

IMPROVING AVIAN SPECIES DISTRIBUTION MODELS BY INCORPORATING
BIOTIC INTERACTIONS

A Dissertation

by

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ABSTRACT

Maps of actual or potential species distributions are crucial for many aspects of natural resource management, land use development, and conservation planning. Species distribution models (SDMs) attempt to predict or statistically associate geographic record of a species with abiotic and biospatial variables of interest over large spatial extents and are utilized in wildlife management as aerial imagery and our understanding of distributional patterns advances. Most distributional models use variables such as soil type, climatic patterns, topography, hydrology, vegetative communities, and other abiotic conditions to identify the predicted geographic range of a species. However, species interactions have yet to be successfully quantified and included in distributional models. It is imperative we include interactions in niche models as certain species relationships (i.e. predation, competition, habitat facilitation) have documented influence on species distribution. I demonstrated techniques to improve traditional SDMs by incorporating intra- and inter-specific biotic interactions using birds as an example. Models that incorporate this biotic influence introduce new code in existing statistical languages that can also be applied to other environments. The methods I developed present a fusion of techniques from multiple fields including ecological modeling, remote sensing, and statistical analyses, the synthesis of which result in a novel and elevated approach to modeling and predicting species distributions.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

Part 1, faculty committee recognition

This work was supervised by a dissertation committee consisting of Professor Michael L. Morrison [advisor], Professor William E. Grant, Dr. Hsiao-Hsuan Wang, and Dr. Tyler A. Campbell of the Department of Wildlife & Fisheries Sciences and Professor David M. Cairns of the Department of Geography.

Part 2, student/collaborator contributions

The vegetative (field) and bird occurrence data used in Chapter 2 and Chapter 3 were collected by East Foundation field crews consisting of various undergraduate and graduate student technicians.

All other work conducted for the dissertation was completed by the student independently.

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CHAPTER I

INTRODUCTION

Distribution ecology intends to answer fundamental questions regarding target species or the use of an area: what is the habitat of the species? How is a specific area, plot, or landscape utilized? Derived from these questions, and their resolutions, are the more applicable conclusions relevant in ecological management: estimating species abundance and predicting trends in the population, understanding and anticipating the behavior of species assemblages, and ultimately determining what leads to a species persistence. Awareness of the presence or absence of a species and how that occupancy changes temporally and spatially is elemental to any higher understanding of the population. Baseline knowledge of occupancy across time enables us to assess the importance of specific geographic and vegetative features in the environment to the target species, as well as evaluate the changes in that value on a temporal scale. Distributional maps offer us visual aide in understanding the spatial definition of the species habitat and, when occurrence data are collected over time, provide visual representation of temporal trends in habitat utilization (Soberon and Peterson 2004). Relevant conclusions can then be used to inform management that better approximate the dynamics of natural ecosystems.

Remote sensing and species occurrence data

The continuing advancements in information technology such as large-scale data digitization, public-access databases, accessibility and improvements of Earth satellite

imagery, and ever-increasing electronic storage capacity have revolutionized how ecologists are using and distributing data (Bisby 2000, Edwards et al. 2000, Krishtalka et al. 2002). The access to an increasing body of remote sensing (RS) data, as well as an imagery archive dating back to the 1960s, has allowed researchers to assess how environments have changed over time. For example, land cover and land use change, grassland conditions, oil-spill response, wildfire impacts, and changes in fragmentation patterns can now be monitored over time (Horning et al. 2010). Furthermore, over 625 Terabytes (TB) of data from the LANDSAT 8 satellite family, alone, have been processed and made available by United States Geological Survey (USGS) (USGS 2015). Technological advances like geographical information systems (GIS) have allowed researchers to develop practical applications that incorporate biodiversity, climate, topography, soils, and vegetation indices data at increasingly finer resolutions (Peterson et al. 2011). The unique capacity of RS data to characterize the Earth's surface from different perspectives and resolutions allows scientists to establish correlates in geographical features and species observation data (Horning et al. 2010). Increasingly, this has made remote sensing a powerful tool for evaluating the status and trends of ecological systems (Peterson and Parker 1998, Turner et al. 2003, McPhearson and Wallace 2008). For example, RS products have been used to develop and simulate multiple management and policy scenarios, including managing protected areas, setting conservation priorities, and identifying ideal locations for protected areas (Menon and Bawa 1997). Among the other broad applications, RS data can be used to link species

occurrence data to specific environmental features and events such as fires or storms through the creation of distributional maps (Horning et al. 2010).

Comprehensive niche modeling

The species niche concept is central to ecology and its history and evolution is discussed in the majority of ecological textbooks and classrooms (Shugart 1998, Chase and Leibold 2003). Loosely defined as the “requirement of a species for existence in a given environment and its impacts on that environment”, the earliest formal niche concept is credited to Grinnell (1917) and Elton (1927). In essence, species persistence is only possible when its ecological requirements are met in its environment (Chase and Leibold 2003). Early niche concept described the full spectrum of environmental conditions in which a species can reproduce and persist (Pulliam 1988). In slight contrast to the Grinnellian niche, Elton defined the niche as the functional role the species plays in its environment as well as its impact on that environment (taking into consideration more complex food web interactions). Hutchinson (1957) introduced the idea that a species niche can be described as an “n-dimensional hypervolume” in which species persistence is limited by a complex combination of biotic and abiotic factors. He is also credited with coining the terms “fundamental” and “realized” niche in which the “realized” niche is the full set conditions actually utilized by a species after interaction forces (e.g. predation or competition) are taken into account.

Most distributional models use variables such as soil type, climatic patterns, topography, hydrology, vegetative communities, and other abiotic conditions to identify

the predicted geographic range of a species (Meier et al. 2010, Zimmermann et al. 2010). This results in a fundamental niche model that resembles early Grinnellian niche concepts, only taking into account environmentally dictated occupancy (Soberón 2007, Guisan and Thuiller 2005, Araújo and Guisan 2006). Some have argued that the outcome of modeling species distributions is a description of the species' realized niche because data of actual occurrence is used and so the model expands conditions associated with species presence into geographical space (Austin 2002, Thuiller et al. 2004, Guisan and Thuiller 2005). The niche is then described statistically and mapped in geographical space representing potential distribution (Araújo and Guisan 2006, Soberón 2007). However, we now understand that the environment does not solely determine species distributions. Instead, a complex network of abiotic and biotic interactions such as predation, competition, facilitation, or otherwise symbiotic relationships (Hutchinson's n-dimensional niche concept) interact to influence occupancy (Hutchinson 1957, Holt 2009, Bascompte, 2009; van Dam, 2009). However, there are conflicting schools of thought as to the exact mechanism by which species are distributed. Diamond's (1975) assembly rules model suggested 7 key mechanisms by which animal communities were distributed of which most are largely attributed to competitive interactions between species. He based his theory on a decade of field observations of bird distributions in the Bismarck Archipelago during which he found species with similar food habits rarely co-occurred. This observation, when applied to broad patterns of occurrence, produced what Diamond called a "checkerboard pattern" attributed mainly to interspecies competition (Morrison 2009). Controversy ensued due to the difficulty in definitively naming

competition as the driving force in the observed species occurrence patterns.

Alternatively, Connor and Simberloff (1979) argued that interspecific competition itself cannot be a major organizing force for avian communities and refutes Diamond's assembly rules model. Connor and Simberloff discounted Diamond's 7 governing assembly rules arguing that their assumptions are baseless, untestable, and "describe situations which would for the most part be found even if species were randomly distributed..." (Connor and Simberloff 1979). Upon release of Diamond's original Bismarck data (Mayr and Diamond 2001), Collins et al. (2011) tested Diamond's theory of competitive exclusion driving observed distributional patterns using binary matrices to test for checkerboard distributions of birds on the archipelago. They found a greater percentage of species exhibiting checkerboard distribution than expected by random chance (Collins et al. 2011). Although unable to refute Diamond's competitive exclusion hypothesis based on the results, they argued insufficient evidence to rule out other hypotheses. A recent meta-analysis (involving 96 presence-absence studies) investigating the application of Diamond's assembly rules model was not able to confirm the mechanism of the model, however the authors did establish a nonrandom frequency of observed co-occurrence (Gotelli and McCabe 2002). It is important to acknowledge the complexity of the determinants that influence a species' distribution. In light of these discussions on assembly rules and the driving forces behind species occurrence patterns, I subscribe to the more comprehensive perspective in which a combination of abiotic and biotic factors determines the occurrence of a species in an area.

Species interactions have yet to be successfully quantified and included in distributional models (Sexton et al. 2009, Paine 2010, Zarnetske et al. 2012). It is imperative we include interactions in niche models as certain species relationships (i.e. predation, competition, habitat facilitation) have documented influence on species distribution (Hopcraft 2012, Pilfold et al. 2014, Bulleri et al. 2016).

Modeling species distribution across spatial extents

Maps of actual or potential species distributions are crucial for many aspects of natural resource management, land use development, and conservation planning (Scott et al. 2002, Franklin 2009). Species distribution models (SDMs) attempt to predict or statistically associate geographic record of a species with abiotic and biospatial variables of interest over large spatial extents and are utilized in wildlife management as aerial imagery and our understanding of distributional patterns advances (Guisan and Zimmerman 2000, Franklin 2009, Peterson et al. 2011). SDMs have diverse applications and can be used to describe both (a) the species niche, and (b) areas of persistence or expansion of presence (Franklin 2009, Rotenberry et al. 2006). Typically using abundance, density, or presence-absence data collected from surveys, models can then be used to extrapolate predictions of habitat or likelihood of a species' presence into areas lacking species occurrence information (Rotenberry et al. 2006). Layering maps of individual species distributions can also reveal correlates among the occurrences of multiple species that can help us better understand the dynamics of whole ecosystems. Expanding the focus from a single species to multiple species distribution can increase our understanding of the local and regional species pool and improve our predictions for

how changes in the environment might impact the ecosystem. These predictions may then help inform management decisions or guide additional survey efforts (Raxworthy et al. 2003, Sinclair et al. 2010). Remotely sensed data provide a crucial tool for the efficient collection of information needed to set conservation and management priorities (Horning et al. 2010). Remotely sensed products allow us to understand environments in a broader landscape or global context and thus are valuable for evaluating the status and trends of ecological systems (Peterson and Parker 1998, Turner et al. 2003, McPhearson and Wallace 2008).

Modeling bird distributions as influenced by biotic interactions in south Texas agricultural landscape

The Rio Grande Plains encompasses the Coastal Sand Plain, Tamaulipas Scrubland, and Lower Rio Grande Valley natural regions of Texas. The low-growing woody plants and dense shrubs that dominate the vegetation in this region have given rise to common vernacular names including “brush country”, “shrublands”, and “thorn scrub” among others (Taylor 2014). Although much of the land is primarily agricultural rangelands, wildlife recreation has become increasingly important to landowners because of the associated economic value (TPWD 2016; Dodd 2009). Due to the relatively high protein content in the forage and large expanses of un-developed land, this region has become popular for producing some of the largest White-tailed deer *Odocoileus virginianus* in the state (TPWD 2016). The area also provides crucial resources for North American migratory and resident birds, as well rare and federally endangered species (e.g. Ocelots *Leopardus pardalis*, Aplomado falcon *Falco femoralis*)

often found nowhere else in the United States (USFWS 1980, TPWD 2016). Birds have become a group of heightened interest due to the recent increased demand for avian game. For example, south Texas landowners that can anticipate an average gross profit of \$11.60 per acre for the deer or exotic ungulate lease can expect an average gross profit of \$51.87 per acre for a quail hunting lease (TPWD 2017). However, woody vegetation encroachment due to overgrazing and fire suppression has been tied to the recent decline in Northern bobwhite *Colinus virginianus* and Scaled quail *Callipepla squamata*, two highly prized game species (Bridges et al. 2002). Thus, understanding of the distributions of game and non-game fauna becomes relevant as landowners and wildlife management agencies balance the needs of cattle ranching, exotic game ranching, and the requirements of sustainable wildlife populations. The biotic influence is crucial in realizing the most accurate ecological niche and it is essential we include species interactions in bird distributional models, especially when important management decisions are at stake. To address this issue, I built baseline species distribution models for resident breeding bird species occurring on a privately managed ranch in south Texas from 2014 through 2017 and then improved the models by quantitatively and spatially representing biotic influences on bird distribution.

I developed techniques to improve traditional SDMs by incorporating intra- and inter-specific biotic interactions using birds as an example. Models that incorporate this biotic influence introduce new code in existing statistical languages that can also be applied to other environments. The methods I developed present a fusion of techniques from multiple fields including ecological modeling, remote sensing, and statistical

analyses, the synthesis of which result in a novel and elevated approach to modeling and predicting species distributions. I achieved this through two over-arching project goals.

A. GOAL: Development of baseline SDMs for breeding and resident birds in the south Texas agricultural landscape.

1) Objective: Build predictive distribution models using avian point count data, environmental conditions, and spatial variables.

B. GOAL: Advance those select SDMs by incorporating biotic interactions.

2) Objective: Identify and quantify known biotic interactions of species present in the dataset using a combination of scientific literature and trends of co-occurrence in the data.

CHAPTER II

MODELING THE INFLUENCE OF LIVESTOCK GRAZING PRESSURE ON GRASSLAND BIRD DISTRIBUTIONS

INTRODUCTION

Domestic livestock are recognized ecosystem engineers in semi-arid rangelands, where they directly and indirectly alter the availability of resources to a wide range of grassland-associated organisms (Derner et al., 2009). Several studies cite the influence of vegetative changes due to livestock grazing on breeding grassland birds since this species group is heavily influenced by vegetative structure (Askins et al., 2007; Brennan and Kuvlesky, 2005; Fuhlendorf et al., 2006; Jansen et al., 1999). Grazing pressure has historically been difficult to quantify due to variable plant responses to grazing and movements of livestock within pastures (Landsberg and Crowley, 2004). However, a review of the effects of water-place distribution on rangelands suggested that distances from water sources (e.g. livestock tanks, troughs) can provide valuable context for interpreting changes in grazed landscapes particularly in areas remote from water sources (James et al., 1999; Landsberg and Crowley, 2004; Ludwig et al., 2000). In south Texas, water sources are scarce. Specifically, the Coastal Sand Plain region of Texas has no natural permanent bodies of freshwater making livestock wells and holding tanks supplied by active ranching operations the only water source for domestic livestock and, thus, it is reasonable to expect water-points to have a substantial impact on the

distribution and intensity of localized grazing (Fulbright et al., 1990; Snelgrove et al., 2013).

Grassland bird populations have experienced precipitous declines on a continental-scale over the last few decades (Brennan and Kuvlesky, 2005; Nocera and Koslowsky, 2011). Although agricultural and livestock operations dominate the south Texas landscape, wildlife-related recreation has become increasingly important to landowners because of the associated economic value (Dodd, 2009; TPWD, 2016). For example, landowners can anticipate an average gross profit of \$4.69 per hectare for a deer or exotic ungulate hunting lease and can expect an average gross profit of \$20.99 per hectare for a quail (e.g., Northern bobwhite *Colinus virginianus*, Scaled quail *Callipepla squamata*) hunting lease (TPWD, 2017). This area also provides crucial resources for other migratory and resident grassland birds (e.g., Cassin's sparrow *Aimophila cassinii*, Grasshopper sparrow *Ammodramus savannarum*, Dickcissel *Spiza americana*) that have declined throughout their ranges due to land use and climate change since 1966 (Brennan and Kuvlesky, 2005; Knopf, 1994). It is essential we advance our understanding of how grassland birds are affected by their environment, inclusive of both their requirements to persist (i.e., resources) and how they interact with environmental features or biotic influences.

Traditionally, species distribution models (SDMs), which statistically associate a species' occurrence with a suite of geospatial predictors, use direct variables, resources that the animal consumes or requires to persist in an area (e.g., shrub density, water availability) to define and project a species' niche and distribution (Austin and Niel,

2011; Elith and Leathwick, 2009). Indirect variables, which are features the animal does not consume or require for persistence but with which it may still interact (e.g., competition, commensalism), are often excluded in SDMs due to the difficulty in identifying the variable ecologically, quantifying the relationship, or in managing collinearity issues adding an interaction factor to a traditional SDM framework may contribute (Austin and Niel, 2011). However, recent advances in machine learning algorithms (e.g., Random Forest) have enabled us to include indirect variables, such as grazing pressure, in SDMs that may have more complicated relationships with the distribution of the target species than traditional resource variables (Miller, 2010).

Our objective was to improve traditional SDMs projecting the distribution of three summer resident south Texas grassland birds (Northern bobwhite *Colinus virginianus*, Eastern meadowlark *Sturnella magna* and Cassin's sparrow *Peucaea cassinii*) by incorporating livestock grazing pressure, an indirect variable. We used a novel approach to spatially quantify localized grazing pressure to include this variable using five SDM algorithms: BioClim, Generalized Linear Model, MaxEnt, Boosted Regression Tree, and Random Forest. Our approach serves as a valuable tool for rangeland managers when the management goal is to promote sustainable livestock grazing and recreational wildlife harvest, while maintaining viable nongame species.

METHODS

Study site

The Coloraditas Grazing Research and Demonstration Area (CGRDA) is a 7,684-ha area located on the 60,000-ha San Antonio Viejo Ranch (SAV) approximately 25 km south of Hebbronville, Texas in Jim Hogg and Starr counties (Fig. 1). SAV is located within the South Texas Plains ecoregion and is managed predominantly as a cow-calf operation. Mean annual temperature within the study site is 22.6 C° and mean annual precipitation is 502.5 mm (PRISM Climate Group, 2018). SAV is one of six properties of the East Foundation that are managed as a living laboratory to support wildlife conservation and other public benefits of ranching and private land stewardship. The CGRDA is representative of south Texas rangeland ecosystems and encompasses the Coastal Sand Plain and Texas-Tamulipan Thronscrub ecoregions. Low-growing woody plants, dense shrubs (*Prosopis glandulosa*, *Acacia greggii*, *Celtis ehrenbergiana*, *Colubrina texensis*, *Aloysia gratissima*, *Lantana urticoides*), and cacti (*Opuntia engelmannii* var. *lindheimeri*, *Opuntia leptocaulis*) dominate the vegetation in this area. The CGRDA is comprised of 10 pastures each assigned to 1 of 4 grazing systems (Fig 1). Four pastures were assigned to a continuous grazing system with 2 pastures (Rodeo and Tia Nena) maintained under a high stocking rate (1 Animal Unit [AU] /14 ha) and 2 pastures (San Juan and Calichera) under a moderate stocking rate (1 AU/20 ha). Six pastures were assigned to a rotational system with 3 pastures, 1 herd maintained under the high stocking rate (Coloraditas, Desiderio, and Guadalupe units) and 3 pastures, 1 herd maintained under the moderate stocking rate (San Rafael, Loma, and Tequileras

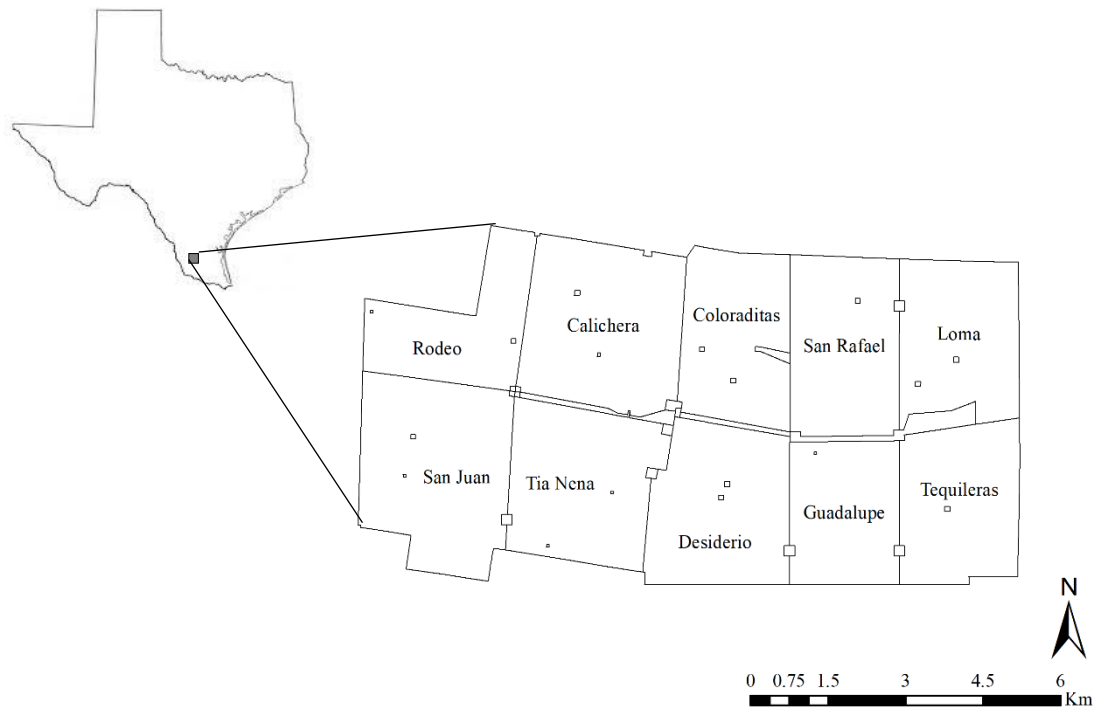


Figure 1. Locality and pasture composition of East Foundation's Coloraditas Grazing Research and Demonstration Area (CGRDA). Four pastures were assigned to a continuous grazing system with 2 pastures (Rodeo and Tia Nena) maintained under a high stocking rate (1 Animal Unit [AU] /14 ha) and 2 pastures (San Juan and Calichera) under a moderate stocking rate (1 AU/20 ha) in December 2015. Six pastures were assigned to a rotational system with 3 pastures, 1 herd maintained under the high stocking rate (Coloraditas, Desiderio, and Guadalupe units) and 3 pastures, 1 herd maintained under the moderate stocking rate (San Rafael, Loma, and Tequileras units).

units). Grazing was deferred on all pastures for two years prior to the onset of livestock grazing in December 2015.

Environmental predictors

We used canopy height, shrub density, grass *spp.* coverage, cacti *spp.* coverage, and bare ground coverage recorded from ground surveys in 2016 as environmental predictors in SDMs. We collected vegetation composition and structure data from 141 permanent 20-m transects in October 2016. We allocated transects proportional to the area of ecological sites that occur in each pasture using stratified sampling resulting in 12–16 transects per pasture (Bonham, 2013). We marked each transect start and collected data in a random, predetermined direction (N, S, E, W). On each transect we sampled 5, 20×50 cm quadrats (5 m spacing) randomly placed at either 0, 0.5, 1, 1.5, 2, or 2.5 m from the left side of the tape and facing away from the transect start, visually recording percent cover of woody, herbaceous (later classified by grass *spp.*), and bare ground in each quadrat.

We also documented woody canopy cover along each of the 20 m transects by visually recording the amount of the ground (in centimeters) covered by woody plant materials (leaves and branches) and succulent (cacti) that intercepted the line transect by species (Canfield, 1941; Higgins et al., 2012). If a gap in the canopy exceeded 0.5 m for an individual, we recorded separate cover measurements. We calculated percent canopy cover by summing the intercept measurements for an individual species, dividing by total line length and converting to a cover percentage. We calculated total percent cover

by adding cover percentages for all species, which sometimes exceeded 100% when overlapping canopies by different species were recorded (Coulloudon et al., 1999).

Additionally, we used elevation, topographic relief (30-m² resolution), and Optimized Soil Adjusted Vegetation Index (OSAVI, a measure of LAI) produced from remotely sensed imagery collected during the same growing season as the ground surveys. We acquired one Landsat 8-OLI tile (< 6% cloud cover) that encompassed the study area (courtesy of U.S. Geological Survey) and processed this in ENVI 5.1 (NASA Landsat Program, 2016). We corrected for atmospheric conditions and converted the original image format of Digital Numbers (DN) to radiance and then surface reflectance. We first resized the image to the rectangular extent of the CGRDA pasture complex and then extracted by the study area mask in ESRI ArcGIS ArcMap 10.5. We then spatially subset the extracted image by bands 2-5 corresponding to Landsat 8-OLI band designations: blue, green, red, and NIR. Bands were stacked and the OSAVI was calculated using the band math tool in ENVI 5.1. This index for LAI follows the standard formula $[(\text{NIR}-\text{Red})/(\text{NIR}+\text{Red}+0.16)]$ and uses a reflectance constant of 0.16 to adjust for high background reflectance (e.g., areas with sparse vegetation and high soil reflectance) (Rondeaux et al., 1996). In south Texas, this vegetation index outperformed other, more common vegetation indices (e.g., Normalized Difference Vegetation Index [NDVI]) in overall image classification accuracy and herbaceous coverage estimations (Fern et al., 2018).

Locations of water sources (e.g., livestock wells) within the study site and cattle stocking rates were provided by the East Foundation. To calculate water proximity, we

gridded the spatial extent of the CGRDA into a fishnet (30-m² resolution). We performed a proximity analysis on each pixel centroid using the Near tool in ArcMap 10.5 to determine distance of each centroid to location of nearest water source, usually a livestock well and holding tank as no natural surface water exists within the study site, and very little exists on the Coastal Sand Plain region of Texas as a whole (Snelgrove et al., 2013). We made considerations for seasonality as not all groundwater pumps are operational year-round on large south Texas cattle ranches and ensured only those wells known to be active during the summer of 2016 were used in the analysis.

Quantifying grazing pressure

Several studies have cited the strong, predictable relationship between localized grazing pressure and proximity to water sources, especially in semi-arid rangelands (James et al., 1999; Landsberg and Crowley, 2004; Locatelli et al., 2016; Ludwig et al., 2000). This spatially un-even use of the pasture by the livestock is even visible in satellite imagery as one study termed the zone of high livestock impact attenuating away from each water point a ‘piosphere’ (Andrew, 1988). Piospheres are areas of high ‘hoof-action’ and generally have higher accumulation of livestock feces, soil compaction, and defoliation (Andrew and Lange, 1986; Graetz and Ludwig, 1978). Due to the absence of natural water sources on the CGRDA, the known stocking rates of each pasture, and the well-documented relationship between localized grazing pressure and water sources in semi-arid rangelands, we used water proximity to create a surrogate index for localized grazing pressure.

To quantify grazing pressure to incorporate into SDMs, we used the distance to nearest water source previously calculated by the proximity analysis and 30-m² fishnet grid across the CGRDA. This ensured that resulting surface value estimates were the same spatial resolution as the other environmental rasters. We divided the distance value (m) of each fishnet pixel centroid by the density of grazing livestock (i.e. stocking rate) in each pasture using the raster math tool in ArcMap.

Bird occurrence data

Avian point counts consisted of 10 12-point transects (centrally located per pasture within the CGRDA). We used point count data collected on the CGRDA from April to June 2016 to build baseline SDMs. Each point was located 400-m apart, 2 observers recorded visual and auditory occurrences of birds within 200-m of each point simultaneously yet independently. We used occurrence records rather than abundance or density since the distributional modeling algorithms required presence/absence or presence only data. We used a traditional framework in which each occurrence was counted as a ‘presence’ record at each point, omitting the duplicate records from the double observer design, and disregarding the transect construct by subsampling the data by a 400-m cell-size. This granted us a finer spatial resolution of the data set to thoroughly investigate the impacts of grazing pressure on grassland bird presence. We used only grassland-obligate species with an adequate number of presence records within the CGRDA during the study period for distribution models: Northern bobwhite, Eastern meadowlark, and Cassin’s sparrow.

Data processing and analyses

We imported values for each predictor (canopy height, shrub density, bare ground coverage, grass *spp.* coverage, cacti *spp.* coverage, water proximity, and grazing pressure) into ArcMap 10.5 and used Kriging interpolation to minimize spatial sampling bias and create continuous surface layers of environmental predictor values. Kriging, or Gaussian process regression, is a geostatistical method through which interpolated values are modeled by a Gaussian process governed by covariances. This method of spatial interpolation estimates a continuous surface of values directly based on values at surrounding points weighted according to spatial covariance (Van Beers and Kleijnen, 2004). The Kriging interpolation algorithm is optimal for most eco-spatial modeling because it produces an unbiased prediction and calculates the spatial distribution of uncertainty allowing for an accurate estimate of error at any particular point (Mahmoudabadi and Briggs, 2016). We exported the resulting GeoTIFFs and read these into the R statistical language as raster layers (R Core Team, 2013). We also read the GeoTIFFs representing the spatial values of elevation and topographic relief into R and all layers were stacked to create the occurrence predictor rasters for the baseline SDMs.

We imported occurrence data for Northern bobwhite, Eastern meadowlark, and Cassin's sparrow into R and used the predictor raster stack to build SDMs using five different algorithms: BioClim (BC), Generalized Linear Model (GLM), MaxEnt, Boosted Regression Tree (BRT), and Random Forest (RF). Table 1 outlines the basic mathematical approach of each modeling algorithm and provides a comparison of the advantages of each model in the occupancy framework. We generated 'background data

Table 1. Comparison of mathematical approach for each modeling algorithm being used to project species distributions in this study. Data requirements and advantages are also listed.

Model	Data type	Approach/mechanism	Advantages
BioClim (BC)	Presence only	This method uses a parallelepiped classifier to define species potential presence as the multi-dimensional environmental spaces bounded by the minimum and maximum values for all occurrences and gives a binary classification of suitable environment and unsuitable environment (Busby, 1986; 1991).	Interpretations are straightforward and the model is relatively simple to execute. More recently, this approach has proven useful in predicting biological invasions and distribution of widespread diseases (Robertson et al., 2004; Zhao et al., 2006)
Generalized Linear (GLM)	Presence/absence	This is a generalization of the multiple regression model that uses the “link” function to accommodate non-linear relationships between the predictor and response variables. Using various transformations of the predictors (e.g., Logit, Poisson, Gaussian) interactions between predictors can also be specified.	This approach is often ideal since occupancy modeling almost always involves multiple predictors, non-linear response functions, and response variables that are binary (Austin and Cunningham, 198; Margules et al., 1987; Franklin 2009).
Random Forest (RF)	Presence/absence	An ensemble machine-learning method in which a large number (500-2000) of decision trees are grown with subsets of the data (e.g., species occurrences) containing a random subset of candidate predictor variables (Breiman, 2001). Each tree votes for a binary outcome and the resulting predictions are averaged.	This method makes no assumptions on data distribution and instead uses bootstrap aggregation to subsample the given data. This approach has been shown to have higher prediction accuracy than ordinary decision trees in SDM and other applications. (Prasad et al., 2006; Gislason et al., 2006).
MaxEnt	Presence only	A machine-learning algorithm based on the principle from statistical mechanics and information theory that states that the probability distribution with maximum	Recent investigations have shown the MaxEnt algorithm to be mathematically identical to that of the GLM (Poisson distribution) (Renner and Warton, 2013). Its unique ability to accept

		entropy is the best approximation of an unknown distribution (Phillips et al., 2006).	environmental gradients as part of the prediction process make its application to ecological niche modeling ideal (Saatchi et al., 2008; Evangelista et al., 2009).
Boosted Regression Tree (BRT)	Presence/absence	An ensemble, regression-based method that combines the strengths of two commonly used algorithms: regression trees (models that define the response to predictors using binary splits) and boosting (a method for combining multiple simple models to improve performance). An initial regression tree is fitted and iteratively improved upon in a forward stagewise manner (boosting) by minimizing the variation in the response not explained by the model at each iteration.	This approach can easily accommodate different types of predictor variables, missing data, and outliers as well as fit complex nonlinear relationships automatically handling collinearity between predictor variables. BRT interpretations can be easily summarized to provide powerful ecological insight (Franklin, 2009).

to produce the non-presence class required by the logistic models. Background data do not attempt to guess at absence locations, but instead are used to characterize the study region (Phillips and Elith, 2011; Phillips et al., 2009; Ward et al., 2009). These established the environmental domain of the study and are independent of occurrence data while presence data established the conditions under which a species is more likely to be present than a null, or completely random, model would predict. After building baseline SDMs for each species, we added the grazing pressure raster to the occurrence predictor raster stack and re-ran the models to assess any improvement or degradation in the predictive performance of each algorithm. Pair-wise correlation coefficients between predictors are reported in Appendix A. Prior to building SDMs, we performed preliminary analyses for each species to ensure only predictors that added to the explanatory power of the models and did not add to the overall deviance were used in each SDM. This included the use of *a priori* Gradient Boosting Machine (GBM) analyses and step-wise regression variable dropping and selection for each model and species.

Model evaluation

We evaluated performance of each model using the Area Under the Receiver Operator Curve (AUROC or AUC) and true sensitivity statistic (TSS). The AUC (range from 0 to 1) is a measure of rank-correlation. In unbiased data, a higher AUC value indicates that areas with high predicted suitability values tend to be sites of known presence (Phillips et al., 2006). The TSS is an approach based on maximizing the sum of sensitivity and specificity independent of species prevalence (Liu et al., 2013). Many

distributional model evaluation approaches (e.g., *kappa*) are threshold-dependent; a value above a user-set threshold indicates a prediction of presence and a value below the threshold indicates absence. However, different models assign different weight to false absences or false presences making it hard to compare models directly. The TSS is considered an alternative to the traditionally used *kappa* to assess model performance, since it has the advantage of being threshold and prevalence independent. This becomes especially meaningful when building SDMs for rare or endangered species that may have low prevalence across a given range or study area as the default threshold, usually 0.5, for many models (e.g., logistic regression-based GLM) may not be appropriate. In these cases, studies have suggested the use of binary species presence/absence maps as input may be preferred for interpretation in building conservation plans, reservation networks, or sanctuaries as opposed to a continuous representation of probability of species presence (Fernandez et al., 2006; Mladenhoff and He, 1999; Wilson et al., 2005). Although not prevalence independent, the AUC can be valuable in determining optimal threshold criteria. For example, Freeman and Moisen (2008) found that for SDMs projecting distributions of species with high prevalence (50%), default threshold criteria tended to converge. However, for species with low prevalence (e.g., 10%), the threshold where Sensitivity + Specificity is maximum offered the ideal probability threshold for species presence. In the R workspace output, this is typically read as “Max TPR+TNR” and can be exceedingly valuable for accurately modeling distributions of rare or endangered species.

RESULTS

We recorded a total of 1,565 occurrences for all three species within the CGRDA in the summer of 2016 (Northern bobwhite = 996, Eastern meadowlark = 179, Cassin's sparrow = 390). Predictive maps generated by each algorithm are produced in Appendix B (Fig.5-9). Machine learning models (MaxEnt and RF) had the highest combinations of AUC and TSS for all species, with RF being the most consistent for each analysis (Table 2). In comparison of AUC values, the environmental envelope model (BC) and the GLM remained constant or only marginally improved with the addition of the grazing pressure raster. However, the TSS for these algorithms markedly improved with the addition of the grazing pressure raster for the Northern bobwhite ($\Delta\text{TSS} = +0.93$) and Eastern meadowlark ($\Delta\text{TSS} = +0.08$) SDMs (Table 2). The predictive power of both machine learning models and the BRT improved with the addition of the grazing pressure raster for all species, with the exception of MaxEnt and Eastern meadowlark (Maxent: Northern bobwhite [$\Delta\text{AUC} = +0.06$], Cassin's sparrow [$\Delta\text{AUC} = +0.02$]; Random Forest: Northern bobwhite [$\Delta\text{AUC} = +0.01$], Eastern meadowlark [$\Delta\text{AUC} = +0.05$], Cassin's sparrow [$\Delta\text{AUC} = +0.02$]; Random Forest: Northern bobwhite [$\Delta\text{AUC} = +0.03$], Eastern meadowlark [$\Delta\text{AUC} = +0.04$], Cassin's sparrow [$\Delta\text{AUC} = +0.03$]. Random Forest had the highest explanatory power (AUC) across all species but was, however, outperformed in sensitivity (TSS) by the other algorithms for all species for models including the grazing pressure raster (Table 2).

Northern bobwhite distribution, the species of highest prevalence ($n = 996$), was best explained by Random Forest model inclusive of grazing pressure (AUC = 0.84; TSS = 0.48). However, the bobwhite distribution was better explained by the addition of the grazing pressure raster by all algorithms as evidence in the measurable increase in AUC

Table 2. Results of species distribution model (SDM) performance for Bioclim, Generalized Linear Model (GLM), MaxEnt, Boosted Regression Tree (BRT), and Random Forest (RF) algorithms in predicting occurrence of Northern bobwhite (NOBO), Eastern meadowlark (EAME), and Cassin's sparrow (CASP) on East Foundation's Coloraditas Grazing Research and Demonstration Area (CGRDA) in the summer of 2016. Model performance metrics (area under curve [AUC] and true sensitivity statistic [TSS]) are compared for SDMs using environmental predictors only and environmental predictors stacked with a raster representing localized grazing pressure (denoted by '+').

		BioClim		GLM		MaxEnt		BRT		RF	
		<u>AUC</u>	<u>TSS</u>	<u>AUC</u>	<u>TSS</u>	<u>AUC</u>	<u>TSS</u>	<u>AUC</u>	<u>TSS</u>	<u>AUC</u>	<u>TSS</u>
NOBO		0.54	0.032	0.64	0.034	0.61	0.056	0.59	0.04	0.81	0.42
	+	0.58	0.96	0.67	0.24	0.67	0.18	0.60	0.57	0.84	0.48
EAME		0.81	0.41	0.78	0.62	0.79	0.61	0.84	0.46	0.91	0.62
	+	0.81	0.49	0.78	0.80	0.78	0.75	0.89	0.80	0.95	0.67
CASP		0.58	0.13	0.44	0.18	0.69	0.24	0.62	0.21	0.78	0.22
	+	0.62	0.15	0.44	0.18	0.71	0.29	0.64	0.67	0.81	0.23

and TSS in each model ($\Delta\text{AUC} = +0.01\text{-}0.06$, $\Delta\text{TSS} = +0.04\text{-}0.93$; Table 2). Eastern meadowlark distribution, the species of lowest prevalence ($n = 179$), was also best explained by the Random Forest model inclusive of grazing pressure ($\text{AUC} = 0.95$; $\text{TSS} = 0.67$). The SDM explanatory power for this species' distribution was not improved with the addition of grazing pressure using the BioClim, GLM, and MaxEnt algorithms. Cassin's sparrow distribution, the species of moderate prevalence ($n = 390$), was also best explained by the Random Forest model inclusive of grazing pressure ($\text{AUC} = 0.81$; $\text{TSS} = 0.23$). However, the SDM explanatory power for this species' distribution was not improved with the addition of grazing pressure using the GLM algorithm. Additionally, other algorithms (BRT and MaxEnt) produced higher TSS values ($\text{TSS} = 0.67$ and 0.29 , respectively).

DISCUSSION

Our novel approach to spatially quantify localized grazing pressure improved the prediction accuracy and sensitivity of SDMs projecting the distribution of Northern bobwhite, Eastern meadowlark, and Cassin's sparrow. Of the three algorithms used, Random Forest performed best for explaining presence regardless of species prevalence and should be preferred by rangeland managers seeking to promote sustainable livestock grazing while balancing the needs of sensitive wildlife populations. It is important to note the varying model performance with relation to species prevalence. For example, SDMS built to project distributions of Northern bobwhite, the species of highest prevalence in this study varied widely in predictive performance (AUC) and sensitivity (TSS) across algorithms. Rangeland managers should consider both metrics (AUC and

TSS) when assessing model performance since both provide valuable insight into the over utility of the model (i.e., AUC describing explanatory power and TSS describing model stability, or sensitivity to the predictors). Although, both, AUC and TSS are theoretically prevalence independent, for species like Northern bobwhite that are often locally abundant where they are present, machine-learning models that can accommodate non-linear relationships (e.g., Random Forest) should be preferred in modeling distributions. In an ecological context, the improvement in model sensitivity and explanatory power seen with the addition of grazing pressure to Northern bobwhite SDMs should be considered meaningful by rangeland ecologists. The direct impacts of livestock grazing (e.g., changes in vegetative structure and composition) on the distribution of Northern bobwhite is well recognized (Baker and Guthery, 1990; Coppedge et al., 2008; Flanders et al., 2005; Lusk et al., 2002). However, with the inclusion of grazing pressure as an indirect variable and the subsequent increase in explanatory power across all algorithms ($\Delta\text{AUC} = +0.01\text{-}0.06$), our findings suggest this species' distribution is also indirectly affected by livestock grazing activities. Thus, future investigations into Northern Bobwhite distribution or populations should consider the presence and localized intensity of livestock grazing.

The addition of grazing pressure as a variable also increased the explanatory power and sensitivity of some SDMs built to project distributions of Cassin's sparrow, the species of moderate prevalence in this study (BioClim, MaxEnt, BRT, RF). However, any improvements in model performance were marginal ($\Delta\text{AUC} = +0.0\text{-}0.4$). Our findings suggest indirect effects of livestock grazing on Cassin's sparrow presence,

though marginally detectable, were negligible. Rangeland managers should consider the unique ecological circumstances of each rangeland and livestock grazing system when investigating Cassin's sparrow distribution or presence. Although both machine learning models (MaxEnt and Random Forest) and Boosted Regression Tree performed relatively well, compared to the envelope (BioClim) and logistic algorithms (Generalized Linear Model), the BRT produced the highest model sensitivity. This is likely due the innate accommodation of missing and limited data in this algorithm, which makes it ideal for species of lower (or unknown) prevalence. In these cases, the Boosted Regression Tree provides a superior, yet conservative SDM for rangeland ecologists seeking to project distributions of species with low to moderate or unknown prevalence.

Distributions of Eastern meadowlark, the species of lowest prevalence in this study, were better explained by the addition of grazing pressure only in the Boosted Regression Tree and Random Forest SDMs. Although previous studies have suggested a neutral effect of livestock grazing activity on the presence of Eastern meadowlark, this species has also been known to alter behavior and be particularly susceptible to brood-parasitism (usually by Brown-headed cowbird *Molothrus ater*) in heavily grazed pastures (Baker and Guthery, 1990; Coppedge et al., 2008). Further, Roseberry and Klimstra (1970) found substantial differences in Eastern meadowlark nest densities between lightly grazed and heavily grazed pastures of similar vegetation composition and area. While direct impacts of livestock grazing (e.g., changes in vegetative structure) may not be as evident in the distributions of this species as they are in others (e.g., Northern bobwhite), our findings suggest some indirect influence of livestock grazing

activity on Eastern meadowlark presence. The Random Forest algorithm, in the accommodation of missing data and low presence values, produced the SDM with the highest explanatory power for this species and it should be preferred for other species of low prevalence.

BioClim

This algorithm is traditionally used as an environmental envelope method to model large scale distributions and invasions (Hijmans et al., 2001; 2005). However, recent improvements in the algorithm (in the R package ‘Dismo’ [Hijmans et al., 2017]) have allowed analyses of single species occurrences at finer resolutions. The binary output also makes it especially well-suited for species with low prevalence. For example, it performed best (AUC = 0.81) with the Eastern meadowlark, the species of lowest prevalence in this study. For this species, this model did not improve with the addition of grazing pressure as a predictor. Since other models showed improvement with the addition of grazing pressure (BRT and RF), this may suggest some disadvantage to the linearity of this algorithm. BioClim also had the poorest predictive performance (AUC = 0.54; 0.58; with and without grazing pressure, respectively) for Northern bobwhite. This species had the highest prevalence in the study and, thus, may suggest a saturation limitation for this algorithm as large sample sizes have been recognized to de-stabilize similar models (Mateo et al., 2010).

GLM (binomial)

The SDMs built using this logistic regression-based algorithm, generally, performed poorly, especially for Cassin's sparrow ($AUC = 0.44$). Additionally, GLM SDMs for Eastern Meadowlark and Cassin's sparrow did not improve with the addition of grazing pressure despite the improvement seen in other models. Although this algorithm can theoretically accommodate non-linear relationships between predictor and response variables, it has been recognized to over-fit distribution models producing biased or inaccurate results (Austin and Cunningham, 1981; Elith and Graham, 2009).

MaxEnt

SDMs built using this machine-learning algorithm projecting Northern bobwhite and Cassin's sparrow distributions improved with the addition of grazing pressure as a predictor. However, predictive power of the Eastern meadowlark SDM decreased with the addition of grazing pressure ($AUC = 0.79, 0.78$; respectively) while the TSS remained high ($0.61, 0.75$; respectively). Although not a rare or endangered species, this was the species of lowest prevalence in the study and supports the concept suggested by Freeman and Moisen (2008) that default probability thresholds may not be appropriate at low prevalence and that the intersection where Sensitivity + Specificity is maximum could serve as a more ideal probability threshold for species presence. We did not perform this analysis here but is an area of interest for future research in improving SDMs.

Boosted Regression Tree (BRT)

The BRT performed best with Eastern meadowlark SDMs (AUC = 0.89) and all species' models improved with the addition of grazing pressure as a predictor. This algorithm has the unique advantage to accommodate collinearity among predictors and fit complex nonlinear relationships between response and predictor variables (Elith et al., 2008; Franklin, 2009). Among the SDMs projecting Cassin's sparrow distribution, the BRT had the highest model sensitivity (TSS = 0.67). The BRT requires two user-input parameters: learning rate (lr), which determines the contribution of each decision tree to the overall model, and tree complexity (tc), which controls whether interactions are fitted (Elith et al., 2008). Ideally, parameters should be optimized based on sample size, number of predictors, intended use of the model, etc. to avoid overfitting the model. However, for the purposes of this study, we maintained consistent parameters to directly compare model performance ($lr = 0.001$, $tc = 6$). This may have contributed to the poor predictive performance of the BRT in projecting Northern bobwhite distribution relative to the other two species.

Random Forest (RF)

This regression-based machine-learning algorithm performed best for Eastern meadowlark SDMs (AUC = 0.95) and produced the most powerful SDMs for all species. All models built using this algorithm improved with the addition of grazing pressure as a predictor and model sensitivity was relatively consistent compared to the output of the other SDMs. Whereas the BRT requires the user to alter input parameters to ensure the model is not over fitted, RF has the advantage of a built-in 'safe-guard' against overfitting in that each decision tree uses a random bootstrap aggregation to subsample

the given data (Breiman, 2001; Prasad et al., 2006). RF is growing in popularity among ecologists for SDM and shows great promise for advanced SDM applications since it makes no assumptions on data distributions.

Implications

Our findings suggest livestock grazing has indirect influence on grassland bird species' distributions and should be included in SDMs as an indirect variable in addition to direct, associated vegetative changes. This is especially important for ground-dwelling species (e.g., Northern bobwhite). For instance, more advanced boosting or machine-learning algorithms (e.g., Boosted Regression Tree, Random Forest) that can accommodate limited data, complex and non-linear relationships, and collinearity among predictors could inform a rangeland ecologist if the redistribution, or absence of breeding quail on a property is more heavily influenced by the absence of rainfall during drought conditions (an indirect effect) or the resulting senescence of vegetation (a direct effect of drought). Algorithms that can tease apart these effects can help inform effective, science-based management. Our approach to quantifying localized grazing pressure, however, did not capture more fine-scale variability in livestock distribution within each pasture (e.g., animals seeking shade in the afternoon, tendency toward a favored vegetation type with heterogeneous distribution across the pasture). Improvements to these models would more represent the movements of livestock within each pasture on a finer scale.

Further, model selection for SDM should include consideration of species prevalence and machine-learning algorithms should be preferred when the target species is of low or unknown prevalence. For example, rangeland ecologists building SDMs for a species that is either rare across its range or of unknown abundance are able to select or alter the probability threshold of species presence in machine-learning algorithms. This is especially valuable since SDMs build based on the default probability threshold (0.5) used for rare or endangered species could lead to misinformed conservation plans and refuge networks. This new approach in spatially quantifying and including livestock grazing pressure as an indirect variable in SDMs has broad implications in rangeland ecology since it addresses a weakness in the current SDM framework – the exclusion of biotic and indirect relationships. With this, we can better estimate the effects of varying grazing regimes on grassland bird populations and more accurately predict the distribution of species of interest

CHAPTER III

MODELING THE TEMPORAL INFLUENCE OF COMPETITION IN CONSPECIFIC NESTING BIRDS

INTRODUCTION

Traditionally, species distribution models (SDMs), which statistically associate a species' occurrence with a suite of geospatial predictors, use resource variables, resources that the animal consumes or requires to persist in an area (e.g., shrub density, water availability) to define and project a species' niche and distribution (Austin & Niel, 2011; Elith & Leathwick, 2009). Indirect variables, which are features the animal does not consume or require for persistence but with which it may still interact (e.g., competition or predation), are often excluded in SDMs due to the difficulty in identifying the variable ecologically, quantifying the relationship, or in managing collinearity issues adding an interaction factor to a traditional SDM framework may contribute (Austin & Niel, 2011). However, recent advances in machine learning algorithms (e.g., Random Forest) have enabled us to include indirect variables or biotic relationships, such as competitive exclusion, in SDMs (Miller, 2010). Complex, biotic interactions are notably excluded from SDMs as they are often difficult to quantify and accommodate in a traditional modeling framework, especially those with a temporal component (i.e., an interaction or relationship that changes through time).

The principle of competitive exclusion, a term coined by G. Hardin (1960), asserts that two species of the same ecology cannot live together in the same place (i.e.,

complete competitors cannot coexist). Competition between sympatric species often include contest for limited resources (e.g., territory, food, water). In birds, availability of nesting space or materials presents a unique competitive challenge in that the degree of contest between species has a temporal aspect: breeding seasons. For example, competition for nest-sites is often observed in sympatric bird species with similar nesting ecology that would otherwise partition resources the remainder of the year (Martin, 1993; McArthur, 1958). Inferior competitors are then frequently pushed to sub-optimal nest-sites that may be more vulnerable to predation or exposure (Newton, 1994).

One such example is the relationship between breeding Cactus wren *Campylorhynchus brunneicapillus*, a large (32-47 g), territorial wren native to the desert southwestern United States, and Verdin *Auriparus flaviceps*, a small (5-8 g) penduline tit native to the southwestern United States and northern Mexico (Anderson & Anderson, 1973; Lockwood & Freeman, 2004; Williamson, 2000). Most of the year, the disparity in size and general morphology of these two species allows for territorial and food resource partitioning. Cactus wren, for instance, are typically found in semi-open areas with low-growing shrub, sifting the ground leaf litter and debris for beetles, weevils, and grasshoppers as well as the occasional fruit from cacti, hackberry, and other fruit-bearing desert species (Anderson & Anderson, 1973; Bent, 1948). In contrast, Verdin inhabit small thickets of woody desert vegetation, gleaning smaller insects (e.g., ants) from the foliage (Lockwood & Freeman, 2004; Webster, 1999). Both, the Cactus wren and Verdin, prefer areas of dense Cholla cacti (*Opuntia spp.*) for nesting but will also utilize Palo Verde (*Cercidium spp.*), large mottes of mixed cacti, and other spiny plants

(Anderson & Anderson, 1973; Wise-Gervais, 2005). The territorial nature of breeding Cactus wren is well-documented and typically involves nest usurping (i.e., destruction) of conspecifics (McGee, 1985; Simons & Simons, 1990). Due to their similar nesting ecology, breeding Verdin are frequently the target of such behavior and are often forced to retreat to alternative nest-sites (McGee, 1985; Simons & Simons, 1990). Our objectives were to understand 1) how the density of Cactus wren influenced the distribution of Verdin during the breeding season and, 2) whether this influence changes throughout the breeding season; if so, can this be incorporated into an SDM framework.

METHODS

Study site

We conducted our study on the East Foundation's 61,000-ha San Antonio Viejo Ranch (SAV), located approximately 25 km south of Hebbronville, Texas in Jim Hogg and Starr counties (Fig. 2). SAV is located within the South Texas Plains ecoregion and is managed predominantly as a cow-calf operation. Vegetation composition and structure within our study area is characteristic of this ecoregion and consists of a mosaic of grassland and thornscrub. SAV is representative of south Texas rangeland ecosystems and encompasses the Coastal Sand Plain and Texas-Tamulipan Thornscrub ecoregions. Low-growing woody plants, dense shrubs (*Prosopis glandulosa*, *Acacia greggii*, *Celtis ehrenbergiana*, *Colubrina texensis*, *Aloysia gratissima*, *Lantana urticoides*), and cacti (*Opuntia engelmannii* var. *lindheimeri*, *Opuntia leptocaulis*) dominate the vegetation in this area. Mean annual temperature within our study site is 22.6 C° and mean annual

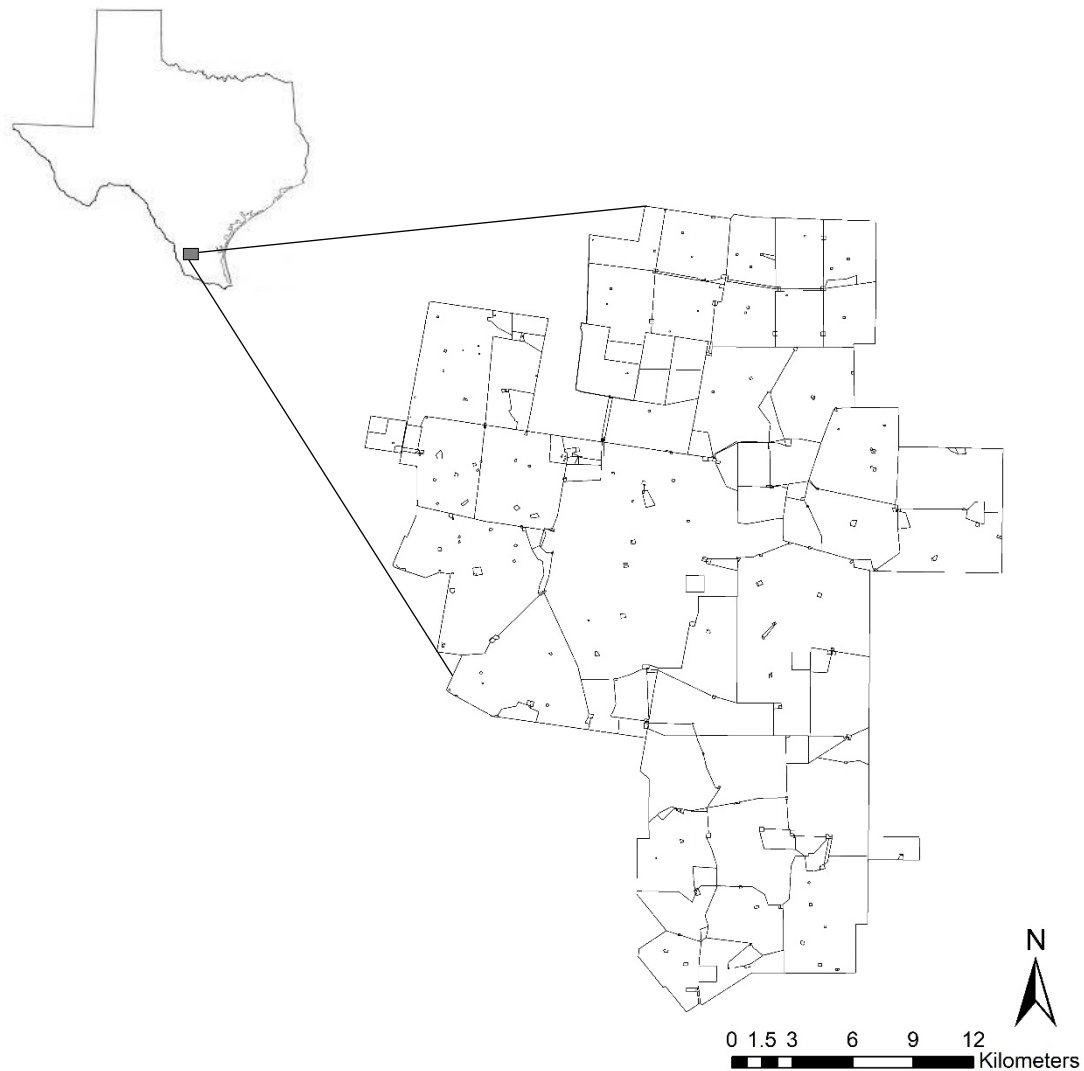


Figure 2. Locality and representation of study site, East Foundation's San Antonio Viejo Ranch, in south Texas.

precipitation is 502.5 mm (PRISM Climate Group, 2018). Mean monthly temperature during our study period (April-July 2015 and 2016) was 27.2 C° with a maximum daily high of 32.8 C° (PRISM Climate Group, 2018). Mean monthly precipitation during our study period was 77.1 mm with a maximum daily high of 93.1 mm (PRISM Climate

Group, 2018). SAV is one of six properties of the East Foundation that are managed as a living laboratory to support wildlife conservation and other public benefits of ranching and private land stewardship.

Environmental predictors

We used canopy height, shrub density, water proximity, grass *spp.* coverage, and cacti *spp.* coverage recorded from ground surveys as well as local topographic relief and an Optimized Soil Adjusted Vegetation Index (OSAVI) calculated using remotely sensed imagery in 2015 and 2016 as environmental predictors in SDMs. We collected vegetation composition and structure data from 141 permanent 20-m transects in October 2016. We allocated transects proportional to the area of ecological sites that occur in each pasture using stratified sampling resulting in 12–16 transects per pasture (Bonham, 2013). We marked each transect start and collected data in a random, predetermined direction (N, S, E, W). On each transect we sampled 5, 20×50 cm quadrats (5 m spacing) randomly placed at either 0, 0.5, 1, 1.5, 2, or 2.5 m from the left side of the tape and facing away from the transect start, visually recording percent cover of woody and herbaceous (later classified by grass *spp.*) in each quadrat.

We also documented woody canopy cover along each of the 20 m transects by visually recording the amount of the ground (in centimeters) covered by woody plant materials (leaves and branches) and succulent (cacti) that intercepted the line transect by species (Canfield, 1941; Higgins et al., 2012). If a gap in the canopy exceeded 0.5 m for an individual, we recorded separate cover measurements. We calculated percent canopy

cover by summing the intercept measurements for an individual species, dividing by total line length and converting to a cover percentage. We calculated total percent cover by adding cover percentages for all species, which sometimes exceeded 100% when overlapping canopies by different species were recorded (Coulloudon et al., 1999). Locations of water sources (e.g., livestock wells) within the study site were provided by the East Foundation. To calculate water proximity, we gridded the spatial extent of the CGRDA into a fishnet (30-m² resolution). We performed a proximity analysis on each pixel centroid using the Near tool in ArcMap 10.5 to determine distance of each centroid to location of nearest water source, usually a livestock well and holding tank as no natural surface water exists within the study site, and very little exists on the Coastal Sand Plain region of Texas as a whole (Snelgrove et al., 2013). We made considerations for seasonality as not all groundwater pumps are operational year-round on large south Texas cattle ranches and ensured only those wells known to be active during the summer of 2015 and 2016 were used in the analysis.

We imported values for each predictor (canopy height, shrub density, water proximity, grass *spp.* coverage, and cacti *spp.* coverage) into ArcMap 10.5 and used Kriging interpolation to minimize spatial sampling bias and create continuous surface layers of environmental predictor values. Kriging, or Gaussian process regression, is a geostatistical method through which interpolated values are modeled by a Gaussian process governed by covariances. This method of spatial interpolation estimates a continuous surface of values directly based on values at surrounding points weighted according to spatial covariance (Van Beers & Kleijnen, 2004). The Kriging interpolation

algorithm is optimal for most eco-spatial modeling because it produces an unbiased prediction and calculates the spatial distribution of uncertainty allowing for an accurate estimate of error at any particular point (Mahmoudabadi & Briggs, 2016). We then calculated the mean values for each predictor within the 2015 and 2016 study periods using the raster algebra tool in ArcMap 10.5.

We acquired one Landsat 8-OLI tile (< 6% cloud cover) that encompassed the study area (courtesy of U.S. Geological Survey) for each year (2015 and 2016) and processed this in ENVI 5.1 (NASA Landsat Program, 2015; 2016). We corrected for atmospheric conditions and converted the original image format of Digital Numbers (DN) to radiance and then surface reflectance. We first resized the images to the rectangular extent of the SAV and then extracted by the study area mask in ESRI ArcGIS ArcMap 10.5. We then spatially subset each extracted image by bands 2-5 corresponding to Landsat 8-OLI band designations: blue, green, red, and NIR. Bands were stacked and the OSAVI was calculated using the band math tool in ENVI 5.1 for each image. This index for LAI follows the standard formula $[(\text{NIR} - \text{Red}) / (\text{NIR} + \text{Red} + 0.16)]$ and uses a reflectance constant of 0.16 to adjust for high background reflectance (e.g., areas with sparse vegetation and high soil reflectance) (Rondeaux et al., 1996). In south Texas, specifically, this vegetation index outperforms other, more common vegetation indices (e.g., Normalized Difference Vegetation Index [NDVI]) in, both, overall image classification accuracy and herbaceous coverage estimations (Fern et al., 2018). We calculated the mean OSAVI values for the 2015 and 2016 study periods using the raster algebra tool in ArcMap 10.5.

Bird occurrence data

Avian point counts consisted of 25 12-point transects arranged in a stratified-random design across SAV, stratified by vegetation type. Each transect was surveyed 3 times throughout the breeding season: first visit between April and mid-May, second visit between mid-May and mid-June, and third visit between mid-June and mid-July. We used point count data collected from April to July 2015 and 2016 to build baseline SDMs. Each point was located 400-m apart, 2 observers recorded visual and auditory occurrences of birds within 200-m of each point simultaneously yet independently. We used a traditional framework in which each occurrence was counted as a ‘presence’ record at each point, omitting the duplicate records from the double observer design, and disregarding the transect construct by subsampling the data by a 400-m cell-size. This granted us a finer spatial resolution of the data set to thoroughly investigate the influence of conspecific (Cactus wren) density on the presence of Verdin. Cactus wren density was calculated using observed abundance at each transect point divided by the total space surveyed (200-m^2). We used the occurrence of Verdin and the calculated density of Cactus wren during the breeding seasons of 2015 and 2016 for SDMs.

Data processing and analysis

We exported the rasters of all predictors as GeoTIFFs and read these into the R statistical language as raster layers (R Core Team, 2013). All layers were stacked to create the occurrence predictor stack for SDMs. Parallel analyses were also performed by time period within the breeding season: early (April through mid-May), peak (mid-

May through mid-June), and late (mid-June through mid-July) to investigate temporal changes in Cactus wren influence on Verdin distribution. Bird occurrence data were subset appropriately. We imported occurrence data for Verdin into R and used the predictor raster stack to build SDMs using three different algorithms: MaxEnt, Boosted Regression Tree (BRT), and Random Forest (RF). Table 3 outlines the basic mathematical approach of each modeling algorithm and provides a comparison of the advantages of each model in the occupancy framework. We generated ‘background data’ to produce the non-presence class required by the logistic models. Background data do not attempt to guess at absence locations, but instead are used to characterize the study region (Phillips & Elith 2011; Phillips et al., 2009; Ward et al., 2009). These establish the environmental domain of the study and are independent of occurrence data while presence data establish the conditions under which a species is more likely to be present than a null, or completely random, model would predict. After building baseline SDMs, we added the raster representing Cactus wren density to the occurrence predictor raster stack and re-ran the models to assess any improvement or degradation in the predictive performance and sensitivity of each algorithm. For each breeding period, we also calculated relative influence and significance of each predictor using a mixed-model

Table 3. Comparison of mathematical approach for each modeling algorithm being used to project species distributions in this study. Data requirements and advantages are also listed.

Model	Data type	Approach/mechanism	Advantages
MaxEnt	Presence only	A machine-learning algorithm based on the principle from statistical mechanics and information theory that states that the probability distribution with maximum entropy is the best approximation of an unknown distribution (Phillips et al., 2006).	Recent investigations have shown the MaxEnt algorithm to be mathematically identical to that of the GLM (Poisson distribution) (Renner & Warton, 2013). Its unique ability to accept environmental gradients as part of the prediction process make its application to ecological niche modeling ideal (Evangelista et al., 2009; Saatchi et al., 2008).
Boosted Regression Tree (BRT)	Presence/absence	An ensemble, regression-based method that combines the strengths of two commonly used algorithms: regression trees (models that define the response to predictors using binary splits) and boosting (a method for combining multiple simple models to improve performance). An initial regression tree is fitted and iteratively improved upon in a forward stagewise manner (boosting) by minimizing the variation in the response not explained by the model at each iteration.	This approach can easily accommodate different types of predictor variables, missing data, and outliers as well as fit complex nonlinear relationships automatically handling collinearity between predictor variables. BRT interpretations can be easily summarized to provide powerful ecological insight (Franklin, 2009).
Random Forest (RF)	Presence/absence	An ensemble machine-learning method in which a large number (500-2000) of decision trees are grown with subsets of the data (e.g., species	This method makes no assumptions on data distribution and instead uses bootstrap aggregation to subsample the given data. This

occurrences) containing a random subset of candidate predictor variables (Breiman, 2001). Each tree votes for a binary outcome and the resulting predictions are averaged.

approach has been shown to have higher prediction accuracy than ordinary decision trees in SDM and other applications. (Gislason et al., 2006; Prasad et al., 2006).

approach. We calculated relative influence of each predictor on Verdin presence using a BRT analysis and the significance of highly influential variables through logit generalized linear regression analyses. The BRT has the unique advantage to accommodate collinearity among predictors and fit complex nonlinear relationships between response and predictor variables making it ideal for determining the relative contribution of each predictor (Elith et al., 2008; Franklin, 2009). Pair-wise correlation coefficients between predictors are reported in Appendix A. Generalized linear models, based on generalized multiple linear regression, also accommodate non-linear relationships through use of the “link” function in which predictors can be transformed based on response data distribution (Austin & Cunningham, 1981; Franklin, 2009; Margules et al., 1987). We used the logit distribution (binary response or presence/absence) to determine significance of each predictor.

Prior to building SDMs, we performed preliminary analyses to ensure only predictors that added to the explanatory power of the models and did not add to the overall deviance were used in each SDM. This included the use of a priori Gradient Boosting Machine (GBM) analyses and step-wise regression variable dropping and selection for each model and time period. We also performed time-fixed effects (FE) regression analysis to identify any significant effects between years in occurrence response to predictor variables. There was no significant effect in Verdin occurrence response to predictor variables between years ($p = 0.79$), thus eliminating the need to separate data per year or accommodate for time-FE in SDMs. Occurrence data were pooled for the 2015 and 2016 breeding seasons.

Model evaluation

We evaluated performance of each model using the Area Under the Receiver Operator Curve (AUROC or AUC) and true sensitivity statistic (TSS). The AUC (range from 0 to 1) is a measure of rank-correlation. In unbiased data, a higher AUC value indicates that areas with high predicted suitability values tend to be sites of known presence (Phillips et al., 2006). The TSS is an approach based on maximizing the sum of sensitivity and specificity independent of species prevalence (Liu et al., 2013). Many distributional model evaluation approaches (e.g., kappa) are threshold-dependent; a value above a user-set threshold indicates a prediction of presence and a value below the threshold indicates absence. However, different models assign different weight to false absences or false presences making it hard to compare models directly. The TSS is considered an alternative to the traditionally used kappa to assess model performance, since it has the advantage of being threshold and prevalence independent.

RESULTS

We recorded a total of 981 occurrences of Verdin throughout the 2015 and 2016 breeding seasons: 351 during the early breeding period (April through mid-May), 322 during the peak breeding period (mid-May through mid-June), and 308 during the late breeding period (mid-June through mid-July). Estimated Cactus wren densities ranged from 0.06 to 2.9 individuals per 200-m². Predictive maps generated by each algorithm are produced in Appendix C (Fig. 9-12). Of the three algorithms used, Random Forest (RF) produced the highest predictive performance SDMs for all three breeding periods

(Table 4). Boosted Regression Tree (BRT) produced the lowest performing model overall for the early breeding period, both, in terms of predictive power (AUC = 0.60, 0.63; with and without Cactus wren density included a predictor, respectively) and

Table 4. Results of species distribution model (SDM) performance for MaxEnt, Boosted Regression Tree (BRT), and Random Forest (RF) algorithms in predicting occurrence of Verdin *Auriparus flaviceps* on East Foundation's San Antonio Viejo Ranch (SAV) during the early (April through mid-May), peak (mid-May through mid-June), and late (mid-June through mid-July) breeding seasons of 2015-2016. Model performance metrics (area under curve [AUC] and true sensitivity statistic [TSS]) are compared for SDMs using environmental predictors only and environmental predictors stacked with a raster representing Cactus wren *Campylorhynchus brunneicapillus* density (denoted by '+').

		MaxEnt		BRT		RF	
		<u>AUC</u>	<u>TSS</u>	<u>AUC</u>	<u>TSS</u>	<u>AUC</u>	<u>TSS</u>
Early		0.74	0.40	0.60	-0.02	0.81	0.23
	+	0.76	0.49	0.63	0.15	0.82	0.47
Peak		0.80	0.14	0.89	0.48	0.89	0.59
	+	0.89	0.34	0.95	0.73	0.99	0.67
Late		0.81	0.27	0.73	0.31	0.88	0.59
	+	0.86	0.93	0.77	0.46	0.98	0.73

model sensitivity (TSS = -0.02, 0.15; with and without Cactus wren density included as predictor, respectively).

All models improved in both predictive power ($\Delta\text{AUC} = 0.01\text{-}0.10$) and model sensitivity ($\Delta\text{TSS} = 0.09\text{-}0.66$) with the inclusion of Cactus wren density as a predictor of Verdin presence (Table 4). However, magnitude of improvement in model performance varied by breeding period. During the early breeding period (April through mid-May), SDMs that included Cactus wren density as a predictor performed only slightly better than those that included environmental features alone (MaxEnt: $\Delta\text{AUC} = +0.02$, $\Delta\text{TSS} = +0.09$; BRT: $\Delta\text{AUC} = +0.03$, $\Delta\text{TSS} = +0.17$; RF: $\Delta\text{AUC} = +0.01$, $\Delta\text{TSS} = +0.24$). SDMs that included Cactus wren density as a predictor for the peak breeding season (mid-May through mid-June), as opposed to those including environmental features only, produced larger increases in model performance, relative to the early breeding period (MaxEnt: $\Delta\text{AUC} = +0.09$, $\Delta\text{TSS} = +0.20$; BRT: $\Delta\text{AUC} = +0.06$, $\Delta\text{TSS} = +0.25$; RF: $\Delta\text{AUC} = +0.10$, $\Delta\text{TSS} = +0.08$). SDMs built for the late breeding period (mid-June through mid-July) produced similar, yet less pronounced improvements in performance for models that included Cactus wren density as a predictor as opposed to environmental features alone (MaxEnt: $\Delta\text{AUC} = +0.05$, $\Delta\text{TSS} = +0.66$; BRT: $\Delta\text{AUC} = +0.04$, $\Delta\text{TSS} = +0.15$; RF: $\Delta\text{AUC} = +0.10$, $\Delta\text{TSS} = +0.14$).

Water proximity was the most influential (+), and significant ($p < 0.001$), feature in predicting Verdin presence during the early breeding period (Fig. 3). Verdin presence during the peak breeding season was most influenced by Cactus wren density (-) and green biomass (+), represented by the OSAVI ($p = 0.037$ and $p = 0.048$, respectively). Cactus wren density (-) and green biomass (+) remained significant in the late breeding period ($p = 0.028$ and $p = 0.041$, respectively), however, shrub density (+) and cactus

spp. coverage (-) also became significant predictors for Verdin presence ($p = 0.002$ and $p = 0.027$, respectively).

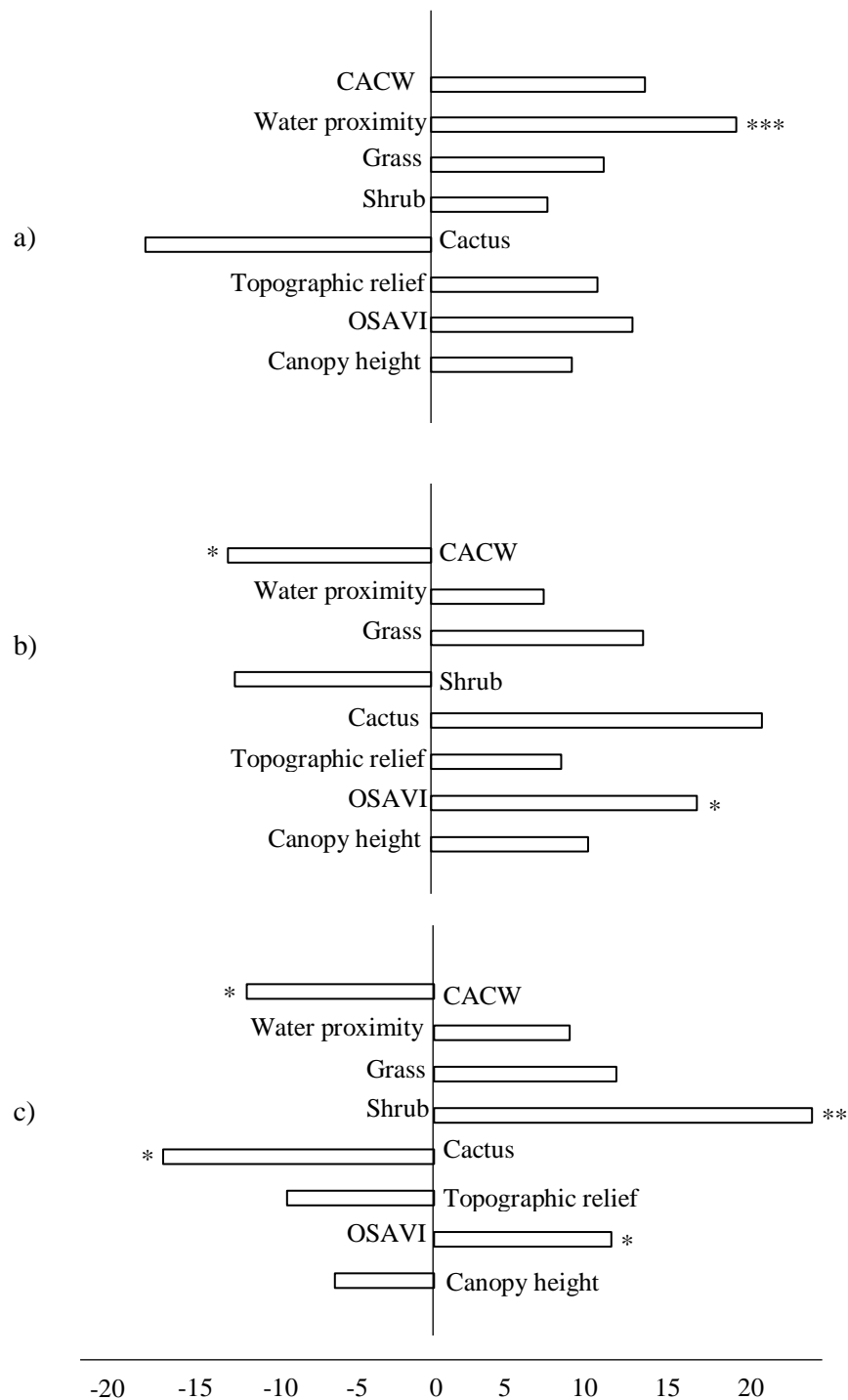


Figure 3. Relative influence, as calculated by boosted regression tree analysis (BRT), of environmental features and Cactus wren *Campylorhynchus brunneicapillus* (CACW) density on the presence of Verdin *Auriparus flaviceps* on East Foundation's San Antonio Viejo Ranch during the early (a; April through mid-May), peak (b; mid-May through mid-June), and late (c; mid-June through mid-July) 2015-2016 breeding seasons; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

DISCUSSION

Our results indicate that Cactus wren density had a significant, negative influence on the distribution of Verdin during the peak (mid-May through mid-June) and late (mid-June through mid-July) breeding season. However, Cactus wren density was not a negatively correlated predictor for Verdin presence during the early breeding season (April through mid-May). This may have biologically meaningful implications for understanding how these two conspecifics interact during nest-site selection. More specifically, this suggests that optimal nest-site selection may not necessarily be the source of the observed competition pressure. Observational studies suggest that Cactus wren usurp conspecific nests in an effort to maximize predator-free nest space (McGee, 1985; Simons & Simons, 1990). Our findings support this assertion as the potential source of competitive pressure since Verdin presence was not negatively affected by Cactus wren density until after the initial breeding period. Further, predation is the

primary cause of nest failure in birds so it is reasonable to expect species able to minimize predation pressure will have a substantial competitive advantage (Davis, 2017; Newton, 1994).

The ubiquity and importance of competition as a primary driver in species persistence and coexistence among birds have been debated for decades (Collins et al., 2011; Conner & Simberloff, 1979; Martin, 1993; Wiens, 1989). However, nest predation is considered a significant evolutionary force (i.e., natural selection favoring birds having life history traits that reduce predation pressure; Martin, 1993; Nilsson, 1986; Slagsvold & Wiebe, 2017). Thus, incorporating these biotic interactions, as well as their temporal trends, is essential in efforts to monitor or conserve bird species with similar nesting ecologies. Ecologists should not only consider the environmental requirements for species persistence, but also the presence of conspecifics with which they are known to interact during various life history stages (e.g., fledging periods, nest-site selection or initiation). Further, modeling algorithms that can accommodate complex, non-linear relationships (e.g., Random Forest) should be preferred in SDM development and application. Random Forest routinely outperforms other machine-learning and linear algorithms, both, in our study and others involving non-normal data distribution and complex predictor interactions (Breiman, 2001; Mi et al., 2014; Prasad et al., 2006).

Understanding how and when competitive pressure impacts the distribution of sympatric species is crucial for informed management. For example, severe drought conditions may disproportionately affect smaller, less territorial birds during sensitive fledging periods. Also, livestock grazing may disproportionately affect obligate ground

nesters during the early breeding season, or nest initiation, relative to the late breeding season. It is imperative we include such biotic relationships, as well as their temporal components, in the modelling framework for accurate SDMs.

CHAPTER IV

SUMMARY

Maps of actual or potential species distributions are crucial for many aspects of natural resource management, land use development, and conservation planning. Species distribution models (SDMs) attempt to predict or statistically associate geographic record of a species with abiotic and biospatial variables of interest over large spatial extents and are utilized in wildlife management as aerial imagery and our understanding of distributional patterns advances. Most distributional models use variables such as soil type, climatic patterns, topography, hydrology, vegetative communities, and other abiotic conditions to identify the predicted geographic range of a species. However, species interactions have yet to be successfully quantified and included in distributional models. It is imperative we include interactions in niche models as certain species relationships (i.e. predation, competition, habitat facilitation) have documented influence on species distribution.

Our novel approach to spatially quantify localized grazing pressure improved the prediction accuracy and sensitivity of SDMs projecting the distribution of Northern bobwhite, Eastern meadowlark, and Cassin's sparrow. Of the three algorithms used, Random Forest performed best for explaining presence regardless of species prevalence and should be preferred by rangeland managers seeking to promote sustainable livestock grazing while balancing the needs of sensitive wildlife populations. Our findings suggest livestock grazing has indirect influence on grassland bird species' distributions and

should be included in SDMs as an indirect variable in addition to direct, associated vegetative changes. This is especially important for ground-dwelling species (e.g., Northern bobwhite). For instance, more advanced boosting or machine-learning algorithms (e.g., Boosted Regression Tree, Random Forest) that can accommodate limited data, complex and non-linear relationships, and collinearity among predictors could inform a rangeland ecologist if the redistribution, or absence of breeding quail on a property is more heavily influenced by the absence of rainfall during drought conditions (an indirect effect) or the resulting senescence of vegetation (a direct effect of drought). Algorithms that can tease apart these effects can help inform effective, science-based management.

Cactus wren density had a significant, negative influence on the distribution of Verdin during the peak (mid-May through mid-June) and late (mid-June through mid-July) breeding season. However, Cactus wren density was not a negatively correlated predictor for Verdin presence during the early breeding season (April through mid-May). This may have biologically meaningful implications for understanding how these two conspecifics interact during nest-site selection. More specifically, this suggests that optimal nest-site selection may not necessarily be the source of the observed competition pressure. Observational studies suggest that Cactus wren usurp conspecific nests to maximize predator-free nest space (McGee, 1985; Simons & Simons, 1990). Our findings support this assertion as the potential source of competitive pressure since Verdin presence was not negatively affected by Cactus wren density until after the initial breeding period.

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Understanding how and when competitive pressure impacts the distribution of sympatric species is crucial for informed management. For example, severe drought conditions may disproportionately affect smaller, less territorial birds during sensitive fledging periods. Also, livestock grazing may disproportionately affect obligate ground nesters during the early breeding season, or nest initiation, relative to the late breeding season. It is imperative we include such biotic relationships, as well as their temporal components, in the modelling framework for accurate SDMs.

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APPENDIX A

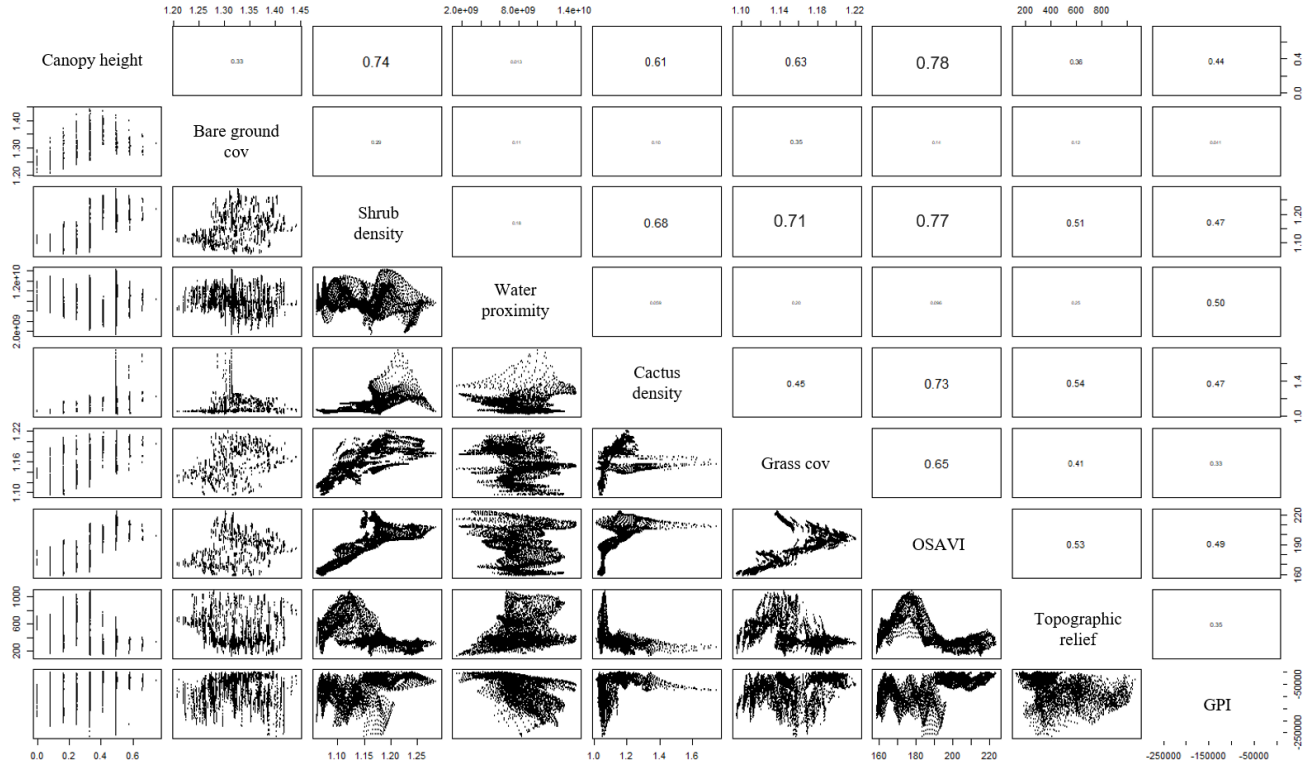


Figure 4. Correlative relationships (R values [top panel] and scatter plots [bottom panel]) of predictors used in species distribution models for Northern bobwhite *Colinus virginianus*, Cassin's sparrow *Peucaea cassinii*, Eastern meadowlark *Sturnella magna*, and Verdin *Auriparus flaviceps* during the 2016 and 2017 breeding seasons on East Foundation's San Antonio Viejo Ranch. OSAVI = Optimized Soil Adjusted Vegetation Index; GPI = Grazing Pressure Index.

APPENDIX B

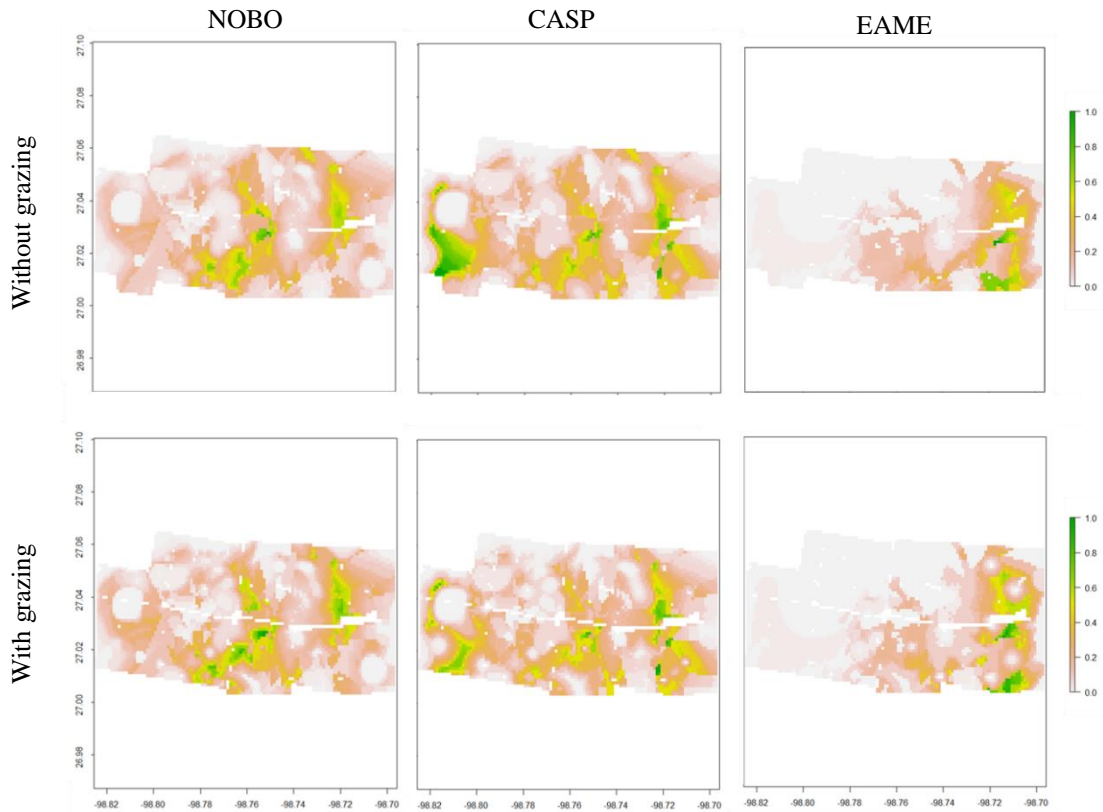


Figure 5. Predictive maps generated by the BIOCLIM algorithm using environmental predictors only (without grazing) and environmental predictors + livestock grazing pressure (with grazing) across the Coloraditas Grazing Research and Demonstration Area (CGRDA) on East Foundation's San Antonio Viejo Ranch during the 2016 breeding season for Northern bobwhite (NOBO), Cassin's sparrow (CASP), and Eastern meadowlark (EAME).

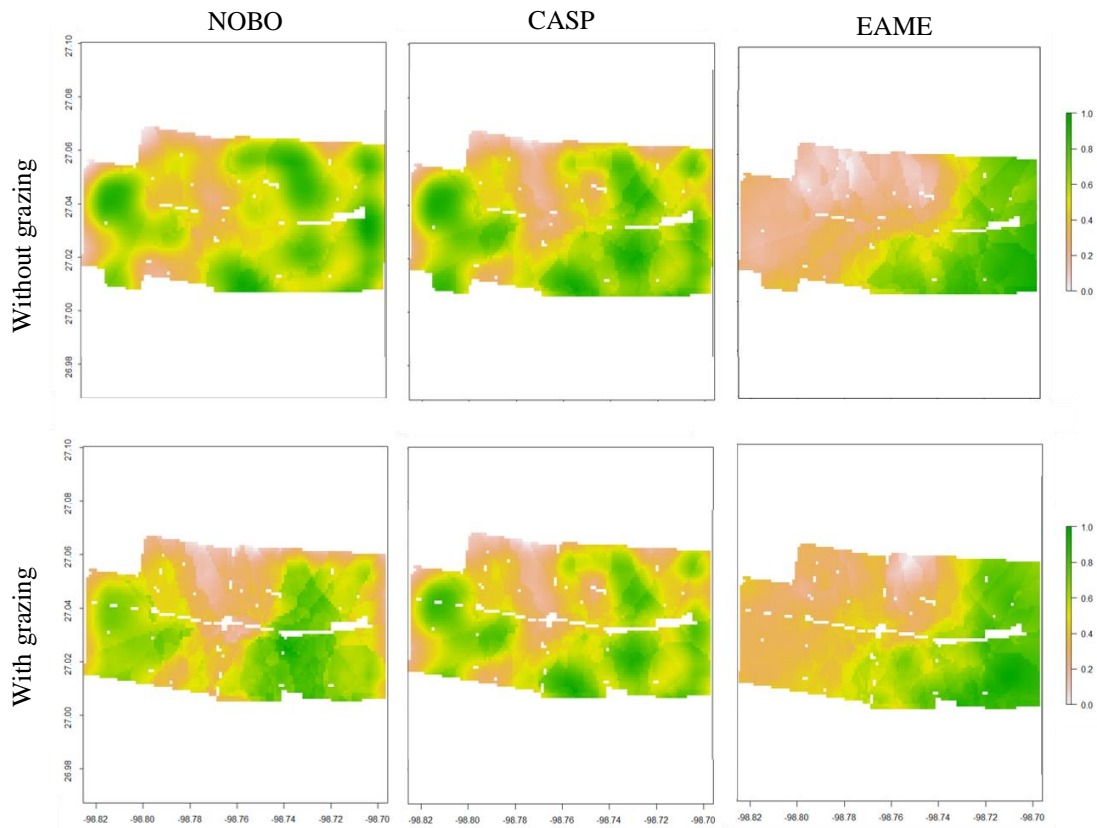


Figure 6. Predictive maps generated by the Generalized Linear Model (GLM; binomial distribution) algorithm using environmental predictors only (without grazing) and environmental predictors + livestock grazing pressure (with grazing) across the Coloraditas Grazing Research and Demonstration Area (CGRDA) on East Foundation's San Antonio Viejo Ranch during the 2016 breeding season for Northern bobwhite (NOBO), Cassin's sparrow (CASP), and Eastern meadowlark (EAME).

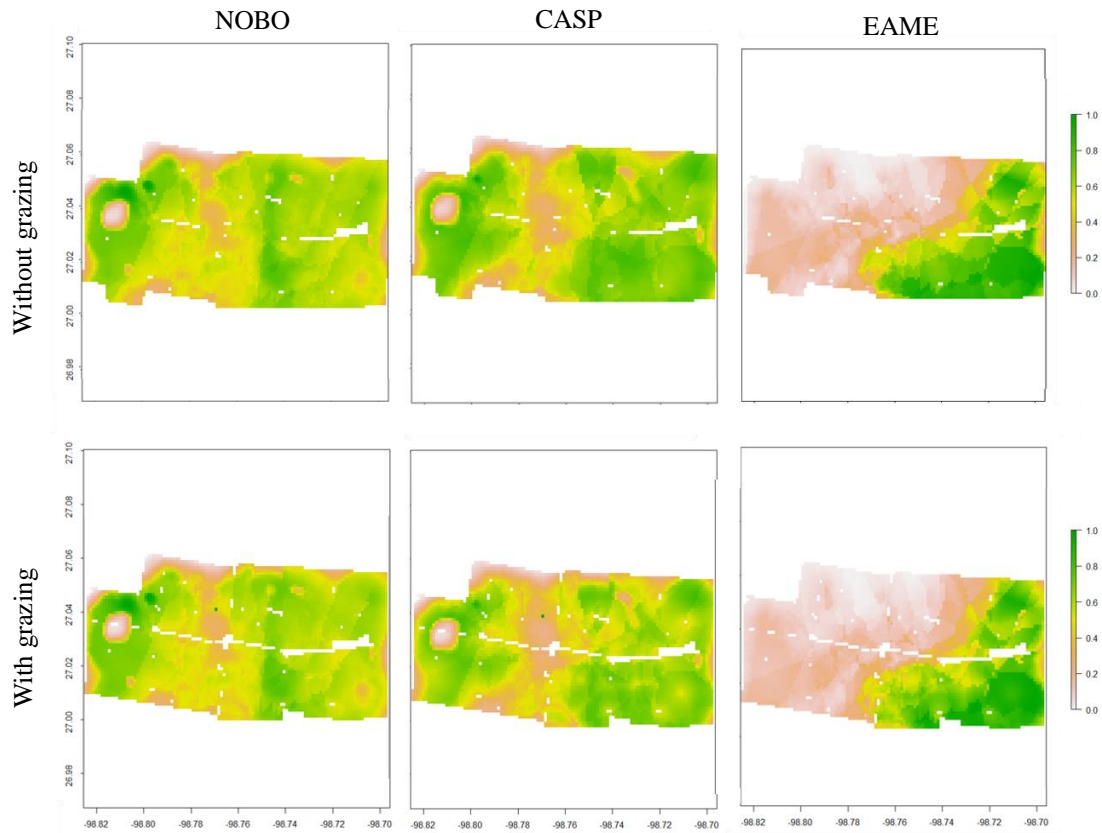


Figure 7. Predictive maps generated by the MaxEnt algorithm using environmental predictors only (without grazing) and environmental predictors + livestock grazing pressure (with grazing) across the Coloraditas Grazing Research and Demonstration Area (CGRDA) on East Foundation’s San Antonio Viejo Ranch during the 2016 breeding season for Northern bobwhite (NOBO), Cassin’s sparrow (CASP), and Eastern meadowlark (EAME).

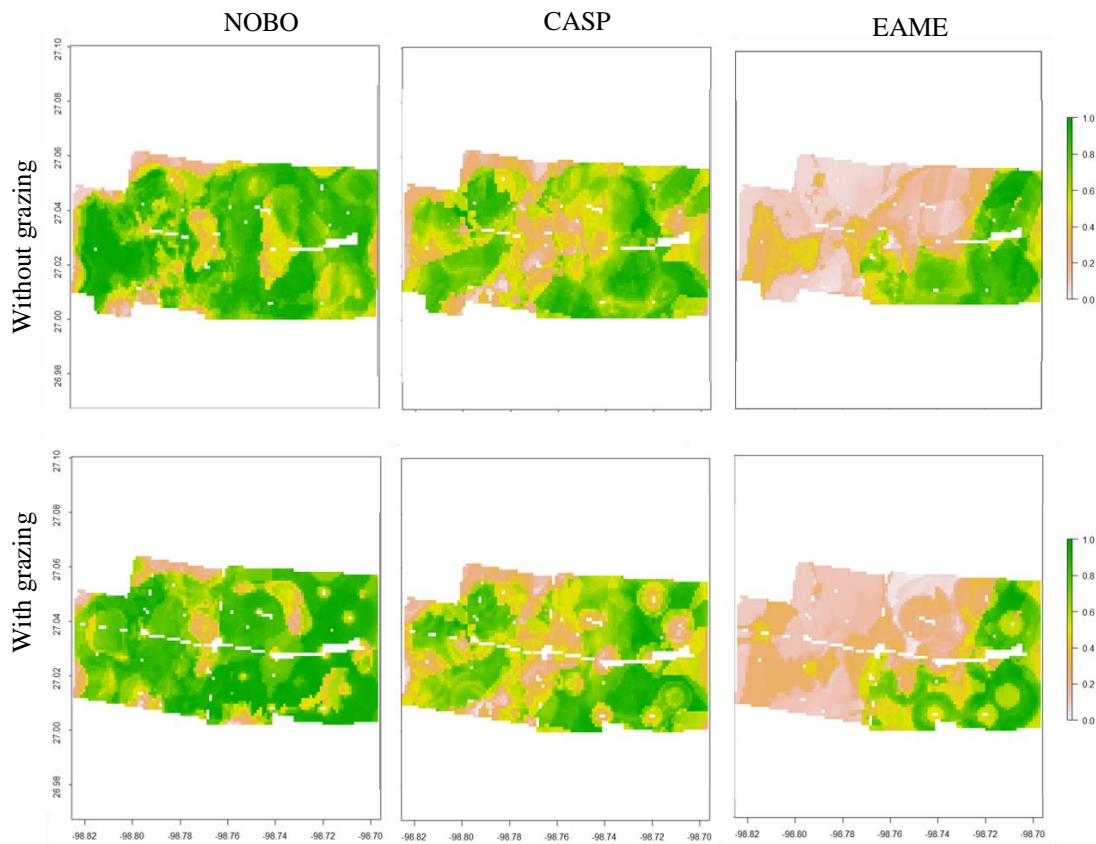


Figure 8. Predictive maps generated by the Boosted Regression Tree (BRT) decision tree algorithm using environmental predictors only (without grazing) and environmental predictors + livestock grazing pressure (with grazing) across the Coloraditas Grazing Research and Demonstration Area (CGRDA) on East Foundation’s San Antonio Viejo Ranch during the 2016 breeding season for Northern bobwhite (NOBO), Cassin’s sparrow (CASP), and Eastern meadowlark (EAME).

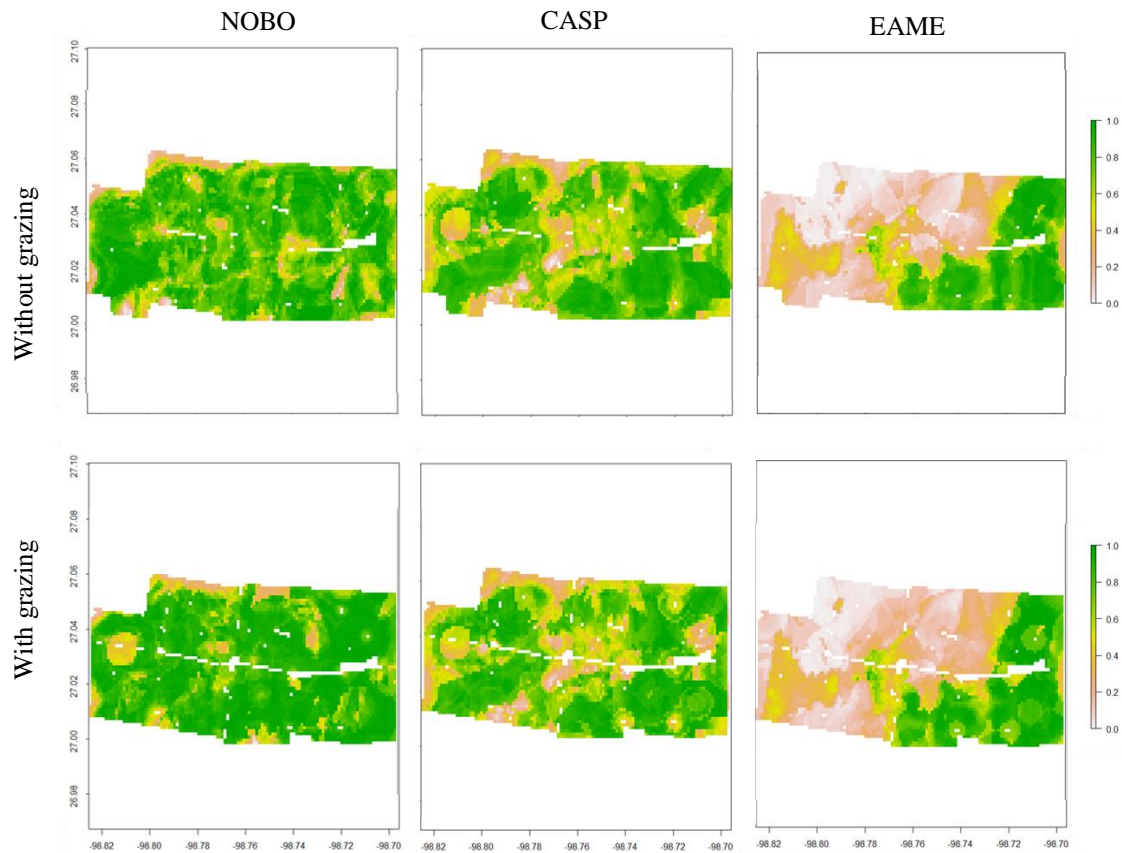


Figure 9. Predictive maps generated by the Random Forest (RF) algorithm using environmental predictors only (without grazing) and environmental predictors + livestock grazing pressure (with grazing) across the Coloraditas Grazing Research and Demonstration Area (CGRDA) on East Foundation’s San Antonio Viejo Ranch during the 2016 breeding season for Northern bobwhite (NOBO), Cassin’s sparrow (CASP), and Eastern meadowlark (EAME).

APPENDIX C

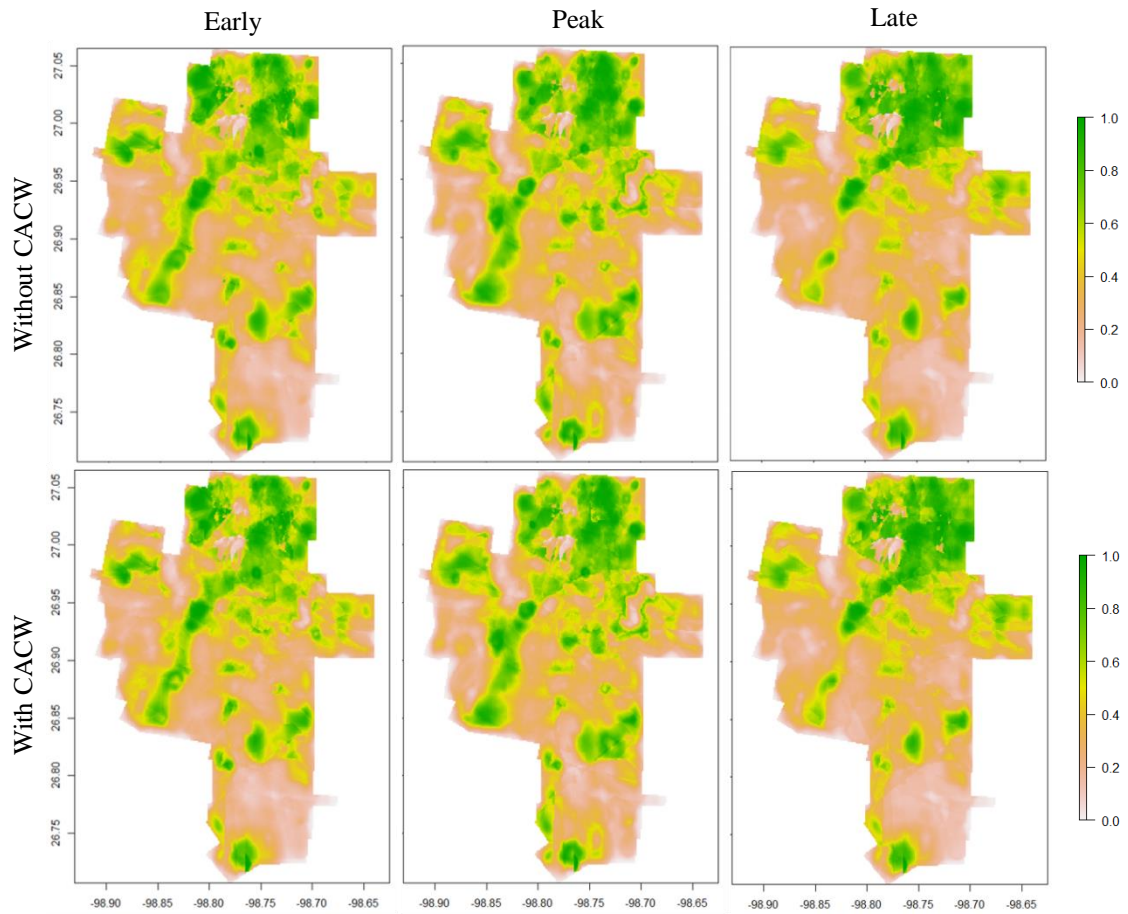


Figure 10. Predictive maps generated by the MaxEnt algorithm using environmental predictors only (without CACW) and environmental predictors + Cactus wren density (with CACW) on East Foundation's San Antonio Viejo Ranch during the 2016 and 2017 breeding season for *Verdin Auriparus flaviceps*.

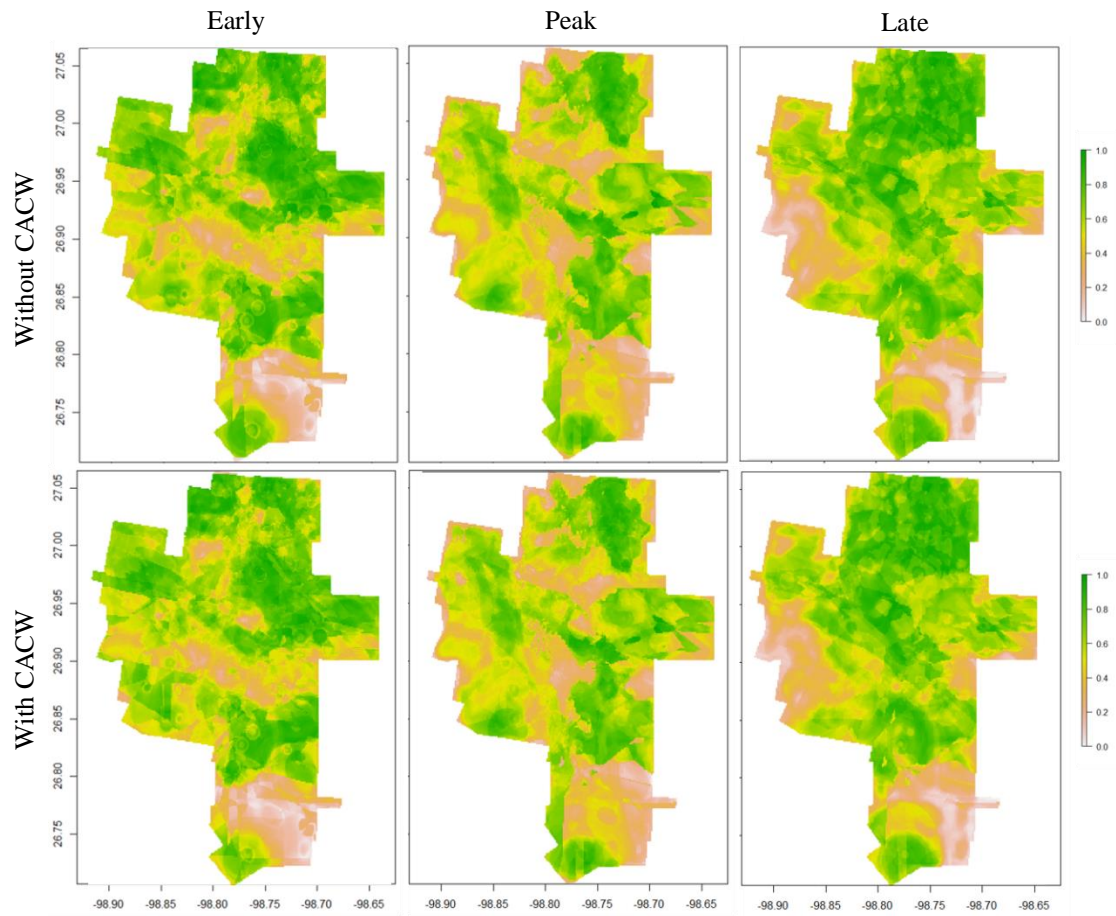


Figure 11. Predictive maps generated by the Boosted Regression Tree (BRT) decision tree algorithm using environmental predictors only (without CACW) and environmental predictors + Cactus wren density (with CACW) on East Foundation’s San Antonio Viejo Ranch during the 2016 and 2017 breeding season for Verdin *Auriparus flaviceps*.

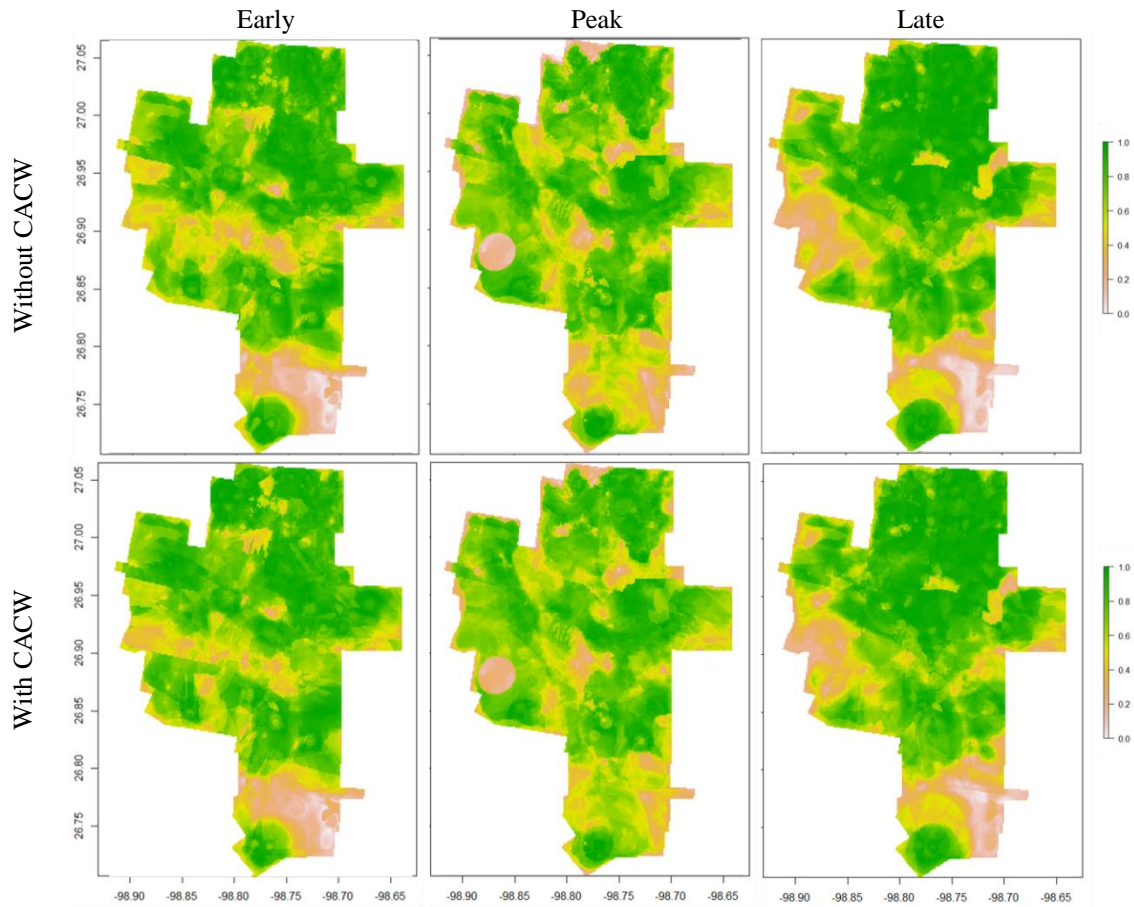


Figure 12. Predictive maps generated by the Random Forest (RF) algorithm using environmental predictors only (without CACW) and environmental predictors + Cactus wren density (with CACW) on East Foundation’s San Antonio Viejo Ranch during the 2016 and 2017 breeding season for Verdin *Auriparus flaviceps*.