Predicting Human-Carnivore Conflict: a Spatial Model Derived from 25 Years of Data on Wolf Predation on Livestock

ADRIAN TREVES,*†§§ LISA NAUGHTON-TREVES,*†‡ ELIZABETH K. HARPER,§ DAVID J. MLADENOFF,** ROBERT A. ROSE,‡ THEODORE A. SICKLEY,** AND ADRIAN P. WYDEVEN††

*Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460-1090, U.S.A.
†Center for Applied Biodiversity Science, Conservation International, Washington, D.C., 20036, U.S.A.
‡Department of Geography, University of Wisconsin–Madison, 550 North Park Street, Madison, WI 53706, U.S.A.
§Department of Fisheries and Wildlife, 200 Hodson Hall, 1980 Folwell Avenue, University of Minnesota, St. Paul, MN 55108, U.S.A.
**Department of Forest Ecology and Management, University of Wisconsin–Madison, 120 Russell Labs, 1630 Linden Drive, Madison, WI 53706, U.S.A.
††Wisconsin Department of Natural Resources, Box 220, Park Falls, WI 54552, U.S.A.

Abstract: *Many carnivore populations escaped extinction during the twentieth century as a result of legal protections, habitat restoration, and changes in public attitudes. However, encounters between carnivores, livestock, and humans are increasing in some areas, raising concerns about the costs of carnivore conservation. We present a method to predict sites of human-carnivore conflicts regionally, using as an example the mixed forest-agriculture landscapes of Wisconsin and Minnesota (U.S.A.). We used a matched-pair analysis of 17 landscape variables in a geographic information system to discriminate affected areas from unaffected areas at two spatial scales (townships and farms). Wolves (*Canis lupus*) selectively preyed on livestock in townships with high proportions of pasture and high densities of deer (*Odocoileus virginianus*) combined with low proportions of crop lands, coniferous forest, herbaceous wetlands, and open water. These variables plus road density and farm size also appeared to predict risk for individual farms when we considered Minnesota alone. In Wisconsin only, farm size, crop lands, and road density were associated with the risk of wolf attack on livestock. At the level of townships, we generated two state-wide maps to predict the extent and location of future predation on livestock. Our approach can be applied wherever spatial data are available on sites of conflict between wildlife and humans.*

Predicción de Conflicto Humano–Carnívoro: un Modelo Espacial Basado en 25 Años de Datos de Depredación de Ganado por Lobos

Resumen: *Muchas poblaciones de carnívoros lograron evitar la extinción durante el siglo veinte debido a protecciones legales, restauración de hábitat y cambios en las actitudes del público. Sin embargo, los encuentros entre carnívoros, ganado y humanos están incrementando en algunas áreas, lo cual es causa de preocupación en cuanto a los costos de la conservación de carnívoros. Presentamos un método para predecir los sitios de conflictos humanos - carnívoro a nivel regional, utilizando como ejemplo los paisajes mixtos de bosques-agricultura de Wisconsin y Minnesota (E. U. A.). Utilizamos un análisis apareado de 17 variables del paisaje en un sistema*

§§*Current address: Living Landscapes Program, Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, NY 10460-1090, U.S.A., email atreves@wcs.org*
Paper submitted May 7, 2002; revised manuscript accepted June 9, 2003.

*de información geográfica para discriminar áreas afectadas de áreas no afectadas a dos escalas espaciales (municipios y establecimientos). Los lobos (*Canis lupus*) depredaron selectivamente el ganado en municipios con proporciones altas de pasto y altas densidades de venado (*Odocoileus virginianus*) combinadas con proporciones bajas de terrenos agrícolas bosques de coníferas, humedales herbáceos y cuerpos de agua abiertos. Estas variables, junto con la densidad de caminos y el tamaño del establecimiento, permitieron además predecir el riesgo para establecimientos individuales cuando analizamos solamente el estado de Minnesota. En Wisconsin, solamente el tamaño del establecimiento, los terrenos agrícolas y la densidad de caminos se asociaron con el riesgo de ataque al ganado por lobos. Al nivel de municipios, generamos dos mapas estatales para predecir la extensión y la localización futura de depredación del ganado. Nuestro método es aplicable dondequiera que haya disponibilidad de datos espaciales sobre conflictos entre vida silvestre y humanos.*

Introduction

Under the U.S. Endangered Species Act and other legal protections, populations of large carnivores in North America have recovered from near extinction in the last century (Aune 1991; Mech 1995). As their populations expand or humans encroach on their habitats, carnivores encounter more domestic animals and humans (Halfpenny et al. 1991; Treves et al. 2002). Such encounters can pose a danger to humans (Jorgensen et al. 1978; Beier 1991) and cost millions of dollars annually (Tully 1991; Mech 1998). People often respond to this conflict by poisoning, shooting, and trapping carnivores, techniques that kill nontarget animals in high proportions (Sacks et al. 1999; Treves et al. 2004). Killing carnivores can undermine endangered-species protections and draws criticism from many fronts (Haber 1996; Torres et al. 1996; Fox 2001). As a result, natural resource managers and researchers are seeking methods to prevent some or all carnivore predation on domestic animals at the outset.

Prevention depends on identifying the conditions promoting human-carnivore conflict and focusing outreach and interventions accordingly. Previous researchers have identified husbandry practices, human activities, and carnivore behaviors as attributes that increase the risk of conflict (Jackson & Nowell 1996; Linnell et al. 1999). But modifying many farmer's practices and the behavior of many individual carnivores appears impractical across regions containing thousands of carnivores and farms. A more efficient approach would be to anticipate the locations of human-carnivore conflict and focus interventions in this smaller set of areas. This requires that we identify the intersection of human and carnivore activities in space or consistent landscape features associated with human-carnivore conflicts (Albert & Bowyer 1991; Jackson et al. 1996; Stahl & Vandel 2001).

Here we present a regional model that predicts future sites of human-carnivore conflict in relation to landscape features such as human land use and vegetation types. We base our model on the sites of past wolf (*Canis lupus*) attacks on livestock in Wisconsin and Minnesota, in the Midwest of the United States. A small portion of the Minnesota wolf population survived the widespread extirpation of wolves throughout the coterminous United States (Young & Goldman 1944). This remnant population began to recover from the northeast portion of Minnesota without direct, human intervention recolonizing almost half of Minnesota, the northern third of Wisconsin, and Michigan's Upper Peninsula in the past 30 years (Fuller et al. 1992; Wydeven et al. 1995; Berg & Benson 1999). In recent years (1996–2000), wolves caused a mean of 12.6 depredations in Wisconsin and 96.2 depredations in Minnesota annually (Paul 2000; Treves et al. 2002). The economic costs of wolf predation on livestock have increased as the wolf population has expanded in this region (Fritts et al. 1992; Mech 1998; Treves et al. 2002). Wisconsin spent an annual average of $51,000 in compensation between 1998 and 2002, and Minnesota spent $84,000 in compensation in 2000 (Paul 2000; Treves et al. 2002). Control operations may double these expenditures (Treves et al. 2002). Predicting where conflict is likely to arise in the future may reduce the costs of control and compensation, and also political controversy over wolves.

Wisconsin and Minnesota contain a variety of land uses and habitat types, including publicly and privately owned forests, agricultural areas, and rural housing. This mixture has favored recolonization by wolves (Mladenoff et al. 1997), but it complicates the management of conflict because there is no clear edge or boundary between wolf habitat and human land uses. Beef cattle and poultry operations are often situated in forested pastures or adjacent to forested lands and overlap wolf population range. We take advantage of this intermingling of human and wolf habitat to test predictions about carnivore behavior in human-modified ecosystems.

Dense vegetative cover appears to favor livestock predation by wolves and other large carnivores (Jackson et al. 1996; Bangs & Shivik 2001; Stahl & Vandel 2001); likewise, placing pastures around vegetated waterways may promote coyote (*C. latrans*) predation on sheep (Robel et al. 1981). Researchers also report a negative association between carnivore predation on livestock and the density of human roads and settlements (Robel et al. 1981; Jackson et al. 1996; Stahl & Vandel 2001). Therefore, we predict that proximity to wetlands and forest will elevate the risk of wolf predation on livestock, whereas lower risk is expected near dense networks of roads and human populations. Low densities of wild prey also appear to promote livestock predation (Mech et al. 1988*a*; Meriggi & Lovari 1996), although the opposite is true for some lynx (*Lynx lynx*) (Stahl & Vandel 2001). Many researchers have found that larger herds of livestock and larger landholdings face disproportionate risk from wolves (Ciucci & Boitani 1998; Mech et al. 2000).

Methods

To identify the landscape features associated with past sites of wolf attacks on livestock, we combined three sets of spatial data from Wisconsin and Minnesota: (1) the range of the 1998 wolf population (163,676 km^2), (2) locations of 975 verified sites of wolf predation on livestock over the past 25 years, and (3) census and remotely sensed land-cover data.

The Wisconsin and Minnesota Departments of Natural Resources (hereafter, WDNR and MDNR) mapped the 1998 wolf population range and collected systematic data on 975 verified incidents of wolf attack on livestock from 1976 to 2000 (Fritts et al. 1992; Paul 2000; Treves et al. 2002). The WDNR used radiotelemetry, winter track surveys, and summer howl surveys to estimate wolf pack home ranges (Wydeven et al. 1995). The MDNR mapped wolf range less precisely, with questionnaires for land-management agencies and scent-station track analyses (Sargeant et al. 1998; Berg & Benson 1999). Neither data set can rule out the occurrence of wolves in a particular area because not all wolves were radiocollared and wolf dispersal and extraterritorial movements can be extensive (Merrill & Mech 2000).

Records of bison, cattle, poultry, and sheep losses were verified and georeferenced by field staff from the WDNR, MDNR, and cooperating federal agencies (Willging & Wydeven 1997; Paul 2000). Field staff recorded locations in DTRS (direction, township, range, and section) coordinates from widely available maps of public land surveys. Of the 975 verified wolf attacks on livestock, 52 occurred in Wisconsin (1976–2000) and 923 in Minnesota (1979–1998). This disparity reflects both the larger size of the Minnesota wolf population—estimated at 2600 in 1999 (Berg & Benson 1999) versus Wisconsin's 257 in 2000—and the more recent recolonization of Wisconsin (Wydeven et al. 1995). Otherwise, the two states are similar in per capita rates, targets, and costs of wolf predation on livestock (Treves et al. 2002). We used the spatial information to analyze conflicts at the scale of farms and their vicinity (10.24 km^2) and of townships (92.16 km^2). These scales of analysis correspond to real geopolitical units and reflect levels of decision-making by livestock producers and wildlife managers alike.

Landscape variables included (1) agricultural census data at the scale of counties—average farm size in square kilometers, density of beef, dairy, and unspecified cattle as head per square kilometer (U.S. Department of Agriculture 1997); (2) land-cover classification at 30-m resolution (National Land Cover Data [NLCD] 1992/1993 classified Landsat TM data: Vogelmann et al. 2001), expressed as percentage of deciduous forest, coniferous forest, mixed forest, brush (grassland, shrubs, and transitional), pasture (pasture and hay field), crops (row crops and small grains), forested wetlands, emergent wetlands, unusable land (residential, commercial, urban grassy areas, and barren areas), and open water (ponds and lakes); (3) population density in humans per square kilometer by census block group for Wisconsin or census minor civil division for Minnesota (U.S. Census Bureau TIGER/line files 1992); (4) deer (*Odocoileus virginianus*) density in head per square kilometer at a resolution of deer management units (1136 km^2) in Wisconsin (WDNR 1999*b*), or permit areas (1707 km^2) in Minnesota (MDNR 2001); and (5) road density in km per square kilometer (U.S. Census Bureau TIGER/line files 1992).

We compared affected townships to randomly selected, contiguous, unaffected townships. In this region, townships were surveyed and mapped in a rectangular grid, visible on commercially available road atlases. Townships were also useful because they were 50–60% of the average wolf pack home range (average winter estimates excluding single forays >5 km from core areas: Wisconsin $=$ 137 km^2, range 47–287; Minnesota $=$ 180 km^2, range 64–512; Wydeven et al. 1995; Berg & Benson 1999; Wydeven et al. 2002); hence, neighboring townships could be encompassed by a single wolf pack. We matched affected and randomly selected neighboring unaffected townships under the assumption that wolves had equal access to either township. By employing a matched-pair design, we avoided potentially confounding differences in wolf residence length, wolf pack attributes, and differences in human land uses across different regions of the two states. No precise data were available on length of wolf residence in Minnesota, so a traditional logistic-regression model was unsatisfactory, although we calculated it for comparison purposes. A logistic regression compares regions with a long history of wolf residence to regions where wolves arrived recently, thereby introducing confounding variation related to the length of exposure to wolves, differences in wolf control, and differences in livestock production across the entire region. For example, Minnesota farms are larger on average than Wisconsin farms, but variation is marked in both states. Hence, a significant difference in the mean size of affected farms versus unaffected ones (Mech et al. 2000) would be masked by the interstate difference in mean farm size and its variability. By contrast, our matched-pair design controls for interregional and interstate variation by drawing comparisons only between neighboring townships.

We mapped all 975 verified incidents of wolf attack on livestock (Fig. 1). Several occurred outside the published

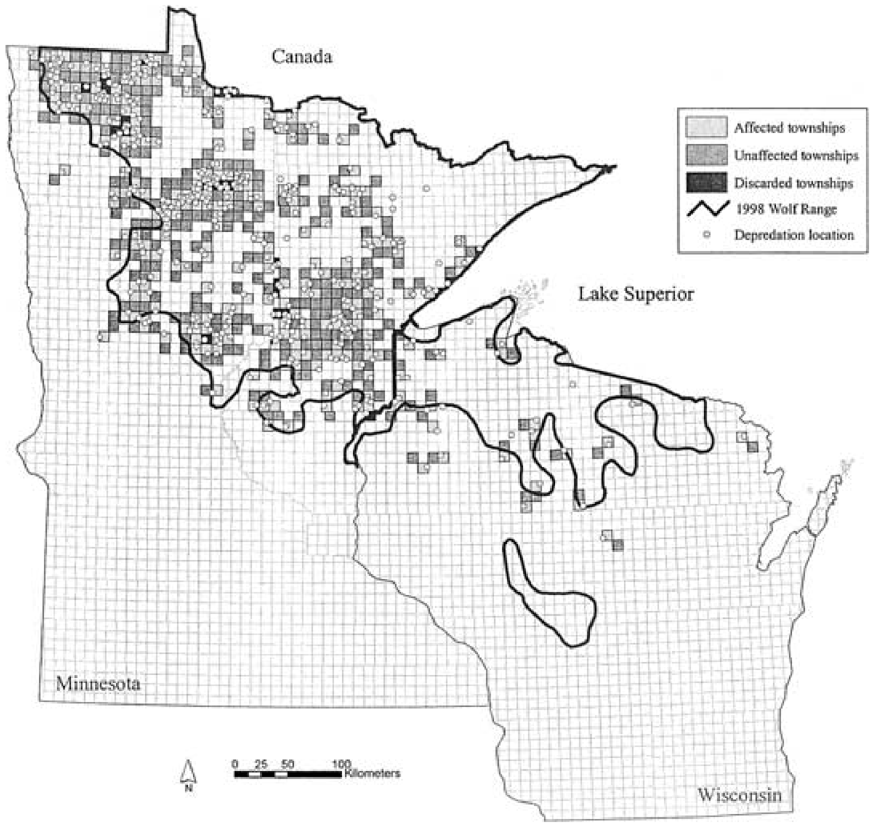

Figure 1. Wisconsin and Minnesota (U.S.A.) townships and the 252 matched pairs of townships used in our analyses. Twenty-five affected townships (dark, irregular polygons) bordering the meridian, Canada, or Lake Superior or lacking eligible, unaffected, neighboring townships were not used in our model (see Methods). Depredations before 1986 or after 1998 were excluded from analyses. Verified depredations outside the wolf range reflect predation by dispersing wolves or fluctuations in the wolf range over time.

range of the wolf population in 1998. These attacks on livestock falling outside the presumed wolf range may reflect fluctuations in the wolf range or the actions of lone wolves missed in range and population estimates (Berg & Benson 1999; Wydeven et al. 2002). To minimize discrepancies between the time of attack and the time at which the landscape data were collected, we considered only those affected townships with verified wolf attacks on livestock between 1986 and 1998. Townships that had only verified wolf predation on livestock before 1986 or after 1998 were not used as unaffected townships but were instead excluded from analyses because we could not be confident of landscape features. Iteratively, we selected unaffected townships randomly from those remaining townships that were contiguous to each affected township. In theory, up to 8 unaffected townships could be contiguous to each affected township. In practice, up to 8 townships were ineligible as matches because they were affected townships themselves, they had already been chosen for another pair, or >50% of their area lacked applicable data (Canada, Lake Superior, or a large body of open water). In addition, 5 affected townships were excluded because of their irregular shape: due to curvature in the earth's surface, surveyors reset the reference meridian running through central Minnesota, and townships near this meridian were <50% of the size of other townships. We excluded these irregular, smaller townships to avoid comparing townships of different sizes to one another. After these exclusion and random assignment steps, 25 affected townships (1 in Wisconsin and 24 in Minnesota) had no eligible neighbors (Fig. 1); they were set aside. Our final sample for analysis consisted of 22 pairs in Wisconsin and 230 in Minnesota (504 townships in total = 42.9% of all 1716 townships within and adjacent to the 1998 wolf population range; Fig. 1).

We see a few potential sources of error in the selection of affected and unaffected townships. First, a livestock loss may have been mistakenly attributed to wolves (Fritts et al. 1992; Treves et al. 2002). This should be a random error, not a systematic one. Second, an unaffected township may have had wolf predation that was not reported or verified. This error is difficult to estimate, but the compensation given to farmers should give an incentive to report losses (Fritts et al. 1992; Treves et al. 2002). Moreover, it is a conservative error because it would obscure the distinction between affected and unaffected townships. Also, we may have lost valuable information if the 25 townships without eligible neighbors all came from one area. However, they were mostly dispersed around national boundaries, lake margins, and the meridian (Fig. 1).

To collect landscape features at a finer scale, we also conducted fieldwork around affected farms. Two teams of observers visited a subset of affected farms (22 in Wisconsin and 41 in Minnesota) and identified a nearby, unaffected neighbor with a similar operation (e.g., both producing beef cattle). They took global positioning system locations on each of the 126 properties and interviewed farmers about husbandry (Mech et al. 2000). The median distance between matched farms in Wisconsin was 5.6 km (range 0.1–12.0 km), and in Minnesota it was 3.2 km (range 0.1–15.6 km; Mann-Whitney U test, $Z = -1.47$, $p = 0.14$). For our analysis, the vicinity of each farm was defined as the section in which it was situated plus 0.8 km on each side (10.24 km^2). No affected farm lay within the vicinity of another. In 14 of 63 matched pairs of farms (22%), the vicinities of affected and unaffected farms overlapped. Such overlap may reduce differences between affected and unaffected farms, so it is a conservative error.

The variables identified as important at the township level were used in our analysis at the farm level because we had a larger sample of affected townships ($n = 252$) than affected farms ($n = 63$). Also, the geographic information system data were more variable across townships than across neighboring farms, reducing the power of our tests to discriminate between affected and unaffected farms. Finally, townships are fixed units visible on statewide atlases, which makes the outputs of our model (maps) usable in the field by any stakeholder (Turner et al. 1995).

Statistical Procedures

We computed univariate tests of association with the one-sample t test (affected minus unaffected) and the sign test. The two statistics provided complementary information. The t value indicated whether the mean difference between affected farm or township landscape features and unaffected farm or township landscape features were statistically different from zero, whereas the sign test revealed whether the variable in question discriminated matched pairs of townships with better than chance probabilities (>57.3% given the sample size of 252 township pairs or >61.9% for the 63 farm pairs). Any variable that passed one or both tests was included in the second stage of analysis, to which we applied a Bonferroni correction for the number of tests ($p < 0.01$).

Using the subset of variables significant in one or both univariate tests, we performed a single-sample discriminant-function analysis following that of Morrison (1990:132–136). Our discriminant-function analysis took the following form:

$$t = \begin{pmatrix} a_1\ b_1\ c_1 & \cdots & j_1 \\ a_2\ b_2\ c_2 & \cdots & j_2 \\ a_3\ b_3\ c_3 & \cdots & j_3 \\ & \cdots & \\ & \cdots & \\ & \cdots & \\ a_i\ b_i\ c_i & \cdots & j_i \end{pmatrix} \begin{pmatrix} u \\ v \\ w \\ x \\ . \\ . \\ z \end{pmatrix} - \begin{pmatrix} a'_1\ b'_1\ c'_1 & \cdots & j'_1 \\ a'_2\ b'_2\ c'_2 & \cdots & j'_2 \\ a'_3\ b'_3\ c'_3 & \cdots & j'_3 \\ & \cdots & \\ & \cdots & \\ & \cdots & \\ a'_i\ b'_i\ c'_i & \cdots & j'_i \end{pmatrix} \begin{pmatrix} u \\ v \\ w \\ x \\ . \\ . \\ z \end{pmatrix}, \quad (1)$$

where $a_i, b_i, c_i \cdots j_i$ are the known values of each significant landscape variable $a \cdots j$ for the affected townships, and $a'_i, b'_i, c'_i \cdots j'_i$ are the known values of the same landscape variables for unaffected townships ($i = 252$ for township analyses). The vectors of coefficients $u, v, w, x \cdots z$ are unknown values that give relative weight to each landscape variable $a \cdots j$. The unknown t is a single value that characterizes the difference between affected and unaffected townships given any vector of coefficients. To combine all variables in the same equation, we standardized them across both affected and unaffected areas. Because the vector of coefficients $(u, v, w, x \cdots z)$ is the same for both affected and unaffected areas, we can simplify the matrices in two steps to generate two vectors:

$$t = (\Delta_a \Delta_b \Delta_c \cdots \Delta_j) \begin{pmatrix} u \\ v \\ w \\ x \\ . \\ . \\ z \end{pmatrix}, \quad (2)$$

where $\Delta_a = \Sigma(a_i - a'_i)/i$ or the mean difference across areas for each variable $a \cdots j$. To most effectively discriminate affected from unaffected townships, we sought t_{max}. This value is unique (Morrison 1990) and corresponds to the inverse of the variance/covariance matrix of $\Delta_{a \cdots j}$ (Morrison 1990:132–136). The inverse matrix is not the simple algebraic inverse, but the matrix algebraic inverse. Many statistical packages compute the variance/covariance matrix and its inverse matrix. We used R, the shareware version of S-plus software (Insightful Corp., Seattle, WA).

If no variable $a \cdots j$ distinguished affected from unaffected areas, t_{max} would not differ significantly from zero by a single-sample t test. If a significant t_{max} results, one might then discriminate affected townships from unaffected ones, and the resulting vector of coefficients $(u \cdots z)$ would provide the coefficient indicating the relative importance of each landscape variable. It is this linear combination of landscape variables with weighting coefficients that can be used to predict future risk (R) of wolf predation on livestock. We repeated this entire procedure for our 63 farm pairs.

To indicate the biological significance of our results (beyond their statistical significance), we calculated effect size for each landscape variable by computing the average percent difference within affected and unaffected pairs.

Mapping Procedures

We used the results of the township analyses to generate two predictive maps. The maps can be used to forecast future wolf predation on livestock. To generate the maps, we extrapolated from the 252 affected townships to the universe of townships in the states of Wisconsin and Minnesota. We assumed that landscape features and wolf-livestock interactions will not change over time. We also assumed that our matched-pair results translated into a linear estimate of relative risk that can be applied across townships.

Because the index of relative risk (R) was calculated in units of sample standard deviation, we color-coded townships as follows: red townships had $R > 2$ SD above the sample mean for the 252 affected townships; orange townships had $R > 1$ SD above that sample mean; yellow townships had R_t within ± 1 SD of that sample mean; green townships had $R > 1$ SD below that sample mean; and blue townships had $R > 2$ SD below that sample mean. Scrutiny of landscape data for both states revealed that 312 townships (<0.3% of the universe of townships) contained <0.1% pasture. These townships were mainly residential or industrial areas, unlike the townships in our affected sample. To avoid spurious estimates of risk for townships with <0.1% pasture, we color-coded these as blue, or lowest risk. In sum, our maps distinguished townships according to whether they matched the landscape features found at sites of past wolf predation on livestock.

Our first map depicted the risk of wolf predation on livestock if wolves occupy any township. This was not conservative because it did not distinguish townships unlikely to contain wolves from those likely to contain wolves. Our second map was more conservative because it assigned a likelihood of wolf occupancy to each township. This likelihood was based on road density.

Roads affect wolf ranging (Thurber et al. 1994) and predict wolf territory establishment (Thiel 1985; Mladenoff et al. 1997). Although there have been some challenges to the predictive power of road density (Mech et al. 1988*b*), it remains an effective predictor of where wolves will establish territories in the Lake Superior region. Therefore, in our second map, we recolored blue those townships with road density of >0.88 km/km^2 (highly unlikely for wolf territory establishment), and all townships with lower road density (possible wolf territory) retained the color assigned in our first map. The value of 0.88 km/km^2 was chosen from a study of the density of roads within confirmed wolf pack territories in Wisconsin (Wydeven et al. 2001). Some estimates from Minnesota were as high as 0.88, whereas the highest confirmed value for a radio-tracked wolf pack overlapping public access roads is 0.73 km/km^2. In sum, our second map indicated the relative risk of wolf predation on livestock, assuming that wolf use of townships continues to follow current trends. We present both, so the reader skeptical of the importance of road density may judge the relative risks.

Results

Township-Level Risk

At the level of townships, six landscape variables significantly distinguished affected from unaffected townships in univariate tests (Table 1). We randomly divided our

Table 1. Landscape features of townships in Wisconsin and Minnesota, comparing those with verified wolf predations on livestock to contiguous, randomly selected, unaffected townships.[a]

	Wisconsin (22 pairs)		*Minnesota (230 pairs)*		*Overall (252 pairs)*		
Predictor	*affected average*	*unaffected average*	*affected average*	*unaffected average*	*sign test* D *(%)*	*paired test* (p)	*predicted relationship*[b]
Farm size	0.10	0.10	0.17	0.16	12.9	0.17	+
All cattle	10.30	9.72	4.86	4.99	11.1	0.98	+
Beef cattle	0.88	0.83	1.57	1.58	11.5	0.93	+
Dairy cattle	4.03	3.78	0.75	0.78	9.5	0.68	+
Deciduous forest	44.30	46.91	25.96	24.96	52.8	0.41	+
Conifer forest	6.30	7.40	3.30	3.80	49.6	0.03[c]	+
Mixed forest	9.50	11.10	4.00	4.25	48.8	0.09	+
Brush	0.90	0.80	1.60	1.80	53.2	0.26	+
Pasture/hayfield	12.54	7.82	11.85	8.46	70.2[c]	0.0001[c]	−
Crops	10.90	6.53	14.40	13.72	60.7[c]	0.28	−
Forested wetland	9.51	10.17	25.54	25.60	56.7	0.91	+
Emergent wetland	2.89	3.81	8.64	8.54	59.5[c]	0.98	+
Unusable	0.48	0.75	0.37	0.50	43.3	0.20	−
Open water	2.65	4.69	4.17	8.10	57.1	0.0001[c]	−
Human density	6.65	9.05	3.09	3.67	46.0	0.11	−
Deer density	4.16	4.14	4.25	4.10	36.5	0.049[c]	−
Road density	0.69	0.70	0.51	0.54	52.4	0.46	−

[a] *Variables and units detailed in Methods section. Key:* D, *percentage of pairs that differ in the same direction;* +, *positive correlation;* −, *negative correlation.*
[b] *Rationale detailed in Introduction.*
[c] *Retained for use in next stage of analysis (farms).*

township data into two equal halves and used the first half to compute the linear combination of the six variables that best discriminated affected from unaffected townships (with Eq. 2). This linear combination (Eq. 3) distinguished 73.8% of affected townships from their matched, unaffected townships (sign test $p < 0.0001$; $t_{\max}$: $t_{1,125} = 6.69, p < 0.0001$):

$$R = 0.63 \text{ pasture/hayfield} + 0.22 \text{ deer density} - (0.10 \text{ conifer} + 0.29 \text{ crops} + 0.12 \text{ emergent wetland} + 0.14 \text{ open water}). \quad (3)$$

When applied to the second half of the data set, Eq. 3 correctly discriminated 76.5% of the affected townships (sign test $p = 0.0001$; $t_{1,125} = 4.65$, $p < 0.0001$). Affected townships contained greater amounts of pasture and numbers of deer with lesser amounts of coniferous forest, crop lands, herbaceous wetland, and open water than did unaffected townships. The validity of Eq. 3 is further bolstered by our finding that Wisconsin and Minnesota showed concordant patterns despite disparate sample sizes and wolf population sizes. Wisconsin's affected townships were significantly discriminated from unaffected ones (86% discrimination, sign test $p = 0.0009$; $t_{1,21} = 4.17, p = 0.0004$). The same held for Minnesota's affected townships (70.0% discriminated, sign test $p < 0.0001$; $t_{1,229} = 7.39, p < 0.0001$). Finally, the 25 townships set aside prior to analysis had an average value from Eq. 3 of 0.08, which fell closer to the affected townships than unaffected townships (affected average = 0.16, unaffected average = −0.16). In particular, the 25 townships set aside had significantly more pasture than the average unaffected townships ($t_{1,275} = 2.40, p = 0.0175$) and did not differ significantly from affected townships in any of the relevant variables of Eq. 3.

The effect size or real difference between affected and unaffected townships cannot be judged from the overall means presented in Table 1. Instead, one must consider the average differences between pairs, which shows that affected townships had 34.5% more pasture on average, 63.7% less open water, 16.1% less coniferous forest, 7.4% more cropland, 0.2% more emergent wetland, and 3.4% more deer (equivalent to 13 more deer per township). Certain landscape variables (e.g., crops, emergent wetland) showed a positive association in univariate tests, but their eventual contribution to the model was negative (Eq. 3). This apparent contradiction was resolved by the discriminant-function analysis, which identified the residual effects of croplands and emergent wetland once the very strong effect of pasture was controlled statistically. For example, when we divided our 252 township pairs into the majority (70.8%) in which affected townships had more pasture than their unaffected neighbor and the minority (29.8%) with the reverse pattern, we found a significant difference in crop lands across the two groups. In the majority, affected townships had more crop lands than unaffected neighbors, but in the minority the pattern was reversed so that the majority and minority were significantly different in relative proportion of croplands (unpaired $t_{1,251} = 4.16, p < 0.0001$). In other words, crop lands provided no additional information when affected townships had more pasture than their unaffected neighbors, but the remainder of affected townships had both less pasture and less cropland than their unaffected neighbors. These conditions might describe livestock operations within wilder areas, compared with areas of high agricultural use. Townships with less pasture and less croplands were less transformed by humans than their neighbors, apparently raising their risk of wolf predation on livestock.

Farm-Level Risk

The 44 Wisconsin farms averaged 1.36 km^2 in area (SD 1.73, range 0.13–8.44), with an average of 86 head of cattle (SD 81, range 6–400). The 82 Minnesota farms ranged from 2.9 to 4.9 km^2, with 82–158 head of cattle. The two states' values are not directly comparable because Wisconsin farmers reported their pasture acreage, whereas the Minnesota farmers reported total landholdings. The affected farms in Wisconsin had significantly larger landholdings and larger herds than their paired, unaffected neighbors (Wilcoxon signed-ranks test, $Z = 2.26$, $p = 0.036$). The same association with herd size occurred among the Minnesota farms (Mech et al. 2000). Due to differences in methods used by the two independent teams, we did not analyze farm size or herd size alongside other landscape variables.

We used the six landscape variables that distinguished affected townships (Eq. 3) and added one additional variable (road density) that was significant in univariate tests (Table 2). With these seven landscape variables, risk of wolf predation on livestock at the scale of farms was estimated as follows:

$$R_f = 0.10 \text{ conifer} + 0.13 \text{ open water} + 0.13 \text{ deer density} - (0.16 \text{ pasture/hayfield} + 0.58 \text{ crops} + 0.13 \text{ emergent wetland} + 0.41 \text{ road density}). \quad (4)$$

Equation 4 distinguished 71.4% (sign test $p = 0.0009$; $t_{1,62} = 4.04, p = 0.0001$) of the affected farms across both states. But Minnesota's farms had an overwhelming effect on this result (Minnesota 73.2%, sign test $p = 0.0043$). On the other hand, Eq. 4 did not predict risk for farms in Wisconsin (68.2%, sign test $p = 0.13$). For Wisconsin, the univariate tests that identified croplands, road density, and herd size were more informative than the discriminant-function analysis (Table 2). For Wisconsin, the effect size of croplands was 26% and that of road density 4%. For Minnesota, effect sizes were as follows: emergent wetland, 36%; croplands, 30%; open water, 26%; roads, 12%; coniferous forest, 10%; pasture, 8%; and deer, 0.1%.

Table 2. Landscape features of farms in Wisconsin and Minnesota, comparing those with verified wolf predation on livestock to neighboring farms with similar operations but unaffected by wolf predation.[a]

Predictor	Wisconsin (22 pairs) affected average	Wisconsin (22 pairs) unaffected average	Minnesota (41 pairs) affected average	Minnesota (41 pairs) unaffected average	Overall (63 pairs) sign test D (%)	Overall (63 pairs) paired test p	Overall (63 pairs) predicted relationship[b]
Farm size	0.1	0.1	0.2	0.2	9.5	0.93	+
All cattle	8.7	8.4	4.6	5.0	11.1	0.12	+
Beef cattle	1.0	1.0	1.5	1.6	11.1	0.43	+
Dairy cattle	3.2	3.1	0.7	0.9	11.1	0.33	+
Deciduous forest	47.7	43.5	24.8	23.7	55.6	0.14	+
Conifer forest	4.1	3.9	1.8	1.5	42.9	0.47	+
Mixed forest	8.1	6.9	2.9	3.3	44.4	0.64	+
Brush	0.9	0.8	1.2	0.7	46.0	0.36	+
Pasture/hayfield	14.3	15.2	22.9	24.4	57.1	0.26	−
Crops	11.6	15.2	14.4	18.5	63.5[c]	0.0041[c]	−
Forested wetland	8.4	8.5	18.6	16.2	55.6	0.12	+
Emergent wetland	2.4	3.8	11.9	9.3	50.8	0.35	+
Unusable	1.2	1.1	0.9	1.0	27.5	0.54	−
Open water	2.1	2.1	0.9	1.3	52.4	0.48	−
Human density	3.6	5.9	1.6	4.3	57.1	0.057	−
Deer density	4.6	4.5	3.7	3.7	20.6	0.73	−
Road density	0.6	0.6	0.4	0.5	59.6	0.0096[c]	−

[a] *Variables and units detailed in Methods section. Key:* D, *percentage of pairs that differ in the same direction, +, positive correlation, −, negative correlation.*
[b] *Rationale detailed in Introduction.*
[c] *Retained for use in next stage of analysis (farms).*

Maps of Risk

Our first statewide map estimated risk for every township in Wisconsin and Minnesota, assuming wolves could occupy any township (Fig. 2). Within our known sample of 504 affected and unaffected townships, Fig. 2 identified 2 (0.4%) as red, 60 (11.9%) as orange, 348 (69.0%) as yellow, 70 (13.9%) as green, and 24 (4.8%) as blue (Fig. 2). This approached a normal distribution, as expected. The remaining 3836 townships in Fig. 2 consisted of 129 (3.4%) red, 752 (19.6%) orange, 1578 (41.1%) yellow, 785 (20.5%) green, and 592 (15.4%) blue. Wisconsin appeared to face higher relative risk than Minnesota because Wisconsin contained 296 of 1809 (16.4%) townships classified as blue or green (lowest risk), whereas Minnesota contained 1175 out of 2531 (46.4%) such townships (Fig. 2). The reverse held among the orange and red classes (32.8% of Wisconsin townships compared to 13.8% for Minnesota).

Red and orange townships were concentrated around the southern borders of the 1998 wolf population range for Minnesota but were particularly dense in southwestern Wisconsin and parts of central and eastern Wisconsin (Fig. 2). Conversely, green and blue townships within the 1998 wolf population spanned northern Minnesota and portions of northern Wisconsin (Fig. 2).

When we incorporated road density to exclude some townships from likely wolf occupation, overall risk of predation on livestock dropped precipitously (Fig. 3). Across both states, 62.2% of townships faced the lowest risk level (blue), 9.2% were classified as green, 24.4% as yellow, 3.8% as orange, and 0.3% as red. In Fig. 3, the two states faced similar predicted levels of risk of wolf predation on livestock, in contrast to findings from Fig. 2. Wisconsin contained 0.3% red, 4.0% orange, 25.2% yellow, 6.5% green, and 63.7% blue townships. Minnesota's values were 0%, 3.7%, 23.9%, 11.2%, and 61.2% respectively. Only 11 townships were red, and all were located in Wisconsin.

Discussion

Wolf attacks on livestock in Wisconsin and Minnesota were not randomly distributed in space. Rather, wolves preyed on livestock in townships sharing a consistent set of landscape features across both states, despite dramatic differences in the two states' wolf population sizes, wolf control policies, and farm sizes. More than 70% of the affected townships displayed a mixture of human-modified habitats (approximately 25%) and unmodified habitats (approximately 75%) with a slightly higher density of deer. This confirms the costs of conserving large carnivores amidst mosaics of human-modified and natural vegetation.

Pasture area was strongly and positively correlated with risk to livestock, probably because it is a proxy for cattle densities. Perhaps wolves select areas with many head of livestock (Mech et al. 2000). Alternately, deer prefer a

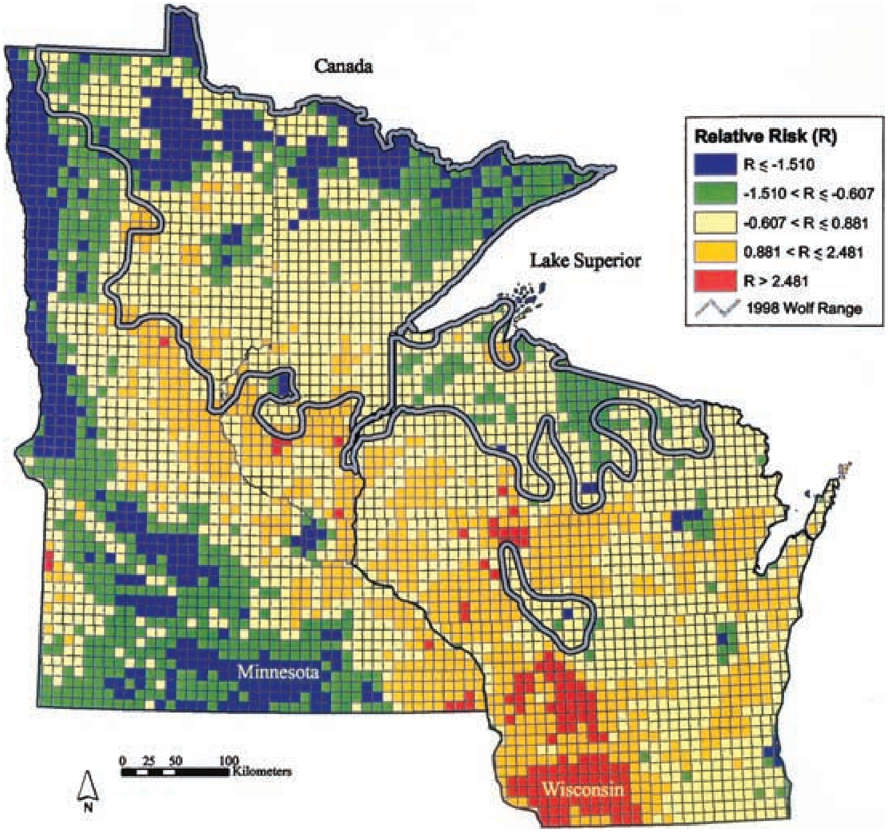

Figure 2. Relative risk of wolf predation on livestock across Wisconsin and Minnesota, assuming continuous statewide distribution of wolves. Relative risk was estimated from Eq. 3 such that risk values >2 SD above the mean of our sample of 252 affected townships were coded as highest risk (red), those >1 SD above the sample mean were coded medium-high risk (orange), those within ±1 SD of the sample mean were coded as medium risk (yellow), those >1 SD below the mean were coded as low risk (green), those >2 SD below the sample mean were coded as lowest risk (blue), and those townships with <0.1% pasture were coded as lowest risk regardless of their other landscape attributes. Other features are identical to those of Fig. 1.

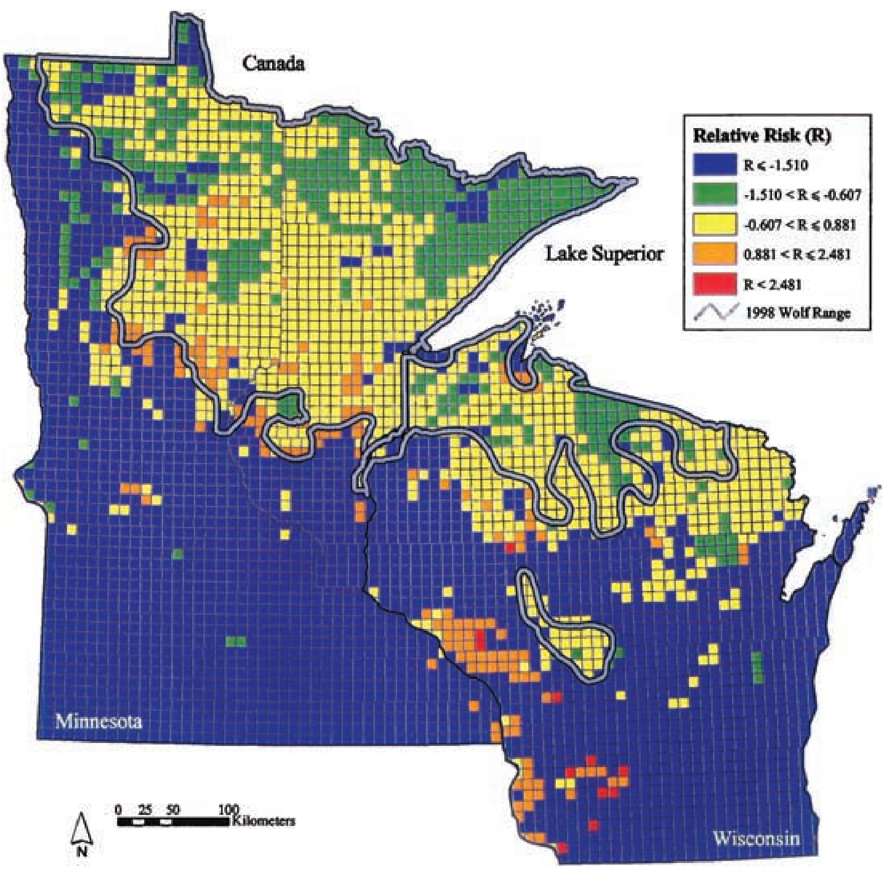

Figure 3. Relative risk of wolf predation on livestock, assuming wolves only occupy territories with a road density of <0.88 km/km^2 Any township with a road density of >0.88 was assigned the lowest risk class (blue), whereas all other townships retained the same colors as in Fig. 2.

mixture of forests and pastures (Mladenoff et al. 1997), so that wolves following the deer encounter cattle incidentally. This is consistent with our finding that affected townships had high densities of deer, but it runs counter to studies that link wild prey shortages to wolf predation on livestock (Mech et al. 1988*a*; Meriggi & Lovari 1996). A study in France found that lynx predation on sheep was associated with higher densities of wild prey (Stahl & Vandel 2001). We could not assess either causal explanation because we lacked township data on cattle and deer densities. Moreover, the Landsat images could not resolve pasture from hayfield. The roles of pasture and deer in wolf predation deserve further scrutiny.

Coniferous forest, herbaceous wetland, and open water were all associated with lower risk for livestock across matched townships, but open water and coniferous forest were associated with higher risk across matched farms. Positive associations at one scale and negative at another may reflect reality if, for example, wolves alter their behavior from travel to a more deliberate search for prey as they approach farms. We place less confidence in our farm analyses, however, because of the smaller sample size ($n = 63$) and inconsistency between the two states. Road density, crop lands, and herd size appeared predictive for both states, but a larger sample will be needed to determine if other variables are truly influential. Road density also deserves further attention because farms near many roads faced substantially lower risk, but township road density was not predictive. The inconsistent role of road density may reflect its variable association with pastures: road density and pasture were correlated more strongly among townships ($r = 0.56$) than among farms ($r = 0.34$).

Testing conjectures about the causal mechanisms underlying the observed associations in this study will require behavioral and experimental data. Nonetheless, we believe that our correlations are sufficient to guide interventions by wildlife managers, livestock producers, and other stakeholders.

Mapping Risk

Our two maps serve complementary purposes. They can be viewed as alternative scenarios. The first map can be used to anticipate problems if any given township is occupied by wolves (Fig. 2). This map is free of assumptions about where wolves will be found. Thus, Fig. 2 can help policymakers define zones of relative risk within and beyond the current wolf population range. By contrast, the second map (Fig. 3) offers a more immediate estimate of the relative risk of wolf predation on livestock by limiting attention to those areas likely to contain wolves (Wydeven et al. 2001). It can be used to anticipate sites of conflict and to focus outreach, deterrence, and mitigation efforts on the subset of higher-risk townships (approximately 25% of the total).

Each map has a weakness. Figure 2 depicts risk as widespread and likely to grow in extent in the near future. It is not useful for assessing the current extent of the problem or for planning management effort. By contrast, Fig. 3 can be used to put the problem of wolf predation on livestock in statewide or regional perspective in the near future because it closely matches the observed wolf population range. But Fig. 3 is hampered somewhat by its dependence on road density; this can generate a false sense of confidence about a given area. For example, Fig. 3 classified a number of townships in northwestern Minnesota on the edge but outside the 1998 wolf population range as lowest risk (blue). Yet Fig. 1 showed that verified incidents occurred in these townships in the past, whereas Fig. 2 correctly identified this region as green or yellow. Errors in Fig. 3 may indicate that road density is not a perfect predictor of where wolves will travel and perhaps encounter livestock but rather of where wolves have established territories (Wydeven et al. 2001). Attacks on livestock are known to occur during extraterritorial movements (Fritts et al. 1985; Treves et al. 2002), and some areas with high road density do not experience high levels of traffic. If wolves will someday establish territories in areas of higher road density—as several researchers have predicted (Mech et al. 1988*b*; Berg & Benson 1999)—then Fig. 2 will supersede Fig. 3 in utility. In this way, our two maps are complementary, and neither one should be used in isolation from the other.

Together, our maps of risk suggest that further spread of wolves in either state will result in a substantial increase in livestock losses because many red, orange, and yellow (higher-risk) townships lie adjacent to currently occupied wolf territories (Fig. 2). On the other hand, if wolves continue to establish territories as they have for the past 25 years (Wydeven et al. 2001), we predict that the same townships will face recurrent predation on livestock (Fig. 3). The main areas where wolves will establish new territories and prey on livestock will be in northeastern and perhaps southwestern Wisconsin. The risk to livestock in these areas will be high (Fig. 3). Furthermore, townships thus far free of wolf predation on livestock may not remain so. For example, no livestock have fallen prey to wolves in the southernmost extent of the 1998 wolf population range (central Wisconsin; Fig. 1). Yet this area faces the same level of risk as affected townships in our sample (mainly yellow). Livestock in this area may therefore be at risk. Such risk could be minimized by proactive interventions such as the use of guard animals, improved fencing, and aversive-stimulus deterrents.

As a check on our results, maps can be compared with the historical distribution of wolf predation on livestock (Fig. 1). Expanses of blue and green townships in Fig. 2 occur where there were few or no verified cases of wolf predation on livestock. This result of Fig. 2 is not circular because the townships in question played no part in the calculation of Eq. 3. Furthermore, 10 affected townships lay outside the 1998 wolf population range (Fig. 1). All but one fell within neighborhoods of townships classified as yellow, orange, or red, suggesting that dispersing wolves or those expanding beyond the known range continued to target livestock in the same way as the main, resident population.

Neither map can reliably predict the frequencies of livestock loss because we did not distinguish multiple incidents within townships from single events. For example, in 2000 Wisconsin had eight verified attacks on livestock, whereas Minnesota had 95 verified incidents (Paul 2000; Treves et al. 2002). This ratio of 1:11.9 was much closer to a ratio derived from their populations (1:10.1) than to a ratio derived from the proportions of red, orange, and yellow townships in each state (1:1.3). However, spatial distribution of risk is important when staff and resources are allocated to control operations.

Broader Implications

Currently, wolf policymakers define zones in which all wolves should be removed based on coarse-resolution assessments of agricultural activities and human population densities (WDNR 1999*a*; MDNR 2001). Policymakers can use maps such as ours to define more precise management zones (Haight et al. 1998). For example, public hunts of wolves might be directed to areas with high expected rates of conflict to limit the severity of conflict and maintain the state wolf population at politically acceptable and established levels. Indemnification programs and incentive schemes could be designed more precisely across broad regions with spatial information such as that provided in Fig. 3. Locally, wildlife managers, researchers, and farmers could use our spatial models to tailor research and interventions according to local conditions. Farmers may want to weigh the costs and benefits of raising livestock on forested pastures, explore the use of nonlethal deterrents (Meadows & Knowlton 2000; Musiani & Visalberghi 2000), and evaluate land purchases or set-asides in light of our results about farm vulnerability. For managers, outreach and extension efforts should focus on those communities living in moderate- to high-risk zones, diverting precious time and resources away from the majority low-risk townships. High-priced interventions may prove cost-effective when targeted to only the riskiest sites (Angst 2001; Bangs & Shivik 2001). Likewise, efforts to monitor and study wolves can benefit from spatial models that include habitat and human land-use information.

Our methods can easily be modified for other wildlife species or ecosystems if spatially explicit data on sites of conflict are available. By combining field measurements, census data, and remote-sensing data with a matched-pair design, we optimized the trade-off between spatial precision and regional scope. By selecting two scales of analysis that reflect decision-making, we expect that our results can be applied directly by managers, policymakers, and livestock producers. In addition to predicting where carnivores will attack livestock, researchers and wildlife managers can use similar techniques to map the locations of human-wildlife encounters such as those leading to crop loss (Naughton-Treves et al. 2000) or human-caused mortality of endangered species. Anticipating the sites of human-wildlife conflict is important to preventing conflict, garnering support for conservation agendas, and planning multiple-use areas in rural settings.

Acknowledgments

The authors thank R. Willging and W. Paul of U.S. Department of Agriculture Wildlife Services for data on locations of wolf attacks. A.T. and L.N.T. were supported by funding from the Wildlife Conservation Society, the Center for Applied Biodiversity Science–Conservation International, Environmental Defense, and the University of Wisconsin–Madison. We are grateful to the farmers who permitted us to interview them and survey their properties. L. D. Mech and T. J. Meier generously provided access to data for Minnesota farms. P. Benson, L. D. Mech, and D. Wilcove provided helpful comments on the manuscript. M. Clayton provided crucial advice on statistical methods.

Literature Cited

Albert, D. M., and R. T. Bowyer. 1991. Factors related to grizzly bear-human interaction in Denali National Park. Wildlife Society Bulletin **19:**339–349.

Angst, C. 2001. Electric fencing of fallow deer enclosures in Switzerland: a predator-proof method. Carnivore Damage Prevention News **3:** 8–9.

Aune, K. E. 1991. Increasing mountain lion populations and human-mountain lion interactions in Montana. Pages 86–94 in C. E. Braun, editor. Mountain lion–human interaction symposium and workshop. Colorado Division of Wildlife, Denver.

Bangs, E., and J. Shivik. 2001. Managing wolf conflict with livestock in the northwestern United States. Carnivore Damage Prevention News **3:**2–5.

Beier, P. 1991. Cougar attacks on humans in the United States and Canada. Wildlife Society Bulletin **19:**403–412.

Berg, W., and S. Benson. 1999. Updated wolf population estimation for Minnesota 1997–1999. Minnesota Department of Natural Resources, Grand Rapids.

Ciucci, P., and L. Boitani. 1998. Wolf and dog depredation on livestock in central Italy. Wildlife Society Bulletin **26:**504–514.

Fox, C. H. 2001. Taxpayers say "no" to killing predators. Animal Issues **32:**1–2.

Fritts, S. H., W. J. Paul, and L. D. Mech. 1985. Can relocated wolves survive? Wildlife Society Bulletin **13:**459–463.

Fritts, S. H., W. J. Paul, L. D. Mech, and D. P. Scott. 1992. Trends and management of wolf-livestock conflicts in Minnesota. Resource publication 181. U.S. Fish and Wildlife Service, Washington, D.C.

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.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology **10:**1068–1081.

Haight, R. G., D. J. Mladenoff, and A. P. Wydeven. 1998. Modeling disjunct gray wolf populations in semi-wild landscapes. Conservation Biology **12:**879–888.

Halfpenny, J. C., M. R. Sanders, and K. A. McGrath. 1991. Human-lion interactions in Boulder County, Colorado: past, present and future. Pages 10–16 in C. E. Braun, editor. Mountain lion-human interaction symposium and workshop. Colorado Division of Wildlife, Denver.

Jackson, P., and K. Nowell. 1996. Problems and possible solutions in management of felid predators. Journal of Wildlife Research **1:**304–314.

Jackson, R. M., G. G. Ahlborn, M. Gurung, and S. Ale. 1996. Reducing livestock depredation in the Nepalese Himalayas. Pages 241–247 in Proceedings of the Vertebrate Pest Conference **17:**241–247.

Jorgensen, C. J., R. H. Conley, R. J. Hamilton, and O. T. Sanders. 1978. Management of black bear depredation problems. Proceedings of the Eastern workshop on black bear management and research **4:**297–321.

Linnell, J. D. C., J. Odden, M. E. Smith, R. Aanes, and J. E. Swenson. 1999. Large carnivores that kill livestock: do "problem individuals" really exist? Wildlife Society Bulletin **27:**698–705.

Meadows, L. E., and F. F. Knowlton. 2000. Efficacy of guard llamas to reduce canine predation on domestic sheep. Wildlife Society Bulletin **28:**614–622.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf 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., S. H. Fritts, and W. J. Paul. 1988*a*. Relationship between winter severity and wolf depredations on domestic animals in Minnesota. Wildlife Society Bulletin **16:**269–272.

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

Mech, L. D., E. K. Harper, T. J. Meier, and W. J. Paul. 2000. Assessing factors that may predispose Minnesota farms to wolf depredations on cattle. Wildlife Society Bulletin **28:**623–629.

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.

Merrill, S. B., and L. D. Mech. 2000. Details of extensive movements by Minnesota wolves (*Canis lupus*). American Midland Naturalist **144:**428–433.

Minnesota Department of Natural Resources. 2001. Minnesota wolf plan. MDNR, Division of Wildlife, and the Minnesota Department of Agriculture. Available at http://www.timberwolfinformation.org/info/archieve/newspapers/miplan.pdf (accessed September 2003).

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

Morrison, D. F. 1990. Multivariate statistical methods. McGraw-Hill, New York.

Musiani, M., and E. Visalberghi. 2000. Effectiveness of fladry on wolves in captivity. Wildlife Society Bulletin **29:**91–98.

Naughton-Treves, L., R. A. Rose, and A. Treves. 2000. Social and spatial dimensions of human-elephant conflict in Africa: a literature review and two case studies from Uganda and Cameroon. World Conservation Union, Gland, Switzerland.

Paul, W. 2000. Wolf depredation on livestock in Minnesota: annual update of statistics—2000. U.S. Animal and Plant Health Inspection Service, Animal Damage Control, Grand Rapids, Minnesota.

Robel, R. J., A. D. Dayton, F. R. Henderson, R. L. Meduna, and C. W. Spaeth. 1981. Relationship between husbandry methods and sheep losses to canine predators. Journal of Wildlife Management **45:**894–911.

Sacks, B. N., K. M. Blejwas, and M. M. Jaeger. 1999. Relative vulnerability of coyotes to removal methods on a northern California ranch. Journal of Wildlife Management **63:**939–949.

Sargeant, G. A., D. H. Johnson, and W. E. Berg. 1998. Interpreting carnivore scent station surveys. Journal of Wildlife Management **62:**1235–1245.

Stahl, P., and J. M. Vandel. 2001. Factors influencing lynx depredation on sheep in France: problem individuals and habitat. Carnivore Damage Prevention News **4:**6–8.

Thiel, R. R. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. American Midland Naturalist **113:**404–407.

Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomasina. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin **22:**61–68.

Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. Wildlife Society Bulletin **24:**457–460.

Treves, A., R. R. Jurewicz, L. Naughton-Treves, R. A. Rose, R. C. Willging, and A. P. Wydeven. 2002. Wolf depredation on domestic animals: control and compensation in Wisconsin, 1976–2000. Wildlife Society Bulletin **30:**231–241.

Treves, A., R. Woodroffe, and S. Thirgood. 2004. Evaluation of lethal control for the reduction of human-wildlife conflict. In S. Thirgood, R. Woodroffe, and A. Rabinowitz, editors. People and wildlife, conflict or coexistence? Cambridge University Press, Cambridge, United Kingdom.

Tully, R. J. 1991. Results, 1991 questionnaire on damage to livestock by mountain lion. Pages 68–74 in C. E. Braun, editor. Mountain lion–human interaction symposium and workshop. Colorado Division of Wildlife, Denver.

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

U.S. Census Bureau. 1992. TIGER/line files. U.S. Census Bureau, Washington, D.C.

U.S. Department of Agriculture (USDA). 1997. Census of agriculture. USDA, Washington, D.C.

Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie, and N. van Driel. 2001. Completion of the 1990s National Land Cover Data Set for the coterminous United States from Landsat thematic mapper data and ancillary data sources. Photogrammetric Engineering & Remote Sensing **67:**650–652.

Willging, R., and A. P. Wydeven. 1997. Cooperative wolf depredation management in Wisconsin. Pages 46–51 in C. D. Lee and S. E. Hygnstron, editors. Thirteenth great plains wildlife damage control workshop proceedings. Kansas State University Agricultural Experiment Station and Cooperative Extension Service, Lincoln, Nebraska.

Wisconsin Department of Natural Resources (WDNR). 1999*a*. Wisconsin management plan. WDNR, Madison.

Wisconsin Department of Natural Resources (WDNR). 1999*b*. Wisconsin's deer management program. WDNR, Madison.

Wydeven, A. P., R. N. Schultz, and R. P. Thiel. 1995. Monitoring a recovering gray wolf population in Wisconsin, 1979–1995. 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 Circumpolar Institute, Edmonton, Alberta.

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., J. E. Wiedenhoeft, R. N. Schultz, R. P. Thiel, S. R. Boles, and B. E. Kohn. 2002. Progress report of wolf population monitoring in Wisconsin for the period October 2001–March 2002. Wisconsin Department of Natural Resources, Park Falls.

Young, S. P., and E. A. Goldman. 1944. The wolves of North America. Dover, New York.