

PREDICTING GRAY WOLF LANDSCAPE RECOLONIZATION: LOGISTIC REGRESSION MODELS VS. NEW FIELD DATA

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Abstract. Recovery of populations of wolves (*Canis lupus*) and other large, wide-ranging carnivores challenges conservation biologists and resource managers because these species are not highly habitat specific, move long distances, and require large home ranges to establish populations successfully. Often, it will be necessary to maintain viable populations of these species within mixed-use landscapes; even the largest parks and reserves are inadequate in area. Spatially delineating suitable habitat for large carnivores within mixed, managed landscapes is beneficial to assessing recovery potentials and managing animals to minimize human conflicts.

Here, we test a predictive spatial model of gray wolf habitat suitability. The model is based on logistic regression analysis of regional landscape variables in the upper Midwest, United States, using radiotelemetry data collected on recolonizing wolves in northern Wisconsin since 1979. The model was originally derived from wolf packs radio-collared from 1979 to 1992 and a small test data set of seven packs. The model provided a 0.5 probability cut level that best classified the landscape into favorable (road density < 0.45 km/km²) and unfavorable habitat (road density > 0.45 km/km²) and was used to map favorable habitat with the northern Great Lake states of Wisconsin, Minnesota, and Michigan. Our purpose here is to provide a better validation test of the model predictions based on data from new packs colonizing northern Wisconsin from 1993 to 1997. In this test, the model correctly classified 18 of 23 newly established packs into favorable areas. We used compositional analysis to assess use of the original habitat probability classes by wolves in relation to habitat class availability. The overall rank of habitat preference classes (P , the percentage favorability from the original model), based on the new packs, was probability class 2 ($P = 75\text{--}94\%$) > 3 ($P = 50\text{--}74\%$) > 1 ($P = 95\text{--}100\%$) > 4 ($P = 25\text{--}49\%$) > 5 ($P = 10\text{--}24\%$) > 6 ($P = 0\text{--}9\%$). As more of the landscape becomes occupied by wolves, classes of lower probability than the 95% class, but above the favorability cut level, are slightly more favored. The 95% class is least abundant on the landscape and is usually associated with larger areas of classes 2 and 3. Wolves may continue to occupy areas of slightly lower habitat probability if adequate population source areas are present to offset the greater mortality in these lower quality areas. The model remains quite robust at predicting areas most likely to be occupied by wolves colonizing new areas based on generally available road network data. The model has also been applied to estimate the amount and spatial configuration of potential habitat in the northeastern United States.

Key words: *Canis lupus*; conservation biology; endangered species; gray wolf; Great Lakes Region; habitat suitability; landscape ecology; logistic regression; recolonization; source–sink; species recovery.

INTRODUCTION

Conservation biologists and resource managers face particularly complex challenges in managing the recovery of large, wide-ranging mammalian carnivores. Habitat needs of such species are not usually well-accommodated by even the largest reserves (Peterson 1988, Fritts and Carbyn 1995, Mech 1995). These species often are not particularly habitat specific, moving over large regions containing good and poor habitat. Furthermore, the value of corridors to large carnivores

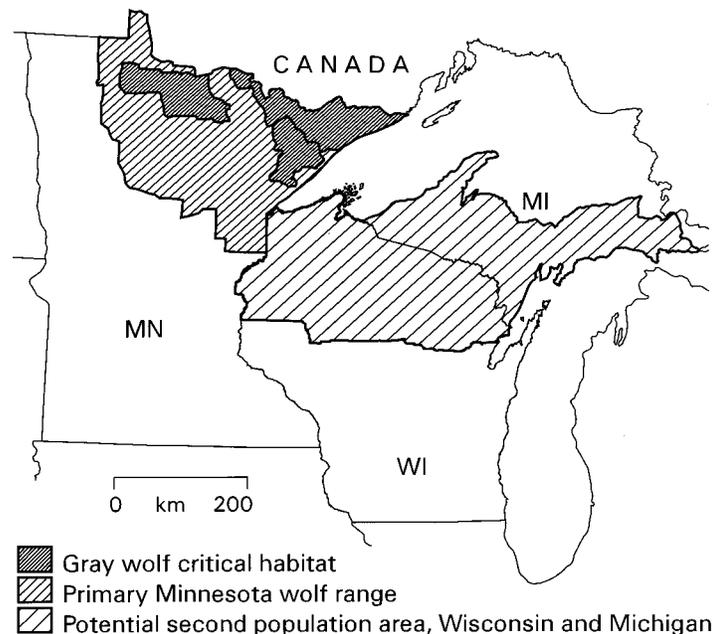
is not clear (Simberloff et al. 1992, Mech et al. 1995, Mladenoff et al. 1997). Management across regions and disjunct areas of suitable habitat is often necessary because these large carnivores have large spatial habitat requirements. These wide-ranging species can benefit from large-scale evaluation and mapping of habitat quality at regional and landscape scales.

The gray wolf (*Canis lupus*) is a species that typifies this group of large, wide-ranging carnivores. The gray wolf has been protected under the U.S. Endangered Species Act (ESA) of 1973 since 1974. At that time, the only U.S. wolf populations outside of Alaska were in northeastern Minnesota and Isle Royale National Park, in Lake Superior (Fig. 1). Elsewhere, the wolf

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FIG. 1. Wolf recovery zones in northern Minnesota, Wisconsin, and upper Michigan, United States (redrawn from U.S. Fish and Wildlife Service 1992).



had been extirpated throughout its former U.S. range, which had covered most of the country (Mech 1970, Fritts and Carbyn 1995). By 1980, the growing Minnesota population was recolonizing northwestern Wisconsin, and the Wisconsin Department of Natural Resources (DNR) began monitoring wolves by radiotelemetry (Wydeven et al. 1995). Recovery in Wisconsin was initially slow, with a decline during the mid-1980s from 24 to 15 animals, presumably due to a parvovirus outbreak (Wydeven et al. 1995). Since 1985, the population has increased 20% per year, and in 1996–1997 was at ~150 wolves.

Our objective here is to present validation results of a spatial, predictive model of favorable wolf habitat. Favorable habitat in a region being newly colonized is defined as landscape areas with the significant characteristics of those portions of the landscape occupied by wolves. We previously derived the model using multiple logistic regression analysis, digital data on landscape characteristics, and long-term radiotelemetry data collected in Wisconsin from 1979 to 1992 (Mladenoff et al. 1995). Our original analysis focused on northern Wisconsin (59 148 km²) and upper Michigan (41 984 km²), a total contiguous area of >100 000 km² (Fig. 1). The region is dominated by mixed hardwood and conifer forests that have been logged during the past 100–150 yr (Mladenoff and Pastor 1993). The relatively young forests and continuing timber harvest provide food for a large population (typically 5–15 deer/km²) of white-tailed deer (*Odocoileus virginianus*), the preferred prey species of wolves in this region (Mech 1970).

Wisconsin DNR biologists have been successful in radio-collaring animals in most wolf packs as they be-

came established, producing a valuable database on a new, recolonizing population (Wydeven et al. 1995). We used this database in a geographic information system (GIS) analysis to examine the correlation of spatial landscape features with existing wolf pack territories. We then derived a logistic regression model (based on Mladenoff et al. 1995) to predict the extent and amount of similar, presumably favorable, habitat areas throughout northern Wisconsin, northern Minnesota, and upper Michigan (Fig. 2). Recently, wolves have been recolonizing upper Michigan as well as Wisconsin (Ham-mill 1995).

In further work, we used the potential habitat prediction and relationships of wolf population density, habitat area, and prey abundance to estimate potential wolf population numbers for Wisconsin and Michigan, and discussed issues concerning species restoration in altered ecosystems (Mladenoff et al. 1997). We also subsequently applied the model to the northeastern United States, estimating potential habitat and wolf abundance for the region from upstate New York to Maine as a further test of the model and to assess the region for future re-establishment of wolves (Mladenoff and Sickley 1998). Here, we present validation testing of the model (based on 1979–1992 data), with data representing newly established packs from 1993 to 1996. We also include a test subset of data from 1979 to 1992 not used in building the original model. Elsewhere, we have examined related issues of wolf population persistence in fragmented landscapes, using a simulation model based on wolf life history characteristics, assuming variability in mortality and immigration due to landscape characteristics (Haight et al. 1998).

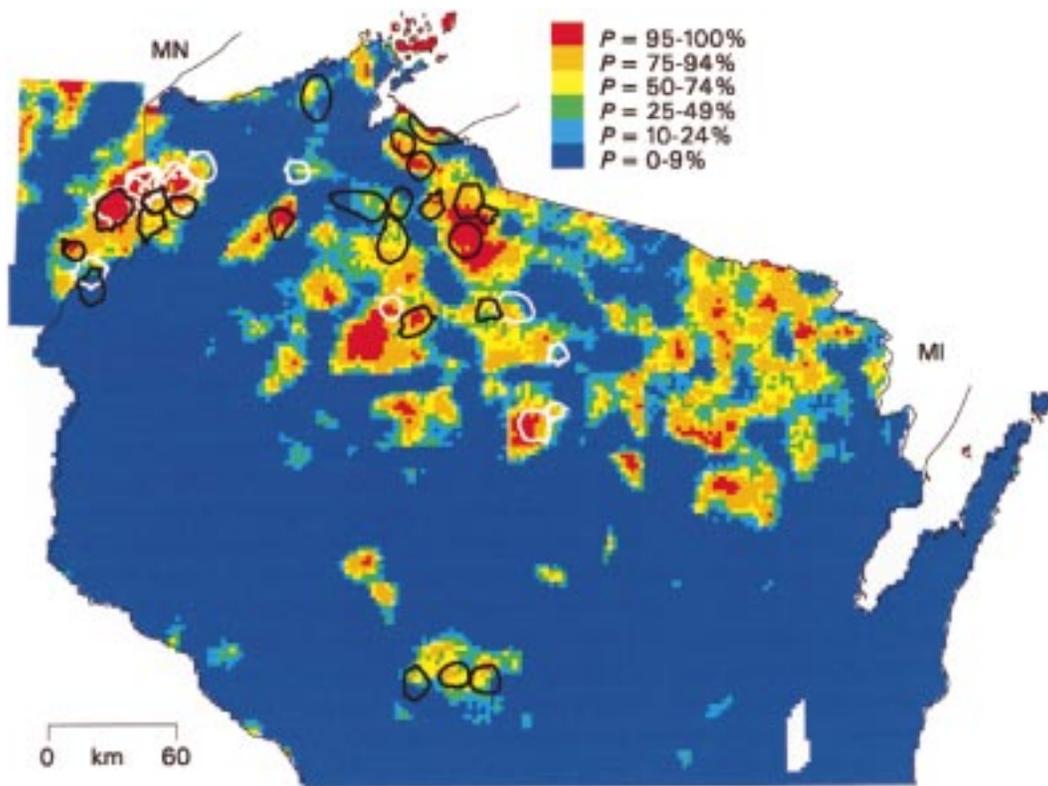


FIG. 2. Map of wolf habitat (by percentage favorability classes) based on the logistic regression road-density model (redrawn based on Mladenoff et al. [1995], with additional data). All areas in which $P > 50\%$ (>0.5 probability of being occupied) are considered favorable habitat, and are above the cut level of the logistic regression model that best classified both occupied and unoccupied areas of the landscape. Polygons with white boundaries are wolf pack territories used in creating the model (1979–1992 packs). Polygons with black boundaries are existing wolf pack territories in Wisconsin, originating since 1993, used in this test of the model and not used in the previous model creation.

METHODS

Data sources and preparation

Radiotelemetry data collected by Wisconsin DNR biologists from 1979 to 1992 were digitized into the ArcInfo GIS. Wolf packs with <50 data points over at least two seasons were not used for analysis. Home ranges of 14 packs met our criteria, and 14 nonpack areas were randomly chosen, but were required to be ≥ 10 km from existing packs (Mladenoff et al. 1995). Pack home ranges or territories were delineated using the harmonic-mean method (Dixon and Chapman 1980), with the 80% use isopleth defining pack territories (Mladenoff et al. 1995). During the original analysis, only a limited set of seven pack areas, which did not meet our minimum criteria for inclusion in the analysis, was available for model testing. Road density was based on a roads coverage derived from the U.S. Census Bureau (1991) TIGER/Line files. This coverage includes those roads indicated by solid lines on U.S.G.S. 1:100 000 quadrangle maps, i.e., roads passable by auto, but excluding unimproved forest roads or trails. Further details on data preparation are in Mladenoff et al. (1995).

In the present work, we apply our methodology to radiotelemetry data collected since model creation, from 1993 to 1996, to provide a more complete test of model performance. Criteria for data inclusion and procedures for delineation of pack home ranges were the same as in the previously work described. We found new data from 13 packs to be suitable. We also included as a separate group 10 packs without radio-collared wolves (field mapped), whose pack territories were mapped based on field tracking and other observations (Fig. 2).

Original model creation

The logistic regression model (SAS Institute 1989, Agresti 1990) was tested in the original analysis by classification performance of the response variable (wolf pack presence/absence), χ^2 goodness-of-fit ($P = 0.0001$), and parameter tests ($P = 0.018$). The roads model was based on the constant relation and the roads variable of the form

$$\text{logit}(P) = -6.5988 + 14.6189R \quad (1)$$

where P is the probability of occurrence of an event

and R is road density. Various probability values were then calculated by

$$P = 1/[1 + e^{\logit(p)}] \quad (2)$$

where e is the base of the natural logarithms. In the original analysis, the probability cut level of $P = 0.50$ yielded the least misclassification error, correctly classifying 12 of 14 pack areas ($P > 0.50$) and 12 of 14 nonpack areas ($P < 0.50$). Six of seven pack areas of a limited test data set were correctly classified (Mladenoff et al. 1995).

Current analysis

Here, we tested wolf landscape use as defined by the six probability classes (0–9%, 10–24%, 25–49%, 50–74%, 75–94%, and 95–100% favorability) from the model, which are based on road density (Eqs. 1 and 2; Fig. 2). For example, areas with road density values between 0.37 and 0.45 km roads/km² fall in the 50% probability class and have a 50–75% chance of supporting a wolf pack. As in the original analysis, we used the 50% cut level from the model as the threshold defining favorable (>0.5 probability) and unfavorable (<0.5 probability) habitat (Mladenoff et al. 1995). In effect, the six probability classes are treated in this analysis as if they were different habitat types; we are interested in assessing wolf preference of these classes. In this way, we can examine the usefulness of the original model, testing whether new wolf location data still indicate nonrandom use of the landscape, as predicted by the habitat class probability rankings.

We calculated road density for all of the new pack territories as a first attempt at evaluating the model's predictive power. We compared these values with the model cut level of $P = 0.50$, calculated for road density values <0.45 km/km² from Eqs. 1 and 2, to assess the overall classification accuracy of the model in classifying areas now occupied by new packs. We then examined the model reliability in finer detail by assessing landscape use by these new wolf packs among the predicted probability classes that we defined previously using the model. We intersected our newly delineated wolf pack home ranges with the habitat probability map, and calculated proportions of probability classes within each home range. This constituted habitat use. Habitat availability was defined by the proportions of the six probability classes found throughout the Wisconsin study area. We used compositional analysis (Aebischer and Robertson 1992) to compare wolf habitat use to availability for the 23 new wolf packs in Wisconsin.

Aebischer et al. (1993) discuss the use of compositional analysis for comparing wildlife habitat use to availability. A set of components or proportions that sums to 1 is defined as a composition. For a given home range, the proportions of D habitat classes can be expressed as x_1, x_2, \dots, x_D . The use of habitat i as measured by x_i is not independent of the use of other hab-

itats. This non-independence limits statistical tools that may be used. To circumvent this limitation, the proportional data can be passed through a log-ratio transformation to make the compositions linearly independent from each other, allowing for the use of statistical procedures that assume independence of variables as well as multivariate normality. The log-ratio transformation y_i is calculated as $y_i = \ln(x_i/x_j)$ ($i = 1, 2, \dots, D, i \neq j$). The variable x_j can be any of the D habitat classes present. In this way, the method avoids problems with non-independence of class proportions that affect other methods of assessing habitat use and availability (Aebischer et al. 1993).

Aebischer et al. (1993) also identify several assumptions that underlie compositional analysis of habitat use (Aitchison 1986). The first is that each animal represents an independent measure of habitat use within the population. Aebischer et al. (1993) caution the use of compositional analysis for gregarious or territorial animals. Because wolves are territorial, an area colonized by one pack is then unavailable to other packs. We subtracted the areas inhabited by wolf packs in 1993, when we began this study, from the total amount of available habitat in the study area.

The second assumption mentioned is that compositions calculated from different animals are equally accurate. For compositions calculated directly from radio-collar locations, the number of locations between animals should be similar. Our compositions were calculated from home range polygons of wolf packs; by extension, the home range areas should be equally accurate. Home ranges for 13 packs were developed from at least 50 radio-collar locations recorded over at least a full calendar year (Wydeven et al. 1995). Previous research (Fuller and Snow 1988) has shown that the size of a home range does not change significantly as the number of radio-collar points used to define that home range increases over 35. Home ranges for 10 additional packs were developed from field data. The mean areas of these two sets of home ranges are not significantly different (two-tailed $P = 0.1548$, assuming equal variances; two-tailed $P = 0.1518$, assuming unequal variances), in spite of the different methods used to define them.

The third assumption of compositional analysis is that the residuals display multivariate normality. Our data passed the Mahalanobis squared-distance measure test for multivariate normality:

$$D^2 = (x_i - \bar{x})'S^{-1}(x_i - \bar{x})$$

as described by Morrison (1990).

Compositional analysis allowed us to determine whether or not wolf habitat use was random or in proportion to overall availability. When use was significantly nonrandom, the analysis allowed us to rank habitat classes on how strongly they were selected for (or against) by wolf packs in comparison to availability of the classes in the landscape overall. Random habitat

TABLE 1. Road densities (km of road per km²) for wolf pack territories of 13 radio-collared and 10 field-mapped packs in Wisconsin from 1993 to 1996.

Collared packs	Uncollared packs
0.18	0.37
0.33	0.47†
0.23	0.24
0.71†	0.17
0.22	0.52†
0.19	0.54†
0.28	0.30
0.23	0.26
0.20	0.42
0.11	0.24
0.41	
0.33	
0.58†	

Notes: Road densities < 0.45 km/km² are predicted by the model to be favorable wolf habitat, above the $P > 0.5$ cut level in the model. Road densities of packs territories delineated with radiotelemetry data (collared wolves) and those mapped using field techniques (uncollared wolves) are not significantly different ($t = 0.698$, $P = 0.493$).

† Pack locations incorrectly classified as unsuitable by the model.

use was evaluated by comparing the differences in habitat use and availability log-ratios simultaneously over all habitat classes. The average log-ratio difference over all wolf packs would equal 0 under random habitat use. We calculated Wilks' lambda (Λ), a multivariate analog to the t test, to test this difference (Aebischer and Robertson 1992). The natural log of this value multiplied by $-N$, the number of packs, can be compared to a chi-squared distribution with $df = 5$ (the number of habitat classes minus 1) to determine if overall wolf habitat use is significantly nonrandom.

RESULTS AND DISCUSSION

In our original work (Mladenoff et al. 1995), we examined a large suite of mapped landscape variables, using both univariate and multivariate statistical methods. Our variables included eight land use/land cover classes, five land ownership/management classes, road density, human population density, and deer abundance. We found that agricultural lands, small-parcel private ownership, road density, and human population density were negatively related to existing wolf pack territories. Forests with a conifer (evergreen) component, and county-managed forest lands were positively related to wolf pack locations. In the logistic regression, a simple model with road density as the best predictor variable correctly classified 12 of 14 existing pack areas and 12 of 14 randomly selected nonpack areas. The model had a road density threshold of 0.45 km/km² that best classified pack and nonpack areas (Mladenoff et al. 1995), with existing pack territories usually within areas of road densities < 0.45 km/km². Others have shown that this negative relationship between roads and wolves is one based on human contact as a factor detrimental to wolf survival (Thiel 1985,

Mech et al. 1988). Wolves will use roads to ease travel, but road density is an index of human contact and roads contributes to wolf mortality through increased intentional or accidental killing. There is some evidence that wolves may select or avoid roads based on the amount of human use (Thurber et al. 1994). There is evidence that wolves will gradually occupy areas of relatively greater road density (>0.58 km/km², but <1.0 km/km²) (Mech 1989), if a large region of low road density serves as a wolf population source. This suggests that areas of higher road density may be biological sinks (Pulliam 1988) that are not sustainable habitat on their own without constant input (Mladenoff et al. 1997).

The logistic regression model identified landscape classes according to probabilities of suitability for wolves. The wolf packs used in the analysis occupied a subset of the landscape in these habitat classes (Fig. 2). The original logistic model correctly classified into favorable habitat areas 11 of 13 of these new packs delineated with telemetry data and 7 of 10 packs mapped in the field (Table 1). Seven (54%) of the more precisely mapped radio-collared packs had mean road densities < 0.25 km/km², within the $P > 0.95$ probability level of the logistic model (Mladenoff et al. 1995) (Figs. 2, 3). Lower precision of the field-mapped sample makes misclassification and actual road density values difficult to assess. Generally, field-mapped pack

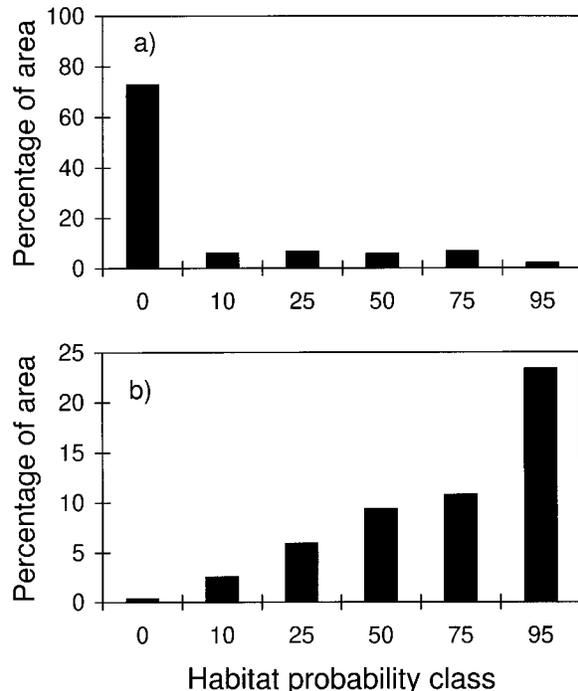


FIG. 3. Landscape percentages of the northern Wisconsin study region in various habitat favorability classes, based on the original logistic regression model (Fig. 2; see Mladenoff et al. 1995). (a) Available habitat (1997); areas occupied by packs established in 1979–1992, used in creating the model, are removed from these totals. (b) Habitat occupied by new (1993–1997) packs used here in testing the model.

TABLE 2. Mean log-ratio differences for habitat probability class use within northern Wisconsin wolf pack territories (1993–1996), based on compositional analysis (see *Methods*). Classes are from the original logistic regression model (Mladenoff et al. 1995).

Class	Habitat probability class					Rank	
	0	10	25	50	75		95
0		-3.13	-4.60	-6.76	-7.19	-5.09	0
10	3.13		-1.48	-3.63	-4.07	-1.96	1
25	4.60	1.48		-2.16	-2.59	-0.48	2
50	6.76	3.63	2.16		-0.44	1.67	4
75	7.19	4.07	2.59	0.44		2.11	5
95	5.09	1.96	0.48	-1.67	-2.11		3

Notes: The number of positive elements occurring in each row determines the rank of that row class. The row for habitat probability class 75% contains the maximum of five positive elements and, thus, is the highest ranked class.

territories are more conservatively delineated (larger), and result in more conservative test results (i.e., packs are more likely to be misclassified).

The compositional analysis of wolf use by landscape probability class reveals model sensitivity at finer levels. Use of the probability classes by wolves was significantly nonrandom (Wilks' lambda (Λ) = 0.406, and $-N \ln(\Lambda) = 20.708$, $P < 0.001$, $df = 5$; Fig. 3). Compositional analysis also indicates that the habitat classes differ in their rank order of relative preference (Table 2). The number of positive elements (positive log-ratio difference values) that occur in each row of Table 2 determines the rank of that row class. The fifth row, for habitat probability class 75%, contains the maximum possible five positive elements and is therefore the highest ranked class. The first row, for habitat class 0%, contains no positive elements and is therefore the lowest ranked class. The overall rank order of habitat class preference was: 75 > 50 > 95 > 25 > 10 > 0%, where the 75% probability class was the most preferred class, the 50% probability class was somewhat less preferred, etc. The 95% probability class, although the most likely type of habitat to sustain a wolf pack, ranked third in preference by new packs. Spatially, little of this class is available to colonizing wolf packs, and this class is always associated with surrounding areas of the more abundant 75% and 50% classes (Fig. 2). The 75% and 50% probability classes may be more

preferred where they are associated with a core of the 95% class, given that they are adequate in their characteristics and much more abundant.

As a result, ranks of the habitat class preferences deviate, in part, from the original model classes (Table 3). The 75% class (ranked first) is not significantly preferred over the 50% class (ranked second), but it is significantly preferred over the rest of the classes. The 50% class is not significantly preferred over the 95% class (ranked third), but it is significantly preferred over the rest of the classes ranked below it. The preference significances may skip a class because the habitat classes represent ordinal data (a continuous range of probability values that have been divided into classes) rather than discrete, categorical classes (such as grassland, forest, water, wetland). There is, then, an inherent similarity between adjacent habitat classes.

The model remains a reliable predictor of favorable wolf habitat based on road density values. Favorable habitat areas within Wisconsin (Fig. 2) are much smaller and more fragmented than those in upper Michigan or Minnesota (Mladenoff et al. 1995). As the Wisconsin wolf population continues to saturate more of the most favorable areas, it is possible that wolves will begin to occupy areas of higher road density, as has occurred in Minnesota (Mech 1989, Mech et al. 1995). Such a phenomenon is not presently occurring to a significant degree, and the model remains robust in predicting locations for wolf packs in this recolonizing population. It may be that broader colonization will not occur easily in northern Wisconsin, where habitat is fragmented, mortality is high, and a large source wolf population is not directly adjacent as in Northeastern Minnesota.

Although the model was developed on a limited area of northern Wisconsin, it appears to apply well in the larger Great Lakes region (Minnesota, Wisconsin, Michigan). The model agrees well with past mapping of critical habitat and overall favorable wolf range identified in Minnesota (Fuller et al. 1992, U.S. Fish and Wildlife Service 1992, Mladenoff et al. 1995). Further analysis after our original work has correctly identified an outlier of favorable habitat in a small, forested region in central Wisconsin that has been colonized by three packs. This habitat island is 100 km disjunct from

TABLE 3. Ranking matrix for preference of habitat probability classes for northern Wisconsin wolf packs (1993–1996), based on log-ratio differences in Table 2. Significance levels indicate deviation from random preference for a given class in the left-hand column over other classes in the matrix.

	Habitat probability class					Rank	
	0	10	25	50	75		95
0		---	---	---	---	---	0
10	+++		--	---	---	-	1
25	+++	++		---	--	-	2
50	+++	+++	+++		-	+	4
75	+++	+++	++	+		+++	5
95	+++	+	+	-	---		3

Notes: (+++, --- $P < 0.01$; ++, -- $P < 0.05$).

the rest of the occupied wolf range in the state (Fig. 2). Colonization of such an isolated area probably means that wolves are dispersing throughout the regional landscape to a great extent, perhaps exceeding our expectations of wolf movement through unfavorable landscapes (Mech et al. 1994, Mech 1995). This suggests that, although wolves examine much of the landscape, they continue, through both selection and avoidance, as well as direct and indirect human-related mortality factors, to colonize areas of low road density first, over less favorable locations (Mladenoff et al. 1997). In Michigan, the model has been qualitatively evaluated and is reported to be performing equally well, and the state of Michigan has adopted the predicted favorable habitat map (Mladenoff et al. 1995) as a part of its official wolf recovery plan (J. Hammill, Michigan DNR, *personal communication*).

Habitat quality is best defined by a combination of species density, individual survival, and productivity (Van Horne 1983). Wolf pack home ranges provide ideal units for testing habitat quality at landscape scales, because wolves are strongly territorial and their home ranges represent areas where all life history activities occur throughout the year. At least 17 of the 23 territories examined in this study were known to produce pups that survived to the end of the first year. However, our model only predicts areas that are suitable for breeding habitat, not dispersal habitat. Therefore, transient wolves can be expected to occur well outside the blocks of suitable habitat illustrated (Fig. 2). Characteristics of habitat suitable for dispersal are not well known, but wolves have been shown to disperse hundreds of kilometers through landscapes generally known to be unfavorable for their establishment and successful breeding (Wydeven 1994, Mech et al. 1995).

Testing a model with new data, as we have done here, is one approach to evaluating model reliability. An ideal further test is to apply the model in another region. We have done so to make initial predictions of favorable habitat in the northeastern United States, from upstate New York to Maine. The model results estimate potential wolf habitat equal in extent to that in Michigan and Wisconsin (Mladenoff and Sickley 1998). The northeastern United States is a region that was generally identified in the revised recovery plan for the gray wolf in the eastern states as a potentially viable area for wolf restoration (U.S. Fish and Wildlife Service 1992). Currently, wolves are not known to exist in the northeastern United States (Mech et al. 1994), although occasional sightings are reported (Glowa 1996).

In a general sense, the northeastern United States has a climate, land cover, forest types, and human land uses that are similar to those of the northern Great Lakes states, suggesting that similar use patterns by wolves could occur if the region were colonized. Several differences also exist between the upper Midwest, where

the model was derived, and the Northeast. Topographic relief is greater in many areas of the Northeast, and this may affect prey abundance and availability throughout the year, road placement, and, thereby, the way in which wolves use the landscape (Mladenoff and Sickley 1998). We speculate that the model may prove useful in the Northeast, but may not be applicable in regions that differ further from the upper Midwest, such as areas in the western United States where climate, vegetation, prey, and land use may all differ significantly from the upper Midwest and Northeast. Actual confirmation of the model predictions in this new location will need to await possible recolonization of the northeastern United States by wolves.

CONCLUSIONS

The relationship between wolf use of the landscape and road density is a robust predictor of suitable wolf habitat, particularly in a region where suitable areas are fragmented and a large source population of wolves is not immediately nearby. Although wolves will use roads for movement, particularly in areas with low human use, road density is an indicator of human contact, and wolf mortality. We now know that wolves do not require wilderness to survive, but require adequate prey and reduced killing by humans (Peterson 1988, Mech 1995). These facts will mean that, with legal protection, wolves can occupy more of the landscape than was initially assumed, and will require active management to minimize conflict with humans (Mech 1995, Haight et al. 1998).

Identifying areas suitable for wolves through the relatively simple model we have presented can provide a useful tool for resource planners charged with managing restoration of wolves. The model may be useful for other large carnivores that may be negatively affected by human contact, and more successful in relatively wild areas that need to be identified in a spatially explicit manner. Such predictions can now be made with considerable ease and spatial accuracy using GIS and available digital data sets. Habitat preference maps generated from the model can be useful in identifying the extent and location of priority areas for management, as well as focusing field inventory efforts. This can be helpful to conservation planning and monitoring in newly colonizing areas, as wolves expand in the Midwest, and if they begin colonizing the northeastern United States.

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