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Spatial risk modeling of cattle depredation by black vultures in the midwestern United States

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Abstract

Negative economic impacts resulting from wildlife disrupting livestock operations through depredation of stock are a cause of human-wildlife conflict. Management of such conflict requires identifying environmental and non-environmental factors specific to a wildlife species' biology and ecology that influence the potential for livestock depredation to occur. Identification of such factors can improve understanding of the conditions placing livestock at risk. Black vultures (*Coragyps atratus*) have expanded their historical range northward into the midwestern United States. Concomitantly, an increase in concern among agricultural producers regarding potential black vulture attacks on livestock has occurred. We estimated area with greater or lesser potential for depredation of domestic cattle by black vultures across a 6-state region in the midwestern United States using an ensemble of small models (ESM). Specifically, we identified landscape-scale spatial factors, at a zip code resolution, associated with reported black vulture depredation on cattle in midwestern landscapes to predict future potential livestock depredation. We hypothesized that livestock depredation would be greatest in areas with intensive beef cattle production close to preferred black vulture habitat (e.g., areas with fewer old fields and early successional vegetation paired with more direct edge between

Health Inspection Service, Wildlife Services, National Wildlife Research Center

older forest and agricultural lands). We predicted that the density of cattle within the county, habitat structure, and proximity to anthropogenic landscape features would be the strongest predictors of black vulture livestock-depredation risk. Our ESM estimated the relative risk of black vulture-cattle depredation to be between 0.154–0.631 across our entire study area. Consistent with our hypothesis, areas of greatest predicted risk of depredation correspond with locations that are favorable to vulture life-history requirements and increased potential to encounter livestock. Our results allow wildlife managers the ability to predict where black vulture depredation of cattle is more likely to occur in the future. It is in these areas where extension and outreach efforts aimed at mitigating this conflict should be focused. Researchers and wildlife managers interested in developing or employing tools aimed at mitigating livestock-vulture conflicts can also leverage our results to select areas where depredation is most likely to occur.

KEYWORDS

cattle, *Coragyps atratus*, ensemble modeling, human-wildlife conflict, livestock, predictive modeling

Conflicts with wildlife have the potential to pose serious problems for humans (Peterson et al. 2010, White and Ward 2010, Redpath et al. 2015). Furthermore, challenges with wildlife are increasing as human populations grow (Treves et al. 2009, Gehring et al. 2010, Margalida et al. 2014). Such conflicts arise frequently when wildlife species have a direct impact on human interest, such as economic damage caused by wildlife feeding on crops or livestock (Baker et al. 2008, White and Ward 2010, Pooley et al. 2021). In some cases, resulting economic losses cause negative attitudes towards wildlife (Treves and Bruskotter 2014, Goljani Amirkhiz et al. 2018, Bhatia et al. 2020). In turn, negative human attitudes can lead to persecution of wildlife (Cerri et al. 2017, Bhatia et al. 2020, Bhatia 2021). Many human-wildlife conflicts involving predators such as large mammalian carnivores and birds of prey (including vultures) occur when these wildlife species feed on livestock (Margalida et al. 2014, Miller et al. 2016). For example, Mitchell et al. (2004) estimated that in the United States, coyotes (*Canis latrans*) are responsible for >$40 million in damages to livestock producers each year. Investigating the patterns and spatiotemporal drivers of crop and livestock depredation can improve understanding and facilitate mitigation of these conflicts (Chen et al. 2016, Huang et al. 2018, Duriez et al. 2019).

Beginning in the 1990s, black vulture (*Coragyps atratus*) populations increased in abundance and expanded (Avery 2004, Rushing et al. 2020) their historical range to include midwestern and northeastern portions of the United States (areas where black vultures were historically absent or occurred at low densities; Toledo et al. 2013, Duriez et al. 2019, Zimmerman et al. 2019, McClure et al. 2021). As black vulture populations increased their geographic range, an increase in the frequency of reports of livestock depredation by black vultures occurred (Avery 2004, Zimmerman et al. 2019, Kluever et al. 2020). In the United States, livestock producers have identified black vulture depredation on neonatal cattle, horses, sheep, goats, domestic swine, and farm-raised deer

(Lowney 1999, Avery and Cummings 2004). Cattle producers in 18 states reported black vulture depredation (Spires 2014), and increasing black vulture-livestock depredation (both perceived and actual loss) is a main concern for human-vulture conflict among agricultural producers (Zimmerman et al. 2019, Kluever et al. 2020).

There is little information on the total extent and frequency of black vulture depredation on livestock (Humphrey et al. 2004). In Virginia between 1990 and 1996, farmers reported 115 incidents between black vultures and livestock (Lowney 1999); comparatively, researchers reported 226 incidents between livestock and wolves (*Canis lupis*) between 1987 and 2002 in Idaho, Montana, and Wyoming, USA (Muhly and Musiani 2009). Furthermore, data compiled from reports to the United States Department of Agriculture (USDA), Animal Plant and Health Inspection Service, Wildlife Services (WS) indicate that the numbers of livestock lost to black vultures has increased (Humphrey et al. 2004). From 2010–2019 requests for United States Fish and Wildlife Services (USFWS) depredation permits to mitigate human-vulture conflict increased nearly 3-fold (Kluever et al. 2020). Of those requests 17% (n = 20) related to agricultural and livestock production in 2010, whereas in 2019 they related to 30% (n = 98). In 2010, the USDA reported that 11,900 cattle deaths were caused by vultures nationwide (U.S. Department of Agriculture USDA National Agriculture Statistics Service 2010). Furthermore, a survey of 3,000 cattle ranchers from Florida, USA, reported 36% of them lost cattle to conflict with black vultures (Milleson et al. 2006). This rate of reported livestock lost to black vultures is similar to the estimated 49% of producers reporting loss of cattle to wolves in Canada (Stronen et al. 2007), the 32% reported rate of livestock lost to pumas (*Puma concolor*) in Patagonia (Llanos et al. 2020), and the 21% reported rate of livestock lost to mammalian carnivores in Bhutan (Wang and Macdonald 2006).

Predicting why and where black vulture depredation events involving livestock are likely to occur will become increasingly important for management and mitigation as black vultures expand their range. Several studies have investigated black vulture movements, habitat, and behavior, particularly at the home-range spatial extent (Holland et al. 2017, 2019; Byrne et al. 2019); however, little is known about landscape variables associated with vulture-livestock depredation, and black vultures are an understudied species (Buckley et al. 2022). Black vultures forage by sight and consequently often forage in open areas (Coleman and Fraser 1987) where they congregate in large groups around carcasses (Buckley 1996). They most frequently fly over clear cuts, edges between cover types, open coastal areas, wooded wetlands, and areas where land ruggedness creates favorable updrafts (Table 1). Black vultures are often associated with anthropogenic features such as roads, highly disturbed forest, and landfills and they frequently use updrafts generated by thermal power plants, which may underlie their frequent use of such structures as roosts (Table 1). They also roost on cell towers, communication towers, water towers (Table 1), and within quarries (Charette et al. 2011). Most of this previous work, however, involves tracking vultures captured near airports to improve understanding of aviation strike risk (DeVault et al. 2005, Avery et al. 2011, Novaes et al. 2020). Therefore, some of these established habitat relationships may differ from vulture populations that are more active in rural locations where agricultural production dominates land use. By identifying the role of landscape factors that increase the risk of reported depredation of livestock by black vultures, we can provide missing knowledge to help target area-specific management to reduce attacks on livestock by vultures. Such insights can also help plan for increases in resources needed to mitigate livestock depredation by black vultures and to target areas for outreach and extension for mitigating this conflict (Miller 2015, Treves and Rabenhorst 2017, Goljani Amirkhiz et al. 2018).

In the midwestern United States, where black vultures have expanded their range, researchers know little regarding their land use and foraging strategies (Kluever et al. 2020). This region contains a large number of livestock operations where potential attacks by black vultures could occur. The objective of this study was to identify landscape-scale spatial factors associated with reported black vulture depredation on livestock in midwestern agricultural landscapes to predict future hotspots of potential conflict. We hypothesized that depredation risk will be greatest in areas with intensive beef cattle production close to preferred black vulture habitat. We predicted that the density of cattle within the county, habitat structure, and proximity to anthropogenic landscape features would be the strongest predictors of black vulture livestock-depredation risk.

TABLE 1 Variables important for vulture habitat use included in our ensemble of small models (ESM), to characterize black vulture-livestock conflict risk within a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN), 2013–2020.

Habitat variable	Impact on vulture occurrence	References
Agricultural lands	Increased vulture occurrence	Thiollay (2007), Holland et al. (2019)
Cattle density	Increased vulture occurrence	Toledo et al. (2013), Piana and Marsden (2014)
Wooded wetlands	Increased vulture occurrence	Thiollay (2007), Holland et al. (2019)
Forests	Increased vulture occurrence	Thompson et al. (1990), Kirk and Currall (1994), Roen and Yahner (2005), Byrne et al. (2019), Holland et al. (2019)
Clear cuts	Increased vulture occurrence	Thiollay (2007), Byrne et al. (2019)
Edge sites	Increased vulture occurrence	Thiollay (2007)
Open landscapes	Increased vulture occurrence	Coleman and Fraser (1987), Thiollay (2007), Holland et al. (2019)
Updrafts	Increased vulture occurrence	Thompson et al. (1990)
Roads	Increased vulture occurrence	Kirk and Currall (1994), Lambertucci et al. (2009), Holland et al. (2019)
Landfills	Increased vulture occurrence	Novaes and Cintra (2013, 2015), Byrne et al. (2019), Holland et al. (2019)
Thermal power plants	Increased vulture occurrence	Lambertucci et al. (2009), Novaes and Cintra (2015), Holland et al. (2019)
Cell towers	Increased vulture occurrence	Ball (2009), Novaes and Cintra (2013), Kushwaha et al. (2019)
Quarries	Increased vulture occurrence	Charette et al. (2011)
Wind farms	Decreased vulture occurrence	Villegas-Patraca et al. (2014), Cabrera-Cruz and Villegas-Patraca (2016), Hoen et al. (2018)
Water and communication towers	Increased vulture occurrence	Avery and Lowney (2016), Hill et al. (2021)
Dams	Increased vulture occurrence	Hameem et al. (2018)

STUDY AREA

We modeled black vulture-livestock depredation risk across a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN) using data from 2013–2020. We selected this region because it represents the northern limit of vulture conflict reports within the Midwest (Avery 2004, Kluever et al. 2020, eBird 2021). The study area contained 3,605 zip code polygons that encompassed 509,594.79 km^2. Within our study area, individual zip code polygons ranged from 0.023 km^2 to 1,777.06 km^2 with an average size of 141.36 ± 158.48 (SD) km^2. Our study area encompassed an area that is south of most recent glacial events in North America (Dyer 2006). After the last glacial retreat, this region's dominant land cover was forest (McEwan et al. 2007). European settlement resulted in forests being cleared for agricultural plots and development resulting in a change in land use to a mixed agricultural, urban, forest landscape (Rhemtulla et al. 2009, Morefield et al. 2016, Goring and Williams 2017). Forests within this region are classified as central hardwoods (Dyer 2006). Although the midwestern region of the United States is generally flat, it contains major landforms that vary in topography, such as mountains, rolling hills, valleys, plains, plateaus, and large lakes. The average elevation within our study area ranged from 180 m to 270 m. Dominant wildlife species present within our study area include coyotes, black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), and many avian species. The dominant native vegetation in central hardwood forests consists of a variety of upland hardwood species, predominantly oaks (*Quercus* spp.), shagbark hickory (*Carya ovata*), bitternut hickory (*Carya cordiformis*), elms (*Ulmus* spp.), black cherry (*Prunus serotina*), red maple (*Acer rubrum*), white ash (*Fraxinus americana*), green ash (*Fraxinus pensylvanica*), basswood (*Tilia americana*), hackberry (*Celtis occidentalis*), and sugar maple (*Acer saccharum*; Clark and Hutchinson 1989, Wisconsin Department of Natural Resources 2021). Although much of the original forest was cleared for agriculture, woodlands remain a dominant feature of the landscape (Dyer 2006). This vast richness of plants and animals that inhabit this area is the result of a wide diversity of soils, geography, and climate. The current climate of the Midwest is mainly governed by latitude, continental location, large-scale circulation patterns, and in the northeastern area by the presence of the Great Lakes (Andresen et al. 2012). Weather patterns are typically influenced by the formation and position of the polar jet stream in the winter (Dec–Mar) and transition seasons, with somewhat less influence in the summer (Jun–Sep), when the region is also influenced by frequent intrusions of warm, humid air masses of tropical origin (Andresen and Winkler 2009).

METHODS

Vulture depredation records and risk variables

In May 2020, we contacted WS and requested records from 2013–2020 for all requests for assistance by livestock producers due to black vulture depredation concerns for livestock for Illinois, Indiana, Kentucky, Missouri, Ohio, and Tennessee. In May of 2020, we also contacted the USFWS, Migratory Birds Division, Region 3, and requested records for all depredation permits issued to livestock producers to mitigate black vulture depredation on livestock for the same times and locations. Personal identifiable information (PII) restrictions and concerns put forth by both agencies only allowed us to examine conflict data at the zip code spatial extent. We considered zip codes including permits or WS requests for assistance for multiple years as one known conflict zip code. This resulted in 223 unique black vulture-conflict zip codes, 50 from WS and 173 from USFWS across our 6-state study area. For our study, we considered only reports of conflict related to livestock depredation. Our decision to disregard permits and consultations associated with airports or other buildings restricted the extent of reported conflict to areas from the southern half of Ohio, Indiana, and Illinois. To ensure that we restricted our model to a spatial extent over which we had observation of conflict, we limited the northern boundary of our study area to a 1-county buffer north of Interstate 70. This extent corresponds to the area where black vultures are commonly reported in the midwestern United States (eBird 2021).

To estimate depredation risk, we modeled differences in conditions between zip codes with reported conflict (depredation permits issued, consultations requested) relative to available zip codes throughout the study area. Initially, we selected 41 predictor variables that previous researchers suggested may be important for vulture habitat use (Table S1, available in Supporting Information). We calculated these variables using 3 different approaches: proportional composition of a land cover type within each zip code polygon, proportion composition of a land cover type within a polygon defined by a 6.8-km (radius of a circle the size of an average black vulture home range; Alarcón and Lambertucci 2018) buffer around each zip code, and the average distance from each zip code to nearest point feature or cover type (Table S1).

We used ArcGIS Pro (ArcGIS Pro 2.7, Esri, Redlands, CA, USA) for geoprocessing steps associated with creating variables. To calculate the proportion of land cover type of each zip code polygon, we used the tabulate area tool (ArcGIS Pro 2.7) to calculate the area (m^2) within each zip code polygon of each land cover type from the National Land Cover Database raster (Dewitz 2019). We used the calculate field tool to calculate the percent area of each land cover variable. We repeated these steps for waterbodies using the National Hydrography Dataset (U.S. Geological Survey 2020). To calculate the density of all roads and non-highway roads (U.S. Census Bureau 2019) in each zip code polygon, we used the intersect tool to create a new shapefile with the roads (U.S. Census Bureau 2019) found in each zip code polygon. We used the summary statistics tool (ArcGIS Pro 2.7) to calculate the sum length (m) of roads for each zip code polygon. To calculate the density of roads within a zip code polygon, we used the calculate field tool (ArcGIS Pro 2.7). To calculate the density of cattle (USDA 2020) within a zip code polygon, we divided the number of all estimated cattle within a county by the county's area (km^2) and used this measure of density to assign an average density of cattle to each zip code polygon. To characterize the landscape composition within a typical black vulture home range size, we repeated the above steps for each variable (Table S1) within the previously described 6.8-km buffer around each zip code polygon and calculated the proportion of habitat within that entire buffer.

Estimates of the proximity of a polygon to other features like cover types or relevant linear (e.g., road) or point (e.g., cell tower) features can be accomplished in numerous ways. Ecological niche models (ENMs) most often require input data consisting of point locations of species occurrence. When exact locations are not available, geographical centroids of respective spatial units are typically used as a substitute (Cheng et al. 2021). Ecological niche models built using spatial unit centroids often suffer from introduced error, and whenever possible, central tendency values (mean, median) that represent the whole spatial unit rather than a single point location should be considered (Cheng et al. 2021). We used ArcMap 10.5.1 (Esri) to create variables for proximity of features of interest to zip code polygons throughout the study area. We used the subdivide polygon tool (ArcGIS Pro 2.7) to create 30 equally spaced points within each zip code polygon and split those zip code polygons into 30 equally sized polygons. We then used the feature to point tool (ArcGIS Pro 2.7) to extract the centroid of each equally sized sub zip code polygon and create a point. We used the near tool (ArcGIS Pro 2.7) to calculate the distance (m) from each point to the nearest variable. We calculated the average of the 30 points within each zip code polygon using the summary statistics tool (ArcGIS Pro 2.7). We then assigned these values to the zip code polygon (Cheng et al. 2021) and statistically compared values from black vulture-livestock conflict zip codes to the population of all available zip codes. We used this approach because Euclidean distance analysis based on random sampling can be unreliable with low and arbitrary numbers of random points (Benson 2013). Furthermore, a systematic approach more efficiently measures habitat availability by making calculations from all possible locations and eliminates uncertainty due to sampling error (Benson 2013).

We categorized our original list of potential descriptive variables into classes including zip code size, cattle density, urban cover type, agriculture, forest, wetlands, open water, dams, all roads (including non-highway roads), non-highway roads, cell towers, communication towers, water towers, power plants, quarries, wind turbines, and landfills (Table S1). Before model development, we calculated Pearson correlation coefficients for all 41 potential descriptor variables (Table S1). We then recursively identified each pair of descriptor variables that was most highly correlated. We then ran ensembles of small models (ESMs) of each individual descriptor variable and eliminated the descriptor variable from the pair with the lower predictive power based on area under the receiver operating characteristic curve (AUC; Swets 1988) and the continuous Boyce index (Hirzel et al. 2006). After eliminating an individual descriptor variable, we recalculated Pearson correlation coefficients for the remaining variables and reiterated the above process until we ended with a set of variables that were not correlated at a threshold value of >0.48. This procedure resulted in 17 variables that we used for modeling risk of livestock depredation by black vultures. To model the risk of potential livestock depredation by black vultures, we calculated values for all selected variables for each zip code polygon (as described above) across the entire 6-state area (south of Interstate 70). We then compared zip codes where black vulture-livestock depredation was observed to all other zip codes across our study area.

Ensemble of small models

To determine black vulture-livestock depredation risk, we fit an ESM in the Ecospat package in R (Di Cola et al. 2017). The strength of ESMs is that they create 1 final model that combines the most supported results from >1 statistical technique by averaging the best predictions of all bivariate combinations of each environmental variable

(Lomba et al. 2010). Breiner et al. (2015) identified the highest support for ESMs with single techniques; however, we tested combinations of multiple techniques to construct the ESM supported best by our data (Lomba et al. 2010). This approach improves predictive power for distribution models when there is a limited number of known locations (Breiner et al. 2015, 2018). We used the ESM approach in part because of the low numbers of individual black vulture depredation permits or WS requests for assistance across the 6 states ($n = 223$).

We used the final 17 predictor variables (Figure 1), to model vulture-livestock depredation risk in our ESM at known vulture-livestock conflict zip codes (used) compared to background zip codes (available). We computed ESM models with 10 replicates of the 136 bivariate models and using 80% of the occurrence data for calibration and 20% for evaluation (Collart et al. 2021). For each of the 10 replicates, Ecospat constructed an ensemble prediction from the weighted average of the 136 bivariate models using a Somer's D value. Models with Somer's D values ≤0 indicated that results were equal or worse than a random model and were excluded from the ensemble model (Collart et al. 2021).

To construct our final ESM, we selected the 5 highest performing techniques: generalized linear models (GLM), gradient boosting machines (GBM), classification tree analysis (CTA), artificial neural networks (ANN), and Maxent as implemented by Phillips et al. (2006) and Breiner et al. (2018). We then used a backwards elimination approach starting with all techniques and dropping the technique with the lowest support after each analysis. We selected the most-supported model based on 2 metrics used in prior studies (Breiner et al. 2015, 2018; Collart et al. 2021):

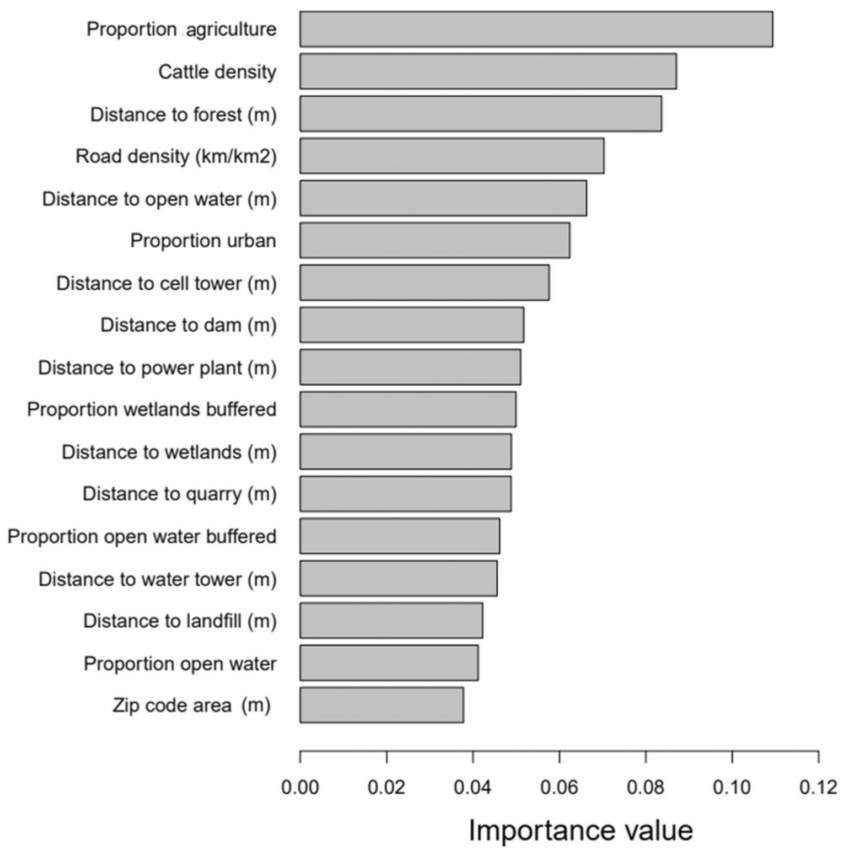

FIGURE 1 Predictive variables retained for the ensemble of small models (ESM), and their importance values ordered from largest to smallest characterizing black vulture-livestock conflict risk within a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN), 2013–2020.

AUC (Swets 1988) and Boyce index (Hirzel et al. 2006). Area under the curve is commonly used and correlates with other performance metrics (true skill statistic [TSS], sensitivity, specificity) except for the Boyce index (Breiner et al. 2015). We used the Boyce index as a second metric of model performance to confirm results of the first (Scherrer et al. 2019). The Boyce index is valuable because it was designed for presence-only data and is not prone to overestimation for small datasets (Hirzel et al. 2006). We then tuned the model for our dataset using the BIOMOD_tuning function in the Biomod2 package in R (Thuiller et al. 2016) and repeated our backwards elimination approach with tuned parameters to select the final model. We obtained importance values and created partial dependence plots for each predictor from output of the final ESM model. We then applied predictions from our ESM to each zip code across our 6-state region to create a raster map of the vulture-livestock depredation probability in this large-scale landscape.

RESULTS

The black vulture-livestock conflict areas included 223 zip codes that spanned 55,460.956 km^2 (~10.88% of the study area). Five polygons (white polygons in Figure 2) that were current or former military installations lacked zip code data and comprised an area of 340.20 km^2 (~0.07% of the study area). Ensemble of small model predictions of the potential risk of livestock depredation by black vultures across our study area ranged from 0.154–0.631 (Figure 2). These predicted values are relative and not absolute. We categorized the range of potential depredation risk in to 3 subcategories: low (0.154–0.315), medium (0.316–0.415), and high depredation risk (0.416–0.631). The number of zip code polygons categorized as low, medium, and high potential depredation risk was 786 (110,418.56 km^2; ~21.7% of the study area), 1,850 (261,418.81 km^2; ~51.3% of the study area), and 969 (137,907.16 km^2; ~27.1% of the study area), respectively.

Model outputs are primarily interpreted in terms of importance of the predictor variables, which broadly relate to vulture habitat needs and human land use. The influence of features related to vulture life history is apparent in a number of the top predictor variables that have high importance. Landscape factors including the proportion of agriculture, the distance to forest, and the distance to open water (Figure 1), relate to edge habitat and correspond to an increase in vulture occurrence (Table 1). Descriptive variables that were ranked higher in importance were

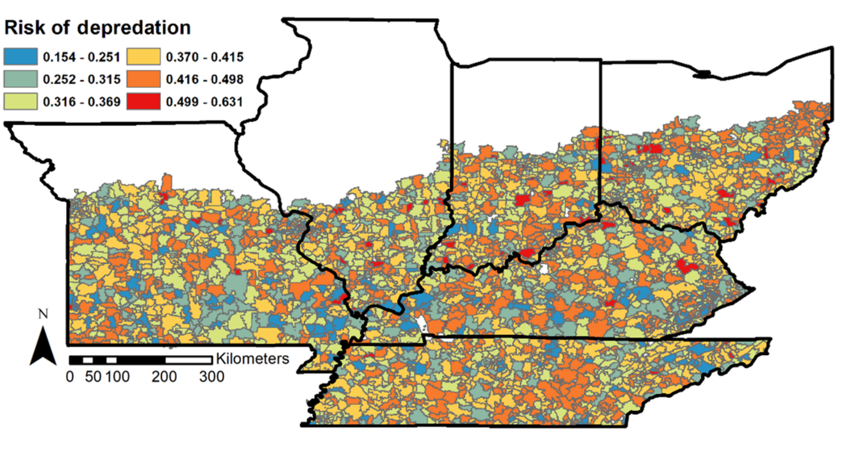

FIGURE 2 Risk map characterizing the relative probability of a reported vulture-livestock conflict within the study period. Our model quantifies the relative probability of livestock depredation risk by black vultures at a zip code resolution based on an ensemble of small models (ESM) within a 6-state region (IL, IN, KY, MO, OH, TN), south of Interstate 70 in the midwestern United States, 2013–2020. White areas within the study area represent current or former military installations without zip code data.

generally associated with factors that increase the opportunity for livestock depredation by black vultures to occur. Variables that aligned with human land use provide features that facilitate vulture behavior such as roosting and thermal soaring. Predictor variables such as road density and the proportion of urban cover (Figure 1) align with human land uses and provide feeding opportunities for vultures (Novaes and Cintra 2015, Hill et al. 2021). Descriptive variables that capture features of human land use such as distance to cellphone towers, distance to dams, and distance to powerplants also correspond with vulture roosting behavior (Avery et al. 2002, Hill et al. 2021).

Ensembles of small models constructed using 4 techniques (CTA, GBM, GLM, Maxent) received the most support among the methods considered (Table 2). The final ESM revealed pronounced non-linear trends in the 6 descriptor variables of highest importance for risk of putative black vulture depredation across our 6-state study area. Proportion of agriculture, cattle density, distance to forest, road density (km/km^2), distance to open water (m), and the proportion of urban cover (high intensity 80–100% impervious surface) within a zip code buffer were the highest-ranked variables by importance value (Figure 1). Zip code area size, a function of networks of streets served by post offices as a tool for mail delivery (U.S. Census Bureau 2000), had the lowest importance value among all variables we included in our modeling (Figure 1).

The partial dependence plots of many descriptor variables exhibited plateaus (Figure 3) and peak values (Figure 4) of the relative probability that a zip code would have a black vulture-livestock conflict within the study period. The variable with the largest importance value, proportion of agriculture, had a plateau of elevated probability of depredation risk across a wide range of values, from approximately 0.15 to 0.65 (Figure 3A). Cattle density, the second most important variable, peaked and remained stable near 0.65 risk probability from approximately 10–50 cattle/km^2 (Figure 3B). Distance to forest, the third most important predictor, exhibited an initial peak from 0.60 to 0.65 probability of depredation risk within 50 m of forest, declined to 0.60 probability of depredation risk at approximately 200 m from forest, and then remained flat (Figure 4A).

Non-highway road density, distance to open water, distance to dams, and distance to power plants exhibited plateaus of elevated probability of depredation risk between 0.60 and 0.65 across their respective ranges (Figure 3C–F). The proportion of urban cover, the proportion of wetlands within a buffer, the distance to the nearest quarry, the proportion of open water within a buffer, and zip code size all exhibited initial increases in probability of depredation risk but stabilized at a relative probability of depredation within our study period between 0.60 to 0.65 (Figure 4B–F). All remaining descriptor variables exhibited relatively flat trends in values at approximately 0.60–0.65 relative probability of depredation within our study period across their respective value ranges (Figure 5).

TABLE 2 Summary of ensemble of small models (ESM) performance characterizing black vulture-livestock conflict risk within a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN), 2013–2020. Models include generalized linear models (GLM), gradient boosting machines (GBM), classification tree analysis (CTA), artificial neural networks (ANN), and Maxent. Model performance was based on the area under the receiver operating characteristic curve (AUC; Swets 1988) and the continuous Boyce index (Hirzel et al. 2006).

Model	Techniques included	AUC	Boyce	Sum of values
5 techniques	ANN, GBM, GLM, Maxent	0.783	0.843	1.626
4 techniques	CTA, GBM, GLM, Maxent	0.781	0.877	1.659
3 techniques	CTA, GBM, Maxent	0.780	0.847	1.627
2 techniques	GBM, Maxent	0.774	0.869	1.643
1 technique	GBM	0.759	0.870	1.629

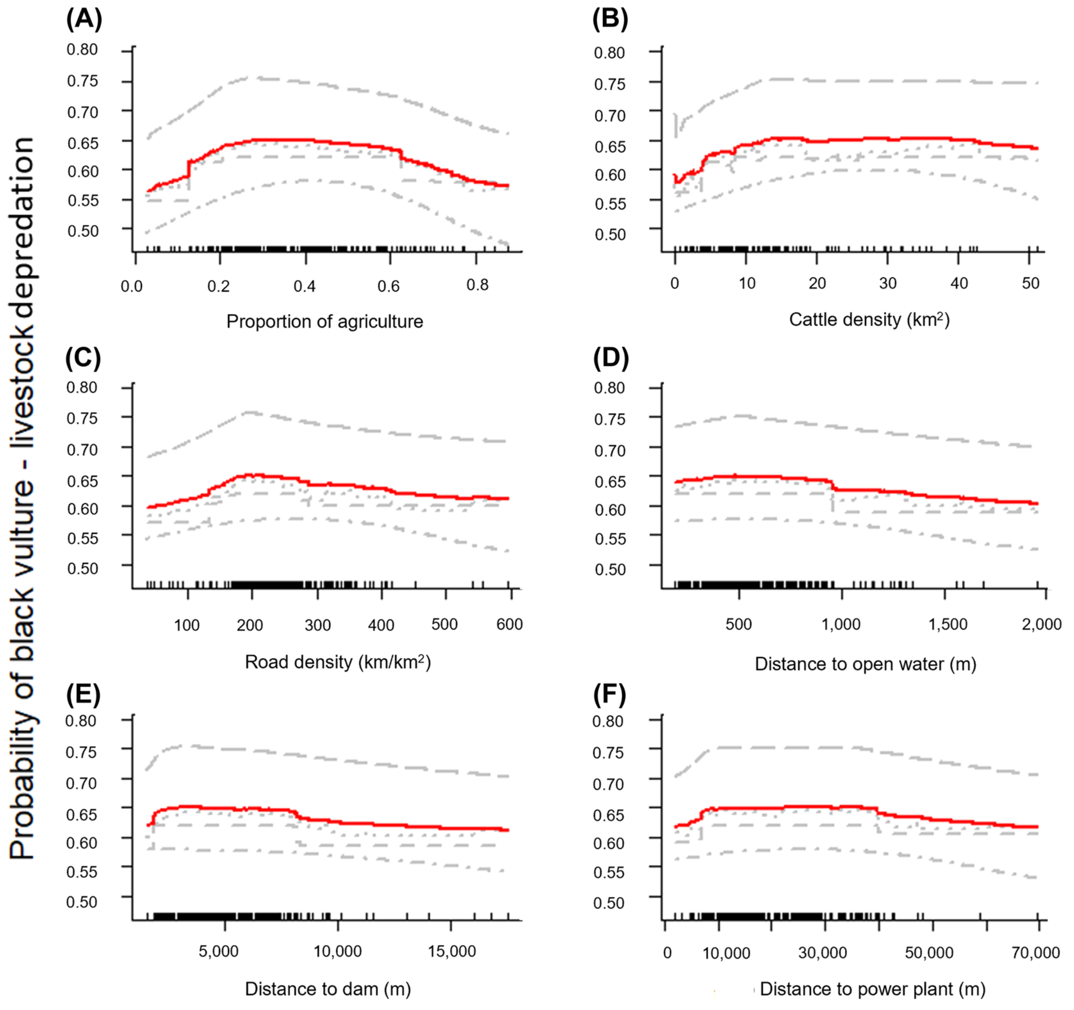

FIGURE 3 Partial dependence plots (A–F) for 6 of 17 variables with importance values depicting plateaus and characterizing livestock depredation risk by black vultures in an ensemble of small models (ESM) within a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN), 2013–2020. The risk of livestock depredation represents the relative probability that a zip code would have a reported vulture-livestock conflict within the study period. The ESM represents combined results of the most supported bivariate models (solid red lines) from 4 statistical techniques, including classification and regression trees (short, dashed lines), generalized boosted models (dotted lines), generalized linear models (dash, dotted lines), and Maxent (long dashed lines).

DISCUSSION

The results of our spatial predictions supported our hypothesis that livestock depredation risk by black vultures would be greatest in areas that provide suitable habitat and opportunities for conflict to occur (i.e., increased cattle density). We observed increased probability of depredation in areas of agricultural and cattle production, close to forested edge sites, and in areas that provide roosting habitat for black vultures. The prevention or reduction of livestock depredation by black vultures depends on the ability to define the conditions that underlie these conflicts (Linnell et al. 1999, Goljani Amirkhiz et al. 2018), and an understanding of the mechanisms underlying species use of environments is important for effective management and mitigation of human-wildlife conflicts (Novaes and Cintra 2015). Our results document that

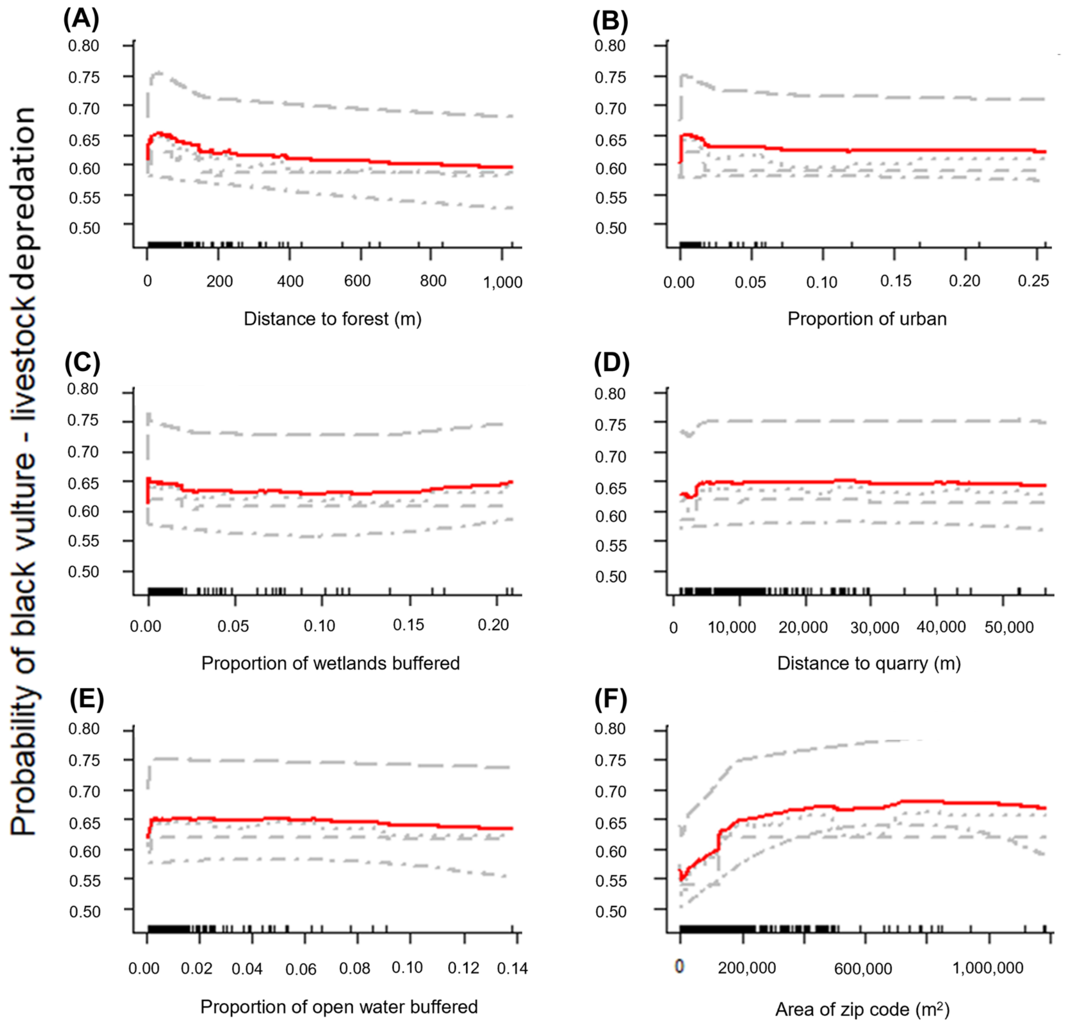

FIGURE 4 Partial dependence plots (A–F) for 6 of 17 variables with importance values depicting peaks and characterizing livestock depredation risk by black vultures in an ensemble of small models (ESM) within a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN), 2013–2020. The risk of livestock depredation represents the relative probability that a zip code would have a reported vulture-livestock conflict within the study period. The ESM represents combined results of the most supported bivariate models (solid red lines) from 4 statistical techniques, including classification and regression trees (short, dashed lines), generalized boosted models (dotted lines), generalized linear models (dash, dotted lines), and Maxent (long dashed lines).

depredations are likely where factors such as food abundance, habitat structure, vegetation cover, and roost site availability influence habitat use by vultures, bringing them closer to livestock (Coleman and Fraser 1987, DeVault et al. 2004). While these relationships are intuitive, existing documentation of them is based upon anecdotal observations. Therefore, our research addresses the need to quantify these relationships.

Consistent with our hypothesis, our risk of depredation map (i.e., risk map) identifies potential livestock depredation hotspots that correspond to areas of higher quality vulture habitat and urban land use, which increase potential for conflict (Roen and Yahner 2005, Thiollay 2007, Byrne et al. 2019, Holland et al. 2019). In other geographical regions, researchers have indicated the importance of similar habitat and land use factors when

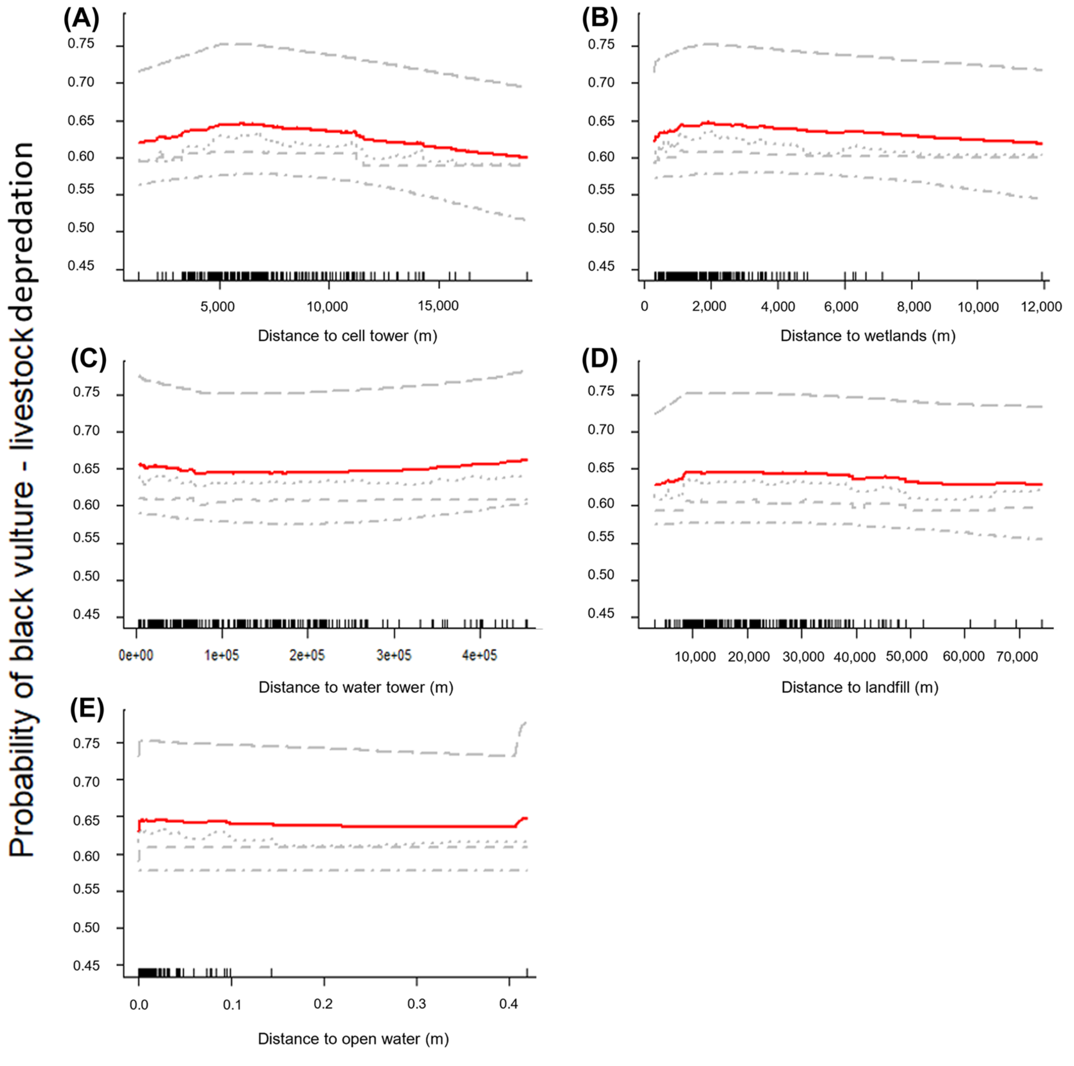

FIGURE 5 Partial dependence plots (A–E) for 5 of 17 variables with importance values depicting stable trends and characterizing livestock depredation risk by black vultures in an ensemble of small models (ESM) within a 6-state region in the midwestern United States (IL, IN, KY, MO, OH, TN), using data from 2013–2020. The risk of livestock depredation represents the relative probability that a zip code would have a reported vulture-livestock conflict within the study period. The ESM represents combined results of the most supported bivariate models (solid red lines) from 4 statistical techniques, including classification and regression trees (short, dashed lines), generalized boosted models (dotted lines), generalized linear models (dash, dotted lines), and Maxent (long dashed lines).

determining where the potential for wildlife-livestock conflict is greatest (Azevedo and Murray 2007, Hemson et al. 2009, Treves et al. 2009, Li et al. 2013). According to our risk map, areas of greatest predicted risk of depredation corresponded with locations that are favorable to vulture life-history requirements and increased potential to encounter livestock. Our 2 most important predictors are proportion of agriculture and cattle density. These results are intuitive in terms of the opportunity for conflict based upon vulture habitat needs and human land use. The influence of vulture habitat needs upon the risk of depredation is further supported by several of our other highly important predictors, such as distance to forest and density of roads, which are related to vulture foraging

(Lambertucci et al. 2009, Byrne et al. 2019, Holland et al. 2019). Factors including the proportion of agriculture, the distance to forest, and the distance to open water presumably reflect proximity to open habitat edges where vultures forage, soar, and roost (Roen and Yahner 2005, Thiollay 2007, Byrne et al. 2019, Holland et al. 2019, Hill et al. 2021). Other influential variables including the proportion of urban land cover, proximity to cell phone towers, quarries, dams, and power plants may provide potential roosting sites and conditions favorable for updrafts (Lambertucci et al. 2009, Novaes and Cintra 2015, Hameem et al. 2018, Holland et al. 2019, Hill et al. 2021).

Three of the most important predictors related to open water or the presence of dams. These variables likely indicate man-made reservoirs because there are few natural bodies of water aside from rivers in the study area. These results correspond with anecdotal data and author experience, in that a few of the known vulture hotspots in Indiana are adjacent to reservoirs (M. L. Wahl, Purdue University, personal observation). With the suitable configuration of agricultural and forested land, the presence of reservoirs potentially increases the favorability of the habitat matrix by adding water and roosting structures (e.g., dams, towers, buildings), and possibly foraging opportunities along the shoreline. The driving mechanism related to black vulture affinity for man-made water sources in our study area requires further exploration.

Our descriptor variables associated with vulture habitat requirements and human land use provided insight into where potential livestock depredation by black vultures might occur. The partial dependence plot for proportion of agriculture had a range of peak values from 0.15 to 0.65 (Figure 3A). Within our study area, some zip codes consisted of up to 85% agricultural cover. In zip codes that are >65% agriculture, the landscape is most likely dominated by an overabundance of row crops. Zip codes <15% are likely dominated by urban cover or forest cover; both conditions are less suitable to black vulture life history (Thiollay 2007, Holland et al. 2019).

Human land use associated with cattle production and increased cattle density across the landscape provides increased opportunities for black vultures to encounter livestock, thus increasing the potential for conflict to arise. The average cattle density across all zip codes within the study area was 10.1 ± 9.82 (SD) cattle/km^2, which is within peak probability of depredation risk values in our ESM. Furthermore, our ESM suggests a potential threshold of approximately 0.60–0.65 relative probability that a zip code would have a black vulture-livestock conflict within the study period once cattle density reaches or exceeds 10.1 cattle/km^2.

The complexity of the conflict between livestock depredation and black vulture populations necessitates several considerations. First, black vultures consume live prey, including livestock, but they are predominately scavengers (Latterman 2019, Buckley et al. 2022). Further, producers sometimes overestimate livestock losses to vultures in other systems, including griffon vultures (*Gyps fulvus*) in France (Duriez et al. 2019) and Andean condors (*Vultur gryphus*) in Argentina (Ballejo et al. 2020). Thus, it is important that future work estimate the actual rate of loss of livestock to black vulture depredation to provide an appropriate context in which to consider the risk map this research provides. Second, black vultures come into conflict with humans for causes other than livestock depredation, including causing structural damage to private and infrastructure-based property, and colliding with aircraft (Lowney 1999, Avery and Cummings 2004, Avery and Lowney 2016). Our model only addresses conflicts associated with livestock depredation that are producer reported rather than field-based empirical investigations, so any inference related to our model should be restricted to that form of conflict.

Other predictor variables may be equally or more important in understanding these other varieties of conflict. For example, when numerous descriptor variables generate an effect that changes the abiotic environment, the aggregated effect itself might be a better descriptor for the action of the species (Linder et al. 2012). Thus, our descriptor variables that indicate potential roosting sites (e.g., cell towers, communication towers, water towers, power plants, quarries), might have increased importance if they were aggregated into a single layer of roosting habitat and we believe this merits investigation in future studies.

All interpretations resulting from our ESMs are completed at the resolution of the zip code because of privacy concerns related to the data we used. This feature could have potential implications because ESMs perform best with geographical point locations of species occurrence as input data because they assume that the whole study area was sampled consistently with these precise locations of occurrences (Yackulic et al. 2013, Cheng et al. 2021).

Without exact point locations, spatial uncertainty can lead to false estimations of species-environment relationships (Dormann et al. 2008, Beale and Lennon 2012, Tulowiecki et al. 2015). The magnitude of these false relationships is determined by the level of spatial autocorrelation of the environmental variables at a local scale (Naimi et al. 2011, 2014). Although we were unable to use more precise locations to develop our ESMs, we incorporated central tendency values from 30 uniformly distributed points within each zip code polygon that represented the zip code polygon as a whole, rather than a single point location (Cheng et al. 2021). In general, larger administrational spatial units (ASUs) such as zip code polygons, have higher spatial heterogeneity, which is associated with higher value frequency mismatch of explanatory variables between true locations and centroids (Cheng et al. 2021). Mean and median metrics of explanatory variables are significantly better fits for approximating values for explanatory variables within an ASU when compared to centroids (Park and Davis 2017, Cheng et al. 2021). For example, Park and Davis (2017) determined that species distribution models using mean climatic data at a county level were most similar to models using actual coordinate data when compared to models using a county centroid that tended to overpredict a species' range.

In our ESMs, known locations were from permits issued by USFWS or consultations with WS; however, in remote or rural locations depredations may be unrepresented because of a lower likelihood that depredation is observed or reported (Goswami et al. 2015). Thus, depredation risk may exceed our estimates. We included positive zip codes with known vulture-livestock conflicts as one known occurrence within a zip code even though some zip codes contained multiple reports of requests for consultations or depredation permits over multiple years. This may have resulted in underestimating the potential of putative depredation risk in these areas but was the most appropriate approach given our presence-absence modeling approach.

Despite the aforementioned limitations, our models document strong relationships that provide meaningful insight into potential livestock depredation by black vultures across the midwestern United States. Overall, our ESM indicates that throughout our entire study area, there is a 15–60% relative probability of livestock depredation by black vultures, with a medium (0.316–0.415) to high (0.416–0.631) relative probability across 78.36% of the study area. The implication of this finding is that some level of conflict can be expected across the majority of zip codes in our study area. Actual reported rates of livestock lost to vultures (5.4%) are less than that of coyotes (53.1%) but greater than the risk attributed to wolves (3.7%) or bears (*Ursus* spp.; 1.3%; USDA National Agriculture Statistics Service 2010).

The basic principle of ESMs is to model species distributions based on multiple small, simple models and combine all possibilities into an ensemble (Lomba et al. 2010, Breiner et al. 2015). This makes it a particularly well-suited approach for the development of wildlife-livestock conflict models. Our approach to ESM modeling using zip codes as known positive location polygons provides a process of conflict risk modeling where exact locations are not known or are limited because a species' presence coincides with a recent range expansion. The probability distributions for used and available polygons across our study area and over time provide information on the proportion of the landscape with increased risk of future livestock depredation by black vultures. Furthermore, our approach has potential relevance farther north as black vulture populations continue to expand their range given predicted climate change and land use change. We suggest that potential livestock depredation by black vultures in the midwestern United States will likely occur in areas with cattle density ≥10 cattle/km^2 and where human land use and the natural habitat matrix promote vulture life-history requirements (e.g., decreases in old fields and early successional vegetation paired with increases in more direct edge between older forest and agricultural lands). The greatest proportions of landscape that are of highest conflict risk are associated with intermediate agricultural cover, increased forested land, moderate to high cattle production, and low to moderate urban cover. Our data has potential in assisting outreach efforts of governmental agencies and industry groups to make livestock producers aware of potential conflict risk so that they can take measures to reduce potential interactions with black vultures on their landscape. This would further help managers plan for dispersal events following roost management activities (Kluever et al. 2020) and has potential to decrease conflict risk. Managers could use these results to refine allowable take models to account for spatial heterogeneity in risk of conflict across the region either at the species level or more local or regional levels that coincide with stakeholder interests (Zimmerman et al. 2019).

By identifying the role of landscape factors that increase the risk of conflict between black vultures and livestock, we can provide missing knowledge to help target area-specific management to reduce vulture-livestock depredation (e.g., prompt removal of afterbirth and carcasses [Avery and Cummings 2004, Humphrey et al. 2004], livestock protection dogs [Milleson et al. 2006], hanging a vulture effigy [Tillman et al. 2002], unmanned aircraft systems [Pfeiffer et al. 2021], dispersal of roosts using pyrotechnics, lasers, and when authorized limited lethal removal [Avery and Lowney 2016]). Such insights can also help plan for increases in resources needed to mitigate black vulture-livestock conflict (Miller 2015, Treves and Rabenhorst 2017, Goljani Amirkhiz et al. 2018). Furthermore, we demonstrate that data sources such as depredation permits have increasing potential to provide spatiotemporal records for black vulture conflict, which has implications for other avian species. Using reported black vulture-livestock conflicts and predictive spatial modeling that incorporated landscape variables important to vulture habitat use, we evaluated habitat characteristics associated with conflict across landscapes.

Beyond the scope of this manuscript, we believe that our novel method of using zip codes as known positive location polygons within an ESM framework may provide a process for dealing with invasive exotic species. In areas where information about a species' ecology in their new habitat is limited, similar models have the potential to be used to predict where managers should invest mitigation resources by providing baseline variables that predict range expansion and areas of elevated potential conflict.

MANAGEMENT IMPLICATIONS

We suggest that managers and researchers use our results to identify areas of potential nest and roosting locations close to livestock operations. In addition, our results can guide where research efforts aimed at testing tools for mitigating vulture-livestock conflict should occur (i.e., areas where depredation risk is relatively high). Maintaining stable populations of black vultures is a statutory-based requirement of the USFWS by way of the Migratory Bird Treaty Act; therefore, further determination of non-lethal means to mitigate black vulture livestock depredation risk is important to meet this requirement and retain the valuable ecosystem services black vultures provide.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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