forested wetland, and shrubland within the WDNR's GIS WISCLAND land cover classification system (http://www.dnr.state.wi.us/org/at/et/geo/data/wlc.htm) was calculated. These 12 categories were consolidated from the original 28 categories present within the H53SA.

This consolidation was conducted based on the following 3 criteria. Any cover type that represented less than 0.10% of all territories being examined and which was present in the den and random site buffers in less than 4 pack territories was excluded from analysis. Any cover type category, which based on traditional paradigms of wolf ecology, would not be used by wolves for denning (i.e., open water and urban) was excluded from the analysis. Similar cover types that represented little variability in resources to wolves were combined (i.e., red oak *Quercus rubra* and northern pin oak *Quercus ellipsoidalis*). The proportion of each cover type category was examined for differences between buffers around dens and random unused points with a T-test ($\alpha = 0.10$).

The calculated proportions of each land cover category, presence or absence of and density of roads within 1212 m of den or random site, and placement within or outside the 25% inner core of the territory were all entered into a forward step logistic regression analysis to further determine which measured variables influence den site selection. All non-categorical and non-binomial variables were analyzed with a Pearson rank correlation analysis to identify variables that were correlated before entering them into the logistic analysis.

A compositional analysis (CA) (Aebischer et al. 1993) was conducted ($\alpha = 0.10$) to examine selection of the 12 consolidated cover types in areas around dens and random sites. CA involves a use vs. availability approach to delineate and quantify selection, while avoiding the problem of non-independence of proportions calculated for use and availability in many habitat selection techniques. The proportions of each cover type in the buffers around den sites represented "use" in this analysis. The proportion of the entire territory classified as each cover type category of interest represented "availability." These proportions were calculated by determining the area of each pack territory in a land cover category within ArcView and dividing by the total area of the territory. The calculations for CA were conducted using ReSelect software (http://ces.iisc.ernet.in/hpg/envis/resdoc1120.html).

## RESULTS

### Den Site Location and Delineation

Nine dens were located during 1998-2000. The locations of 5 additional dens from 1993-1996 that could not be analyzed during the Unger (1998) study were provided by D. Unger (Alderson Broaddus College, Phillipi, VA.), resulting in 14 den sites for analysis. Forty-three (1-7 per territory based on 1/4000 ha) random unused points corresponding to den sites were generated. Using a 1212m radius to buffer dens and random sites resulted in buffers of 461 ha for analysis of land cover category.

### Variables Influencing Den Site Selection

Den sites (11 of 14, 78%) were more likely ($p = 0.002$) to fall within the 25% inner core of a territory than random points (15 of 44, 35%). Dens (7 of 14, 50%) were also less likely ($p = 0.029$) to occur within 1212 m or less of a road than random points (33 of 43, 76%). Average road density within buffers around dens was less ($p = 0.095$) than around random points (0.37km/km$^2$ vs. 0.61km/km$^2$, respectively).

Analysis of the proportion of land covers within buffers around dens and random points indicated that pine, oak, and shrub categories comprised higher proportions of buffers around dens sites (Table 4.1). This analysis also indicated that lowland shrub comprised lower proportions of buffers around den sites than random sites (Table 4.1).

Table 4.1 Land cover category composition in 1212m radius buffers around gray wolf dens (n =14) and corresponding random sites (n =43) in the H53SA in northwest Wisconsin 1993-2000.

| Land cover category | $\bar{x}$ % composition (SE) of den buffers | | $\bar{x}$ % composition (SE) of random point buffers | | $p^A$ |
|---|---|---|---|---|---|
| Oak | 3.3 | (1.1) | 3.0 | (1.0) | 0.014 |
| Pine | 8.1 | (2.9) | 5.6 | (1.6) | 0.071 |
| Shrub | 6.3 | (2.5) | 3.6 | (1.5) | 0.093 |
| Lowland shrub | 10.1 | (2.3) | 16.0 | (1.8) | 0.068 |
| Aspen | 22.1 | (2.2) | 26.9 | (2.2) | 0.194 |
| Forested wetland | 12.1 | (1.8) | 12.1 | (1.0) | 0.579 |
| Mixed/other coniferous | 1.4 | (0.4) | 1.4 | (0.3) | 0.286 |
| Grassland | 6.7 | (0.9) | 6.9 | (1.2) | 0.331 |
| Maple | 1.5 | (0.4) | 1.5 | (0.4) | 0.661 |
| Emergent wet meadow | 2.5 | (0.9) | 3.1 | (0.7) | 0.743 |
| Mixed deciduous/coniferous | 3.9 | (1.1) | 5.8 | (1.0) | 0.736 |
| Mixed/other deciduous | 15.1 | (3.9) | 13.9 | (1.8) | 0.949 |

$^A$ Significant at $\alpha = 0.10$ t-test

No other differences in land cover category composition between den and random sites were observed (Table 4.1).

The Pearson rank correlation matrix of variables being considered for inclusion in the logistic regression indicated that no variables were highly correlated (r in all cases < 0.5). When all landscape and land cover type variables were entered into the forward step logistic procedure, the final model output consisted of the logistic generated intercept and binomial response for location within or outside of the 25% inner core of the territory. A backward step regression procedure resulted in the same combination of variables. The equation for this model was: $p = \dfrac{-2.268 + 1.959(C)}{1 - 2.268 + 1.959(C)}$

With a logit of: p = -2.268 +1.959 (C) where C is the binomial response of within or outside the 25% inner core of the territory. Tests of classification accuracy for logistic models involve converting the output of the logistic equation for each observation to a binomial (0/1, success/failure, den/random) response through the use of a cutpoint (*c*) (Hosmer and Lemeshow 2000) between 0.0 and 1.0. If the output of the logistic regression equation for an individual observation falls below *c*, the observation is predicted to be in group 0 (failure, in this case a random unused point). If the logistic output is above this *c*, the observation is predicted to be part of group 1 (success, in this case a den site). The actual groups that each individual observation belongs to are compared to the predicted groups to determine the classification accuracy of the logistic model. The ability to vary the *c* between the 0.0-1.0 probability interval allowed me to determine the optimal value of *c* for successfully classifying used and unused sites (Pereiara and Itami 1991). The maximum classification accuracy for the logistic equation based on inner 25% core location was reached at a *c* of 0.40. Using this *c*, the model correctly classified 11 of 14 den sites (79%) and 29 of 43 random sites (67%) for an overall classification accuracy of 70%.

Results from the CA indicated that mixed deciduous, aspen, and lowland shrub categories were the three most selected cover types and that maple, grassland, and oak were the three least selected cover types by wolves (Table 4.2 and Appendix B).

**DISCUSSION**

My findings that wolves tend to place dens near the center of their territory support the findings of Ballard and Dau (1983), Gehring (1995), and Unger (1998), but refute those of Ciucci and Mech (1992) who found that within an area encompassing the inner 60% of monitored territories, dens were located randomly. The use of the 60% inner core by Ciucci and Mech (1992) compared to the inner 25% inner core in this study and by Unger (1998) makes direct comparisons of results problematic.

Ciucci and Mech (1992) suggested that the tendency to place dens in the center of territories was related to the comparatively larger territory sizes of the Alaskan wolves observed by Ballard and Dau (1983). Wolves must repeatedly bring food sources to the den to support the pups (Mech 1970, Groebner 1991) and have been shown to travel long straight line distances when bringing prey to the den (Mech 1970, Young and Goldman 1944). Therefore, the benefits of a centrally located den to travel and foraging efficiency when supporting the alpha female and pups at the den seem evident, but may not be entirely dependent on territory size. Both Unger (1998) and I documented the tendency to locate dens in the center of territories even though the observed territory size in both studies (202km/km$^2$ and 142 km/km$^2$, respectively) were comparable to those observed in

Table 4.2. Compositional analysis rankings (1 most preferred, 12 least preferred) of land cover category selection at gray wolf den sites within the Highway 53 Study Area in northwest Wisconsin 1993-2000.

| Cover Type Category | CA Ranking |
|---|---|
| Mixed/other broad-leaved deciduous | 1 |
| Aspen | 2 |
| Lowland shrub | 3 |
| Emergent wet meadow | 4 |
| Mixed deciduous/coniferous | 5 |
| Shrubland | 6 |
| Mixed/other coniferous | 7 |
| Forested wetland | 8 |
| Pine | 9 |
| Oak | 10 |
| Grassland | 11 |
| Maple | 12 |

Minnesota (Van Ballenberghe et al. 1975, Fritts and Mech 1981, Berge and Kuehn 1982, Fuller 1989) and smaller than those observed in Alaska (Peterson et al. 1984).

The other hypothesis explaining the tendency of wolves to place dens in the center of territories is that this tendency is a mechanism to avoid contact and conflict with wolves from other packs (Ciucci and Mech 1992, Unger 1998). Past authors have shown that buffer zones between packs are often the site of interpack aggression and occasional mortality (Peters and Mech 1975, Fritts and Mech 1981). Ciucci and Mech (1992) also found that neighboring packs had a major influence on territory use and the distribution of kills and hypothesized that adjacent packs could also influence den location. My data seem to support the hypothesis that wolves tend to place dens in the center of territories because this lowers the probability of wolves not in the natal pack encountering the den. Of the 3 dens that were not located in the 25% inner core of the territory, 2 were in territories, which to my knowledge had no other territories directly abutting them. The lack of the threat of aggression from wolves directly neighboring these packs may have allowed placement of the den in other than the center of the territory.

The lower road densities in buffers around pack territories than in buffers around random sites is consistent with the documented avoidance of roads related to overall wolf ecology (Mladenoff et al. 1995, 1999, Chapters 2 and 3, this document) as well as past research in the H53SA (Unger 1998). The avoidance of roads during such a sensitive segment of the wolf life cycle as denning, is not surprising since wolves avoid roads and the associated human activity when establishing territories (Mladenoff et al. 1995, 1999, Chapters 2 and 3, this document).

The results from CA and the comparison of land cover category composition between den and random sites indicated that wolves are selecting for cover types indicative of well-drained upland soils. This is consistent with Unger's (1998) findings in the same area and is likely related to the nearly exclusive use of excavated burrows as dens in the H53SA. Unger (1998) observed that 11 of 12 dens he located were burrows and all of the dens analyzed in this study were burrows. Excavating a den is presumably easier and more efficient in well-drained upland soils than more lowland areas.

## SUMMARY AND MANAGEMENT IMPLICATIONS

Disturbance of den sites may have an effect on the denning behavior of wolves (Stephenson 1974, Joslin 1966, 1967). This coupled with the importance of the den site and denning behavior of wolves on the local wolf population (Harrington and Mech 1982) emphasizes the importance of being able to predict potential den sites. If potential denning areas can be identified, limitations on highly disruptive human activities during the denning season can be imposed in these areas. Areas with a high likelihood of den site usage could also potentially be protected by limiting access on a longer-term basis or by limiting road density as management priorities dictate.

Based on the results of this study and that of Unger (1998), the most useful indicator of wolf den site placement is location within the inner 25% core of a pack territory. Delineating this core area requires the estimation of the boundaries of the territory of interest. This is easiest when radio telemetry locations on the pack are available, but as the wolf population in the upper Great Lakes region continues to increase and is reclassified under the Endangered Species Act, progressively smaller percentages of the population will be monitored via radio telemetry. Although this increases the effort required to determine the inner 25% core, the WDNR already estimates the boundaries of approximately 35% of the pack territories in the state using techniques other than radio telemetry (i.e., track surveys, howling surveys) as part of their population monitoring program (A. Wydeven, J. Wydenhoff, WDNR, pers. commun). This indicates that territory boundaries and the inner 25% core of a territory can be determined during normal management activities.

Once the inner 25% core of a territory has been located, other factors affecting den site selection (land cover type category, road density) can be used to further refine predictions of likely den sites. This insight into potential denning areas will prove useful whether the objective of determining the den site is to restrict access to the area, locate the den for research purposes, or any other management activity.

The majority of cattle depredations by wolves in the H53SA during the course of my study occurred during the denning period. This was apparently due to the combination of wolves foraging to bring constant food sources back to the den and the availability of young and relatively vulnerable cattle during this period. Unger (1998) suggested that the tendency of wolves to place dens in the 25% inner core of a territory could prove useful to managers when dealing with depredation problems. He suggested "Given that wolves may be selecting the inner core of their territory for a den site to minimize interpack conflict, recorded wolf howling and/or distribution of wolf scat may deter wolves from placing the den in an undesirable location," the undesirable location referring in this case to den placement in proximity to cattle farms. Additionally, farms located within the 25% inner core of territories could be targeted for educational programs and funding for measures targeted at preventing depredation such as improved cattle enclosures, guarding dogs, and wolf exclusion techniques.

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Appendix A. Original and consolidated land cover categories used for compositional analysis in 1212m buffers around den and random points within the Highway 53 Study Area in northwest Wisconsin.

| WISCLAND code | Description | Consolidated code |
|---|---|---|
| 100 | URBAN/DEVELOPED | Excluded from analysis |
| | High Intensity | |
| 104 | Low Intensity | |
| 110 | AGRICULTURE | Excluded from analysis |
| 113 | Corn | |
| 118 | Other row crops | |
| 124 | Forage crops | |
| 150 | GRASSLAND | 150 |
| 160 | PINE | |
| 162 | Jack Pine (*Pinus banksiana*) | 162 |
| 163 | Red Pine (*P. resinosa*) | |
| 166 | WHITE SPRUCE (*Picea glauca*) | Excluded from analysis |
| 173 | MIXED/OTHER CONIFEROUS | 173 |
| 176 | ASPEN (*Populus spp.*) | 176 |
| 177 | OAK (*Quercus spp.*) | 177 |
| 179 | Northern pin oak (*Q. palustris*) | |
| 180 | Red oak (*Q. rubra*) | |
| 183 | MAPLE (*Acer spp.*) | 183 |
| 185 | Sugar Maple (*Acer saccharum*) | |
| 187 | MIXED/OTHER BROAD LEAVED DECIDUOUS | 187 |
| 190 | MIXED DECIDUOUS/CONIFEROUS | 190 |
| 200 | OPEN WATER | Excluded from analysis |
| 211 | EMERGENT/WET MEADOW | 211 |
| 212 | Floating aquatic vegetation | |
| 217 | LOWLAND SHRUB | 217 |
| 218 | Broad-leaved deciduous | |
| 219 | Broad-leaved evergreen | |
| 220 | Needle-leaved | |
| 222 | FORESTED WETLAND | 222 |
| 223 | Broad-leaved deciduous | |
| 229 | Coniferous | |
| 234 | Mixed deciduous/coniferous | |
| 240 | BARREN | Excluded from analysis |
| 250 | SHRUBLAND | 250 |

Appendix B. Compositional analysis based pair-wise comparisons of land cover category by denning gray wolves in the Highway 53 Study Area of northwest Wisconsin 1993-2000[A].

| Land cover[B] category | 150 | 162 | 173 | 176 | 180 | 183 | 187 | 190 | 211 | 217 | 222 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 162 | + | | | | | | | | | | |
| 173 | + | + | | | | | | | | | |
| 176 | +* | + | + | | | | | | | | |
| 180 | + | - | - | -* | | | | | | | |
| 183 | - | - | -* | -* | - | | | | | | |
| 187 | +* | + | + | + | +* | +* | | | | | |
| 190 | + | + | + | - | + | +* | - | | | | |
| 211 | +* | + | + | - | + | +* | - | + | | | |
| 217 | + | + | + | - | + | +* | - | + | + | | |
| 222 | + | + | - | - | + | +* | - | - | - | - | |
| 250 | + | + | + | - | + | +* | - | - | - | - | + |

[A] + indicates category in left column was preferred over category in top row.
- indicates category in top row was preferred over category in the left column.
* indicates preference was a significant based on a $t$ distribution at $\alpha = 0.05$.

[B] Definitions of WISCLAND land cover category codes:

150 Grassland
162 Pine
173 Mixed/other coniferous
176 Aspen
180 Oak
183 Maple
187 Mixed/other broad-leaved deciduous
190 Mixed/deciduous coniferous
211 Emergent/wet meadow
217 Lowland shrub
222 Forested wetland
250 Shrubland

# CHAPTER 5

# SYNTHESIS AND FUTURE RESEARCH DIRECTION

## SYNTHESIS

This final chapter is intended to provide a place to recap and consolidate the information presented in the previous chapters of this dissertation. It is also intended to provide me the opportunity to present some thoughts and or hypotheses on the implications of these data and their potential impacts on management actions. The final segment of this chapter will present suggestions for future research directions or topics that have been suggested by the results of the research conducted during this project.

Human tolerance of or legal protection of wolves and the density of large ungulate prey species are the two major limiting factors on most wolf population (Fuller 1989). Current forestry practices in Wisconsin are maintaining white-tailed deer populations at densities that can support wolf populations larger than the target population set by WDNR (Mladenoff et al. 1997, Wisconsin Department of Natural Resources 1999). Therefore, no change in forest management practices is currently required to support ungulate densities that can maintain healthy wolf populations in the state. However, maintaining current white-tailed deer populations within the state will have negative affects on other aspects of forest ecology, especially regeneration of browse species preferred by deer browse (Anderson and Loucks 1979, Verme and Johnson 1986, Alverson et. al. 1988, Tilghman 1989, Pregitzer, 1990). These problems should be considered when decisions regarding deer population management and the resultant effect on wolf populations are made.

Managing wolf populations at a level that promotes high levels of human tolerance is a more difficult task than managing for adequate prey populations. The wolf population in Wisconsin has consistently increased during the past 10 years (Wisconsin Department of Natural Resources 1999) and likely will exceed the target population set by WDNR in the near future. This target population was set at least in part in an attempt to maintain the wolf population below social carrying capacity and therefore to maintain high levels of public tolerance of wolves. If the wolf population is to be maintained at or below this level after ESA reclassification, it is likely that individuals will have to be removed from the population. This can be accomplished by paying professional hunters or trappers to cull animals or by implementing some form of public harvest. While the logistics of a public harvest would likely be problematic, the potential monetary savings and more importantly the potential gain in support for healthy wolf populations among the hunting and trapping public make a public harvest a viable management option. Due to the potential difficulties in establishing a public harvest of wolves (resistance by some segments of the public, and logistic concerns including harvest levels, harvest methods, and harvest zones) I recommend that WDNR begin exploring the possibility of a public harvest. Beginning to explore the possibility of and examine solutions to the difficulties of establishing a public harvest now will avoid lag time after ESA reclassification when a public harvest may be a needed population management option.

As predicted by their habitat generalist nature and normal avoidance of humans, land cover selection by wolves appears to be driven by the acquisition of prey and the avoidance of human activity. During this study, wolves selected forested wetland and lowland shrub when placing territories on the landscape. Areas of forested wetland are generally not hospitable to human activity that requires movement away from roads due to difficulty in walking, high biting insect populations in the summer, and the general lack of human development. This suggests that the selection of forested wetland areas is as much a result of low human activity and the corresponding lower probability of human disturbance or contact as a result of the cover type itself. This is also the likely causal factor behind lowland shrub, and emergent wet meadow being in the top five most selected cover types at the landscape level of selection. The selection of forested wetland areas by wolves may also have been influenced by prey densities in these areas due to the typical use of lowland conifer areas as yarding areas by white-tailed deer in severe winters. Wolves also highly selected aspen at the landscape level and within territories, presumably at least in part because of the high use of aspen areas by white-tailed deer and the resultant access to prey in these areas. Therefore, observed preferences in land cover category by wolves may actually reflect the importance of these land cover types to white-tailed deer, which is the main prey species of wolves in Wisconsin (Mandernack, 1983).

Under current levels of human tolerance and legal protection, wolves appear to be expressing their adaptable nature and colonizing areas that in the past would have been viewed as unsuitable. While this will likely lead to larger wolf populations that are less likely to experience catastrophic population declines that might force reevaluation of current efforts to reclassify them under the ESA, there are also potential negative effects of this expansion of wolf populations and range. It is generally accepted that human tolerance and the resulting level of human induced mortality is a major limiting factor on wolf population levels. As the wolf population in the Great Lakes region expands its geographic range into more human dominated areas, the potential for human/wolf conflict will increase. This in turn may lower levels of human tolerance and have negative impacts on the wolf population in the region, which may require resource agencies to adjust current management practices.

**Future Research Directions**

As with most research projects, the results I observed brought to mind additional questions. Investigating the answers to these questions could provide useful insight into wolf resource use and selection in Wisconsin. The following is a list of those questions and brief suggestions on how to address them.

The GIS model predicting favorable wolf habitat in PWR within Wisconsin generally matches existing wolf pack territories in the state (Chapter 2). However, there are 5 territories that occur in areas that are classified by the model as being in the lowest habitat suitability category. Assuming these territories are persistent, it seems that there must be some characteristic(s) of these areas that set them apart from other areas that the model classifies as being low suitability wolf habitat. Since wolves appear to be successfully using these areas, research into what sets them apart from other low suitability areas could provide insight into where wolves may occur in the future. Since a major component of the model is road density (as a surrogate for human activity), it is likely that wolves establishing territories in areas classified as containing low suitability habitat will have a higher likelihood of contact and conflict with humans. Increasing our understanding of what leads wolves to establish territories in these "high risk" areas will allow us to minimize the potential for human/wolf conflict.

In an attempt to avoid excessive "fishing" within my data and produce the most parsimonious model in Chapter 2, I only included 5 land cover categories in the analysis. The selection of land cover categories to be included in analysis was based on my understanding of their importance in wolf ecology. However, these 5 categories only encompassed approximately 55% of monitored pack territories and 25% of examined unused areas. It is possible that land cover categories occupying the rest of the landscape may have an impact on wolf territory placement. If this is true, a reanalysis of the data and reformulation of the logistic model underlying my GIS-based habitat model could provide a model with more predictive power.

In the logistic analysis of factors influencing den site placement (Chapter 4), location within the inner 25% core of a territory was identified as the main variable influencing den site placement. As noted in that chapter, the use of a 25% inner core versus any other measure of core area was based on past research in the H53SA (Unger 1998) and was arbitrary. Examining the affect of core areas of varying sizes could provide further insight into wolf den site placement.

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