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Research Article



Regional-Based Mitigation to Reduce Wildlife–Vehicle Collisions

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ABSTRACT Vehicular collisions with large ungulates pose serious challenges for managing and conserving large ungulates throughout the world. Despite the global frequency, mitigation efforts are mostly limited to localized hotspots and not effective on broad scales. Our goal was to determine whether dynamic, regional attributes could inform broader focus for mitigation efforts. We applied a spatiotemporal dynamic model to examine the regional influences on white-tailed deer (Odocoileus virginianus)-vehicle collisions (DVCs) throughout the Midwest United States from traffic, abundance of deer, and composition and configuration of the landscape during 2000-2011. The regions included eco-zones representing landscape dominated by shelter-forage habitats with ubiquitous and abundant distribution of deer (i.e., forest-agriculture matrix), landscape dominated by agriculture with sparse refugia (i.e., agriculture), and landscape dominated by forests with seasonal migration for deer (i.e., northern forest). We found little fluctuation in the factors affecting collisions through time but substantial differences among regions. In the forest-agriculture matrix eco-zone, fragmentation of the landscape was the most important predictor of collisions. In the agriculture eco-zone, traffic and abundance of deer best predicted collisions. In the northern forest eco-zone, the predictors of collisions were variable and likely related to winter severity and deer migration. This research provides new justification for broadening the focus of current mitigation measures to regional extents. In regions dominated by forest and agriculture, new policies that reduce habitat fragmentation should be the primary focus for reducing collisions. Reducing abundance of ungulates will have the most direct effect in regions dominated by agriculture. Finally, a variety of seasonal and local mitigation measures will be most effective in northern forests where large ungulates migrate. © 2018 The Wildlife Society.

KEY WORDS accident, collision risk, dynamic process, *Odocoileus virginianus*, road ecology, spatiotemporal model, white-tailed deer.

Vehicular collisions with large ungulates such as deer (*Odocoileus* spp.), moose (*Alces alces*), and elk (*Cervus canadensis*) are widespread and increasingly pervasive human-wildlife interactions throughout North America and Europe (Bruinderink and Hazebroek 1996, Seiler 2004, Bissonette et al. 2008, Conover 2010). Since 1990, human fatalities from these collisions (mostly deer) have more than

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²Current affiliation: USDA/APHIŠ/Wildlife Services, National Wildlife Research Center, 4101 LaPorte Ave., Fort Collins, CO 80521, USA doubled (Sullivan 2011). Numerous ungulates are killed, with an estimated 92% mortality rate following collisions (Allen and McCullough 1976). Additionally, wildlife-vehicle collisions comprise one of the largest sources of economic loss caused by wildlife, averaging \$6,717 (USD)/ collision and \$8 billion/year in property damage (Huijser et al. 2008).

Most strategies for mitigating vehicular collisions focus on reducing collisions at localized hotspots (Huijser et al. 2008). These strategies include localized wildlife fencing, underpasses and overpasses, animal detection systems, vegetation management, wildlife hunting or culling, and dynamic or static warning signs. These techniques have highly variable effectiveness for reducing collisions at hotspots, ranging from 0–100% effective (Huijser et al. 2008). Despite decent effectiveness in some areas, the regional odds for motorists being involved in collisions with ungulates have remained

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high (e.g., for deer: State Farm[®] https://www.statefarm. com/about-us/newsroom/2015/09/14/deer-collision-data).

Recent studies have linked regional features of the landscape (e.g., landscape connectivity) to wildlife-vehicle collision (WVC) locations (Grilo et al. 2011, Girardet et al. 2015), but suggestions for regional mitigation strategies are limited. Regional strategies for improving road infrastructure, such as road optimization by decommissioning some roads, are being suggested to improve habitat quality for ungulates (D'Amico et al. 2016), and may reduce WVCs. Furthermore, predictive models have suggested that mitigation measures should be applied across large geographic spaces to reduce WVCs throughout the world (Malo et al. 2004, Hothorn et al. 2012, Visintin et al. 2016), but these measures may be regional-specific.

Vehicular collisions with white-tailed deer (*O. virginianus*; deer) exemplify the pervasive problem of widespread WVCs without an effective means of mitigation (Conover 2010). An estimated >1 million deer-vehicle collisions (DVCs) occur each year throughout the United States (Conover et al. 1995) and are rising (Huijser et al. 2008). The Midwest region of the United States experiences the highest rates of DVCs, and therefore some states manage for publicly tolerable levels of DVCs. For example, Illinois implemented a deer-management objective in 2008 to keep the rate of DVCs at \leq 207 DVCs/billion kilometers traveled (University of Illinois Extension 2013), although success of this management is uncertain.

We hypothesized that regional attributes of the landscape, abundance of deer, and anthropogenic factors are associated with widespread extents of DVCs, and these associations vary by region. For instance, increased abundances of deer have resulted from changes in landscape structure and wildlife management during the past several decades (Coulson 1999), and led to increases in DVCs. Meanwhile, human populations have increased and dispersed away from centralized cities (i.e., suburbanization; Jordan et al. 1998, Alig et al. 2004, Baum-Snow 2007). These partially developed, suburban environments maintain high abundances of deer by providing food, shelter, and refuge from hunting (Cornicelli et al. 1996, Lovely et al. 2013). In addition, agricultural activities throughout the Midwest continue to maintain high densities of deer (Roseberry and Woolf 1998) especially when coupled with interconnected patches of forests (Walter et al. 2009). The current trajectory of suburbanization (Alig et al. 2004), agriculture, and reduced winter severity from climate change (Thompson et al. 1998) are all likely to influence DVCs across regional scales; therefore, a broader understanding of these factors is needed to develop broader solutions for reducing DVCs.

Two unanswered questions have limited our ability to understand variation in the frequency of DVCs across large regional extents. Is the frequency of DVCs influenced by the temporally dynamic nature of environmental predictors at regional extents? Do environmental predictors influence the frequency of DVCs differently across large regions? Our objectives were to answer each of these questions by examining the spatiotemporal influences on DVCs using



Figure 1. Study area for examination of dynamic, space-time influences of white-tailed deer-vehicle collisions at the county level throughout the Midwest, USA, 2000–2011.

12 years of data in 3 eco-zones throughout the Midwest United States (i.e., forest-agriculture matrix, agriculture, and northern forest). Specifically, we examined changes in the regional factors influencing DVCs through time and across space. We hypothesized that mitigation measures for DVCs could be region-specific, providing broader guidance for reducing collisions with large ungulates at large spatiotemporal scales.

STUDY AREA

The study area (584,493 km²) was comprised of 355 counties from Illinois, Iowa, Michigan, and Wisconsin, USA (Fig. 1). The area was generally classified as a humid continental climate with cold winters and warm to hot, wet summers (Kottek et al. 2006), and topography that was gently rolling to flat with elevation ranging from 85–603 m above sea level. This area contained varying land uses and land covers, primarily dominated by agriculture, forests, or both (Table 1). The most ubiquitous and abundant ungulate in this region was white-tailed deer (Kays and Wilson 2009). Overall, this region included approximately 981,765 km of roads for an overall road density of 1.68 km/km².

Table 1. Proportion of reclassified land-cover and land-use types for 3 ecozones in the Midwest United States from the 2001 and 2006 National Land Cover Databases.

Proportions of land use and land cover by year						
	Northern forest		Forest-agriculture matrix		Agriculture	
Class	2001	2006	2001	2006	2001	2006
Agriculture	0.16	0.16	0.56	0.56	0.78	0.78
Forest	0.68	0.67	0.24	0.24	0.10	0.10
Developed	0.05	0.05	0.13	0.13	0.08	0.08
Rangeland	0.05	0.05	0.02	0.02	0.03	0.03
Wetlands	0.02	0.02	0.01	0.01	0.00	0.01
Water	0.03	0.03	0.02	0.02	0.01	0.01
Other	0.00	0.00	0.00	0.00	0.00	0.00

We divided the region into 3 eco-zones: forest-agriculture matrix, agriculture, and northern forest based on the province divisions of ecoregions for the United States (Bailey 1983, 1995). The forest-agriculture matrix eco-zone was within the eastern broadleaf forest (continental) ecosystem province. The land cover and land use of this province was a mix of oak (Quercus spp.)-hickory (Carya spp.) stands with maples (Acer spp.) and American beech trees (Fagus grandifolia), and corn, soybean, wheat, and livestock production. The agricultural eco-zone was within the prairie parkland (temperate) ecosystem province. This province was dominated by corn, soybean, and livestock production, and intermixed patches of native grasslands such as big bluestem (Andropogon gerardii), little bluestem (A. scoparius), switchgrass (Panicum virgatum), and Indian grass (Sorghastrum nutans). The northern forest eco-zone was within the Laurentian mixed forest ecosystem province. The land cover and land use of this province was dominated by stands of conifers, deciduous trees, and mixed coniferdeciduous trees, such as balsam fir (Abies balsamea), pines (Pinus spp.), black spruce (Picea mariana), eastern white cedar (Thuja occidentalis), maples, yellow birch (Betula alleghaniensis), and American beech.

For the purposes of this study, each eco-zone was representative of differences in ungulate ecology based on regional attributes. The forest-agriculture matrix was associated with ubiquitous distribution and use of deer (Alverson et al. 1988, Roseberry and Woolf 1998). The juxtaposition of forests and agriculture provide ample refugia, foraging, and edge habitats that deer prefer (Williamson and Hirth 1985), and therefore generate high population abundances. The agriculture eco-zone was dominated by a single type of land use, agriculture, and therefore provided sparse forests for refugia. In this landscape, the distribution and movements of deer are largely reflective of the sparsely located forests (Nixon et al. 1991, Brinkman et al. 2005). The northern forest eco-zone was associated with primarily forested land covers with small intermixed agriculture. Deer undergo seasonal migration to winter deeryards (Verme 1973, Van Deelen et al. 1998) located in the southern portions of this eco-zone, dependent on climatic conditions (Brinkman et al. 2005).

METHODS

Data Collection

We collected data from several sources, which were compiled annually at the county level for the states of Illinois, Iowa, Michigan, and Wisconsin during 2000–2011 (Appendix 1). We excluded Menominee County, Wisconsin because no reports of DVCs were obtained. We considered DVCs as the reported numbers of traffic accidents involving deer during each year. Counts of DVCs were biased low because not all collisions were reported. Reporting rates of DVCs have been estimated to be 42–50% (Decker et al. 1990, Romin and Bissonette 1996, Marcoux and Riley 2010), but statistical models of DVCs were reported to be robust with only \leq 30% of collisions being reported (Snow et al. 2015); therefore, we

amount of property damage exceeded a certain amount. The amounts of property damage varied by state and year (Appendix 1), but the average amount of damage from DVCs exceeded the minimum amounts required for reporting in all cases (Huijser et al. 2008). We compiled records of antlered and antlerless deer harvested in each county each year. Fewer restrictions were placed on the number of individuals allowed to purchase licenses to burt antlered deer, which the majority of burters

harvested in each county each year. Fewer restrictions were placed on the number of individuals allowed to purchase licenses to hunt antlered deer, which the majority of hunters prefer to harvest (Fawley and Rudolph 2014). Therefore, in the absence of consistently developed annual deer populations at the county level, we used the number of antlered deer harvested during year t as an index to represent the abundance of deer during year t (abundance). Antlerless permits were more regulated with intent to remove a number of female deer to achieve desired effects on population abundance (Brown et al. 2000). Therefore, we used the number of antlerless deer harvested during year t-1 as an index for the effect of management on the population of deer during year t (antlerless lag).

did not expect reporting rates to be problematic. We used the

reported number of DVCs per county to represent an index

of the true frequency of collisions. Collisions with deer were reported when a human injury or death occurred, or the

We compiled shapefiles depicting locations of all roads in each state to identify public roads using ArcGIS (version 10.1; Environmental Systems Research Institute, Redlands, CA, USA). We used National Functional Classification categories to exclude private roads. We calculated the length of roads and road density for each county (km/km²) using the Geospatial Modeling Environment program (version 0.7.2.1, Spatial Ecology LLC). We used estimates of annual vehicle kilometers traveled (traffic) compiled from the Department of Transportation for each state to measure the intensity of motorists on roadways in each county during each year. We also examined traffic² to identify any nonlinear effects from traffic. We considered the interaction (traffic × abundance) to examine the interacting relationships between the volume of traffic and the abundance of deer on the frequency of DVCs. Lastly, we compiled the numbers of registered vehicles in each county (vehicles registered) to provide an additional index of the number of motorists on roads.

We used ArcGIS to reclassify the 2001 and 2006 National Land Cover Database (Homer et al. 2007, Fry et al. 2011) from 16 to 7 classes (i.e., agriculture, forest, rangeland, developed, wetlands, water, and other; Table 1) that represented important land cover and land use classes for deer (Anderson et al. 1976). We used the 2001 database to represent the time 2000–2005, and the 2006 database to represent 2006–2011. We calculated 5 landscape metrics using program FRAGSTATS (version 4.1, University of Massachusetts, Amherst, MA, USA) to quantify important land covers and configurations for deer in each county. We calculated the proportions of agriculture (agriculture), forest (forest), and developed (developed) land covers in each county. The contrast-weighted edge density (edge density) represented the sum of the borders between cover types multiplied by a corresponding contrast weight (i.e., weight = 1 for agriculture, rangeland, and forest cover types, and weight = 0 for all other cover types) divided by the area of the county (km/km²). We used contagion as an index of the spatial aggregation and interspersion of similar patch types. A contagion value of 0 represented a highly fragmented and intermixed landscape, whereas a value of 100 represented a landscape comprised of a single patch.

Study Design and Data Analysis

Counties and years were our spatial and temporal units of observation, respectively. Each county was associated with an annual response variable (count of DVCs), 10 main effects (traffic, traffic², abundance, antlerless lag, vehicles registered, agriculture, forest, developed, edge density, and contagion), and 2 interactions (traffic × abundance, and contagion × abundance). We standardized the main effects before calculating the interaction and quadratic terms. We conducted an intercorrelation analysis of the data and excluded the predictor(s) that were less correlated with DVCs from any correlated pair of predictors from our models (i.e., $|r| \ge 0.60$; Program R version 2.15.1; R Development Core Team, Vienna, Austria). We used all remaining predictors in subsequent models.

We used a hierarchical Bayesian modeling framework to develop a dynamic, space-time model for each eco-zone (e=1, 2, ..., E) to examine influences on DVCs at the county level. For our model, we used the counts of DVCs observed in each county (s=1, 2, ..., N) during each year (t=1, 2, ..., T) as the response variable using MATLAB (version R214a; The MathWorks, Natick, MA, USA). We incorporated the offset $O_{s,t}$ of area (km^2) of each county to account for differences in areas of counties. The model was structured as:

$$y_{s,t} \sim Poisson(O_{s,t}e^{\eta_{s,t}});$$

$$\eta_{s,t} = x'_{s,t}\beta_{e,t} + w_{s,t};$$
 (1)

for county *s* in eco-zone *e*, where $x'_{s,t}$ is comprised of columns vectors $(x^1_{s,t}, \ldots x^p_{s,t})$ for *p* regressors including the

intercept $(x_{s,t}^1 \equiv 1)$ with fixed effect $\beta_{e,t}$; $w_{s,t}$ represents observation-level random effects to model potential spatial correlation and overdispersion for count response (Harrison 2014). The temporal structure for the coefficients and spatial random effects followed:

$$eta_{e,t} = eta_{e,t-1} + u_{e,t}, u_{e,t} \sim N\left(0, \sum_{u}\right);$$
 $w_{s,t} = w_{s,t-1} + v_{s,t};$
(2)

so that the priors of $\beta_{e,t}$ and $w_{s,t}$ were dynamically informed by the posteriors of $\beta_{e,t-1}$ and $w_{s,t-1}$, respectively. We assumed the increment $v_{s,t}$ admits the conditional autoregressive (CAR) structure (Besag et al. 1991), which is frequently adopted to capture the spatial correlation for areal data. We employed the CAR specification parameter dependence with a spatial (Castro to alleviate spatial confounding: et al. 2015) $v_{s,t} \sim N\left(0, \tau_t^2 (M - \gamma_t W)^{-1}\right)$, where *W* is the binary adjacency matrix, *M* is the diagonal matrix with number of adjacent counties for individual county, τ_t^2 captures unmodeled sources of variation by Poisson distribution to account for overdispersion, and γ_t measures the spatial dependence (0 = no dependence). We assumed both parameters τ_t^2 and γ_t to be year-specific as the increments $v_{s,t}$ can vary by scale across a different year t. To identify the most parsimonious model for making inference, we compared 4 models for best fit using 5 predictive scoring rules for count data (i.e., logarithmic, quadratic, spherical, ranked probability, and Dawid-Sebastiani score) and root mean squared error (definitions provided in Czado et al. 2009). These scoring rules represent unique summary measures to evaluate the probability forecasts from the models based on predictive distributions and observed data (Czado et al. 2009). We selected the top performing model as the model with the best fit from the majority of the scoring rules:

Model 1: log(offset) + state effect + intercept Model 2: log(offset) + state effect + intercept + main effects

Table 2. Annual averages and standard errors for white-tailed deer-vehicle collisions (DVCs) and associated predictors for counties within 3 eco-zones in the Midwest United States during 2000–2011.

		Northern forest	Forest-agriculture matrix	Agriculture
Number of counties		78	140	137
DVCs	\overline{x}	358.3	471.0	158.9
	SE	9.9	38.4	30.2
Road density (km/km ²)	\overline{x}	1.5	2.2	1.3
·	SE	0.1	0.1	0.02
Human density (people/km ²)	\bar{x}	20.7	85.1	26.7
	SE	3.9	20.0	3.6
Abundance of deer (antler harvest)	\overline{x}	2,748.8	1,736.9	575.2
	SE	149.6	119.4	31.8
Traffic (million km traveled)	\overline{x}	552.6	1,766.3	622.9
	SE	62.2	328.7	69.3
Proportion of agriculture	\overline{x}	17.7	56.8	77.2
	SE	2.1	1.5	1.0
Contagion (fragmentation)	\overline{x}	63.3	62.9	72.6
	SE	1.0	0.6	0.7

Table 3. Comparison of model validation metrics for 4 models not including spatial random effects (NS) and including spatial random effects (SP) for predictive models of white-tailed deer-vehicle collisions (DVCs) by counties within 3 eco-zones in the Midwest United States during 2000–2011. Values with asterisks represent the top competing model for each metric.

Comparison of model validation metrics

	Mo	del 1	Model2		Model 3		Model 4	
Measure	NS	SP	NS	SP	NS	SP	NS	SP
Logarithmic	6.5906	6.5569	6.5439	6.5287*	7.3996	7.6072	7.5020	7.7089
Quadratic	-0.0053	-0.0059^{*}	-0.0046	-0.0047	-0.0045	-0.0047	-0.004	-0.0041
Spherical	-0.0922	-0.0937^{*}	-0.0899	-0.0905	-0.0893	-0.0901	-0.0872	-0.0877
Ranked probability	22.0500	21.9025	21.2988	21.2248*	23.6649	23.8274	24.4949	24.7695
Dawid-Sebastiani	12.1613	12.0577	11.9941	11.9772*	13.3603	13.6344	13.5387	13.8105
Root mean squared error	40.4243	40.3410	38.0943	38.0550*	48.1740	49.9735	49.4911	51.5529

Model 3: log(offset) + state effect + intercept + main effects + quadratic

Model 4: log(offset) + state effect + intercept + main effects + quadratic + interactions

We also compared each of these models with spatial and nonspatial random effects. We included a state effect for each model to account for differences among DVC reporting requirements for each of the 4 states, with Iowa considered the state of reference. We assessed model performance using 10-fold cross validation by randomly partitioning the N=355 observations for the last year (2011) into 10 bins containing 10% of the observations for each state.

We examined 3 Markov chain Monte Carlo (MCMC) runs of 20,000 iterations with burn-ins of 15,000 and thinned by 5 iterations. We examined the median and 95% credible intervals (CrIs) from the distributions of the estimated regression coefficients to identify influences from the environmental predictors on the frequency of DVCs. Specifically, we examined any overlap of zero by the 95% CrIs to indicate influences on the count of DVCs. We used the final year of the analysis (2011) to examine effect plots for each of the environmental predictors. The final year included the most information from the time-evolving priors, and was most pertinent for current management strategies.

RESULTS

Overall, 1,387,948 DVCs were reported during our 12-year study averaging 115,662 DVCs/year. The average count of DVCs was highest in the forest-agriculture matrix, followed by the northern forest and then agriculture eco-zones (Table 2). We excluded antlerless lag, vehicles registered, developed, edge density, and forest from analysis because of collinearity with other predictor variables. The remaining predictors examined were traffic, abundance, agriculture, and contagion.

Each of the 4 models had better model fit when the spatial random effects were included (Table 3). Model 2 with the spatial random effects, including the main effects without the quadratic or interaction terms, was considered the top performing model. We therefore used model 2 to make subsequent inferences. The estimates of regression coefficients and 95% CrIs were stable throughout the 12 years for each eco-zone (Fig. 2), although in some cases the estimates changed between overlapping zero or not.

Traffic had a positive effect in the northern forest eco-zone (during the first 7 years), and a smaller positive effect in the agriculture eco-zone (Fig. 2). Traffic had minimal influence in the forest-agriculture matrix eco-zone where the values of traffic were largest (Fig. 3). Agriculture had a positive effect on the frequency of DVCs in the eco-zone with the least amount of agriculture (i.e., northern forest) only during the



Figure 2. Estimates of regression coefficients and 95% credible intervals from dynamic models for examining the influences of environmental predictors on the frequencies of white-tailed deer–vehicle collisions at a county level throughout the Midwest, USA, 2000–2011. Contagion is an index of fragmentation among land covers per county per year where lower values represent more fragmented landscapes.



Figure 3. Predicted counts of deer–vehicle collisions (DVCs) in counties throughout 3 eco-zones in the Midwest, USA during 2010 using the best fitting model. Solid lines indicate that the relationship was identified as being statistically influential in that eco-zone. Traffic is represented as annual average vehicle kilometers traveled. Contagion is an index of fragmentation among land covers per county per year where lower values represent more fragmented landscapes.

last 4 years (Figs. 2–3). Similarly, abundance had a positive effect in the eco-zones with the lowest index of deer (i.e., northern forest and agriculture eco-zones) only for 3 years. Contagion had a negative effect in the eco-zone with the most fragmentation (i.e., forest-agriculture matrix) during all 12 years, and during a few years in the other eco-zones.

We found obvious differences in reporting of DVCs by state, necessitating the inclusion of the state effect into the models. Michigan had the strongest positive effect on the frequency of DVCs, followed by Illinois (Fig. 4). Reporting of DVCs was similar in Iowa and Wisconsin. The posterior median with 95% credible interval of the spatial dependence parameter suggested positive effects during 9 of the 12 years, indicating that the spatial arrangement of counties influenced where DVCs occurred. For most counties, the bestfitting model (Table 2) predicted the count of DVCs during 2011 with a high degree of accuracy from 10-fold cross validation (Fig. 5). In Iowa the model predicted less well where there was little variation in the ubiquitously low counts of DVCs reported across the state, and therefore influential trends for DVCs were difficult and detect and predict at this regional scale.

DISCUSSION

Results provide empirical evidence that the determinants of vehicular collisions with wildlife, such as large ungulates, are dependent on broader-scale ecological processes than previously realized and managed. Localized investigations also found similar factors influence DVCs (Sudharsan et al. 2005, Farrell and Tappe 2007), and moose–vehicle collisions (Seiler 2004) on smaller-scales but have not associated larger-scale patterns across eco-zones. Our analysis reveals that the effectiveness of mitigation measures is dependent on the regional characteristics of eco-zones.

The highest frequency of DVCs was reported in the ecozone with the most abundant deer (i.e., forest-agriculture matrix), which also had the highest volume of traffic. The only detectable influence on DVCs was increasing landscape fragmentation, which corresponded with more collisions. Fragmentation in this landscape is attributed to a mosaic of land covers and land uses, mostly from intermixed forest and agriculture. These landscapes are associated with the ubiquitous use and distribution of deer (Alverson et al. 1988, Roseberry and Woolf 1998) and also with high



Figure 4. Estimates of regression coefficients and 95% credible intervals for random state effects and random spatial effects for examining the spatial influences of environmental predictors on the frequencies of white-tailed deer–vehicle collisions at a county level throughout the Midwest, USA, 2000–2011.



Figure 5. Observed and predicted number of white-tailed deer–vehicle collisions (DVCs), and measure of model uncertainty (i.e., spread of 95% credible intervals), for model validation in the Midwest, USA, 2011. Red stars indicate counties where the observed number of DVCs was outside of the predicted 95% credible intervals.

frequencies of DVCs (Bashore et al. 1985, Finder et al. 1999, Farrell and Tappe 2007), suggesting the risk of DVCs is widespread throughout this eco-zone. In the forest-agriculture matrix eco-zone, we detected no effects from traffic, proportion of agriculture, or abundance of deer. In particular, a lack of effect from traffic is contrary to other studies on smaller scales (Farrell and Tappe 2007, Ng et al. 2008) and likely stems from the mixture of high volumes of traffic and high abundance of deer that were characteristic throughout this region. We expect that this mixture generated an underlying high frequency of DVCs across the region, and any localized variations in these predictors did not change this frequency in a detectable manner.

Within the eco-zone dominated by agriculture, DVCs were highest in counties with more traffic volume and deer abundance. Therefore, for a region that is mostly comprised of a single type of land use used by ungulates for foraging, variation in traffic and abundance are better predictors of DVCs than composition of the landscape. However, within this region counties with more forest and riparian land covers have higher localized abundances of deer, especially after crops are harvested (Vercauteren and Hygnstrom 1998), which may influence DVCs. These results corroborate the findings of a similar study in Arkansas, USA that exhibited similar characteristics as this eco-zone (Farrell and Tappe 2007). We found no relationship between DVC and the proportion of agriculture, suggesting that the underlying frequency of DVCs is not related to county-specific variations in the amount of agriculture.

Within the eco-zone with seasonally migrating deer (i.e., northern forest), DVCs were highest in counties with higher traffic volume, proportion of agriculture, deer abundance, and landscape fragmentation. Collisions were highest in the southern counties with more agriculture and landscape fragmentation, likely because these landscapes sustain more deer (Alverson et al. 1988). However, the seasonal movements of ungulates in this region could be influencing the frequencies of collisions. For instance, relationships between the predictors and DVCs somewhat varied throughout time, more so than other in eco-zones. One possible explanation is that less severe winters result in less migration into the southern counties of this eco-zone, therefore lessening the

impact that agriculture and fragmentation have on DVCs. Examination of the relationship between climate and interannual DVCs in the northern forest represent a line of important future research.

Temporally, the influences on collisions with deer were mostly stable during the last 12 years. Previous studies identified spatial patterns to DVCs (Huijser et al. 2008, Ng et al. 2008, Danks and Porter 2010, Snow et al. 2014) but none have linked findings to any temporal trends. Twelve years may not be sufficient to observe major shifts in the distributions of DVCs, especially considering a large-scale analysis of influences. Anthropogenic changes to the landscape have occurred during much of the last century (Harris 1943); therefore, long-term collection of collision data is needed to relate with those changes. However, our findings indicate that the frequencies of collisions with large ungulates are unlikely to diminish in any regions in the absence of effective mitigation.

MANAGEMENT IMPLICATIONS

Our results confirm that permanent mitigation strategies specific to each eco-zone are best for widespread reduction in collisions. Specifically, in the forest-agriculture matrix with ubiquitous distributions of ungulates, roads, and collisions, policies and planning that reduce habitat fragmentation should be the primary focus for reducing collisions. In the highly agricultural landscapes, reducing the abundance of ungulates will have the most direct effect for reducing collisions. In the northern forest eco-zone, mitigation strategies will need to be most dynamic, including reduction of traffic, reduction of ungulate abundance, and enhanced policies that reduce habitat fragmentation particularly from agriculture. Regardless of the eco-zone, our results corroborate that upfront investments in mitigation measures should result in long-term reductions in collisions because regional influences are temporally stable. In turn, these investments may unlock long-term safety for motorists and economic gains (Schwabe et al. 2002, Huijser et al. 2009). Indeed, a national commitment has been proposed for development of wildlife crossing structures on large scales demonstrating these benefits (ARC Solutions 2017). Finally, our results exhibit the importance of consistent reporting of WVCs to

enhance the development of larger-scale and more efficient mitigation strategies. More consistent reporting is needed across larger geographic scales.

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APPENDIX 1

Description and sources of data used to examine the dynamic, space-time influences of white-tailed deer-vehicle collisions (DVCs) throughout the Midwest, USA, 2000-2011.

Location	Data ^a	Description	Data source
IL	DVCs	Vehicle crashes involving deer with >\$500 in property damage (2000–2009), >\$1,500 for insured drivers and >\$500 for uninsured drivers (2009–2012), or bodily injury	Illinois Department of Transportation
	Deer harvest	Estimated number of antlerless and antlered deer harvested by firearm and archery	Illinois Department of Natural Resources
	Traffic	Estimated annual vehicle kilometers traveled on roads by all vehicles	Illinois Department of Transportation
	Registered vehicles Roads	Number of registration counts 2011 shapefile of roads with federal functional classification representing public roads	Illinois Secretary of State Illinois Department of Transportation
IA	DVCs	Vehicle crashes involving deer with >\$1,000 in property damage (2000–June 2010), >\$1,500 (July 2010–2012), or bodily injury	Iowa Department of Natural Resources
	Deer harvest	Estimated number of antlerless and antlered deer harvested by firearm and archery	Iowa Department of Natural Resources
	Traffic	Estimated annual vehicle kilometers traveled on roads by all vehicles	Iowa Department of Transportation
	Registered vehicles Roads	Number of registration counts 2006 shapefile of roads with federal functional classification representing public roads	Iowa Department of Transportation Iowa Department of Natural Resources Geographic Information Systems Library
MI	DVCs	Vehicle crashes involving deer with >\$400 in property damage (2000–2003), >\$1,000 (2003– 2012), or bodily injury	Michigan State Police
	Deer harvest	Estimated number of antlerless and antlered deer harvested by firearm and archery	Michigan Department of Natural Resources
	Traffic	The estimated total number of kilometers traveled annually by motor vehicles on Michigan trafficways	Michigan Department of Transportation
	Registered vehicles	Number of registration counts excluding trailers and trailer coaches	Michigan State Police, Office of Highway Safety Planning
	Roads	2012 shapefile of roads with national functional classification representing public roads	Michigan Center for Geographic Information
WI	DVCs	Vehicle crashes involving deer with >\$1,000 in property damage (2000–2012) or bodily injury	Wisconsin Department of Transportation
	Deer harvest	Estimated number of antlerless and antlered deer harvested by firearm and archery	Wisconsin Department of Natural Resources
	Traffic	The estimated total number of kilometers traveled annually by motor vehicles on Wisconsin trafficways	Wisconsin Department of Transportation
	Registered vehicles	Numbers of current and non-expiring registrations	Wisconsin Department of Transportation, Bureau of Vehicle Services
	Roads	2013 shapefile of roads with roadway categories representing public roads.	Wisconsin Department of Transportation
Region	County boundaries	2010 seamless national file with no overlaps or gaps between parts, designed to stand alone as an independent data set, or can be combined to cover the entire nation	U.S. Census Bureau (TIGER/Line Shapefile)
	Land-cover and land-use maps	30-m resolution land use and land cover maps for the conterminous United States generated from remote sensing with 79% (2001) and 78% (2006) overall accuracy	U.S. Geologic Survey (2001 and 2006 National Land Cover Database)

^aThe response variable was the number of DVCs per county per year. Explanatory predictors were the numbers of antlered deer harvested per county per year as an index of deer population, annual vehicle kilometers traveled (traffic) per county per year as an index of traffic volume, number of registered vehicle per county per year as an index of the number of motorists, maps of all public roads for each county to calculate the densities of roads per county (km/km²), maps of the boundaries of counties, and maps of the land cover and land use for each county.