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Predicting spatial factors associated with cattle depredations by the Mexican wolf (*Canis lupus baileyi*) with recommendations for depredation risk modeling

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ABSTRACT

Aim: Predation on livestock is one of the primary concerns for Mexican wolf (*Canis lupus baileyi*) recovery because it causes economic losses and negative attitudes toward wolves. Our objectives were to develop a spatial risk model of cattle depredation by Mexican wolves in the USA portion of their recovery area to help reduce the potential for future depredations.
Location: Arizona and New Mexico, USA.
Methods: We used a presence-only maximum entropy modeling approach (Maxent) to develop a risk model based on confirmed depredation incidents on public lands. In addition to landscape and human variables, we developed a model for annual livestock density using linear regression analysis of Animal Unit Month (AUM), and models for abundance of elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginiana*) using Maxent, to include them as biotic variables in the risk model. We followed current recommendations for controlling model complexity and other sources of bias.
Results: The primary factors associated with increased risk of depredation by Mexican wolf were higher canopy cover variation and higher relative abundance of elk. Additional factors with increased risk but smaller effect were gentle and open terrain, and greater distances from roads and developed areas.
Main conclusions: The risk map revealed areas with relatively high potential for cattle depredations that can inform future expansion of Mexican wolf distribution (e.g., by avoiding hotspots) and prioritize areas for depredation risk mitigation including the implementation of active non-lethal methods in depredation hotspots. We suggest that livestock be better protected in or moved from potential hotspots, especially during periods when they are vulnerable to depredation (e.g. calving season). Our approach to create natural prey and livestock abundance variables can facilitate the process of spatial risk modeling when limitations in availability of abundance data are a challenge, especially in large-scale studies.

1. Introduction

Large carnivores can cause conflicts with humans by preying on livestock, which causes economic losses and, in some cases, negative attitudes toward carnivores (Treves and Bruskotter, 2014; Dickman et al., 2013). A variety of non-lethal approaches to reduce human-carnivore conflicts are available. Some studies show that non-lethal methods were often more effective than lethal methods (Treves et al., 2016; Santiago-Avila et al., 2018), however, other studies report that there is high variation, indeterminacy and lack of scientific evidences in non-lethal methods effectiveness (Miller et al., 2016; Eklund et al., 2017; Eeden et al., 2018). Moreover, depredation on livestock by wolves may be a learned behavior and therefore may be difficult to stop if all individuals in a pack are involved (Harper et al., 2005). An

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alternative approach is to prevent conflicts from occurring, which may be more efficient and less costly than trying to reduce conflict after it has occurred. Prevention of conflicts depends on recognizing the conditions that promote these conflicts (Linnell et al., 1999). Therefore, predicting future depredations from their past patterns can lead to optimum interventions for reducing carnivore-livestock conflicts (Treves and Rabenhorst, 2017). Predictive spatial models find relationships between ecological variables and spatial processes and are commonly used tools to plan strategies for wildlife management (Guisan and Zimmermann, 2000). Risk maps, created by spatial models, predict spatial distributions of potential conflicts between humans and carnivores, and provide an opportunity for early warning (Edge et al., 2011; Treves et al., 2004; Treves et al., 2011; Miller, 2015). Moreover, identifying the role of landscape, natural prey, and livestock characteristics in depredation can help inform management of livestock and wildlife to reduce depredations (Miller et al., 2015; Treves and Rabenhorst, 2017).

The Mexican wolf (*Canis lupus baileyi*) is an example of a carnivore that is being restored to part of its native range, but which can cause conflicts with humans. Historically, the Mexican wolf occurred in portions of the American Southwest and south through central Mexico, although there is disagreement about precise historical range limits (Heffelfinger et al., 2017; Hendricks et al., 2016; Parsons, 1998). Historical efforts to eradicate Mexican wolves due to conflicts with livestock resulted in their extirpation from the United States by 1970 (Bednarz, 1988; Brown and Shaw, 2002). The Mexican wolf was listed as endangered under the US Endangered Species Act in 1976 upon which the last individuals were captured from the wild in Mexico to initiate a captive breeding program (McBride, 1980). The first releases of captive-bred Mexican wolves occurred in 1998 within a primary recovery zone in the Apache National Forest in east-central Arizona. Wolves were allowed to disperse throughout the Blue Range Wolf Recovery Area (BRWRA), which included additional areas of the Apache and Gila National Forests in Arizona and west-central New Mexico (see Fig. S1. 1 of Appendix S1 in Supporting information). The small founding population and low gene diversity have been a concern in Mexican wolf recovery efforts (Harding et al., 2016). In 2015, revisions to the regulations for the nonessential experimental population of the Mexican wolf resulted in a dramatic increase in the area where Mexican wolves would be allowed to occupy, from the former BRWRA to the Mexican Wolf Experimental Population Area (MWEPA), which includes areas of Arizona and New Mexico south of Interstate Highway 40 (Appendix S1; U.S. Fish and Wildlife Services [USFWS], 2015). This expansion will increase Mexican wolf-livestock conflicts (USFWS, 2015). From 1998 to 2017 the Mexican wolf population in the US has generally increased from an initial 11 wolves in 3 packs to a maximum of 114 wolves within 22 packs during 2017 (USFWS, 2017). Residents of Arizona and New Mexico that oppose Mexican wolf restoration, do so primarily because of concerns about livestock and human safety (Schoenecker and Shaw, 1997). Depredation by Mexican wolves on livestock occurs throughout the year on private and public lands. Prior to 2007 management removal of wolves from the population was negatively impacting population growth. Protocols were altered to emphasize non-lethal and proactive strategies and minimize removals (USFWS, 2017).

The overarching goal of this study was to develop a model that explains landscape scale spatial factors associated with Mexican wolf depredation on livestock. Specific objectives included: 1) predict relative density of livestock and predict relative abundance of potential natural prey, including elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginiana*), in Arizona and New Mexico with the aim of using estimates from these models as part of the initial suite of variables that were tested for inclusion within the risk model, 2) develop a risk model of Mexican wolf depredation on cattle to understand factors associated with increased risk and to illustrate spatial arrangement of depredation conflict hotspots, and 3) make recommendations for future wolf recovery and livestock management to reduce potential conflicts. Our study was important in several ways. First, the depredation risk model provides information about areas with high potential for conflict before the distribution of Mexican wolf has expanded within the revised MWEPA. This provides an opportunity to inform future management actions that can reduce potential conflicts before they occur. Second, fine scale spatial data on abundance of livestock and natural prey are rarely available for large regional study areas. We developed models for livestock density and natural prey abundance, which were tested as predictors in the risk model. Third, few studies have applied maximum entropy modeling (i.e., Maxent; Phillips et al., 2006) using current recommendations (Morales et al., 2017; Yackulic et al., 2013). We incorporated all currently recommended modeling criteria, including correcting sampling bias, defining background extent based on study goals and assumptions, testing model complexity, and avoiding overestimation in model evaluation.

2. Methods

2.1. Study area

The study area was the states of Arizona and New Mexico, USA. The risk model was developed based on depredation incidents that occurred on public lands within and near the former BRWRA and then was extrapolated as a risk map to the study area (Appendix S1).

2.2. Occurrence records

We focused our analysis on depredations on cattle by Mexican wolves because cattle represent the majority of livestock production, both in terms of numbers of animals and economic value, and because the majority of depredation incidents attributed to Mexican wolves involve cattle (USFWS, 2017). We analyzed 186 confirmed lethal depredation incidence locations (yearlings $n = 2$, heifers $n = 2$, calves $n = 108$, bulls $n = 3$ and cows $n = 71$) verified by Wildlife Services as part of the Interagency Field Team from 1998 to February 2017. To reduce the effect of sampling bias, we used spatial filtering to randomly remove all but one depredation record within each 1 km^2 pixel. After rarefaction, 162 depredation points remained in the dataset.

2.3. Independent variables

We modeled depredation risk as a function of 6 biotic (relative abundance of elk, mule deer and white-tailed deer, annual livestock density, land cover type, land cover variety, canopy cover, and cover variety), 4 human (distance to and density of roads, distance to and density of developed areas) and 6 landscape (elevation, slope, terrain ruggedness index [TRI], aspect, distance to and density of water resources) variables (see Appendix S2 in Supporting information for hypotheses, variable sources, and variable calculations).

Spatial data on the abundance of livestock was not available for the entire study area and is probably not obtainable given the large number of livestock operations and variation in how livestock are managed. Consequently, we developed a spatial layer “annual livestock density” that represents the annual capacity for livestock production as a proxy for actual livestock abundance. We applied generalized linear models and used AIC_c to model annual livestock capacity on basis of Animal Unit Month (AUM) data for 3876 allotments (covering 39% of the study area) on lands managed by the US Forest Service and Bureau of Land Management and then interpolated to the 61% remainder of our study area (see Appendix S3 in Supporting information for details of methods and results). Similarly, spatial data on the abundance or density of the primary natural prey of the Mexican wolf (elk, mule deer and white-tailed deer) were not available for the entire study area. Maxent's raw output can be directly interpreted as a model of relative abundance

(Phillips et al., 2017). Consequently, we used available occurrence data for each prey species in Maxent to generate species distribution models that estimate their relative abundance. Development of the prey relative abundance models followed similar procedures as used for the risk model (see Appendix S4 in Supporting information for details of methods and results). The original pixel size of all variables was 30 m, except annual AUM density, which was 1 km. All variables were scaled to 1 km pixel size.

2.4. Modeling approach

Depredation risk models are usually developed in the same manner as correlative species distribution models, but based on depredation locations rather than species occurrence locations (Miller, 2015). The decision-making framework for such modeling is dependent on the purpose of the model and is determined by the type of survey data available (either presence-absence or presence-background) and how the survey data interact with sampling bias and imperfect detection (Guillera-Arroita et al., 2015). Early risk models were usually developed based on presence-absence survey data (Miller, 2015). Indeed, presence-absence survey data can estimate probability of occurrence, which is the highest level of information content possible, but this is only achievable when detection probability is perfect (Guillera-Arroita et al., 2015). Detection probability for depredation events by Mexican wolves is low and it varies primarily by producer (Breck et al., 2011). Our goal was to produce a map of the study area that correctly ranks locations for risk of depredation on cattle by Mexican wolves. Such ranking models have high information content and good ability to discriminate between depredation and non-depredation sites and these models may be created using either presence-absence or presence-background datasets (Guillera-Arroita et al., 2015). We did not have data on locations where Mexican wolves and livestock overlapped but depredation had not occurred, and therefore did not have absence data. Consequently, we used presence-background data in Maxent to model depredation risk. In addition to be being consistent with our modeling objectives, this approach also reduced the risk of including false absence data in the model.

Maxent is a machine-learning program that uses the principle of maximum entropy to estimate the distribution of a species (or occurrences such as depredation events) based on occurrence points (Phillips et al., 2006; Elith et al., 2011). Maxent typically has better performance in comparison with other presence-background methods, it performs well with small samples, and it is robust to spatial errors and biased sampling (Elith et al., 2006, 2011). In addition, Maxent can use both categorical and continuous data and it can incorporate interactions between variables (Phillips and Dudík, 2008). However, Maxent has been criticized because many users have failed to understand and address model assumptions, control model complexity, and report relevant results (Yackulic et al., 2013; Morales et al., 2017). Maxent only performs well if its assumptions are met and its settings are tuned (i.e., to find and use optimal model parameters; Merow et al., 2013; Morales et al., 2017). Thus, we incorporated all currently recommended modeling criteria for our Maxent analyses, including correcting sampling bias, defining background extent based on study goals and assumptions, testing model complexity, and avoiding overestimation in model evaluation (Merow et al., 2013; Radosavljevic and Anderson, 2014).

2.4.1. Sampling bias

A key assumption of species distribution models generated via Maxent is that all locations on the landscape have equal chance to be sampled (Royle et al., 2012). Sampling bias can result in overfitting the model toward areas with clustered points and, thus, inaccurate models (Phillips et al., 2009). To reduce the effect of sampling bias on the depredation risk model, we used spatial filtering to randomly decrease the number of presence points in oversampled regions (Boria et al., 2014; Radosavljevic and Anderson, 2014), and removed all but one depredation record within each 1 km pixel. In this way, we could retain 85% of depredation points in the model.

2.4.2. Background extent

Maxent compares conditions at the locations of the dependent variable to randomly selected locations within a background area. The extent of the area in which background points are selected should be determined according to the objectives of the study and characteristics of the environmental conditions that are desired to be discriminated from presence points (Merow et al., 2013). To define the background extent, we created a buffer around each depredation point using the mean home range size for Mexican wolves (17.6 km radius, USFWS, 2017). We chose this buffer based on a tradeoff between needing background points that represent a range of variation, while restricting the background extent to only areas where wolves occur.

2.4.3. Model complexity

Maxent is capable of fitting highly complex models. However, less complicated models are more interpretable and less sensitive to sampling bias (Yackulic et al., 2013). We addressed three sources of model complexity, multicollinearity, β multiplier, number and type of features, by applying sample size corrected Akaike Information Criteria (AIC_c; Akaike, 1974; Burnham and Anderson, 2007) in a stepwise fashion. First, we used the R package MaxentVariableSelection (Jueterbock, 2015) to obtain a set of models. Each model included variables that were not highly correlated ($r \leq 0.7$) and that had a model contribution > 5% individually. We repeated the process of variable selection for a range of β multipliers from 0 to 15 at an increment of 0.5. The β multiplier is a penalty coefficient to reduce overfitting (Tibshirani, 2011). MaxentVariableSelection is able to consider multicollinearity, model contribution and β multiplier, but it is not able to include specified feature sets. Thus, we considered the variables of the model with lowest AIC_c as the input for the next step. Next we used the R package ENMeval (Muscarella et al., 2014) to find the optimum set of features from an a priori set of features and retuned the β multiplier for the variables selected by MaxentVariableSelection. Maxent calculates five models for each independent variable known as features: linear (L), quadratic (Q), product (P), threshold (T) and hinge (H). We tested 9 sets of feature classes: L, H, LQ, LQT, LP, HP, LQP, LQTP. We considered L because one side of the unimodal curve might not be included in the background data (Elith et al., 2010). We examined H since avoiding T may improve the model performance and lead to a simpler and smoother model (Phillips et al., 2017). We considered LQ because responses of species to environmental variables are mostly nonlinear and unimodal, as observed in fundamental niches (Austin, 2007). We included LQT since some environmental conditions may limit species distribution (e.g. highly rugged areas). We added P to L, H, LQ, LQT feature sets since it may negligibly improve model performance, although it makes model interpretation difficult (Phillips et al., 2017).

2.4.4. Model evaluation

We did not use Maxent's default model evaluation, random partitioning k-fold cross-validation, because it leads to overestimation of performance (Boria et al., 2014). Instead, we evaluated the accuracy of model predictions by applying spatially independent k-fold cross-validation with R package ENMeval using the ‘block’ method (Muscarella et al., 2014). The block method was chosen because our aim was projecting models developed for a small region (i.e., depredation incidences where Mexican wolves currently occur) to the entire study area (i.e., areas where depredations by Mexican wolves could eventually occur; Wenger and Olden, 2012). The block method partitioned our presence points and background points into four bins of equal numbers based on latitude and longitude lines.

We assessed the accuracy of predictions of models via threshold-independent and threshold-dependent omission rates. For the threshold-independent evaluation methods we used Area Under the

Curve of the Receiver Operating Characteristic plot (AUC) to evaluate the overall model performance (Phillips et al., 2006). We also measured overfitting by calculating AUC difference, which is the difference between AUC calculated on training localities and AUC calculated on evaluation localities (Warren and Seifert, 2011). Threshold-dependent omission rates quantify discriminatory ability and overfitting of models. These rates are based on two threshold criteria: 10% omission rate of the training records and lowest presence threshold. The former is a value that excludes the 10% of localities with the lowest predicted values and its expected omission rate is 0.10. The latter is the minimum predicted value for any pixels, including training points, with an expected value of zero for test presence points. Generally, models with lower omission exhibit better discrimination between suitable and unsuitable areas, while models with higher omission rates indicate overfitting (Anderson and Gonzalez, 2011). For both threshold-independent and threshold-dependent measures, we used the averaged values across the four geographic bins. Maxent models assume that species are at equilibrium with the environmental variables used to fit the model. Extrapolation outside the range of variation represented by the environmental variables can lead to errors. Thus, we ran a Multivariate Environmental Similarity Surface analysis (MESS, Elith et al., 2010) using package Dismo (Hijmans et al., 2017) to find where our model is violating this assumption. MESS analysis quantifies the degree of similarity between the range of variables at occurrence locations and projection data set. Predictions outside of the similar domain may not be reliable (Elith et al., 2010).

3. Results

The model with the lowest AIC_c used a β multiplier = 3.5; linear, quadratic and product features, and it had 6 uncorrelated variables with a contribution > 5% including canopy cover variation, elk abundance, land cover, slope, density of roads and density of developed areas (Tables 1 and 2). The most important variables in discriminating high depredation risk from low depredation risk areas were canopy cover variation and relative abundance of elk (33.1% and 29.3% contribution, respectively), both of which had a positive linear relationship with depredation risk (Fig. 1). Land cover majority type had 13% contribution to the model, with montane grassland having the highest probability of depredation (90% probability), and pine woodland having the lowest probability of depredation (60% probability). There also was > 65% chance of depredation in areas with a land cover majority of mixed conifer forest, basin/playa, chaparral, desert/semi desert scrub, disturbed, pinyon-juniper woodland, riparian, rock and savanna grassland. In contrast, depredation risk was negatively related to slope, density of roads and density of developed areas (9.4%, 9.4% and 5.5% contribution, respectively; Fig. 1).

The mean AUC of the model was 0.81 indicating that the model had good overall performance (Araújo et al., 2005) in distinguishing areas with high depredation risk from areas with low depredation risk (Table 1). The AUC difference was low (0.05) suggesting that the model was not affected by overfitting toward depredation points and, thus, had a good transferability in space (Warren and Seifert, 2011). Threshold-dependent measures indicated that the model had low overfitting and high discriminatory ability at 10% omission rate (0.15) and lowest presence threshold (0.006).

Table 2
Percent contribution of variables in the risk model for cattle depredation by the Mexican wolf (*Canis lupus baileyi*).

Variables	Percent of contribution
Canopy cover variation	33.1
Elk (*Cervus canadensis*) abundance	29.3
Land cover	13.7
Slope	9.5
Density of roads	9.5
Density of developed areas	5.5

The risk map revealed that most of the depredation hotspots are located within public lands managed by the U.S. Forest Service (Fig. 2). Within the MWEPA (i.e., south of I-40), the highest depredation risk hotspots were in portions of the Mogollon Highlands (i.e., vicinity of the former BRWRA). A large area with moderate risk was on the Mogollon Plateau near Flagstaff, Arizona. Other smaller hotspots of low to moderate risk are in the Zuni Mountains, Magdalena Mountains, San Mateo Mountains, Manzano Mountains, and parts of the Sacramento Mountains in New Mexico, and the Nantanes Pleateau and Pinaleno Mountains in Arizona (Fig. 2). According to the MESS analysis, areas near large cities (except Flagstaff) had values for variables most outside the range of the depredation points, and hence these areas do not predict well. Based on an examination of individual variable contributions to the MESS analysis, the poor prediction of these areas was a product of all of the variables except slope (see Appendix S5 in Supporting information).

4. Discussion

4.1. Depredation by Mexican wolves

We found that the primary factors associated with increased risk of depredation by Mexican wolves on livestock were higher canopy cover variation and higher relative abundance of elk. The positive relationship between risk of livestock depredation and abundance of elk is consistent with other studies that also found a positive correlation between the abundance of natural prey and depredation risk (Bjorge and Gunson, 1985; Bradley and Pletscher, 2005; Karanth et al., 2013; Stahl et al., 2002; Treves et al., 2004). Elk are the primary prey for Mexican wolves within their currently occupied range in Arizona and New Mexico (Carrera et al., 2008; Reed et al., 2006). Abundance of natural prey is considered a key factor that determines distribution and movement patterns of wolves (Fuller et al., 2010). A number of studies have concluded that depredation on livestock ensues when wolves

Table 1
Settings and evaluation metrics for a spatial risk model of cattle depredation by Mexican wolf (*Canis lupus baileyi*).

Features[a]	β[b]	Full AUC[c]	Mean AUC[d]	Mean AUC Difference[e]	Mean omission rate[f]	Mean minimum omission rate[g]	Number of parameters[h]
LQP	3.5	0.88	0.81	0.05	0.15	0.006	11

[a] L = linear, Q = quadratic, P = product.
[b] β = β multiplier.
[c] AUC (Area Under the Curve of the Receiver Operating Characteristic plot) based on unpartitioned dataset.
[d] AUC based on the testing data averaged across four bins.
[e] Difference between the training AUC (calculated on training localities) and testing AUC (calculated on evaluation localities).
[f] The 10% omission rate of the training records (a value that excludes the 10% of localities with the lowest predicted values).
[g] The lowest presence threshold (the minimum predicted value for any pixels).
[h] The number of parameters in the full model.

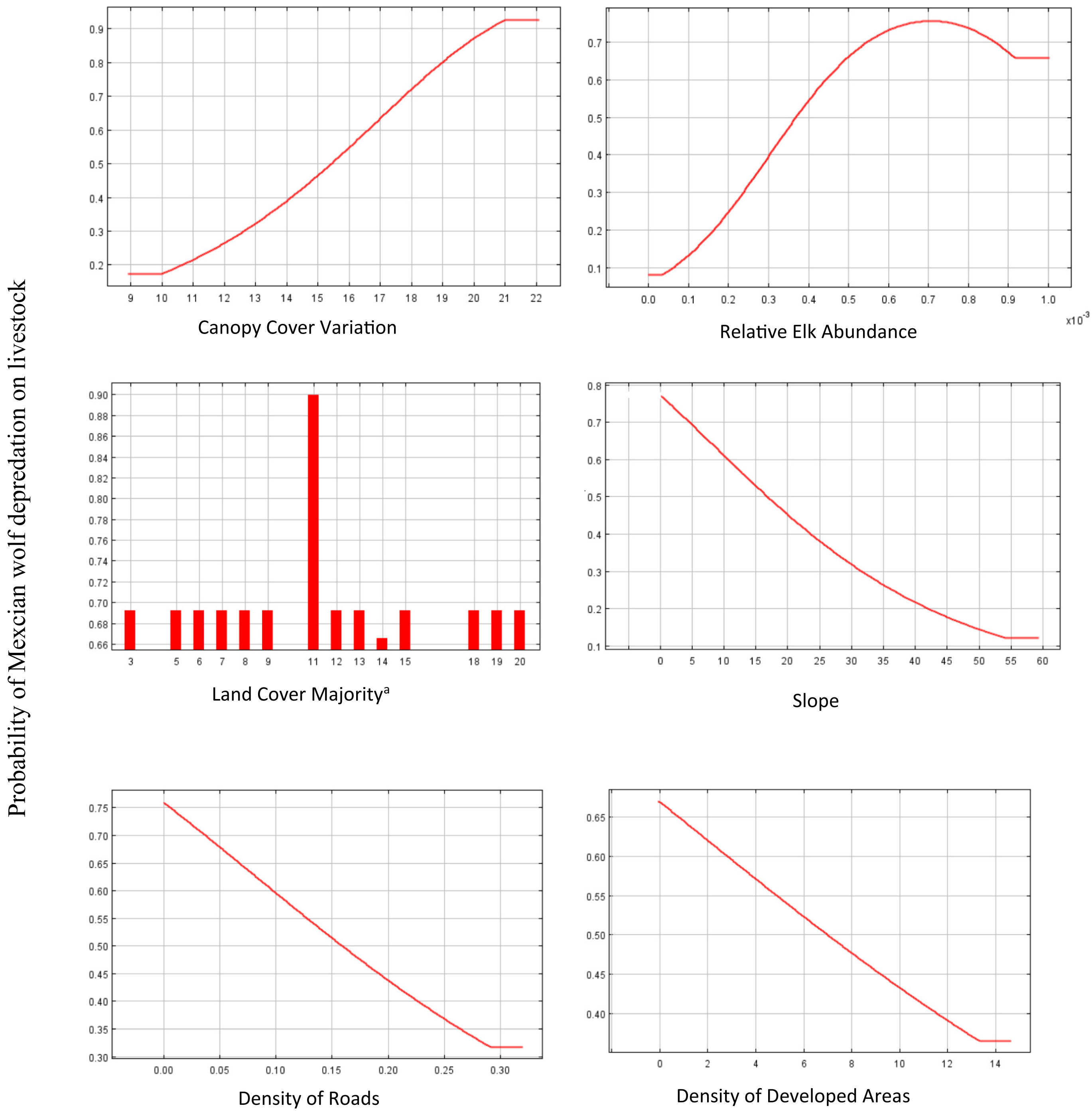

Fig. 1. Response curves of the Maxent model for Mexican wolf (*Canis lupus baileyi*) depredation on cattle. For description of variables see Table S2.1. [a]Land cover majority types: 3, mixed conifer forest; 5, basin/playa; 6, chaparral; 7, desert/semidesert; scrub, 8, arroyo; 9, disturbed; 11, montane grassland; 12, oak woodland; 13, open water; 14, pine woodland; 15, pinyon-juniper woodland; 18, riparian wetland; 19, rock; 20, savanna/semidesert grassland.

pursue their natural prey and unexpectedly confront livestock and shift their pursuit to livestock as an easier prey (Bjorge and Gunson, 1985; Bradley and Pletscher, 2005; Oakleaf et al., 2006; Oakleaf et al., 2003).

Elk, like many other prey species, alter their profitable habitat (open grasslands) in response to predation risk (Mao et al., 2005). Wolves are pursuit predators that prefer to hunt in flat, open areas (Davie et al., 2014; Treves et al., 2011). Consequently, dense forests may be perceived as less dangerous to elk than open grasslands (Mao et al., 2005). In the Greater Yellowstone Ecosystem, Creel et al. (2005) reported that elk used open grasslands in the absence of wolves, but that elk moved into forest and more steep terrain when wolves were present. Similarly, we found higher depredation risk in areas with open land cover (montane grassland) and flatter slopes, and lower depredation risk in forested areas with steeper slopes. Cattle also tend to prefer open grassland and flatter slopes (Bailey et al., 2001; Bailey, 2005). Therefore, it is possible that cattle become more vulnerable to depredation by Mexican wolves when elk vacate open grassland and move into forests or rugged terrain. These relationships also provide an explanation for the positive relationship between canopy cover variation and depredation risk. Areas with higher canopy cover variation might provide ideal conditions for elk, due to comingling of high quality (but high risk) foraging habitats with poor quality (but safer) foraging habitats,

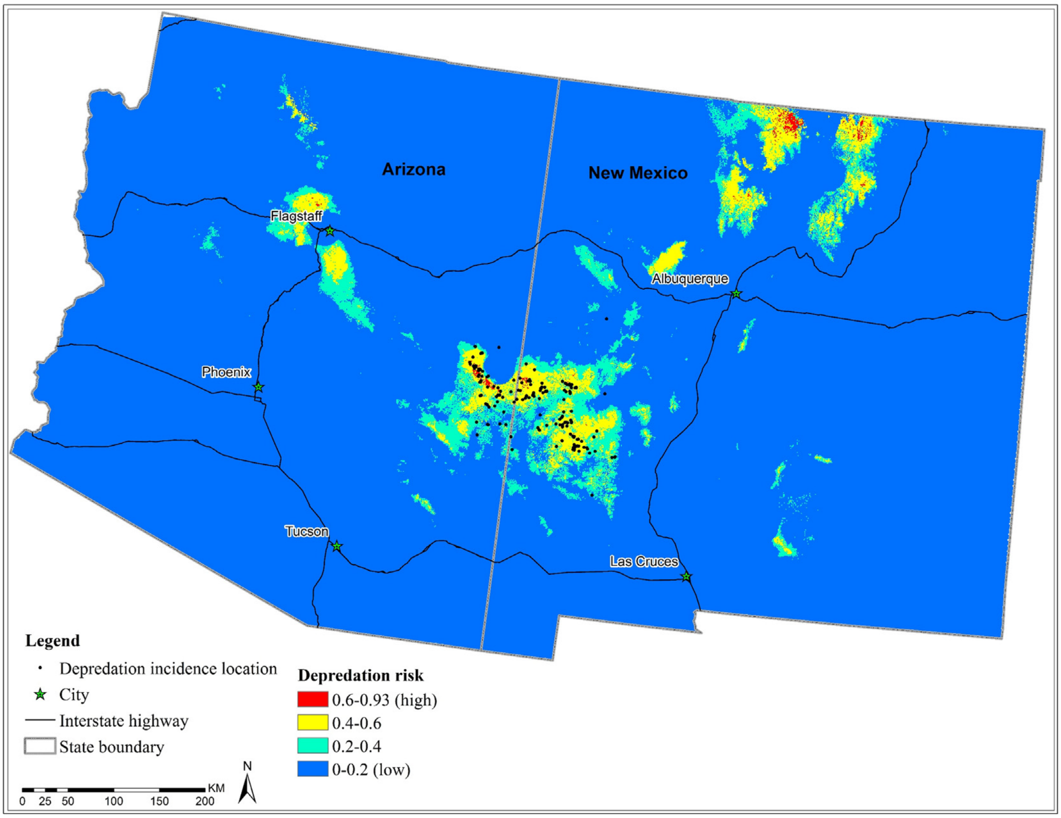

Fig. 2. Map of predicted depredation on cattle by the Mexican wolf (*Canis lupus baileyi*) in Arizona and New Mexico, USA. Lines are major highways and stars are major cities. Depredation risk is highest in areas in red and is lowest in areas in dark blue. Depredation incidences (black dots) are filtered at 1 km scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

resulting in less opportunity for predation on elk by wolves (Mao et al., 2005). This could result in increased risk of livestock depredation. Although the abundance of natural prey and land cover have been recognized as influencing factors associated with depredation risk by wolves in the Southwestern U.S. (our study), Northern Rockies (Bradley and Pletscher, 2005) and Midwest (Treves et al., 2004), the differences in natural prey seasonal movements and livestock husbandry practices may influence this relationship. For instance, in the Northern Rockies depredations are seasonal in relation to how livestock are managed and migration of ungulates (Bradley and Pletscher, 2005; Nelson et al., 2012). In the Midwest, white-tailed deer is the primary prey and livestock are mostly kept in confined pastures on private lands (Treves et al., 2004). In the Southwestern U.S., livestock grazing is mostly year-round on public lands and depredations occur year-round, with an increase in the denning season (USFWS, 2015). In our study, annual livestock density was not an important variable in the best depredation risk model (its contribution to the model was 2%). Other studies on wolf (Behdarvand et al., 2014), cougar (Teichman et al., 2013), and lynx (Linnell et al., 1999; Mao et al., 2005), also reported no relationship between the density of livestock and depredation events. However, some other studies have demonstrated that livestock density is an important factor influencing depredation in areas with different livestock husbandry systems (Miller, 2015). It is possible that livestock density was underrepresented in our model due to the coarse scale and absence of data on seasonal abundance of livestock. Future studies that include variables such as herd size, type of operation, and seasonal grazing patterns may reveal more information about the relationship between livestock density and depredation risk in the Southwestern U.S. We found that depredation risk was higher in areas remote from human development and with lower road density. Similar results were found by Treves et al. (2004) and Davie et al. (2014). These patterns are likely related to wolf habitat selection. Higher road and human densities can decrease habitat suitability for wolves and, therefore, wolves establish territories in areas with lower road and human densities (Mech et al., 1988; Oakleaf et al., 2006; Wydeven et al., 2001).

The risk map revealed the spatial configuration of depredation hotspots. Depredation hotspots are mostly located within montane areas that are public lands in National Forests. Because these montane areas have similar environmental conditions compared with those surrounding the depredation locations, the model makes robust predictions about depredation risk in most of these areas. Further, many of these montane areas are also considered areas most suitable for Mexican wolves by virtue of their forest cover, high native ungulate density, low livestock density, and low road and human densities (USFWS, 2017). Consequently, our risk map can help inform future expansion of the distribution of Mexican wolves in Arizona and New Mexico in order to minimize potential future conflicts. Moreover, this map can be used to prioritize areas for depredation risk mitigation including the implementation of active non-lethal methods in depredation hotspots. Our results indicate that spatial overlap of livestock in areas with abundant elk was associated with the risk of depredation. Thus, spatiotemporal management of livestock grazing to reduce this overlap could decrease the risk of depredation. For instance, depredations might be reduced by releasing livestock into pastures within hotspot areas after elk calving has occurred and elk become more dispersed. Other strategies for reducing depredation risk include limiting the exposure of young livestock to open range situations where they may be more prone to being attacked by wolves (Oakleaf et al., 2003), increasing human presence while simultaneously using non-lethal tools in an adaptive and proactive fashion (Stone et al., 2017) and preventing Mexican wolves from denning around areas of higher depredation risk (USFWS, 2003).

Spatial risk models demonstrate the interactions between predators and livestock in a dynamic system (Miller, 2015). Therefore, with the expansion of Mexican wolves' distribution, the depredation risk map should be updated by adding new data and the results of management feedback. Mexican wolves may adjust their hunting patterns in response to alteration in patterns of natural prey and livestock distribution and density. In areas where deer are the primary prey, the relationship between depredation risk, natural prey abundance and livestock may change. Landscape variables are only part of the picture. Complimentary studies on the effect of individual and population level aspects (e.g., breed, size, and age of livestock; management of livestock; wolf pack makeup) on depredation risk will be required with an expansion of Mexican wolf distribution.

There are several caveats or limitations to our study. First, our depredation risk model was developed at a 1 km resolution landscape scale based on GIS layers. Therefore, the model does not consider other factors at the individual or population level that can contribute to depredation risk, such as breed, sex, age, or management of livestock (De Azevedo and Murray, 2007; Ogada et al., 2003; Teichman et al., 2013) or demographics of wolves (Marucco and McIntire, 2010). Second, our risk map assumes Mexican wolves are present throughout the entire study area. Obviously, there is no risk of depredation by wolves where they are not actually present. Third, the depredation risk model was built based on environmental conditions around depredation locations that occurred from 1998 to 2017, which were primarily within the former BRWRA. Thus, the accuracy of the model's predictions outside of this range depends on the degree of similarity of the environmental variables within and outside of this range. The MESS analysis demonstrated that the model predicts well in all areas of the study area except around some (but not all) major cities, where wolves are unlikely to occur. Finally, the relative abundance of mule deer and white-tailed deer were not important predictors in our model, probably because elk are the primary prey species in vicinity of the former BRWRA. However, deer are the primary prey for Mexican wolves where elk are absent (Bednarz, 1988; Brown and Shaw, 2002). Therefore, we urge caution in interpreting the model in areas, such as the Sky Island region of southeastern Arizona, where elk are generally absent and deer would provide the primary natural prey for wolves.

4.2. Recommendations for risk modeling

We developed the risk model for Mexican wolf depredation on livestock by 1) selecting variables based on a full spectrum of specific well-rationalized biological hypothesis related to factors that may influence depredation risk, 2) creating important variables that were not otherwise available (e.g., livestock density and prey abundance), 3) developing Maxent models by adhering to all current recommendations for reducing biases and overfitting, and 4) using multiple model evaluation metrics. Our approach can serve as a model for other future depredation risk modeling studies.

1. When developing a depredation risk model, it is important to include a predictor variable related to livestock abundance. Our results did not support our assumption that depredation risk was related to livestock abundance. However, because we tested this relationship using fine scale data on livestock abundance, it provides stronger support for our key findings that wolf depredation was primarily associated with abundance of natural prey rather than livestock. This suggests that management to reduce depredation could preferentially focus on areas with high natural prey abundance, rather than areas with high livestock abundance. Detailed data on livestock abundance are generally not available. This problem may be more challenging for large regional study areas, for areas with free range livestock grazing (such as public lands allotment grazing management in western U.S.), or where there is a mosaic of various land ownership, in comparison with areas where livestock are raised on small farms or in small fenced pastures. Our model of annual livestock density is the first model to rigorously predict livestock abundance at a large regional scale. We demonstrated that AUM stocking rates can be predicted by environmental variables. Stocking rate data, such as AUM, are available in many areas under managed livestock grazing. Modeling stocking rate using appropriate methods and predictors can fill the gap of livestock abundance data in human-wildlife conflict studies.
2. Abundance of natural prey is perhaps the most important variable to incorporate in depredation risk modeling (Miller, 2015). In our study, relative abundance of elk was a primary predictor of depredation risk. However, actual data on abundance of natural prey are rarely available, except in small study areas where field studies have occurred. Estimates of abundance of natural prey over large study areas, such as those based on game management units, may be too crude or have too much uncertainty to fulfill study goals (Pearce and Boyce, 2006). Maxent's raw output can be interpreted as an estimate of relative abundance (Phillips et al., 2017). Therefore, species distribution models created with Maxent can serve as a surrogate for prey abundance in the absence of detailed field data. However, the performance of Maxent depends on the quality of dependent and independent variables and proper configuration of its settings (Merow et al., 2013). An advantage of using Maxent is that the dependent variable (species occurrence data) is usually already available from a variety of sources (e.g., Global Biodiversity Information Facility). However, these data have their own constraints, especially spatial bias, which must be addressed to obtain accurate results (Beck et al., 2014). Our study showed that Maxent's raw output can fill the gap of natural prey abundance in human-wildlife conflict studies. More research is needed to understand the relationships between Maxent output and actual animal abundances. Also, future studies should use independent data to validate our models.
3. In this study, we incorporated all current recommendations for improving Maxent performance including correcting sampling bias, defining background extent, evaluating model complexity (reducing multicollinearity, tuning beta parameter, tuning feature classes), and performing unbiased model evaluation (Merow et al., 2013; Radosavljevic and Anderson, 2014). Few studies of any kind (including to our knowledge no spatial risk modeling studies) have implemented all recommendations for producing unbiased and robust Maxent models (Morales et al., 2017). Using Maxent's default settings can lead to overly complex models that reveal odd relationships between variables and depredation risk as a result of overfitting, and consequently potentially lead to incorrect conclusions (Radosavljevic and Anderson, 2014).
4. Based on our prey model results, we suggest that when developing species distribution models over large areas it is important to test performance of models generated based on different background extents and scales of rarification. In addition, our results support conclusions of others that Maxent models be evaluated using multiple metrics including expert evaluation (Muscarella et al., 2014; Radosavljevic and Anderson, 2014).

5. Conclusions

Negative human-wildlife interactions can reduce the perceived value of a species (Conover, 2001). Therefore, employing creative and less costly approaches such as spatial risk models can help to reverse this process (Treves et al., 2011). We showed that spatial risk models can be created using available data. However, the quality of predictions depends on the quality of predictor variables and the modeling approach. Our approach to create natural prey and livestock abundance variables can facilitate the process of spatial risk modeling when limitations in availability of prey abundance data are a challenge, especially in large-scale studies.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.06.013.

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