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16. Abstract <p>The grasslands of Nebraska are highly altered due to anthropogenic development and degradation. The loss and degradation of grasslands has significantly impacted populations of swift fox (<i>Vulpes velox</i>), a Nebraska Natural Legacy Plan Tier-1 at risk species. We began a project to document the occurrence of swift fox in Nebraska and identify the anthropogenic and ecological factors that limit swift fox distribution through the development of a species distribution model. Over two years we conducted four surveys on 200 public and private sites within Western Nebraska. From nearly 5 million images representing 22,670 trap nights, we only detected swift fox on roughly 3.5% of our surveys. Although we were able to make a visual model of the estimated distribution of swift fox in Nebraska, the low numbers of presence data resulted in a model that performed poorly in predicting swift fox habitat suitability. Because swift fox are a species of concern, errors of omission are extremely important, and therefore we argue that predicted distribution map should interpreted and used cautiously.</p>			
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BACKGROUND:

Temperate grasslands, such as the prairies of Nebraska, are among the most imperiled ecosystems on earth (Hoekstra et al. 2005). With half the world's grasslands altered due to anthropogenic development and degradation, and less than five percent under preservation (Hoekstra et al. 2005), the future of grassland ecosystems remains in question. In the United States, the loss of temperate grasslands exceeds 99% in some areas, with 85% of the remaining grasslands in private ownership (Sampson and Knopf 1994). As a result, the conservation of grasslands and the wildlife which rely upon them is highly dependent on private land stewardship, as 90% of a species distribution can occur on private lands.

In Nebraska, the loss and degradation of grasslands has significantly impacted many grassland species, including the swift fox (*Vulpes velox*). A Nebraska Natural Legacy Plan Tier-1 at risk species (Schneider et al. 2011), swift fox are estimated to occupy as little as 20-25% of their historic range (Sovada et al. 2009); however, despite their Tier-1 status, little is known about the true distribution of swift fox. With increasing interest in developing infrastructure in Western Nebraska there is a clear need to document the distribution of swift fox, and identify threats to swift fox populations.

Traditional studies of species distribution focus on identifying the habitat attributes, most notably vegetation, that best predict the spatial patterns observed in nature. However, in canid systems, there is clear evidence that intraguild interactions play an important role in predicting species distribution and habitat use, especially for smaller canid species. As the largest extant canid in the shortgrass prairie, coyote are dominant to swift fox and often cited as an important source of mortality. As such, increases in the abundance and distribution of coyote following the development of the western Nebraska may have inadvertently restricted the range of swift fox despite the availability of suitable vegetative conditions.

Starting in 2013, the Nebraska Game and Parks Commission, the Nebraska Department of Roads, the Nebraska Environmental Trust, and the U.S. Forest Service - Nebraska National Forests and Grasslands working in collaboration with the Nebraska Cooperative Fish and Wildlife Research Unit, the University of Nebraska-Lincoln and Chadron State College began project to document the occurrence of swift fox in Western Nebraska and identify the anthropogenic and ecological factors that limit swift fox distribution.

PROJECT OBJECTIVE:

1. Create a predictive map of swift fox distribution in Nebraska

To achieve the overarching objective of the project requires several stages of development to secure the appropriate data to develop the outlined species distribution models including 1) developing *a priori* habitat suitability models, 2) securing access to sampling locations based on random sampling design, 4) implementing the sampling regime, 5) cataloging camera trap photos, 6) analyzing and developing current species distribution models based on ecological relationships, and finally 7) share what we are learning with the people of Nebraska. Below we inform the underlying approach of each of stage of project.

1) *A priori* habitat suitability model

Space-use patterns describe the distribution of individuals across habitats, while habitat selection refers to an animals' innate and learned behavioral responses that result in the disproportionate use of specific habitat types (Hutto 1985, Block and Brennan 1993, Jones 2001). As such, space-use is the end product of the habitat selection processes (Jones 2001). To understand the distribution of canid populations it is necessary to examine space-use patterns and the underlying habitat selection mechanisms that drive species-habitat relationships. Increasingly empirical evidence suggests that many factors (e.g. landscape structure, predation and competition) influence habitat decision, which rarely happens in an "ideal" or "free" fashion (Karr and Freemark 1983, Pulliam and Danielson 1991, Petit and Petit 1996 *in*: Jones 2001). The general theory of ecology presents at least four fundamental principles that constitute a basic framework to address questions concerning space-use and distribution of a species: (i) all species have a heterogeneous distribution at some spatial scale; (ii) heterogeneous distribution is caused and a cause of other ecological processes; (iii) organisms interact with the abiotic and biotic environments; and (iv) the ecological properties of species are the results of evolution (Scheiner and Willing 2008). There are, as well, a number of ecological theories (e.g., the theory of habitat selection, the ideal free distribution theory, the theory of optimal foraging, and the metabolic theory) considered relevant in explaining spatial patterns; however, one of the central ideas related to what causes species distribution and use of space is the species niche concept.

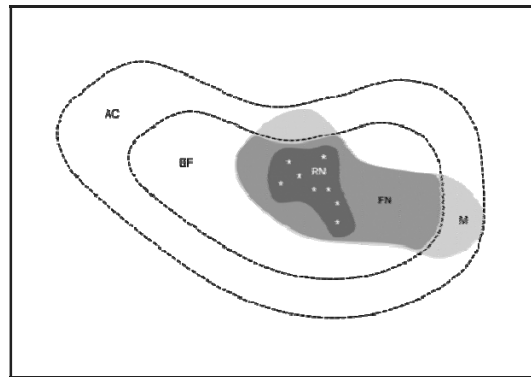


Figure 1. Ecological niche model for a hypothetical species. The AC area represents the geographic region with the appropriate set of abiotic conditions for the species. BF area is the region where the right combination of biotic factors (e.g., interacting species) occurs. The light and medium gray shaded areas represent the "accessible" areas to the species in some ecological sense (M), without barriers to movement and colonization, and the fundamental niche (FN). The dark gray shaded area is the region that has the right set of abiotic and biotic factors and that is accessible to the species, and is equivalent to the potential geographic distribution of the species. Using distributional information (i.e., known occurrences sampled from the actual distribution, represented with white asterisks) it is possible to identify the geographic extent of the realized niche (RN) and the potential distribution of the species (Modified from Soberón and Peterson 2005 and Hirzel and Le Lay 2008).

In general terms, the ecological niche of a species refers to the range of conditions and resources where the species can survive and reproduce based on physiological and morphological adaptations (Stearns 1992) such that differences among species niches (either their requirements or their impacts or both) determine the outcome of species interactions, species distribution and abundance, as well as the functional role of species in ecosystems (Chase and Leibold 2003). In other words, ecological niche theory predicts that critical characteristics of species' biology, such as physiology, feeding ecology, and reproductive behavior, define the fundamental ecological niche (Hutchinson 1957, Hutchinson 1978), and that there should be a strong relationship between a species' actual space use and distribution, and the environmental conditions which describe the species' realized niche (Fig.1, Hutchinson 1957, Soberón and Peterson 2005, Araújo and Guisan

2006). Accordingly, we expect species to be present in areas where the abiotic conditions are favorable (i.e., density-independent fitness is positive), an appropriate suite of species is present (e.g., prey and other food resources) and absent (e.g., competitors and predators), and the areas are accessible to the species (i.e., no dispersal limitation, Soberón and Peterson 2005).

Swift foxes live in the same habitat year-around and are strongly den dependent (Carby 1998, Dark-Smiley and Keinath 2003), placing dens in easily excavated sandy and friable soil (Hines and Case 1991, Pruss 1999). Swift foxes often associate den sites with roads, potentially to minimize encounters with coyotes, which tend to avoid roads and human contact (Hines and Case 1991, Pruss 1999). Swift foxes prefer open and flat shortgrass and mixed grass prairies with sparse vegetation, habitat conditions that presumably improve visibility to avoid predators (Dark-Smiley and Keinath 2003). Therefore, we expect higher occupancy by swift foxes in relatively flat areas (i.e., $< 10\%$ of slope) of shortgrass and mixed grass prairies such that swift fox occupancy increases when the percentage of suitable prairie landscapes increases. Similarly, because swift foxes select areas with short and sparse vegetation, we also expect to find them in heavily grazed pastures or fallow cultivated lands adjacent to shortgrass prairies (Carbyn 1998, Sovada et al. 1998).

Habitat suitability for swift fox is also related to prey availability, particularly small mammals, and den availability, which are generally constructed by other fossorial mammals such as prairie dogs (*Cynomys ludovicianus*), ground squirrels (*Spermophilus* spp.), and American badgers (*Taxidea taxus*) that swift foxes then modify (Carbyn 1998). Therefore, we expect higher occupancy and detection probability of swift fox in areas with well-drained friable and sandy-loamy soils also occupied by prairie dogs, ground squirrels and badgers (Hines and Case 1991).

To develop a predictive habitat suitability model for swift fox, we conducted an extensive literature review to identify key habitat structure and landscape predictors of species occurrence and abundance. Using the best available information on species habitat needs, we used geographic information systems (GIS) tools to correlate known vegetative associations and landscape characteristics from the literature with available landcover data.

Using the predicted habitat suitability model as a base layer we divide the study area into grids of 31 km^2 (Following Findley et al. 2005), which will allow us to potentially identify individual foxes in the site and be able to estimate number of foxes in a particular area. Swift fox home ranges in Nebraska average 32.3 km^2 for males and 27.5 km^2 for females (Hines and Case 1991) although these estimates are larger than other found in the literature – 7.6 km^2 in Colorado (Kitchen et al. 1999) and 11.7 km^2 in Wyoming (Pechacek et al. 2000). Using a 31 km^2 grid we are able to sample swift foxes over a large geographic area and compare our results with studies conducted in other areas within swift fox distribution range (Finley et al. 2005; Martin et al. 2007; Stratman 2012). We classified the grids by the percentage of potential suitable habitat. A grid was defined as “suitable” if it was composed of $\geq 25\%$ suitable landcover (i.e., shortgrass and mixed grass prairie) and $\geq 45\%$ suitable slope (i.e., $< 10\%$ of slope) because they are habitat characteristics that reliably predicts occupancy and detection of swift foxes (Findley et al. 2005, Martin et al. 2007, Knox and Grenier 2011). Then, we used the Create Spatially Balanced Points tool, an ArcGIS 10.0 Geostatistical Analyst extension by Esri, to select 100 locations from all available grids.

The Spatially Balanced Points tool was developed based on the Reverse Randomized Quadrant-Recursive Raster algorithm (Stevens and Olsen 2004) that is used to map two-dimensional space into a one-dimensional space in which successive samples are randomly and spatially balanced according to an unequal inclusion probability of the grids. The Reverse Randomized Quadrant-Recursive Raster algorithm works in a three-step process that includes: generating a sequence grid or raster, filtering the sequence generated against a probabilistic grid (i.e., probability of observing the target species in a specific location), and generating sample site locations (ESRI 2010). In this way the grids were selected based on perceived importance relative to other locations in the raster.

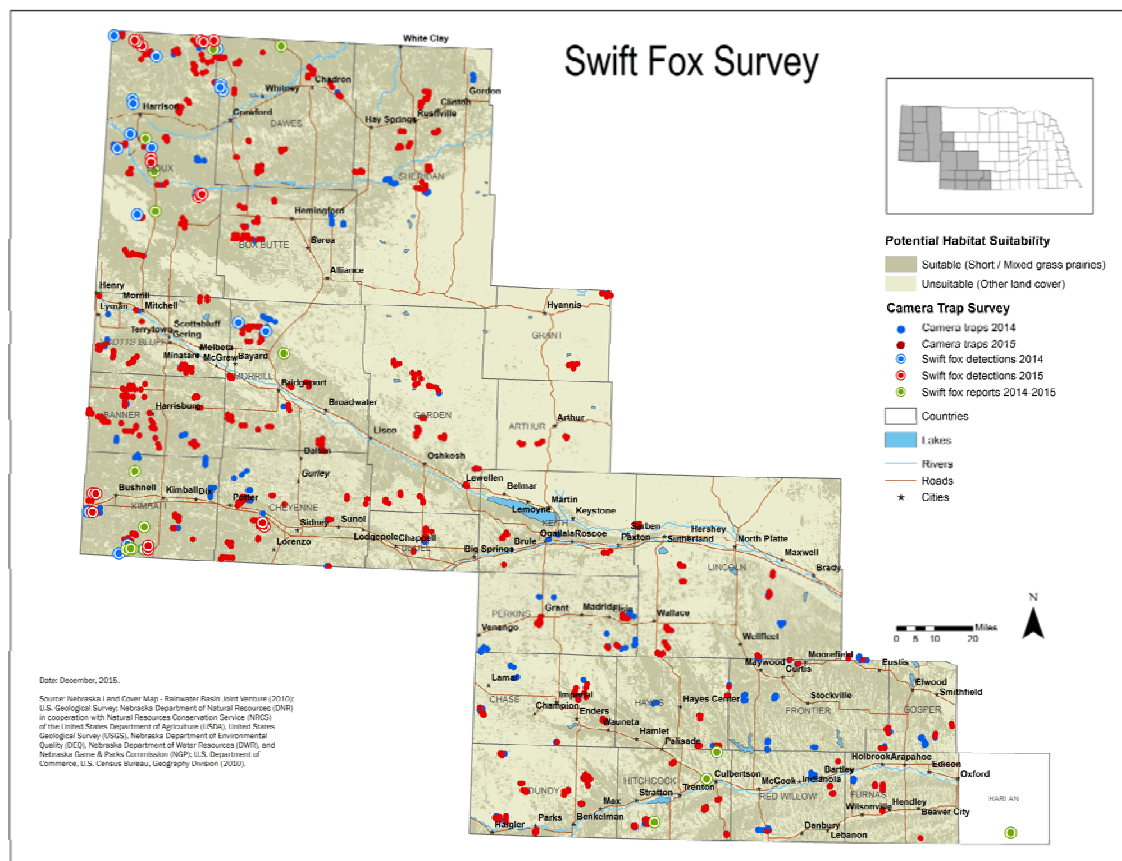


Figure 2. Swift fox *a priori* habitat suitability model with locations of sampling sites based on a balanced sampling design. Large dots represent locations where either swift fox were reported or confirmed with camera traps.

Spatially Balanced Sampling selects sample points by taking into account the potential spatial pattern of the population and optimizing the sampling based on the probability of observing a target species in a specific point. Spatially Balanced Sampling is intended to provide more information per sampling unit with less spatial autocorrelation effects (Theobald and Norman 2006) while allowing for flexibility in survey design, so that if there is a need to remove a location from the survey, a new one will replace it with another replicate of the site, conserving the randomness and spatial balanced qualities (i.e., it makes it possible to update sample locations according to accessibility of the sites, budget, etc.).

2) Private and public lands access

Because of the geographic scope of the project, a great deal of effort was necessary to secure access to the 100 study sites defined by the random sampling design. Beginning in December, 2013, we sent letters to more than 200 private landowners. Using public databases of landownership, landowners were selected if they owned property within any of the 100, 31 km² sampling grid. The letter acted as a first round of contact, and was followed by a phone call requesting access to place camera traps. Acceptance rates were low, access was not available at all random sites. As such we generated replacement sites (see above for protocol) and sent an additional letter to potential landowners, again followed by a phone call. To facilitate landowner engagement and information transfer, we developed a website (swiftfox.unl.edu) outlining the overall objectives of the project. The website acts as means to help landowners understand the project and provides them information on the researchers and collaborators that are involved as well as the protocols we use for setting up cameras.

In addition to private lands, we also secured permission to sample for canids on public lands. This included securing permissions and associated permits from Nebraska Game and Parks, U.S. Forest Service, the U.S. Fish and Wildlife Service, and U.S. National Park Service.

In total we secured public and private permission from 130 landowners to sample nearly 200 sites within the study area.

3) Sampling

To assess the presence and relative abundance of various canid species, we employed a standardized camera trap protocol. Surveys were conducted two times per year to coincide with two main seasons: (i) breeding season between February and June to detect resident adults, because the persistence of swift fox populations depends on the distribution and abundance of breeding adults; and (ii) during juvenile dispersal between September and November, in an attempt to maximize detection probabilities (Finley et al. 2005, Martin et al. 2007) because during the fall pups forage on their own, juveniles start to disperse, and adults are more active and range farther from the den (Olson et al. 2003).

We used an array of 5-10 trail cameras (Bushnell Trophy Cam HD and Moultrie M-880) within each 31 km² sampling location. The cameras were hung on posts 40 cm above ground and deployed to take advantage of the presence of fences, posts, gates, intersections, etc., because canids tend to travel using such landscape features. A wooden stake was placed 3 m from each camera exposed 40 cm above the ground to

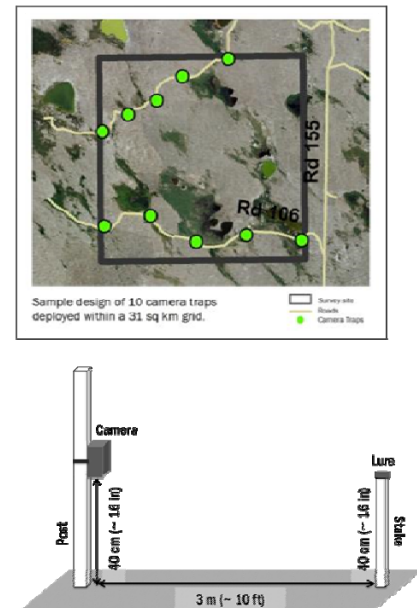


Figure 3. Example of camera trap effort within a sampling location and the appropriate method of camera deployment.

serve as a base for the lure as well as a focal point for the camera and a metric for estimating animal body size. The lure consists of approximately 15 ml of a skunk-based attractant produced by heating 385 ml of petroleum jelly to liquid form, adding 15 ml of skunk essence (F&T Fur Harvester's Trading Post, Alpena, MI), and allowing the lure to solidify. Cameras were set up to take bursts of 3 photographs no less than 5 seconds apart each time motion and/or heat signature is detected and left for 10 consecutive nights as this maximizes the trade-off between detection probability (i.e., reducing false negatives) and sampling time.

Starting in April 2014, we began deploying camera traps across the western third of Nebraska. In the spring of 2014, we deployed 455 cameras on 108 sites. We increased our effort in the fall of 2014 and we were able to deploy 804 cameras on 187 sites. During 2015 we deployed a total of 1,422 cameras (spring and fall) surveying at the same sites 2014. We deployed a total of 2,267 cameras representing 197 survey sites across two seasons (spring and fall) for two years (2014 and 2015). From these cameras we have collected nearly more than 5 million images representing 22,670 trap nights. At each site we also conducted vegetation and infrastructure assessments.

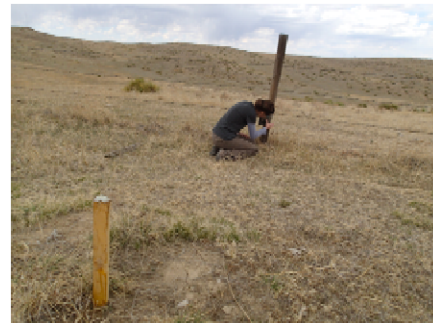


Figure 4. Camera trap being deployed by graduate student Lucia Corral on private land in northwest Nebraska.

4) Photo catalog

To associate occupancy with ecological conditions, all pictures were downloaded and captures recorded by species, as well as GPS coordinates, location and habitat code, and total number of photos taken for each camera. The resulting data for each camera is recorded as detection histories; i.e., vectors of 1's and 0's, where "1" represents that at least one individual was detected and a "0" the failure to detect any individual during the survey. The binary database forms the basis to develop predictive models that relate the occurrence of all canid species with habitat attributes the distribution of other canids.



Figure 5. Coyote caught on a camera trap in northwest Nebraska.

We have cataloged data to collect information not only on swift fox, but a suite of species commonly attracted to scent stations. We have cataloged nearly 5 million photos and entered data on occupancy for twenty different species, including confirmed locations for swift fox (Figure 2).

5) Current species distribution model

Predictive models of species distribution (i.e., Species Distribution Models – SDM) have become an increasingly important tool to study distribution patterns and the processes that predict species occurrence (Guisan and Thuiller 2005). Species distribution models are low-dimensional

abstractions that describe empirical correlations between species occurrence or abundance and environmental variables. SDMs are constructed in accordance with ecological knowledge of the factors limiting species occurrence (Scott et al. 2002, Franklin 2009). Therefore, one of the outcomes of SDM is a characterization of the species niche, because we use data on actual species occurrence to produce the models and then extrapolate the results in geographical space. Once the realized niche for the species is described and modeled, it can be mapped to produce potential distribution or habitat suitability maps (Franklin 2009), and subsequently used to predict the likelihood that a species occurs at a location (i.e., the probability of the species presence in an area).

Model Development

We used occurrence data of swift fox from camera trap surveys conducted in 2014 and 2015. The resulting data for each camera was recorded as detection histories (i.e., vectors of 1's and 0's, where "1" represents that at least one individual was detected and a "0" the failure to detect any individual during the survey). The data on presence/absence of swift fox was the response variable for our analysis, while the data on environmental and landscape characteristics at each location formed the basis of the explanatory variables.

The explanatory or predictor variables were chosen to represent characteristics of the landscape and climatic conditions likely to be important determinants of the distribution of swift foxes. Climatic variables were obtained from the WorldClim database (Hijmans, et al. 2005, O'Donnell, et al. 2012), which provides a variety of climatic data averaged over the years 1950-2000 converted into 19 bioclimatic variables. Because the Worldclim variables are derived from a common set of temperature and precipitation data, they present strong multicollinearity. Therefore, before selecting the variables, we created a Spearman rank correlation matrix to explore the relationships between the 19 variables. We removed all the variables that were significantly correlated (Spearman $\rho > 0.50$, $p < 0.01$) and that were less likely to be biologically significant in contributing to or limiting swift fox. We used four bioclimatic variables in modeling: annual mean temperature, temperature annual range, annual precipitation and precipitation coefficient of variation (see <http://www.worldclim.org/bioclim>).

The landscape variables were obtained from landcover, soil type and slope layers. Shortgrass prairie and flat terrains are reliable predictors for probability of occupancy and detection of swift foxes (Findley et al. 2005, Martin et al. 2007, Knox and Grenier 2011, Stratman 2012). We used the landcover data set developed by the Rainwater Basin Joint Venture landcover (version 10.1) and modified later by NGPC (2013). The soil type layer was based on the Soils of Nebraska map published by the Natural Resources Conservation Service (NRCS) of the United States Department of Agriculture (USDA). This map presents the main soil associations of the state directly related to topographic characteristics of each area. Finally, we created a slope layer from the Nebraska Digital Elevation Model (DEM) using the slope function from ArcToolbox (ArcGIS 10.3.1). The slope function calculates the maximum rate of change from every cell to its neighbors, in degrees (0-90), which is a measure of vertical rise over the horizontal run. All layers were modified so that each data set layer had the same spatial resolution, extent, and projection (coordinate reference system). We use ArcGIS Spatial Analyst resampling function to

perform a nearest neighbor analysis to match all layers to the coarsest resolution (~ 1km) from input datasets.

We used Zero-inflated Generalized Linear Mixed Models to assess the relationships between swift fox presence/absence and the explanatory variables. Our modeling approach was chosen because it is suitable for overdispersed data due to an excess of zero values, allows the analysis of multilevel data structure (e.g., repeated measures), accounts for temporal and spatial correlation between the observations, includes fixed and random effects, allows for a response variable with a binomial distribution (i.e., presence/absence), and predictors variables can be either categorical, numerical or both (Zuur et al. 2009, 2012).

We assumed that (1) the source of zeros in our data is structural (structural zeros), which means they represent positive zeros, true zeros, or true negatives that are not due to the difficulty to detect swift foxes, and (2) the logit of the “success” or positive detection probability is linearly related to the predictor variable.

We used an information-theoretic approach to examine which variables are important determinants of swift fox distribution and to identify a suitable and parsimonious approximating model. We used Akaike information criterion (AIC) to select the “best model” from a multiple model comparisons. The “best” model chosen was:

$$\begin{aligned} \text{logit}(p_{ij}) &= \alpha + \beta_1 + \beta_2 \times \text{cover}_{ij} + \beta_5 \times \text{temp_am}_{ij} + \beta_6 \times \text{temp_ar}_{ij} + \beta_7 \times \text{prec_as}_{ij} + \\ &\beta_8 \times \text{prec_cv}_{ij} + a_i \\ a_i &\sim N(0, \sigma_a^2) \end{aligned}$$

Where logit stands for the logistic link, p_{ij} is the probability that a swift fox j is present on a location i (loc_id), cover_{ij} is the landcover, temp_am_{ij} is the annual mean temperature, temp_ar_{ij} is the annual range temperature, prec_as_{ij} is the annual precipitation, and prec_cv_{ij} is the precipitation coefficient of variation. All predictor variables considered fixed effect, and a_i is the random intercept. Since the same camera-trap location was surveyed repeatedly, the location (loc_id) was used as random effect.

We used the glmm function from glmmADMB package (version 0.6.5) in R (version 3.2.2), built on the open source AD Model Builder nonlinear fitting engine, for fitting generalized linear mixed models. We then made predictions using the glmm object and created a raster object with predictions from the fitted model to be able to visualize occurrence probabilities (Figure 6).

Model Evaluation

To evaluate the quality of the predictions, we calculated six threshold dependent metrics (see below) and compared four different methods to select the optimal thresholds (Table 1). All accuracy metrics were obtained using the PresenceAbsence package in R (version 3.2.2). Model accuracy metrics:

1. Percent Correctly Classified – overall predictive capability
2. Omission – failure to predict true presence
3. Commission – over-prediction of presence
4. Sensitivity – ability to predict true presence
5. Specificity – ability to predict true absence
6. Prevalence – refers to species frequency (presence)

Table 1. Estimates of optimal thresholds values

Methods for threshold selection	Threshold
Mean occurrence prediction ^a	0.22
10% omission ^b	0.10
Sensitivity = Specificity ^c	0.15
Max. Sensitivity + Specificity ^d	0.14

a. the mean prediction for the occurrence (presence) records

b. the threshold that excludes approx. 10 percent of the occurrence records

c. the threshold value or range in values where sensitivity is equal to specificity

d. the threshold value or range in values that maximizes sensitivity plus specificity

The estimates obtained for Percent Correctly Classified (53-84%), omission (88-93%), and commission (0-2%) suggest a relatively poor performing model. As most of our data reflect locations where swift fox are not present (numerous zeros in the input data) our model performs relatively well when predicting zeros, but only because the low prevalence of swift fox (0.14-0.30) makes it likely that any place surveyed will not contain a fox. Subsequently, the low numbers of presence data were nearly impossible to predict given our predictors and model structure (9-11% correctly predicted presences). This means the current model is not a reliable model to accurately predict the presence of swift fox, but it is extremely accurate in showing where foxes are not. This preliminary output is not surprising considering that the model is strongly influenced by the low occurrence of swift fox (84 presence / 2282 absences). Because swift fox is a species of concern, errors of omission are extremely important, and therefore we should interpret and use the predicted distribution map cautiously. It is crucial to take into consideration that (1) the predictive map is a static product in space and time, (2) the model selected is subject to several assumptions and dependent on the predictor variables used, and (3) the current validation is subject to the selected thresholds.

Our poorly-fitting model may indicate:

- 1) The assumptions of model family fitted (zero-inflated binomial) may not accurately reflect the structure of the data; our model fitting procedure assumed a single constant value for zero-inflation across the dataset which may not be a valid assumption.
- 2) Our selected predictors cannot adequately separate presences from absences, either because they are unrelated to the presence of swift fox or because the functional form of the relationship (linear) was inappropriate.
- 3) We are missing important predictor variables that would explain swift fox distribution patterns.

We will continue to improve the model by reevaluating the predictor variables selected and evaluating new variables (e.g., percent of each type of landcover). Additionally, we will investigate non-linear relationships using models that offer greater flexibility in the modeled relationships (e.g., generalized additive models). Furthermore, we will explore machine learning methods (e.g., classification trees and random forest), which may be suited for modeling rare species and can potentially offer improvements to predictive accuracy.

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