# L. D. Mech Critique of Our Work Lacks Scientific Validity

**DAVID J. MLADENOFF,**[1] *Department of Forest Ecology & Management, University of Wisconsin–Madison, Madison, WI 53706, USA*
**MURRAY K. CLAYTON,** *Departments of Plant Pathology and Statistics, University of Wisconsin–Madison, WI 53706, USA*
**THEODORE A. SICKLEY,** *Department of Forest Ecology & Management, University of Wisconsin–Madison, Madison, WI 53706, USA*
**ADRIAN P. WYDEVEN,** *Wisconsin Department of Natural Resources, Park Falls, WI 54552, USA*

## Abstract

*An accompanying article in this issue of the Bulletin (Mech 2006) purports to critique our past research. L. D. Mech attempts to show that our model of prospective, preferred gray wolf (*Canis lupus*) habitat (Mladenoff et al. 1995, 1997, 1999, Mladenoff and Sickley 1998) has been incorrect. We first state clearly that we are not opposed to the re-assessment of our work based on new data. However we believe the Mech paper contains both serious conceptual and methodological flaws that render its conclusions invalid. Our own analysis, based on logic and current techniques (Mladenoff et al. 2005), shows that the model has behaved according to our predictions and continues to successfully predict wolf recolonization in Wisconsin, USA, over more than 25 years. However, the serious flaws of Mech (2006) alone show that he is incorrect in his putative critique of our work.* (WILDLIFE SOCIETY BULLETIN 34(3):878–881; 2006)

## Key words

Canis lupus, *geographic information systems, model, recolonization, spatial analysis, United States lake states, Wisconsin, wolf.*

In previous work we developed an empirically based model using logistic regression and spatial wolf recolonization data (1979–1992) for northern Wisconsin, USA (Mladenoff et al. 1995). The analysis took advantage of a unique data set, where all re-colonizing wolf packs were known and mapped for the state beginning in 1979 (Wydeven et al. 1995). Gray wolves had been extirpated in the state since the 1950s but began to reinvade in the mid-1970s, presumably from the newly protected population in northern Minnesota, USA. In our work we asked the simple question: can characteristics of the landscape where wolves were newly colonizing help us identify similar such areas in the state and assist in better quantifying the amount and distribution of such habitat (Mladenoff et al. 1995)? We used geographic information systems (GIS) to spatially analyze available data on land-cover types and configuration and road density. The most significant, simplest model was based on road density. This relationship had been shown before (Thiel 1985). We extended this approach by using the information to map habitat-probability classes for northern Wisconsin, where the classes of highest probability of future wolf use were those with fewer roads (Mladenoff et al. 1995). Similar to Mech's (2006) own observations, we stated no assumption that wolves require such areas; indeed, as he has, we noted that it has been repeatedly shown that wolves can live in many areas with surprisingly high road and human population density if not persecuted and if wolf fecundity and immigration are greater than mortality. However, it is clear that any animal species will have differential survival and population growth due to many factors across a variable landscape of habitat quality. In our case we make no assumption that wolves intentionally seek out more remote areas or require them, merely that survival and growth have higher probabilities in such areas, even assuming random dispersal (Mladenoff et al. 1995). Further research also has demonstrated that there are relationships between risk of human-caused mortality and such landscape factors as road density (Wydeven et al. 2001). This is fully consistent with what we know of the effects of habitat variables on the population dynamics of all wildlife species.

Over the past decade, the mapped data we produced have successfully guided wolf management in Wisconsin, and also anticipated areas of greatest wolf recolonization that has followed in upper Michigan. Most recently, a detailed re-examination of wolf habitat in upper Michigan using new data on prey (deer; *Odocoileus* spp.) abundance allowed Potvin et al. (2005) to improve our potential wolf-density estimates. Yet their results show that after a decade our original (1995) habitat estimations were within 10% of the new results. Also, in Minnesota an apparent halt in wolf-range expansion has been detected (Erb and Benson 2004), contrary to speculations of Mech (1998, 2001). This halt corresponds to our mapped primary habitat in Minnesota made over 10 years ago (Mladenoff et al. 1995). Since the appearance of our original paper, the same or similar approaches have been used by many others for wolves and other wide-ranging carnivores where the use of broad-scale mapped data analysis is appropriate (e.g., Corsi et al. 1999, Carroll et al. 2001). We have always stated that our analysis is empirical in nature, based on data on the regional landscape and a dynamic wolf population. We have repeatedly emphasized that we expect the ability of such a static model to predict areas of wolf recolonization over time to change and that our estimates are conservative, given that wolves will, in fact, occupy less favorable areas as well. Indeed, we performed the first such reassessment of the model to examine this in Mladenoff et al. (1999). Also, we have cautioned that extension of the results to very different species, landscapes, or carnivore populations at a different stage of growth and colonization may not be valid (Mladenoff and Sickley 1998).

In the 1999 paper, we tested our predictions using actual data of new wolf packs that had colonized northern Wisconsin (1993–1997) after our model creation, based on habitat-class use and availability relationships. The model clearly continued to predict the locations of ongoing wolf recolonization based on our determination of favored habitat in 1995. In his current paper, Mech (2006) suggests that sufficient additional time has passed

[1] *E-mail: djmladen@wisc.edu*

and an additional assessment of our model was warranted. We wish to state clearly that we are not opposed to this and, in fact, agree that after a decade of dramatic wolf population change, valuable information may be gleaned from any apparent change in the predictive ability of the model. We have stated before that we expect complex interactions over time and space to affect more recent wolf colonization (Mladenoff et al. 1999). These include wolf population increase and spatial spread, changing landscape characteristics, primary habitat occupancy, and changing human behavior (Mladenoff et al. 1997, 1999).

## Discussion

### Flaws in the Mech Paper

We believe that the approach taken by Mech (2006) is seriously flawed. As such, it does not qualify as a test or refutation of our work.

*Conceptual premise*.—Mech (2006:874–875) states that the basis of our model is flawed because "It is clear that wolves do not require wilderness..." and "apparently because it failed to consider the adaptability of wolves," suggesting that these were the assumptions of our work. They are not. In fact, we have repeatedly stated our agreement with these statements and that wolves are not habitat-specific (Mladenoff et al. 1995, 1997, Mladenoff and Sickley 1998). In 1999 we emphasized that "We now know that wolves do not require wilderness to survive, but require adequate prey and reduced killing by humans (Peterson 1988, Mech 1995). These factors mean that, with legal protection, wolves can occupy more of the landscape than was initially assumed..." thus agreeing with the adaptability premise (Mladenoff et al. 1999:43).

Mech himself has pointed out that wolves are limited by human-caused mortality, intraspecific strife, disease, starvation, and prey abundance (Mech 1970, 1977), all points with which we agree. But it appears that Mech's current, unarticulated hypothesis is that all of these factors and the result—successful wolf colonization—are random in relation to habitat and the regional landscape. We contend that this makes no biological sense, according to accepted, basic principles of wildlife biology (Andrewartha and Birch 1954, Caughley and Sinclair 1994). Analytically, Mech's argument may benefit from consulting more recent, dynamic approaches (see, e.g., McCullough 1996, Boitani and Fuller 2000, Gittleman et al. 2001, Manly et al. 2002). Our suggestion, empirically derived, is that differential wolf survival will occur in some areas and not others, largely due to reduced human-caused mortality, either accidental or deliberate. This does not contradict these principles. As noted above, further research has shown that mortality by humans is more likely in certain landscape areas than others (Wydeven et al. 2001). Finally, we argue that Mech's putative analysis ignores the very fundamental principal that assessing significance of use of habitat classes or other resources by an animal can only be done in the context of relative availability (Morrison et al. 1992, Aebischer et al. 1993, Manly et al. 2002) and, in this case, how availability has dramatically changed over time. This is the most serious conceptual flaw in his argument.

*Methodology*.—Mech (2006) bases his critique of our work on an approach that we contend is too imprecise and does not meet currently acceptable standards. We argue that the methodology he used created multiple levels of error. The causes of these errors include the following:

1. Mech (2006) has photocopied 2 letter-sized, published maps of northern Wisconsin to carry out this exercise. These maps are approximately 4 × 6 inches (10 ×16 cm) in size, one from an unpublished annual report of the Wisconsin Department of Natural Resources (DNR) showing wolf packs (Wydeven and Wiedenhoeft 2004), and fig. 2 from Mladenoff et al. (1999) showing our wolf favorability classes mapped on the landscape. A photocopy machine was then used to "... [enlarge] the habitat-suitability map to the same size and scale as the pack territory map" (Mech 2006:874).
2. We cannot know if the 2 maps were created with accuracy and precision suitable for analysis because they are merely copies of illustrations taken from publications. We are not told what the cartographic projections of the 2 maps are or if they are the same.
3. It is not possible to assess, of course, the further errors of precision and accuracy that accumulate when attempting to overlay, by hand, a "transparent acetate copy" of the pack territory map onto the habitat map (Mech 2006:874).
4. The errors described in the previous point are exacerbated because the polygons of interest (pack areas) and their critical locations in a complex matrix of habitat classes are small fractional areas of the total map.
5. Mech (2006) made subjective estimates of how much each pack territory intersected a given habitat class, and each pack was assigned to a habitat category on that basis. Given the imprecision described above, this approach cannot be assessed for accuracy.
6. Two distinct, subjective methods of habitat-class assignment are described in adjacent sentences: "Where a territory boundary enclosed areas of more than one probability, [Mech] scored the probability encompassing the greatest portion of the territory for that territory" followed by, "If a territory enclosed areas of several probabilities, [Mech] used integrated probability." (Mech 2006:874). It is unclear which approach was used, or how the subjective integration was performed; details are not provided.
7. Mech does not include in his paper a figure of the copy-machine-based map overlay to allow reader assessment. Only a numerical summary of the subjective results are provided (Mech 2006, table 1), and these form the basis of the putative refutation of our model.
8. No statistical methods are used to test or validate the claims and conclusions. Moreover, at the scale at which this was performed, and using this subjective approach, we were unable to replicate Mech's numerical results.

Most seriously, this flawed technique has been combined with the fatal conceptual error: ignoring the necessity of assessing habitat-class use versus availability and treating the data as changing relative proportions of habitat classes and wolf abundance over time. Thus, we argue that, due to several cumulative errors and conceptual and methodological flaws, the paper lacks validity. This conclusion is not based on a need for highly technical GIS methods but is based on a lack of fundamental principles of map use and analysis that have existed for decades (Robinson et al. 1995), and basic principles of wildlife ecology. Indeed, an anonymous reviewer of our earlier draft pointed out that "the two maps (figures 1 and 2) that he [Mech] shows lack sufficient common control points to properly overlay. . . . I believe that Mech reads too much into his interpretation, by ignoring registration error and the functional scale of models such as Mladenoff's. . . . Mech should re-evaluate his interpretation of the data he has presented. The fact that 60% of wolf polygons actually occurred in areas of habitat (regardless of probability) says that the model is working. His figure 2 supports this conclusion since the vast majority of his black circles are within predicted habitat."

Certainly though, GIS capability and the appropriate expertise to carry out valid work currently is available to Mech, as are the public data needed for the analysis. Similarly, many such applications of high-quality work exist in the peer-reviewed literature (Boyce and McDonald 1999, Corsi et al. 1999, Carroll et al. 2001).

Regardless of the validity of the data Mech generated, no statistical evaluation of habitat use and availability was performed. The least-suitable habitat class is by far the largest area of 6 classes and itself constitutes over half of the map (>54%). The fact that after 25 years some wolves are occupying this class is neither surprising, as the reviewer has noted, nor is it evidence of the model failure. It is, in fact, expected by chance and, therefore, trivial. Indeed, since remaining high-quality areas are now generally scattered habitat fragments which may not be functional, it is surprising to us that the model still performs significantly; we did not expect this (Mladenoff et al. 2005). Thus, even if they were valid data, a correct interpretation of Mech (2006) does not disprove our model.

Elsewhere, we have presented an appropriate analysis of Wisconsin wolf recolonization from 1979–2002 (Mladenoff et al. 2005). The results are intriguing in revealing how the performance patterns of the model have changed over time, as the number of wolf packs has changed from 5 to 82 and the number of wolves in Wisconsin increased from 25 to 327 (425 as of 2005). The changes are consistent with those we predicted would occur over time (Mladenoff et al. 1999), yet continue to significantly predict continuing wolf occupation of the landscape (Mladenoff et al. 2005). Thus, Mech (2006) is incorrect in his assertion that the model has not been consistent with our predictions. We are left puzzled that this work, by a noted wolf biologist, was submitted and passed the review and editorial process.

### *Summary*

We have shown that the paper by Mech (2006) lacks any reasonable theoretical basis or hypothesis, and conflicts with what is broadly known about animal behavior and population dynamics. It is based on imprecise, subjective methods that are not acceptable by current scientific standards, nor is it necessary to use methods of such poor quality. Only incomplete, un-replicable results are provided by Mech (2006) and, therefore, we contend any interpretations and conclusions are meaningless. We presented an appropriate analysis and results at the recent annual meeting of The Wildlife Society (Mladenoff et al. 2005) showing model behavior has changed, as expected, but has continued to successfully predict wolf recolonization over more than 25 years in Wisconsin. We argue that, even aside from our own analysis, Mech's (2006) flawed work cannot form the basis for a valid critique of our work, and he is incorrect in stating that the model has not been consistent with our predictions.

## Acknowledgments

We thank an anonymous reviewer for helpful comments, and the current Editor-in-Chief for the invitation to reply.

## Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radiotracking data. Ecology 74:1313–1325.

Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. University of Chicago, Illinois, USA.

Boitani, L., and T. Fuller. 2000. Research techniques in animal ecology. Columbia University, New York, New York, USA.

Boyce, M. S., and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecological Applications 11:961–980.

Caughley, G., and A. R. E. Sinclair. 1994. Wildlife ecology and management. Blackwell, London, United Kingdom.

Corsi, F., E. Dupre, and L. Boitani. 1999. A large-scale model of wolf distribution in Italy for conservation planning. Conservation Biology 13:150–159.

Erb, J., and S. Benson. 2004. Distribution and abundance of wolves in Minnesota, 2003–2004. Minnesota Department of Natural Resources, St. Paul, USA.

Gittleman, J. L., S. M. Funk, D. Macdonald, and R. K. Wayne. 2001. Carnivore conservation. Cambridge University, United Kingdom.

Manly, B. F. J., L. MacDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic, Dordrecht, The Netherlands.

McCullough, D. R. 1996. Metapopulations and wildlife conservation. Island, Washington, D.C., USA.

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

Mech, L. D. 1977. Productivity, mortality, and population trends of wolves in northeastern Minnesota. Journal of Mammology 58:559–574.

Mech, L. D. 1995. The challenge and opportunity of recovering wild populations. Conservation Biology 9:270–278.

Mech, L. D. 1998. Estimated costs of maintaining a recovered wolf population in agricultural regions of Minnesota. Wildlife Society Bulletin 26:817–822.

Mech, L. D. 2001. Managing Minnesota's recovered wolves. Wildlife Society Bulletin 29:70–77.

Mech, L. D. 2006. Prediction failure of a wolf landscape model. Wildlife Society Bulletin 34:874–877.

Mladenoff, D. J., M. K. Clayton, T. A. Sickley, and A. P. Wydeven. 2005. Evaluating a model of gray wolf increase and spread in Wisconsin. The Wildlife Society Annual Meeting, September 2005, Madison, Wisconsin, USA.

Mladenoff, D. J., R. G. Haight, T. A. Sickley, and A. P. Wydeven. 1997. Causes and implications of species restoration in altered ecosystems. BioSience 47: 21–31.

Mladenoff, D. J., and T. A. Sickley. 1998. Assessing potential gray wolf habitat 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.

Mladenoff, D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf colonization: logistic regression models vs. new field data. Ecological Applications 9:37–44.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 1992. Wildlife–habitat relationships. University of Wisconsin, Madison, USA.

Peterson, R. O. 1988. The pit or the pendulum: issues in large carnivore management in natural ecosystems. Pages 105–117 *in* J. K. Agee and D. R. Johnson, editors. Ecosystem management for parks and wilderness. University of Washington, Seattle, USA.

Potvin, M. J., T. D. Drummer, J. A. Vucetich, D. E. Beyer, Jr., R. O. Peterson, and J. J. Hammill. 2005. Monitoring and habitat analysis for wolves in upper Michigan. Journal of Wildlife Management 69:1660–1669.

Robinson, A. H., J. L. Morrison, P. C. Muehrcke, A. J. Kimerling, and S. C. Guptill. 1995. Elements of cartography. Sixth edition. John Wiley, New York, New York, USA.

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

Wydeven, A. P., D. J. Mladenoff, T. A. Sickley, B. E. Kohn, R. P. Thiel, and J. L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes region. Endangered Species UPDATE 18:110–114.

Wydeven, A. P., R. N. Schultz, and R. P Thiel. 1995. Gray wolf (*Canis lupus*) population monitoring in Wisconsin 1979–1991. Pages 147–156 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and conservation of wolves in a changing world. Canadian Circumpolor Institute, University of Alberta, Edmonton, Canada.

Wydeven, A. P., and J. E. Wiedenhoeft. 2004. Status of the timber wolf in Wisconsin. Wisconsin endangered resources performance report 1 July 2003 through 30 June 2004. Wisconsin Department of Natural Resources, Park Falls, USA.

***David J. Mladenoff*** is the Beers-Bascom Professor of Conservation in the Department of Forest Ecology & Management at the University of Wisconsin (UW)-Madison. He earned his Ph.D. from the UW-Madison in 1985, and held positions in The Nature Conservancy as Western Region Science and Stewardship Director, and the University of Minnesota Natural Resources Research Institute in Duluth. He manages the Forest Landscape Ecology Lab at UW-Madison and teaches a graduate course in landscape ecology. Besides 20 years of wolf research, his research addresses sustainable forest issues such as old-growth forest characteristics, developing and testing methods for reconstructing past forests and change, and modeling of future forests under climate change. He was Editor-in-Chief of the journal *Landscape Ecology* from 1999–2005, and is an editor for *Ecological Applications*. ***Murray K. Clayton*** is a professor of statistics and the Professor and Chair of Plant Pathology at UW-Madison. He received a B. Math. (hons) in statistics and pure mathematics from the University of Waterloo in 1979 and a Ph.D. in statistics from the University of Minnesota in 1983. His research focus is on the application of statistics to the biological sciences, especially with respect to spatial statistics. He has authored or co-authored over 100 articles in the statistics and science literature. ***Theodore A. Sickley*** has been a Geographic Information Systems (GIS) scientist in the Department of Forest Ecology and Management at UW-Madison since 1995. He has worked extensively on GIS applications to natural resource issues. ***Adrian P. Wydeven*** is a mammalian ecologist with the Wisconsin Department of Natural Resources (1990 to present). He earned a B.S. in Wildlife Management and Biology from the University of Wisconsin–Stevens Point (1976), an M.S. from Iowa State University in Wildlife Ecology (1979), and was a wildlife manager in Missouri and Wisconsin from 1980–1990. He has been a member of The Wildlife Society since 1976, and was past president of the Wisconsin Chapter.