CROSSING PATHS:

GRAY WOLVES AND HIGHWAYS IN THE MINNESOTA-WISCONSIN BORDER REGION

Submitted by:

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This thesis is arranged into two papers: (1) *Patterns in highway crossings by wolves in northwestern Wisconsin* and (2) *The influence of highways on estimates of suitable wolf habitat*. Both papers are formatted to Journal of Wildlife Management specifications.

Abstract

Highways may threaten wolf (*Canis lupus*) habitat connectivity in the Great Lakes Region. Highways may further define the useable amount and arrangement of habitat within areas identified as suitable habitat. The two papers of this thesis explored wolf habitat with respect to roads by: (1) inferring wolf habitat connectivity across a major highway from predictions of crossing habitat, and (2) identifying how highways influenced suitable habitat choices and within-territory movements.

Track searches, radio-telemetry, and observations identified 62 crossings of 4 major highways in northwestern Wisconsin between March 1991 and February 1999. Selected crossings (n=33) were visited to identify local crossing site characteristics. Compared to paired random sites wolves were equally likely to cross through forested and open landscapes ($p = 0.192$). In their immediate crossing environment, wolves favored factors related to visibility and ease of movement — less visual obscurity ($p = 0.003$) and less deciduous canopy cover ($p = 0.038$). Among the variables not significantly correlated with crossing sites were margin slope, maximum distance visible, shrub cover, and the presence/absence of trails or fences nearby. Satellite imagery data were used to map habitat composition and pattern within 25-400 ha of crossing sites. Patch density, an index to human-induced fragmentation, was the most significant and consistent indicator of crossing habitat across 5 landscape sampling resolutions ($p < 0.005$). Crossing landscapes had fewer patches, less open water, less developed land, and more forested or unforested wetlands than the available landscape matrix. Generally predictive ability increased with increased sampling area indicating that wolves perceived and reacted to landscape pattern at larger spatial scales. Some differences between

highways were noted, e.g., traffic volume and resident wolf activity in neighboring habitat, but the model captured elements of habitat selection specific to individual highways and common to all. Disperser and resident wolf crossings were equally represented by the model. Along U.S.H. 53 (a recently widened highway which bisects the primary wolf dispersal corridor in WI) the model mapped 68% of the road-adjacent habitat to have moderate-high crossing potential indicating a high degree of habitat connectivity. Highway crossing mitigations, e.g., widened medians and a highway underpass, were located where crossing potential was at least moderate. Only 20% (14 km) of the highway had high crossing potential of which 2 areas did not have any structural mitigations to aid crossings. The model was proved valid by 19 crossings reserved from analyses. Highway design may prove critical for continued connectivity as recreational and commercial use of the landscape increases in combination with increased traffic volume and vehicle speeds.

Along the Minnesota-Wisconsin border, individual wolves from 4-12 wolf packs were radio-monitored between 1992-96. Resident wolf locations (n=3,448) were compared to unused locations (n=3,535) – outside of known wolf territories – with respect to the amount of major highways, minor highways, and non-highway public roads found within 200-ha of each location. Univariate logistic regression models indicated that highways did not strongly influence suitable habitat choices (less than 22% accuracy for unused habitats) but the density of non-highway public roads did (74% overall accuracy). Overall road density was still the best predictor of suitable habitat (77% overall accuracy). No improvement in classification accuracy was achieved by segregating highways from non-highway public roads. Males and pups demonstrated less

tolerance for roads than females and older wolves ($p < 0.001$). All wolves combined demonstrated less tolerance for roads during the breeding and nomadic months ($p < 0.001$). These results indicated that not all habitats were equally available to wolves at all times — a critical consideration when estimating the total amount of useable wolf habitat in a given area. Sequential radio-locations (12-48 hours apart) were connected to investigate how often wolves crossed roads within their annual home ranges. Although highways were not a major factor in population-level habitat selection they strongly influenced within-territory movements ($p < 0.001$) which in turn affects the geographic arrangement of wolf territories in the landscape. All territories contained some non-highway public roads, and wolves were either indifferent or attracted towards such roads. In contrast only one-half of the territories contained a major highway. Minor highways were strongly avoided in regular movements ($p < 0.001$). Potential highway tolerance limits for this population were identified as 0.09 km/km^2 of major highways and 0.15 km/km^2 of minor highways within territories. Considering the amount and arrangement of highways in the landscape could further help to define the subset of "suitable" wolf habitat (based on overall road densities) which is truly "useable" habitat to the population.

Key words: gray wolf, connectivity, habitat selection, highways, Minnesota, movements, predictive model, roads, Wisconsin

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PAPER ONE: Patterns in highway crossings by wolves in northwestern Wisconsin.

PATTERNS IN HIGHWAY CROSSINGS BY WOLVES IN NORTHWESTERN WISCONSIN

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Abstract: Highways may threaten wolf habitat connectivity in the Great Lakes Region. Habitat choices at known highway crossing locations in northwestern Wisconsin were used to map crossing likelihoods along a recently widened section of U.S. Highway 53 — a highway which intersected the primary wolf dispersal corridor. Wolves crossed U.S.H. 53 year-round through a variety of habitats. Wolves were equally likely to cross highways through forested and open landscapes ($p = 0.192$). In their immediate crossing environment, wolves favored areas with little visual obstruction ($p = 0.003$) and less deciduous canopy canopy cover ($p = 0.038$). In the surrounding landscape, patch density — an index to human-induced fragmentation — was the most significant and consistent indicator of crossing habitat ($p < 0.005$) across 5 sampling resolutions ranging from 25-400 ha. Overall crossing landscapes had fewer patches, less open water, less developed land, and more forested or unforested wetlands than the available landscape matrix. Using the 200-ha sampling resolution, a multiple-variable, logistic model indicated that 68% of the U.S. Highway 53 expansion project had moderate-high crossing potential. Although connectivity is currently at a high level, suitable crossing areas will shrink over time with expanded human development and increasing recreational or commercial uses of the landscape. Key crossing areas were identified which require landscape-level habitat management to insure connectivity into the future.

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Keywords: gray wolf, habitat connectivity, highways, landscape pattern, mitigation, movements, predictive model, scale

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Practically unparalleled in their ability to exploit diverse ecosystems, gray wolves (*Canis lupus*) once successfully occupied the entire state of Wisconsin from boreal forests in the north to oak savannas in the south. Extensive human settlement coupled with intolerance for wolves led to drastic declines in wolf numbers and range. By 1970 the only wolves remaining in the midwestern United States had been relegated to wilderness areas in northern Minnesota (Mech 1970). Federal protection under the 1974 Endangered Species Act and concurrent education efforts allowed wolf populations to gradually rebound across the northern portions of Minnesota, Wisconsin, and Michigan (Mech and Nowak 1981, Schadler and Hammill 1996, Wydeven 1996).

Wolves began recolonizing Wisconsin in the late 1970s (Thiel 1993). Repatriating wolves first occupied wilderness areas in northern-western and north-central Wisconsin. Population growth was hindered initially by high human-caused mortality and high disease levels – both of which abated in the late 1980s (Wydeven et al. 1992, Thiel 1993). Recent generations of wolves, those protected from harvest and raised in less hostile environments, are demonstrating increased tolerance for human presence in the landscape (Mech 1989, Fuller et al. 1992, Haight et al. 1998, United States Fish and Wildlife and Wildlife Service 1992). The expanding wolf population in Wisconsin reached state recovery goals in 1995 and continues to grow (Wydeven and Boles 1998). Growth of this protected population is ultimately limited by 2 factors: (1) the amount and arrangement of suitable habitat, and (2) the ability to offset mortality with natality and immigration.

Wolves are habitat generalists, but they are not reclaiming the vast wilderness landscape of their ancestors (Haight et al. 1998). Suitable habitats today are those areas in which wolf and human uses of land are compatible. Although several physical features can be linked to wolf use of the landscape, road density – an index to human accessibility – remains the single best predictor of wolf habitat in the Great Lakes region (Fuller 1995; Mladenoff et al. 1995, 1998). Using road densities, Mladenoff et al. (1995) mapped 14,864 km^2 of discontinuous wolf habitat scattered across northern Wisconsin. This fragmented distribution of habitat forces the Wisconsin wolf population to function in disjunct units subject to metapopulation dynamics (Gilpin and Hanski 1991, USFWS 1992, Mladenoff et al. 1995, Haight et al. 1998). Long-term viability of this fragmented wolf population depends upon continued immigration of wolves from Minnesota and Michigan in addition to successful intra-state dispersal. Models indicated that immigration of as few as 2 dispersers per year greatly increased the pool of available mates, compensated for mortality, and reduced extinction probabilities in small, disjunct populations (Haight et al. 1998). Successful immigration requires connectivity of suitable habitats. To ensure connectivity the Wisconsin Timber Wolf Recovery Plan requested that agencies maintain conditions suitable for the natural movement of wolves in the Great Lakes region (Wisconsin Timber Wolf Recovery Team 1989). Highways form 'semi-permeable barriers' to wolves dispersing across northern Wisconsin (Mladenoff et al. 1995). Habitat connectivity and thus population viability would be compromised if wolves refused to cross highways, were frequently killed along highways, or were deflected into inhospitable landscapes because of highways and their associated human habitation patterns.

U.S. Highway 53 (U.S.H. 53) was a north-south, primary arterial highway connecting the interstate highway system at Eau Claire with the Superior/Duluth metropolitan areas in northwestern Wisconsin. The highway separated a large, local population of wolves along the Minnesota/Wisconsin border from suitable habitat and other wolves in north-central, north-eastern, and central Wisconsin. In 1990, the Wisconsin Department of Transportation (WDOT) decided to improve U.S.H. 53 to meet national standards which required expanding residual 2-lane sections to 4-lanes (WDOT 1990). Continued wolf dispersal across the highway was of immediate concern. Following a Biological Assessment of the improvement project, the mitigation proposal for wolves included: (1) constructing 3 ballooned medians which separated north and south-bound lanes by at least 75 m and retained mixed forest cover, (2) creating one highway underpass by extending an existing bridge overland 200 m to provide 15-50 m of clearance, (3) restricting fences and highway access roads to those present in 1990, and (4) posting warning signs in potential crossing areas (WDOT 1990). This research was conducted to help managers evaluate these mitigations by: (1) documenting when and where wolves crossed U.S.H. 53, (2) describing local and landscape habitat characteristics of highway crossing sites, and (3) using landscape patterns to map wolf crossing potential along the U.S.H. 53 improvement corridor.

STUDY AREA

The U.S.H. 53 expansion project extended 71 km from just north of Trego in Washburn County to approximately Hawthorne in Douglas County, Wisconsin (Figure 1). An approximately 7,000 km^2 study area was delineated to include the entire project and comparable portions of Wisconsin State Highways 35 (WI 35) and 27 (WI 27).

The St. Croix River formed a natural division between lowland boreal forests in the northern portion of the study area and upland deciduous/coniferous forests to the south. The study area was dominated by deciduous, coniferous or mixed upland forests (58%) but also contained substantial complexes of forested and non-forested wetlands (11%). Wisconsin's northern forest associations primarily included aspen/birch or maple/birch with interspersions of pine barrens, oak, and boreal forest (Wydeven et al. 1992). Shrub and grasslands (5%), large lakes and rivers (4%), and agricultural, urban, or barren areas (<1%) were scattered across the generally flat to rolling landscape.

While northern Wisconsin contained an extensive road network (Wydeven et al. 1992) the study area retained a large, semi-wild section of relatively low road densities. This area coincided with state, county and private forests north of the St. Croix National Scenic Riverway and extended west into the Nemadji State Forest and St.Croix State Park of Minnesota. Study area lands south of the St. Croix River contained higher densities of lakes, roads, and humans while lands to the north of the managed forests encroached on the suburbs of Superior and Duluth.

METHODS

Crossing Locations

Wolves were radio-monitored in the study area and across the Minnesota border from March 1991 through February 1999. Radioed wolves were relocated a minimum of 1-3 times/week, year-round via aerial and ground telemetry surveys. Wolves moving towards a highway were monitored more intensively as were animals whose territories were adjacent to a highway. When a highway crossing was detected, the area was searched for wolf sign to accurately locate the crossing site. In some instances the exact crossing location could not be found and a straight line between radio-locations obtained immediately before and after crossing was used to estimate the crossing location. In addition, crossing locations were identified by: (1) standardized winter track searches along U.S.H. 53 and WI 35, (2) intermittent, non-standardized winter searches along MN 48, WI 27, and WI 77, and (3) observations reported by local residents.

Highway Approaches. -- Winter crossings were backtracked where possible to determine if wolves travelled along the highway edge to selectively choose their crossing location. Anecdotal observations were recorded along winter wolf trails to further describe movement patterns.

Habitat Associations at Crossing Sites

Local-area habitat associations. -- Selected elements of the biotic and abiotic environment were quantified within the immediate vicinity of crossing sites. Crossing sites were paired with random sites to standardize against major changes in vegetation, topography, or traffic intensities (Bashore et al. 1985). The direction and distance of paired sites were randomly selected along the highway to fall within 100-1200 m of the actual crossing site.

At the interface between natural vegetation and maintained highway margin (edge), the following variables were quantified: *margin slope* (%), *margin width* (m) *distance to opposite edge* (m), and *maximum distance visible* (km). The latter two variables were measured from a height of 1-m to simulate wolf eye height. Engineering standards differed for these 3 highways so estimates of *margin width* and the *distance to opposite edge* were considered independently by highway. *Relative topography* of the site was recorded as flat (no perceptible slope), rolling (kettle and moraine), or sloping. *Snow depth* (cm) and *snow compaction* (unitless; Verme 1969) were also measured when applicable. Measurements related to habitat structure were obtained within a 0.6 ha sampling area centered 20 m into the natural vegetation (perpendicular to the highway). *Shrub cover* (%) at 1-m height was measured by line-intercept along 2 15-m transects (Heady et al. 1959). A dichotomous *canopy cover* variable documented the presence or absence of overstory trees at the sample site. *Deciduous canopy cover* (%) and *coniferous canopy cover* (%) were estimated by the frequency of occurrence above 16 equally spaced sample points (Bonham 1989). A canopy 'hit' indicated at least 25% canopy cover at that sample point. *Visual obscurity* (%) was estimated using a modified optical density board (Nudds 1977). Ten meters from the center of the sampling area the density board was observed in 3 directions: (1) towards the highway, (2) towards oncoming traffic, and (3) away from oncoming traffic. The percent of board obscured by vegetation or debris was estimated from a viewing height of 1 m and the 3 directional estimates were averaged. The presence or absence of *fences* and *deer* (evidenced by pellets or trails) were recorded within each sampling area. Additional variables indicated the presence of *trails* (lightly used dirt roads, maintained trails, or fallow roads) within 25 and 100 m of the sample site and *human development* (paved roads, driveways, or parking lots) within 100 m of the sample site.

Differences between used and paired-random sites were detected using Wilcoxin matched-pairs signed rank tests (continuous variables), Pearson chi-square (categorical variables), and Pearson chi-square tests with Yates correction for continuity (binary variables; Zar 1984). A Spearman rank correlation matrix was produced to explore interrelationships between local-area habitat variables.

Landscape Associations. -- Crossing site coordinates were used to create an Arc/Info (Environmental Systems Research Inc., Redlands, CA) point coverage which was refined to match a coverage of improved-surface roads (1:100K, provided by Ted Sickley, Wisconsin Department of Natural Resources). Comparison sites were randomly selected along a given highway at a ratio of 2 random sites per crossing site. Greater environmental variability was expected for the sample of available sites because they extended over much greater area than used sites. A sampling ratio greater than 1 was used to compensate for these differences in sample variabilities (Pereira and Itami 1991).

A nested, or concentric, sample design was used because the "scale" of an investigation may have profound effects on the patterns detected (Wiens 1989, Kotliar and Wiens 1990, Lehmkuhl and Raphael 1993, Baker et al. 1995, Meyer et al. 1998). Squares were centered around each crossing and random site to define increasingly larger sampling areas of 25, 50, 100, 200, and 400 ha. An increase in sampling area was expected to reduce effects from undetected sample error and individual wolf movements, increase the general applicability of detected habitat associations, and increase power (Wiens 1989, Baker et al. 1995). Crossing and random sites were considered independent of overlap with neighboring sites, i.e., sampling with replacement, which increased the Type I error rates of statistical inferences.

A satellite-based vegetation map (WISCLAND) was used to represent landcover of the study area at a minimum mapping unit of 5 ha. These data averaged 87% accuracy for major upland classes and 79% accuracy for major wetland classes (Heather Reese, Wisconsin Department of Natural Resources, personal communication). The original data were reclassed to 5 major landcover components to: (1) provide the greatest contrast between cover types, (2) reduce the number of variables required to characterize landscape composition and pattern, and (3) allow for clear interpretation of pattern metrics. Reclassification also increased the accuracy of any given cover type.

Raster-based FRAGSTATS (McGarigal and Marks 1995) was used to compute landscape composition and pattern metrics within each sampling area (Appendix I). Landscape composition was measured by the percent of each sampling area comprised of upland deciduous or coniferous forest (*UPFOREST*), forested or non-forested wetland (*LOWLAND*), open water (*WATER*), developed land (*URBAN*), or shrub/grassland (*OPEN*) cover types. Landscape pattern metrics were selected to describe patch size, shape, and dispersion based on their hypothesized importance to wolves. The selected pattern variables included patch density (*PD*), mean patch size (*MPS*), edge density (*ED*), mean patch fractal dimension (*MPFD*), Simpson's diversity index (*SIDI*), patch richness (*PR*), Shannon's evenness index (*SHEI*), and contagion (*CONTAG*).

Road densities were also quantified within sampling areas. The improved-surface roads coverage was reclassed to depict *non-highway public road densities* and *county highway densities*. These 2 road classes attempted to standardize roads by their relative traffic intensities and human uses. Non-highway public roads included improved-surface roads visible on 1:100K USGS topographical quadrangles. Public roads were typically grated, gravel forest roads or paved town roads which received year-round use by forest managers and local residents in additional to seasonal use by hunters and recreationists. County highways were 2-laned, paved roads which almost exclusively connected other highways. The surface and margin of county highways were maintained less frequently than those of state or interstate highways which typically supported higher traffic volumes and faster vehicle speeds. State and interstate highway densities were excluded from analyses.

The St. Croix River and associated lakes formed a prominent, atypical landscape feature which crossed and then paralleled U.S.H. 53 north of Gordon. A binomial variable, *STCROIX*, accounted for any effects the river may have on wolves dispersing in its vicinity. *STCROIX* was assigned a value of 1 if the sample site occurred from Gordon to just north of Solon Springs and a 0 otherwise. The value of this variable remained constant across scales because it was set by geographic position rather than sampling resolution.

A univariate logistic regression model was created for each variable (n=16), within each of the 5 sampling resolutions (Hosmer and Lemshow 1989). Coefficients and *p*-values indicated the sensitivity of an individual pattern variable to changes in sampling resolution. Those variables showing univariate significance at $p < 0.25$ were retained as predictor variables for multiple-variable logistic regression analyses (Hosmer and Lemeshow 1989).

Scatterplots were explored to identify outlying or unusually influential sites. Spearman rank correlations were calculated and variable pairs with $r > 0.75$ were not simultaneously entered into multiple-variable procedures. Non-correlated groups of variables were run through a backwards selection, logistic regression protocol (entry $p < 0.25$, removal $p < 0.10$). Models were compared using Akaike's Information Criterion (AIC; Burnham and Anderson 1992). The goal was to produce a straight-forward, biologically meaningful, and parsimonious model. No transformed variables, higher order terms, or interaction terms were considered because they obscured biological interpretation.

Wolf choice of a crossing site may be influenced by highway-specific circumstances such as the amount and arrangement of road-adjacent habitat. Random sites on U.S.H. 53 were compared to those on WI 35 using Mann-Whitney U tests (Zar 1984) to document differences between highways. Highway-specific habitat selection was identified by comparing used sites to random sites on each highway using Mann Whitney U tests.

Crossing Likelihoods

A resource selection function (RSF) was calculated using the multiple-variable logistic regression model with the lowest AIC (Manly et al. 1993). Since sampling probabilites were unknown in this study a probability function could not be calculated, hence β_0 was dropped from the logistic equation to form the RSF as $w(x) = \exp(\beta_1 x_1 +$

$\beta_2x_2 + \ldots \beta_nx_n$). Resulting RSF values were considered relative to each other rather than as specific probability estimates.

To graphically depict wolf crossing likelihoods points were: (1) systematically placed every 100 m along U.S.H. 53 between Trego and U.S.H. 2, (2) queried for landscape composition and pattern, (3) assigned RSF values based on the modified logistic function, and (4) grouped into high, moderate, and low crossing potential based on natural breaks in the distribution of RSF values. A sample of U.S.H. 53 crossings was reserved to validate model predictions.

RESULTS

Wolf Crossings of U.S.H. 53

A total of 37 crossings of U.S.H. 53 were accurately located between March 1991 and February 1999 by radio-monitoring (n=12), observation (n=14), and winter track searches (n=11). All crossings discovered prior to June 1996 (n=19) were known or suspected dispersal movements. In contrast, 61% of the crossings discovered since June 1996 (n=18) were known or suspected to be resident wolf crossings. The true number of crossings was inestimable; however, between December 1992 and July 1996 the located sample of crossings accounted for only 34% of the total number of crossings detected for radio-collared wolves.

The majority of crossings (76%) occurred along 3 stretches of highway: (1) from 3 to 13 km south of Minong (n=13), (2) from the St. Croix River north approximately 6 km (n=6), and (3) from 1 to 9 km north of Solon Springs (n=8). The remaining crossings (n=9) were more dispersed. Only 3 car-kill mortalities resulted from attempted crossings during this study period – all occurred in 1998 south of Minong. Among those killed were a yearling disperser and 2 residents (1 yearling, 1 pup).

Peak crossing periods. -- Although sampling techniques were biased towards winter, crossings of U.S.H. 53 were detected in every month (Figure 2). Dispersal crossings were most numerous during January-February (31%) and October-November (27%) which coincided with peak dispersal times reported in the Great Lakes Region — February-April and October-November for northeastern Minnesota (Gese and Mech 1991) and fall-early winter for Wisconsin (Wydeven et al. 1992). Although resident wolf crossings were spatially constrained to areas immediately adjacent to pack territories they did not correspond temporally with peak dispersal times.

Highway Approaches. -- Nine winter crossings on WI 35 (n=4), MN 48 (n=3), and U.S.H. 53 (n=2) were backtracked a total of 20 km. No clear break in general travel pattern was witnessed as wolves approached a highway. Wolves did not travel back and forth along the highway before chosing an appropriate crossing location. Anecdotal observations indicated that wolves opportunistically used features of the landscape as they approached highways — 37% of the total length of trails followed coincided with groomed snowmobile trails, plowed roads, or railroad tracks (16%); deer trails or individual ski/snowmobile tracks (7%); or other linear features such as streams, ridgelines, frozen lakes, or gas-line right-of-ways (14%).

Habitat Associations at Highway Crossing Sites

Local-area associations. -- Thirty-three crossings of WI 35 (n=19), U.S.H. 53 (n=8), and MN 48 (n=6) were visited during 1995 and 1996 to assess local-area, habitat selection by wolves when crossing highways. Wolves crossed WI 35 where the *margin width* and *distance to opposite edge* were greater than found at random ($p = 0.045$ and 0.017, Table 1). Too few sites were visited on U.S.H. 53 and MN 48 to reliably detect such differences. Distances crossed on U.S.H. 53 were nearly twice those crossed on WI 35.

The non-significant *canopy cover* variable ($p = 0.192$) indicated that wolves were as likely to cross highways through open landscapes as through forested ones. Wolves preferred an open landscape at eye level when approaching highways as evidenced by lower estimates of *visual obscurity* then expected ($p < 0.001$). Wolves also preferred sites with less *deciduous canopy cover* then expected ($p = 0.038$). *Visual obscurity,* which could relate to ease of movement as well as to visibility, was highly correlated with *shrub cover* ($r = 0.77, p < 0.001$) and both variables were correlated with *deciduous canopy cover* ($r = 0.54$ and $0.64, p < 0.001$). *Coniferous canopy cover* had no significant association with either *visual obscurity* ($p = 0.126$) or crossing location ($p = 0.925$). Other visibility-related variables, e.g., *maximum distance visible, margin percent slope,* and *relative topography*, were not significantly associated with crossing site selection (all $p \geq 0.116$). Snow was significantly more compact at crossing sites than expected ($p = 0.0281$) which may be directly related to ease of movement. Although wolf movements in this study area have been previously associated with trails (Gehring 1996; Bruce Kohn, Wisconsin Department of Natural Resources, personal communication) preferential use of trails when crossing highways was not apparent ($p = 0.450$). Trails do provide wolves with the local-area habitat elements they preferred when crossing highways (less visual obscurity, more compacted snow cover, less deciduous overstory) and it is reasonable to expect that wolves would opportunistically use trails which coincide with their intended direction of movement even if that leads them across a highway.

Landscape associations. -- Forty-three wolf crossings of WI 35 (n=23), U.S.H. 53 (n=18), WI 77 (n=1), and WI 27 (n=1) collected between March 1991 and June 1996 were used for landscape analyses. Eighty-six sites were randomly selected for comparison. Generally, as sampling area increased so did the number of significant univariate regressions (Table 2). Six variables were consistently significant ($p < 0.25$) across all sampling resolutions; *URBAN, WATER, PD, ED,* and *PR* which were negatively associated with crossings (–), and *MPS* which was positively associated (+). *STCROIX* (+) was also significant (and did not change with sampling area). *PD* (–) and *WATER* (–) were consistently significant across sampling resolutions while *LOWLAND* (+), *URBAN* (–), *ED* (–), *CONTAG* (+), and *MPS* (+) increased in significance with increased sampling area. *MPFD* (–) and *non-highway public road density* (–) were significant for only 1 sampling resolution making them less consistent habitat indicators. *County highway density* was not a stable habitat indicator as the coefficient sign changed from one sampling resolution to the next.

High, significant correlations ($r > 0.75$, $p < 0.05$) were detected between *ED, MPS,* and *PD* and between *SHEI* and *CONTAG*. These sets of variables were not simultaneously entered into stepwise procedures. Additionally, 2 crossing locations were excluded from multiple-variable analyses: (1) a highly influential site on WI 35 which was discovered by track search but may not have been a wolf, and (2) an outlying site on WI 35 where a wolf crossed the highway through a gas station parking lot. Combinations of 1 to 4 variables were retained in multiple-variable logistic models created for each of the 5 sampling resolutions (Table 3). As sampling area increased typically the number of variables in models increased (from 1 to 4) while AIC decreased (from 146 to 109). The 400-ha sampling area reversed this trend with 1 less variable and a slightly increased AIC. *PD* (–) was retained by all 5 multiple-variable models. *WATER* (–) and *URBAN* (–) were the second most commonly retained variables followed by *LOWLAND* (+). Consistencies in multiple-variable models indicated that crossing landscapes had fewer patches, less open water, less developed land, and more forested or unforested wetlands than the available landscape matrix.

Differences by highway. -- Between March 1991 and June 1996, crossings discovered on U.S.H. 53 were predominantly dispersal movements (97%) while those of WI 35 were predominantly resident wolf movements (84%). Habitat along WI 35 supported 5 wolf packs during this time period whereas habitat adjacent to U.S.H. 53 supported only 1 pack. U.S.H. 53 also maintained a higher average daily traffic volume (4,075 vehicles/day in 1995) compared to WI 35 (900 vehicles/day in 1993; Marc Hershfield, Wisconsin Department of Transportation, personal communication).

The relative distribution and pattern of landcover differed between these 2 highways. Sampling landscapes along U.S.H. 53 had more *WATER* in the form of lakes and large rivers than landscapes along WI 35 ($p = 0.025$). Wolves avoided water when crossing U.S.H. 53 ($p < 0.001$) while those crossing WI 35 did not ($p = 0.187$). The amount of *OPEN* ($p = 0.433$), *LOWLAND* ($p = 0.120$), *URBAN* ($p = 0.459$), and *UPFOREST* ($p = 0.070$) did not differ between highways; even so, wolves crossing WI 35 selected for greater amounts of *LOWLAND* ($p = 0.004$) and lower amounts of both *OPEN* ($p < 0.001$) and *URBAN* ($p = 0.004$) while wolves crossing U.S.H. 53 did not (all

$p > 0.175$). Generally lower *PD* and greater *MPS* occurred within U.S.H. 53 landscapes compared to WI 35 (all $p < 0.030$) yet wolves crossing both highways preferred low *PD* and larger *MPS* (all $p < 0.028$). The full sample model (all highways) captured elements important on U.S.H. 53 (*WATER*) and WI 35 (*URBAN, LOWLAND*) individually as well as one element common to both (*PD*).

Crossing Likelihoods

The greatest number of significant univariate regressions and the lowest multiple-variable AIC was obtained from the 200-ha sampling area. RSF values were calculated as: $w(x) = \exp(-1.0853*WATER - 0.4295*PD - 0.2215*URBAN + 0.0635*LOWLAND)$. Some crossing sites had much higher scaled, relative likelihoods of use (mean = 7.96; range 0.11-42.02) than available sites (mean = 1; range 0.00-12.29). Sites were categorized as having relatively high, moderate, or low crossing potential (Figure 3). Sites with RSF values > 3.000 (60% of the known crossings) were labeled "high crossing potential" which equated to 20% of the U.S.H. 53 corridor between U.S.H. 2 and Trego (Figure 4). Sites with values between 0.111 and 3.000 (40% of the known crossings) were labeled "moderate crossing potential" which equated to an additional 48% of the highway corridor. A high degree of overlap between used and available sites was accepted for the moderate crossing potential category because of the variability in wolf crossings, the relatively low sample size, and the fact that unused sites could not be identified. Sites with values <0.110 (0% of the known crossings) were considered to have low crossing potential which covered the remaining 32% of the highway.

Model validation. -- The model was validated by 15 crossings of U.S.H. 53 identified between July 1996 and February 1999 (provided by Bruce Kohn, Wisconsin Department of Natural Resources) in addition to 4 crossings observed prior to June 1996. Eleven crossings (58%) occurred in areas of high crossing potential, 5 (26%) in areas of moderate crossing potential, and 3 (16%) in areas of low crossing potential consistent with the expected distribution ($\chi^2 = 1.704$, $p = 0.427$). Five of 7 resident crossings (71%) and 4 of 6 disperser crossings (67%) occurred in high crossing potential areas indicating that the model equally represented these 2 segments of the wolf population.

Mitigation placement. -- All widened median and underpass mitigations occurred within or partially overlapped at least moderate crossing potential habitats. One large section of high potential habitat (north of the St. Croix River) and several smaller sections do not contain any crossing mitigations. Given unequal crossing frequencies it was impossible to infer a survival benefit from crossing mitigations in the present study.

DISCUSSION

Wolves crossed highways year-round through a variety of habitats. Wolves did not assess the suitability of individual sites before selecting a crossing location. Crossing habitat is likely consistent with habitats used during dispersal, food search, and territory maintenance — behaviors manifested at larger spatial scales (Ims 1995). The majority of detected U.S.H. 53 crossings were made by dispersing wolves who were inherently naïve to their environment. Compared to resident animals disperers are wider-ranging and typically less habitat specific. Resident wolves may be more locally selective because they have a cognitive map of their surrounding landscape. These 2 components of the wolf population may select different landscape features when crossing highways because of their differing motives and knowledge of the landscape. Given differing traffic volumes and road-adjacent habitat configurations it was impossible to segregate dispersal crossing choices from resident wolf choices using this sample set. Test sites indicated that both components of the wolf population were equally well represented by the crossing model. Combining resident and disperser crossings, as well as crossings of more than one highway, likely overgeneralized crossing habitat. Crossing predictions should therefore be considered generous estimates of suitable crossing habitat.

Patch density was the most consistent indicator of crossing habitat. In north-western Wisconsin patch density was directly related to human-induced landscape fragmentation. Forest cuts, log landings, roads, agricultural fields, grazing allotments, airstrips, cranberry bogs, cabin sites, homes, and gravel pits all acted to break the primarily forested landscape into smaller patches which contrasted with the surrounding matrix. Wolves clearly avoided patchy landscapes when crossing highways consistent with larger-scale studies which documented wolf habitat as areas where human and road densities were low (Thiel 1985, Mladenoff et al. 1995). Strong avoidance of open water when crossing U.S.H. 53 may further be related to human fragmentation due to intensive lakeshore development common in northern Wisconsin. The positive association with the St. Croix River was likely influenced by the extensive lowland complexes protected along the St. Croix National Wild & Scenic Riverway. Although lowland complexes were the most preferred crossing habitats, large patches of non-preferred habitat (shrubland, grassland and upland forest) were also used because they provided wolves with the distance from human activity that they required when moving through the landscape. Model fit improved with increased sampling area indicating that wolves perceived and reacted to landscape pattern at larger spatial scales. Local characteristics may influence small-scale, immediate movement choices but the larger landscape dictates movement limitations and is the level at which management actions would be most effective.

The crossing model showed 68% of the U.S.H. 53 expansion project to have at least moderate crossing potential. That so much of the highway had a good chance of being crossed, and indeed has been crossed, indicated high connectivity between habitats east and west of the highway. However, these estimates of potential crossing habitat were likely overestimated. Expanding human populations and increasing recreational or commercial use of the landscape will also narrow suitable crossing areas over time. Structural mitigations — widened medians and underpasses — may play a more strategic role in providing connectivity should suitable crossing areas narrow into discrete corridors while traffic volumes and vehicle speeds continue to increase. Presently only 14 miles of U.S.H. 53 from Trego to Superior occur within high potential crossing habitat. Proactive, landscape management is required to insure these key crossing areas are not degraded over time. Continued monitoring is necessary to document wolf use of crossing areas as human habitation and land use patterns change.

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Table 1. Habitat choices within 0.6 ha of highway crossing locations (n=33) along WI 35, USH 53 and MN 48. Paired random sites were compared to used sites by Wilcoxon matched-pairs signed rank tests (A), Pearson chi-square (B), or Pearson chi-square tests with Yates correction for continuity (C).

Continuous Variable (A)	Used Mean	±SD	Random Mean	±SD	*p*-value
Margin width (m)					
WI Highway 35 (n=19)	14.36	7.65	11.40	6.49	0.045
U.S. Highway 53 (n=8)	16.76	6.99	16.60	8.91	0.889
MN Highway 48 (n=6)	6.82	1.51	7.47	1.06	0.345
Distance to opposite edge (m)					
WI Highway 35 (n=19)	46.14	17.91	37.72	8.40	0.017
U.S. Highway 53 (n=8)	82.38	43.61	64.38	49.20	0.263
MN Highway 48 (n=6)	21.38	4.49	21.16	4.58	0.600
Margin slope (%)	-9.97	15.49	-3.00	10.52	0.116
Maximum distance visible (km)	0.48	0.35	0.56	0.32	0.194
Snow depth (cm; n=12)	30.91	23.21	38.88	22.83	0.092
Snow compaction (unitless; n=12)	0.41	0.43	0.88	0.64	0.028
Shrub cover (%)	4.89	7.82	5.91	6.35	0.170
Deciduous canopy cover (%)	28.41	34.16	41.66	34.82	0.038
Coniferous canopy cover (%)	10.79	22.76	11.36	21.22	0.925
Visual obscurity (%)	21.17	15.65	29.15	14.56	0.003

Categorical Variable (B)	Count Used (Random) Flat	Rolling	Sloping	*p*-value
Relative topography	12 (18)	11 (11)	10 (4)	0.152

Binary Variable (C)	Count Used	(Random)	*p*-value
Canopy cover	19	(25)	0.192
Fences	7	(5)	0.740
Deer	12	(14)	0.801
Trails within 25 m	9	(8)	1.000
Trails within 100 m	15	(11)	0.450
Human development within 100 m	5	(7)	0.750

Table 2. Univariate logistic significance of landscape composition and pattern variables within 5 sampling resolutions around gray wolf highway crossings in northwestern Wisconsin, 1992-1996.

	---------------- *p*-value (sign of regression coefficient) ----------------				
Variable	25-ha	50-ha	100-ha	200-ha	400-ha
UPFOREST					
LOWLAND		0.2153 (+)	0.0891 (+)	0.0307 (+)	
OPEN					
URBAN	0.1175 (–)	0.1335 (–)	0.1009 (–)	0.0390 (–)	0.0341 (–)
WATER	0.1580 (–)	0.0591 (–)	0.0438 (–)	0.0697 (–)	0.0444 (–)
PD	0.0048 (–)	0.0021 (–)	0.0001 (–)	0.0004 (–)	0.0003 (–)
ED	0.0880 (–)	0.0618 (–)	0.0280 (–)	0.0124 (–)	0.0058 (–)
SHEI		0.1008 (–)	0.0919 (–)		
PR	0.0069 (–)	0.0524 (–)	0.0014 (–)	0.0071 (–)	0.0764 (–)
CONTAG		0.0429 (+)	0.0148 (+)		
MPFD		0.0752 (–)			
SIDI					
MPS	0.0408 (+)	0.0511 (+)	0.0095 (+)	0.0036 (+)	0.0009 (+)
Highway density	0.1299 (–)	0.1200 (+)	0.2296 (–)		
Public road density		0.0118 (+)			
*STCROIX**	0.1377 (+)	0.1377 (+)	0.1377 (+)	0.1377 (+)	0.1377 (+)

* *STCROIX* was a dichotomous variable that retained the same value regardless of sampling resolution.

Table 3. Multiple-variable logistic models of landscape composition and pattern within 5 sampling resolutions around gray wolf highway crossings in northwestern Wisconsin, 1992-1996.

	β-coefficient				
Variable	25-ha	50-ha	100-ha	200-ha	400-ha
URBAN			−0.1092	−0.2215	−0.5079
LOWLAND				0.0635	0.0385
WATER		−0.4138	−0.8007	−1.0853	
PD	−0.0660	−0.0861	−0.1911	−0.4295	−0.3239
PR			−0.7618		
Constant	1.1414	1.2329	6.0909	4.0625	5.3852
Akaike's Information Criterion	146.500	144.110	115.439	109.339	120.400

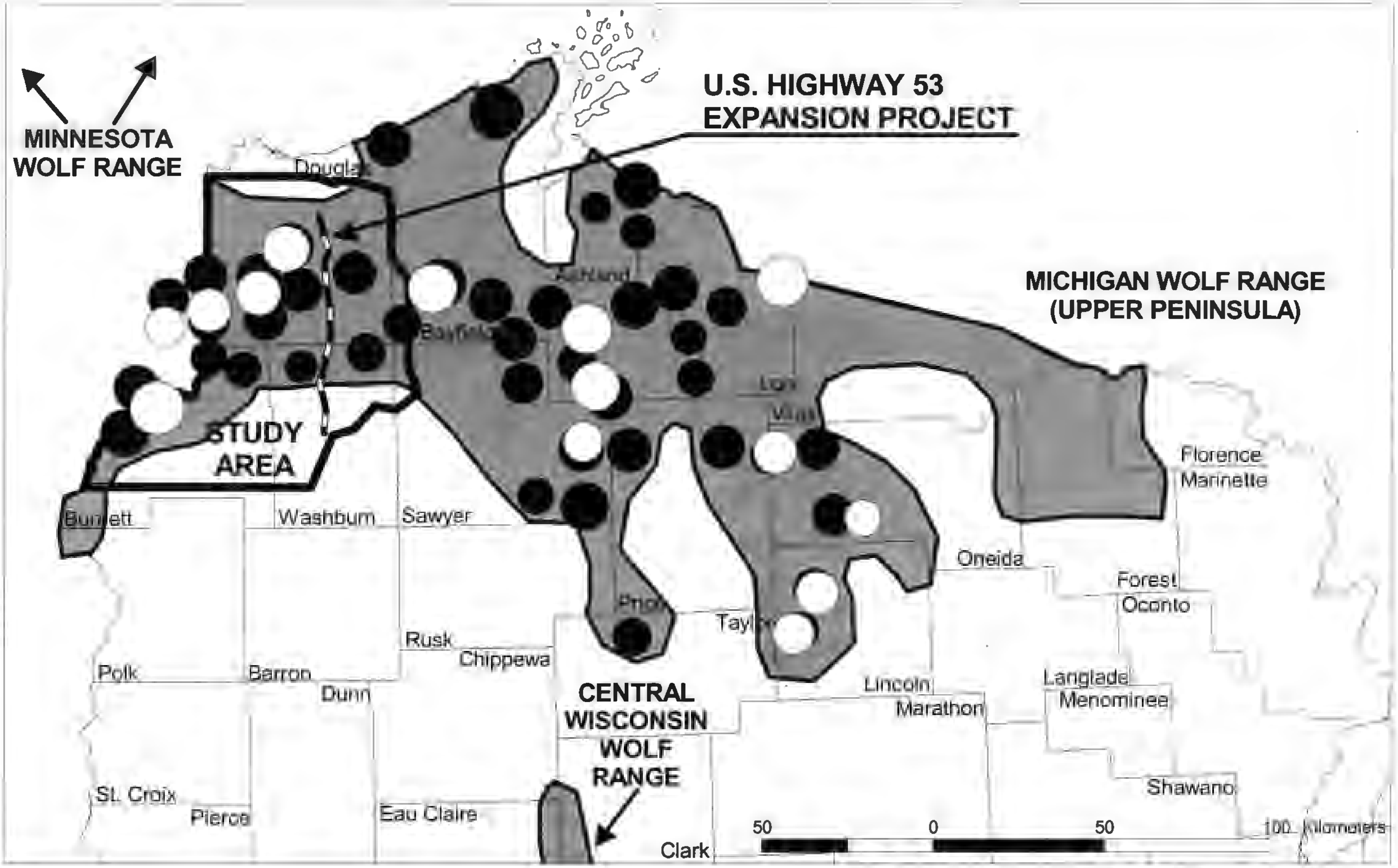


Figure 1. Location of the U.S. Highway 53 expansion project and study area. Gray shading depicts the estimated extent of wolf habitat in northern Wisconsin. Areas of known wolf pack activity are shown for 1992 (white circles) and 1998 (black circles).

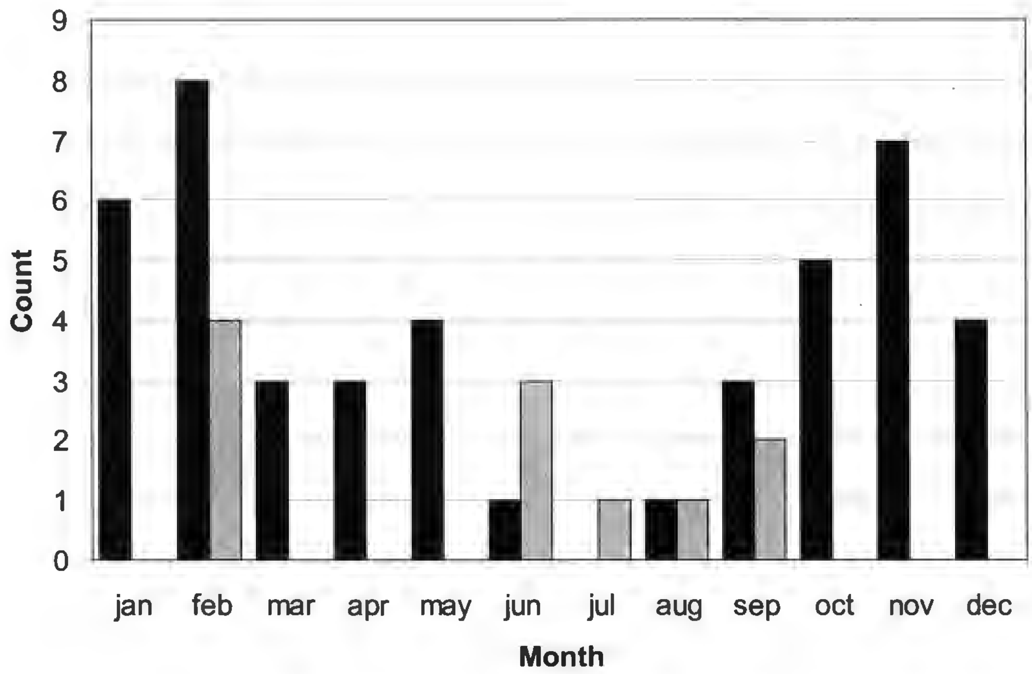
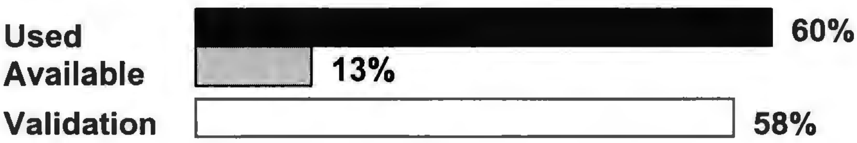


Figure 2. Distribution of U.S.H. 53 wolf crossings detected between March 1991 and February 1999 by radio-telemetry (n=34), track search (n=11), and observation (n=11). Bars indicate known or suspected dispersal crossings (black) and resident wolf crossings (gray).

HIGH CROSSING POTENTIAL

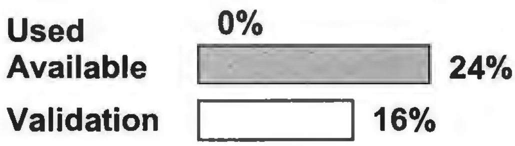


Variable	WATER	PD	URBAN	LOWLAND
Mean ± SD	0.12 ± 0.23	8 ± 2	0.93 ± 1.00	25.05 ± 25.13
Max. Value	1%	15	4%	82%

MODERATE CROSSING POTENTIAL

Variable	WATER	PD	URBAN	LOWLAND
Mean ± SD	0.49 ± 0.66	12 ± 3	2.30 ± 2.44	18.74 ± 16.00
Max. Value	3%	21	16%	54%

LOW CROSSING POTENTIAL



Variable	WATER	PD	URBAN	LOWLAND
Mean ± SD	6.80 ± 8.12	14 ± 3	6.90 ± 9.41	12.16 ± 11.27
Max. Value	27%	24	46%	40%

Figure 3. Distribution of high, moderate, and low likelihood of use (crossing potential) categories. The bar graph indicates the percent of used (crossing, n=41), available (random, n=82), and validation (crossing, n=19) sites falling within each category. Tables show the within-category mean, standard deviation, and maximum value for each variable within 200-ha of the 814 sites used to map crossing potential on U.S.H. 53.

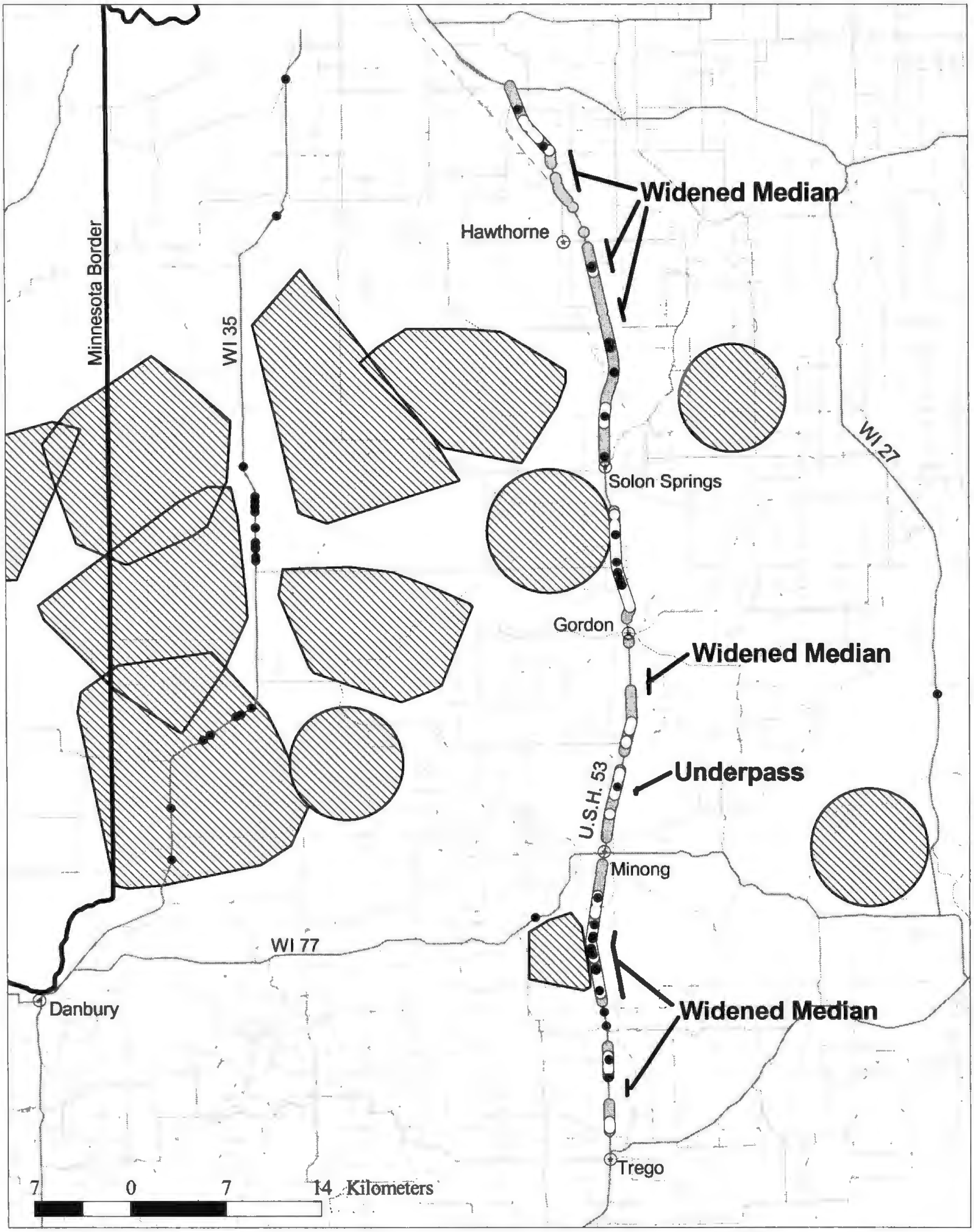


Figure 4. Location of known highway crossings (black dots), pack territories (hatched polygons), and U.S.H. 53 crossing mitigations. U.S.H. 53 wolf crossing potential is shown as high (white polygons) and moderate (gray polygons).

Appendix I. Landscape composition and pattern metrics calculated by FRAGSTATS (McGarigal and Marks 1995).

Metric	Calculation[1]	Units	General Interpretation
Class Percent of Landscape	*URBAN*, *FOREST*, *OPEN*, *LOWLAND*, *WATER* $= P_i = \dfrac{\sum_{j=1}^{n} a_{ij}}{A} \bullet (100)$	percent	The areal extent of each class within the specified sample landscape.
Patch Density	$PD = \dfrac{N}{A} \bullet (10{,}000) \bullet (100)$	#/100 ha	*PD* expresses the number of patches per unit area to allow comparisons among landscapes of various sizes. Increased *PD* indicates greater spatial heterogeneity
Edge Density	$ED = \dfrac{E}{A} (10{,}000)$	m/ha	*ED* is 0 if the entire landscape consists of a single patch. As *ED* increases so does the spatial complexity of the landscape.
Mean Patch Size	$MPS = \dfrac{A}{N} \bullet (1/10{,}000)$	ha	*MPS* is inversely related to the degree of landscape fragmentation.

Metric	Calculation[1]	Units	General Interpretation
Mean Patch Fractal Dimension	$MPFD = \dfrac{\sum_{i=j}^{m} \sum_{j=1}^{n} \dfrac{2\ln(0.25p_{ij})}{\ln a_{ij}}}{N}$	none	*MPFD* approaches 1 for patches with very simple perimeters, and approaches 2 for patches with highly convoluted perimeters. *MPFD* is an alternative to the regression approach and is based on the fractal dimension of each patch.
Simpson's Diversity Index	$SIDI = 1 - \sum_{i=1}^{m} (P_i^2)$	none	*SIDI* equals 0 when the landscape contains only one patch. It approaches 1 as the number of different patch types (*PR*) increases and the proportional distribution of area among patch types becomes more equitable
Patch Richness	$PR = m$	#	*PR* equals the number of different patches present in the landscape.
Shannon's Evenness Index	$SHEI = \dfrac{-\sum_{i=1}^{m} (P_i \bullet \ln P_i)}{\ln(m)}$	none	*SHEI* equals 1 when the landscape contains only one patch or the distribution of area among patch types is perfectly even. It approaches 0 as the distribution of area among the different patch types becomes increasingly uneven (dominated by 1 type).

Metric	Calculation[1]	Units	General Interpretation
Contagion		percent	*CONTAG* approaches 0 when the distribution of adjacencies among unique patch types becomes increasingly uneven. It equals 100 when all patch types are equally adjacent to all other patch types.

$$CONTAG = \left[1 + \frac{\sum_{i=1}^{m}\sum_{j=1}^{m} \left[(P_i) \left[\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}} \right] \right] \bullet \left[\ln(P_i) \left[\frac{g_{ik}}{\sum_{k=1}^{m} g_{ik}} \right] \right]}{2 \ln(m)} \right] (100)$$

[1] Notation used in formulas: P_i = proportion of landscape occupied by class i, n = n_i = number of patches in the landscape of class i, a_{ij} = area (m^2) of patch ij, A = total landscape area (m^2), N = total number of patches in the landscape, E = total length (m) of edge in the landscape (excludes boundary segments unless they represent true edge), m = number of class types present in the landscape, p_{ij} = perimeter (m) of patch ij, g_{ik} = number of adjacencies (joins) between pixels of classes i and k.

THE INFLUENCE OF HIGHWAYS ON ESTIMATES OF SUITABLE WOLF HABITAT

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Abstract: The most widely accepted estimates of suitable wolf habitat in the Great Lakes Region and northeastern United States were based solely on overall road densities. Roads in these models were broadly defined to include everything from gravel forest roads to multi-lane interstate expressways. This research investigated how highways and non-highway public roads influenced suitable habitat choices by comparing used areas (defined by 4-12 packs between 1992-96) to unused areas outside of known wolf territories using logistic regression. Sequentially connected radio-locations (collected 12-24 hours apart) were used to further explore how highways influenced regular wolf movements within annual home ranges.

The density of non-highway public roads better explained habitat selection at the population level (74% accuracy) than either major or minor highway densities (which could not adequately differentiate used and unused areas). Overall road density was still the best predictor of suitable wolf habitat (77% accuracy). No improvement to classification accuracy or model fit was achieved by segregating highways from non-highway public roads. Certain components of the wolf population were less tolerant of all roads (males and pups, $p < 0.001$) and in general wolves were less tolerant of roads during certain time periods (breeding and nomadic months, $p < 0.001$). These patterns indicated that not all "suitable habitat" areas were available to wolves during all times —

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a critical consideration when estimating how much habitat is truly available to a given wolf population.

Although not a major factor in population-level habitat selection, highways strongly influenced regular wolf movements ($p < 0.001$) which in turn affects the geographic arrangement of territories within any patch of suitable habitat. All territories contained some non-highway public roads and these roads were crossed mostly in proportion to their occurrence ($R^2 = 0.48$, $p < 0.001$). Only one-half of the wolf territories contained major highways and minor highways were avoided during regular wolf movements ($p < 0.001$). Potential within-territory tolerance limits for highways were identified around 0.09 km/km^2 for major highways and 0.15 km/km^2 for minor highways. The amount and arrangement of highways in the landscape could help to identify a subset of "suitable" wolf habitat which is actually useable by a given wolf population.

Key words: gray wolf, habitat selection, Minnesota, movements, predictive model, roads, Wisconsin

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Road densities have served as an index to a wide spectrum of human-induced pressures on large mammals (Brocke et al. 1988, Bennett 1991). Displacement of brown bear (*Ursus arctos*), black bear (*U. americanus*), and mountain lion (*Felis concolor*) from potential habitat has been linked to the presence of roads and the human activities associated with them (Van Dyke et al. 1986, Mclellan and Shackleton 1988, Brody and Pelton 1989). Increased harvest vulnerability (legal and illegal) has been documented as a function of road density for populations of black bear, moose (*Alces alces*), and white-tailed deer (*Oidocoileus virginianus*) (Crete et al. 1981, Timmerman and Gollath 1982, Sage et al. 1983, Brocke et al. 1988). Thiel (1985) identified a critical road density (0.56 km/km^2) above which gray wolf populations failed to sustain themselves in Wisconsin. Subsequent supporting evidence for this road density threshold was provided by studies of wolf populations in Michigan, Minnesota and Ontario (Jensen et al. 1986, Mech et al. 1988). In a more recent study, landscape composition, spatial patterns, human densities, prey densities, and land ownership could not explain wolf presence or absence in the landscape as well as road densities (Mladenoff et al. 1995).

Accurate estimates of available habitat are crucial when determining reintroduction feasibility, long-term carrying capacities, and management alternatives for gray wolf populations. In the Great Lakes Region and the northeastern United States, the most recent and widely accepted estimates of suitable wolf habitat relied solely on overall road densities (Wisconsin Timber Wolf Recovery Team 1989, United States Fish and Wildlife Service 1992, Mladenoff et al. 1995, Hosack 1996, Mladenoff and Sickley 1998). For these models roads were broadly defined as permanent roads requiring routine maintenance which were passable year-round by 2-wheel drive vehicles (Fuller 1995) — more specifically these roads appeared as solid lines on 1:100,000 scale USGS topographic quadrangles (Mladenoff et al. 1995). This definition covered a gradient from gravel forest roads through interstate highway systems. Yet roads differ markedly in traffic volume, vehicle speeds, widths and surfaces, types of motorized use, access restrictions, and human uses of neighboring lands.

Bobcats (*Lynx rufus*), black bear, brown bear and gray wolves have all been shown to react differently to roads based on traffic levels — they generally avoided roads with heavy vehicle traffic while demonstrating indifference or attraction towards low-traffic roads (McLellan and Shackleton 1988, Brody and Pelton 1989, Thurber et al. 1994, Lovallo and Anderson 1996). Wolves have been known to use dirt roads and trails year-round, likely as efficient travel, transport, and hunting routes (Mech 1970). Highways pose semi-permeable barriers to wolf movements and may thus limit the amount and arrangement of suitable habitat. To assume that a low-traffic country road and a multi-lane interstate expressway exert the same degree of influence on wolf habitat choice may be too broad a generalization that might lead to erroneous estimates of available wolf habitat.

This research focused on how highways influenced wolf habitat use. Two levels of habitat use with respect to roads were explored: (1) population-level selection of suitable habitat from the roaded landscape matrix, and (2) within-territory road avoidance by individual wolves. Habitat use by individuals can be considered a higher order selection dependent upon what qualified as suitable habitat for the population (Johnson 1980).

STUDY AREA

A 9100 km^2 study area was selected which overlapped the Minnesota-Wisconsin border and encompassed from 4-12 wolf packs between 1992-1996 (Figure 1). The study area had an overall road density of 0.64 km/km^2 and contained 9 major and numerous minor highways. The St. Croix National Wild & Scenic River bisected the study area separating lowland boreal forests north of the river from mixed deciduous/coniferous forests to the south. Much of the area north of the river was managed as state, county, or private forest land. The most northern extent of the study area encroached upon the suburbs of Duluth, Minnesota and Superior, Wisconsin. Extensive lakeshore development and recreational opportunities supported a growing road network south of the river.

METHODS

An ArcInfo roads coverage (provided by T. Sickley, University of Wisconsin – Madison) was reclassed to major highways (state and interstate), minor highways (county), and non-highway public roads (those visible as solid lines on 1:100,000 scale USGS topographic maps). These categories standardized roads by basic structure, human use, and traffic intensity (volume and speed). Major highways were either 2-lane undivided or multi-lane divided highways which connected metropolitan areas or other major highways. Minor highways were 2-lane county roads (paved in Wisconsin, unpaved in Minnesota). Minor highway surfaces and margins were not maintained as frequently as major highways therefore vehicle speeds on minor highways were slower and vegetation extended closer to the road surface. While concentrated urban centers (villages, towns, cities) were located primarily along major highways, minor highways were more likely to have year-round houses or seasonal cabins alongside. The non-highway public roads category included everything between dirt forest roads to paved town roads. Paved roads in this category did not typically have painted center or margin lines and posted speeds were lower than 55 MPH.

Wolves were captured and fitted with radio collars (Telonics, Mesa, Arizona) from 1992 through 1996. Commonly ≥1 wolf was collared/pack/year. Wolf relocations were obtained 1-3 times/week using fixed-wing mounted Yagi antennas. Aerial locations had associated, unquantified errors due to plane velocity, height above ground, and position-fix delays but were considered consistent with ground-based telemetry locations. More frequent locations were obtained for individual wolves using a vehicle-mounted telemetry system. Ground locations were estimated from 2-4 bearings taken ≤20 minutes apart and solved using LOCATE II (Pacer, 1990, box 1767, Truro, Nova Scotia, Canada, B2N 5Z5). Error ellipses around ground locations averaged 3 ± 3 ha with no ellipses exceeding 15 ha. Only resident wolf locations were retained for analyses — dispersal locations and extreme extraterritorial locations were excluded. Locations of only 1 wolf/pack were used in analyses to insure independence. Additionally, only locations ≥12 hours apart were used to reduce the effects of spatial autocorrelation (White and Garrott 1990).

Population Level Selection of Suitable Habitat

Resident wolf locations were obtained from 4-12 packs between 1992-1996. Each location was buffered by 200-ha — a sampling resolution successfully used in an associated wolf habitat study (Frair 1999). Each wolf area (buffered location) was queried within an ArcInfo GIS for the density (km/km^2) of major highways, minor highways, and non-highway public roads.

A comparatively sized sample of unused sites (outside of known wolf territories) was randomly selected such that used and unused areas did not overlap. Differences between used and unused areas were identified through Mann-Whitney U tests (Zar 1984). Densities of major highways, minor highways, non-highway public roads, and overall roads (all highways + public roads) were used to create univariate logistic regression models. Additionally, a multiple-variable model was created by the combination of the 3 individual road class variables. Models were compared by Akaike's Information Criterion (AIC; Burnham and Anderson 1992) and classification accuracies using a cutoff of $P > 0.50$.

Limiting population components. -- Habitat choices may be affected further by non-spatial factors such as the internal state of the individual, its age, or its life cycle (Ims 1995). This sample of wolf locations supported investigating habitat choices with respect to roads based on sex, age, and season.

At the time of capture wolf age was estimated as pup (<12 mo), yearling (12-24 mo), or adult (>24 mo) based on a combination of body weight, tooth eruption and tooth wear. Telemetry relocations were parsed into 4 biologically-meaningful seasons: (1) breeding, January – April; (2) denning, May – June; (3) rendezvous, July – September; and (4) nomadic, October – December (Mech 1970, Van Ballenberghe 1975). For this analysis road densities were categorized as none ($x = 0$ km/km^2), low ($0 > x \leq 0.56$ km/km^2), or high ($x > 0.56$ km/km^2) based on the threshold road density identified by Thiel (1985). Differences were detected using chi-square tests of independence (Zar 1984).

Avoidance of Roads in Regular Wolf Movements

Annual minimum convex polygon home ranges (Mohr 1947) were generated to enclose ≥30 radio-locations collected from at least 2 seasons (Fuller and Snow 1988). Sequentially connected locations (within 12-48 hrs) were used to estimate the minimum number of times each wolf crossed each of the 3 road classes within their territories. Expected numbers of road crossings were calculated following Lovallo and Anderson (1996) as:

$$X_k = C * \frac{\sum_{i=1}^{m} \sum_{j=1}^{n} (p_{ij} * RD_{ijk})}{\sum_{k=1}^{r} \left[\sum_{i=1}^{m} \sum_{j=1}^{n} (p_{ij} * RD_{ijk}) \right]}$$

where X_k is the expected number of crossings for road class k, C is the total number of road crossings observed during the study period, p_{ij} is the proportion of the total distances moved by wolf i during year j, and RD_{ijk} is the density of road class k within the annual home range of wolf i during year j. Observed and expected numbers of crossings were compared using a chi-square goodness of fit test (Zar 1984) with Bonferroni-z confidence intervals (White and Garrott 1990).

The total distance moved and number of crossings observed for each wolf were partially a function of the frequency with which radio-locations were obtained. To standardize observed numbers of crossings by sampling intensities a road crossing index was calculated as:

$$I_{ijk} = \frac{X_{ijk}}{M_{ij}} * 100$$

where I_{ijk} is the road crossing index for wolf i during period j for road class k, X_{ijk} is the minimum number of crossings by wolf i during period j for road class k, and M_{ij} is the total distance moved (km) by wolf i during period j (Lovallo and Anderson 1996). Simple linear regression and scatterplots were used to examine wolf responses to increasing road densities. If roads were not avoided, i.e., a given road class was crossed proportionate to the level it occured within a home range, then the expected distribution of I_{ijk} should be represented by a positive, linear function. Deviances from this function would indicate an effect of that road class upon wolf movements.

RESULTS

A total of 3,448 independent radio-locations were obtained. Seasonal distributions of radio-locations were unequal due to differing season lengths and sampling intensities (36% breeding, 20% denning, 22% rendezvous, and 22% nomadic). Four pups (2M, 2F), 5 yearlings (1M, 4F), and 16 adults (8M, 8F) were monitored. Two pups and 3 yearlings were monitored through adulthood and several adults were monitored for consecutive years. Overall, the 18 resident wolves monitored equated to 28.25 wolf years of study.

Suitable Habitat Selection

Used areas were compared to 3,535 unused areas. No roads of any kind were detected for 77% of the used areas compared to only 22% of unused areas. Compared to unused areas, used areas contained lower densities of major highways (0.02 ± 0.11 vs.

0.10 ± 0.27 km/km^2; $p < 0.001$), minor highways (0.03 ± 0.14 vs. 0.14 ± 0.30 km/km^2; $p < 0.001$), and other public roads (0.09 ± 0.25 vs. 0.58 ± 0.56 km/km^2; $p < 0.001$). Each road class yielded a significant univariate logistic regression model (Table 1). However, the major highway density and minor highway density variables could not effectively discriminate between used and unused habitats. Of the 3 road classes, the density of non-highway public roads was the most useful predictor variable (AIC = 7585, 74% accurate). The best univariate model contained the overall road density variable (AIC = 6948, 77% accurate) which yielded only an 8% lower AIC and 3% higher classification accuracy from the other public roads model. The multivariate model containing all 3 road class variables (AIC = 6936, 77% accurate) yielded no improvement over the overall road density model.

Limiting population components. -- Female wolves (n = 1,406) tolerated higher overall road densities than males (n = 2,042; $p < 0.001$). Adults (n = 2,720) and yearlings (n = 377) tolerated higher overall road densities than pups (n = 350; $p < 0.001$). Higher overall road densities were also tolerated during the denning (n = 691) and rendezvous months (n = 759) compared to breeding (n = 1,274) or nomadic months (n = 724; $p < 0.001$).

Within-Territory Road Avoidance

Between 1992-1996, 15 different wolves were monitored yielding 1,916 sequentially connected locations obtained 12-48 hours apart. Annual MCP home ranges averaged 215 ± 125 km^2. Only 54% of the delineated territories contained major highways (ave. density 0.03 ± 0.05 km/km^2) compared to 81% which contained minor highways (ave. density 0.08 ± 0.08 km/km^2). All territories contained non-highway public roads (ave. density 0.14 ± 0.08 km/km^2). A total of 100 major highway, 136 minor highway, and 425 non-highway public road crossings were detected. Crossings did not occur proportionate to road class prevalence within territories ($p < 0.001$). Confidence intervals indicated clear avoidance of minor highways and a slight attraction to non-highway public roads, however, strong avoidance of one class may force the observed selection for another.

A linear function did not adequately explain the relationship between major highway crossing index and major highway density ($R^2 = 0.13$, $p = 0.070$). The scatterplot indicated a possible within-territory tolerance limit for major highways around 0.09 km/km^2 (Figure 2a). Only 1 pack occupied a territory which exceeded this threshold value and individuals within that pack were not detected to cross the highway with any regularity. Excluding the most outlying point slightly improved the regression to ($R^2 = 0.30$, $p = 0.005$). Below 0.09 km/km^2, wolves demonstrated highly individual tolerances for major highways at least partly due to geographic location (how many highways occur in the vicinity of the territory) and personal experience with highways.

A linear function also failed to explain minor highway crossing index as a function of minor highway density ($R^2 = 0.02$, $p = 0.454$). The scatterplot indicated a possible within-territory tolerance limit for minor highways around 0.15 km/km^2 (Figure 2b). Again, only 1 pack occupied a territory above the threshold value and deleting that outlying point improved the regression ($R^2 = 0.27$, $p = 0.008$). Below the threshold value, only individuals from 2 packs indicated a willingness to frequently cross minor highways while the majority seemed to avoid these highways.

Non-highway public roads were generally crossed in proportion to their occurrence in home ranges ($R^2 = 0.48$, $p < 0.001$). The scatterplot indicated a small degree of individual variation in response to non-highway public roads but overall agreement as to the positive, linear nature of the relationship (Figure 2c). With 1 outlier removed, the scatterplot showed that crossing indices did not continue to increase when road densities reached 0.2 km/km^2 — perhaps when such roads become more common wolves suffered from exposure to humans and became selective about which public roads they used. No wolves occupied territories with public road densities greater than 0.3 km/km^2.

DISCUSSION

The majority of areas used by wolves contained no roads at all. Contrary to expectations highways did not drive population-level habitat selection — non-highway public roads did. Public roads received more prolonged human use compared to highways because they were used for sight-seeing, hunting, and motorized or non-motorized recreation. Humans built houses and cabins along these roads and spent more time out of their cars near non-highway public roads than near highways. Wolves likely perceived more of a threat near a concentrated residential area than they did when encountering a 4-lane highway through a large tract of county forest. No predictive benefit was obtained by segregating roads into classes. Overall road density remained the single best predictor of suitable wolf habitat.

To be most effective habitat-based models should be applied to the most limiting population component (Kolasa and Waltho 1998). This dataset showed males and pups to have lower road density tolerances. Tolerances were also lower during the breeding and nomadic time periods (roughly coinciding with winter). After leaving the den pups are cached at rendezvous sites. Females and older wolves may recognize energy benefits by relying on roads as efficient travel routes for hunting and transporting food during the critical pup-rearing months. Social status may also influence resource partitioning with sub-dominant wolves using sub-optimal habitats. Regardless of the mechanism, these differences in road tolerances indicated that not all "suitable habitat" areas were available to all wolves during all time periods — an important consideration when estimating the extent of suitable habitat.

Once suitable habitat has been established, territories were formed based on the arrangement of resource patches and individual tolerance limits for adverse conditions. All wolf territories contained non-highway public roads. Some attraction towards these roads was detected but generally public roads did not affect regular, within-territory wolf movements. Only one-half of the wolf population occupied territories which contained a major highway. Major and minor highways often defined the edges of pack territories and only a few wolves repeatedly crossed highways. Tolerance limits for highways may have partially dictated the geographic positioning of pack territories in the landscape thus affecting the true carrying capacity.

Focusing suitable habitat estimates on limiting population components and then considering the distribution of highways in the landscape may help managers better identify "useable" habitat from the universe of "suitable" habitat.

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Table 1. Logistic regression models to estimate available wolf habitat based on road densities in northwestern Wisconsin and eastcentral Minnesota. All $p < 0.001$.

Road Variable	β	S.E.	Constant	AIC	Percent Correctly Classified[1] used	unused	overall
Univariate Models							
Major Highway	-2.2516	0.1649	0.0857	9419	96	14	55
Minor Highway	-2.4641	0.1398	0.1546	9245	95	22	58
Non-Highway Public Roads	-3.1027	0.0886	0.8025	7585	87	62	74
Overall Roads	-2.9249	0.0732	1.1467	6948	83	72	77
Multivariate Model							
Major Highway	-2.3622	0.1807					
Minor Highway	-2.6992	0.1495					
Non-Highway Public Roads	-3.0967	0.0885	1.1467	6936	83	71	77

[1] Classification cutoff at P > 0.50.

Table 2. Differences in overall road tolerance with respect to wolf sex, age, or season. Differences tested using a chi-square test of independence.

Factor	Category	n	Road Density[1] none	low	high	χ^2	*p*
Sex	Male	2,042	80	8	12		
	Female	1,406	72	12	16	31.31	< 0.001
Age	Pup	351	87	5	8		
	Yearling	377	78	8	14		
	Adult	2,720	76	11	14	24.93	< 0.001
Season[2]	Breeding	1,274	81	9	10		
	Denning	691	74	9	16		
	Rendezvous	759	66	13	21		
	Nomadic	724	85	7	8	98.84	< 0.001

1 Road density categories: none = 0 km/km^2, low = 0.01-0.56 km/km^2, high = >0.56 km/km^2.

2 Bioligically-meaningful seasons: breeding = January-April, denning = May-June, rendezvous = July-September, nomadic = October-December.

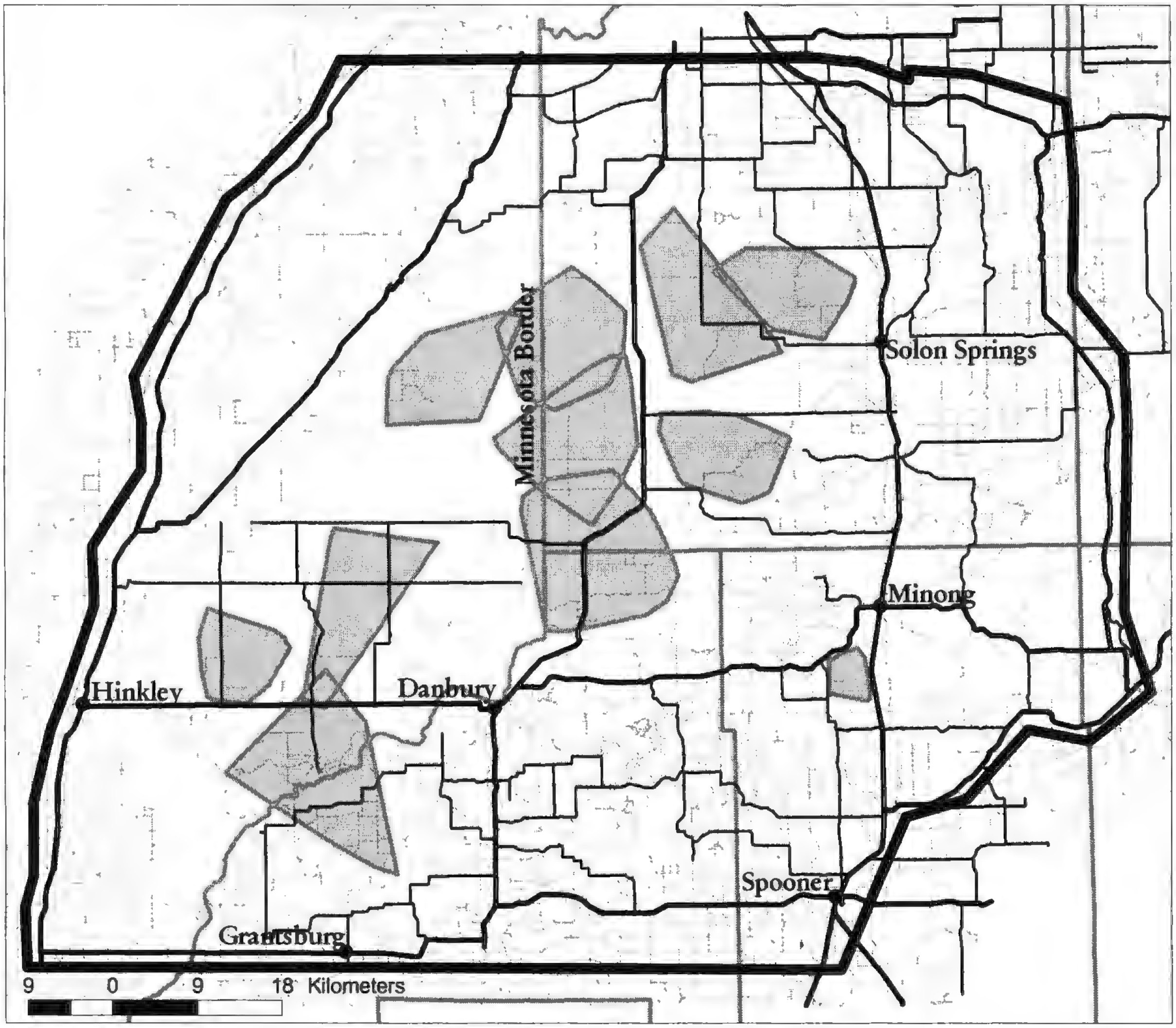
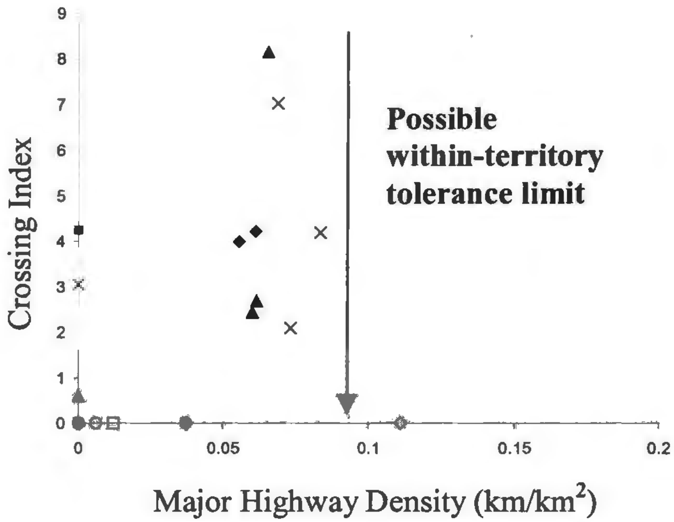
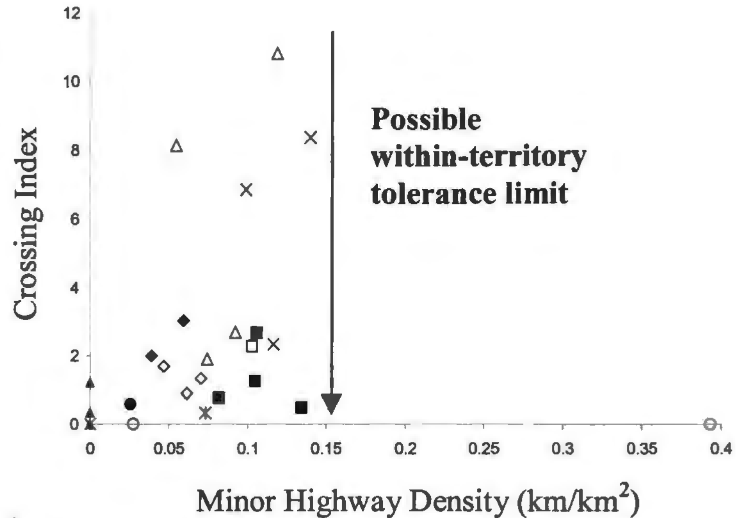


Figure 1. The study area road network. Heavy black lines indicate major (state and interstate) highways, thin black lines indicate minor (county) highways, and gray dashed lines indicate non-highway public roads. Gray polygons represent the location of wolf territories in the study area between 1992-1996.

a



b



c

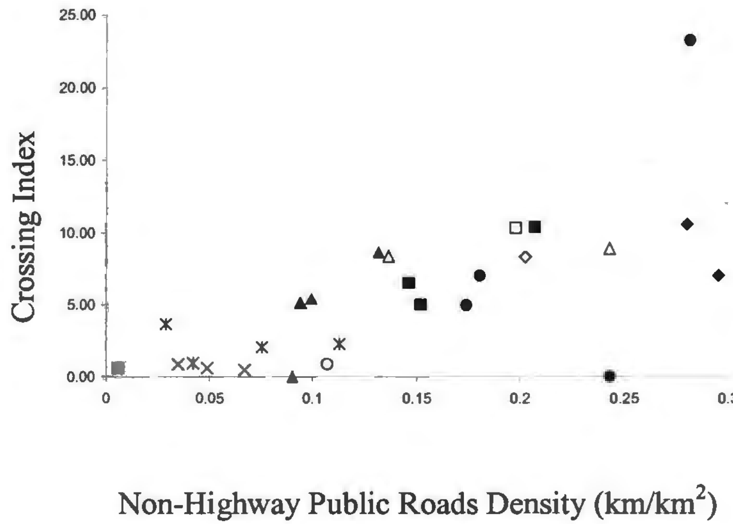


Figure 2. Scatterplot of crossing index against road density for (a) major highways, (b) minor highways, and (c) non-highway public roads. Each pack is represented by a unique symbol (different pack members may have been monitored at any given time).