Modeling Gray Wolf (Canis lupus) Habitat in the Pacific Northwest, U.S.A

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Journal of Conservation Planning Vol 2 (2006) 17—33

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ABSTRACT: Gray wolves (*Canis lupus*) were once widespread throughout most of North America including the Pacific Northwest. Wolves were extirpated from the Pacific Northwest in the early 20th century and have been absent for over 60 years. The success of reintroduction efforts in Idaho and the greater Yellowstone area, however, has caused wolf populations in these regions to rise dramatically, giving way to wolf dispersal into Oregon. This study used a Geographic Information System (GIS) and wolf pack locations from the Rocky Mountain region to model gray wolf habitat. *A priori* models were created under the hypotheses that wolf habitat (1) will include a relatively high prey density, (2) will be limited by human influence, (3) will include favorable landscape characteristics such as forest cover and public ownership, and (4) may be influenced by some combination of these factors. Logistic regression was used to select the best model for predicting wolf habitat. The resulting model was tested in Idaho, Montana, and Wyoming and applied to Oregon to reveal approximately 68,500 km2 of potential wolf habitat that could support a population of approximately 1450 wolves. The final model, which included variables of forest cover and public lands, was applied to the greater Pacific Northwest to identify possible locations for wolf colonization throughout the area. The model may be relevant for other parts of the world where wolf reintroductions are planned or recolonizations are taking place. In addition, the methods presented in our study may be applicable to other wide-ranging large carnivores in other regions.

Keywords: Canis lupus, geographic information systems, habitat modeling, logistic regression, Oregon, Pacific Northwest, wolf, wolves

INTRODUCTION

Gray wolves (*Canis lupus*) historically had the most extensive range of any land mammal. Originally ranging over much of the northern hemisphere, their range has since been reduced significantly over the centuries by humans (Mech and Boitani 2003). Wolves were extirpated from the conterminous United States with the exception of a small population in northern Minnesota in the early 20th century (Mech et al. 1995, Mladenoff and Sickley 1998). Since gaining protection from the Endangered Species Act (1974) and being reintroduced into Yellowstone and central Idaho (1995 – 1996), wolves have begun to recolonize areas in the northern Great Lake states and the Rocky Mountain region (Fuller 1995, Mech et al. 1995, Mladenoff et al. 1995, Pletscher et al. 1997, USFWS et al. 2002). An increase of wolf populations in Idaho has resulted in some wolves dispersing into Oregon to seek out new habitat (ODFW 2003). These dispersing wolves have ignited much controversy regarding the potential of gray wolf recovery in Oregon. Our study focused on ecological factors to assess the potential wolf habitat in Oregon.

Because wolves are habitat generalists, they can live in most places in North America that have a sufficient prey base (Fuller et al. 1992, Haight et al. 1998). Conflicts typically occur, however, when they occupy areas close to humans. The majority of wolf mortality is human-caused whether accidental, intentional or indirectly through disease (Mech and Goyal 1993, Mladenoff et al. 1995). Predicting favorable wolf habitat thus becomes a process of locating areas that contain sufficient prey and provide security from humans to lessen conflict (Mladenoff et al. 1995).

Prey Availability

The single most important factor for considering wolf habitat is the availability of prey. A review of documented wolf studies from the various regions throughout North America shows that approximately two-thirds of the variation in wolf density can be explained by variation in prey biomass (Keith 1983, Fuller 1989, Fuller et al. 2003). Although wolves are generally not prey-specific, large ungulates make up the majority of their diet (Fuller et al. 1992, Haight et al. 1998, Corsi et al. 1999, Fuller et al. 2003). In the eastern portion of North America, white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) in single prey systems typically constitute the majority of a wolf's diet (Mech 1970, Peterson 1999). However, in the northern and western portions, many different combinations of ungulate species including elk (*Cervus elaphus*), moose, caribou (*Rangifer tarandus)*, muskox (*Ovibos moschatus)*, white-tailed deer, mule deer (*Ododcoileus hemionus*), black-tailed deer (*O. h. columbianus*), bighorn sheep (*Ovis canadensis*), and bison (*Bison bison*) can be available to wolves in a multi-prey system (Ballard et al. 1987, Weaver 1994, Fuller et al. 2003). In addition, beaver (*Castor canadensis*) and hares (*Lepus americanus and L. othus*) are important secondary prey in the spring and summer seasons (Fuller 1989, Weaver 1994, Jedrzejewski et al. 2002). Due to the relatively small biomass of beavers and hares, however, ungulates (primarily immature ungulates) still make up the greater prey biomass during these times (Fuller 1989, Mech and Peterson 2003).

Several studies in western North America have found that in terms of biomass, elk are the most important prey species for wolves (Huggard 1993, Weaver 1994, Smith et al. 2000, Peterson and Ciucci 2003). In a review of western North America studies, Weaver (1994) found wolf predation on elk and deer to be roughly equal in numbers (42%), but the elk were far more important in terms of biomass (56% for elk compared to 20% for deer).

Human Presence

Road Density

In addition to prey availability, wolves require areas that minimize wolf-human conflicts (Mech 1995, Mladenoff et al. 1995). One of the most important factors in determining suitable wolf habitat is road density (Theil 1985, Fuller et al. 1992, Mladenoff et al. 1995). In some cases lightly traveled roads can be used as travel corridors by wolves, but wolves often avoid roads that are heavily traveled and easily accessible by humans (Thurber et al. 1994, Mladenoff et al. 1995). Human interactions with wolves are a primary source of wolf mortality due to legal, illegal, and accidental killings or indirectly through disease (Theil 1985, Mech 1989, Mladenoff et al. 1995).

Theil (1985) found that wolf breeding occurred in areas with a road density of ≤0.59 km/km^2 (linear kilometers of roads per square kilometer) in 13 northern Wisconsin counties. Other studies in Minnesota and Michigan provided similar results and a basis for assessing wolf habitat suitability in the Lake States (Jensen et al. 1986, Mech et al. 1988). Dispersing wolves, however, have been shown to travel through areas of high road densities in order to find suitable habitat (Mech et al. 1995). Since wolves are not necessarily deterred by the roads themselves, but rather humans that use the roads, the difficulty with measuring road density for habitat models becomes an issue of human activity. And, while the level of road usage may be a relatively accurate measure for habitat modeling, such information is rarely available.

Human Density

In the Great Lakes region, Fuller et al. (1992) found that most wolf packs (88%) in Minnesota were located in areas where human density was ≤8 humans/km^2. Mladenoff et al. (1995) found that the mean human density in wolf pack areas in the Great Lakes region was 1.5 humans/km^2. Light and Fritts (1994) found dispersing wolves in the Dakotas to be in areas with a mean human density of 3.5 humans/km^2, with 8.2 humans/km^2 being the greatest human density. Human density can be difficult to assess because most data are only available at the census tract/block or county level which can vary significantly in size between tracts/blocks or counties.

Landscape Characteristics

Several landscape characteristics have also been found to be associated with wolf habitat. These characteristics may not be a requirement by wolves per se, but rather may provide additional security from human contact (Singelton et al. 2002, Boitani 2003). Mladenoff et al. (1995) found that public land ownership was strongly related to favorable wolf habitat in the Great Lakes region. Houts (2000) also found that land ownership was significantly different between wolf and non-wolf locations in the northern Rocky Mountain region. Low human density and low road density, in addition to a greater amount of wilderness areas, make public land generally suitable for wolf habitat. Mladenoff et al. (1995) also found that private industrial forest ownership was strongly related to favorable wolf habitat.

Forest cover has also been shown to be strongly related to wolf habitat since it provides habitat for avoiding humans (Boitani 2003). In the Great Lakes region, Mladenoff et al. (1995) found that although most pack areas were located within mixed or deciduous forest, over 92% of all wolf pack areas were located within some type of forest. In the Rocky Mountain region, Houts (2000) also found forest cover (mainly conifer dominated) to be a significant component of wolf habitat.

Previous Models

Several Geographic Information System (GIS) based models have proven to be effective at predicting habitat suitability for large carnivores including wolves (Clark et al. 1993, Mladenoff et al. 1995, Schadt et al. 2002, Fernandez et al. 2003). Mladenoff et al. (1995) used logistic regression to map the probability of wolf habitat in Wisconsin. Stepwise logistic regression resulted in a model with a road density term to be effective in assessing wolf habitat throughout the region (Mladenoff et al. 1995). Later studies corroborated these earlier results (Mladenoff et al. 1999). Subsequently, other wolf habitat models have been applied to various areas in the northern U.S. Rocky Mountains, southern U.S. Rocky

Mountains, and Italy (Corsi et al. 1999, Houts 2000, Carroll et al. 2003).

Only one study has modeled wolf habitat in Oregon (Carroll et al. 2001). Ungulate density data were based on numbers from a remote sensing "tasseled-cap greenness" technique that were not found to be correlated with ungulate harvest data. In addition, the authors did not test or validate the model, however, with any measure of wolf habitat (e.g. presence/absence data).

The objectives of this study were to provide a more comprehensive model for predicting wolf habitat in Oregon and the Pacific Northwest. Logistic regression was used to select the best approximating wolf habitat model from a set of *a priori* models based on the previous wolf research. These *a priori* models were grouped under the hypotheses that wolf habitat (1) includes relatively high densities of prey (Keith 1983, Fuller 1989, Fuller et al. 2003), (2) is limited by human influence (Theil 1985, Fuller et al. 1992, Mladenoff et al. 1995), (3) includes favorable landscape characteristics such as forest cover and public ownership (Mladenoff et al. 1995, Houts 2000), and (4) may be influenced by some combination of these factors.

METHODS

Study Area

The study area for this project included Oregon, Idaho, Montana, and Wyoming. These states have many similar characteristics including diverse ecosystems, large amounts of public land and wilderness areas, and similar ungulate species. Although wolves have been absent from Oregon for over 60 years, wolves were reintroduced into Yellowstone National Park (31 wolves) and central Idaho (35 wolves) in 1995–1996 (USFWS et al. 2002). In addition, wolves have dispersed from Canada into northwestern Montana and through Glacier National Park (Boyd et al. 1995). Currently, there are an estimated 108 wolves in northwestern Montana, 271 in the Greater Yellowstone ecosystem, and 285 in central Idaho (USFWS et al. 2002, USFWS 2004). Since wolves currently reside in Idaho, Montana, and Wyoming but not in Oregon, the models were created for Idaho, and the best model was tested in Idaho, Montana, and Wyoming and then applied to Oregon.

Spatial Data

Three main factors generally need to be addressed when assessing wolf habitat: sufficient prey available, low levels of human influence, and adequate landscape characteristics (e.g. forest cover and land ownership). In order to address the availability of prey in Oregon, data sets were created illustrating ungulate range and density. Thus, range maps were developed for elk (Cervus elaphus) and deer (*Odocoileus hemionus* and *O. virginianus*), the main source of prey accessible to wolves in Oregon.

Ungulate density data were obtained by applying existing deer and elk population estimates for 68 wildlife management units in Oregon to the area of ungulate range within those management units. An Ungulate Biomass Index (UBI) was used to normalize the relative biomass of deer and elk, in which the relative biomass of elk were the equivalent of the relative biomass of three deer (Keith 1983, Fuller 1989, Mladenoff et al. 1995, Fuller et al. 2003). Therefore, all UBI values were measured in terms of deer biomass. For example, the UBI value for 300 elk in a management unit would be 900; the same value as a management unit containing 900 deer. These ungulate density calculations were undertaken for elk and deer separately. All ungulate data were converted from vector to raster data with a 1 km2 cell size for subsequent analysis.

Road density and human density were used to identify areas with limited human presence. Road densities were calculated from the U.S. Census Bureau 2000 TIGER (Topologically Integrated Geographic Encoding and Referencing) road data (line). These data are equivalent to the solid lines on a USGS 1:100,000 quadrangle (metadata available online at: http://www.census.gov/geo/www/tiger/rd_2ktiger/tlrdmeta.txt). Paved roads and improved unsurfaced roads passable year-round by 2 wheel drive automobiles were included for density calculations, but unimproved forest roads (e.g. logging roads) and trails were omitted. The Spatial Analyst extension of ArcMap (ESRI, Redlands, CA) was used with a search radius of 5 km and output cell size of 1 km2 to calculate road densities in kilometers of road per square kilometer area (km/km2).

Because most human density data are only available at the census block/tract or county level that can vary in size by hundreds of square kilometers, the accuracy of these data may be questionable for habitat modeling purposes. The 2000 U.S. Census data at the block group level were used as a measure for human density to provide a comparable dataset to previous models (Mladenoff et al. 1995) in addition to a human presence variable. In order to test a more accurate measure of human impact, LandScan Global Population 2002 data created by the Oak Ridge National Laboratory were used (Dobson et al. 2000). These data have a resolution of 30 arc seconds (approximately 1 km2) and estimate the number of humans per unit area. The dataset was created from a population model that not only incorporates census data, but also roads, slope, land cover, populated places, lights visible from satellites at night, and other factors to result in a global human density grid (Dobson et al. 2000). Because many variables that measure human impact are used, these data may provide a more accurate assessment for modeling wolf habitat than census data alone.

Landscape variables that were found to be significant in previous models (e.g. public ownership and forest cover) were incorporated to provide additional insight into predicting wolf habitat (Mladenoff et al. 1995, Houts 2000). Land ownership was obtained from the U.S. Bureau of Land Management at a 1:100,000 scale. These data were then queried to include only public lands. Land cover data were obtained from the U.S. Geological Survey National Land Cover Data dataset. These data are derived from 30 m Landsat Thematic Mapper (TM) imagery for the conterminous U.S. The data were queried to include only forest cover. The percentage of forest cover and public ownership were converted to a 1 km2 continuous layer by running the ArcMap Spatial Analyst neighborhood analysis over a three km radius.

Precipitation data were obtained from the Oregon Climate Service to incorporate as a climatic variable. These data were created from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) and represent average annual precipitation over a 29-year period (Daly et al. 2002). Although precipitation was not used in previous models, we investigated its importance with regard to ecosystem productivity. These data were measured in millimeters of precipitation at a resolution of approximately 4 km2.

Topographic variables such as elevation and slope were not included in the analysis although some studies have found them to be of note for certain wolf activities (Paquet et al. 1996). Wolves are likely to be driven from areas of generally low elevations and slopes, however, where human settlements and infrastructures occur (Dobson et al. 2000) and the relationship between topographic features and pack presence/absence on a landscape scale would likely be reversed due to the greater need of wolves to avoid humans.

In order to test the models, wolf pack data were obtained for wolf populations in the Rocky Mountains (Idaho, Montana, and Wyoming). These data were based on GPS and radio-collared tracking locations obtained by National Park Service and US Fish and Wildlife in 2003 (USFWS et al. 2004). The radio-collared wolves were tracked by aircraft a minimum of two times per month and many were tracked more frequently from the ground (USFWS et al. 2004). Wolf pack polygons were created by the minimum convex polygon procedure in the “Animal Movement” extension for ArcView. Where packs were known to exist, but lacked radio-collared locations, polygons of average wolf pack size were created to represent pack locations (Steve Carson, personal communication).

Model Selection

In order to find the best overall model for wolf habitat, *a priori* models were separated into four categories (Table 1). The first category was grouped under a hypothesis that the probability of wolf occupancy will increase with some measure of prey availability (H1). To test this hypothesis, models were based on elk, deer, and overall ungulate densities. The second category of models was grouped under a hypothesis that the probability of wolf occupancy will decrease with increasing human presence (H2). To test this hypothesis, models were based on road density, human density, and human impact. The third category was grouped under a hypothesis that the probability of wolf occupancy will increase with favorable landscape characteristics (H3). To test this hypothesis, models were based on percent of forest cover, percent of public ownership, and precipitation. The fourth category of models was grouped under the hypothesis that there may be an additive effect of prey availability, human presence, and/or favorable landscape characteristics (H4). Therefore, the models with the best-fit values from each of the first three categories were used in all combinations (i.e., H1 + H2; H1 + H3; H2 + H3; and H1 + H2 + H3) to measure the additive effects.

Logistic regression methods were used to compare pack locations with non-pack locations. Non-pack locations were based on random polygons (equal in size to the mean wolf pack size) at least 10 km away from pack polygons in order to minimize spatial autocorrelation (Mladenoff et al. 1995). The Information Theoretic approach following Burnham and Anderson (2002) was used to select the best models. Small sample size adjusted Akaike's Information Criterion (AICC), delta AICC and Akaike's weights were used to rank models (Burnham and Anderson 2002). The best model was selected based on lowest AICC values for each hypothesis. Finally, the best models from each hypothesis were compared to each other to find the best overall wolf habitat model.

TABLE 1 Summary of Variables Used in Logistic Regression Models

Models*	Definition of variables
Hypothesis 1 (H1) - Prey availability	
UngD	Density of elk and deer per square km (UBI/km^2)
ElkD	Density of elk per square km (UBI/km^2)
DeerD	Density of deer per square km (UBI/km^2)
Hypothesis 2 (H2) - Human presence	
RdD	Linear km of road per square km (km/km^2)
HuD	Number of humans per square mile from census block group data (humans/km^2)
HuP	Measurement of human presence based on LandScan data (humans/km^2)
RdD + HuD	
Hypothesis 3 (H3) - Landscape characteristics	
%For	Percentage of forest cover
%Pub	Percentage of public land
Precip	Annual precipitation (mm)
%For + %Pub	
%For + Precip	
Hypothesis 4 (H4) - Additive effects	
H1 + H2	
H1 + H3	
H2 + H3	
H1 + H2 + H3	

*Models based on hypotheses that wolf habitat will be identified by that availability of prey (H1); will be restricted by the presence of human activity (H2); that some landscape characteristics are favorable to wolf habitat (H3); and that there may be an additive effect of prey availability, human presence, or favorable landscape characteristics (H4).

Model Application

The *a priori* model selected to be the best approximating wolf habitat model was applied to Idaho in order to test the accuracy of the model against the wolf pack and random polygons. In addition, the model was applied to Montana and Wyoming and tested against packs and random polygons as a means of validating the model. Success was measured by assessing the mean probability for wolf pack occurrence calculated by the model for observed wolf packs versus the mean probability for wolf pack occurrence calculated by the model for random polygons. The model would be considered successful if the model predicted a high probability (>50%) where wolves are present and predicted a low probability (<50%) where wolves are not present. Finally, the model was applied to Oregon in order to identify potential wolf habitat in the state.

Estimating Capacity

Predicting how many wolf packs a given amount of habitat will support can be difficult. Wolves are social animals so pack dynamics are very complex to model. In order to avoid predicting the social complexity of wolf packs, estimates of wolf density can be based on the numbers of wolves in relation to prey abundance. Fuller et al. (2003) compiled data from previous research to study the relationship between wolf density and prey availability (Keith 1983, Fuller 1989). Results yielded the following equation:

$$W = 3.5 + 3.27U$$

where W is the number of wolves/1000 km^2 and U is the UBI/km^2 (r^2 = 0.64, 31 df, P < 0.001). This equation was used to estimate the number of wolves that could initially be supported in potential habitat in Oregon based on current prey population estimates. Estimates were grouped together into five regions for analysis: the northeast region, the Cascade region, the Siskiyou/ Klamath (southwest) region, the central coastal region, and the northern coastal region. Patches of wolf habitat with a capacity less than four wolves were eliminated from further analysis. This ensured all areas of wolf habitat contained enough prey density to support at least a small number of wolves since prey densities were not included in the final model.

RESULTS

Spatial Data

Univariate statistics (Kruskal-Wallis rank sum test) show that most variables included in the models were significantly different (P < 0.001) between pack and non-packs (Table 2, page 24) (Mladenoff et al. 1995, Fernandez et al. 2003). The exceptions were deer density and ungulate density which did not show significant differences (P = 0.070 and 0.065 respectively). Elk density, percent forest, percent public land, and precipitation were all found to be higher in wolf pack areas than in random polygons (P < 0.001). Road density, human density, and human presence were all found to be lower in wolf pack areas than random polygons (P < 0.001). These results supported the initial hypotheses. Deer density and ungulate density, however, were found to be at similar levels between wolf packs and random polygons.

Model Selection

The best model from the prey availability hypothesis set included elk density (Table 3, page 25). This model was 8 AIC_C lower than the next best model and received 98% of the Akaike's weight from this group of models. This elk density variable was retained for inclusion in our final modeling step of building additive models associated with the three main hypotheses. The best model from the human presence hypothesis set included human density based on the 2000 US census data. The model was 3 AIC_C lower than the next best model and received 57% of the Akaike's weight from this group of models. The next closest model was road density and human density, but a correlation matrix showed these variables to be highly

TABLE 2 Statistical Comparisons for Habitat Variables between Packs (n = 50) and Random Non-pack Polygons (n = 50)

Variable	Packs *	Non-Packs *	X^2	P
RdD (km/km^2)	0.12 ± 0.12	0.39 ± 0.30	12.82	<0.001
HuD ($hu./km^2$)	0.23 ± 0.32	3.33 ± 4.56	17.98	<0.001
HuP ($hu./km^2$)	0.11 ± 0.18	2.33 ± 3.69	15.62	<0.001
UngD (UBI/km^2)	3.76 ± 2.02	2.79 ± 2.35	3.40	0.065
ElkD (UBI/km^2)	2.87 ± 1.32	1.33 ± 1.79	11.50	<0.001
DeerD (UBI/km^2)	0.85 ± 1.19	1.20 ± 1.26	3.29	0.07
%For (%)	85.42 ± 18.44	19.67 ± 33.26	27.50	<0.001
%Pub (%)	93.75 ± 12.62	53.30 ± 32.25	22.34	<0.001
Precip (mm)	1012.81 ± 330.95	479.52 ± 267.18	24.58	<0.001

All variables were tested using Kruskal-Wallis rank sum test

*Values are means ± 1 SE

TABLE 3 Summary of Logistic Regression Models for Wolf Habitat vs. Non-habitat in Idaho

Model*	K	AIC_C	Δ_i	Akaike W_i
Hypothesis 1 (H1)				
ElkD	2	62.27	0	0.98
UngD	2	70.92	8.65	0.01
DeerD	2	72.42	10.15	0.01
Hypothesis 2 (H2)				
HuD	2	51.20	0	0.57
RdD + HuD	3	52.68	1.48	0.27
HuP	2	54.22	3.02	0.12
RdD	2	56.49	5.29	0.04
Hypothesis 3 (H3)				
%For + %Pub	3	17.87	0	>0.99
%For	2	34.07	16.20	$3.03 * 10^{-4}$
%For + Precip	3	35.41	17.54	$1.55 * 10^{-4}$
Precip	2	43.26	25.39	$3.06 * 10^{-6}$
%Pub	2	45.88	28.01	$8.25 * 10^{-7}$
Hypothesis 4 (H4)				
HuD + %For + %Pub	4	20.22	0	0.44
ElkD + %For + %Pub	4	20.23	0.02	0.43
ElkD + %For + %Pub + HuD	5	22.69	2.47	0.13
ElkD + HuD	3	47.81	27.59	$4.47 * 10^{-7}$
Final models				
%For + %Pub	3	17.87	0	0.77
ElkD + %For + %Pub	4	20.23	2.36	0.23
HuD	2	51.20	33.33	$4.43 * 10^{-8}$
ElkD	2	62.27	44.40	$1.75 * 10^{-10}$

*Models based on hypotheses that wolf habitat will be identified by the availability of prey (H1); that wolf habitat will be restricted by the presence of human activity (H2); that some landscape characteristics are favorable to wolf habitat (H3); and that there may be an additive effect of prey availability, human presence, or favorable landscape characteristics (H4).

correlated (r = 0.77) as were human density and human presence (r = 0.95). Human density, therefore, was the only model from the second category to be retained for inclusion in the final modeling step. The best model from the landscape characteristics hypothesis included percent forest cover and percent public ownership. The model was 16 AIC_C lower than the next best model and received 99% of the Akaike's weight from this group of models. The percent forest cover and percent public ownership were retained for inclusion in the final modeling step.

The best model from the additive effect hypothesis set included human density, percent forest cover, and percent public ownership. The model was only 0.02 AIC_C lower than the next best model which included elk density, percent forest cover and percent public ownership and received 44% of the Akaike's weight from this group of models as compared to 43% for the next best model. A correlation matrix, however, showed that human density was negatively correlated with public land (r = -0.7). Thus, the best model that contained both parameters was no longer considered for further analyses. The next best model which included elk density, percent forest cover and percent public ownership was used in further analyses.

Comparing the best models from the four hypotheses revealed that the overall best model included percent forest cover and percent public ownership. This model was more than 2 AIC_C lower than the next best model and received 77% of the Akaike weight from this group of models. This final model was considered to be the best approximating model for predicting wolf habitat. The equation for this model is as follows:

$$\text{logit}(P) = -21.10(\pm 10.67) + (0.10\ (\pm 0.05) * \%For) + (0.19\ (\pm 0.11) * \%Pub)$$

Model Application

The probability of wolf habitat was calculated using the equation: $P = e^{\text{logit}(P)} / 1 + e^{\text{logit}(P)}$

This calculation revealed that there was a significant difference between the mean percent probability for packs (89.9% ± 17.9) and the mean percent probability for random polygons (11.9% ± 17.2) in Idaho (X^2 = 35.37; P < 0.001 from Kruskal-Wallis rank sum test).

Testing the model against the packs and random polygons in Montana and Wyoming showed that the model also worked well in those states (Figure 1, page 27). There was a significant difference between the mean percent probability for packs (79.2% ± 11.3) and the mean percent probability for random polygons (5.1% ± 11.3; X^2 = 66.40; P < 0.001 from Kruskal-Wallis rank sum test). In addition, there was no evidence of a difference between pack results in Idaho versus Montana or Wyoming (P = 0.05 from two-sample t-test) or between results of random polygons (P = 0.08 from two-sample t-test).

A wolf pack probability greater than 50% (Mladenoff et al. 1995, Fernandez et al. 2003) was used in estimating wolf habitat in Oregon. Based on this approach, there is approximately 68,500 km^2 of wolf habitat in Oregon. The Cascade region has the greatest amount of wolf habitat (approximately 33,500 km^2) in Oregon (Figure 2, page 27). The northeast region has the next largest portion of wolf habitat (approximately 22,800 km^2) followed by the Siskiyou/Klamath (approximately 6500 km^2), the central coastal (approximately 3200 km^2), and the northern coastal (approximately 2500 km^2) regions.

Estimating Capacity

Applying the equation developed by Fuller et al (2003) to the estimated available habitat, Oregon would be able to support approximately 1450 wolves with an average density of 21 wolves/1000 km^2. The Cascade region would be able to support approximately 600 (18 wolves/1000 km^2) wolves, the northeast region approximately 460 (20 wolves/1000 km^2) wolves, the Siskiyou/Klamath region approximately 120 (18 wolves/1000 km^2) wolves, the central coastal region approximately 144 (45 wolves/1000 km^2) wolves, and the north coastal region approximately 129 wolves (52 wolves/1000 km^2).

FIGURE 1 Modeled wolf habitat >50% in the Rocky Mountain region.

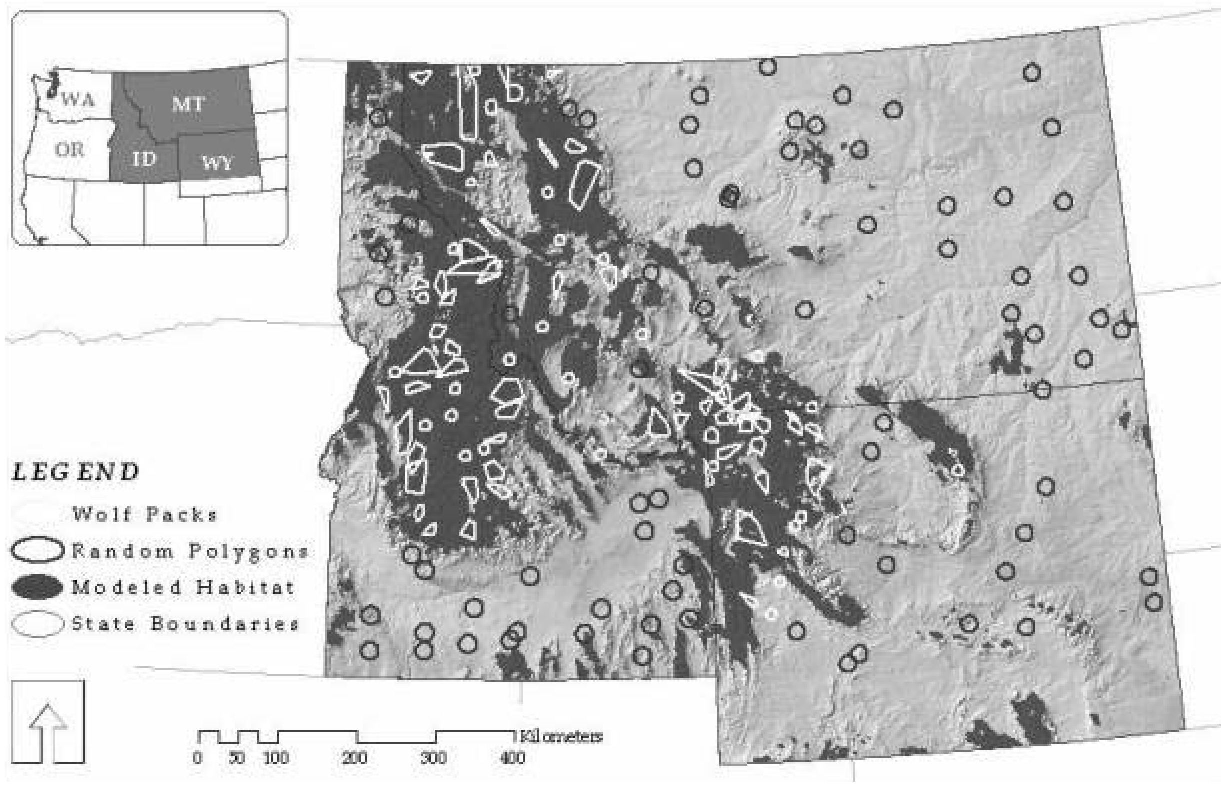
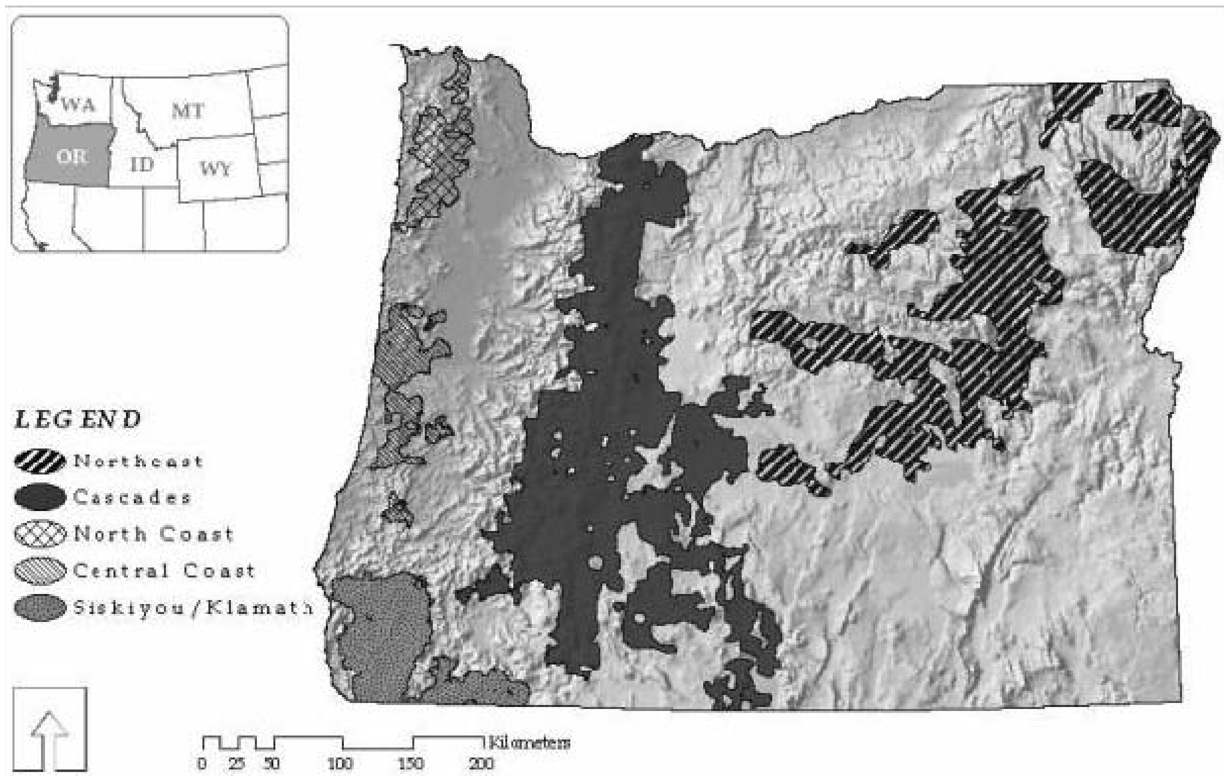


FIGURE 2 Modeled wolf habitat >50% in the Rocky Mountain region.



DISCUSSION

Spatial Data

Mladenoff et al. (1995) found deer density not to be related to wolf distribution (8.58 deer/km^2 in pack territories versus 8.38 deer/km^2 in non-pack territories) and suggested that the ability of deer to live in close proximity to humans may influence this relationship. Our results corroborate the Great Lakes study and found deer to be at similar densities in random polygons and wolf pack locations (p = 0.07, Table 2). Houts (2000) found elk density to be higher in wolf areas than non-wolf areas (p <0.004) in the Rocky Mountain region. Our results were similar; elk density was approximately 2 times higher in wolf pack areas than non-pack areas (p <0.001, Table 2).

Previous studies (Thiel 1985, Fuller et al. 1992, Mladenoff et al. 1995) in the upper-Midwest found road density to be significantly lower in areas where wolves were present (<0.6 km/km^2) than in areas that wolves did not inhabit. Overall, we found road density to be relatively low in our study area compared to the Great Lakes, but road density was still found to be significantly lower in wolf pack locations (0.1 km/km^2) than random polygons (0.4 km/km^2). We also found that road density did not perform as well as human density, which differs from the research in Wisconsin (Mladenoff et al. 1995, Mladenoff et al. 1999). This may be due to the relatively low road density overall in western states compared to the Great Lake states.

We found human density to be much lower in wolf pack areas (0.2 humans/km^2) than non-pack areas (3.3 humans/km^2) in our study area which is consistent with other studies from the Great Lakes region (Fuller et al. 1992, Mladenoff et al. 1995) and the Rocky Mountain region (Houts 2000). Mladenoff et al. (1995) found mean human density in Wisconsin to be 1.5 humans/km^2 in wolf pack areas and 5.2 humans/km^2 in non-pack areas. Our results were likely due to the low relative human population in the northern Rocky Mountain region and the large amount of wilderness areas that wolves inhabit. Although the LandScan human presence data did not perform as well as census blocks in our habitat models, our results suggest that human impact models may be a valuable tool for assessing wolf or other large carnivore habitat. Since the LandScan data are available for the entire globe and consistent at relatively fine resolution, they may represent an efficient and relatively accurate database for assessing potential wolf habitat in other regions of the world.

Houts (2000) found that wolf habitat in the Rocky Mountain region was characterized by forest cover and public land. In addition, Mladenoff et al. (1995) found wolf packs to include higher percentages of forest cover and public ownership in Wisconsin. Our results tend to corroborate these previous studies and our final model included percent forest cover and percent public land.

Since wolves are still expanding in the study area, wolf absence does not necessarily mean an uninhabited area will not provide wolf habitat. As their populations increase in a given region, wolves will likely inhabit areas with higher road and human densities and possibly less public forested land. However, this study does reflect the habitat characteristics that the expanding population has utilized in the Rocky Mountains and will likely use when dispersing to surrounding areas.

Model Selection

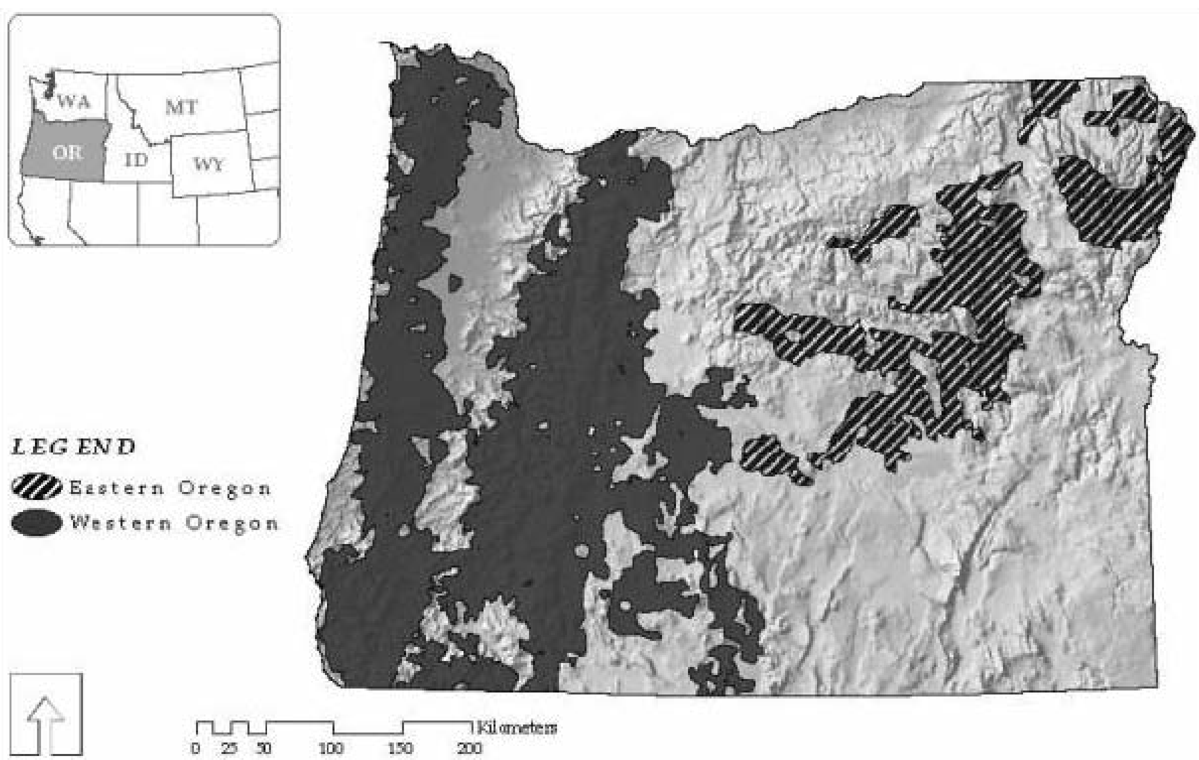
While Mladenoff et al. (1995) successfully used stepwise logistic regression to select a wolf habitat model, most natural resource modeling has since shifted to using *a priori* hypotheses as a means of model creation and selection (Burnham and Anderson 2002). Our study followed the guidelines of Burnham and Anderson (2002) in order to create a robust wolf habitat model for the northwest United States. The selected prediction model used public land and forest cover to identify potential wolf habitat in our study area. Although no human presence data were used in the final model, public lands generally have low road and human densities (r = -0.85 and r = -0.70 respectively). These variables are therefore indirectly taken into account when determining wolf habitat with the final model.

Although no prey densities were used in the final model, most forested areas in our study area contain adequate levels of prey. In fact, applying the second best model that included elk density, percent forest cover, and percent public ownership (*ElkD + %For + %Pub*) in Oregon showed only a 0.5% difference from the first model with regard to predicting wolf habitat probability >50%.

Model Application

When applied to Oregon, the final model predicted over 68,500 km^2 of probable wolf habitat ($P \geq 0.5$). Most of the contiguous land available for wolves is in the Cascade mountain region, while smaller blocks of land are available in the northeast region, the Klamath region, and the central and northern coastal regions. The relatively small amount of wolf habitat in western Oregon may be underestimated due to the large amount of private industrial forest available that may be considered habitat. Mladenoff et al. (1995) found that wolf pack areas contained more private industrial forest land than non-pack areas. Due to the relatively small amount of private industrial forest and lack of data in the study area outside of the Oregon coastal region, private industrial forest lands were not included in the analysis. However, including western Oregon private industrial forests in post hoc analysis (in conjunction with the public land variable) shows that there is a much greater amount of wolf habitat in western Oregon (Figure 3). In fact, including private industrial forests raises the amount of wolf habitat in western Oregon by more than 23,000 km^2 (from 45,700 km^2 to 68,700 km^2). Further research is warranted, however, to study wolves in relation to these land types.

FIGURE 3 Modeled wolf habitat >50% in Oregon including private industrial forests in Western Oregon.



Since the wolf data used in our analyses were collected throughout the year, we used year-round ranges for ungulates instead of winter/summer. Because ungulates in the study area migrate primarily by elevation over relatively short distances versus long distance migrations, the final predicted wolf habitat in our analyses will likely incorporate year-round wolf habitat. At various times of the year wolves may migrate relatively short distances to follow ungulate migration, but we feel these movements will likely be from the center to the perimeter of the predicted wolf habitat areas. Modeling winter versus summer habitat, however, would be beneficial research in the future.

The spatial pattern of available land in Oregon differs from that of Idaho, Montana, and Wyoming. Oregon has less contiguous predicted habitat and more patches spread out over the state which would require wolves to cross areas of unsuitable habitat in order to reach higher quality habitat. Many studies have shown, however, that wolves are able to cross large distances through unsuitable areas while dispersing (Mech 1995, Mech and Boitani 2003). "Pioneering" wolves have been known to disperse over large distances, with mates or in order to find mates, and settle in new habitats far from the nearest source population (Wabakken et al. 2001, Mech and Boitani 2003).

Estimating Capacity

We estimate that Oregon is capable of supporting approximately 1450 wolves based on current elk population estimates. This estimate is based on previous studies in relatively stable predator-prey ecosystems throughout North America (Keith 1983, Fuller 1989, Fuller et al. 2003). Since Oregon does not currently have wolves, the predicted capacity could be overestimated depending on the affect the wolf population has on the ungulate population. Wolves will likely cause a decrease in ungulate numbers which, in turn, would lower the capacity of wolves until some equilibrium is reached. Carroll et al. (2001) estimated the wolf capacity for Oregon to be approximately 790 animals based on a model of deer abundance. Our results, however, were based on current elk and deer estimates for each wildlife management unit. In addition, these results increase to approximately 2200 wolves if private industrial lands are included in the analysis, with about three quarters of the estimated wolves located in western Oregon (Figure 3, page 29).

The estimated capacities of wolves in the coastal areas are relatively high due to the high densities of black-tailed deer in the coastal range where primary productivity is also relatively high. Although deer density was not found to be related to wolf habitat, deer will inevitably make up a significant portion of the prey biomass, particularly in the western portion of the state. It is unusual for wolf density to be greater than 40 wolves/1000 km^2, but there are some exceptions including a study on Isle Royale where wolf densities reached as high as 92 wolves/1000 km^2 (Peterson and Page 1988, Fuller et al. 2003). Fuller (1989) also recorded wolf densities in Minnesota to be as high as 69 wolves/1000 km^2 within the past 25 years.

It is difficult for wildlife biologists to estimate ungulate populations, especially in western Oregon due to the large amounts of forested land cover. Therefore, confidence intervals on ungulate estimates used are fairly large. In addition, the latest black-tailed deer estimates used in our analysis do not reflect the current population losses of deer due to hair-loss syndrome (ODFW 2001). The lower densities of deer would also limit the wolf estimates. These are the best wolf population estimates that can be provided, however, until more accurate assessments of ungulate populations are available. It is also important to note that these analyses are a "snapshot" of wolf habitat and populations under current policies. Any changes in these policies (e.g. lowering protection) would likely affect numbers of wolves.

Our final model of forest cover and public land could likely be applied to the entire western United States as an initial means of analyzing wolf habitat for conservation management. The data used in the final model are consistent across states and easily obtainable. Applying the model to the Pacific Northwest (Figure 4, page 31) shows that there is significant habitat available for wolves with sufficient connectivity between large areas of habitat. Outside of the habitat utilized by the current Rocky Mountain population, most of the available habitat is in the Cascade Range in Washington and Oregon. In addition, there are smaller patches of habitat in northern Washington and northeast to central Oregon that may act as corridors for relatively safe dispersal or small populations linking the larger core habitat areas. Once established in the Cascade Range, dispersal into western Washington and Oregon would be likely.

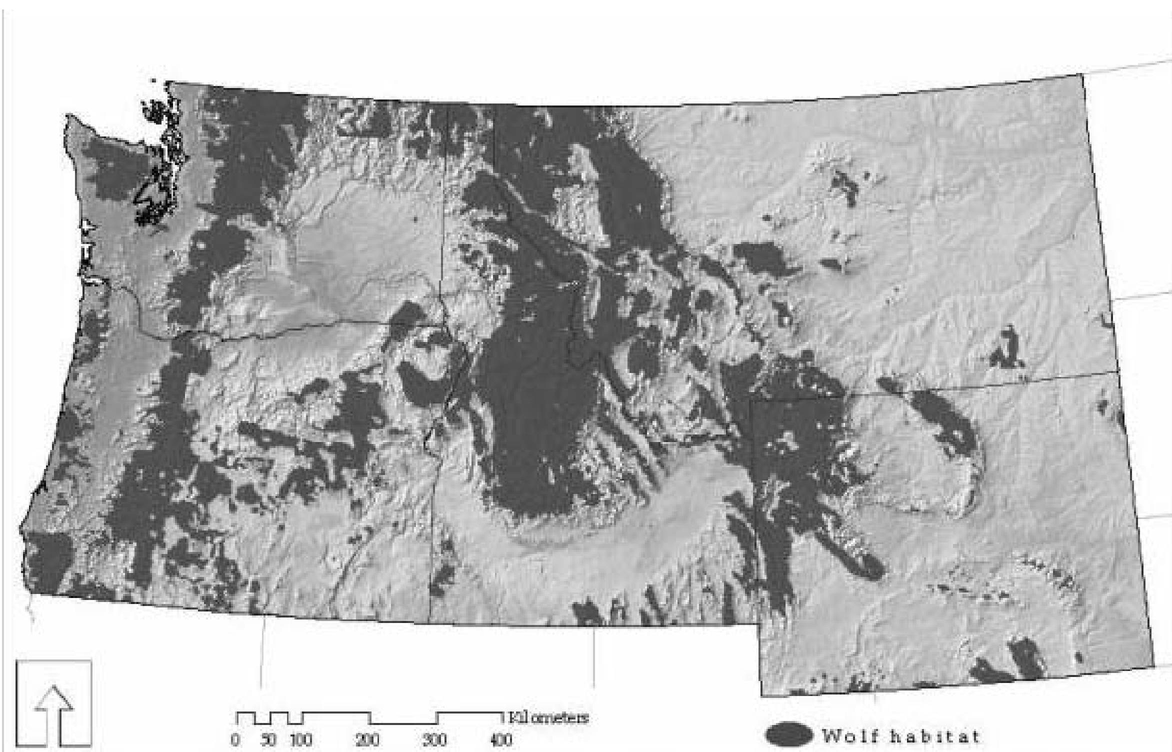
From our wolf habitat analysis it appears that there is a large amount of wolf habitat in the Northwest region of the U.S. The future of wolves in the Pacific Northwest will ultimately depend, however, on the level of human tolerance for dispersing wolves and the policies set forth by governmental agencies.

We envision that our approach to modeling wolf habitat will be of use to biologists and policy makers in developing wolf management plans in other areas of North America. The methods presented in our study may be applicable to other wide-ranging large carnivores. In addition, our model may also be relevant for other parts of the world where wolf reintroductions are planned or wolf recolonizations are taking place.

ACKNOWLEDGEMENTS

We would like to thank the Oregon Department of Fish and Wildlife, the Idaho Department of Fish and Game, the Montana Department of Fish, Wildlife, and Parks, and Todd Black from Utah State University for providing the necessary data for this project. We would also like to thank Robert Beschta, Robert Anthony, Betsy Glenn, Ben Miller, and Katie Dugger for reviewing an earlier draft of this paper.

FIGURE 4 Modeled wolf habitat >50% in the Pacific Northwest.



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