Computer simulation of wolf-removal strategies for animal damage control

Robert G. Haight, Laurel E. Travis, Kevin Nimerfro, and L. David Mech

Abstract Because of the sustained growth of the gray wolf (*Canis lupus*) population in the western Great Lakes region of the United States, management agencies are anticipating gray wolf removal from the federal endangered species list and are proposing strategies for wolf management. Strategies are needed that would balance public demand for wolf conservation with demand for protection against wolf depredation on livestock, poultry, and pets. We used a stochastic, spatially structured, individually based simulation model of a hypothetical wolf population, representing a small subset of the western Great Lakes wolves, to predict the relative performance of 3 wolf-removal strategies. Those strategies included reactive management (wolf removal occurred in summer after depredation), preventive management (wolves removed in winter from territories with occasional depredation), and population-size management (wolves removed annually in winter from all territories near farms). Performance measures included number of depredating packs and wolves removed, cost, and population size after 20 years. We evaluated various scenarios about immigration, trapping success, and likelihood of packs engaging in depredation. Four robust results emerged from the simulations: 1) each strategy reduced depredation by at least 40% compared with no action, 2) preventive and population-size management removed fewer wolves than reactive management because wolves were removed in winter before pups were born, 3) population-size management was least expensive because repeated annual removal kept most territories near farms free of wolves, and 4) none of the strategies threatened wolf populations unless they were isolated because wolf removal took place near farms and not in wild areas. For isolated populations, reactive management alone ensured conservation and reduced depredation. Such results can assist decision makers in managing gray wolves in the western Great Lakes states.

Key words animal damage, *Canis lupus*, control, endangered species, model, recovery, simulation, wolf

As a result of human tolerance, reintroduction, and natural repopulation, gray wolves (*Canis lupus*) have now recolonized parts of Europe and the United States (Promberger and Schroeder 1993, Fritts and Carbyn 1995, Mech 1995). As wolf populations increase and expand their ranges, local decision makers must choose management strategies that balance competing demands for wolf protection and animal damage control (Mech 2001). Wolf management planners in the western Great Lakes states (i.e., Mich., Minn., Wis.) face these conflicting demands. Since the gray wolf received legal protection in 1974, the Minnesota population grew from <1,000 wolves to 2,450 wolves in 1997–1998 and expanded its range from <40,000 km^2 in the northeast to 90,000 km^2 in the northern and central parts of the state (Fuller et al. 1992, Berg and Benson 1999). Wolves recolonized Wisconsin and upper Michigan in the late 1970s, and populations in each state exceeded 200 wolves in 2000 (United

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States Fish and Wildlife Service [USFWS] 2000). As a result, in 1999 wolf numbers and distribution exceeded the goals identified in the recovery plan for the western Great Lakes population (USFWS 2000). In addition, each state adopted a wolf management plan with the primary goal of ensuring the long-term survival of the wolf (Michigan Department of Natural Resources [MDNR] 1997,2001;Wisconsin Department of Natural Resources [WDNR] 1999). In July 2000 the USFWS proposed that the gray wolf be reclassified from endangered to threatened throughout the western Great Lakes region and considered proposing its removal from the federal list of endangered and threatened species (USFWS 2001*a*). Such delisting would give most legal responsibility for wolf management to state and tribal authorities.

Concurrent with increasing wolf numbers in the western Great Lakes states, wolf range expanded into areas with farms and wolf depredations on livestock, poultry, and pets increased. For example, annual cases of depredation increased from 29 farms in Minnesota in the 1980s to 71 farms in the 1990s (Michigan Department of Natural Resources 1997; Minnesota Department of Natural Resources [MDNR] 2001; Wisconsin Department of Natural Resources [WDNR] 1999). To address wolf depredation, the Minnesota and Wisconsin management plans proposed detailed animal damage control programs that added to or enhanced current federal regulations (WDNR 1999, MDNR 2001). Each program divided the state into management zones and defined wolf-control guidelines that depended on habitat and the potential for conflicts with humans.

The relative performances of prescriptions alternative to Minnesota's current animal damage control program (Mech 1998) have not been evaluated. As a result, here we compare 3 types of wolf-removal strategies. Reactive management (wolves removed in summer from farms immediately after depredation occurs) and preventive management (wolves removed in winter from farms in which depredation had occurred at least once in the previous 5 years) are similar to the depredation control measures proposed in management plans, whereas population-size management (wolves removed in winter from all territories surrounding farms, regardless of depredation activity) operates at the population level. We analyzed these removal strategies, applied alone and in combination, using a stochastic, spatially structured, and individually based simulation model of a hypothetical wolf population composed of up to 64 packs in a region with farm and wild areas. Simulations compared removal strategies in terms of occurrence of depredation, wolves removed, population size, and costs. Simulations also included sensitivity analyses with respect to assumptions about wolf immigration, trapping success, and probability that packs become prone to depredation.

Methods

Considerations for model design

Wolves live in packs and defend exclusive territories (Mech 1973). Generally, packs are family groups, with 1 dominant breeding pair and their offspring (Mech 1970). In the western Great Lakes region, midwinter pack size averages 4–8 wolves, with about half being pups (Fuller 1989). Because of territoriality, population density and reproductive rate depend on number and size of territories. Wolves depend on prey availability and can live wherever large herbivores are present, provided humans can tolerate them (Fuller 1995, Mech 1995). Population turnover rates are naturally high, with 6 pups born per pack (Mech 1970) and more than half of pack members lost each year to mortality and dispersal (Mech 1977, Fritts and Mech 1981, Fuller 1989, Gese and Mech 1991). A dispersing wolf might pair with the opposite sex and colonize a vacant territory, or join another pack and replace a missing breeding member (Rothman and Mech 1979, Fritts and Mech 1981, Fuller 1989). Wolf populations are characterized by discrete but interacting packs. In the western Great Lakes region, midwinter pack territories average 150–180 km^2 (Fuller et al. 1992, Wydeven et al. 1995).

Formulation of the wolf simulation model

We designed a stochastic, demographic model of a wolf population consisting of 64 pack territories living in a large, semi-wild landscape with abundant, well-distributed prey. The model was spatially structured (Beissinger and Westphal 1998) because the population was subdivided into packs, which were located in either wild or farm range; however, the model was not spatially explicit because territory shapes and locations were not included. The model was individually based because demographic events were computed 1 wolf at a time. The model was a variant of one developed by Haight and Mech (1997).

Our model simulated mortality, dispersal, and birth of wolves in each pack using estimates

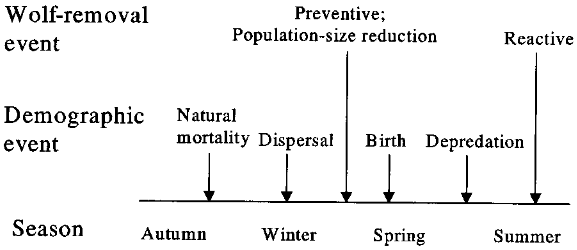

Figure 1. Annual sequence of wolf-removal and demographic events in the wolf-removal model used to evaluate 4 hypothetical removal strategies.

obtained in Minnesota (Fuller 1989) and Wisconsin (Wydeven et al. 1995). State variables for each pack included number of wolves of each sex in 3 age classes: pup (0–12 months), yearling (12–24 months), and adult (>24 months). Individuals of the last 2 age classes could belong to 2 categories: nonbreeding and breeding. The model allowed 1 breeding pair per pack (Mech 1970). Packs in farm territories could have 2 states: a tendency for depredation or not, based on wolf behavior in farm territories (Fritts and Mech 1981). The model assumed an annual probability of 20% that packs with no history of depredation in farm territories initiated this activity.

The annual cycle of events (Figure 1) began in autumn, and all modeled mortality occurred in winter. Whether each wolf died was a Bernoulli random variable with probability depending on wolf age. Mortality rates were 65% and 32% for pups and older animals, respectively (Fuller 1989, Wydeven et al. 1995).

Modeled dispersal occurred in late winter, with probability = 1.0 if the breeding pair died. Otherwise, whether each wolf dispersed was a Bernoulli random variable with probability depending on wolf age: pups (25%), yearlings (50%), and nonbreeding adults (90%; Gese and Mech 1991). Breeders had no probability of dispersal. The model assumed 20% long-distance dispersals, with those wolves being lost from the population. The model annually included 5 immigrants that joined the dispersers.

Each disperser searched the area for a suitable territory (i.e., a vacant one or one with an available mate). The model assumed that each dispersing wolf randomly explored 6 territories (Lande 1987, Lamberson et al. 1994). Unsuccessful dispersers died. The probability of finding a suitable territory was as follows:

$$\text{Prob (success)} = 1 - \left[1 - \frac{\text{(no. suitable territories)}}{\text{(total no. territories)}}\right]^6 .$$

Successful dispersers were assigned to the most suitable territory among the 6 they explored, suitability depending on depredation history. Dispersers coming from packs without tendencies for depredation were assumed to prefer territories with available mates to empty territories without preference for territories in wild or farm areas. The model assumed dispersers originating from packs with a tendency for depredation to select first for territories with available mates and second for territories in farm range.

Breeding pairs produced their pups in spring, and we modeled litter size using a discrete probability distribution, with a mean of 6.5 pups and a range of 0–10 pups (Fuller 1989). The sex of each pup was determined with equal probabilities. When only one member of the breeding pair occupied a territory, it held its territory without reproducing (Smith et al. 1997). The age distribution of each pack was updated after birth.

The propensity for depredation of packs near farms was updated following reproduction. All packs with a history of depredation were assumed to maintain that tendency. Each pack with no history of depredation could switch to a tendency for depredation in one of two ways: if a dispersing wolf with a tendency for depredation joined the pack, or if proximity to farms induced depredation (P = 0.20).

Removal strategies

We modeled wolf-removal strategies over a 20-year horizon, assuming 32 farm territories and 32 wild territories. The initial autumn population had 320 wolves in 32 packs, where each pack had 6 pups, 2 yearlings, and 1 breeding pair of adults. Sixteen packs inhabited farm territories, half of them having tendencies for depredation.

We simulated 3 types of wolf removal: preventive (P), reactive (R), and population-size (S) management. We also evaluated 2 mixed strategies: preventive and reactive management (P–R) and population-size and reactive management (S–R). In addition to these 5 active management strategies, we considered a sixth strategy of no action (N).

We assumed that each removal strategy used trapping or snaring, methods that were not 100%

effective. Simulations assumed capture probabilities of 60% for pups and yearlings and 30% for adults. Trapping stopped when the fate of every wolf in targeted territories had been determined.

The model included two kinds of density dependence. There was partial compensation between natural and human causes of mortality because those two types of mortality events were applied at different points in time. In addition, the fate of dispersers depended on the rate of territory occupancy (i.e., population density).

Analysis of management strategies

We evaluated removal strategies over a 20-year horizon based on livestock loss, wolf removal, and sustainability of the strategies. We ran simulations 1,000 times and computed each performance measure for the final year of the 20-year horizon. Livestock loss from wolf depredation was estimated by counting farm territories in June that were occupied by packs with a tendency for depredation. We determined sustainability of management strategies using mean population size and probability that population size decreased to <100 wolves.

The cost of each removal strategy was also computed for the final year of the 20-year horizon (1998 United States dollars) and included compensation payments for animals lost to wolf depredation and costs of trapping and removing wolves. We assumed that each wolf pack involved in depredation affected 3 farms, which represented $1,680 (assuming compensation averaged $550 per farm; Mech 1998). We also assumed that the cost of trapping and removing each wolf under reactive management was $1,500, based on data collected in Minnesota (Mech 1998). For preventive and population-size management, we used an administrative removal cost of $500 per wolf because such removal imposed fewer restrictions on the location and timing of wolf removal.

Sensitivity analysis

We analyzed the impacts of one-at-a-time changes in selected model parameters. To determine the impacts of changing the immigration rate, we evaluated removal strategies with 0 and 20 immigrants per year. To determine the impacts of increasing trapping success, we increased capture probabilities to 80% for pups and yearlings, and 60% for adults. Finally, we evaluated the removal strategies under 1% and 40% annual probabilities of wolves becoming prone to depredation.

Results

Single strategies

The 3 removal strategies reduced mean depredation by at least 40% compared with the no-action strategy (Table 1). With no action, the populations doubled from 320 wolves in 32 packs (year 0) to an average of 661 wolves in 64 packs (year 20), with depredation occurring in 30 of the 32 farm territories. Preventive and reactive strategies reduced the number of farm territories with depredation to 15–17 packs. Depredation decreased because each strategy removed wolves in territories overlapping farms. As a result, 40–50% of the territories near farms were either free of wolves or included wolves that did not have a tendency for depredation. The population-size strategy reduced depredation to an average of 10 packs because it had fewer restrictions on wolf removal and therefore fewer wolves lived near farms.

Preventive and population-size strategies removed 70–80% fewer wolves than the reactive

Table 1. Mean performance (n = 1,000) in year 20 of hypothetical wolf-removal strategies with the following base-case assumptions: 5 immigrants per year, 60% capture probability for pups and yearlings and 30% for adults, and 20% annual probability of wolves in a farm territory becoming prone to depredation. Standard errors are in parentheses.

	Strategy[a]					
Performance measure	N	P	R	S	P–R	S–R
Packs active in depredation	30 (0.04)	15 (0.11)	17 (0.10)	10 (0.12)	9 (0.09)	5 (0.08)
Wolves removed	0 (0.00)	21 (0.21)	80 (0.58)	17 (0.22)	38 (0.44)	20 (0.34)
Population size	661 (0.98)	382 (1.84)	463 (1.53)	271 (2.41)	357 (1.90)	216 (2.13)
Probability population size<100	0.00	0.00	0.00	0.02 (0.004)	0.00	0.04 (0.006)
Compensation cost ($ thousand)	50.4	25.2	28.6	16.8	15.1	8.4
Removal cost ($ thousand)	0.0	10.5	120.0	8.5	45.0	19.0
Total cost ($ thousand)	50.4	35.7	148.6	25.4	60.1	27.4

[a] Management strategies: N = no action, P = preventive, R = reactive, S = population size reduction.

strategy (Table 1) because removal occurred in winter before birth (Figure 1). On average, about 1 wolf per pack was captured and removed. Because the reactive strategy took place in summer after pups were born, >4 wolves were removed per pack on average, most of which were pups and yearlings.

None of the 3 strategies, applied alone, threatened to extirpate the wolf populations because wolf removal was limited to packs near farms, and the majority of packs lived in the wild area and totaled >100 wolves (Table 1). The population-size strategy reduced the number of wolves in farm territories from 160 in year 0 to an average of 73 in year 20 with annual removal rates of 20-25% of the population in farm territories. Those removal rates were lower than sustainable harvest levels estimated for free-ranging populations (30-50%; Mech 1970, Gasaway et al. 1983, Peterson et al. 1984, Ballard et al. 1987, Larivière et al. 2000).

Combined strategies

Combining preventive or population-size management with reactive management doubled the trapping effort on packs with tendencies for depredation, resulting in <10 packs with such tendencies after 20 years (Table 1). Under such scenarios, >70% of farm territories were either free of wolves or included wolves without tendencies for depredation. Combined strategies reduced wolf removals by 50-75% in year 20 compared with reactive management alone because there were fewer packs with tendencies for depredation. Combined strategies also increased turnover in territories near farms, resulting in smaller packs. Combined strategies did not threaten to extirpate populations, although they produced smaller populations than the single strategies.

Cost

In year 20 compensation payments averaged $50,400 under the no-action scenario (Table 1). The 2 single strategies in which we removed wolves in winter before birth (i.e., preventive and population-size management) reduced costs 30-50% because they resulted in fewer depredating packs and removed fewer wolves. Reactive management was the most expensive because of the large number of wolves removed and the high unit cost of wolf removal.

The 2 combined strategies had different impacts on costs relative to no action (Table 1). Population-size reduction combined with reactive removal reduced costs 46%, while the combination of preventive and reactive removals increased costs 19%. Population-size reduction resulted in fewer wolves in farm territories, thereby reducing the number of high-cost reactive removals.

Standard errors

Number of depredating packs, wolves removed, and population size were averages of outcomes in year 20 obtained from 1,000 independent simulations of the wolf model. With 1,000 replications, standard errors were <2% of the means (Table 1). The estimator for the probability that population size was <100 wolves was the proportion of simulations with populations <100 wolves in year 20. With 1,000 simulations, standard errors of estimated probabilities between 0.20 and 0.80 were 0.012-0.016. Standard errors of estimated probabilities between 0.01 and 0.20 were 0.003-0.012. While we could not compute a standard error for cases in which the estimated probability was 0.00, we can say that if the probability were really >0.01, it would be very unlikely (less than one chance in 10,000) we would observe no instances of these events in 1,000 simulations. Standard errors of the means obtained in the sensitivity analyses were of the same magnitude, so we did not report them.

Sensitivity analyses

The absence of immigration (Table 2) resulted in smaller wolf populations after 20 years under all removal strategies compared with population projections with 5 immigrants per year (Table 1). As a result, fewer wolves colonized territories near farms, fewer packs had tendencies for depredation, and fewer wolves were removed. Without immigration, population growth was very sensitive to the type of wolf removal, the growth rate remaining positive only with reactive removal or no action. The two strategies involving population-size management (S and S-R) resulted in populations with <100 wolves in >60% of the simulations. Without immigration, populations declined without stabilization because many wolves from wild areas dispersed to farm range and were removed before they could reproduce. The wolves remaining in the wild area were not numerous or productive enough to sustain the population.

The influx of 20 immigrants per year amplified trends observed under the scenario of 5 immigrants per year, and wolf populations were larger after 20 years under all removal strategies (Table 2). This

Table 2. Mean performance (n = 1,000) in year 20 of hypothetical wolf-removal strategies under 2 scenarios of the immigration rate; other assumptions as in the base case.

Performance measure	Strategy[a] N	P	R	S	P–R	S–R
			0 immigrants per year			
Packs active in depredation	30	11	14	3	6	1
Wolves removed	0	13	58	5	21	4
Population size	652	254	351	87	214	52
Probability population size <100	0.00	0.10	0.05	0.63	0.17	0.82
Compensation cost ($ thousand)	50.4	18.5	23.5	5.0	10.1	1.7
Removal cost ($ thousand)	0.0	6.5	87.0	2.5	25.5	4.0
Total cost ($ thousand)	50.4	25.0	110.5	7.5	35.6	5.7
			20 immigrants per year			
Packs active in depredation	30	18	18	17	11	10
Wolves removed	0	28	89	30	52	48
Population size	669	463	514	438	438	383
Probability population size <100	0.00	0.00	0.00	0.00	0.00	0.00
Compensation cost ($ thousand)	50.4	30.2	30.2	28.6	18.5	16.8
Removal cost ($ thousand)	0.0	14.0	133.5	15.0	60.0	50.0
Total cost ($ thousand)	50.4	44.2	163.7	43.6	78.5	66.8

[a] Management strategies: N = no action, P = preventive, R = reactive, S = population size reduction.

resulted in more wolves colonizing territories near farms, more packs with tendencies for depredation, and greater wolf removal. The preventive strategy produced the same results as population-size management under the high-immigration scenario because most territories in farm range contained depredating packs.

With an increase in probability of capture (Table 3), relative performance of removal strategies remained the same as in the base case (Table 1). However, increasing the capture probability resulted in fewer depredating packs and fewer wolf removals compared with projections in the base case. Repeated and effective trapping near farms kept the number of packs and the size of those packs relatively small. With fewer depredating packs and wolf removals, the projected cost of each removal strategy was lower than its counterpart with lower capture probability. Strategies involving population-size management cost 75–80% less than the no-action strategy because of lower depredation costs. Finally, increased capture probability reduced population-size projections relative to the base case, especially when wolves were removed near farms without regard for the pack's depredation history.

Increasing the annual probability of a wolf becoming prone to depredation from 20% to 40% produced only small increases in numbers of depredating packs, numbers of wolves removed, and costs. In this case the relative performance of removal strategies remained the same as in the baseline simulations, and we do not present the tabular results. However, decreasing the switching probability to 1% had a dramatic effect (Table 4). Because fewer packs switched to depredation, each removal strategy nearly eliminated the wolves with tendencies for depredation by year 20. As a result, each of the removal strategies produced <5 depredating packs and removed <20 wolves. Strategies involving preventive and reactive removal, which took wolves only in depredating packs, removed fewer wolves than strategies involving population-size management, which took

Table 3. Mean performance (n = 1,000) in year 20 of hypothetical wolf-removal strategies under 80% capture probability for pups and yearlings and 50% for adults; other assumptions as in the base case.

Performance measure	Strategy[a] N	P	R	S	P–R	S–R
Packs active in depredation	30	9	12	3	6	2
Wolves removed	0	19	76	11	33	12
Population size	661	344	474	162	340	156
Probability population size <100	0.00	0.00	0.00	0.16	0.00	0.15
Compensation cost ($ thousand)	50.4	15.1	20.1	5.0	10.1	3.4
Removal cost ($ thousand)	0.0	9.5	114.0	5.5	36.5	9.0
Total cost ($ thousand)	50.4	24.6	134.1	10.5	46.6	12.4

[a] Management strategies:N = no action, P = preventive, R = reactive, S = population size reduction.

Table 4. Mean performance (n = 1,000) in year 20 of hypothetical wolf-removal strategies under a 1% annual probability of wolves in a farm territory becoming prone to depredation; other assumptions as in the base case.

	Strategy[a]					
Performance measure	N	P	R	S	P–R	S–R
Packs active in depredation	29	4	2	2	1	1
Wolves removed	0	10	11	18	6	18
Population size	661	588	643	288	635	278
Probability population size <100	0.00	0.00	0.00	0.01	0.00	0.01
Compensation cost ($ thousand)	48.7	6.7	3.4	3.4	1.7	1.7
Removal cost ($ thousand)	0.0	5.0	16.5	9.0	7.0	10.0
Total cost ($ thousand)	48.7	11.7	19.9	12.4	8.7	11.7

a Management strategies:N = no action, P = preventive, R = reactive, S = population size reduction.

wolves from all packs near farms regardless of depredation tendency. As a result, projected population sizes under preventive and reactive removal were higher than those projected under population-size management.

Discussion

Where recovering wolf populations have expanded their range into areas near farms, wolf management goals may include maintaining wolves and reducing wolf depredation on livestock and pets (WDNR 1999, MDNR 2001, Mech 2001). Programs for reducing wolf depredation usually include prescriptions for wolf removal. Because the relative performance of removal strategies has not been evaluated, we developed a simulation model to evaluate and compare alternative prescriptions. Those prescriptions included reactive management, in which wolves were removed in summer from territories immediately after depredation occurred (similar to the existing program in Minnesota); preventive management, in which wolves were removed in winter from territories in which depredation had occurred at least once in the previous 5 years (similar to the proposed program in Minnesota); and population-size management, in which wolves were removed in winter from all territories surrounding farms regardless of current or previous depredation activity.

Four results emerged from the simulations that were largely robust to changes in assumptions about immigration, trapping success, and likelihood of packs engaging in depredation. First, by focusing wolf removal in territories near farms, each strategy substantially reduced depredation. Compared with a no-action strategy, single strategies reduced depredation by at least 40%, while combined strategies reduced depredation by at least 70%. Second, strategies that included preventive removal or population-size management removed fewer wolves than reactive management, primarily because removal occurred in winter before birth. Third, strategies that included population-size management were least expensive (in terms of compensation for lost animals and cost of wolf removal) because repeated annual application kept most of the territories around farms free of wolves. Finally, because wolf removal took place near farms and not in wild areas, none of the strategies threatened to extirpate populations unless populations were isolated (no immigration). In that case, population-size management caused a steady decline.

Although the wolf model accounted for some compensatory behavior between natural mortality and wolf removal, it likely underestimated the capacity of wolf populations to respond to exploitation. For example, the model predicted a sustainable yield of 20–25% of the wolves in farm territories under the population-size control strategy, but maximum sustainable harvest rates of 30–50% have been estimated for free-ranging populations (Mech 1970, Gasaway et al. 1983, Peterson et al. 1984, Ballard et al. 1987, Larivière et al. 2000). The model likely overestimated natural mortality, which decreases when a wolf population is harvested (Peterson et al. 1984, Ballard et al. 1987, Mech 2001). Further, the model likely underestimated the number of breeding pairs in farm territories because the rate of adult capture was too high or the likelihood of surviving adults finding mates and colonizing territories was too low. As a result, none of the removal strategies may be as effective as the model suggested. Altering the model to increase population productivity would change the magnitude of the performance measures; however, the relative performance of the management strategies probably would not be affected.

Keeping this caveat in mind, the simulation results suggested strengths and weaknesses of each removal strategy. Reactive management, which has been used for animal damage control in Minnesota since 1978, could be relatively expensive because of the high cost of targeted removal and the large numbers of wolves removed in summer after pups are born. However, because reactive management removes wolves only after depredation is confirmed in summer, more wolves can live near farms, and populations are more likely sustainable, especially when isolated.

Although our analysis included a strategy for population-size control, none of the state management plans have proposed such a strategy. Strategies involving population-size control, including public hunting or trapping seasons, will be considered after wolves are removed from the federal endangered species list. The population-size strategy we considered would be similar to implementing a public trapping season if trapping took place in winter and was limited to areas near farms. The simulation results suggested that such a strategy would be relatively inexpensive after repeated annual application because fewer wolves would live near farms and engage in depredation. However, we might have underestimated the administrative costs of public trapping, which could include law enforcement, public relations, and compensation. The simulation results suggested that population-size control in farm territories would not threaten a population that received a small number of immigrants, which are critical to the maintenance of exploited wolf populations (Fritts and Carbyn 1995, Larivière et al. 2000). Although the simulation results suggested that population-size management was not sustainable in isolated populations, it is well known that wolf populations can recover rapidly following cessation of intensive wolf removal (Fritts and Mech 1981, Peterson et al. 1984, Hayes and Harestad 2000). Furthermore, few if any wolf populations in the United States are isolated.

Preventive removal was a mild version of population-size control because wolves were removed near farms only when there had been a history of depredation. As a result, more wolves could live near farms with more chances for depredation and higher cost. On the other hand, because fewer wolves were removed, preventive removal was less likely than population-size control to threaten the sustainability of isolated populations. It should be noted that the preventive removal strategy in our model was more specific about the timing of wolf removal than the preventive strategies described in the wolf management plans, which did not specify time of year when removals could take place. Our simulations suggested that removing wolves in winter before pups are born could reduce the number of wolves removed as well as reduce depredations.

The simulation results have implications for management plans that include the use of agricultural practices to reduce or prevent depredation. In both Wisconsin and Minnesota, management plans proposed depredation prevention activities as well as wolf removal. If effective prevention activities were discovered that could reduce the likelihood that packs near farms engaged in depredation, the simulation results suggested that any one of the removal strategies would nearly eliminate wolves with tendencies for depredation. Further, strategies involving preventive and reactive removal would allow relatively large populations to live near farms without removing many wolves.

Our simulation model represented a wolf population much smaller than the wolf population in the western Great Lakes region. The landscape in the model was bounded by the assumption that it could support a maximum of 64 pack territories in a landscape including farm and wild range. This scale of analysis was consistent with a small portion of the Minnesota wolf population on the frontier of its range or the smaller populations in Wisconsin and Michigan. Therefore, the simulation results should be viewed as predictions of the relative performance of alternative wolf-removal strategies applied to a small subset of the wolves in the western Great Lakes region.

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