A Large-Scale Model of Wolf Distribution in Italy for Conservation Planning

FABIO CORSI,* EUGENIO DUPRÈ,† AND LUIGI BOITANI†‡
*Istituto Ecologia Applicata, Via L. Luciani 41, 00197-Roma, Italy
†Dip. Biologia Animale e Uomo, Viale Università 32, 00185-Roma, Italy

Abstract: *The 400–500 wolves currently living in the Apennine range of peninsular Italy are slowly recolonizing the Alps and are expected to move northward. A nationwide management plan for the Italian wolf population is being prepared, and a zoning system with connecting corridors has been suggested. We developed a large-scale probabilistic model of wolf distribution as a contribution to the planning process. Thirteen environmental variables related to wolf needs and human presence were analyzed in 12 well-studied wolf territories and in 100 areas where the species has been absent for the past 25 years. These two areas were used as a training set in a discriminant analysis to evaluate potential wolf presence throughout the entire country. We used the Mahalanobis distance statistic as an index of environmental quality, calculated as the distance from the average environmental conditions of the wolf territories. Based on the Mahalanobis distance statistics, we constructed an actual and potential spatial distribution of the wolf for all of peninsular Italy. The jackknife procedure was used to assess the stability of the distance model and showed good confidence in our model (coefficient of variation ≤ 13%). Distance from the wolf territories' centroid as an index of environmental quality for the wolf was tested using 287 locations where wolves have been found dead in the past 25 years as a consequence of human action (poison, shotgun, car accidents). A useful contribution to conservation planning resulted from comparing the frequency distribution of the Mahalanobis distance of the dead wolf locations with the percentage of study area within each distance class. This showed how the number of wolf casualties would greatly decrease with protection of only a minor part of the study area and indicated the usefulness of our approach for evaluation of other conservation options, such as core areas and corridor identification.*

Modelo de Larga Escala de la Distribución de Lobos en Italia para la Planeación de la Conservación

Resumen: *Los 400–500 lobos que viven en el rango Apennine de la Italia peninsular están recolonizando lentamente los Alpes y se espera que se muevan hacia el Norte. Se ha preparado un plan de manejo nacional para la población de lobos en Italia y se ha sugerido un sistema de zonación con corredores conectivos. Desarrollamos un modelo probabilístico de gran escala de la distribución de lobos como una contribución al proceso de planeación. Trece variables ambientales relacionadas con las necesidades de los lobos y la presencia de humanos fueron analizadas en 12 bien estudiados territorios de lobos y en 100 áreas donde la especie ha estado ausente en los últimos 25 años. Estas dos áreas fueron usadas como prueba en un análisis discriminante para evaluar el potencial de la presencia de lobos a lo largo de todo el país. Utilizamos la distancia estadística de Mahalanobis como un índice de calidad ambiental, calculada como la distancia de las condiciones ambientales medias de los territorios de lobos. En base a la distancia estadística de Mahalanobis, construímos la distribución espacial actual y potencial de la distribución de los lobos para toda Italia peninsular. El procedimiento de jacknife fue usado para evaluar la estabilidad de la distancia modelo y mostró una confidencia buena en nuestro modelo (CV ≤ 13%). Se evaluó la distancia del centroide de los territorios de lobos como un índice de calidad ambiental empleando 287 localidades donde algunos lobos han sido en-*

‡*Address correspondence to L. Boitani, email boitani@pan.bio.uniroma1.it*
Paper submitted July 7, 1997; revised manuscript accepted May 1, 1998.

contrados muertos en los últimos 25 años como consecuencia de activadades humanas (envenenamiento, caza, atropellamiento). Una contribución valiosa para la planeación de la conservación resultó de la comparación de distribuciónes de frecuencias de las distancias Mahalanobis de localidades con lobos muertos con el porcentaje de área de estudio dentro de cada de distancia. Esto mostró como el número de lobos muertos podría disminuir grandementre con la protección de tan sólo una parte pequeña del área de estudio e indicó lo valioso de nuestra aproximación para la evaluación de otras opciones de conservación, como lo son la identificación de áreas centrales y corredores.

Introduction

The wolf (*Canis lupus*) once ranged throughout most of western Europe, but by the end of the last century it was reduced to only a few small, isolated populations in the Iberian peninsula, Italy, and the Balkans (Promberger & Schröder 1993). In Italy the population is believed to have reached its minimum in the early 1970s, when about 100 wolves were estimated, mostly in the central and southern portion of the peninsula (Zimen & Boitani 1975). After full legal protection was established in 1976, increased acceptance of wolves and a significant increase in wild ungulate populations favored a numerical increase of the wolf and recolonization of large areas of the former distribution range (Boitani 1992). Currently, there are 400–500 animals ranging along the Apennines from the French border to the southern tip of Italy, but distribution is discontinuous and density varies (Boitani & Ciucci 1993; Fig. 1). The natural recolonization of the Italian and French Maritime Alps started in 1992 and is likely to extend northward to the central Alps in the near future (Boitani & Ciucci 1993). In spite of the expanding trend, population viability of the wolf is still threatened by small population size and significant adult mortality caused by illegal hunting (estimated at 15–20% of the total population [Boitani & Ciucci 1993]), and the species has recently been confirmed as "endangered" (Pinchera et al. 1997).

The recolonization of areas where the wolf had been absent for many years has increased conflicts between wolves and humans and has revealed the need for a national management plan (Boitani & Ciucci 1993). As pointed out by Noss (1992), a landscape approach in the range of 10^4–10^5 km^2 is likely to be the most adequate for integrating management of viable populations of wide-ranging animals, and it is evident that an effective management plan for the wolf in Italy should consider all of Italy except its islands (about 250,000 km^2).

The most recent developments in population viability analysis have shown the usefulness of spatially explicit computer simulation and the integration of demographic and dispersal data with a detailed knowledge of the landscape geometry (Lamberson et al. 1992; McKelvey et al. 1992; but see Harrison et al. 1993; Harrison 1994). Only a few studies have modeled spatial factors that determine wolf distribution. Mladenoff et al. (1995) built a multiple logistic regression model to assess the importance of landscape-scale factors in defining favorable wolf habitat in the northern Great Lakes region of the United States and found that road density and fractal dimension were the most correlated variables. The model was also applied to the northeastern United States to predict favorable wolf habitats (Mladenoff & Sickely 1998). A similar result for road density had previously been obtained through simple correlation analyses (Thiel 1985; Mech et al. 1988; Fuller et al. 1992). These studies all aim to define the best habitat descriptor and predictor variables.

We developed a method that uses multivariate analysis of geographic information system data to provide a spatially explicit model of wolf distribution that is applicable when country-wide information is limited. We wanted our model to emphasize spatial patterns rather than hab-

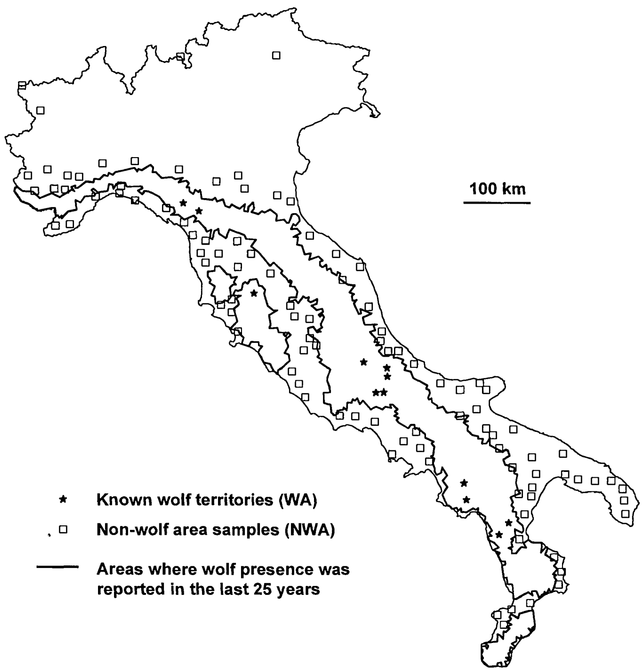

Figure 1. Area of current wolf presence, wolf territories and nonwolf sample areas used in the discriminant analysis.

itat suitability and to contribute to the design of a country-wide conservation plan for the wolf by (1) providing a basis for more advanced spatial and habitat analyses, (2) identifying the broad fragmentation patterns of the wolf distribution, and (3) providing insights into the wolf's likely recolonization of the Alps, an area where the wolf is expected to extend its range in the next few years.

Methods

Our methodology is based on two paradigms. First, given a set of environmental variables that potentially influence wolf distribution, a training set can be built using two groups, one of known wolf territories and the other of areas where the wolf is absent. A model can thus be built, in the multivariate space defined by the variables, that maximizes the difference between the two groups. Second, given an adequate sample of areas where the wolf is found, it is possible to build a "signature" that best describes (and predicts) the areas where the wolf lives, based on the available environmental variables. The results can be used to identify all areas of the country where the environmental conditions are most similar to those of the known territories and to evaluate to what extent each portion of the study area departs from the optimal conditions as defined by those of the territories.

The model, however, is not suitable for analyzing habitat use because no absolute value of the contribution of each environmental variable to the model is obtained. In fact, in changing the set of environmental data or the training sets the relative contribution of each variable is expected to change, whereas the model is expected to maintain overall stability in defining large-scale response (e.g., use of space).

Our study area was all of continental Italy. The country is characterized by a variety of landscapes and ecological features. This is a consequence of the country's north-south extension, the mild coastal climate versus the more continental climate of internal and northern regions, the elevation variation from sea level to 4800 m, and the intense habitat modification produced over thousands of years by human activity.

Data Sets

Constrained by the limited country-wide information available, our data set was composed of three main subsets: data on wolf presence and absence, the environmental variables to be correlated to wolf presence, and a list of 287 locations where dead wolves were collected during the past 25 years.

WOLF PRESENCE AND ABSENCE

To define our training set, two groups of samples were used to describe the environmental features of the wolf areas (WAs) and the nonwolf areas (NWAs). The WAs were obtained using 12 wolf territories previously studied by radio tracking (7) and/or intensive snow tracking (5) in various parts of the wolf range (Zimen 1978; Boitani 1986; Ciucci 1994; L.B., P. Ciucci, and F. Francisci, unpublished data; Fig. 1). A basic assumption is that the diversity of environmental conditions within these territories represents the best average conditions for a stable presence of the wolf in the Apennines, including human influence: all 12 territories were found within areas where wolves either have always been present or have recently (in the last 10 years) and permanently colonized.

Using all available records (direct and indirect signs of wolf presence), we identified any area where no evidence of stable wolf presence had been gathered in the last 25 years (Fig. 1) as a NWA. Considering only the portion of Italy south of the Po River and given the size and shape of the Italian peninsula, it is reasonable to assume that any location within a NWA is within the reach of dispersing wolves (<100 km). Because these areas have not been recolonized in the last 20 years when wolves were expanding their range, it can be assumed that most of the habitat in the NWAs is unsuitable. Therefore, random samples taken within the NWAs south of the Po River should provide samples of areas in which the values of the environmental variables are mostly unsuitable for the wolf. To minimize the risk that this group could include points of suitable wolf habitat and to account for the diversity of habitat conditions, we oversampled the NWA and produced 100 non-overlaying circular areas (Fig. 1) by randomly sampling the centers of the circles within the NWA south of the Po River. The surface of each area (106 km^2) was equal to the average size of the 12 known wolf territories.

Of these 100 samples, 96 (8 times the number of available territories) were chosen randomly. The remaining four were selected at the site of the major icefields in the Alps in order to account for the different topographic conditions of the Apennines and the Alps, the latter exhibiting higher elevations and icefields, which are absent in the Apennines. These differences can conceal the real relationship between an environmental variable and wolf presence.

ENVIRONMENTAL VARIABLES

The second data set was used to describe the environmental characteristics of the training set and to extrapolate the result of the analysis to the entire study area. The 13 variables used (Table 1) to define the multidimensional environmental space were selected not only

Table 1. The 13 environmental variables used in the analysis.

Variable	Used in final model	Origin and resolution of data
Farmland	x	land-use maps (1962–1986), scale 1:200,000
Forest	x	land-use maps (1962–1986), scale 1:200,000
Pasture		land-use maps (1962–1986), scale 1:200,000
Bare soil or water		land-use maps (1962–1986), scale 1:200,000
Urban settlement	x	urban settlement contours (Ente Nazionale Energia Elettrica [ENEL] 1971), scale 1:25,000
Elevation		Italy's Ministry of Environment, resolution 250 m
Human density	x	13° National Census of the Population (Istituto Centrale Statistica 1991), aggregated by *comune*
Road density	x	maps of the Italian Touring Club, scale 1:200,000
Shannon diversity index	x	land-use maps (1962–1986), scale 1:250,000
Shannon dominance index	x	land-use maps (1962–1986), scale 1:250,000
Dumping site density	x	census of the Ministry of Agriculture and Forests (1990), aggregated by region
Sheep density		4° National Census of Agriculture (Istituto Centrale Statistica 1990), aggregated by *comune*
Number of ungulate species	x	species' distribution maps (Ministry of Environment 1993), scale 1:1.250,000

to account for our best knowledge of the basic wolf needs of space, food, and cover, but also with respect to their availability in digital form and degree of national coverage. Although the full influence of each of the 13 variables on wolf distribution cannot be obtained, we assumed that they describe fairly well the high diversity of ecological conditions to which the wolf is known to adapt (Mech 1970; Boitani & Ciucci 1993). Wolf distribution in Italy appears to be influenced primarily by human presence, food availability, and, consequently, type of land use (Boitani & Fabbri 1983). The wolf in Italy has been reported to feed on wild ungulates, livestock, and garbage at dump sites (Boitani 1982; Ciucci 1994; Meriggi & Lovari 1996). Therefore, the selected set of variables included densities of sheep, number of ungulate species present (densities were not available), and density of dumping sites.

Cover was described in terms of percentage of land-use classes (five variables: farmland, forest, pasture, bare soil or water, and urban). Indices of diversity and dominance of land use were included to account for the overall landscape structure. Elevation was also included and interpreted as an ancillary variable highly correlated to both human disturbance and cover availability. Human pressure is probably the most important factor affecting wolf distribution, especially in Italy, where human impact on the environment is substantial (Boitani 1982). Additional variables such as human population and road densities were selected as habitat components to account for human disturbance.

All variables were obtained directly as digital thematic maps from various governmental sources and stored in a geographic information system (GIS) (ArcInfo, ESRI 1992). Some of the data sets were used directly for analysis, such as the land-use map in scale 1:200,000, whereas others were derived from the original digital thematic map by means of basic analyses (e.g., road density was computed from the original road network with a cell grid 10 × 10 km). Human population and sheep densities (Istituto Centrale Statistica 1990, 1991) were aggregated by *comune* (municipality), the median size of which is 21.5 km^2. A digital terrain model with a square cell size of 250 m was used to derive information on elevation, whereas the diversity and dominance indices were calculated using a cell grid 10 × 10 km, following the Shannon-Weaver formula. The maps of dumping-site density and number of ungulate species were available at a broader scale (about 1:1,000,000).

Because data quality and homogeneity were a major concern, all original data sets underwent editing, and all discrepancies were corrected. The final layers were then converted to raster format with a cell size of 250 m.

We characterized the 12 territories and the 100 NWAs by performing simple overlay with the 13 layers and calculating basic statistics (percentage of coverage, mean values, etc.) depending on the type of environmental variable. In order to extend the result of the modeling based on these training sets to the entire study area, map algebra focal functions (Tomlin 1990) were used to replicate the same statistics over the entire study area. Each raster of 13 variables was processed by assuming each pixel to be the center of a hypothetical wolf territory and assigning to that pixel the same statistics used to characterize the training set, and each was calculated within a window of 23-pixel radius. This radius gives an area of 103.8 km^2, the best approximation to the average dimension of the 12 wolf territories (106 km^2) obtainable with a cell size of 250 m.

DEAD WOLF LOCATIONS

The data set of 287 dead wolf locations was obtained by pooling all information collected by various Italian offices and scientists on wolves found dead in the past 25 years. About half of the sample was collected by L.B. Evidence of human-related cause of death (e.g., poison, shotgun, car or train accident) was available for at least 70% of the sample, whereas cause of death for the remaining 30% of the locations was presumed through indirect ancillary information. Although only a portion of the total number of illegally killed wolves was recovered and the collection was not organized through a predefined procedure, the sample can be assumed to reflect the gross spatial distribution of killed wolves. In Italy, a wolf killed illegally or (more rarely) found dead is still an event, and the news is immediately spread; local authorities usually recover the body and file a formal statement. The sample may not accurately represent regional variation in the recovery system and the temporal distribution of killed wolves, but this does not affect the sample utilization in our analysis. The data set on locations of dead wolves was used to explore the correspondence of dead wolf locations to areas of marginal environmental quality, thus providing a tool with which to validate the model and to enhance its conservation interpretation.

Data Analysis

We analyzed the data in three steps. First, to identify the most important areas of wolf presence (actual and potential), we used discriminant function analysis (DFA). This statistical method, although constrained by its inherent limitations, has been applied widely to define a binary use of space—in our case, wolf and nonwolf areas (Verbyla & Litvaitis 1989; Dubuc et al. 1990; Livingston et al. 1990). Similar results could be obtained with logistic regression and less rigorous statistical assumptions, but we preferred to normalize the variables through various transformations (see below) and to use a DFA because of its similarity to the methods adopted in the second step of our analysis (i.e., the Mahalanobis distance). We performed a forward stepwise canonical discriminant analysis on 13 variables, 2 groups, and 112 observations (12 WAs and 100 NWAs). Density of dumping sites and number of ungulate species were normalized with logarithmic transformation, forest and pasture extension with the Freeman and Tukey transformation, and the remaining 9 variables with the Box-Cox transformation with different values (Sokal & Rohlf 1995).

The analysis was run with $F = 0.6$ (F, the probability value of the F statistics) to determine how significant the contribution of a variable to the regression had to be in order to be added to the discriminant function. The DFA results were used to classify the entire study area. The classification was calculated as the posterior probability of each pixel belonging to one of the groups

$$p(t|\boldsymbol{x}) = \frac{\exp(-0.5D_t^2(x))}{\sum_t \exp(-0.5D_t^2(x))}, \qquad (1)$$

where $\boldsymbol{x}$ is the vector containing the values of environmental characteristics for each pixel. The D_t is the generalized squared distance of each pixel from the t group, in which

$$D_t^2(x) = (x-\boldsymbol{m}_t)'\mathbf{S}_t^{-1}(x-\boldsymbol{m}_t), \qquad (2)$$

where $\mathbf{S}_t$ represents the within-group covariance matrix and $\boldsymbol{m}_t$ the vector of the means of the variables of the t group. Equality of covariance matrices was tested by means of the Box M test (Davis 1986). The generalized squared distance (SAS Institute 1985) was used instead of the simple Mahalanobis distance because it accounts for differences in the variance-covariance matrix of the two groups. The a priori probabilities were considered equal, with the threshold set at 50% probability.

In the second step, independently calculated from the previous one, we sought to describe potential interconnections between the areas of wolf presence, and we used the Mahalanobis distance statistic as an index of environmental quality, distance from the best environmental conditions for wolves. The Mahalanobis distance statistic has been used as a multivariate index to rank habitat suitability in GIS raster maps (Clark et al. 1993; Knick & Dyer 1997) and avoids many difficult requirements of discriminant function and logistical regression, particularly those involving incorrect classification of used versus unused habitats (Clark et al. 1993). We used wolf territories rather than a series of animal locations (radio locations, Clark et al. 1993; sightings, Knick & Dyer 1997); our small number of "observations" should be compensated partly by their higher ecological significance (large, stable areas).

We calculated a surface of actual and potential use of space for the entire study area. The environmental centroid of the WAs group represented our best description of the optimal environmental conditions for the wolf; thus, we built an index of environmental quality based on the environmental Mahalanobis distance of any given location from the WAs centroid (the smaller the distance the more similar the environmental conditions of that location to the wolf's ecological profile). The environmental distance was calculated for a continuous raster covering the entire study area.

The third step served as validation of the previous two and as support for their conservation interpretation; it was based on the overlay of the locations of dead wolves to the models produced by the previous analyses.

We evaluated the relationship between the distance from the WAs centroid and the probability of wolf occurrence using the location of dead wolves. For each location the environmental distance from optimal wolf conditions was calculated through interpolation from the continuous surface. The resulting frequency distribution was fitted with different probability density functions to interpret changes in wolf distribution in response to variation in the environmental distances from WAs.

To determine if an increase in population was related to expansion of wolf populations into areas of lower environmental quality, we looked for differences in the environmental quality levels of the areas where dead wolves were found in different time periods. All casualties were ordered chronologically and then grouped in sets of 10, 20, 30, 40, 50, 60, and 70 consecutive locations. Each set was tested for normality and analyzed by analysis of variance, the hypothesis being that if a density-dependent pattern of recolonization is applicable to the wolf in Italy, then the distribution should show a shift toward an increasing number of dead wolves in lower-quality environments.

Finally, a tentative model for wolf management was produced by extrapolating from the distance raster a new raster in which the pixel values represented the expected percent decrease of dead wolves (due to casualties) that would be achieved if all areas falling within the pixel's ecological distance were effectively protected. The index was obtained using the cumulative probability density function derived from the ecological distances of dead wolf locations. Comparing on the same plot the cumulative frequency distribution of areas of increasing ecological distance and the cumulative probability density function of dead wolf locations, the curves represent, for any given value of ecological distance, the percentage of territory that should be protected to achieve an expected percent reduction of wolf casualties. Obviously, this model was applied only to the portion of Italy south of the Po River. The stability of the environmental distance model was assessed by means of jackknife procedures (Cressie 1993; Sokal & Rohlf 1995).

In analyzing the results, we divided the study area into a portion south of the Po River including the peninsular part of continental Italy (Apennines), where most of the current wolf range is, and a portion north of the Po River including the Alps, where the wolf is currently expanding its range.

Results

Areas of Importance for Wolf Presence

Nine of the 13 variables were selected by the stepwise discriminant analysis (Wilks' lambda = 0.567, $F = 8.64$, $p = 0.0001$). The 100 NWAs appeared well separated from the 12 WAs on the first canonical variates, with only a few NWAs within the pertinence of the WAs. The 12 wolf territories were correctly classified; the overall probability of belonging to the wolf group was over 90%. Only 3 of the 96 random NWAs were assigned to the wolf distribution, whereas the 4 nonrandom NWAs were classified, as expected, into the NWAs group.

By applying the classification criterion to the entire study area, we obtained locations of the areas most important for wolf presence (Fig. 2). About 14,200 km^2 (about 5.7% of continental Italy) with an a posteriori probability of more than 50% were found in this category. Of these, 11,300 km^2 are in the peninsular portion of the country (Apennines), whereas 2900 km^2 are located in the Alpine region. These areas of optimal environmental conditions could be considered the core of the wolf distribution (actual and potential) and should be expected to act as a source of wolves for less suitable areas.

Index of Environmental Quality and Surface of Actual and Potential Use of Space

The values of the raster of the distances range from 0 to 2933 (mean = 297, SD = 301). These absolute values have no specific meaning per se and are of interest only when considered in relation to another variable such as the dead wolves' locations. The frequency distribution of these locations fitted a log-normal density function (mean = 3.9068, SD = 0.8644, Kolmogorov-Smirnov d = 0.0124403, not significant; Fig. 3). The right side of the distribution (the decreasing part) indicates density dependence; that is, as we move away from the areas of high environmental quality, wolf numbers and, consequently, deaths tend to decrease. As for the left side, taking into account that all deaths are due to human-related causes, there are several possible explanations: (1) interactions between humans and wolves tend to be less frequent in areas of high environmental quality (lower hu-

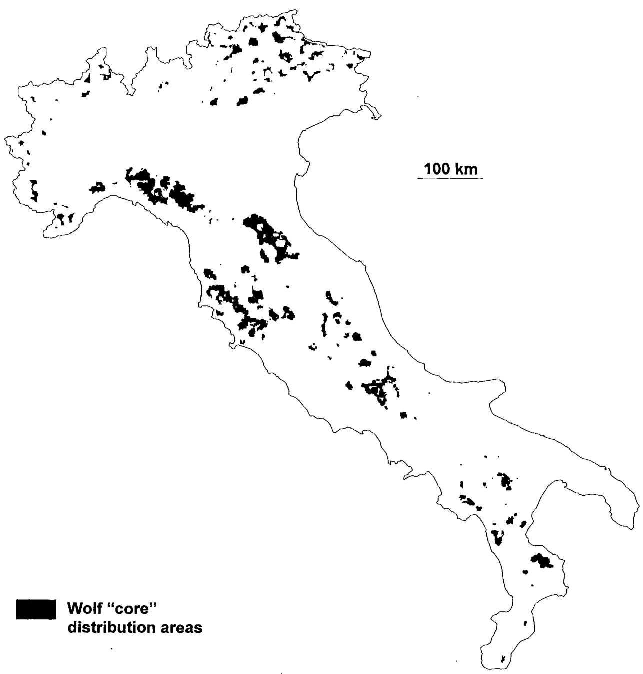

Figure 2. Wolf core distribution areas as obtained from the discriminant analysis model (i.e., with a posteriori probability over 50%).

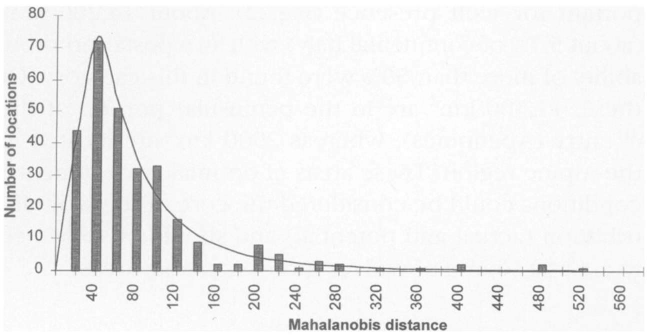

Figure 3. Log-normal distribution fitted to the environmental distances of dead wolf locations. The histograms show the observed distribution; the line shows the fitted log-normal distribution (mean = 3.9068, SD = 0.8644; Kolmogorov-Smirnov d *= 0.0124403, not significant).*

man population density, higher availability of wild prey); (2) the interactions do not cause any casualty (better or more cover availability); and (3) the casualties that result from these interactions are not included in our sample. The first two hypotheses are similar because both reduce the number of casualities. The third should be rejected because the patterns of relatively high human presence throughout the country make it unrealistic to postulate lower efficiency in recovering dead wolves in the best wolf areas.

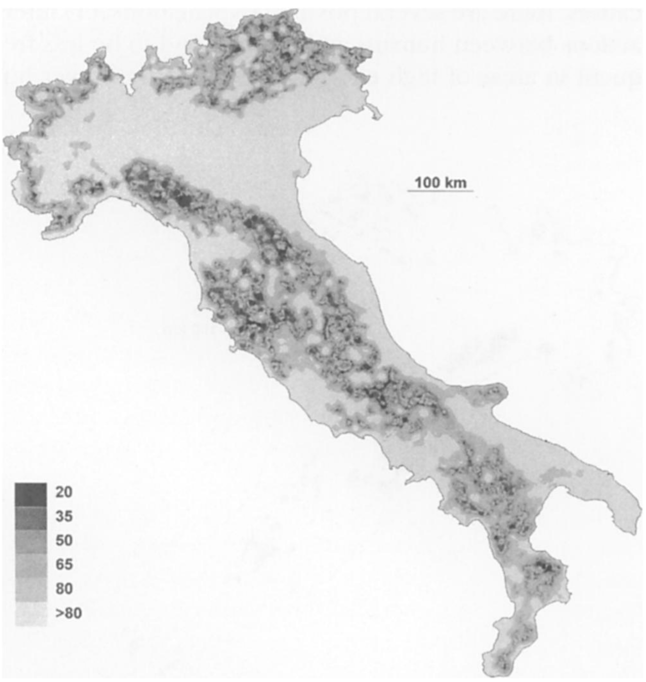

Figure 4. Spatial distribution of the percent reduction in wolf casualties that would be achieved through effective protection of the areas pertaining to each land-use class (Table 1), obtained by calculating the cumulative probability associated with each distance as derived from the log-normal probability function fitted to the ecological distances of the locations of dead wolves.

Table 2. Expected percent reduction in wolf casualties that would be achieved through full protection of the areas pertaining to different classes of environmental quality.

*Percent of study area**	*Expected reduction of casualties (%)*	*Area (km²)*
2.4	<20	6,060
8.9	20-35	16,157
18.0	35-50	22,661
30.6	50-65	31,618
50.2	65-80	49,173
100.0	>80	124,516

**Percentages of study area are given as cumulative figures to the upper limit of the probability class.*

The results of the conversion of the ecological distances based on the probability density function of the ecological distances of the dead wolves' locations are shown in Fig. 4. For management purposes, the conversion can best be read from a map of the percent reduction in wolf casualties that would be achieved through full protection of the areas with different levels of environmental quality (Fig. 4; Table 2).

Based on the cumulative frequency distribution of distance classes throughout continental Italy (Fig. 5), different conservation scenarios can be analyzed by means of a cost-benefit approach. For example, the point of maxi-

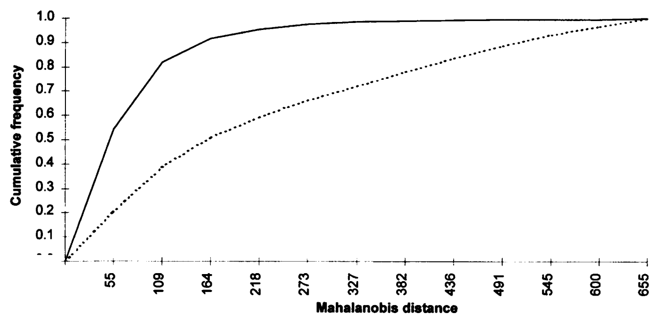

Figure 5. Comparison of the cumulative log-normal distribution of the probability of wolf casualties (solid line) with the cumulative frequency distribution of the environmental distance classes in the study area (limited to the portion south of the Po River; dashed line). The two lines can also be used as a model of expected percent decrease of wolf casualties with increasing size of areas of effective wolf protection. The solid line indicates the expected percent reduction of casualties when increasing quantities of areas of different environmental quality (from best to poor) are effectively protected.

mum "gain" occurs at an environmental distance of 109, where the number of casualties would decrease by more than 80%. Less than 40% of the study area would need to be protected to achieve maximum gain.

Model Validation and Stability

If the pattern of space use in relation to the environmental distances has remained constant in the past 25 years, then wolf densities in the areas included within any given distance level should not have changed over time, and the wolf population should have increased mainly through an increase in its area of occupancy. The results of the analysis of variance applied to groups of sets of 10, 20, 30, 40, 50, 60, and 70 consecutive locations supported this hypothesis: all groupings but the first (with sets of 10 locations each) showed no significant differences among their sets. None of the tests gave significant results ($p > 0.5$). The low significance of the grouping with 10 locations ($p < 0.1$) may be explained as the result of local, random effects (i.e., the temporary occupancy of areas of lower environmental quality during the dispersal phase) due to the excessive subdivision of the sample.

As for the overall stability of the models, the jackknife process showed an expected high variability (coefficients of variation of over 1000%) in the pixel values of the raster of environmental distances. This is not surprising because the relative contribution of the environmental variables varies according to the subset of samples used for the analysis. With the same 12 rasters obtained from the jackknife, we also calculated the probability density function of the dead wolves' locations, and from these we calculated a probability raster for each of the 12 runs of the jackknife. In this last case, the coefficient of variation of each pixel dropped drastically ($\leq$13%) in accordance with an expected stability of the distance values when considered as a relative measure of environmental quality.

Discussion

There are at least two main reasons for adopting a large-scale approach to conservation of the Italian wolf metapopulation (spatially structured; Harrison 1994). First, a large-scale approach is needed to manage fragmentation of suitable habitat and the inevitable metapopulation structure of the resulting population (May 1994), and hence to manage conflicts with human economies and illegal hunting. Second, the future of the wolf in Italy, as well as that of most large carnivores elsewhere, ultimately will depend on our ability to designate a zoning system of areas and connecting "corridors" where the wolf will be managed in ways appropriate to local ecological and economic conditions (Boitani 1982; Mech 1995; Noss et al. 1996; Weaver et al. 1996). An "integrated landscape management" (Saunders et al. 1991; Turner et al. 1995; Wiens 1996) appears to be the only rational approach to ensure the survival of a mobile and adaptable species like the wolf, particularly in a highly fragmented landscape mosaic such as Italy (and Europe).

We have explored a method for obtaining a spatial model of wolf distribution as a contribution to the preparation of a conservation plan. Model building is a deductive-inductive process, with model formulation and validation occurring iteratively (Stormer & Johnson 1986; Clark et al. 1993) and developing through a feedback process with field studies (Price & Gilpin 1996). Good models are the key to good conservation management (Gilpin 1996), yet real-world data are rarely adequate for complex and robust simulations (Dunning et al. 1995). Our method is an example of integration of the inductive and the deductive modeling approaches (Stoms et al. 1992) to maximize the utility of limited data.

The model's predictions for the Alps may not be fully justified due to substantial ecological differences and should be taken only as a first indication of potential wolf distribution. Nevertheless, our model is based on the best current knowledge, and it provides a first insight into the likely evolution of wolf presence in that area. We emphasize that the method is more suited to identifying spatial patterns than critical habitat factors for wolf distribution because a variety of habitat combinations can produce identical distance values.

Even though the human attitude toward wolves is probably one of the most important factors determining wolf distribution (Boitani & Ciucci 1993; Mladenoff et al. 1995), it is not a simple variable and its distribution cannot be mapped. Our method assumes that human attitude is hidden in the other variables (e.g., road density and land use), as suggested by Thiel (1985), Mech et al. (1988), and Mladenoff et al. (1995). This approach implies that human disturbance is a density-dependent variable (i.e., it increases linearly with human density). This is a weak assumption because the human attitude toward wolves can greatly modify this relationship.

Although the GIS and statistical method are becoming more widespread in the ecological literature, we recognize the limits of the interpretations of our results. The core wolf areas as obtained from the discriminant analysis and the 12 wolf territories were characterized by means of the environmental distance surface, showing a conservative effect of the results of discriminant analysis. The average distance from the wolf optimal areas was 16.78 (SD = 6.08) for the core wolf areas and 31.09 (SD = 19.68) for the 12 territories. The high patchiness of these areas is expected in a highly fragmented landscape, but their interpretation as a source of wolves for less suitable areas is constrained by the particular definition of core area.

Caution should also be observed in interpreting the optimal areas as obtained from the means and the variance-covariance matrix of the 12 territories: the definition refers to the statistical method rather than to an analysis of biological factors. Although the jackknife process used to assess the variability of the environmental distance model justifies our good confidence in its statistical stability, the model's best utilization is as a conceptual guide for further insight into the biological and landscape reality of its results.

The output of the environmental distance model should never be interpreted as an absolute value. The high variability evidenced by the jackknife indicates that there is no direct functional relationship between these values and an absolute index of environmental quality. The jackknife, however, also shows that the relative measure of these distances appears to remain constant, allowing their use as a relative index of environmental quality. The environmental distance raster can be interpreted as the relative expectation of wolves being at a given location, lower distances indicating higher expectation.

The general level of spatial fragmentation (i.e., fragment size) appears within the order of magnitude of wolf territory size, allowing for future simulation of the effect of the territorial behavior on interpatch dynamics (Gutierrez & Harrison 1996). The fragmentation pattern in the Alps should be re-analyzed when similar data are available for neighboring countries because ecological continuity may be ensured through management of areas across Italian borders.

The calculations of the percent reductions in wolf casualties achieved through area protection allow for preliminary analysis of various conservation scenarios on a cost-benefit basis, although the results should be viewed with caution due to the simplicity of the model. Assuming that the patterns shown by the frequency distribution of dead wolf locations in the Apennines can be extrapolated to the Alps, we may infer the percentage of area that should be fully protected in order to expect a corresponding percent decrease in the number of dead wolves (Table 2). The distance raster, when analyzed in conjunction with available GIS functions, can be used to address important conservation issues such as areas of occupancy, core areas, areas of least conflict with human activities, conservation options between areas of different quality (source-sink), and the identification of corridors.

Within the limits of the practical utilization of metapopulation conceptual models (Gutierrez & Harrison 1996), our model is currently being used to support the difficult technical and political process of preparing a conservation and zoning plan for the wolf in Italy. Without a critical analysis of their inherent limitations (Price & Gilpin 1996), we strongly support the call for caution in using the appealing predictions of computer models to make real-life decisions.

Literature Cited

Boitani, L. 1982. Wolf management in intensively used areas of Italy. Pages 158–172 in F. H. Harrington and P. C. Paquet, editors. Wolves of the world: perspectives of behaviour, ecology and conservation. Noyes Publishing, Park Ridge, New Jersey.

Boitani, L. 1986. Dalla parte del lupo. Giorgio Mondadori, Milan.

Boitani, L. 1992. Wolf research and conservation in Italy. Biological Conservation **61:**125–132.

Boitani, L., and P. Ciucci. 1993. Wolves in Italy: critical issues for their conservation. Pages 74–90 in C. Promberger and W. Schröder, editors. Wolves in Europe: status and perspectives. Munich Wildlife Society, Ettal, Germany.

Boitani, L., and M. L. Fabbri. 1983. Strategia nazionale di conservazione per il lupo (*Canis lupus*). Ricerche Biologia Selvaggina (Bologna, Italy) **72:**1–31.

Ciucci, P. 1994. Movimenti, attività e risorse del lupo (*Canis lupus*) in due aree dell'Appennino centro-settentrionale. Ph.D. dissertation. University of Rome, Rome.

Clark, J. D., J. E. Dunn, and K. G. Smith. 1993. A multivariate model of female black bear habitat use for a geographic information system. Journal of Wildlife Management **57:**519–526.

Cressie, N. A. C. 1993. Statistics for spatial data revised edition. Wiley & Sons, New York.

Davis, J. C. 1986. Statistics and data analysis in geology. 2nd edition. Wiley & Sons, New York.

Dubuc, L. J., W. B. Krohn, and R. B. Owen, Jr. 1990. Predicting occurrence of river otters by habitat on Mount Desert Island, Maine. Journal of Wildlife Management **54:**594–599.

Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. Ecololgical Applications **5:**3–11.

ESRI. 1992. ArcInfo user's manual. Version 6.1. Redlands, California.

Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and G. B. Joselyn. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Society Bulletin **20:**42–55.

Gilpin, M. 1996. Metapopulations and wildlife conservation: approaches to modeling spatial structure. Pages 11–28 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Gutierrez, R. J., and S. Harrison. 1996. Applying metapopulation theory to Spotted Owl management: a history and critique. Pages 167–186 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Harrison, S. 1994. Metapopulations and conservation. Pages 111–128 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Scientific Publications, Oxford, United Kingdom.

Harrison, S., A. M. Stahl, and D. Doak. 1993. Spotted Owl update: U.S. judge rejects Forest Service plan. Conservation Biology **7:**1–4.

Istituto Centrale Statistica. 1990. 4° Censimento generale dell'agricoltura. Rome.

Istituto Centrale Statistica. 1991. 13° Censimento generale della popolazione. Rome.

Knick, S. T., and D. L. Dyer. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. Journal of Wildlife Management **61:**75–85.

Lamberson, R. H., K. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. Conservation Biology **6:**505–512.

Livingston, S. A., C. S. Todd, W. B. Krohn, and R. B. Owen. 1990. Habitat models for nesting Bald Eagle in Maine. Journal of Wildlife Management **54:**644–653.

May, R. M. 1994. The effects of spatial scale on ecological questions and answers. Pages 1–17 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large-scale ecology and conservation biology. Blackwell Scientific Publications, Oxford, United Kingdom.

McKelvey, K., B. R. Noon, and R. H. Lamberson. 1992. Conservation planning for species occupying fragmented landscapes: the case of the Northern Spotted Owl. Pages 424-450 in P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts.

Mech, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Doubleday, New York.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology **9**:270-278.

Mech, L. D., S. H. Fritts, G. L. Radde, and W. J. Paul. 1988. Wolf distribution and road density in Minnesota. Wildlife Society Bulletin **16**: 85-87.

Meriggi, A., and S. Lovari. 1996. A review of wolf predation in southern Europe: does the wolf prefer wild prey to livestock? Journal of Applied Ecology **33**:1561-1571.

Mladenoff, D. J., and T. A. Sickely. 1998. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. Journal of Wildlife Management **62**:1-10.

Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. Conservation Biology **9**: 279-294.

Noss, R. S. 1992. Issues of scale in conservation biology. Pages 240-250 in P. L. Fiedler and S. K. Jain, editors. Conservation biology the theory and practice of nature conservation, preservation and management. Chapman and Hall, New York.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merril, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10**:949-963.

Pinchera F., L. Boitani, and F. Corsi. 1997. Application to terrestrial vertebrates of Italy of a system proposed by IUCN for a new classification of national Red List categories. Biodiversity and Conservation **6**:959-978.

Price, M. V., and M. Gilpin. 1996. Modelers, mammologists, and metapopulations: designing Stephens' kangaroo rat reserves. Pages 217-240 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Promberger, C., and W. Schröder, editors. 1993. Wolves in Europe: status and perspectives. Munich Wildlife Society, Ettal, Germany.

SAS Institute, Inc. 1985. SAS user's guide: statistics. Version 6.04. Cary, North Carolina.

Saunders, D. A., R. J. Hobbs, and C. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology **5**:18-32.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. W. H. Freeman, New York.

Stoms, D. M., F. W. Davis, and C. B. Cogan. 1992. Sensitivity of wildlife habitat models to uncertainties in GIS data. Photogrammetric Engineering & Remote Sensing **58**:843-850.

Stormer, F. A., and D. H. Johnson. 1986. Introduction: biometric approaches to modeling. Pages 159-160 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison.

Thiel, R. P. 1985. The relationship between road densities and wolf habitat suitability in Wisconsin. American Midland Naturalist **113**: 404-407.

Tomlin, C. D. 1990. Geographic information systems and cartographic modelling. Prentice-Hall, London.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. Ecological Applications **5**:12-16.

Verbyla D. L., and J. A. Litvaitis. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. Environmental Management **13**:783-787.

Weaver, J. L., P. C. Paquet, and L. F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology **10**:964-976.

Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics and management. Pages 53-84 in D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Washington, D.C.

Zimen, E. 1978. Der Wolf, Mythos und Verhalten. Meyster Verlag, Wien, Austria.

Zimen, E., and L. Boitani. 1975. Number and distribution of wolves in Italy. Zeitschrift für Säugetierkunde **40**:102-112.