Wolf depredation on domestic animals in Wisconsin, 1976–2000

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Abstract As wolves (*Canis lupus*) recolonize mixed forest and agriculture areas in the Lake Superior region of the United States, their depredations on livestock are increasing, along with public complaints and compensation payments. We documented 176 complaints about wolves in Wisconsin between 1976 and 2000 and analyzed the regional and temporal patterns for the 87 verified incidents involving the injury or death of 377 domestic animals. Calves were the most frequent target of wolf depredation, but game-farm deer losses demanded higher compensation payments. Sixty-six property owners were affected by wolf depredations over the 25-year period examined. Compensation costs averaged \$96.00 per capita of wolf/year. Two thirds of 71 breeding wolf packs were never suspected of causing depredations, but 4 packs were involved in ≥4 incidents. These data were collated to aid in preventing wolf depredation and provide a foundation for policy-making surrounding the impending federal delisting of the wolf.

Key words Canis lupus, compensation, dogs, human-carnivore conflict, livestock

In the wake of changing public opinion, habitat recovery, and legal protections, wolves (Canis *lupus*) and other large carnivores are recovering in many areas of North America and Europe (Mansfield 1991, Wydeven et al. 1995, Breitenmoser 1998). When recovering populations of carnivores range beyond public lands and recolonize agricultural regions, managers must develop effective strategies to reduce conflicts with local residents. Wolves present such challenges because they adapt to many human land uses (Blanco et al. 1992, Fuller et al. 1992, Thiel et al. 1998). Conflict arises when wolves hunt domestic animals or threaten humans (Meriggi and Lovari 1996, Rajpurohit 1998, Bangs and Shivik 2001). Wildlife managers have traditionally been reactive in controlling these conflicts by trapping or poisoning wolves near depredation sites, a strategy that often forces the state to pay

compensation and outreach costs in addition to the costs of control operations. A pre-emptive strategy might be more effective, but the development of predictive models is a prerequisite.

In Wisconsin, USA, over the past 25 years, wolves have recolonized mixed forest-agriculture habitats and now number approximately 250 animals. Human-wolf conflict has resurfaced as a result. State authorities have monitored wolf population recovery systematically, while recording complaints about wolves from the public. Combining these 2 data sets should improve our understanding of human-wolf conflict in a recovering wolf population. Here we describe all wolf complaints reported to the Wisconsin branch of the Wildlife Services Division of the United States Department of Agriculture's Animal and Plant Health Inspection Service (USDA-WS) and the Wisconsin Department of

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Aerial photo of wolf pack.

Natural Resources (WDNR) from 1976-2000. Our intent was to document the prey, timing, and geographic distribution of depredation incidents by wolves in Wisconsin along with control and compensation efforts by state and federal agencies. These data will aid managers in tracking long-term changes in human-wolf conflict, may help to predict future depredations in Wisconsin, and may help carnivore managers beyond Wisconsin to design control and compensation plans.

Study area

As many as 3,000 to 5,000 wolves once may have inhabited Wisconsin (Wydeven et al. 1995). Between 1865 and 1957, a bounty intensified human persecution of wolves so that no wolves remained by 1960 (Thiel 1993, WDNR 1999). In 1967, the wolf was listed as a federally endangered species by the United States Fish and Wildlife Service, and by 1975 wolves from Minnesota had begun to recolonize Wisconsin (Thiel 1993, WDNR 1999). Annually since 1979, WDNR biologists have determined population size, number of packs, and distribution. These data are collected through a combination of radiotracking, summer howl surveys, winter track surveys, and various population indices (Wydeven et al. 1995, Wydeven and Wiedenhoeft 2000). Identification of wolf packs was possible from long-term population monitoring. Between 1980 and 2000, from 3 to 66 breeding wolf packs occupied Wisconsin. By the winter of 1999-2000, 252±5 wolves were distributed as 13 loners and in 66 packs, with an average pack size of 3.7 animals before pup production (Wydeven et al. 1995, Wydeven and Wiedenhoeft 2000). They inhabited 20 northern and central counties at an average density of 1 wolf/38 km². The occupied region was characterized by deciduous and evergreen forests (79% of land area interspersed with lakes and wetlands) or agricultural areas (21%). Wolf packs defend territories averaging 136 km², primarily on public and private

forested land (Wydeven et al. 1995). Nearly all areas occupied by Wisconsin's wolves had road densities <0.45 km/km², no urban areas, and little agricultural land (Mladenoff et al. 1995, 1997).

Wolves come into conflict with Wisconsin residents in several ways. On one hand, 52% of all wolf mortality was caused by shooting, illegal trapping, and vehicle collision between 1979 and 1998 (n=63 known deaths, WDNR 1999). On the other hand, wolves prey on and injure livestock and dogs. Although no human injuries have been attributed to wild wolves in Wisconsin, some citizens report feeling threatened. The WDNR began paying compensation for losses in 1982.

Central and northern Wisconsin has an average human population density of 28 individuals/km² (United States Bureau of the Census 1991) and



Anesthetized wolf with radiotracking collar.

average cattle density of 12.8 head/km² (United States Department of Agriculture [USDA] 1999) on farms averaging 91 ha (compared to statewide average of 228 ha; USDA 1999, Wisconsin Agricultural Statistics Service [WASS] 2000). In winter, large livestock (e.g., beef cattle, horses, sheep) are generally kept in or near farm buildings, whereas in warmer months they are released onto pastures that are often partially wooded (L. Naughton-Treves, University of Wisconsin-Madison, unpublished data). No livestock grazing occurs on public lands. Typically, parturition and nursing occur in outdoor pastures and beef cattle remain outdoors at night. Smaller stock (e.g., poultry, sheep, pigs) are typically kept in pens near houses.

Methods

Complaints about Wisconsin's wolves for the period 1976-2000 were compiled from federal and state records. Before 1990, WDNR field staff investigated complaints of domestic animal losses (bison [Bison bison], cattle, chickens, dogs [Canis familiaris], farm deer, horses, sheep, and turkeys) that had been telephoned in to regional WDNR offices. After 1990, Wisconsin wolf management and its control were divided in a cooperative agreement between the WDNR and USDA-WS (Willging and Wydeven 1997). After that time, complainants directly telephoned USDA-WS. The WDNR assumed responsibility for compensating complainants and relocating live-captured wolves. USDA-WS assumed responsibility for investigating complaints of depredation and for live capture of depredating wolves (Willging and Wydeven 1997). USDA-WS also advised landowners on abatement practices. In collaboration with livestock producers, the WDNR and USDA-WS disseminated information about wolf depredation and how to report complaints (WDNR 2000).

Field investigations typically followed complaints within 48 hours. Field investigators diagnosed wolf depredation by examining indirect evidence (Bjorge and Gunson 1985, Acorn and Dorrance 1990) including marks on carcasses (e.g., gnawed ribs, canine punctures on rump or throat, subcutaneous hemorrhage), tracks (e.g., size, shape, carcass dragging), and scats (e.g., size, consistency, shape), as well as occasional direct observation of canids near the site. The WDNR staff used these field reports together with radiotelemetry information on the local presence of wolves to decide on compensation. We report WDNR final judgments here, using 4 categories: C=confirmed wolf (assigned when physical evidence was consistent with wolf attack; occasionally, visual sightings of wolves or live-trapping resolved uncertainty about indirect evidence), P=probable wolf (assigned when indirect evidence was consistent with wolves and when prior complaints had been confirmed), NW= not wolf (assigned when loss was attributable to an animal or cause other than wolves), and UNC= unconfirmed (assigned when insufficient evidence was available to determine the cause of death or injury). For the purpose of statistical analyses, we pooled C and P judgments as verified incidents. With 2 exceptions, only C or P cases received compensation.

Compensation payments were initially based on the immediate market value of the lost property, often as calculated by USDA-WS. By 1992, negotiations with livestock producers led state authorities to increase compensation payments to match the eventual autumn market value, even for livestock lost in early spring. The WDNR determined compensation for hunting-dog losses based on recommendations by USDA-WS. The latter considered the dog's breed, age, pedigree, and experience, as well as information about the dog's value provided by the owner and sometimes testimonials from other hunters familiar with the dog's ability.

The cost and time invested in control operations are detailed from USDA-WS records. Estimates of costs per captured wolf should be interpreted carefully, because such calculations fail to account for the benefits of averting future depredations or ameliorating human animosity toward wolves. Furthermore, live capture of problem wolves can be relatively costly because it is immediately initiated to resolve a complaint without regard for field conditions. As a result, trapping efficiency for problem wolves should not be compared to that seen under other conditions. This also partly explains the wide variation in time and financial expenditure among control operations.

We compared our data to those of neighboring Minnesota, the source population for Wisconsin (Thiel 1993), where an extensive database on wolf depredations on livestock is available (Fritts et al. 1992). Minnesota's database describes depredations on domestic animals in detail, but underestimates depredations on dogs (Fritts and Paul 1989). Accordingly, we referred to livestock (domestic animals excluding dogs) when making these comparisons.

Statistical methods

In our analyses, we treated each property owner's complaint as a single incident, regardless of number of domestic animals affected. Complaints about separate incidents on the same property were thus treated as independent incidents. Sample sizes varied as information was occasionally missing from older records. All tests were twotailed. We accepted $P \le 0.05$ as significant. Comparison of slopes was based on a paired *t*-test using standardized values of the response variables. We based tests of correlation on Spearman rank analyses, but calculated slopes of regression using simple linear models. We used nonparametric tests corrected for ties when assumptions of constant variance were not met or when n < 40.

Results

Between 1976 and 2000, the WDNR and USDA-WS received 176 complaints about domestic animal losses from 141 property owners. Of these complaints, 87 (49.4 %) incidents were verified as wolfrelated (i.e., judged C or P), with 52 incidents on livestock and 35 on dogs, affecting 66 property owners. Considering verified incidents only, 52 of the 66 (78.8 %) affected property owners faced only 1 incident, whereas the most frequently hit site faced 7 incidents. For the 14 owners who faced \geq 2 incidents, 8 reported these in different years and 6 in the same year. Considering only verified livestock losses, 19 of 32 property owners (59.4 %) faced only 1 incident. These 32 affected livestock producers represented approximately 0.4 % of the 7,424 full-time producers in the 19 Wisconsin counties with verified wolf incidents and data on livestock production (calculated by averaging 1992 and 1997 census data, WASS 1997).

Property owners blamed wolves for the deaths or disappearances of 575 domestic animals, as well as 37 injuries and 19 cases of harassment. Of these, 59.8% were verified to be wolf depredations (Table 1). This represented <0.1% of the standing cattle in 2000 among the 17 counties providing livestock data that also contained resident breeding wolf packs (WASS 2000). Indeed, this was an overestimate of the impact because the population of all livestock was far greater than that of cattle alone, but data were not available on other types of livestock.

The most common pattern (mode) was loss of a single calf with no repeat. Although most incidents

Table 1. Domestic animal losses from verified wolf depredation in Wisconsin, 1976-2000.

	Type of loss		
Animal	Killed	Injured	Age
Cattle	84	4	All calves <1 year old
Chickens	48		Various
Dogs	29	15	Average 5.0 yrs $(n = 24)$
Farm deer	20		Various
Sheep	12		Various
Turkeys	165		Various
Total	358	19	

involved cattle, more than half of the animals suffering verified depredation (56.50 %) were poultry (chickens and turkeys) preyed upon in 5 incidents. There were 35 verified incidents resulting in death or injury to dogs. Only 2 game-farm deer operations had verified wolf incidents (0.4% of Wisconsin's 486 registered deer farms; A.Wydeven, WDNR, unpublished data). In both cases, depredations on farm deer occurred within fenced enclosures of 275 ha and 335 ha, respectively.

Of Wisconsin's remaining complaints, 49 (27.8 %) were judged unrelated to wolves (NW) and 40 were judged unconfirmed (UNC, 22.7 %). Other predators were suspected in 43 NW incidents (coyotes [*Canis latrans*] 42%; free-roaming dogs or wolf-dog hybrids [*C. lupus x C. familiaris*] 34%; bears [*Ursus americanus*] 8%; fishers [*Martes pennanti*] 2%), while 6 were judged unrelated to predators (e.g., lightning, birth complication, self-inflicted wounds).

Temporal patterns

On average, 9.4 complaints were filed each year (SD=10.0, range 0-34), with the most in 1998. Verified incidents increased at the same rate as other complaints (Figure 1). Most of the 176 complaints (87.5 %) were filed between 1991 and 2000, a period of rapid growth in the Wisconsin wolf population (Figure 2). The number of verified incidents of wolf depredation (r=0.90, Z=4.03, P<0.001) and the annual compensation paid (r=0.88, Z=3.95, P< 0.001) also increased over time. The slope describing annual increase in verified incidents (slope= 0.09) was slightly less steep than the slope describing annual increase in wolf population size (slope= 0.13), but this difference was not significant (t_{20} = 0.35, P=0.50). Sixty-seven of 87 (77.0 %) verified wolf incidents fell between March and September,



Figure 1. Complaints about wolf depredations in Wisconsin 1976–2000: verified incidents (closed circles: y=-1,186.15 + 0.60x) and unconfirmed or nonwolf complaints (open squares; y=-1,037.17 + 0.52x).

with peaks in May and August, which corresponded to calving season and hunting-dog training season on public lands, respectively (Figure 3).

Geographic patterns

Most verified incidents of wolf depredation occurred in the northwestern portion of the state, reflecting the history of colonization from Minnesota eastward and southward (Thiel 1993, Wydeven et al. 1995). Property owners in 27 counties filed complaints about wolves (range 1–41), but only 19 counties had verified wolf depredations (range 1–19). One county (Pine) in Minnesota had verified depredations by Wisconsin's wolves. Of the 20 counties containing breeding packs of wolves as of the 1999-2000 winter count (Wydeven and Wiedenhoeft 2000), 5 had no verified incident. Four counties had no known breeding packs



Figure 2. Number of verified incidents of wolf depredation and population size of wolves in Wisconsin, 1980–2000.



Figure 3. Monthly distribution of verified incidents of wolf depredation in Wisconsin, 1976–2000. The bars are split by the type of domestic animal preyed upon.

of wolves, yet had verified depredations (range 1-4).

Publicity about wolf depredations may promote fraudulent claims for compensation (Bjorge and Gunson 1985; Gipson et al. 1998; Kaczensky 2000); on the other hand, depredations by different carnivores are often difficult to distinguish. We found that number of verified incidents across all 27 counties was correlated positively with number of unconfirmed (UNC) and nonwolf (NW) incidents (r=0.46, Z=2.36, P=0.018). Unconfirmed losses were correlated more strongly with verified wolf incidents (r=0.53, Z=2.71, P=0.007) than were those judged to be nonwolf losses (r=0.36, Z=1.82, P=0.069).

Identifying depredating wolves

Based on tracks, scat, and bite marks, the minimum number of wolves involved in verified depredations averaged 1.7 (median=2, n=35). In 55 of 87 (61.8 %) verified incidents, the WDNR attributed depredation to an identified wolf pack. Twentythree different wolf packs were deemed responsible for these 55 incidents (Figure 4). Between 1990 and 2000, 15 wolf packs preyed on dogs and 14 packs preyed on livestock (including game-farm deer); 6 of the former preyed on both dogs and livestock. No single pack was deemed responsible for more than 5.5 depredations (responsibility was shared if 2 packs were equally likely to have caused the depredation). Of the 71 breeding wolf packs identified between 1990 and 2000, 48 (67.6 %) caused no known depredations. On the other



Figure 4. Distribution of verified incidents of wolf depredation among the 71 identified wolf packs in Wisconsin, 1976–2000.

hand, two-thirds of those packs that preyed on dogs did so ≥ 2 times.

Of the remaining 32 verified incidents, no known wolf pack could be deemed responsible because the depredations occurred outside known ranges and far from recent radio locations (A. Wydeven, WDNR, unpublished data). These incidents were tentatively attributed to loners and dispersing wolves. Wolf-dog hybrids may have been involved in as many as one-fifth of the latter cases, although compensation was paid nonetheless.

Compensation and control

Between 1982 and 2000, WDNR paid \$150,485.75 to property owners (Table 2). Gamefarm deer losses required the greatest total and percapita compensation, followed by hunting dogs. The greatest compensation for a single property owner was \$48,000, paid in 1999 for game-farm deer losses. The maximum paid in 1 year was \$67,374, in 1999. Compensation took an average of

Table 2. Compensation paid (\$) for verified depredations in Wisconsin, 1976-2000.

	Compensation paid		
Animal	Total	Average	
Cattle	33,633.57	410.17	
Chickens	245.00	5.10	
Dogs	46,472.18	1,191.59	
Farm deer	68,250.00	3,412.50	
Sheep	584.00	53.09	
Turkeys	1,301.00	7.88	
Total	150,485.75		

80 days (n=43, SD=52, range=18-292) between filing a complaint and posting the compensation check. The annual cost of recent (1991-2000) compensation per wolf ranged from \$6-329, with a 10year average of \$96 (calculated as annual cost per annual wolf *N*; Mech 1998).

Between 1991 and 2000, 11 wolf control operations were conducted by USDA-WS and WDNR on four properties, resulting in the live capture of 11 wolves (0-5 wolves captured in each operation). USDA-WS control operations required 304 days of trapping (n = 10 operations, average = 30.4 days, range = 11-93) or 1195.25 hours on the property (average = 119.5 hours, range = 42-442). Control operations cost \$24,950 (average = \$2,495, range = \$884-8,141). Also, control operations against wolfdog hybrids were run on 4 occasions. Seven hybrids were captured and either euthanized or placed in captivity.

All 11 captured wolves (F 5 adults and 1 yearling, body mass range=29.5-38.6 kg; M 3 adults and 2 yearlings, body mass range 31.8-40.9 kg) appeared to be healthy at the time of live trapping. Nevertheless, 2 of the original 11 wolves did not survive capture; one was euthanized at the capture site and the other died from capture-related stress. Seven of the 9 survivors were translocated outside their original territories (average = 186 km, range = 74-275km), whereas the remainder were released near the capture site (4.8 km and 6.4 km) because they were lactating females. None of the 9 relocated wolves were known to cause subsequent depredations, yet relocated wolves had low survival (67% mortality). Five of the 9 (44%) relocated wolves died (illegal shooting n=2, vehicle collision n=2, recapture stress n=1) within 176 days (range = 13-516 days) of capture. Three relocated wolves continue to be monitored. The telemetry signal for the ninth wolf was lost after 1 day.

Discussion

Wisconsin's wolves were judged responsible for 377 deaths, disappearances, and injuries of domestic animals between 1976 and 2000. Most of these depredations occurred in the last decade. If the observed trends continue, Wisconsin will contain 350 wolves by 2005 and experience 24–31 verified incidents of wolf depredation annually (resulting in 104–134 animals dead, injured, or missing). Considering both compensation and control, the state should expect to pay \$44,250 to \$61,250 in each of

the next 5 years. These figures do not include costs of field investigation of all complaints. Furthermore, lifting the federal protection of wolves may lead to more frequent demands for trapping. This would further elevate costs.

Comparison with neighboring Minnesota

Wisconsin now stands at a stage of human-wolf conflict similar to Minnesota's between 1980 and 1982, based on the absolute number of complaints and verified losses (see Figure 3b in Fritts et al. 1992). Even today, the 2 states share broad similarities in patterns of human-wolf conflict. Wolves preyed on cattle and turkeys most frequently in both states. Also, field investigators attributed a similar proportion of incidents of depredation to covotes rather than wolves (Wisconsin 13%, n=132) vs. Minnesota 15%, n=600; Fritts et al. 1992). In both states, verified wolf depredations peaked in May, June, and July. This mirrors patterns in other regions with wolves and other large carnivores (e.g., Dorrance 1982, Aune 1991, Halfpenny et al. 1991, Ciucci and Boitani 1998).

Although peaks of wolf depredation coincide in Minnesota and Wisconsin, overall distributions differed somewhat. In Minnesota, 83% of verified wolf incidents on livestock occurred between May and September (Fritts et al. 1992), whereas only 61% of Wisconsin's fell in this season. These data suggest that Wisconsin's livestock are vulnerable for a longer period. This may affect the probability of repeat incidents. Verified incidents were slightly more likely to recur in Wisconsin (41% of livestock owners faced repeated incidents) than in Minnesota (26.9% calculated from Fritts et al. 1992). On the other hand, lethal control operations in Minnesota may have limited repeat incidents. This subject certainly deserves further study.

The greatest difference between patterns of wolf depredation in Wisconsin and Minnesota involved domestic dogs. In Wisconsin, verified incidents involving dogs comprised 40.2% of the sample, whereas Fritts & Paul (1989) report only 4.8%. However, these authors suspect under-reporting of dog depredations because Minnesota did not compensate for dog losses at the time. Furthermore, these authors treated sets of depredations on dogs in the same community over a short time period as single incidents, thereby lowering the apparent frequency of dog losses (Fritts and Paul 1989). Context also appears important. For example, in Minnesota 1979-1987, most of the verified wolf depredations on dogs occurred within sight of their owners' houses, whereas Wisconsin owners most often reported losses while hunting with dogs (32 of 35 verified incidents). Wisconsin permits training of hunting dogs on public forested land during summer and use of dogs to hunt bears, bobcats (*Lynx rufus*), and coyotes in certain regions of the state. Hunting dogs range far from their owners, often through several miles of forest, all of which may increase their vulnerability to wolf depredation. Minnesota is more restrictive of hunting-dog use.

Identifying depredating wolves

Because of Wisconsin's dedicated investment in wolf population monitoring, managers can sometimes attribute depredations to particular wolf packs with confidence. These data provide some insight into the behavioral decisions that lead a carnivore into conflict with humans. Several incidents involving long-established breeding packs suggest that depredations are not caused mainly by desperate animals or those in unfamiliar habitat (loners or dispersers). Capture data suggest that depredations were caused by healthy animals of either sex, not those injured or infirm. The Wisconsin data also show that most packs do not prey on domestic animals, whereas those that do are equally likely to repeat as not to repeat. Therefore, the Wisconsin data conform to and supplement other studies that found male and female wolves in good health causing livestock depredation at equal rates (Fritts et al. 1992, Linnell et al. 1999). Studies using radiocollared livestock and radiocollared wolves found that habitat use, age, and health of killed livestock were critical to their vulnerability (Bangs and Shivik 2001). Wolves and livestock often traveled within a few hundred meters without conflict. In short, not all conditions promote depredations. Elucidating the predisposing factors may aid in prevention and will depend on further behavioral studies of wolves and livestock.

Wolves, like most other canids, are coursing predators that rely on speed and stamina more than on surprise when hunting (Fanshawe and Fitzgibbon 1993, Fitzgibbon and Lazarus 1995). When pursuing wild ungulates in open habitats, coursing predators often approach in plain sight and observe prey movements, searching for individuals that are slow to escape. Thus, they often kill the young, old, or infirm. This supports the recommendation that young, infirm, or periparturient livestock should not be pastured far from human habitations when wolves range nearby (e.g., Bjorge and Gunson 1983). Conversely, prey that cooperate in defense or stand their ground are harder for coursing predators to kill (e.g., Holekamp et al. 1997). Therefore, prey that form defensive rings or move in a coordinated fashion to protect young may suffer fewer successful attacks. Researchers should investigate whether defensive behavior (e.g., escape, aggregation, mobbing, or counter-attack) can be manipulated within existing breeds, or whether wolf depredations can be prevented by introducing exotic breeds as guards (e.g., llamas [Lama glama] [Cavalcanti and Knowlton 1998, Meadows and Knowlton 2000] or guard dogs [Coppinger et al. 1988]).

Management recommendations

Additional funds for reimbursement of depredations and more flexible control of problem wolves will be necessary as the Wisconsin wolf population continues to grow. Mech (1998) suggested that Minnesota had allowed its wolf population (estimated at 2,450 in winter of 1998 [Berg and Benson 1999] to reach a size that exceeded financial, practical, and humanitarian tolerance. Although Wisconsin can not support as many wolves as Minnesota (Mladenoff et al. 1997), it already pays compensation at similar rates. Expressed as cost/wolf in the state, Wisconsin pays an average of \$96/wolf compared to Minnesota's average of \$110/wolf (this study, Mech 1998). Therefore, addressing human-wolf conflict deserves the high priority it currently receives from Wisconsin state officials. However, rising costs signal the need for more flexibility in wolf control.

Federal reclassification of the wolf to threatened, or its removal from the list of endangered species, will increase calls for lethal control. If practical and effective prevention is not found, Wisconsin's managers may have to kill a limited number of depredating wolves once strict criteria for verifying depredations have been met. The best application of lethal control would be to kill only those wolves that cause significant depredations, while protecting those that cause none. Identifying the perpetrators of depredation is difficult, and different stakeholders will urge different levels of retaliation. Nevertheless, the long-term success of wolf conservation in an agricultural region like north-central Wisconsin depends on selecting wolves that coexist peacefully with humans and their domestic animals. Given political and ecological challenges to the application of lethal control (Mech 1995, Haber 1996, Knowlton et al. 1999), a simple solution to carnivore depredations will be elusive (Breitenmoser 1998; Bangs and Shivik 2001; Karanth and Madhusudan, in press). Rather than finding one solution to fit all, each state or province must balance cost-effectiveness with its own public's dynamic perceptions of wildlife (e.g., Mansfield 1991, Manfredo et al. 1998, Mech 1998). Hence, the clearest recommendation for Wisconsin is to continue the existing policy that integrates compensation with prudent application of various forms of control. The existing management plan has public support and a stable funding base (WDNR 1999).

Continued monitoring of wolf populations is to understanding and essential resolving human-wolf conflict. Managers must base decisions about control operations and compensation on scientific information about wolf packs. For this, managers need up-to-date information on wolf pack dynamics and individual wolf ranging. These data are collected through a combination of radiotracking, summer howl surveys, winter track surveys, and various population indices (Wydeven et al. 1995, Wydeven and Wiedenhoeft 2000). Radiotelemetry is the most effective way to monitor wolf populations (Mech 1974, Fuller and Snow 1988), so as many animals as possible should be monitored in areas where human-wolf conflict is likely. In 2000, fewer than half of the 66 wolf packs contained radiocollared individuals (Wydeven and Wiedenhoeft 2000); therefore most wolves in the state were being monitored by less precise methods (e.g., snow tracking and howl surveys).

Legislation and regulation also may improve wolf management in 3 areas: funding for depredation control, strict regulation of wolf-dog hybrids, and liability for farm-deer losses and hunting-dog losses. Delisting will reduce or eliminate federal financial contributions to wolf management at the same time that greater flexibility in control methods is available. Therefore, state legislators must adequately fund control and compensation programs or reduce liability for expensive nonlivestock such as game-farm deer or hunting dogs on public land. Breeding and release of wolf-dog hybrids into the wild should be strictly regulated because of depredation problems and human safety concerns (WDNR 1999). Regulations that require predatorproof fencing on commercial deer farms may reduce incidence of wolf predation on farmed deer

and limit the compensation costs for which the state is held liable. Wildlife agencies should be free to refuse compensation for deer-farm losses that result from inadequate fencing. Such a change would affect only a small proportion of producers but would limit compensation costs substantially (Table 2). Compensating owners for depredations on dogs running free on public land may encourage a practice that has negative ecological consequences (Bowers 1953); instituting a voluntary insurance program for such activities may defray the costs.

Additional research also may assist in mitigating depredation. At a large scale, research that identifies which packs are "sources" crucial to population viability versus those that are "sinks" would help to guide control operations, and research that predicts regions of greater-than-expected conflict would help to concentrate resources. At a finer scale, researchers can help to explore husbandry practices and nonlethal controls that reduce vulnerability of livestock to wolves, predict where problem wolves or wolf packs will emerge, generate field tools for the forensic discrimination of depredating wolves from uninvolved wolves, and measure human tolerance for wolves and for conflict-mitigation policies.

Worldwide, wolf recovery is associated with conflict over domestic animals. Management of this conflict is critical to long-term viability of these carnivore populations, lest affected human populations begin a fresh cycle of persecution and extirpation. Managers must strive for interventions that promote self-sustaining populations of wolves without threats to human safety or significant loss of private property. Wisconsin's management of wolves exemplifies a balanced and cautious approach to a small population of wolves recolonizing a mixed forest-agriculture landscape.

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Literature cited

- ACORN, R., AND M. J. DORRANCE. 1990. Methods of investigating predation of livestock. Alberta Agriculture, Edmonton, Canada.
- 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, 24-26 April, 1991. Colorado Division of Wildlife, Denver, USA.
- BANGS, E., AND J. SHIVIK. 2001. Managing wolf conflict with livestock in the northwestern United States. Carnivore Damage Prevention News 3: 2-5.
- BERG, W., AND S. BENSON. 1999. Updated wolf population estimation for Minnesota 1997-1999. Minnesota Department of Natural Resources, Grand Rapids, USA.
- BJORGE, R. R., AND J. R. GUNSON. 1983. Wolf predation of cattle on the Simonette River pastures in northwestern Alberta. Pages 106-111 *in* L. N. Carbyn, editor. Wolves in Canada and Alaska, Canadian Wildlife Service Report Series 45, Edmonton, Alberta, Canada.
- BJORGE, R. R., AND J. R. GUNSON. 1985. Evaluation of wolf control to reduce cattle predation in Alberta. Journal of Range Management 38:483-486.
- BLANCO, J. C., S. REIG, AND L. CUESTA. 1992. Distribution, status and conservation problems of the wolf *Canis lupus* in Spain. Biological Conservation 60:73-80.
- BOWERS, R. R. 1953. The free-running dog menace. Virginia Wildlife 14:5-7.
- BREITENMOSER, U. 1998. Large predators in the Alps: The fall and rise of man's competitors. Biological Conservation 83: 279–289.
- CAVALCANTI, S. M. C., AND F. F. KNOWLTON. 1998. Evaluation of physical and behavioural traits of llamas associated with aggressiveness toward sheep-threatening canids. Applied Animal Behaviour Science 61:143-158.
- CIUCCI, P., AND L. BOITANI. 1998. Wolf and dog depredation on livestock in central Italy. Wildlife Society Bulletin 26: 504-514.
- COPPINGER, R., L. COPPINGER, G. LANGELOH, L. GETTLER, AND J. LORENZ. 1988. A decade of use of livestock guarding dogs. Proceedings of the Vertebrate Pest Conference 13: 209-214.
- DORRANCE, M. J. 1982. Predation losses of cattle in Alberta. Journal of Range Management 35:690-692.
- FANSHAWE, J. H., AND C. D. FITZGIBBON. 1993. Factors influencing the hunting success of an African wild dog pack. Animal Behaviour 45:479-490.
- FITZGIBBON, C. D., AND J. LAZARUS. 1995. Antipredator behavior of Serengeti ungulates: individual differences and population consequences. Pages 274–296 *in* A. R. E. Sinclair, and P. Arcese, editors. Serengeti II: Dynamics, management and conservation of an ecosystem. University of Chicago, Illinois, USA.
- FRITTS, S. H., AND W. J. PAUL. 1989. Interactions of wolves and dogs in Minnesota. Wildlife Society Bulletin 17:121-123.
- FRITTS, S. H., W. J. PAUL, L. D. MECH, AND D. P. SCOTT. 1992. Trends

and management of wolf-livestock conflicts in Minnesota. United States Fish and Wildlife Service, Resource Publication 181, Washington, D.C., USA.

- FULLER, T. K., W. E. BERG, G. L. RADDE, M. S. LENARZ, AND G. B. JOSE-LYN. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Society Bulletin 20: 42-55.
- FULLER, T. K., AND W. J. SNOW. 1988. Estimating wolf densities from radio telemetry data. Wildlife Society Bulletin 16:367-370.
- GIPSON, P. S., W. B. BALARD, AND R. M. NOWAK. 1998. Famous North American wolves and the reliability of early wildlife literature. Wildlife Society Bulletin 26:808–816.
- HABER, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology 10: 1068-1081.
- 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, 24–26 April 1991, Colorado Division of Wildlife, Denver, USA.
- HOLEKAMP, K. E., L. SMALE, R. BERG, AND S. M. COOPER. 1997. Hunting rates and hunting success in the spotted hyena (*Crocuat crocuta*). Journal of Zoology (London) 242:1-15.
- KACZENSKY, P. 2000. Co-existence of brown bears and men in Slovenia. Dissertation. University of Munich.
- KARANTH, U., AND M. D. MADHUSUDAN. In Press. Mitigating humanwildlife conflicts in southern Asia. Pages 000–000 *in* J. Terborgh, L. C. Davenport and C. P. van Schaik, editors. Making parks work: identifying key factors to implementing parks in the tropics. Island, Covelo, California, USA.
- KNOWLTON, F. F., E. M. GESE, AND M. M. JAEGER. 1999. Coyote depredation control: An interface between biology and management. Journal of Range Management 52: 398-412.
- LINNELL, J. D. C., J. ODDEN, M. E. SMITH, R. AANES, AND J. E. SWEN-SON. 1999. Large carnivores that kill livestock: do "problem individuals" really exist? Wildlife Society Bulletin 27: 698-705.
- MANFREDO, M. J., H. C. ZINN, L. SIKOROWSKI, AND J. JONES. 1998. Public acceptance of mountain lion management: a case study of Denver, Colorado, and nearby foothill areas. Wildlife Society Bulletin 26:964-970.
- MANSFIELD, T. M. 1991. Mountain lion damage to property in California. Pages 75-78 in C. E. Braun, editor. Mountain lionhuman interaction symposium and workshop, 24-26 April 1991, Colorado Division of Wildlife, Denver, USA.
- 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. 1974. Current techniques in the study of elusive wilderness carnivores. Proceedings of the 11th International Conference of Game Biology 11:315-322.
- 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.
- 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., T. A. SICKLEY, R. G. HAIGHT, AND A. P. WUDEVEN. 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., R. G. HAIGHT, T. A. SICKLEY, AND A. P. WYDEVEN. 1997. Causes and implications of species restoration in altered ecosystems. BioScience 47:21-31.
- RAJPUROHIT, K. S. 1998. Child lifting wolves in Hazaribagh, India. Ambio 28:163-166.
- THIEL, R. P. 1993. The timber wolf in Wisconsin: the death and life of a majestic predator. University of Wisconsin, Madison, USA.
- THIEL, R. P., S. MERRILL, AND L. D. MECH. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. The Canadian Field-Naturalist 112:340-342.
- UNITED STATES BUREAU OF THE CENSUS. 1991. Census of Population and Housing 1990: summary tape file 1,Wisconsin. Prepared by the Bureau of the Census,Washington, D.C., USA.
- UNITED STATES DEPARTMENT OF AGRICULTURE. 1999. National Agricultural Statistics Service, 1997 Census of Agriculture AC97-A-49, Volume 1, Geographic Area Series Part 49, Wisconsin State and County Data. Washington, D.C., USA.
- WISCONSIN AGRICULTURAL STATISTICS SERVICE. 2000. Wisconsin Agricultural Statistics Service. Online at http://www.nass usda.gov./wi/. Accessed 2 January 2002.
- WISCONSIN DEPARTMENT OF NATURAL RESOURCES. 1999. Wisconsin wolf management plan. Wisconsin Department of Natural Resources, publication ER-099-99. Madison, USA.
- WISCONSIN DEPARTMENT OF NATURAL RESOURCES. 2000. Wolves in farm country in Wisconsin. Wisconsin Department of Natural Resources, USDA-Wildlife Services, and the Wisconsin Cattlemen's Association, publication ER-103-00. Madison, Wisconsin, USA.
- 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, 16–19 April 1997, Lincoln, Nebraska, USA.
- WYDEVEN, A., AND J. E. WIEDENHOEFT. 2000. Gray wolf population 1999-2000. Wisconsin Wildlife Surveys 10: 130-137.
- 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, Canada.

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