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LETTER

Socioeconomic Benefits of Large Carnivore Recolonization Through Reduced Wildlife-Vehicle Collisions

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Abstract

The decline of top carnivores has released large herbivore populations around the world, incurring socioeconomic costs such as increased animal–vehicle collisions. Attempts to control overabundant deer in the Eastern United States have largely failed, and deer–vehicle collisions (DVCs) continue to rise at alarming rates. We present the first valuation of an ecosystem service provided by large carnivore recolonization, using DVC reduction by cougars as a case study. Our coupled deer population models and socioeconomic valuations revealed that cougars could reduce deer densities and DVCs by 22% in the Eastern United States, preventing 21,400 human injuries, 155 fatalities, and $2.13 billion in avoided costs within 30 years of establishment. Recently established cougars in South Dakota prevent $1.1 million in collision costs annually. Large carnivore restoration could provide valuable ecosystem services through such socio-ecological cascades, and these benefits could offset the societal costs of coexistence.

Introduction

The global decline of large carnivores has led to dramatic ecosystem changes, including increased herbivore abundance and decreased biodiversity (Côté *et al.* 2004; Knight *et al.* 2005; Myers *et al.* 2007; Estes *et al.* 2011; Ripple *et al.* 2014). The potential positive effects of these trophic cascades on human societies remain poorly understood (Treves *et al.* 2013), presenting a persistent roadblock to science-based public policy regarding large carnivore conservation. Although many studies have focused on the economic costs of large carnivores (Dickman *et al.* 2011), appeals to restore large carnivores are largely based on ecological rather than social or economic arguments (e.g., Ripple *et al.* 2014). Large carnivores could provide socioeconomic benefits by reducing overabundant mesopredator or herbivore populations, but to our knowledge, these potential ecosystem services not been quantified.

Human conflicts with proliferating large herbivore populations include damage to crops, competition with livestock, and collisions with vehicles (Côté *et al.* 2004; Gordon 2009). Herbivore–vehicle collisions kill thousands and injure tens of thousands of people annually in areas throughout the world where large carnivores have declined and large herbivores are consequently abundant (Conover *et al.* 1995; Bruinderink & Hazebroek 1996; Gordon 2009). Deer in the United States cause 1.2 million deer–vehicle collisions annually, incurring $1.66

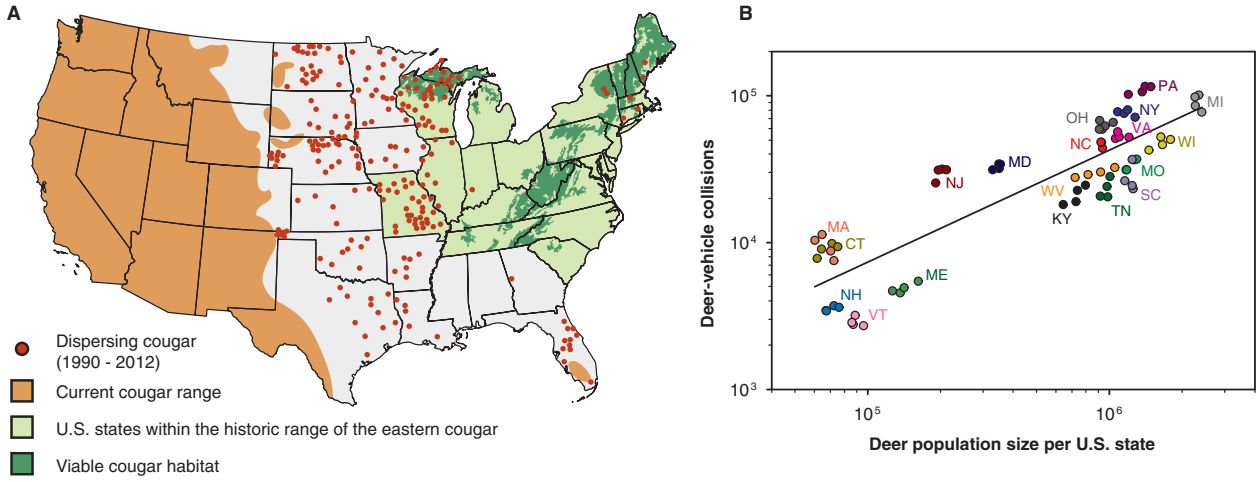

Figure 1 Cougar distribution in the continental United States, and deer–vehicle collision rates in the Eastern United States. (A) Map of current cougar range, confirmed dispersal locations, and viable habitat in the states within the historic range of the eastern cougar, and (B) annual number of deer–vehicle collisions as a function of deer population size in each state within the historic range of the eastern cougar, 2009–2012 ($n = 19$ states, $R^2 = 0.75$).

billion (hereafter all amounts reported in 2014 US$ unless otherwise noted) in damages, 29,000 injuries, and over 200 deaths, and making them the most dangerous large mammal in North America to humans (Conover *et al.* 1995). Annual deer–vehicle collisions (DVCs) in the United States increased by 50% from 1990 to 2004 despite no increase in total vehicle collisions, primarily due to increasing deer numbers (Huijser *et al.* 2008; Figure. 1). Impacts of DVCs are especially severe in eastern states, where overabundant white-tailed deer (*Odocoileus virginianus*, Zimmermann 1780) also damage forest biodiversity, agriculture, forestry, and human health (Côté *et al.* 2004), with estimated costs of $3.1 billion annually in the United States (Conover 1997). While managers in many parts of the Eastern United States seek to control deer populations, others do not due to real and perceived benefits of high deer density for hunters (Riley *et al.* 2003). When attempted, control efforts include costly measures such as administering contraceptives, relocation, construction of fencing and overpasses, culling (Huijser *et al.* 2009), and liberalized hunts (Williams *et al.* 2013), with variable success (Aiken & Harris 2006; Huijser *et al.* 2009). Despite these efforts, the dual problems of deer overabundance and rising DVC rates persist (Huijser *et al.* 2008).

Recolonization by large carnivores could provide an efficient solution to the problem of deer overabundance. Both cougars (*Puma concolor*; Linnaeus 1771) and wolves (*Canis lupus*; Linnaeus 1788) could recolonize the Eastern United States naturally (Mladenoff & Sickley 1998; Laundré 2011). However, cougars may have a better chance of establishment in areas of relatively high human density (Kellert *et al.* 1996; Wilmers *et al.* 2013). Although eastern cougars (*Puma concolor couguar*; Young 1946) were likely extirpated by the early 1900s (LaRue *et al.* 2012), dispersing western cougars (considered by many to also be *P. c. couguar*; Culver *et al.* 2000) have begun to recolonize Midwestern states in the past quarter centuryxbrk (Figure 1). Cougars have dispersed as far eastward as Connecticut (LaRue *et al.* 2012), raising the possibility of breeding populations in the Eastern United States within decades (LaRue & Nielsen 2015). While recolonizing cougars are likely to have both costs to society (e.g., livestock losses; Conover *et al.* 1995), and benefits (e.g., reduction of the negative impacts of deer), we focus our analysis on one potential benefit, reductions in DVCs.

Here, we present a valuation of the ecosystem service provided by large carnivores through reductions in herbivore-vehicle collisions. Using cougars recolonizing the Eastern United States as a case study, we built a model to estimate the impact successful recolonization would likely have on deer density, DVCs, and accompanying human injuries, fatalities, and economic losses (Figures 1 and 2). We then analyzed DVC data from South Dakota, where cougars have recently become established, to empirically test for such a service. We report surprisingly large socioeconomic benefits (Figure 3).

Methods

We compiled vital rates from 19 studies of white-tailed deer in the Eastern United States and created a density-dependent, stochastic matrix model of deer population growth (n = 2,279 radio-collared deer, Table S1). Life stages were categorized as fawn (0–1 years old) or adult (>1 years old), and causes of mortality were categorized

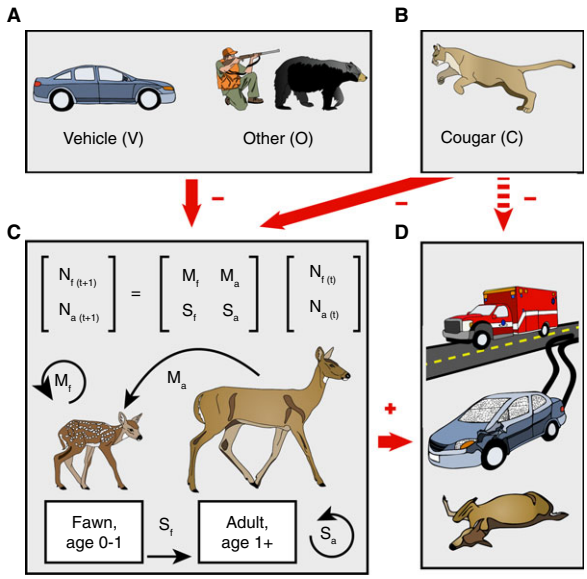

Figure 2 The socio-ecological cascade among cougars, white-tailed deer, and humans. If cougars successfully recolonize the Eastern United States, (A) the current sources of mortality for eastern white-tailed deer are augmented by (B) new mortality from recolonizing cougars. As a result, (C) deer populations, as modeled using a stage-structured population model, would be negatively affected. Thus, cougars would indirectly reduce (D) economic and social costs of deer to humans due to DVCs. Solid arrows show direct positive (+) and negative (–) effects, dashed arrow shows an indirect benefit of cougars to humans through reduced DVCs.

as "vehicle" or "other." We calculated starting deer population sizes by estimating statewide populations from harvest statistics and scaling by the forested proportion of each state (i.e., we assumed deer density was spatially uniform). We then simulated the addition of mortality from cougars using stage-specific predation rates on deer compiled from 11 studies in the Western United States (n = 1,673 radio-collared deer, Table S2). We assumed 75% of the cougar-caused mortality would be compensatory (i.e., replace other causes of death) and 25% would be additive. Deer populations were projected for 30 years (the time needed to reach the new equilibrium density in our models), with 10,000 Monte Carlo iterations.

The value of the ecosystem service provided by cougars was calculated by comparing estimates of deer density and numbers of deer killed by vehicles from models with and without cougar predation. Number of human fatalities and injuries and collision costs (i.e., vehicle damage plus medical and removal costs) avoided due to cougar predation on deer were based on published rates ($7,248 per collision; adjusted from Huijser *et al.* 2008), and these costs were reduced based on estimated improvements to vehicle safety over time.

To ensure modeled predation rates on deer by cougars were realistic, we calculated the density of cougars required to kill the number of deer our models projected. For each state, cougar density (Figure S1) was calculated as the modeled number of deer killed by cougars divided by the average per-cougar kill rate (Table S3) and area of cougar habitat (Table 1). The value of a single cougar was calculated using the per-cougar kill rate of deer, the vehicle mortality rate per deer (Table S1), and the average lifespan of a cougar. Our simulations restricted cougar impacts to areas within eastern states containing large (>2,200 km^2; Beier 1993) tracts of contiguous forest within the historic range of eastern cougars (Table

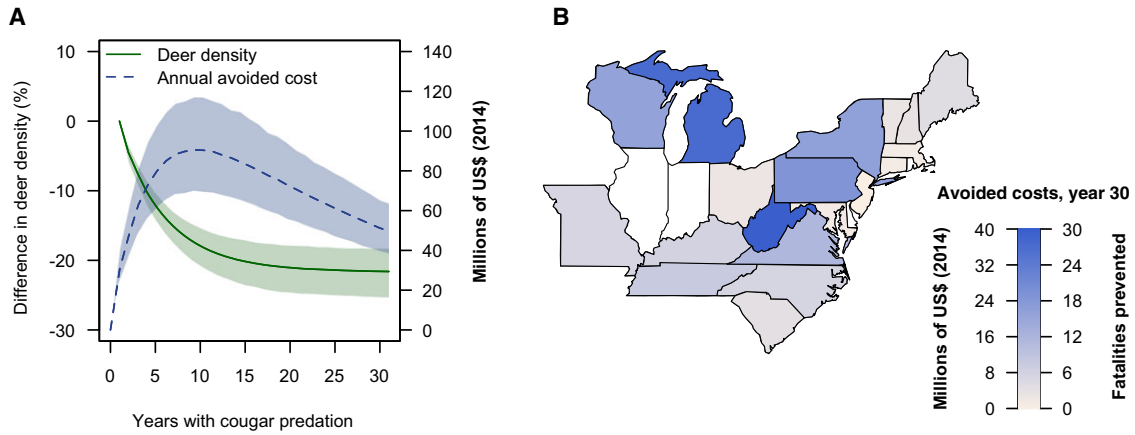

Figure 3 Modeled effects of cougars on deer density and avoided costs of deer–vehicle collisions (DVCs). (A) Reduction in deer density (green line) and increase in avoided costs (blue line) across 19 states in the Eastern United States. Shading shows 95% CIs from 10,000 Monte Carlo simulations. (B) Net present value of cumulative avoided costs (left scale) and numbers of prevented deaths (right scale) due to reduced DVCs during the 30-year period following simulated cougar recolonization in each state.

Table 1 State-specific predictions of cumulative avoided deer-vehicle collisions (DVCs) and associated costs over 30 years

	Model Inputs			30 Year Results				
State	Cougar habitat area (km^2)	Cougar habitat (%)	Starting deer density (per km^2)	Final deer density (per km^2)	Total DVCs prevented (thousands)	Total avoided costs ($US millions)	Total avoided injuries	Total avoided deaths
CT	3,960	32	6.06	5.26 (4.47-6.03)	4.29 (3.56-5.13)	12.93 (5.12-25.12)	130 (51- 252)	1 (0-2)
KY	19,530	19	7.78	6.76 (5.75-7.77)	27.18 (22.52-32.33)	81.80 (32.48-157.99)	821 (325-1,586)	6 (2-11)
ME	51,651	65	1.97	1.71 (1.46-1.96)	18.19 (15.11-21.69)	54.76 (21.69-106.09)	549 (217-1,064)	4 (2-8)
MD	1,827	7	14.68	12.75 (10.86-14.63)	4.80 (4.00-5.73)	14.46 (5.74-28.02)	145 (58-281)	1 (0-2)
MA	6,696	33	3.64	3.16 (2.71-3.62)	4.37 (3.64-5.22)	13.14 (5.21-25.38)	132 (52-255)	1 (0-2)
MI	38,511	26	17.42	15.12 (12.89-17.35)	120.10 (100.07-142.74)	361.52 (143.3-699.98)	3,626 (1,435-7,021)	26 (10-51)
MO	17,298	10	7.88	6.85 (5.85-7.84)	24.39 (20.22-29.09)	73.43 (29.06-142)	737 (291-1,425)	5 (2-10)
NH	17,469	75	3.36	2.92 (2.49-3.34)	10.49 (8.73-12.49)	31.59 (12.56-61.19)	317 (126-614)	2 (1-4)
NJ	432	2	10.3	8.94 (7.63-10.26)	0.79 (0.66-0.96)	2.40 (0.95-4.66)	24 (9-47)	0 (0-0)
NY	37,728	31	10.73	9.31 (7.94-10.67)	72.46 (60.23-86.40)	218.08 (86.9-422.69)	2,188 (870-4,239)	16 (6-31)
NC	16,038	13	8.33	7.23 (6.16-8.3)	23.91 (19.84-28.45)	71.95 (28.48-139.23)	722 (285-1,397)	5 (2-10)
OH	4,959	5	10.66	9.26 (7.89-10.6)	9.47 (7.89-11.27)	28.49 (11.3-55.24)	286 (113-554)	2 (1-4)
PA	33,912	29	12.91	11.21 (9.57-12.87)	78.17 (65.28-92.92)	235.26 (93.21-454.67)	2,360 (934-4,560)	17 (7-33)
SC	5,049	6	16.2	14.07 (11.98-16.11)	14.65 (12.23-17.40)	44.07 (17.44-85.32)	442 (175-856)	3 (1-6)
TN	19,449	18	9.92	8.62 (7.35-9.87)	34.54 (28.58-41.19)	103.93 (41.25-201.27)	1,043 (413-2,019)	8 (3-15)
VT	15,543	65	4.13	3.59 (3.07-4.11)	11.50 (9.60-13.66)	34.62 (13.77-66.88)	347 (138-671)	3 (1-5)
VA	22,644	22	11.95	10.37 (8.85-11.87)	48.40 (40.25-57.57)	145.68 (57.6-282.25)	1,461 (577-2,831)	11 (4-21)
WV	47,070	75	15.37	13.34 (11.34-15.3)	129.76 (107.99-154.80)	390.58 (154.91-756.67)	3,918 (1,551-7,589)	28 (11-55)
WI	31,023	22	12.78	11.10 (9.41-12.76)	71.11 (58.97-84.46)	213.94 (84.51-415.07)	2,147 (847-4,164)	16 (6-30)

Estimates were based on a density-dependent population projection model for Eastern white-tailed deer with simulated cougar predation. Mean estimates are shown (95% CI). *Starting deer density estimates were based on annual Quality Deer Management Association reports, 2009–2013 (Adams et al. 2009, 2010, 2012; Adams & Ross 2013), multiplied by the proportion of cougar habitat in each state. †Net present value in millions of 2014 US dollars, assuming a 3% discount rate (United States Office of Management and Budget 2013).

Conservation Letters, July 2016, 00(0), 1–9

1, Figure 1). Modeling procedures are detailed in the Supporting Information.

We empirically estimated the impact of cougar recolonization on DVC rates in South Dakota (Table S4), where cougars recolonized during the 1990s (Thompson & Jenks 2010; LaRue *et al.* 2012), using a multiyear before-after-control-impact analysis (Schwartz 2014) of county-level per-capita DVC data from 1994 to 2012. Years were categorized as "before" (i.e., during cougar colonization, 1994–2004) or "after" (i.e., after establishment, 2005–2012). Analyses were restricted to the 22 counties west of the Missouri River, because cougars have colonized approximately half of this area and are rarely seen in eastern South Dakota. Counties were categorized as "control" (i.e., outside cougar range, $n = 12$) or "impact" (i.e., within cougar range, $n = 10$). We examined changes in land use and deer hunting between control and impact counties and found no confounding trends. See Supporting Information "Methods" for details.

Results

Our models predicted that successful cougar recolonization of the Eastern United States would reduce deer density and DVCs by 22% (95% CI = 19–24%) over 30 years, stabilizing at a lower equilibrium (Figure 3). Annual DVCs decreased with deer density, from 5,700 DVCs avoided annually (95% CI = 4,383–7,589) in year 1, to 28,000 DVCs avoided annually (95% CI = 21,500–36,000) in year 30 across study area states (Table 1). In total, our simulations predicted 708,600 fewer DVCs (95% CI = 542,500–912,600) over 30 years with cougars than without cougars in the Eastern United States.

These avoided DVCs resulted in estimated annual avoided costs of $50 million (95% CI = $38–64 million, Figure 3) and prevention of 680 injuries (95% CI = 528–883) and 5 deaths (95% CI = 4–6, Figure 3) annually by year 30. Cumulatively, there were 21,400 fewer injuries (95% CI = 16,400–27,600) and 155 fewer deaths (95% CI = 119–200) during the 30-year simulation period. The net present value of these avoided DVCs, injuries and deaths was $2.13 billion (95% CI = $1.63–2.75 billion) assuming a 3% discount rate (Figure S2; see Supporting Information "Methods").

We estimated that a single cougar would kill 259 deer (95% CI = 212–309) over an average 6-year lifespan (see Supporting Information "Methods"), thereby preventing 8 DVCs (95% CI = 7–10) and avoiding costs with a net present value of $37,600 (95% CI = $30,700–44,800, Figure S2). Modeled cougar density declined through time with deer density, from 0.58–5.16 cougars/100 km^2 in year 1 to 0.51–4.59 cougars/100 km^2 in year 30 (Figure S1).

These results concur with our analysis of empirical data from two states recently recolonized by cougars, North and South Dakota (Thompson & Jenks 2010; LaRue *et al.* 2012). In South Dakota, before-after-control-impact analysis showed that cougars reduced DVCs by 9% within 8 years of establishment (Figure 4, Table S4), preventing an estimated 158 DVCs annually, and worth approximately $1.1 million annually to residents of South Dakota in counties with established cougar populations. Data were of insufficient quality in North Dakota to conduct statistical analysis, but the pattern was similar (Figure 4).

Discussion

Here, we present the first valuation of an ecosystem service provided by a large carnivore. Our projection models indicated that cougar recolonization would substantially reduce costs associated with DVCs in the Eastern United States. Further, our analysis of empirical data from South Dakota suggests that cougar recolonization is already providing this valuable ecosystem service. The benefits of this ecosystem service are likely to be shared broadly among members of society (Figure 5), because those not directly involved in collisions pay for more than 75% of costs through taxes, insurance premiums, traffic delays, and other shared costs (Blincoe *et al.* 2015). By reducing large herbivore populations, cougars and other large carnivores already perform this ecosystem service in areas of the world where vehicle collisions with large herbivores occur. Valuation of such socio-ecological cascades provides a novel tool for predicting and presenting outcomes of carnivore conservation to stakeholders. Further, public perceptions of carnivores may become more positive knowing that these predators reduce their odds of crashing into an ungulate, which is a frequent and frightening cause of human injury, death, and property damage.

Our quantitative projections in the Eastern United States should be interpreted with caution due to uncertainties in this emerging predator-prey system and consequential simplifying assumptions. However, we suggest our assumptions ensured conservative estimates while maintaining the validity of analyses. We assumed that 75% of cougar mortality would be compensatory, with only 25% adding to the net mortality rate of deer. Many eastern deer populations are nutritionally limited (Côté *et al.* 2004), and cougar predation may thus be largely compensatory (Bowyer *et al.* 2014); however this rate has not been empirically estimated. We explored the sensitivity of results to compensation rate (Figure S2) and found that lower rates produced lower deer den-

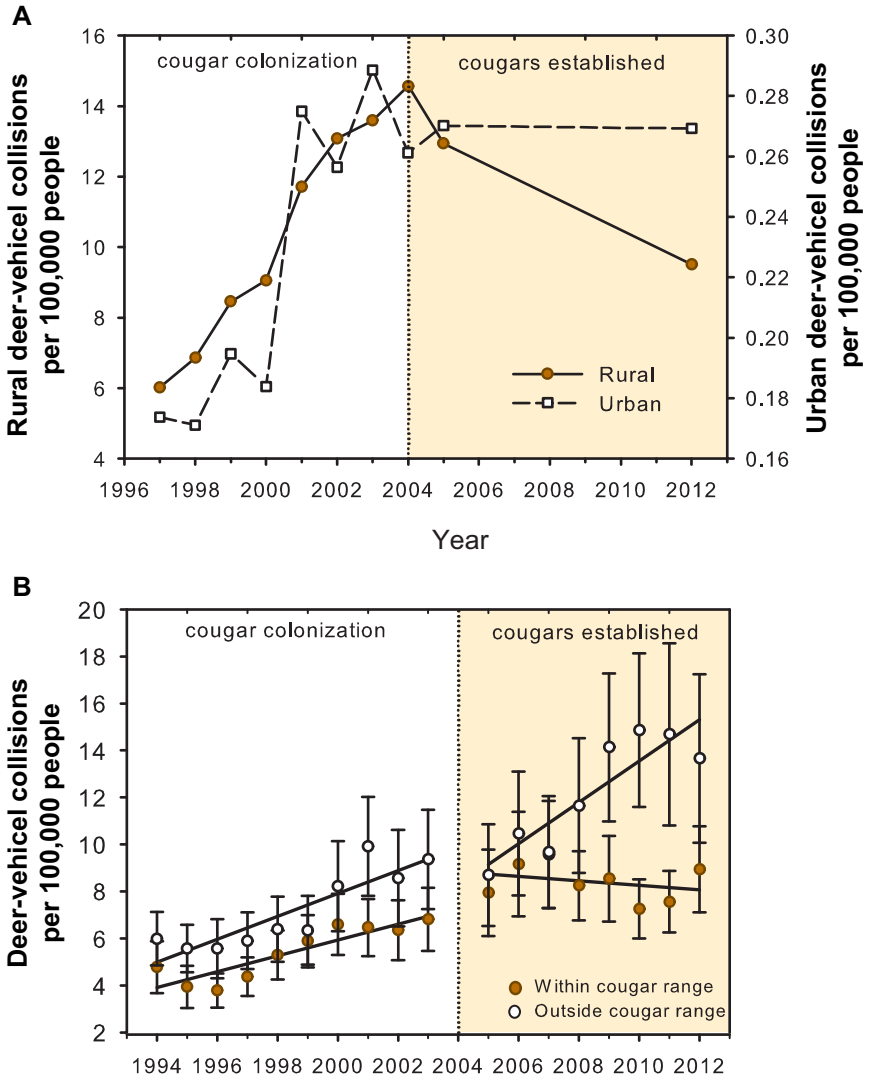

Figure 4 Number of deer–vehicle collisions (DVCs) before and after establishment of cougar populations in (A) North Dakota and (B) South Dakota, 1994–2012. (A) Per capita DVC rates continued to increase in urban areas after cougar establishment but declined in rural areas, where cougars likely had higher impacts. (B) Per capita DVC rates rose at similar rates in counties with and without cougars prior to cougar establishment (1994–2003). After cougar establishment (2004–2012), DVC rates stopped increasing in counties with cougars (filled circles, $n = 10$ counties) but continued to rise in areas without cougars (open circles, $n = 12$ counties). Error bars in (B) show 95% confidence intervals.

sity, higher cougar density, and larger ecosystem services (Figures S1 and S2). Consequently, we used a high compensation rate to ensure conservative results. Cougar predation should become increasingly additive as deer densities decline and nutrition improves (Bowyer *et al.* 2014), and cougars may therefore prevent more DVCs per kill.

Another conservative model assumption was that eastern cougars would be restricted to large forested areas (>2,200 km^2; Figure 1). Yet western cougars prey on deer in suburban landscapes (Wilmers *et al.* 2013; Moss *et al.* 2016), and could do so in eastern states as well. In addition, we modeled deer and hence DVCs as evenly distributed across each state, yet DVC rates are highest in forested areas (i.e., cougar habitat in our model) along with suburban areas (Gunson *et al.* 2011). Moreover, we modeled a decline in injury and fatality rates per DVC due to increases in vehicle safety over time (Figure S3; see Supporting Information "Methods"), but we did not account for increases in health care costs because it was not possible to separate these from other estimated costs of DVCs (Blincoe *et al.* 2015). Health care costs are rising faster than inflation and are projected to increase 6% annually at least through 2023 (Centers for Medicare

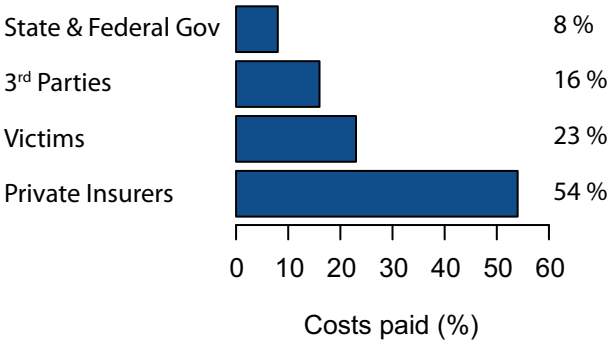

Figure 5 Distribution of the costs of a vehicle collision across society (% of costs paid), broken into categories of state and federal government, third-party individuals and organizations (e.g., charities), crash victims, and private insurers.

& Medicaid Services 2013). Thus, our projections likely underestimated the cost of future DVCs. Finally, we assumed that eastern and western cougars would prey on deer at the same rate. Because alternative large herbivore prey are available in western but not most eastern states, cougar predation rates on eastern deer should be higher. Therefore, our analyses likely estimated the minimum value of the DVC-reduction ecosystem service that cougars could provide.

Although our estimates of cougar effects on deer, DVCs, and associated costs were likely conservative, validations indicated that our models accurately simulated underlying dynamics. We compared the modeled DVC rates without cougar mortality, which were based on vehicle-caused mortality rates of radio-collared deer (Table S1), to reported DVC rates in each state (see Supporting Information "Methods"). Modeled and reported DVC rates were similar ($r = 0.89$, model DVC = 17% lower than true DVC on average; Figure S3). Likewise, in simulations without cougar predation, deer reached equilibrium densities 11% (95% CI = –2% to 23%) higher than current densities, consistent with the slowing growth of many eastern deer populations (Huijser *et al.* 2008). Further, the range of cougar densities modeled in the study region (0.51–5.16 cougars/100 km^2) was within that observed in western states (0.37–7.00 cougars/100 km^2, $n = 27$ studies, Table S5).

Potential socioeconomic benefits and costs of large carnivore recolonization to human society extend well beyond reductions in DVCs. Other benefits include reduced ungulate-caused damage to agriculture and forestry and disease transmission, increased biodiversity-associated services, and new hunting and viewing opportunities of carnivores and trophically benefited species (Côté *et al.* 2004; Ripple *et al.* 2014). Across the Eastern United States, deer damage roughly $3.5 billion annually of crops, nursery plants, landscaping, and tree seedlings (see Supporting Information "Methods"). Recovery of suppressed plants, along with associated animals (e.g., birds, butterflies), would increase forest biodiversity (Côté *et al.* 2004) and possibly enjoyment of outdoor recreationists. Reduced deer density could lower transmission of some diseases, as deer are vectors, or hosts for vectors, of diseases that affect humans and domestic and game animals, including Lyme disease (Côté *et al.* 2004). Finally, cougar hunting is popular in western states and could become so in the east, with associated increases in hunting value (Spiers 2014).

Major costs of large carnivore recolonization include attack on humans, pets, and livestock, and reduced hunting and viewing opportunities of trophically suppressed species (Conover *et al.* 1995; Conover 1997; Aiken & Harris 2006). In the United States and Canada, there were 153 confirmed cougar attacks and 21 human fatalities from 1890 to 2008 (Mattson *et al.* 2011). Yet we estimate cougars would indirectly save far more people from death (5 per year) and injury (680 per year) by reducing DVCs than they would likely directly kill (<1 per year) or injure (~5 per year). However, fear of cougar attacks may reduce enjoyment for some outdoor recreationists. Similarly, cougar depredation of livestock is rare, accounting for only 8.6% and 5.6% of total cattle and sheep depredation, respectively (National Agricultural Statistics Service 2005, 2011). Livestock populations are small in eastern compared to western states, and thus lost livestock values are likely to be lower as well, on the order of $2.35 million per year (see Supporting Information "Methods"). Cougars also attack pets, although this cost is poorly quantified due to low reporting rates (Torres *et al.* 1996). In addition, deer have considerable value to hunters and wildlife viewers (U.S. Fish and Wildlife Service 2011). Deer density and hunter satisfaction are not closely correlated, however, making this cost difficult to value (Van Deelen & Etter 2003; Aiken & Harris 2006; Hammitt *et al.* 2010).

A full cost–benefit analysis was not possible due to the large study region and prospective nature of our analyses. However, such analyses, grounded in empirical data, are important next steps for evaluating the net socioeconomic impacts of large carnivores, and for understanding how the costs and benefits of carnivore restoration are distributed across society. It is likely that livestock producers, rural residents that fear cougars, and hunters bear the brunt of the costs of large carnivores, while agricultural producers, homeowners with landscaping, drivers, local governments, and insurance agencies reap the majority of benefits (Figure 5). Effects of carnivore populations on wildlife viewers, who are increasing as a proportion of the population (U.S. Fish and Wildlife Service

2011), may be mixed, because fear of cougar attacks and lost ungulate viewing opportunities and may be compensated for by increased abundance of other valuable species. If hunter participation and total number of deer hunters continue to decline in the United States (Riley *et al.* 2003; Aiken & Harris 2006), the total cost of cougars via reduced satisfaction of deer hunters will likewise decline, and shouldered by a decreasing segment of the population. Understanding and potentially compensating for inequalities in allocation of costs and benefits could improve conservation outcomes for large carnivores such as cougars as they recolonize.

Large carnivores are highly polarizing in human society (Treves & Bruskotter 2014). In an increasingly human-dominated world, efforts to conserve large carnivores must succeed outside protected areas (Treves & Bruskotter 2014; LaRue & Nielsen 2015). Societal acceptance of large carnivores living in proximity to humans is therefore a critical yet daunting conservation goal (Carter *et al.* 2012; Treves & Bruskotter 2014; Moss *et al.* 2016). While documenting the ecological benefits of carnivores is an important tool for conservation, such benefits do not outweigh the perceived costs of carnivores for many stakeholders (Treves & Bruskotter 2014). Tolerance for large, fierce carnivores may depend on demonstrating, as we do here, that they can provide tangible, valuable ecosystem services to many members of society.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Supporting Information

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