MONITORING AND HABITAT ANALYSIS FOR WOLVES IN UPPER MICHIGAN

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Abstract: Gray wolves (*Canis lupus*) in upper Michigan have been monitored since 1991 when breeding activity in mainland Michigan, USA, was documented for the first time since 1954. Based on winter track counts, the mean annual rate of increase in abundance was 19% from 1995 to 2002, with the population reaching an estimated 278 animals in 2002. Our objectives were to (1) increase the efficiency of wolf management in Michigan by evaluating alternative and less extensive sampling approaches for population estimation, and (2) evaluate habitat for wolves based on occupancy after a decade of recovery. For the first analysis, we created 22 discrete sampling units that cover upper Michigan, and we evaluated abundance estimates based on various sampling plans using known distribution and populations from the 2000–2002 winter track surveys. We evaluated each plan based on the precision, bias, and confidence interval coverage. A random sampling plan with regression estimator returned the most precise estimates, but a stratified sampling plan, using low, medium, and high wolf density strata had the greatest precision at lowest effort. For the habitat evaluation, we compared white-tailed (*Odocoileus virginianus*) deer density and road density between wolf pack locations from 1995 to 2001 to random locations outside of the current wolf range. We estimated white-tailed deer density by a spatial interpolation of pellet group counts. Our resource selection function indicated that probability of wolf occupation of an area was positively correlated with deer density, and it was relatively constant for road densities <0.4 km/km^2 but declined sharply at higher road densities. For areas habitable by wolves in upper Michigan, we predict a road density threshold of 0.7 km/km^2 and a deer density threshold of approximately 2.3–5.8 deer/km^2. We believe that these results will aid managers who need to estimate wolf abundance and predict wolf distribution.

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Population monitoring is central to informed management of wildlife. For example, in the Yukon monitoring allowed managers to document the effects of intensive reduction programs on wolf populations (Hayes and Harestad 2000). In Michigan, extensive monitoring of a recovering wolf population during the 1990s facilitated federal reclassification of the wolf from an endangered to threatened species. Also in Michigan, managers predicted the carrying capacity of wolves with the use of annual population estimates and a Leslie Matrix (Miller et al. 2002).

The most accurate means of population monitoring is a complete census; however, extrapolation from sample counts is more efficient and is usually used for estimating wolf populations across large geographic areas. For example, in Minnesota, where wolves are widely distributed, the population size was calculated by applying an average density from small study areas to an estimated wolf range (Fuller et al. 1992). In northwest Alaska, wolf population sizes were estimated across 2 large wildlife refuges by aerial detection of tracks in snow following a stratified sampling of potential wolf habitat (Becker et al. 1998).

Besides sampling, habitat analysis is another means of increasing the efficiency of population monitoring. For example, habitat evaluation can aid in stratification of sampling for population monitoring, evaluating changes to habitat (Carroll et al. 2003), and delineating management zones (Corsi et al. 1999). In addition, a spatial habitat model has been used to predict areas of recolonization and associated carrying capacities for wolf populations in the upper Great Lakes (Mladenoff et al. 1995, 1997). However, this model is based entirely on road density, so large areas of low prey density in upper Michigan (Doepker et al. 1995) may render this model inaccurate.

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In Michigan, the federal and state wolf recovery and management plans are based largely on wolf population size and distribution (U.S. Fish and Wildlife Service 1992, Weise et al. 1997). Currently, these parameters are estimated by a winter track count covering the entire northern peninsula of Michigan. We describe the methods of the track count that was used to document the recovery of wolves in Michigan. As the wolf population increases the cost and difficulty of this type of survey also increase. Our objectives were (1) to evaluate the bias, precision, and confidence interval coverage of various sampling plans that could be used to estimate wolf abundance, and (2) build a resource selection function using prey density (white-tailed deer) and road density to model the probability of wolf occurrence throughout upper Michigan.

STUDY AREA

Following virtual extirpation in the western Great Lakes and Michigan, breeding wolves were absent from mainland Michigan for 30 years (Schadler and Hammill 1995). Since 1991, the wolf population in upper Michigan has increased steadily, reaching a population of 278 in 2002.

Upper Michigan has an area of 41,984 km^2, a human population of 300,000, and a white-tailed deer (*Odocoileus virginianus*) population that fluctuated around 500,000 (Hill 1999). The area was forested primarily by northern hardwoods and conifers with isolated areas of agriculture in the southern tip and eastern half. Eastern upper Michigan was generally flat and poorly drained, and it supported vast peatlands and swamp forests (Albert 1995). Western upper Michigan has gently rolling hills with altitudes ranging from 184 to 604 m (602–1,980 ft). Federal land, including 2 national forests and a national wildlife refuge, comprised nearly one fifth of upper Michigan. State forests and parks made up another 20%.

METHODS

Field Methods

During 1992–2001, we live-captured and fitted wolves with VHF radiocollars (Telonics Inc., Mesa, Arizona, USA) in spring and summer using methods similar to Kuehn et al. (1986). We live-captured wolves with foot-hold traps modified to reduce injury (Minnesota Trapline 760, also Newhouse Modified 14 and McBride No. 7), and we chemically immobilized (ketamine hydrochloride and xylazine, both at 100 mg/ml) wolves at doses of 0.11 mg/kg and 2 mg/kg, respectively. We also administered penicillin and vaccinations against sarcoptic mange, canine distemper, and canine parvovirus. We concentrated our live-trapping efforts in southwestern upper Michigan, where wolf density was greatest.

We located radiocollared wolves using fixed-wing, single-engine aircraft at intervals of 1–14 days throughout the year. We recorded locations on 1:150,000-scale county maps (1992–1999) or on Global Positioning Systems (GPS; after 1999). Visual observations were rare during summer (15 Apr–14 Sep), and wolves were occasionally observed in winter (<10%; 15 Sep–14 Apr). We assessed the accuracy of the aerial telemetry by determining the mean difference between locations of radiocollars placed at known points and the subsequent aerial telemetry locations.

We conducted the winter track count each winter during snow-cover from 1992 to 2002 on all passable roads and trails throughout upper Michigan using trucks and snowmobiles. To aid trackers in determining pack size and centers of activity in multiple trips to areas with wolf sign such as tracks, scat, or previous sightings, trackers used data on radiocollared wolves, wolf distribution from previous surveys, and public observations. We recorded all wolf signs including scat, scent marks and scratches, tracks, and measurements and estimated the age of the tracks. We followed tracks a minimum of 200 m to discern distinct trails of individual wolves. Aircraft aided the trackers when radiocollared wolves were being tracked. We plotted the centers of activity for each pack on digital maps and estimated the distribution and population.

We considered the population estimates from the winter track survey to be minimum counts due to the potential for missing some wolf packs because of poor accessibility, weather, or time limitations. We avoided double-counting wolves in adjacent areas by using the territory boundaries of radiocollared wolves to distinguish between different groups of animals. In areas without radiocollared wolves, differentiation of adjacent packs depended on finding fresh tracks in their respective areas with no sign of movement between the 2 areas. Trackers also used locations of den sites and territories that were delineated in preceding years to aid them in differentiating between packs.

Deer Density

We estimated deer density and relative distribution from field counts of deer fecal pellet groups conducted in spring 1999 (Hill 1999). Field biologists divided upper Michigan into 3 categories based on approximate deer density. Courses were located within each category based on a stratified random sample. Each course was 4-m wide and 100-m long for an area of 400 m^2. There were 290 courses randomly distributed throughout the 41,984 km^2 study area, or 1 course per 145 km^2.

Software

We mapped and analyzed the geographical data with the GIS software Arcview 3.2 and Arcmap 8.1 (Environmental Systems Research Institute, Redlands, California, USA) and the extensions Spatial Analyst, Geostatistical Wizard (ESRI), Simple Random Sample (Quantitative Decisions, Marion Station, Pennsylvania, USA), and Animal Movement (Hooge and Eichenlaub 1997). For all road density estimates, we used the same digital road coverage as Mladenoff et al. (1995; i.e., U.S. Geological Survey 1:100,000 Digital Line Graphs [DLG]), which included major highways, local, gravel, and improved roads. We performed statistical analyses with SAS (SAS Institute 1999).

Monitoring Plan Evaluation

We used the 3 most recent winter track counts (2000–2002) to simulate 4 sampling plans: simple random, simple random with a regression estimator, stratified random, and hybrid. We assigned each wolf pack to 1 of 22 non-overlapping sampling units covering upper Michigan (Fig. 2). Six packs bordered 2 adjacent units and were assigned to the sampling unit that contained the largest portion of the territory. For each sampling plan and sample size ($n = 6$ and $n = 11$), we used Monte Carlo simulation to generate 10,000 samples (results were similar for up to 1,000,000 samples) and associated abundance estimates and confidence intervals. We constructed 95% confidence intervals using the t-distribution with $n - 1$ degrees of freedom for the simple random sampling plan and $\sum(n_i - 1)$ degrees of freedom for the stratified sampling plan. To evaluate the sampling plans, we compared the mean percent error (half the mean length of 95% confidence intervals/population size), confidence interval coverage (percentage of 95% confidence intervals capturing the true population size), and bias.

The simple random plan abundance estimate is obtained by multiplying the average number of wolves/sampling unit by the total number of sampling units (22). We evaluated this sampling plan using samples of size 6 and 11.

The simple random with regression estimator plan yields abundance estimates in years following a complete census. We used the following notation: N is the population total of sampling units (22), Y is the mean number of wolves per sampled unit, b is the estimated slope of the linear regression model, X is the observed mean number of wolves per sampled unit from the previous survey, and is the mean number of wolves per sampling unit obtained from the previous complete census. The regression estimator is calculated as $N \times (Y + b \times [X - \;])$. The variance of this estimator may be relatively small if a large positive correlation exists within sampling units between years (Cochran 1977).

The stratified plan abundance estimate uses wolf density classes. We stratified the sampling units into 3 wolf density classes (high, medium, low) using cluster analysis with centroid linkage (Seber 1984). In the stratified plan ($n = 11$), we sampled 3 units in each of the high and medium density classes and 5 units in the low density class. In the stratified plan with $n = 6$, we sampled 2 units in each density class so that variance estimates could be obtained. To estimate abundance, we multiplied the mean number of wolves/sampling unit in each density class by the number of units in each density class. and summed the abundance estimates for each density strata to estimate of the population total. We used the standard variance estimator (Cochran 1977).

The hybrid plan abundance estimate was obtained by sampling all units in the high-density class, 2 units from the medium density class and 3 units from the low-density class. To compute the abundance estimate and confidence interval for this plan we treated the high-density class count as a fixed constant that did not contribute to variance, and estimated the total and variance for the randomly selected units using the methodology for stratified sampling.

Habitat Analysis

We analyzed wolf occupancy of upper Michigan using a generalized additive logistic regression model with 2 independent variables – pellet group density of white-tailed deer and road density.

Deer Pellet Group Density.—Our analysis of deer density relied on the spatial interpolation of pellet group data. We interpolated the data using ordinary kriging, which is suited to irregularly distributed data (Isaaks and Srivastava 1989). We analyzed the data using univariate statistics and then transformed the data using the Box-Cox transformation (Johnston et al. 2001) to achieve normality. We constructed a semivariogram model and used this model to estimate values at unmeasured locations. We assessed the interpolation with

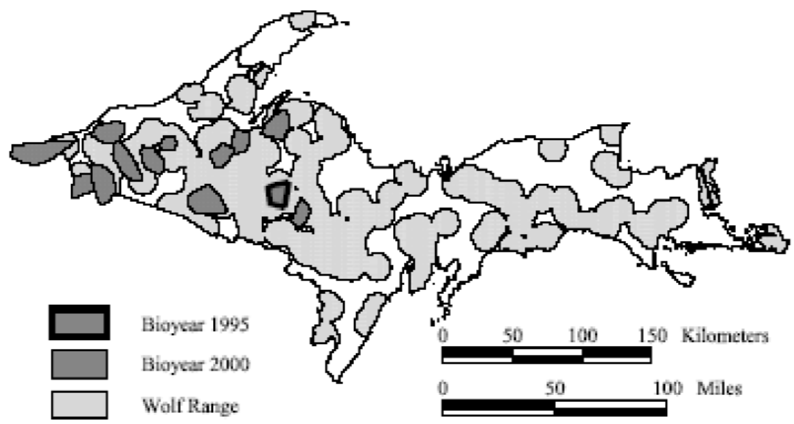

Fig. 1. Territories with >50 locations and geographic range of gray wolves in upper Michigan, USA, 1995–2000. Most packs were monitored for multiple years, but only the most recent territories are represented. The wolf range was delineated by placing circular asymptotic territories on each pack location from the winter track surveys. The asymptotic territories were 287 km^2 and based on nonlinear regression of observation/area curves from territories with >50 telemetry locations.

the use of statistical variances, the nugget, and the partial sill (Isaaks and Srivastava 1989). We assessed the interpolation qualitatively using past maps of deer distribution in upper Michigan (Doepker et al. 1995).

Generalized Additive Model.—To create a map of wolf distribution, we centered a circle the size of the mean asymptotic territory on each pack location from the winter track surveys of 1995 to 2001. We merged these circles, or estimated territories, along with any radiocollared pack territories, to create a wolf distribution.

We estimated the mean asymptotic territory size used to create the estimated territories using observation/area curves and nonlinear regression (Ballard et al. 1998). For each territory, we created observation/area curves by randomly selecting subsets of the telemetry points then calculating the area of a territory constructed for each subset. The number of locations in each subset started at 5 and increased by 5 until it equaled the number of observations in the specific territory. We calculated the mean territory size at each subset by randomly selecting 75 subsets of locations. We modeled the observation/area curves using nonlinear regression and used the asymptote of the curve as the asymptotic territory size.

We determined the road and pellet group densities of the estimated wolf territories and that of an equal number of random locations outside of the wolf distribution. For each random location, we determined the attributes in an area defined by the radius of a circle the size of the asymptotic territory. Territories of wolves and random locations were allowed to overlap. The pellet group densities of all wolf territories and random territories were divided into low, medium and high categories using the 33rd and 66th percentiles of the pellet group distribution.

We used a generalized additive model (GAM; Hastie and Tibshirani 1990) with the logistic link to model the relationship between probability of wolf occupancy and road density and pellet group category. The degree of observed curvature was determined by the response curve and the degrees of freedom associated with the GAM (Hastie and Tibshirani 1990). The degrees of freedom were analogous to the degree of a fitted polynomial. We used up to 5 degrees of freedom. We created interaction terms (pellet group categories by road density) to allow for differing effects of road density across deer pellet group density levels.

Our comparison of occupied and unoccupied areas was an example of separate sampling (Seber 1984). In separate sampling, the constant term of the regression is confounded with the sampling fractions of the 2 groups. For our data, the sampling fraction of the occupied territories was 1.0. The sampling fraction for the random territories was close to 1.0 because the 2 samples combined covered the entire study area; however, the probabilities of occurrence may have been offset by a constant multiplier. Nonetheless, the functional relationships between wolf occupation, road density, and pellet group category were not affected.

We applied our model to upper Michigan using a 2 km by 2 km grid. For each grid, we calculated the pellet group density based on the interpolation and assigned a road density of an area defined by the radius of a circle the size of the asymptotic territory. Using the attributes of each grid, we estimated the total area habitable by wolves in upper Michigan.

RESULTS

We captured 84 wolves in upper Michigan between 1991 and 2001 including 40 males (47.6%) and 44 females (52.4%), of which 18 were pups

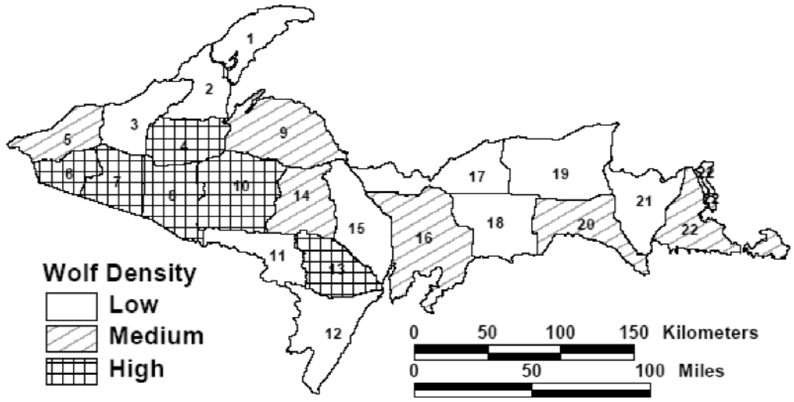

Fig. 2. Sampling units for population estimation of gray wolves in upper Michigan, USA, 2003. Wolf density of the sampling units is based on cluster analysis with centroid linkage of the winter track counts of 2000, 2001, and 2002.

(21.4%). Momitoring yielded 3,478 telemetry locations and 13 different pack territories that had >50 locations in 1 bioyear (starting each year on Apr 15). The mean difference between a known transmitter location and the location plotted from the plane was 433 m (SD = 866, n = 18). Of the 13 territories with >50 locations each, road densities varied from 0.01 to 0.51 km/km^2 and averaged 0.30 km/km^2.

The wolf population increased with an average annual growth rate of 19% during 1995–2002. In 2002, we detected 63 packs with a mean pack size of 4.3 (Table 1). These packs occupied an area of 26,000 km^2 with a general paucity of wolf pack locations in northwestern, northeastern, and central upper Michigan (Fig. 1).

Monitoring Plan Evaluation

Cluster analysis indicated that the highest density of wolves occurred in 6 sampling units in southwestern upper Michigan (Fig. 2). The medium density class consisted of 6 units, and we assigned the remaining 10 units to the low density class. The sampling plan with the lowest mean percent error was the simple random plan with a regression estimator for both sample sizes of 6 and 11 sample units (Table 2). The bias was negligible for all sampling plans, varying from –0.3% to 0.7%. Confidence interval coverage tended to be slightly below the nominal value of 95% but was never <90.5% (Table 2). The simple random plan with a regression estimator also resulted in the highest confidence interval coverage when the sample size was 6. The precision of the regression estimator was probably improved by high positive correlation of counts within units through time. Between the counts of 2000 and 2001 the correlation was 0.92, between 2001 and 2002 it was 0.82, and between 2000 and 2002 it was 0.81.

Among the 3 sampling plans that did not require a complete census in the preceding years, the stratified plan produced the least mean error for sample sizes of 6 and 11. The stratified plan also resulted in the highest confidence interval coverage when the sample size was 6. However, the hybrid plan resulted in the highest confidence interval coverage when the sample size was 11 (Table 2).

Habitat Analysis

Deer Pellet Group Density.—Univariate analysis of the deer pellet group data indicated a left skewed distribution containing primarily zero and low values with a few high values. The data ranged from zero to 129 pellet groups/transect with a mean of 15.9 and a median of 9. We used a coefficient of 0.3 in the Box/Cox transformation to produce a more normal distribution.

The ordinary kriging interpolation indicated deer pellet group density to be highest in southern upper Michigan and lowest in areas of high

Table 1. Composition of the gray wolf population in upper Michigan, USA, 1995–2002 based on winter track surveys. Abundance estimates are considered minimum estimates, packs contain ≥2 wolves, and the standard error of the mean pack size varied between 0.2 and 0.3.

	1995	1996	1997	1998	1999	2000	2001	2002
Minimum population	80	116	113	139	169	216	249	278
Packs	27	33	35	42	52	63	70	63
Pairs	13	13	18	18	25	27	33	17
Lone wolves	6	6	12	7	12	14	5	8
Mean pack size	2.7	3.3	2.9	3.1	3.0	3.2	3.5	4.3
Largest pack size	5	10	5	7	7	7	11	10

Table 2. Percentages of confidence interval coverage (CIC), and mean error (Error) of sampling plans for monitoring gray wolf abundance in upper Michigan, USA. Statistics are based on 10,000 simulations of the winter track surveys, 2000–2002. The CIC is the proportion of 95% confidence intervals of the population estimates that include the true population. Error is half of the length of the 95% confidence interval of the population estimate divided by the true population.

		Year					
		2000		2001		2002	
Sampling plan	*n*	CIC	Error	CIC	Error	CIC	Error
Simple	6	92.3	59.1	92.7	57.9	94.1	47.6
Stratified	6	95.1	30.1	90.5	36.8	92.6	23.1
Reg. Estimator	6	NA	NA	92.0	23.0	93.7	14.9
Simple	11	94.0	32.1	93.4	31.7	95.6	25.7
Stratified	11	92.3	15.3	91.9	18.2	95.2	10.1
Reg. Estimator	11	NA	NA	93.4	12.1	93.7	14.9
Hybrid	11	95.7	13.8	95.1	18.8	96.5	18.4

snowfall near Lake Superior (Fig. 3). The model prediction standard error was 18.1, the nugget was 5.1, and the partial sill was 2.6. The semivariogram of the transformed data showed slightly increasing variance with increasing distance between data points. Both mean prediction errors were near zero, indicating an unbiased estimation.

Generalized Additive Model.—In winter track surveys from 1995 to 2001, we detected 305 wolf packs including those monitored for multiple years. The 13 territories with >50 telemetry locations had a mean number of 112 locations (range 59–166) and a mean asymptotic territory size of 287 km^2. The nonlinear regression model of the observation/area curves was highly significant ($R^2 > 99.0\%$), and the asymptotic territories were 20% larger than territories constructed using minimum convex polygons.

We placed a circular 287 km^2 territory on each of the 305 pack locations and merged them to delineate a wolf range of 26,000 km^2 (Fig. 1). We randomly placed another 305 points outside the wolf range. We estimated the pellet group density and road density within 9.6 km of each of the pack and random locations and created 3 pellet group categories: low (<6.75), medium (6.75–15.52), and high (>15.52).

The generalized additive model indicated that probability of wolf occupation was positively correlated with pellet group density and that a threshold effect existed with respect to road density (Fig. 4). Altering the cutoffs for the pellet group density categories by 2 pellet groups did not change the response curves with respect to road density. The response curves for low and high pellet group densities were approximately parallel, and the interaction term between them was not significant ($P = 0.58$). At medium pellet group densities, the curvature indicated a more complex response between road density and probability of occupancy (Fig. 4), but a threshold appeared to exist in this curve also. The data points corresponding to this anomaly were geographically confined to small specific regions where the local interpolation of pellet groups was based on 1 or 2 pellet group transects and may have yielded unreliable predictions of pellet group density in that area.

We defined an area as habitable by wolves if pellet group densities were above a threshold of 6.75 pellet groups/transect and road densities were below a threshold of 0.7 km/km^2. We excluded the areas below 6.75 pel-

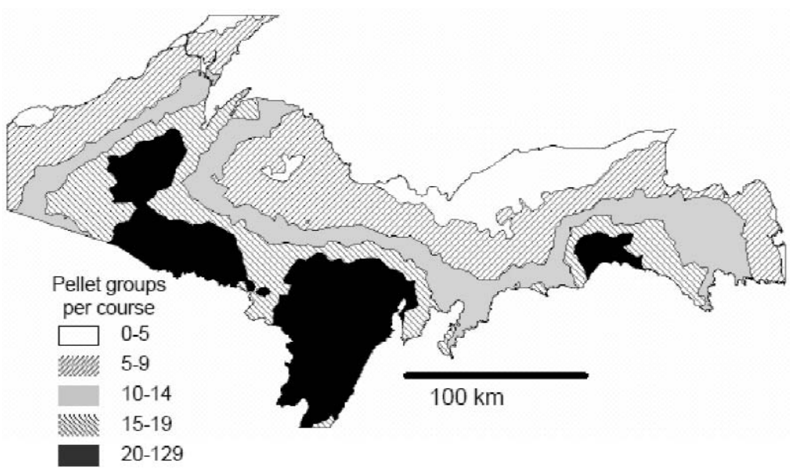

Fig. 3. Density of white-tailed deer based on ordinary kriging of pellet group counts in upper Michigan, USA, 1999. The kriging does not cover the north, east, south, and west extremities due to a lack of transects in these areas.

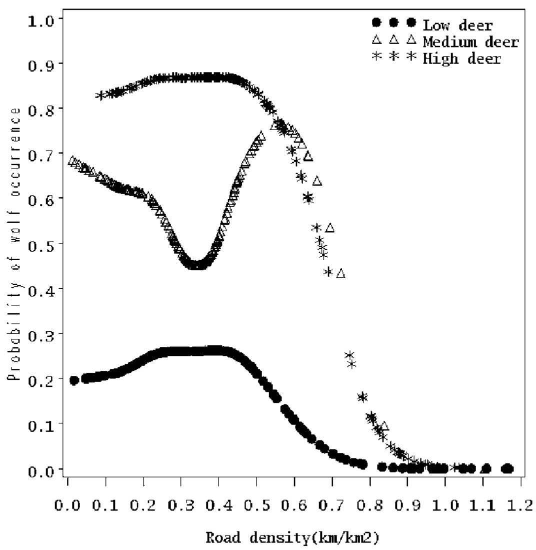

Fig. 4. Response curves for a generalized additive model relating wolf occupancy to road density and pellet group density of white-tailed deer in upper Michigan, USA.

let groups/transect because the probability of occupancy in the response curve for these areas was never >0.25. The response curve for the high densities of pellet groups began to decrease at a road density of 0.5 km/km^2 and leveled off at 0.8 km/km^2 with a midpoint of approximately 0.65 km/km^2 (Fig. 4). The response curve for the medium densities of pellet groups began to decrease at a road density of 0.6 and leveled off at 0.85 km/km^2 with a midpoint of approximately 0.73 km/km^2 (Fig. 4). These 2 response curves were similar in their dramatic decrease and the midpoint of the decrease, so we approximated a threshold for both at 0.7 km/km^2.

Using the pellet group and road density thresholds, the predicted location of habitable areas for wolves in upper Michigan totaled 27,700 km^2. The areas of highest probability of occupancy were in south and southwestern upper Michigan, and these areas were defined primarily by the distribution of deer (Fig. 5). Despite high pellet group densities, road density was high enough (>0.7 km/km^2) to exclude some areas such as a north-south highway corridor in the southern tip of upper Michigan and cities represented by isolated areas of low probability of occurrence.

DISCUSSION

A previously published wolf habitat model relied only on road density to predict probability of wolf occupation (Mladenoff et al. 1995). That habitat model and associated road density threshold of 0.45 km/km^2 (Mladenoff et al. 1995) successfully predicted the location of more recently established radiocollared wolf territories in Wisconsin (Mladenoff et al. 1999). In addition, road densities for 10 of the 13 radiocollared wolf territories in our study were lower than 0.45 km/km^2. Given the results of our habitat analysis and the persistence of human-caused mortality in upper Michigan, we believe that road density is still important in predicting wolf occupation in this area.

The negative impact of roads and the power of road density to predict wolf habitat, however, are variable. In southern Minnesota, wolves utilized areas of high road density on a military base where human caused mortality was virtually eliminated (Merrill 2000). Elsewhere in Minnesota, wolves were also observed in high road density areas (Mech 1989). In Spain, wolves successfully utilized areas near roads within their territories through temporal avoidance of humans (Vila et al. 1995).

A measure of prey density has also been used with other covariates to predict wolf habitat (Corsi et al. 1999). Although many habitat models for small carnivores have not incorporated prey density (Carroll et al. 1999, Nielsen and Woolf 2002, Rowland et al. 2003), wolves are habitat generalists, and occupation of the

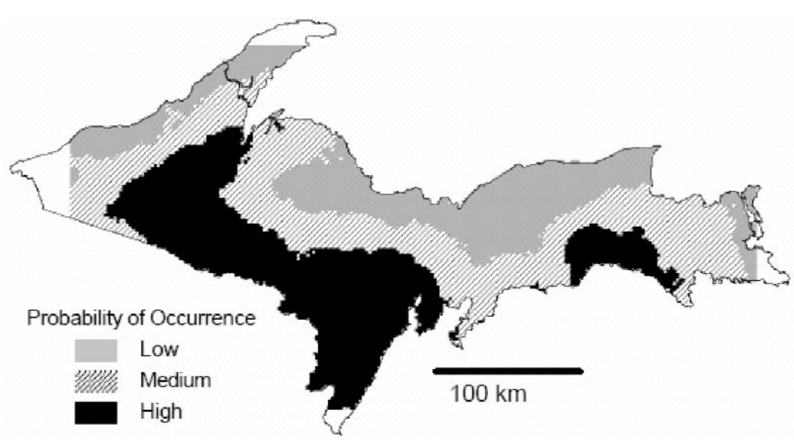

Fig. 5. Probability of occupancy of gray wolves in upper Michigan, USA. Probabilities were determined from a generalized additive model relating wolf occupancy to road density and pellet group density of white-tailed deer.

landscape is not well predicted by characteristics such as cover type or landscape diversity (Mladenoff et al. 1995). We retained deer density, in addition to road density, as a predictor of wolf occupation, whereas deer density was not significant in the previous analysis of Mladenoff et al. (1995). Our study also differed from that of Mladenoff et al. (1995) in the methods used to estimate deer distribution, and in that the study areas that were characterized by different ranges of road and deer density. Mladenoff et al. (1995) used deer densities compiled by deer management units (700 km^2) of relatively homogenous deer densities. These deer distributions may be useful for preliminary estimates of wolf habitat (i.e., Phillips et al. 2000). Indeed, in upper Michigan many of the areas of high wolf density predicted by Mladenoff et al. (1995, 1997) corresponded roughly to our predicted areas of high probability of occupancy. However, based on deer densities from deer management units, Mladenoff et al. (1995, 1997) predicted suitable habitat and densities of 20–30 wolves/1,000 km^2 in large areas of upper Michigan that were virtually devoid of deer according to our interpolation of pellet counts. We suggest that spatial interpolation of pellet counts may be a more accurate method of estimating deer distribution for modeling wolf habitat. Although the reliability of pellet counts as a predictor of deer density has been questioned (Fuller 1991, but see White 1992), long-term research on moose suggests a correlation between pellet counts and aerial surveys (Jordan et al. 1993). Our spatial interpolation of pellet counts was qualitatively similar to previous estimates of deer distribution in upper Michigan (Doepker et al. 1995). In addition, a concurrent study of deer distribution in northeastern upper Michigan reported similar pellet density values to those of our interpolation (Steve Windels, Michigan Technological University, personal communication).

Our deer density data exhibited more spatial heterogeneity than those in the study by Mladenoff et al. (1995). High deer densities occurred in southern upper Michigan, but we also identified extensive areas of low deer density that may approach a prey biomass of 2.4 deer/km^2 at which wolves are nutritionally stressed (Messier 1987). In regions of such low deer density, probability of occupancy is probably equally low for most road densities. The range of road densities in the northern Wisconsin study area of Mladenoff et al. (1995) was generally higher than in upper Michigan (Mladenoff et al. 1995). These differences between study areas probably contributed to the differing results of our analyses.

Based on the response curves (Fig. 4), we hypothesize a higher road density threshold for wolf occupation (0.7 km/km^2) than the previous estimates of 0.58 km/km^2 in Wisconsin (Thiel 1985) and 0.45 km/km^2 predicted more recently in Wisconsin (Mladenoff et al. 1995). We also defined a deer density threshold of 6.75 pellet groups/400 m^2 transect. This pellet group value was equivalent to 2.3–5.8 deer/km^2 based on varying reported defecation rates (Ryel 1972, Rogers 1987). In upper Michigan, using these thresholds, we predicted a habitable area of 27,700 km^2, similar to 29,348 km^2 predicted by Mladenoff et al. (1995). However, Mladenoff et al. (1995) predicted many habitable areas to occur in northern upper Michigan, whereas we predicted nearly all habitable areas to occur in southern upper Michigan where deer density was greatest. Of course, wolves may occur outside of the areas we predicted to be habitable. However these wolves may not contribute consistently to the sustainability of the wolf population in upper Michigan.

Mladenoff and Sickely (1998) extrapolated the Mladenoff et al. (1995) model of wolf habitat to the northeastern United States where prey densities were generally low, especially at high altitudes. As in upper Michigan, areas of low prey density may be erroneously classified as favorable habitat. In Michigan, the total area habitable by wolves differed by only 10% between our predictions and the habitat model of Mladenoff et al. (1995). However, where variance of prey density within management units was high, we believe that the habitat model of Mladenoff et al. (1995) overestimated the probability of occupation by wolves in upper Michigan as well as in the northeastern United States. The corresponding carrying capacities could also be overestimated if there were many small areas of low prey density that were not portrayed by average densities of management units.

Currently, the deer population in Michigan is relatively high, contributing to a potentially high carrying capacity for wolves but negatively impacting other environmental values such as forest structure and composition (Frelich and Lorimer 1985, Alverson et al. 1988). In the future, deer density may decline for various reasons such as management to reduce the population (Rudolph 2002), severe winters (DelGiudice et al. 2002), predation (Mech and Karns 1977), or disease (Gross and Miller 2001). Mladenoff et al. (1997) noted that at high prey densities, wolf territories are small (Fuller 1989), enabling wolf packs to subsist in small isolated patches of favorable habitat. However, if prey density decreases and territory size increases, the same patches of habitat may not be large enough to support a pack. In upper Michigan, the large, homogenous areas habitable by wolves that our analysis predicted indicate that decreases in deer density, while probably resulting in lower wolf densities, may not significantly reduce the overall area habitable by wolves.

MANAGEMENT IMPLICATIONS

We recommend using a wolf population abundance estimator that is based on ground sampling of wolf tracks for estimating large wolf populations in areas where aerial tracking is not ideal, such as where prey density and forest cover are high. We recommend using experienced trackers and conducting surveys with adequate road access and suitable snow for tracking. Data from aerial telemetry is also important for aiding trackers in delineating territories.

Our evaluation of several sampling plans indicates that probability sampling of land areas may be useful for obtaining abundance estimates. All sampling plans rely on accurately assigning a wolf pack to a single sampling unit. We assigned each pack to the sampling unit that contained the largest portion of its territory. This assignment requires intensive tracking of pack territories that are close to the sampling unit borders. We suggest using a randomization procedure if it is unclear to what sampling unit a pack should be assigned.

The quality of the stratified and hybrid sampling plans depended on the stratification of wolf density. Currently, the stratification of wolf density indicates highest densities in the sampling units of southwestern upper Michigan (Fig. 2). If wolf distribution changes, sampling unit boundaries may need to be adjusted in the future, and the density classification may need to be updated.

The Recovery Plan for the Eastern Timber Wolf (U.S. Fish and Wildlife Service 1992) suggests maintaining areas with road densities <0.6 km/km^2 for wolf habitat. Our results confirm that core habitat for wolves in upper Michigan occurs where road density is similarly low, but only where deer density is adequate. In addition, with adequate deer densities, wolves may occupy areas with road densities approaching 0.7 km/km^2 and higher associated human densities. In these areas, where conflicts between wolves and humans may intensify, public education and management of problem-causing wolves will be critical for successful coexistence of wolves and humans.

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