Wolves make roadways safer, generating large economic returns to predator conservation

Jennifer L. Raynor[a,1] , Corbett A. Grainger[b] , and Dominic P. Parker[b]

[a]Department of Economics, Wesleyan University, Middletown, CT 06459; and [b]Department of Agricultural and Applied Economics, University of Wisconsin–Madison, Madison, WI 53706

Recent studies uncover cascading ecological effects resulting from removing and reintroducing predators into a landscape, but little is known about effects on human lives and property. We quantify the effects of restoring wolf populations by evaluating their influence on deer–vehicle collisions (DVCs) in Wisconsin. We show that, for the average county, wolf entry reduced DVCs by 24%, yielding an economic benefit that is 63 times greater than the costs of verified wolf predation on livestock. Most of the reduction is due to a behavioral response of deer to wolves rather than through a deer population decline from wolf predation. This finding supports ecological research emphasizing the role of predators in creating a "landscape of fear." It suggests wolves control economic damages from overabundant deer in ways that human deer hunters cannot.

economic impact | trophic cascade | deer–vehicle collision | gray wolf (*Canis lupus*) | white-tailed deer (*Odocoileus virginianus*)

Populations of apex predators have declined across the world's landscapes over the past 200 y due to government bounty programs, hunting pressure, habitat loss, and declines in prey populations (1, 2). Ecologists are beginning to unravel the far-reaching ecological effects of these changes (1–5), but little is known about the economic effects. While many of the costs attributable to predators are salient and quantifiable, such as predation on livestock and pets, estimating and valuing the often subtle and indirect beneficial effects of predators is more difficult (6, 7).*

The recent expansion of the gray wolf (*Canis lupus*) offers a unique opportunity to concretely measure the cascading benefits of a predator whose reintroduction is controversial. Wolves once ranged over most of the Northern Hemisphere, but humans nearly eradicated the species from the continental United States and Europe by the 1960s (10). Legal protections strengthened during the latter half of the 20th century, and wolf populations returned to 10 coterminous US states and 28 European countries (11, 12). As of 2019, there are about 5,500 wolves in the United States and 11,000 in Europe. More jurisdictions, such as the state of Colorado, are proposing or already planning reintroductions (13).

Restoring wolves could benefit humans who enjoy seeing wolves in their natural habitat or who value knowing of their existence (14, 15), but in this study we focus on the potential for wolves to generate indirect benefits by controlling overabundant deer populations. Deer populations have surged in the United States, increasing from about 2 to 4 deer per km^2 in the precolonial era (16) to 15 to 50 deer per km^2 in some areas today (17). Overabundant deer populations affect ecosystems by suppressing forest regeneration, altering the composition of tree and herbaceous plant species, and contributing to the spread of invasive species (18–20). Deer also generate economic costs for humans through deer–vehicle collisions (DVCs), Lyme disease (which is transmitted through deer ticks), and damage to agriculture, timber products, and landscaping (21).

This study focuses on DVCs, which are the largest known economic cost of deer (*SI Appendix*, Table S1). About 1 million DVCs occur every year in the United States, causing 29,000 human injuries, 200 human fatalities, and nearly $10 billion in total economic losses (21, 22).† Europe experiences similar problems,

with a lower frequency of collisions with ungulates (such as deer and moose) but a higher rate of fatalities and injuries (23). The problem has worsened over time, with DVCs rapidly increasing since around 1990 (22, 23). If wolves reduce DVCs even modestly, the social and economic benefits could be sizable.

We focus on two channels through which wolves could affect DVCs. The first is changes to deer abundance. We hypothesize that larger wolf populations reduce deer abundance directly through predation (18, 24, 25), which in turn reduces DVCs (26–28). The second channel is through changes to deer behavior because wolves create a "landscape of fear" for deer (29–31). Wolves use roads, pipelines, and other linear features as travel corridors, which increases wolves' travel efficiency and the kill rate of prey near these features (32–36). We hypothesize that wolf presence affects deer movement near these features (34, 37, 38), thereby reducing collision risk for a given number of deer on the landscape. The behavioral effect is important because, through it, wolves can suppress economic damage from deer in ways seasonal human deer hunters cannot.

Significance

Measuring the economic benefits conveyed by predators is difficult—often, effects are indirect and operate through complex ecological changes. As a result, debates about the expansion of predators have pit salient costs against more speculative estimates of benefits that might be dismissed as unreliable or ideologically motivated. We quantify the indirect benefits of wolves (*Canis lupus*) to human lives and property through reductions in deer-vehicle collisions. Moreover, we decompose the effect into two components: changes in prey behavior versus prey abundance. This decomposition is important when effective policy depends on whether hunters can replicate the effects of predators. In the case of wolves, we conclude that human deer hunters cannot.

*Recent research on the cascading benefits generated by recovering sea otters provides a case in point (8, 9). As keystone species, otters provide carbon sequestration benefits via predation on fish that reduce kelp production. Because this benefit is subtle and indirect, it may not resonate with stakeholders who more readily recognize the concrete adverse effects of otters on fish populations that have commercial value.

†All dollar estimates referenced in this study are converted to 2019 US dollars using the Bureau of Labor Statistics' Consumer Price Index.

Our empirical analysis focuses on Wisconsin, where wolves began to recolonize naturally around 1975 (Fig. 1) (39). Wisconsin provides an interesting, if not ideal, case study for several reasons. Foremost, the results from Wisconsin should generalize to other settings where wolves are (or could be) allowed to spread naturally into areas of human communities rather than only into wilderness. Much of the prior research on the effects of wolves in the United States focuses on Isle Royale and Yellowstone National Parks; however, the effect of wolves in national parks "would have little relevance to most of wolf range because of overriding anthropogenic influences there on wolves, prey, vegetation, and other parts of the food web" (40). By contrast, the spread of wolves across Wisconsin was natural and unimpeded by wildlife managers. As a result, contiguous wolf range in Wisconsin spans a human-dominated landscape more than 6 times the size of Isle Royale and Yellowstone combined (41). Second, the wolf population in Wisconsin is likely close to ecological carrying capacity (42, 43), which suggests the wolf effects we measure represent a long-term steady state rather than only transitional effects. Finally, if the benefits of a reduction in DVCs outweigh the costs of wolf predation in Wisconsin, then there may be economic justification for allowing wolves to expand not just in the state but also potentially in other states that have suitable wolf habitat and high DVCs (e.g., the northeastern United States) (44). Although verified predation on livestock and pets in Wisconsin is costly (recently, about $174,000 per year, on average) (45), DVC losses are orders of magnitude larger (almost $200 million per year, based on the national average cost per DVC) (22, 46).

Results

Testing for the effects of wolves requires spatial-temporal data on DVCs, wolf presence, and deer populations. Our preferred study period begins in 1988 (the earliest available DVC data) and ends in 2010 (the last available data on detailed wolf pack locations due to subsequent wolf harvests) (*Materials and Methods*). As we explain below, the findings are similar when we include years after 2010.

Motivating Visualizations. Two differential trends across counties where wolves eventually colonized (wolf counties) and counties where wolves never colonized (nonwolf counties) support our hypotheses regarding wolf effects on DVCs (Fig. 2 *A–D*). First, deer population trends began to diverge in the 1990s, with the populations growing in nonwolf counties and stabilizing in wolf counties. This pattern suggests wolves may be suppressing the trend toward deer overabundance. Second, DVCs were stable in wolf counties but grew in nonwolf counties. By contrast, vehicle collisions not caused by deer (non-DVCs) declined at similar rates in areas with or without wolves, suggesting the proportion

of vehicle collisions involving deer grew faster in nonwolf counties.

To further motivate the potential effect of wolves, we examine the share of vehicle collisions involving deer before and after wolf entry in each county (Fig. 2 *E* and *F*). Wolves entered 29 counties by 2010. To visualize the effect of wolf entry, we normalize the year when wolves were first recorded as time $t = 0$ for each county. We exclude three counties for which wolves exit and re-enter at some point during the study period to avoid assumptions about which entry year(s) should be set to $t = 0$. Then, we plot the proportion of collisions attributable to deer during each of the 10 y before and after wolf entry (Fig. 2*E*). The plot reveals a sharp decline in DVC shares that begins in $t = −1$. Although this is 1 y earlier than expected, the plot is consistent with evidence that dispersing wolves traveling outside heavily forested areas are not immediately detected by the state management agency (43). Analysis of these data demonstrates that, on average, collisions attributable to deer dropped significantly after wolf arrival ($t \geq 0$), relative to years before arrival ($t < 0$) (Fig. 2*F*). The decline in DVC shares stabilized about 5 y after reintroduction, which is suggestive evidence that deer behavior eventually adapts to wolf presence.

Net Effect. To quantify the effects of wolves on DVCs, we apply panel data econometric techniques with 63 counties (29 wolf counties and 34 nonwolf counties) and 22 y (1988 to 2010). We regress DVCs on annual measures of wolf presence, weather conditions, non-DVCs, and deer populations. All models include fixed effects for each county to control for time-invariant characteristics (such as relatively fixed differences in road characteristics across counties) and year-specific effects to control for common, statewide changes over time (such as improvements in vehicle safety or changes in fuel prices).

The preferred model uses a triple-differences approach commonly employed in applied econometrics (47, 48). Applied to our setting, this technique measures whether there is a change in the frequency of DVCs before versus after wolf entry (first difference) in wolf versus nonwolf counties (second difference). Then, it compares whether this "difference-in-differences" is larger for DVCs than for non-DVCs (third difference). For example, if DVCs decline by 30% when wolves enter a county and stay the same in all other counties, then a difference-in-differences estimate would suggest that wolf presence was responsible for a 30% reduction in DVCs. However, if non-DVCs declined by, say, 10% more in nonwolf counties when compared to wolf counties, then the DVC reduction attributed to wolves by the model is 20%. By subtracting the third difference, the model purges the effects of other confounding changes in roadway safety in a specific county that may have occurred at the same time as wolf expansion (e.g., a change in speed limits, road use, driver composition, or road quality).
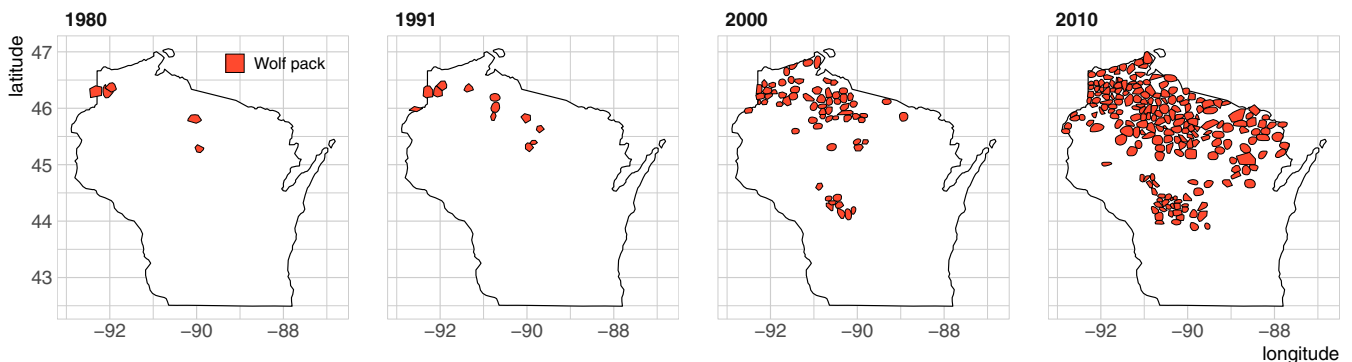
Fig. 1. Wolf packs spread across Wisconsin between 1980 and 2010. Wolf packs are concentrated in the forested areas in the northern and central parts of the state. The rest of the state is predominantly nonforested agricultural or urban areas.
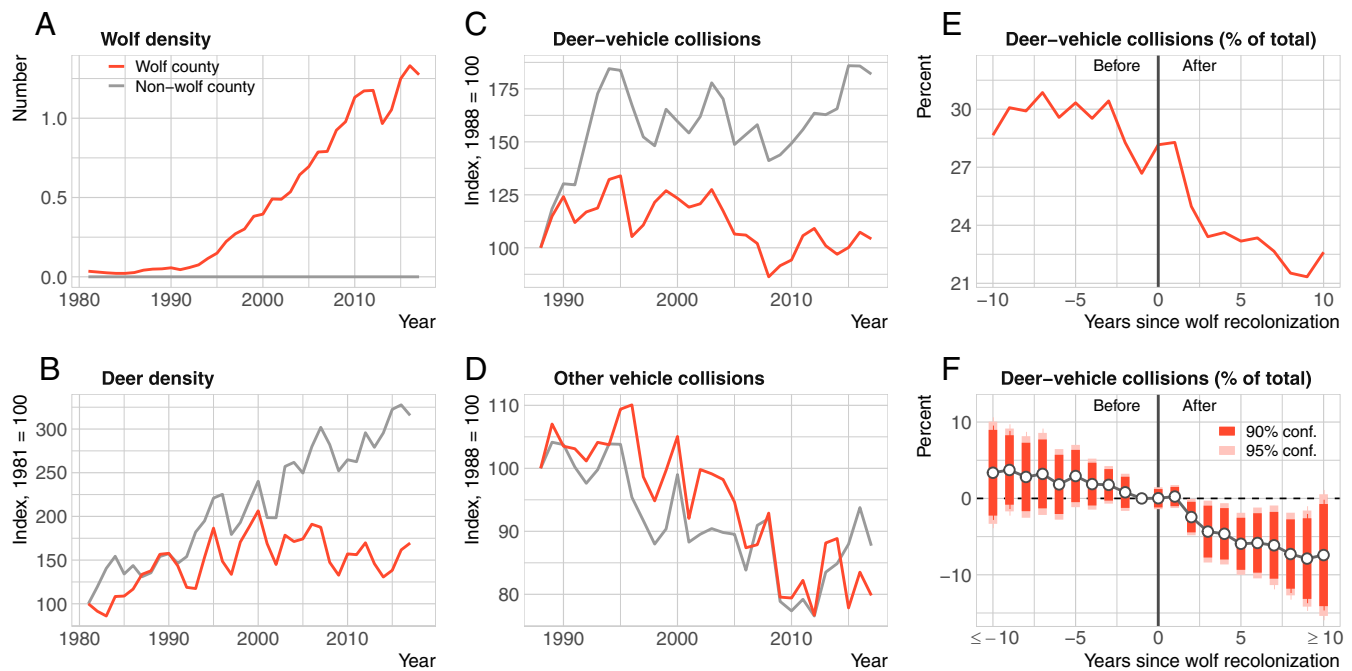
Fig. 2. Trends in wolf abundance, deer abundance, and roadway collisions. (*A*) Winter wolf population per 100 km² of deer range. Deer range is defined as permanent cover at least 4 ha in size in 1993, the only year available. (*B*) Prehunt deer population per km² of deer range. (*C*) Vehicle collisions caused by deer. (*D*) Vehicle collisions not caused by deer. (*E*) Percent of vehicle collisions caused by deer before and after wolves enter a county, 1988 to 2010. (*F*) Percent of vehicle collisions caused by deer regressed on indicator variables for years since wolf recolonization, county, and year, 1988 to 2010. SEs clustered at the county level. (*E* and *F*) Data exclude three counties with wolf exit at some point during the period.

Intuitively, the triple-differences model allows us to control for all time-varying factors that affect roadway safety in general but that, unlike wolves, would not specifically affect DVCs.

We first estimate the net effect of wolves on DVCs through changes in both deer population and deer behavior (Fig. 3*A*). The preferred model shows that wolf presence reduces DVCs by 23.7% for the average county, on net (model 1). The estimated net effect is robust to changes in model specification as indicated by the similar results for models 2 to 5. Model 2 excludes the three counties for which wolves exit at some point during the study period to avoid assumptions about the persistence of the effect of past wolf presence. Model 3 excludes the 13 nonwolf counties on the boundary of wolf counties to rule out possible spatial spillover effects of wolves on neighbor counties. Model 4 flexibly allows wolf counties to have different nonparametric time trends (separate year effects) than nonwolf counties to further allow unobserved annual factors to affect each region differently. Model 5 extends the time series to 2016 rather than concluding in 2010. Collectively, the results suggest that wolves reduced DVCs by 17.9 to 27.3% and that specification choice has little effect on the point estimate. These results are also robust to the inclusion of eight counties with suspected data-quality issues (*Materials and Methods* and *SI Appendix,* Fig. S2*A*).

The net effect of wolf presence on DVCs is economically significant. For the average county with wolves present, a 23.7% reduction in DVCs translates to 38 fewer DVCs per year (Table 1, column 1). Based on the national average loss per DVC ($9,960) (22), the presence of wolves leads to more than a $375,000 reduction in DVC losses per county per year; this translates to a savings of about $11 per person or $808 per million vehicle miles traveled in 2010. Across the 29 counties with wolves present, these savings generate a $10.9 million aggregate reduction in DVC losses each year.

Decomposed Effect. The net effect of wolves on DVCs embeds a population and behavioral effect. Decomposing the effect is useful for determining whether or not human deer hunting might be a good substitute for wolves in reducing DVCs. If most of the effect on DVCs comes from reductions in deer abundance, then deer hunters could reproduce the benefits of wolves (conditional on sufficient hunting participation). Currently, recreational hunting is the main source of deer population control in the United States (49). If the effect mainly results from changes in deer behavior, then wolves are serving a unique ecological function that seasonal human deer hunters cannot replace.

Controlling for deer abundance in the DVC model separates the behavioral effect of wolves from the population effect (Fig. 3*B*). This set of models does so by estimating the effect of wolf presence on DVCs conditional on the number of deer on the landscape, thereby purging any effect that wolves have on DVCs through their influence on deer abundance; any remaining effect depends on how wolves change deer behavior. The results suggest that wolf presence reduces DVCs primarily through a behavioral effect; in the preferred model, DVCs fall by 17.4% for the average county (model 1). As with the net effect, the point estimate for the behavioral effect is essentially unchanged across a range of robustness checks (Fig. 3*B* and *SI Appendix,* Fig. S2*B*). For the average county with wolves present, this percentage reduction translates to 28 fewer DVCs per year (Table 1, column 2). The change is valued at about $276,000 per county per year or $8 million per year statewide.

The difference between the net effect and the behavioral effect represents the percentage decline in DVCs attributable to the influence of wolf presence on deer populations (or the "population effect") (Table 1, column 3). Based on this method, wolf presence reduces DVCs by 6.3% through changes in deer abundance. For the average county with wolves present, this translates to 10 fewer DVCs per year, about one-quarter the size of the behavioral effect.
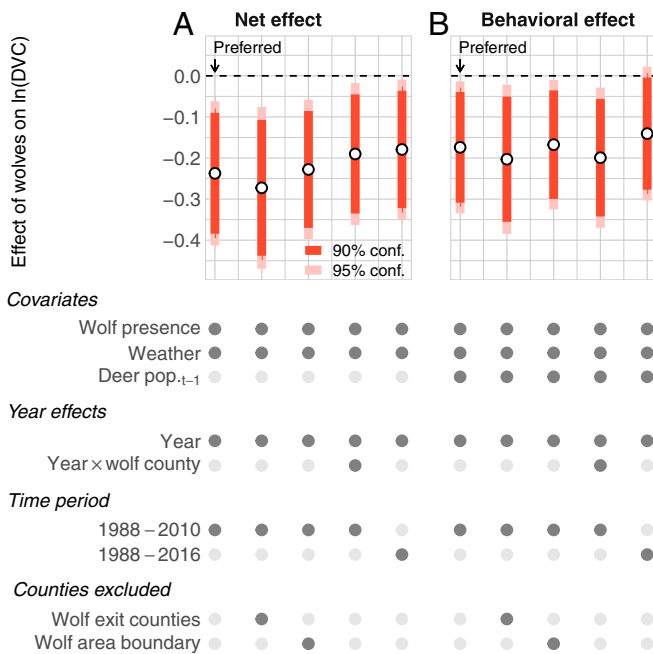
Fig. 3. Wolf presence reduces the frequency of DVCs through changes in deer abundance and behavior. (*A*) The "net effect" occurs through changes in both mechanisms. (*B*) The "behavioral effect" occurs through changes in deer behavior only. Subtracting *B* from *A* provides the "population effect," which occurs through changes in deer abundance only. (*A* and *B*) Model 2 excludes three counties with wolf exit at some point during the period. Model 3 excludes 13 counties that never have wolf presence (nonwolf counties) on the boundary of counties that have wolf presence for at least 1 y during the study period (wolf counties). SEs clustered at the county level.

Predator–Prey Theory. To further evaluate the dominance of the behavioral effect, we estimate the reduction in deer abundance that would be needed to generate the net effect of wolves on DVCs through the population channel only. Then, we compare this benchmark to the estimated effect of wolves on deer abundance from three predator–prey models (*SI Appendix*). A 1% decrease in deer abundance leads to a 0.32% reduction in DVCs in the preferred DVC model (*SI Appendix*, Fig. S1). Therefore, wolf presence would have to reduce deer abundance by 74% to generate the net effect of wolf presence on DVCs if wolf presence had no behavioral effect (i.e., $0.32 \times 74.2 = 23.7$). Equivalently, given the average number of wolves present in a county (14.5), each wolf would need to reduce the deer population by about 5% on average (i.e., $74.2 / 14.5 = 5.1$). However, the predator–prey models show that each wolf reduces the deer population by no more than 1.1% (*SI Appendix*, Table S2). Overall, the predator–prey models confirm that the effect of wolves on deer abundance is much too small to explain the large effect of wolves on DVCs.

Wolf Presence versus Wolf Abundance. Does the effect of wolves on DVCs depend on the number of wolves in a county? To examine this question, we add to the triple-differences model the annual estimate of wolf populations in addition to the indicator for wolf presence (*SI Appendix*, Fig. S3 *A* and *B*). Results indicate that simultaneous inclusion of both measures leaves the effect of wolf presence essentially unchanged (compare model 2, coefficient 1 to the preferred model). The effect of wolf population is statistically insignificant in this model (model 2, coefficient 2), as well as a model that excludes wolf presence (model 3). We interpret these results as suggestive evidence that wolf presence is sufficient to induce behavioral changes in deer that reduce DVCs.

Table 1. Wolf presence reduces the economic losses from DVCs

	(1)	(2)	(3)
	Net effect	Behavioral effect	Population effect
Change in DVCs			
Percent	−23.7%	−17.4%	−6.3%
No.	−38	−28	−10
Economic value	$375,972	$275,715	$100,257

Notes: The wolf effect operates through changes in: (1) both deer population and deer behavior, (2) deer behavior only, and (3) deer population only.

Discussion

Ecologists and economists alike recognize the potential for apex predators to deliver cascading economic benefits to humans but providing concrete evidence has proven difficult. Unfortunately, the benefits of predators usually become salient only after they are removed from an ecosystem. This was the case in Kern County, California, for example, where government programs sought to protect livestock and pet owners by decimating skunks, foxes, badgers, weasels, snakes, owls, ravens, and hawks. Only after the program was it clear that these efforts facilitated the proliferation of mice populations. The mice damaged the local industries that were supposed to benefit from the predator control programs (50).[‡]

Our study suggests that systematic elimination of wolves from North America has also caused unintended damages. Wolves appear to induce an economically significant reduction in the economic losses associated with DVCs. Wolf presence reduces DVC losses by an average of $375,000 per county per year and by $10.9 million per year in aggregate across the 29 wolf counties. As a point of comparison, the state paid $3.1 million in compensation to individuals for verified deaths or injuries caused by wolves of livestock, hunting dogs, and pets between 1985 and 2019, or an average of $174,000 per year over the last 5 y (45).[§] The economic benefit of reduced DVCs exceeds the economic costs of verified wolf predation by a ratio of 63:1. This ratio is relevant because economics matters for listing, delisting, and management decisions for endangered species, if only as implicit considerations (56, 57).

The beneficial reduction in DVCs concentrates in rural areas where livestock predation also occurs. This finding may help dampen political polarization around wolf reintroduction that generally pits rural and urban voters against one another, as was the case with the November 2020 vote on wolf reintroduction in Colorado (58). In contrast to studies that focus on the economic benefits to humans in urban areas who value knowing of wolf existence (14), our study's focus may be of more practical use to policy makers trying to balance competing constituent interests when setting policy.

Furthermore, the findings imply that wolves may provide a solution to an intractable traffic safety engineering problem, namely that traditional DVC mitigation measures often are not scalable over large regions. Out of more than 40 types of traditional

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[‡]In the jargon of economics, the excessive damage resulting from predator removal is an "ecosystem externality," given the effects of this activity on third parties (50).

[§]Compensation programs are the most common metric used to estimate the economic costs of wolf predation on livestock, hunting dogs, and pets (51); however, this measure likely underestimates the true effect. For example, it does not account for some direct but unverifiable losses, such as missing livestock (rules about compensation for missing calves vary over time in Wisconsin). It also does not account for indirect effects of stress on the growth, reproduction, and health of livestock (52). These indirect effects are difficult to estimate but may be as large or larger than direct costs (53). Compensation programs also do not account for the time and money spent by producers to defend their herds and reduce the consequences of attacks (54). Nor does it account for the distress of livestock and pet owners caused by lost animals and their willingness to pay to avoid wolf predation (55). Although these and other indirect costs of wolves are difficult to measure, they should be considered in management decision making.

mitigation measures, only 13 are effective at reducing collisions with large ungulates (22).¶ Of these strategies, most are cost effective (meaning, the present value of benefits exceeds the present value of costs) only if deployed in DVC hotspots (59); hence, information and funding constraints limit the widespread use of mitigation strategies not involving wolves. Newer technologies, such as machine learning models that identify the presence of deer on roads (60, 61) and rear-facing illumination systems that make vehicles more visible to deer (62), have shown promise in reducing DVCs. It remains unclear how quickly and widely these technologies can be deployed.

In any case, the changes in deer behavior induced by wolf presence could have additional positive effects beyond reducing DVCs. Deer regularly forage on the edges of agricultural fields (16, 63), which tend to be near roads. When wolves are present, deer may retreat from the fields to wooded areas with better cover (64, 65). This behavioral change could be a substantial benefit to farmers, as deer cause 90% of all wildlife damage to agriculture in Wisconsin (66).# Wolves may also reduce the incidence of Lyme disease by changing the ecology of small mammal hosts (68).‖ Lyme disease has annual economic costs of $4.4 to $7.9 billion (69–71). Wolves also can mitigate the harmful effects of overabundant deer on forest ecosystems (3–5).

Importantly, our study implies that wolves regulate deer populations and behavior in ways that a waning number of human deer hunters cannot. In many areas, deer are considered overabundant (18, 19), and managers have struggled to incentivize recreational hunters to reduce deer numbers to a level that would reduce the harmful ecological effects of deer (72–74). A sharp decline in deer hunting participation in recent years will make it more challenging to rely on recreational hunters (75, 76). More fundamentally, deer hunters have limited ability to change deer behavior. Although deer avoid roads when deer hunters are present (77, 78), most hunting activity (and therefore any potential effect on DVCs) is compressed into a few weeks each year. In contrast, wolves alter deer behavior year-round. This explains why most (73%) of the estimated effect of wolves on DVC reductions is attributable to their effects on deer behavior.

The finding that wolves reduce DVCs primarily by changing deer behavior rather than by reducing deer abundance is likely good news for policy makers. It implies they do not need to choose between a $20.6 billion nationwide recreational deer hunting industry (79) and DVC benefits from wolves. At least in Wisconsin, it seems that wolves and deer hunters can coexist with safer roadways. This is consistent with research from Europe, suggesting the potential for successful coexistence with wolves on that continent as well (11).

Materials and Methods

Literature.

Wolf–deer interactions. A growing body of literature finds that the recolonization of wolves precedes dramatic ecological changes in forested areas, such as increases in aspen, willow, and cottonwood tree recruitment (4, 80–82), forb and shrub species richness (5), and balsam fir growth (3). The theory is that prey are more cautious in ecosystems with wolves, which leads to less time spent in any one place and in areas with high predation risk. This avoidance behavior reduces herbivory pressure on preferred food sources, which in turn affects other aspects of the ecosystem, a process known as a trophic cascade. Although debate remains about whether wolves caused these observed ecosystem changes or were merely correlated with them (40, 83), there is strong circumstantial evidence that wolves have important and quantifiable impacts on a variety of ecological outcomes.

There are direct and indirect channels through which wolves could affect DVCs through a trophic cascade. The direct mechanism is changes to deer abundance. It is intuitive that wolf predation would decrease deer abundance, but in reality, this relationship is complicated and difficult to identify empirically. There is some evidence that wolves can suppress elk (*Cervus canadensis*), deer (*Odocoileus* spp.), and moose (*Alces alces*) populations (18, 24, 25, 84), but this effect may be mediated by many factors, such as the relative levels of predator and prey, forage availability, and weather (85–87). The effect of a reduction in deer abundance on DVCs could be economically significant. The only prior study of which we are aware that examines the impact of carnivores on DVCs predicts, using theoretical simulations, that the reintroduction of cougars (*Puma concolor*) to the eastern United States could reduce DVC losses by $2.3 billion over 30 y through reductions in deer density (28).

The indirect mechanism is changes to deer behavior. Areas with high road density are generally poor habitats for wolves (88–92); however, wolves also use roads, pipelines, and other linear features as travel corridors, which increases wolves' travel efficiency and the kill rate of prey near these features (32–36). As such, prey may avoid these features when wolves are present (34, 37, 38). It makes sense that these behavioral changes also would cause deer to avoid roads, thereby reducing DVCs; however, to our knowledge this effect has yet to be measured. The behavioral effect is particularly important because it suggests that wolves suppress economic damage from deer in a way that hunters cannot. *DVCs.* Economists have investigated many factors that influence traffic safety, such as mandatory seatbelt laws and speed limits, drunk driving, fuel economy standards, vehicle size, and daylight saving time (93–97). Most prior economic studies focus on fatal collisions, which are critical to understand because mitigating such collisions prevents the loss of human life; but fatal collisions only account for 0.2% of all collisions (98). Research on the remaining 99+% of collisions could illuminate strategies to minimize the impacts of crashes on a large segment of the population. DVCs constitute 7% of all vehicle collisions and 24% of single-vehicle collisions (22, 99).

Three categories of variables describe the main determinants of DVCs in the literature: exposure, road characteristics, and land cover (26, 100–116). Intuitively, both larger deer populations and higher traffic volume tend to increase DVCs by increasing the probability a driver will encounter (or be exposed to) a deer. Road characteristics such as curvature, steepness, and number of lanes affect DVCs by influencing driver reaction times or changing deer movement patterns.** The effects of land cover on DVCs is mixed, with some studies finding positive impacts and some finding negative impacts of agricultural, forested, and urban areas. Landscape diversity and fragmentation appear to be more important and tend to increase DVCs; however, these variables may be proxies for deer abundance because deer tend to prefer landscapes that are more heterogeneous.

The effects of weather on nondeer vehicle collisions is well established (117–127), but only three animal–vehicle collision (AVC) studies of which we are aware examine weather (128–130). Collectively, these studies demonstrate that weather affects both deer and driver behavior, sometimes in opposing ways, and the impacts of weather on DVCs is context specific and poorly understood.††

¶Effective measures include seasonal wildlife warning signs; vegetation removal; fence, gap, and crosswalk; population culling; relocation; anti-fertility treatment; fence; fence, underpass, and jump out; fence, under- and overpass, and jump out; animal detection system (ADS); fence, gap, and ADS; elevated roadway; and road tunnel. Effectiveness ranged from 26 to 100% (59).

#Deer-inflicted crop damage was last valued at $74 to $92 million per year in 1996, when deer populations were substantially lower than they are today (67).

‖The theorized impact of wolves on Lyme disease operates through changes in predator–prey interactions (68). In short, the absence of wolves has led to rapid growth in coyote (*Canis latrans*) populations. Coyotes suppress the abundance of several small mammal predators, such as red fox (*Vulpes vulpes*), which leads to increases in small mammal populations. These small mammals are thought to infect the majority of ticks that spread Lyme disease.

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*Bridges, drainage ditches, jersey barriers, gullies, and right-of-way fencing (less than 1.5 m or 5 ft tall) are associated with higher DVCs, as are roads with higher curvature, more than two lanes, or short or obstructed sight lines. Roads with steeper or groomed rights-of-way tend to decrease DVCs.

††There is a consensus that rain increases the frequency of vehicle collisions by causing slippery conditions and reduced visibility, but no AVC study includes rain. Snow can either increase or decrease vehicle collisions, depending on driver defensive behaviors. Snow also increases both moose–vehicle collisions (MVC) and AVCs (128, 129), but the effect on DVCs is unknown. Cold temperatures increase vehicle collisions but may decrease fatal collisions (118, 123, 125). Cold temperatures increase MVCs because moose increase movement at low temperatures (129); the effect on DVCs is unknown. High temperatures (greater than 26.7 °C or 80 °F) increase vehicle collisions, likely by increasing driver irritability and reaction times. Summer temperatures did not affect MVCs in Norway (129); however, deer decrease activity or seek thermal cover at these temperatures (131), which would tend to reduce DVCs. Positive phases of the North Atlantic Oscillation increase DVCs in spring in Norway, but the relative contributions of temperature, precipitation, and snow depth in this relationship is unknown (130).

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https://doi.org/10.1073/pnas.2023251118

Most previous research on DVCs focuses on identifying the characteristics of "hotspots" or short stretches of roads with especially frequent crashes (132). Understanding these characteristics helps traffic safety engineers target mitigation strategies (e.g., fences and deer warning signs) and design safer roads. Risk maps also shed light on the biological mechanisms causing DVCs, and they may have long-lasting predictive power (133, 134). However, it is difficult to extrapolate hotspot risk maps regionally. As a result, there is a gap in understanding how to prevent DVCs cost effectively over large regions, especially in the presence of an apex predator.

As described in more detail below, we estimate the relationship between wolves, deer abundance, and DVCs at a broader spatial scale—counties in Wisconsin. This is important because location-specific interventions could displace DVCs to different areas, and research focused on specific locations will fail to encompass these displacement effects. In addition, it is difficult to estimate deer population in a small roadside buffer; using a larger unit of analysis allows us to better measure deer population. A handful of previous studies measure how county-level characteristics affect the frequency of ungulate–vehicle collisions (27, 129, 130, 135–138). The findings from these studies are generally in line with the hotspot literature.

The existing county-level studies provide a foundation for identifying determinants of DVCs at a broad geographic scale; however, several data and methodological limitations may introduce undesirable properties of coefficient estimates. Small sample sizes [N = 9 (135) and N = 5 (130)], imprecisely measured covariates (27, 129, 130, 137, 138), replication of data values across years as proxies for missing values (27), and inclusion of few covariates (130, 137) could all contribute to biased or inconsistent coefficient estimates. Lastly, most of these studies pooled data across time for spatial analysis and across counties for time series analysis. In contrast, we develop a unique panel dataset covering 72 counties over 28 y, which allows us to control for a bundle of county-level characteristics that might affect DVCs using modern econometric techniques; none of the existing studies use the panel data methods employed here.

Data. We assembled an annual, county-level data set for 1979 through 2016 that includes DVCs, deer and wolf populations, and weather. The study period is limited by data availability before 1988 for DVC's and after 2010 for detailed wolf pack locations. Although we can estimate county-level wolf presence data for 2010 to 2016, the source data are collected on a different basis during that period; this change increases measurement error. Below, we describe each data set.

DVCs. The Wisconsin Department of Transportation provided county-level, police-reported DVCs for 1988 through 2013. The Wisconsin Traffic Operations and Safety Laboratory at the University of Wisconsin-Madison provided crash-level data for 1994 through 2016. All overlapping years are identical.

We exclude 8 of 72 counties because police in these counties apparently stopped attending DVC crash scenes during the study period, except when the crash causes a road hazard, human injury, or fatality, based on discrete structural breaks in the data. The main results are robust, however, to inclusion of these counties, as a comparison of Fig. 3 with *SI Appendix*, Fig. S2 makes clear.

We also exclude Menominee County, which is coterminous with the boundaries of the Menominee Indian Reservation. The state of Wisconsin does not have reliable data on the variables of interest for this region.

Deer population. The Wisconsin Department of Natural Resources (WDNR) provided posthunt white-tailed deer population by Deer Management Unit (DMU) for 1981 through 2016. Historically, Wisconsin's DMU boundaries followed roads or other natural features that would be easy for hunters to identify in the field. In 2013, the WDNR revised DMUs to follow primarily county boundaries. At that time, they estimated deer population for the new DMUs for 2002 onward by distributing each old DMU's deer population to the new DMUs it overlaps based on an area-weighted measure. We replicated this procedure for 1981 onward. The procedure assumes that deer are distributed uniformly across the deer range in each DMU. Deer range includes all permanent cover—forest, woodlot, brush-covered land, or marsh—at least 4 ha in size in 1993, the only year available. We also converted population estimates from posthunt to prehunt using the WDNR's formula for this conversion (139), namely prehunt population = posthunt population + harvest × 1.15.

Wolf population. WDNR provided midwinter wolf pack locations and populations for the winter spanning 1979 and 1980 through the winter spanning 2010 and 2011. This is the last year for which WDNR publishes individual wolf pack locations, likely due to legislative changes. The federal government temporarily delisted wolves from the Endangered Species Act on January 27, 2012 (43). The state legislature designated the gray wolf as a game species and authorized wolf harvest on April 2, 2012 (140). Then, WDNR stopped

publishing wolf pack locations in the September 2012 data release, which covers wolf status during the winter spanning 2011 and 2012 (141). Beginning with that release, WDNR provides only the number of wolves in survey blocks. These data sets include some lone wolves; however, WDNR's monitoring methods focus on wolf packs, and lone wolves likely remain undercounted (43).

In most models, the main variable of interest is a dummy variable for wolf presence. The preferred models define county-level wolf presence based on wolf pack locations. If at least one wolf pack's territory crosses a county boundary, we define that county as having wolf presence. We also extend the time series using the wolf survey block data as a robustness check; namely, for 2011 to 2016, if any populated wolf survey block overlaps a county boundary, we define that county as having wolf presence. This procedure implicitly assumes that wolves range across the entire survey block.

Finally, we calculate wolf population using the same procedures as wolf presence, except we assign wolf pack or survey block population to counties using a spatially weighted measure. The population measure allows us to test the hypothesis that wolf presence alone is sufficient to alter deer behavior, even though higher wolf abundance may be required to reduce deer abundance.

Weather. Daily minimum temperature, maximum temperature, and precipitation (rain + melted snow) are available online as 4 km grid raster files from the Parameter-elevation Regressions on Independent Slopes Model (PRISM) Climate Group at Oregon State University beginning on January 1, 1981. We calculate spatially weighted averages for each variable, county, and day. Then, we calculate total annual precipitation (centimeters), the number of days with a minimum temperature below 0 °C (32 °F), and the number of days with a maximum temperature above 26.7 °C (80 °F) for each county and year. The rationale for using these weather covariates is described in the literature review above.

Conceptual Models and Estimation Methods.

Net effect. As a starting point for identifying the net impact of wolves on DVCs through changes in deer abundance and deer behavior, we begin with a difference-in-differences (fixed-effects) model that is commonly used in modern econometrics (47, 48). Applied to our setting, this technique measures whether there is a change in the frequency of DVCs before versus after wolf entry (first difference) in wolf versus nonwolf counties (second difference). Rather than trying to include measures for every factor that could affect DVCs within a particular county, this model uses nonparametric methods—indicator variables for each county—to control for all time-invariant factors that could affect average differences in DVC rates across counties (e.g., differences in average roadway curvature across counties). The standard model also uses nonparametric methods—indicator variables for each year—to control for time-variant factors that could affect DVCs across the entire state of Wisconsin (e.g., gasoline prices, improvements in vehicle safety, or annual weather fluctuations). The standard model is as follows:

$$\ln(DVC_{it}) = \alpha WolfPresence_{it} + \beta' \boldsymbol{W}_{it} + \theta_i + \delta_t + u_{it},\qquad[\mathbf{1}]$$

where DVC_{it} is the number of vehicle collisions in county i at time t, $WolfPresence_{it}$ is a dummy variable indicating whether a wolf pack is present, θ_i is a vector of county effects, δ_t is a vector of year effects, and u_{it} is the idiosyncratic error. Although δ_t accounts for annual differences in weather severity across Wisconsin, we also include the matrix $\boldsymbol{W}_{it}$ to account for annual differences in severity within each county. $\boldsymbol{W}_{it}$ includes the natural log transformation of the following covariates: total annual precipitation (centimeters), the number of days with a minimum temperature below 0 °C (32 °F), and the number of days with a maximum temperature above 26.7 °C (80 °F). All weather variables are always greater than zero. The rationale for using these weather covariates is described in the literature review above. We hypothesize that α, the net effect of wolf pack presence on the frequency of DVCs, is negative. Note that the model estimates the effects of deer and wolves on DVCs net of drivers adapting to changing risks of collision. As such, the estimates will not reflect the economic costs of avoidance behaviors (e.g., driving at different times or taking different routes to avoid deer) and will therefore understate the full economic benefits of any wolf-induced reduction in DVCs.

To summarize, the empirical strategy in Eq. **1** is based on within-county variation in DVCs over time based on wolf entry and exit over time within a given county. For the most part, this variation is based on initial entry to the county because wolves tend to stay in a county permanently. However, there are three counties for which wolf packs entered and exited multiple times. These are likely cases where wolf pack territories are straddling the

county boundary. The model captures these dynamics. If wolves exit a county, the wolf-presence dummy variable switches to zero; it switches back to one if wolves re-enter.

The main limitation is that the estimation strategy in Eq. **1** does not control for time-varying factors that might have differentially affected roadway safety across counties within Wisconsin for reasons unrelated to deer and wolves. Such factors could include changes in the relative amount of roadway traffic, changes in the relative maintenance and quality of roads, or changes in the relative demographic composition of drivers. We address this limitation by utilizing the annual county-level data on non-DVCs. Our assumption is that changes in non-DVCs will reflect time-varying changes in road safety conditions that are unrelated to deer abundance and wolf presence.

Controlling for changes in non-DVCs builds our estimated model into the triple-differences model given by Eq. **2**. Triple-differences estimators can "generate a more convincing set of results than a traditional [difference-in-differences] analysis" (47). They are also widely used in the econometrics literature, appearing in over 900 peer-reviewed papers since 2000 (48). The model is as follows

$$\ln(VC_{it}) = \alpha_{11} WolfPresence_{it} + \beta'_{11} W_{it} + \theta_{11i} + \delta_{11t}$$

$$+ (\alpha_{12} WolfPresence_{it} + \beta'_{12} W_{it} + \theta_{12i} + \delta_{12t}) \times DVCDummy_{it} + u_{it},$$
[2]

where VC_{it} is the number of vehicle collisions (of any type) in county i during year t, and $DVCDummy_{it}$ is an indicator variable indicating whether a collision was caused by deer. By interacting the weather matrix W_{it} with $DVCDummy_{it}$, we allow weather to have a different effect on DVCs versus non-DVCs. This flexible approach allows weather to affect accidents not only through its effects on general roadway-safety conditions but also through its effects on deer behavior and abundance. The difference-in-differences estimate of α_{11} measures changes in vehicle collisions of any type, DVC or non-DVC, before versus after wolf arrival (first difference) in wolf versus nonwolf counties (second difference). We have no hypothesis about the sign of α_{11} because this coefficient estimate will capture any generic changes in roadway safety that correlate with the timing of wolf arrival and presence in a county. We hypothesize that α_{12} is negative. It is the triple-differences coefficient that assesses how the number of DVCs changes relative to non-DVCs before versus after wolf arrival in wolf versus nonwolf counties (the third difference). Intuitively, this model allows us to control for all time-varying factors that affect roadway safety in general but that, unlike wolves, would not specifically affect DVCs. For comparison with other models, discussed below, we convert the proportional effect of wolf presence to a level effect by multiplying the point estimate for α_{12} by the annual number of DVCs in the average county in which wolves are present.

We estimate a number of robustness checks to account for other factors that could possibly confound the estimates of how wolf presence affected DVCs. First, we exclude three counties for which wolves exit at some point during the study period to avoid assumptions about the persistence of the effect of past wolf presence. Second, we exclude 13 nonwolf counties on the boundary of wolf counties to rule out possible spatial spillover effects of wolves on neighbor counties. Third, we use separate year effects for counties that ever get wolves versus those that do not to allow for the possibility that DVCs were trending differently in wolf versus nonwolf counties before wolves arrived, even relative to non-DVCs. Finally, we extend the study period through 2016 to examine the impact of timing on the model estimate. For all models, we cluster SEs at the county level.

One concern could be that wolves are spreading spatially in response to changes in deer populations. However, two studies in Wisconsin fail to find a significant difference in deer density between wolf pack areas and non-wolf pack areas. The studies also find that deer density is not a significant predictor of wolf habitat suitability (89, 90). This finding is helpful for causal identification because it suggests there is not reverse causation with wolves responding to deer abundance.[‡‡]

Behavioral effect. To measure the effect of wolves on DVCs through changes in deer behavior, we control for deer abundance in Eq. **2**. In other words, what

is the effect of wolves on the frequency of DVCs for a given number of deer on the landscape? The model is as follows:

$$\ln(VC_{it}) = \alpha_{21} WolfPresence_{it} + Y_{21} \ln(DeerPop_{t-1}) + \beta'_{21} W_{it} + \theta_{21i} + \delta_{21t}$$

$$+ (\alpha_{22} WolfPresence_{it} + Y_{22} \ln(DeerPop_{t-1}) + \beta'_{22} W_{it} + \theta_{22i} + \delta_{22t})$$

$$\times DVCDummy_{it} + u_{it},$$
[3]

where $DeerPop_{it-1}$ is the prehunt deer population for county i during year $t-1$, and the other variables are defined as previously. Deer population is lagged for two reasons: 1) to reduce potential endogeneity between vehicle collisions, which typically result in the death of the deer, and deer populations and 2) because contemporaneous wolf presence cannot affect lagged deer populations. We hypothesize that α_{22}, the effect of wolf presence on the frequency of DVCs through changes in deer behavior, is negative. For comparison with other models, we convert the proportional effect of wolf presence to a level effect by multiplying the point estimate for α_{22} by the annual number of DVCs in the average county with wolves present over the study period. We also estimate the same robustness checks for this model as we did for the net-effect model, described above. For all models, we cluster SEs at the county level.

Population effect. The difference between the net effect and the behavioral effect represents the preferred estimate of wolf presence on DVCs through changes in deer population (or the "population effect"). We calculate this effect by subtracting the point estimate for α_{22} (Eq. **3**) from α_{12} (Eq. **2**). Note that this effect represents how wolf presence affects DVCs through changes in deer abundance, assuming that deer behavior has simultaneously changed in response to wolves. As before, for comparison with other models, we convert the proportional effect of wolf presence to a level effect by multiplying the point estimate for the population effect by the annual number of DVCs in the average county with wolves present over the study period.

Predator–prey theory. To corroborate the relative magnitudes of the population effect versus the behavioral effect, we estimate the effect of wolves on county-level deer populations using three predator–prey models (*SI Appendix*). The first estimate is the simplest (and most naïve). It assumes that one additional wolf reduces the deer population by the average number that it eats, which is 20 deer per year in Wisconsin (142). The naïve model ignores compensatory mortality (i.e., wolves kill some deer that would have died of other causes) and non-consumptive effects of wolves on deer (e.g., effects of energetically costly avoidance behaviors and stress on reproductive success) (52). The second estimate applies a dynamic predator–prey model to predict deer abundance at the county level based on changes in lagged deer abundance, wolf abundance, and winter severity (139, 143, 144). In contrast to the simple estimate, the dynamic model also accounts for indirect effects that wolves have on deer populations (e.g., by reducing the reproductive success of deer). Although this type of predator–prey model is standard in the ecological literature, including both lagged deer and lagged wolf abundance in one specification may bias the coefficient estimates, as these two variables are simultaneously determined. As such, the third estimate excludes lagged deer abundance from the predator–prey model. Finally, we compare the ecological models to the implied reduction in deer population needed to reproduce the net effect of wolves from the DVC model, converted to a per-wolf basis by dividing the effect of wolf presence by the average number of wolves present.

Wolf presence versus wolf abundance. To examine whether the effect of wolves on DVCs increases with wolf abundance, we test the effects of two wolf data transformations on the net-effect model in Eq. **2** and the behavioral-effect model in Eq. **3**. The first specification includes wolf presence; this is the preferred model, as defined above. The second specification includes both wolf presence and wolf population; this model provides insight on the relative importance of wolf presence versus wolf abundance. The third specification includes wolf population. Comparing model results helps us determine if wolf presence is the main driver of DVC changes.

Economic effects. For all models, we estimate the economic effects of changes in DVCs by multiplying the level change in DVCs by the national average of economic losses per DVC, $9,960 (22). Economic losses include vehicle repair costs, towing and law enforcement services, monetary value of the animal, and carcass removal and disposal. They also include "lost earnings, lost household production, medical costs, emergency services, travel delay, vocational rehabilitation, workplace costs, administrative and legal costs, and pain and lost quality of life."[§§]

[‡‡]The literature's finding that temporal colonization of wolves across Wisconsin appears to be exogenous to changes in deer abundance and DVCs adds to our confidence that the effects we estimate are causal. We emphasize, however, that our results should be interpreted as an average effect for counties with suitable wolf habitat, rather than an effect that could be projected to counties without suitable wolf habitat. In econometric jargon, we are most credibly estimating an average treatment effect on the treated counties rather than an average treatment effect applicable to all counties. The difference between the two estimates is described in modern econometrics textbooks (notably, ref. 47).

[§§]The value of these costs is estimated using "willingness-to-pay cost," which represents "the costs people are willing to pay for safety improvements to avert a fatality or injury" (145). This measure does not quantify the costs associated with the emotional distress of people and animals involved in DVCs, nor the costs of cultural values impacted by wounded animals (22).

1. J. A. Estes et al., Trophic downgrading of planet Earth. Science 333, 301–306 (2011).
2. W. J. Ripple et al., Status and ecological effects of the world's largest carnivores. Science 343, 1241484 (2014).
3. B. E. McLaren, R. O. Peterson, Wolves, moose, and tree rings on Isle Royale. Science 266, 1555–1558 (1994).
4. W. J. Ripple, E. J. Larsen, R. A. Renkin, D. W. Smith, Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biol. Conserv. 102, 227–234 (2001).
5. R. Callan, N. P. Nibbelink, T. P. Rooney, J. E. Wiedenhoeft, A. P. Wydeven, Recolonizing wolves trigger a trophic cascade in Wisconsin (USA). J. Ecol. 101, 837–845 (2013).
6. J.-L. Martin, S. Chamaillé-Jammes, D. M. Waller, Deer, wolves, and people: Costs, benefits and challenges of living together. Biol. Rev. Camb. Philos. Soc. 95, 782–801 (2020).
7. S. Gilbert, N. Carter, R. Naidoo, Predation services: Quantifying societal effects of predators and their prey. Front. Ecol. Environ., https://doi.org/10.1002/fee.2336 (2021).
8. J. A. Estes, L. P. Carswell, Costs and benefits of living with predators. Science 368, 1178–1180 (2020).
9. E. J. Gregr et al., Cascading social-ecological costs and benefits triggered by a recovering keystone predator. Science 368, 1243–1247 (2020).
10. L. Boitani, "Wolf Conservation and Recovery" in Wolves: Behavior, Ecology, and Conservation, L. D. Mech, L. Boitani, Eds. (University of Chicago Press, 2003), pp. 317–340.
11. G. Chapron et al., Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 1517–1519 (2014).
12. US Fish and Wildlife Service, Gray Wolf: Current Population in the United States. https://www.fws.gov/midwest/wolf/aboutwolves/WolfPopUS.htm. Accessed 27 July 2020.
13. Colorado Proposition 114, Gray Wolf Reintroduction Initiative. Ballotpedia (2020). https://ballotpedia.org/Colorado_Proposition_114,_Gray_Wolf_Reintroduction_Initiative_(2020). Accessed 7 November 2020.
14. C. M. Chambers, J. C. Whitehead, A contingent valuation estimate of the benefits of wolves in Minnesota. Environ. Resour. Econ. 26, 249–267 (2003).
15. C. L. Kling, D. J. Phaneuf, J. Zhao, From Exxon to BP: Has some number become better than no number? J. Econ. Perspect. 26, 3–26 (2012).
16. W. S. Alverson, D. M. Waller, S. L. Solheim, Forests too deer: Edge effects in Northern Wisconsin. Conserv. Biol. 2, 348–358 (1988).
17. E. S. Long, D. R. Diefenbach, C. S. Rosenberry, B. D. Wallingford, M. D. Grund, Forest cover influences dispersal distance of white-tailed deer. J. Mammal. 86, 623–629 (2005).
18. A. Leopold, L. K. Sowls, D. L. Spencer, A survey of over-populated deer ranges in the United States. J. Wildl. Manage. 11, 162–177 (1947).
19. S. D. Côté, T. P. Rooney, J.-P. Tremblay, C. Dussault, D. M. Waller, Ecological impacts of deer overabundance. Annu. Rev. Ecol. Evol. Syst. 35, 113–147 (2004).
20. K. M. Averill et al., A regional assessment of white-tailed deer effects on plant invasion. AoB Plants 10, plx047 (2017).
21. M. R. Conover, W. C. Pitt, K. K. Kessler, T. J. DuBow, W. A. Sanborn, Review of human injuries, illnesses, and economic losses caused by wildlife in the United States. Wildl. Soc. Bull. 23, 407–414 (1995).
22. M. P. Huijser et al., "Wildlife-vehicle collision reduction study: Report to Congress" (Tech. Rep. FHWA-HRT-08-034, Federal Highway Administration, 2008).
23. G. W. T. A. Groot Bruinderink, E. Hazebroek, Ungulate traffic collisions in Europe. Conserv. Biol. 10, 1059–1067 (1996).
24. W. J. Ripple, R. L. Beschta, Large predators limit herbivore densities in northern forest ecosystems. Eur. J. Wildl. Res. 58, 733–742 (2012).
25. F. Messier, The significance of limiting and regulating factors on the demography of moose and white-tailed deer. J. Anim. Ecol. 60, 377–393 (1991).
26. A. J. DeNicola, S. C. Williams, Sharpshooting suburban white-tailed deer reduces deer–vehicle collisions. Hum.- Wildl. Confl. 2, 28–33 (2008).
27. A. Hussain, J. B. Armstrong, D. B. Brown, J. Hogland, Land-use pattern, urbanization, and deer-vehicle collisions in Alabama. Hum.- Wildl. Confl. 1, 89–96 (2007).
28. S. L. Gilbert, et al., Socioeconomic benefits of large carnivore recolonization through reduced wildlife-vehicle collisions. Conserv. Lett. 10, 431–439 (2016).
29. J. L. Atkins et al., Cascading impacts of large-carnivore extirpation in an African ecosystem. Science 364, 173–177 (2019).
30. J. W. Laundré, L. Hernández, The landscape of fear: Ecological implications of being afraid. Open Ecol. J. 3, 1–7 (2010).
31. K. M. Gaynor, J. S. Brown, A. D. Middleton, M. E. Power, J. S. Brashares, Landscapes of fear: Spatial patterns of risk perception and response. Trends Ecol. Evol. 34, 355–368 (2019).
32. J. Whittington et al., Caribou encounters with wolves increase near roads and trails: A time-to-event approach. J. Appl. Ecol. 48, 1535–1542 (2011).
33. M. Dickie, R. Serrouya, R. S. McNay, S. Boutin, Faster and farther: Wolf movement on linear features and implications for hunting behaviour. J. Appl. Ecol. 54, 253–263 (2017).
34. A. R. C. James, A. K. Stuart-Smith, Distribution of caribou and wolves in relation to linear corridors. J. Wildl. Manage. 64, 154–159 (2000).
35. K. Bojarska et al., Opportunity and peril: How wolves use a dense network of forest roads. Mamm. Biol. 100, 203–211 (2020).
36. E. J. Newton et al., Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. PLoS One 12, e0186525 (2017).
37. C. A. DeMars, S. Boutin, Nowhere to hide: Effects of linear features on predator-prey dynamics in a large mammal system. J. Anim. Ecol. 87, 274–284 (2018).
38. J. A. Dellinger et al., Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. Oecologia 189, 487–500 (2019).
39. Wisconsin Department of Natural Resources, Wisconsin Wolf Management Plan (1999). https://p.widencdn.net/hspl5b/ER0099. Accessed 31 August 2018.
40. L. D. Mech, Is science in danger of sanctifying the wolf? Biol. Conserv. 150, 143–149 (2012).
41. J. E. Wiedenhoeft, D. M. MacFarland, N. S. Libal, J. Bruner, "Wisconsin Gray Wolf Monitoring Report: 15 April 2016 through 14 April 2017" (Wisconsin Department of Natural Resources, Madison, WI).
42. T. R. Van Deelen, "Growth characteristics of a recovering wolf population in the Great Lakes region" in Recovery of Gray Wolves in the Great Lakes Region of the United States: An Endangered Species Success Story, A. P. Wydeven, T. R. Van Deelen, E. J. Heske, Eds. (Springer, 2009), pp. 153–166.
43. National Archives and Records Administration, Endangered and threatened wildlife and plants; revising the listing of the gray wolf (Canis lupus) in the western Great Lakes. Fed. Regist. 76, 81666–81726 (2011).
44. D. J. Mladenoff, T. A. Sickley, Assessing potential gray wolf restoration in the northeastern United States: A spatial prediction of favorable habitat and potential population levels. J. Wildl. Manage. 62, 1–10 (1998).
45. Wisconsin Department of Natural Resources, Wisconsin annual wolf damage payment summary (2020). http://dnr.wi.gov/topic/wildlifehabitat/wolf/documents/wolfdamagepayments.pdf. Accessed 8 April 2020.
46. Wisconsin Department of Natural Resources, Wisconsin Deer Metrics. Deer Veh. Collis. https://dnr.wi.gov/wideermetrics/DeerStats.aspx?R=Collision. Accessed 2 November 2020.
47. J. D. Angrist, J.-S. Pischke, Mostly Harmless Econometrics: An Empiricist's Companion (Princeton University Press, 2009).
48. A. Olden, J. Moen, The Triple Difference Estimator, SSRN Electron. J. (2020) https://doi.org/10.2139/ssrn.3582447. Accessed 30 October 2020.
49. T. L. Brown et al., The future of hunting as a mechanism to control white-tailed deer populations. Wildl. Soc. Bull. 28, 797–807 (2000).
50. T. Crocker, J. Tschirhart, Ecosystems, externalities, and economies. Environ. Resour. Econ. 2, 551–567 (1992).
51. P. J. Baker, L. Boitani, S. Harris, G. Saunders, P. C. White, Terrestrial carnivores and human food production: Impact and management. Mammal Rev. 38, 123–166 (2008).
52. I. Laporte, T. B. Muhly, J. A. Pitt, M. Alexander, M. Musiani, Effects of wolves on elk and cattle behaviors: Implications for livestock production and wolf conservation. PLoS One 5, e11954 (2010).
53. J. R. Steele, B. S. Rashford, T. K. Foulke, J. A. Tanaka, D. T. Taylor, Wolf (Canis lupus) predation impacts on livestock production: Direct effects, indirect effects, and implications for compensation ratios. Rangeland Ecol. Manag. 66, 539–544 (2013).
54. M. Widman, M. Steen, K. Elofsson, Indirect costs of sheep depredation by large carnivores in Sweden. Wildl. Soc. Bull. 43, 53–61 (2019).
55. L. Naughton-Treves, R. Grossberg, A. Treves, Paying for tolerance: Rural citizens' attitudes toward wolf depredation and compensation. Conserv. Biol. 17, 1500–1511 (2003).
56. J. F. Shogren et al., Why economics matters for endangered species protection. Conserv. Biol. 13, 1257–1261 (1999).
57. A. W. Ando, Waiting to be protected under the Endangered Species Act: The political economy of regulatory delay. J. Law Econ. 42, 29–60 (1999).
58. D. Main, Gray wolves to be reintroduced to Colorado in unprecedented vote. Natl. Geogr. (2020). https://www.nationalgeographic.com/animals/article/colorado-approves-gray-wolf-reintroduction. Accessed 8 November 2020.
59. M. P. Huijser, J. W. Duffield, A. P. Clevenger, R. J. Ament, P. T. McGowen, Cost–benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada; a decision support tool. Ecol. Soc. 14, 15–50 (2009).
60. W. J. Hans, N. Venkateswaran, V. S. Solomi, On-road deer detection for advanced driver assistance using convolutional neural network. Int. J. Adv. Comput. Sci. Appl. 11, 762–773 (2020).
61. J. Chen et al., Deer crossing road detection with roadside LiDAR sensor. IEEE Access 7, 65944–65954 (2019).
62. T. L. DeVault, T. W. Seamans, B. F. Blackwell, Frontal vehicle illumination via rear-facing lighting reduces potential for collisions with white-tailed deer. Ecosphere 11, e03187 (2020).

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https://doi.org/10.1073/pnas.2023251118

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63. A. P. Wywialowski, Wildlife damage to field corn in 1993. *Wildl. Soc. Bull.* **24**, 264–271 (1996).

64. J. S. Mao *et al.*, Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *J. Wildl. Manage.* **69**, 1691–1707 (2005).

65. D. Fortin *et al.*, Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* **86**, 1320–1330 (2005).

66. Wisconsin Department of Natural Resources, "Wisconsin's deer management program: The issues involved in decision-making" (Tech. Rep. PUBL-SS-931-98, Wisconsin Department of Natural Resources, 1998).

67. J. Yoder, Estimation of wildlife-inflicted property damage and abatement based on compensation program claims data. *Land Econ.* **78**, 45 (2002).

68. T. Levi, A. M. Kilpatrick, M. Mangel, C. C. Wilmers, Deer, predators, and the emergence of Lyme disease. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 10942–10947 (2012).

69. H. J. Kilpatrick, A. M. LaBonte, K. C. Stafford, The relationship between deer density, tick abundance, and human cases of Lyme disease in a residential community. *J. Med. Entomol.* **51**, 777–784 (2014).

70. E. R. Adrion, J. Aucott, K. W. Lemke, J. P. Weiner, Health care costs, utilization and patterns of care following Lyme disease. *PLoS One* **10**, e0116767 (2015).

71. K. Berry, J. Bayham, S. R. Meyer, E. P. Fenichel, The allocation of time and risk of Lyme: A case of ecosystem service income and substitution effects. *Environ. Resour. Econ. (Dordr)* **70**, 631–650 (2018).

72. T. R. Van Deelen *et al.*, Effects of earn-a-buck and special antlerless-only seasons on Wisconsin's deer harvests. *J. Wildl. Manage.* **74**, 1693–1700 (2010).

73. D. R. Diefenbach, W. L. Palmer, W. K. Shope, Attitudes of Pennsylvania sportsmen towards managing white-tailed deer to protect the ecological integrity of forests. *Wildl. Soc. Bull.* **25**, 244–251 (1997).

74. B. Blossey, P. Curtis, J. Boulanger, A. Dávalos, Red oak seedlings as indicators of deer browse pressure: Gauging the outcome of different white-tailed deer management approaches. *Ecol. Evol.* **9**, 13085–13103 (2019).

75. M. Fuller, "Deer hunting in the United States: Demographics and trends: Addendum to the 2011 National Survey of Fishing, Hunting, and Wildlife-Associated Recreation" (Tech. Rep. 2006-10, US Fish and Wildlife Service, 2016).

76. US Department of the Interior, US Fish and Wildlife Service, and US Department of Commerce, US Census Bureau, "2016 National survey of fishing hunting, and wildlife-associated recreation" (Tech. Rep. FHW/16-NAT, US Fish and Widlife Service and US Census Bureau, 2018).

77. S. Ciuti *et al.*, Human selection of elk behavioural traits in a landscape of fear. *Proc. R. Soc. B Biol. Sci.* **279**, 4407–4416 (2012).

78. J. C. Kilgo, R. F. Labisky, D. E. Fritzen, Influences of hunting on the behavior of white-tailed deer: Implications for conservation of the Florida panther. *Conserv. Biol.* **12**, 1359–1364 (1998).

79. Southwick Associates, Hunting in America: an economic force for conservation (2012). http://www.southwickassociates.com/wp-content/uploads/downloads/2013/01/Hunting-Econ-Impacts-NSSF-Southwick-FINAL.pdf. Accessed 18 December 2017.

80. H. L. Beyer, E. H. Merrill, N. Varley, M. S. Boyce, Willow on Yellowstone's northern range: Evidence for a trophic cascade? *Ecol. Appl.* **17**, 1563–1571 (2007).

81. W. J. Ripple, E. J. Larsen, Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biol. Conserv.* **95**, 361–370 (2000).

82. W. J. Ripple, R. L. Beschta, Restoring Yellowstone's aspen with wolves. *Biol. Conserv.* **138**, 514–519 (2007).

83. E. Marris, Rethinking predators: Legend of the wolf. *Nature* **507**, 158–160 (2014).

84. F. Messier, Ungulate population models with predation: A case study with the North American moose. *Ecology* **75**, 478–488 (1994).

85. L. L. Eberhardt, R. A. Garrott, D. W. Smith, P. J. White, R. O. Peterson, Assessing the impact of wolves on ungulate prey. *Ecol. Appl.* **13**, 776–783 (2003).

86. J. A. Vucetich, R. O. Peterson, The influence of top-down, bottom-up and abiotic factors on the moose (Alces alces) population of Isle Royale. *Proc. Biol. Sci.* **271**, 183–189 (2004).

87. J. A. Vucetich, M. Hebblewhite, D. W. Smith, R. O. Peterson, Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf-ungulate systems. *J. Anim. Ecol.* **80**, 1236–1245 (2011).

88. R. P. Thiel, Relationship between road densities and wolf habitat suitability in Wisconsin. *Am. Midl. Nat.* **113**, 404–407 (1985).

89. D. J. Mladenoff, T. A. Sickley, R. G. Haight, A. P. Wydeven, A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conserv. Biol.* **9**, 279–294 (1995).

90. D. J. Mladenoff, T. A. Sickley, A. P. Wydeven, Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data. *Ecol. Appl.* **9**, 37–44 (1999).

91. B. E. Kohn, E. M. Anderson, R. P. Thiel, "Wolves, roads, and highway development" in *Recovery of Gray Wolves in the Great Lakes Region of the United States: An Endangered Species Success Story*, A. P. Wydeven, T. R. Van Deelen, E. J. Heske, Eds. (Springer, 2009), pp. 227–242.

92. A. P. Wydeven *et al.*, Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes region. *Endanger. Species Update Ann Arbor* **18**, 110–114 (2001).

93. R. Michener, C. Tighe, A Poisson regression model of highway fatalities. *Am. Econ. Rev.* **82**, 452–456 (1992).

94. S. D. Levitt, J. Porter, How dangerous are drinking drivers? *J. Polit. Econ.* **109**, 1198–1237 (2001).

95. M. R. Jacobsen, Fuel economy, car class mix, and safety. *Am. Econ. Rev.* **101**, 105–109 (2011).

96. S. Li, Traffic safety and vehicle choice: Quantifying the effects of the 'arms race' on American roads. *J. Appl. Econ.* **27**, 34–62 (2012).

97. A. C. Smith, Spring forward at your own risk: Daylight saving time and fatal vehicle crashes. *Am. Econ. J. Appl. Econ.* **8**, 65–91 (2016).

98. L. Blincoe, T. R. Miller, E. Zaloshnja, B. A. Lawrence, "The economic and societal impact of motor vehicle crashes, 2010 (Revised)" (Tech. Rep. DOT HS 812 013, National Highway Traffic Safety Administration, Washington, D.C., 2015).

99. National Highway Traffic Safety Administration, "National motor vehicle crash causation survey" (Tech. Rep. DOT HS 811 059, US Department of Transportation, 2008).

100. R. E. Allen, D. R. McCullough, Deer-car accidents in southern Michigan. *J. Wildl. Manage.* **40**, 317–325 (1976).

101. T. L. Bashore, W. M. Tzilkowski, E. D. Bellis, Analysis of deer-vehicle collision sites in Pennsylvania. *J. Wildl. Manage.* **49**, 769–774 (1985).

102. A. P. Clevenger, M. Barrueto, K. E. Gunson, F. M. Caryl, A. T. Ford, Context-dependent effects on spatial variation in deer-vehicle collisions. *Ecosphere* **6**, 47 (2015).

103. M. C. Farrell, P. A. Tappe, County-level factors contributing to deer–vehicle collisions in Arkansas. *J. Wildl. Manage.* **71**, 2727–2731 (2007).

104. R. A. Finder, J. L. Roseberry, A. Woolf, Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. *Landsc. Urban Plan.* **44**, 77–85 (1999).

105. R. Found, M. S. Boyce, Predicting deer-vehicle collisions in an urban area. *J. Environ. Manage.* **92**, 2486–2493 (2011).

106. K. Gkritza, R. R. Souleyrette, M. J. Baird, B. J. Danielson, Empirical Bayes approach for estimating urban deer-vehicle crashes using police and maintenance records. *J. Transp. Eng.* **140**, 04013002 (2014).

107. K. Gkritza, M. Baird, Z. N. Hans, Deer-vehicle collisions, deer density, and land use in Iowa's urban deer herd management zones. *Accid. Anal. Prev.* **42**, 1916–1925 (2010).

108. T. W. Grovenburg *et al.*, Factors affecting road mortality of whitetailed deer in eastern South Dakota. *Hum.- Wildl. Confl.* **2**, 48–59 (2008).

109. T. Hothorn, J. Müller, L. Held, L. Möst, A. Mysterud, Temporal patterns of deer-vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. *Accid. Anal. Prev.* **81**, 143–152 (2015).

110. M. W. Hubbard, B. J. Danielson, R. A. Schmitz, Factors influencing the location of deer-vehicle accidents in Iowa. *J. Wildl. Manage.* **64**, 707–713 (2000).

111. Y. Lao, G. Zhang, Y.-J. Wu, Y. Wang, Modeling animal-vehicle collisions considering animal-vehicle interactions. *Accid. Anal. Prev.* **43**, 1991–1998 (2011).

112. J. J. Mckee, D. M. Cochran, The role of landscape in the distribution of deer-vehicle collisions in south Mississippi. *Southeast. Geogr.* **52**, 327–340 (2012).

113. W. J. McShea, C. M. Stewart, L. J. Kearns, S. Liccioli, D. Kocka, Factors affecting autumn deer-vehicle collisions in a rural Virginia county. *Hum. Wildl. Interact.* **2**, 110–121 (2008).

114. J. W. Ng, C. Nielson, C. C. St Clair, Landscape and traffic factors influencing deer-vehicle collisions in an urban enviroment. *Hum.- Wildl. Confl.* **2**, 34–47 (2008).

115. C. K. Nielsen, R. G. Anderson, M. D. Grund, Landscape influences on deer-vehicle accident areas in an urban environment. *J. Wildl. Manage.* **67**, 46–51 (2003).

116. K. Sudharsan, S. J. Riley, H. Campa III, Relative risks of deer–vehicle collisions along road types in southeast Michigan. *Hum. Dimens. Wildl.* **14**, 341–352 (2009).

117. J. Aguero-Valverde, P. P. Jovanis, Spatial analysis of fatal and injury crashes in Pennsylvania. *Accid. Anal. Prev.* **38**, 618–625 (2006).

118. M.-P. Andreescu, D. B. Frost, Weather and traffic accidents in Montreal, Canada. *Clim. Res.* **9**, 225–230 (1998).

119. J. Andrey, S. Yagar, A temporal analysis of rain-related crash risk. *Accid. Anal. Prev.* **25**, 465–472 (1993).

120. J. Bertness, Rain-related impacts on selected transportation activities and utility services in the Chicago area. *J. Appl. Meteorol.* **19**, 545–556 (1980).

121. D. Eisenberg, The mixed effects of precipitation on traffic crashes. *Accid. Anal. Prev.* **36**, 637–647 (2004).

122. L. Fridstrøm, J. Ifver, S. Ingebrigtsen, R. Kulmala, L. K. Thomsen, Measuring the contribution of randomness, exposure, weather, and daylight to the variation in road accident counts. *Accid. Anal. Prev.* **27**, 1–20 (1995).

123. B. Leard, K. Roth, "Weather, traffic accidents, and climate change" (Tech. Rep. RFF DP 15-19, Resources for the Future, 2015).

124. N. Levine, K. E. Kim, L. H. Nitz, Daily fluctuations in Honolulu motor vehicle accidents. *Accid. Anal. Prev.* **27**, 785–796 (1995).

125. N. V. Malyshkina, F. L. Mannering, Markov switching multinomial logit model: An application to accident-injury severities. *Accid. Anal. Prev.* **41**, 829–838 (2009).

126. V. Shankar, F. Mannering, W. Barfield, Effect of roadway geometrics and environmental factors on rural freeway accident frequencies. *Accid. Anal. Prev.* **27**, 371–389 (1995).

127. L. A. Sherretz, B. C. Farhar, An analysis of the relationship between rainfall and the occurrence of traffic accidents. *J. Appl. Meteorol.* **17**, 711–715 (1978).

128. J. Biggs, S. Sherwood, S. Michalak, L. Hansen, C. Bare, Animal-related vehicle accidents at the Los Alamos National Laboratory, New Mexico. *Southwest. Nat.* **49**, 384–394 (2004).

129. C. M. Rolandsen, E. J. Solberg, I. Herfindal, B. Van Moorter, B.-E. Sæther, Large-scale spatiotemporal variation in road mortality of moose: Is it all about population density? *Ecosphere* **2**, 113 (2011).

130. A. Mysterud, Temporal variation in the number of car-killed red deer *Cervus elaphus* in Norway. *Wildl. Biol.* **10**, 203–211 (2004).

131. K. L. Parker, C. T. Robbins, Thermoregulation in mule deer and elk. *Can. J. Zool.* **62**, 1409–1422 (1984).

132. K. E. Gunson, G. Mountrakis, L. J. Quackenbush, Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. *J. Environ. Manage.* **92**, 1074–1082 (2011).

133. A. Treves, K. A. Martin, A. P. Wydeven, J. E. Wiedenhoeft, Forecasting environmental hazards and the application of risk maps to predator attacks on livestock. *Bioscience* **61**, 451–458 (2011).

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https://doi.org/10.1073/pnas.2023251118

134. A. Treves, M. F. Rabenhorst, Risk map for wolf threats to livestock still predictive 5 years after construction. *PLoS One* **12**, e0180043 (2017).

135. A. L. Iverson, L. R. Iverson, Spatial and temporal trends of deer harvest and deer-vehicle accidents in Ohio. *Ohio J. Sci.* **99**, 84–94 (1999).

136. J. Raynor, *Measuring the Economic Impacts of Keystone Species* (University of Wisconsin-Madison, Madison, WI, 2017).

137. K. A. Schwabe, P. W. Schuhmann, M. J. Tonkovich, E. Wu, "An analysis of deer-vehicle collisions: the case of Ohio in Human Conflicts with Wildlife: Economic Considerations" *Proceedings of the Third NWRC Special Symposium*, L. Clark, *et al*, Eds.. (National Wildlife Research Center, Fort Collins, CO, 2002), pp. 91–103.

138. A. Seiler, Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildl. Biol.* **10**, 301–313 (2004).

139. Wisconsin Department of Natural Resources, *Management Workbook for White-Tailed Deer* (Wisconsin Department of Natural Resources, 2001).

140. 2011 Wisconsin Act 69 (October 7, 2020).

141. A. P. Wydeven, J. E. Wiedenhoeft, R. N. Schultz, J. Bruner, S. Boles, "Status of the timber wolf in Wisconsin: Performance report 1 July 2011 through 30 June 2012" (Tech. Rep. 143, Wisconsin Endangered Resources, Wisconsin Department of Natural Resources, Madison, WI, 2012).

142. Wisconsin Department of Natural Resources, "Wolves and deer in Wisconsin (2009)." http://dnr.wi.gov/topic/wildlifehabitat/wolf/documents/wolvesdeer2009.pdf. Accessed 29 April 2021.

143. B. Dennis, M. R. Otten, Joint effects of density dependence and rainfall on abundance of San Joaquin kit fox. *J. Wildl. Manage.* **64**, 388–400 (2000).

144. T. M. Hegel *et al*., Seasonal effects of Pacific-based climate on recruitment in a predator-limited large herbivore. *J. Anim. Ecol.* **79**, 471–482 (2010).

145. US Department of Transportation, *Technical advisory T 7570.2. Motor vehicle accident costs* (US Department of Transportation, Federal Highway Administration, Washington, D.C., 1994).