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# Supplementary Information for
## Wolves make roadways safer, generating large economic returns to predator conservation

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## Supplementary Information Text

## Methods

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. The first estimate is the simplest (and most naïve). It assumes that one additional wolf leads to 20 fewer deer, the number of adult-sized deer the average wolf eats in a year (1). Note, this is likely an over-estimate of the consumptive effect of wolves because some proportion of deer mortality is compensatory (i.e. wolves kill some deer that would have died of other causes). However, it may not over-estimate the total effect of wolves because predator-avoidance behaviors may be energetically costly and lead to reduced productivity, which would tend to reduce the deer population further (2). For comparison with other models, we calculate the change in deer abundance as a percent of the annual prehunt deer population in the average county with wolves present over the study period (Table S2, column 1).

The second estimate is based on the predator-prey model from (3):

$$N_{t+1} = N_t \exp(r + rN_t/K + \zeta P_t + \boldsymbol{\gamma}'\boldsymbol{W_t} + \sigma Z_{t+1}) \qquad [1]$$

where $N_t$ is the prey population at time $t$, $r$ is the instantaneous rate of growth in $N$, $K$ is the carrying capacity of the environment for $N$, $P_t$ is predator abundance, $\boldsymbol{W_t}$ is a vector of weather variables, and $Z_{t+1}$ represents stochastic environmental shocks other than observed weather with $Z_{t+1} \sim N(0, \sigma^2)$. When $\boldsymbol{\gamma}' = 0$ and $\sigma = 0$ (i.e. weather has no effect on subsequent abundance), this model reduces to the classic density-dependent Ricker logistic growth model with Type 1 (linear) predation. Reorganizing the equation yields the following relationship:

$$\ln(N_{t+1}/N_t) = \beta_0 + \beta_1 N_t + \zeta P_t + \boldsymbol{\gamma}'\boldsymbol{W_t} + \sigma Z_{t+1} \qquad [2]$$

In other words, prey abundance, predation, and weather affect the annual growth rate of the prey species.

The Wisconsin Department of Natural Resources employs a version of Eq. [2], excluding wolves, to predict the change in deer population between the current posthunt population and the following prehunt population (4). They use an index of winter severity as the relevant weather variable, defined as the number of days with a minimum temperature of –17.8 °C (0 °F) or lower plus the number of days with at least 45.72 cm (18 in) of snow on the ground between December 1 and April 30. Deer conceive in October to November and give birth the following May to June. Severe conditions during the winter can cause the starvation of adult deer; it can also negatively affect the health of pregnant does and reduce fawn survival and recruitment the following spring. Exposure to temperatures less than –17.8 °C and snow deeper than 45.72 cm are important thresholds beyond which the metabolic rate of deer increases and the likelihood of population effects increases (5). We estimate the following approximation to this relationship:

$$\ln(DeerPopPrehunt_{it}) = \beta_1 \ln(DeerPopPosthunt_{it-1}) + \zeta WolfPop_{it-1} + \boldsymbol{\gamma}'\boldsymbol{W_{it-1}} + \theta_i + \delta_t + u_{it} \qquad [3]$$

where $DeerPopPrehunt_{it}$ is the prehunt deer population for county $i$ at time $t$, $DeerPopPosthunt_{it-1}$ is the posthunt deer population measured at time $t-1$, $WolfPop_{it-1}$ is the mid-winter wolf population (with $t$ defined according to the start year of the relevant winter), and the matrix $\boldsymbol{W_{it-1}}$ includes the natural log transformation of the following covariates: total winter precipitation (centimeters) and the number of days with a minimum temperature of –17.8 °C (0 °F) or lower. Ideally, the model would include snow depth rather than winter precipitation, but data are not available for the full study period. We hypothesize that $\zeta$ is negative. Standard errors are clustered at the county level. For comparison with other models, we convert the proportional effect of wolf abundance to a level effect by multiplying the point estimate for $\zeta$ by the annual prehunt deer population in the average county with wolves present over the study period (Table S2, column 2).

Although this model is standard in the ecological literature, the simultaneous determination of lagged deer and lagged wolf abundance through predator-prey interactions may bias the coefficient estimates. The third estimate excludes lagged deer abundance from Eq. [3] to evaluate potential bias. As before, we examine the level effect based on the size of the prehunt deer population in the average county with wolves present over the study period (Table S2, column 3).

For each of the three ecological models, we then calculate the effect of the estimated changes in deer abundance on deer-vehicle collisions (DVCs) (the “population effect” refers to the effect on DVCs of changes in deer population, not the change in the deer population itself, as discussed in the main text). To estimate the effect on DVCs, we multiply the percentage change in deer abundance (Table S2) by the point estimate of the effect of a one percent change in deer abundance on DVCs (Fig. S1). We also examine the level effect based on the number of DVCs in the average county with wolves present over the study period.

Finally, we compare the ecological models to the implied reduction in deer population needed to produce the net effect of wolf presence on DVCs. First, we determine what percentage change in deer population would be required to generate the net effect of wolves on DVCs, if there was no behavioral effect of wolves. To do so, we divide the effect of wolf presence on DVCs (Fig. 3*A*, model 1) by the effect of a one percent reduction in deer abundance on DVCs (Fig. S1) (i.e. 23.7 / 0.32 = 74.2 percent reduction in deer abundance). Then, we convert the estimated effect of wolves on DVCs and the implied effect of wolves on deer abundance to a per-wolf basis by dividing by the number of wolves in the average county with wolves present over the study period (14.5 wolves). We also examine the level effects based on the number of DVCs and the prehunt deer population in the average county with wolves present over the study period (Table S2, column 4).

## Discussion

The results confirm that wolf effects on deer abundance are much too small to account for the net effect of wolves on DVCs. The ecological models show that one additional wolf above the mean reduces deer abundance by 0.06 to 1.07 percent (20 to 330 deer for the average county with wolves present). Based on the DVC model, a 1 percent decrease in deer abundance leads to a 0.32 percent reduction in DVCs (Fig. S1). Therefore, the ecological models suggest that each wolf reduces DVCs by 0.02 to 0.34 percent through changes in deer abundance. However, each wolf reduces DVCs by about 1.6 percent on net. If the only mechanism for this effect was a change in deer abundance, each wolf would need to reduce the deer population by 5.1 percent (1,584 deer at the mean). Overall, the ecological models confirm the population effect alone is insufficient to account for the large effect of wolves on DVCs.

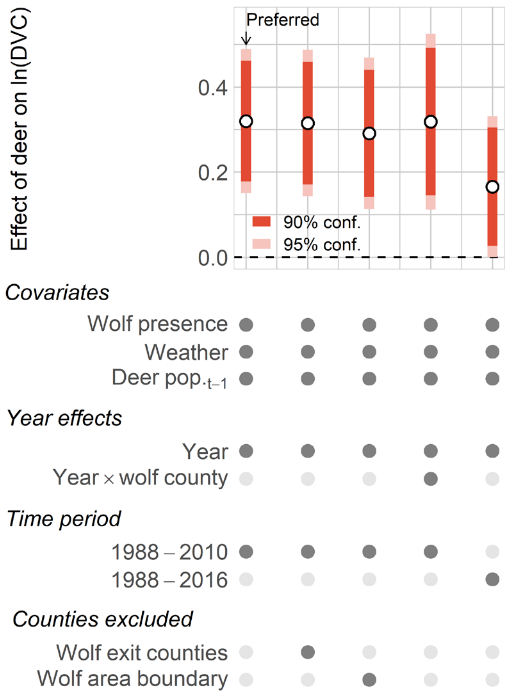

**Fig. S1.** Decreases in deer abundance reduce the frequency of deer-vehicle collisions (DVCs). Model 2 excludes three counties with wolf exit at some point during the period. Model 3 excludes 13 counties that never have wolf presence (non-wolf counties) on the boundary of counties that have wolf presence in at least one year during the study period (wolf counties). Standard errors clustered at the county level.

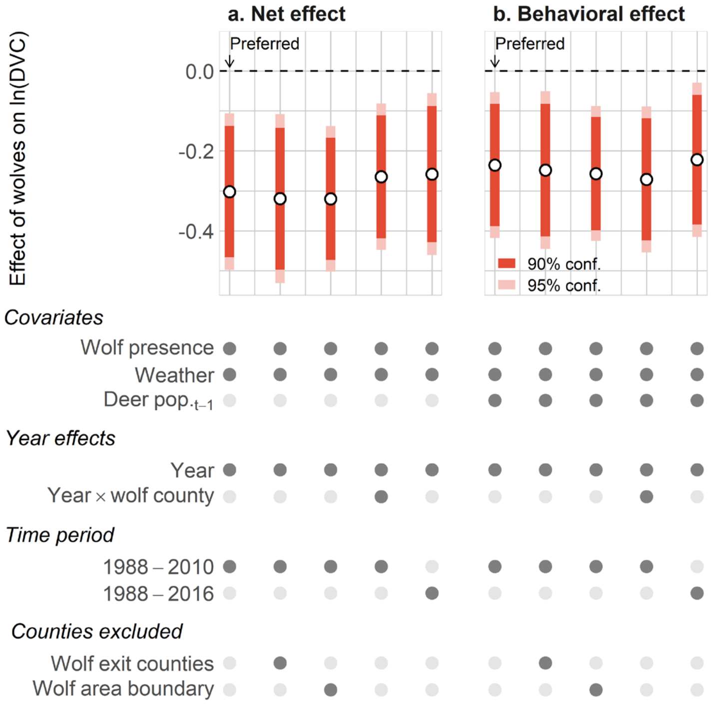

**Fig. S2.** The effect of wolf presence on the frequency of deer-vehicle collisions (DVCs) is robust to county coverage. The results in this figure include eight counties that the main results exclude due to data quality issues (see *Materials and Methods*). The results are otherwise analogous to those in Fig. 3. Standard errors clustered at the county level.

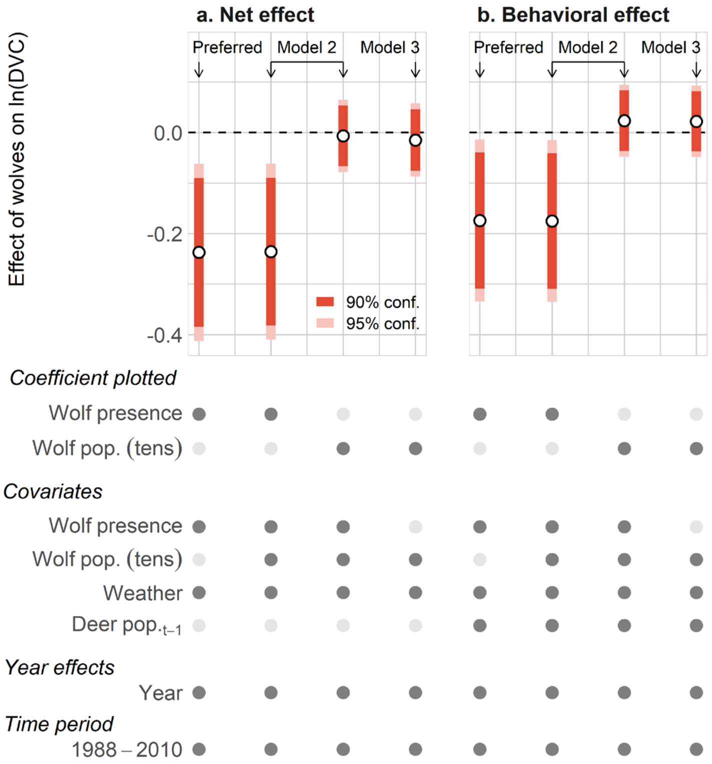

**Fig. S3.** Wolf presence is sufficient to reduce the frequency of deer-vehicle collisions (DVCs); increases in wolf abundance ("Wolf pop.") do not have an additional effect. **a**, the "net effect" occurs through changes in both deer population and deer behavior. **b**, the "behavioral effect" occurs through changes in deer behavior only. Subtracting panel **b** from panel **a** provides the "population effect," which occurs through changes in deer abundance only. Standard errors clustered at the county level.

**Table S1.** Annual Aggregate Economic Effects of Deer in the United States (Billions of 2019 Dollars).

| Category[*] | Annual Effect | |
|---|---|---|
| | Low | High |
| **Costs**[†] | **16.2** | **19.7** |
| Deer-vehicle collisions (6) | 10.0 | 10.0 |
| Deer-aircraft collisions[‡] (7) | 0.004 | .004 |
| Lyme disease | 4.4 | 7.9 |
| Medical costs (8) | 0.8 | 1.5 |
| Avoidance behavior (9) | 3.6 | 6.3 |
| Agricultural damage (10) | 0.3 | 0.3 |
| Timber productivity losses (11) | 1.2 | 1.2 |
| Damage to metropolitan households (11) | 0.4 | 0.4 |
| **Benefits** | **66.6** | **66.6** |
| Deer hunting | 60.4 | 60.4 |
| Direct expenditures (12) | 20.6 | 20.6 |
| Indirect and induced effects of expenditures (12) | 24.7 | 24.7 |
| Consumer surplus[§] (13, 14) | 15.1 | 15.1 |
| Wildlife viewing expenditures[#] (11, 15) | 6.2 | 6.2 |

Notes: [*]Aggregate benefits minus costs does not represent net economic benefits. Most costs presented here include transfers (e.g. some portion of DVC losses to drivers are benefits to mechanics). Likewise, expenditures represent a transfer between consumers and producers. [†]Cost estimates exclude effects of overabundant deer on forest ecosystems, which are significant but difficult to monetize (16–20). [‡]Estimate based on dividing total damage between 1990 to 2009 by the number of years in this period. [§]Estimate based on multiplying the mean consumer surplus for one day of deer hunting by total days of deer hunting. [#]Estimate based on attributing 10 percent of wildlife viewing expenditures to deer as a conservative estimate per Conover (11). Indirect and induced effects from these expenditures and consumer surplus are available for wildlife watching (14, 15); however, it is not possible to determine what fraction of these effects are attributable to deer.

**Table S2.** Changes in deer population alone are insufficient to explain the effect of wolves on deer-vehicle collisions (DVCs).

| | (1) | (2) | (3) | (4) |
|---|---|---|---|---|
| Deer population basis | Deer consumed per year | Predator-prey model | Predator-prey model (excl. lagged deer) | Deer-vehicle collision model (net effect) |
| Change in deer pop. | | | | |
| Percent | -0.06% | -0.14% | -1.07% | -5.13% |
| Number | -20 | -44 | -330 | -1584 |
| Change in DVCs | | | | |
| Percent | -0.02% | -0.05% | -0.34% | -1.64% |
| Number | -0.03 | -0.07 | -0.5 | -2.6 |

Notes: Columns 1-3 show the effect of each additional wolf above the mean on deer abundance, and how the changes in deer abundance affect the frequency of DVCs. The estimated changes in deer abundance are based on: (1) the average number of adult-sized deer a wolf eats in a year, (2) a predator-prey model that predicts deer abundance based on lagged deer abundance, wolf abundance, and weather, and (3) a predator-prey model that excludes lagged deer abundance. Column 4 shows the effect of the average wolf on DVCs, and estimates the change in deer abundance implied by this change, assuming wolves only affect deer abundance not deer behavior.

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