Species distribution modelling supports “nectar corridor” hypothesis for migratory nectarivorous bats and conservation of tropical dry forest

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Funding information
T&E Inc.; New Mexico Native Plant Society Otero Chapter; U.S. Bureau of Land Management; New Mexico State University

Abstract
Aim: The Mexican long-tongued bat (Choeronycteris mexicana), Mexican long-nosed bat (Leptonycteris nivalis) and lesser long-nosed bat (Leptonycteris yerbabuenae) (Phyllostomidae: Glossophaginae) undertake long-distance migrations from south-central Mexico to the south-western United States. It is proposed that these bats migrate along a nectar corridor of columnar cacti and Agave species, but this has not been tested with independent data and the spatiotemporal nature of this relationship is poorly understood. Our goal was to test this nectar corridor hypothesis and determine the relative importance of food plant and abiotic variables to the distribution and seasonal movements of these migratory nectarivores.

Location: Mexico and the south-western United States.

Methods: We generated species distribution models (SDMs) of documented food plants for these bats. We then created SDMs for each bat following a model selection approach, using food plant and abiotic predictor variables. We modelled migration pathways for C. mexicana and L. yerbabuenae using circuit theory and seasonal SDMs based on seasonally available food plants.

Main conclusions: Food plants were more important than climatic and topographic variables in shaping the distribution of these bats. The most important predictors of distribution were Agave, columnar cacti and species richness of food plants. Species richness of food plants was the most consistently important variable, but the components of this diversity varied by bat species: Choeronycteris mexicana was influenced by Agave and cacti; Leptonycteris nivalis was influenced solely by Agave; Leptonycteris yerbabuenae was influenced more generally by cacti, Agave and C3 plants. Migration models for C. mexicana and L. yerbabuenae provided independent support for the nectar corridor hypothesis and indicate shifts in relative importance of specific food plants throughout the year. These results suggest that conservation of these bats should focus more broadly on management for species richness of food plants, especially in tropical dry forests.
1 | INTRODUCTION

Migration is the predictable, seasonal and synchronized movement between two regions in which different life-history events take place in order to maximize fitness (Dingle, 1996; Dingle & Drake, 2007; Greenberg & Marra, 2005; Lennox et al., 2016). Across a wide range of taxa, migration is favoured over residency when the distribution of resources changes seasonally (Dingle & Drake, 2007; Shaw & Couzin, 2012). Though migration takes place throughout the animal kingdom, most insights are from birds, fishes and insects (Dingle & Drake, 2007). While it is difficult to track long-distance movement of animals with small body masses with current technology (Holland & Wikelski, 2009), research on migratory birds has been revolutionized by light-level geolocators (Akesson, Klaassen, Holmgren, Fox, & Hedenström, 2012; Tettrup et al., 2012). However, the utility of these devices is limited to the diurnal environment. Consequently, our ability to study long-distance migration in the only mammals capable of true flight, bats, is still limited.

Though <1 percentage of bat species undertake long-distance migrations (Bisson, Safi, & Holland, 2009; Krauel & McCracken, 2013), the need to better understand bat migration is paramount to their conservation. Most mass mortality events of bats are attributable to human activity, and migratory bats may be particularly vulnerable to anthropogenic disturbances (O’Shea, Cryan, Hayman, Plowright, & Streicker, 2016). Humans can disrupt bat migration in many ways, such as by interfering with magnetic navigation (Lennox et al., 2016; Voigt et al., 2017), increasing light pollution (Lacoeuilhe, Machon, Julien, Bocc, & Kerbiiriou, 2014), developing wind farms along migration corridors (Cryan & Brown, 2007; Hayes, Ozenberger, Cryan, & Wunder, 2015; Santos, Rodrigues, Jones, & Rebelo, 2013), reducing food availability through deforestation (Trejo & Dirzo, 2000), overharvesting nectar resources (Nabhān & Fleming, 1993) and implementing land management practices that result in the degradation of food sources (Martin, Peters, Palmer, & Illsley, 2011; Martínez-Morales & Meyer, 1985; Russo, Bosso, & Ancillotto, 2018). In order to mitigate threats to migratory bats, a better understanding of their overall and seasonal distribution is necessary.

The Mexican long-tongued bat (*Choeronycteris mexicana*), Mexican long-nosed bat (*Leptonycteris nivalis*) and lesser long-nosed bat (*Leptonycteris yerbabuenae*) undertake long-distance migrations from south-central Mexico to the south-western United States and play important ecological roles as pollinators and seed dispersers throughout their ranges (Fleming, Geiselman, & Kress, 2009; Godínez-Alvarez & Valiente-Banuet, 2000; Horner, Fleming, & Sahley, 1998; Howell & Roth, 1981; Rocha et al., 2006; Rojas-Martínez, Godínez-Alvarez, Valiente-Banuet, Arizmendi, & Acevedo, 2012; Valiente-Banuet, Arizmendi, Rojas-Martínez, & Domínguez-Canseco, 1996). *Leptonycteris nivalis* is currently listed as endangered in the United States and is listed as threatened by Mexico (SEMARNAT, 2010; U.S. Fish and Wildlife Service, 1988; U.S. Fish and Wildlife Service, 2016). *Leptonycteris yerbabuenae* was recently delisted by Mexico and the United States (U.S. Fish and Wildlife Service, 2017; U.S. Fish and Wildlife Service, 2018). Under the International Union for Conservation of Nature (IUCN), *L. nivalis* is listed as endangered, while *C. mexicana* and *L. yerbabuenae* are listed as near-threatened (Arroyo-Cabrales & Perez, 2008; Medellin, 2016a, 2016b).

*Choeronycteris mexicana*, *L. nivalis* and *L. yerbabuenae* are thought to undertake long-distance migrations from south-central Mexico to the south-western United States following seasonal availability of food sources (Ammerman, Hice, & Schmidly, 2012; Bogan, Cryan, Weise, & Valdez, 2017; Fleming, Núñez, & Stenberg, 1993). While the southernmost populations may not undergo long-distance latitudinal migrations due to the availability of food throughout the year (Cajas-Castillo, Kraker-Castañeda, López-Gutiérrez, Pérez-Consuerga, & Grajeda-Godínez, 2015; Rojas-Martínez et al., 2012; Rojas-Martínez, Valiente-Banuet, Arizmendi, Alcántara-Eguren, & Arita, 1999; Stoner, O.-Salazer, R.-Fernández, & Quesada, 2003), their northern counterparts migrate up to 1,200 km along a supposed “nectar corridor” of columnar cacti and Agave species primarily in the Sonoran and Chihuahuan deserts (Fleming et al., 1993; Moreno-Valdez, Grant, & Honeycutt, 2000). Similar to migratory terrestrial birds, nectarivorous bats rely on a matrix of stopover foraging grounds and roosting habitat along the migratory pathway. The degradation of stopover habitat can result in energetic depletion and competition for limited resources during a period in which animals are most vulnerable (Lennox et al., 2016). Preserving and restoring stopover habitat for long-distance migrants is often the only way to mitigate threats to long-term population viability (Smith, Miller, Merchant, & Sankoh, 2015), yet the locations of migratory routes for these bats are largely unknown. Despite the ecological importance of preserving migratory corridors for *C. mexicana*, *L. nivalis* and *L. yerbabuenae*, their small body mass restricts the ability to track migratory movements with current technology (Arita & Santos-del-Prado, 1999; Holland & Wikelski, 2009).

Recent studies have directly mapped foraging movement in *L. yerbabuenae* using GPS technology (Eger-Berg et al., 2018). However, monitoring is limited to a small number of bats over a nightly foraging distance and does not reflect migratory scale movement. Despite technological developments, most inferences regarding migration in nectarivorous bats are drawn from indirect methods due to technological and financial limitations. Originally, the theory that *L. yerbabuenae* migrates latitudinally following a nectar corridor of columnar cacti and paniculate Agave spp. was based mainly on
stable isotope analysis. Fleming et al. (1993) discovered that L. yerbabuenae feeds on plants of the C3 photosynthetic pathway in the southern portion of its range during the winter months and on those of the Crassulacean acid metabolism (CAM) photosynthetic pathway as they become available throughout the spring and summer months in the Sonoran and Chihuahuan deserts. Using mitochondrial DNA analysis, Wilkinson and Fleming (1996) theorized that L. yerbabuenae follows divergent migration routes along the Pacific coast of Mexico and along the foothills of the Sierra Madre Occidental. Rojas-Martínez et al. (1999) refined the theory using geographic analysis of plant phenology and capture records, suggesting that L. yerbabuenae populations occurring north of 30° migrate, while those around 21° are likely resident.

Though migratory routes ought to be spatially and temporally predictable (Fleming et al., 1993), we still lack a spatially explicit framework with which to test the theory of generalized latitudinal migration. Hence, the overall influence of forage resource phenology on nectarivorous bat distribution and migration has not been substantiated. Simultaneously, recent extralimital occurrence records of all three species at the northern edge of their range suggest these bats may have a broader range than previously described (Bogan & Cryan, 2006; Ramsey & Whiteman, 2011; Bogan et al., 2017). A better understanding of the distribution and potential migratory pathways among seasonal habitats would inform conservation efforts for these bats.

Our objectives were to: (a) model the overall distribution of C. mexicana, L. nivalis and L. yerbabuenae to gain a better understanding of their geographic distribution and to test the relative importance of food plants vs. abiotic variables to their distribution; and (b) model seasonal habitats and migratory pathways between seasonal habitats to test the theory of latitudinal migration based on available food resources and to test the presence of divergent migration routes. We used presence-only data with species distribution and corridor modelling tools to test this theory. The models generated in this study shed light on the ecological relationships governing the distribution of migratory nectarivorous bats, enhance our ability to monitor populations throughout their range by providing a spatiotemporal framework with which to prioritize habitat conservation and allocate survey efforts, and provide a spatial model with which to test theories on migratory strategies.

### 2 | METHODS

#### 2.1 | Study area

Our study area encompassed the entire potential migratory range of C. mexicana, L. nivalis and L. yerbabuenae including all of Mexico and the south-western United States. This region is typified by a transition in plant communities and increasing plant richness along elevation, temperature and humidity gradients (Sánchez-González & López-Mata, 2005). Elevations range from sea level to about 3,190 m (Silva-Flores, Pérez-Verdin, & Wehenkel, 2014). From the tropics of southern Mexico to the Sonoran and Chihuahuan deserts, biomes shift from tropical evergreen, semideciduous and deciduous forests to thorn forest and xeric shrubland with Neotropical savanna and warm temperate grasslands interspersed with sky islands of coniferous forests and Madrean montane grassland (Brown & Makings, 2014). Within these biomes, plant communities are highly variable based on aspect and soil characteristics, with high diversity of xerophytic plants along limestone escarpments (Gehlbach, 1967; Sánchez-González & López-Mata, 2005).

#### 2.2 | General approach

We used MAXENT 3.3.3 to generate species distribution models (SDMs) (Phillips, Anderson, & Schapire, 2006). Species distribution modelling is widely used in ecology to better understand the relationship between organisms and environmental variables, shedding light on how this relationship influences the likelihood of presence across the landscape (Elith & Leathwick, 2009; Elith et al., 2010). While there are many methods with which to generate SDMs (Guisan & Thuiller, 2005), MAXENT has become the most popular for both its ease of use and functionality (Morales, Fernández, & Baca-González, 2017). MAXENT is a machine learning algorithm that allows SDMs to be generated using presence-only data, making it an effective tool for predicting species distribution when obtaining presence-absence data is logistically impractical (Clemente et al., 2019; Kabir et al., 2017; Zhang, Yao, Meng, & Tao, 2018).

Though widely applied in ecological studies, models produced with MAXENT can be prone to bias when parameters are not properly tuned (Anderson & Gonzalez, 2011, 2011; Morales et al., 2017; Warren & Seifert, 2011; Warren, Wright, Seifert, & Shaffer, 2014). Background data, feature types, regularization, sampling bias, model output types and evaluation metrics must be effectively dealt with, though few studies do this in practice (Merow, Smith, & Silander, 2013; Morales et al., 2017). If these issues are addressed in the modelling process, the SDMs will have limited bias, appropriate complexity, ecological relevancy and the ability to remain relevant in novel climates and geographic environments (Anderson & Gonzales, 2011; Kramer-Schadt et al., 2013; Boria, Olson, Goodman, & Anderson, 2014; Radosavljevic & Anderson, 2014; Warren & Seifert, 2011; Warren et al., 2014).

Species distribution modelling has recently been applied to better understand the distribution of bat species (Razgour, Rebelo, Febbraro, & Russo, 2016), yet only a few studies deal with migratory bats (Cryan, 2003; Cryan and Diehl, 2009; Cryan et al., 2014; Hayes, Cryan, & Wunder, 2015; Roscioni et al., 2014; Santos et al., 2013). Modelling the distribution of species throughout multiple seasons at a continental or global scale can help reveal important patterns of seasonal habitat preferences at a scale more relevant to animal migration (Fink et al., 2010). Many studies assess the relationship between species occurrences and climatic variables to predict potential distribution across the landscape (Abolmaali, Tarkehs, & Bashari, 2018; Bosso et al., 2018; Thapa et al., 2018), but the specialized diets of nectarivorous bats may render food plants more biologically relevant to their distribution (Arita & Santos-del-Prado, 1999). Hence,
we used the distribution of plants that have been documented in the diet of these bats as explanatory variables, in addition to more commonly used bioclimatic, topographic and land cover variables, to generate SDMs of *C. mexicana*, *L. nivalis* and *L. yerbabuenae*. We used the SDMs to test the relative importance of these variables to each bat and to predict migratory corridors by establishing resistance surfaces derived from the SDMs, which can adequately estimate wildlife corridors when more precise information, such as telemetry data, is unavailable (Zeller et al., 2018). We chose to use circuit theory over least-cost methods because although nectarivorous bats have strong spatial memory (Henry & Stoner, 2011), shifting phenology of food resources would prevent these bats from always following the most efficient route along the migratory corridor.

### 2.3 Predictor layers

We used 51 food plant variables, along with food plant richness, bioclimatic variables, topographic and land cover variables to model the distribution of *C. mexicana*, *L. nivalis* and *L. yerbabuenae*. These included 19 bioclimatic variables (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), distance to karst (Weary & Doctor, 2014), elevation (GTOPO30; Earth Resources Observation and Science Center 1997) and land cover (Colditz et al., 2014), amounting to 76 initial variables. Some studies have excluded bioclimatic variables that combine precipitation and temperature variables due to odd spatial patterns (Escobar, Lira-Noriega, Mdeina-Vogel, & Peterson, 2014). However, we chose to include these variables because we did not observe any odd spatial patterns and because of their combined influence on agave and cactus physiology (Nobel, 1988) and on bat foraging and migration (Frick et al., 2012; Pettit & O’Keefe, 2017). As distance to variables may improve model performance for central-place foragers such as bats (Rainho & Palmeirim, 2011) and nectarivorous bats rely on a matrix of foraging grounds and roosting habitat, we used karst as a surrogate variable for roosting habitat by creating a layer of distance to karst using the Euclidean distance tool in **arCGIS** 10.4.1 (ESRI, 2016). We also used elevation and land cover as predictor variables due to their influence on habitat selection and the supposed segregation of these species based on elevational gradients (Arita, 1991; Baker & Cockrum, 1966).

We created SDMs of food plants to approximate food plant distribution. To generate these models, we determined plants that might be used as food by *C. mexicana*, *L. nivalis* and *L. yerbabuenae* based on information from the literature (Arias-Cóyotl, Stoner, & Casas, 2006; Bustamante & Bürquez, 2008; Cajas-Castillo et al., 2015; Casas, Valiente-Banuet, Rojas-Martínez, & Dávila, 1999; Cruz & Pavon, 2013; Eguizábal & Burquez, 1987; England, 2012; Fleming, Sahley, Holland, Nason, & Hamrick, 2001; Gentry, 1982; Lemke, 1984; Lobo et al., 2003; Molina-Freaner & Eguizábal, 2003; Munguía-Rosas & Sosa, 2010; Peñalba, Molina-Freaner, & Rodríguez, 2006; Rojas-Martínez et al., 1999; Sánchez & Medellín, 2007; Stoner et al., 2003; Valiente-Banuet et al., 1996; Valiente-Banuet, Rojas-Martínez, Casas, Coro Arizmendi, & Dávila, 1997; Valiente-Banuet, Rojas-Martínez, Coro Arizmendi, & Dávila, 1997; Valiente-Banuet, Santos Gally, Arizmendi, & Casas, 2007). These included plants of Agavoideae (CAM pathway, 20 spp.), Bignoniaceae (C3 pathway, 3 spp.), Bombacaceae (C3 pathway, 1 sp.), Cactaceae (CAM pathway, 18 spp.; all but *Hylocereus undatus* are columnar cactus), Convolvulaceae (C3 pathway, 2 spp.), Fabaceae (C3 pathway, 3 spp.) and Malvaceae (C3 pathway, 4 spp.).

We developed SDMs for each plant species based on occurrence records obtained from herbaria (gbif.org and swbiodiversity.org/seinet). We followed the taxonomy of the World Checklist of Selected Plant Families (https://wcsp.science.kew.org/home.do) to identify synonyms of outdated herbarium records. We used plant occurrence records in **MAXENT** to generate an SDM for each plant species, using bioclimatic, topographic and land cover variables as explanatory variables in each (see Appendix S1). To avoid generating overly complex models, we tuned regularization parameters (β) and eliminated highly correlated and unimportant explanatory variables using **ENMTools** (Warren, Glor, & Turelli, 2008, 2010), following the methods of Warren et al. (2014). The same model tuning steps were followed for each plant species.

We also generated food plant richness models from the SDMs to use as explanatory variables (Zhang et al., 2016). Species richness of food plants is positively associated with nectarivorous bat presence (Gómez-Ruiz & Lacher, 2016). We generated food plant richness models by applying a presence threshold to each food plant SDM using the maximum sum of sensitivity and specificity method to create binary presence–absence models (Liu, Newell, & White, 2016). We then used the raster calculator in **arCGIS** 10.4.1 to aggregate binary models into an overall food richness model. We generated seasonal food richness models based on the seasonal availability of each food plant to nectarivorous bats to later use as covariates in our winter, spring, summer and fall seasonal bat distribution models (see Appendix S1).

**Table 1** Sample sizes of total occurrence records and spatially rarefied (50 km) occurrence records for overall species distribution models and seasonal distribution models
2.4 | Bat occurrence records

Because Leptonycteris spp. are frequently misidentified (Arita, 1991), we only used specimen records of this genus that were examined and verified by us or were included in the revision by Arita and Humphrey (1988). We differentiated L. nivalis and L. yerbabuenae using the length of the last digit of the third phalange (Hinman & Snow, 2003; Medellín, Arita, & Sanchez, 1997). We verified specimens from the Museum of Southwestern Biology Division of Mammals, Texas Tech Natural Science Research Laboratory, the University of Arizona Mammals Collection, the University of Texas El Paso Biodiversity Collections, the American Museum of Natural History and the Texas A&M Biodiversity and Teaching Collections. We also included records of L. yerbabuenae from Ramsey and Whitman (2011), which included measurements that allowed for reliable identification, as well as records in Bogan et al. (2017) and Bogan and Cryan (2006).

Choeronycteris mexicana is readily distinguished from Leptonycteris based on the presence of a skirted uropatagium (Medellín et al., 1997). We found no misidentifications of C. mexicana in the museums we visited to confirm records of Leptonycteris. Consequently, to increase our sample size of C. mexicana we used specimen records from the following museums: California Academy of Sciences, Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Centro de Investigación en Biodiversidad y Conservación, Universidad Autónoma del Estado de Morelos, Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León, Instituto de Historia Natural y Ecología, Kansas University Natural History Museum, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Universidad de la República del Uruguay, Instituto de Investigaciones Biológicas, Universidad de Concepción, and Universidad de Chile. The skirted uropatagium also allowed for the identification of C. mexicana using photographs. We used photographs to verify records of C. mexicana from Midland and Hays counties, Texas (L. Balin, Texas Parks and Wildlife Department personal communication; B. Mayes, Texas Department of State Health Services personal communication). We also included occurrence records of C. mexicana from Cryan and Bogan (2003).

To maintain adequate sample sizes, we did not discard bat occurrence records with low precision because this has limited impact on model performance for volant animals with high dispersal potential (Hayes, Ozenberger, et al., 2015). However, many of our records were spatially clustered. To limit potential sampling bias, we spatially rarefied occurrence records for each species to 50 km to approximate daily dispersal distance (Horner et al., 1998; Medellín et al., 2018). This resulted in sample sizes which were sufficient for generating reliable MAXENT models (Van Proosdij, Sosef, Wieringa, & Raes, 2015) and allowed minimally for the implementation of hinge, linear and quadratic feature classes (Merow et al., 2013; Phillips & Dudik, 2008; Scheglovitova & Anderson, 2013; see Table 1).

2.5 | Generating bat SDMs

We defined the background extent for each SDM as all of Mexico, Texas, New Mexico, Arizona and California south of the latitude of the northern border of Arizona. We did not restrict this extent further because these highly mobile bats could theoretically reach any given area in the study region given their migratory capabilities of 1,200 km (Cockrum, 1991; Moreno-Valdez et al., 2000). Simultaneously, recent extralimital records of each species indicate poorly documented distributions and a broad background extent prevented us from inadvertently truncating potential ranges. We followed a series of steps to tune each model. First, we removed highly correlated variables ($r > |0.90|$) a priori based on biological relevance to limit redundancy (Fourcade, Engler, Rödder, & Secondi, 2014). We followed the methods of Warren et al. (2014) to create SDMs that controlled multicollinearity and model complexity. Using the uncorrelated predictor variables, we made 76 models for each species wherein we adjusted

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**TABLE 2** | Regularization parameters ($\beta$), feature classes, block-partitioned AUC evaluation metric, sensitivity, specificity and true skill statistic for species distribution models for Choeronycteris mexicana, Leptonycteris nivalis and Leptonycteris yerbabuenae, and seasonal distribution models for Choeronycteris mexicana and Leptonycteris yerbabuenae.

| Species               | Season | $\beta$ | Features | AUC    | Sensitivity | Specificity | TSS  |
|-----------------------|--------|---------|----------|--------|-------------|-------------|------|
| Choeronycteris mexicana | Overall | 4.2     | H, L, Q, P, T | 0.8083 | 0.8468 | 0.6219 | 0.4687 |
| Leptonycteris nivalis  | Overall | 6.0     | H, L, Q  | 0.8905 | 0.8400 | 0.7912 | 0.6312 |
| Leptonycteris yerbabuenae | Overall | 2.6     | H, L, Q, P, T | 0.8154 | 0.7355 | 0.7198 | 0.4554 |
| Choeronycteris mexicana | Winter | 2.6     | H, L, Q  | 0.9004 | 0.6667 | 0.8719 | 0.5386 |
| Choeronycteris mexicana | Spring | 2.8     | H, L, Q  | 0.8478 | 0.8684 | 0.6678 | 0.5362 |
| Choeronycteris mexicana | Summer | 3.8     | H, L, Q  | 0.8729 | 0.8871 | 0.7276 | 0.6147 |
| Choeronycteris mexicana | Fall   | 3.2     | H, L, Q  | 0.7805 | 0.8857 | 0.6527 | 0.5384 |
| Leptonycteris yerbabuenae | Winter | 3.2     | H, L, Q  | 0.9286 | 0.9394 | 0.8266 | 0.7660 |
| Leptonycteris yerbabuenae | Spring | 2.2     | H, L, Q  | 0.8187 | 0.8710 | 0.5917 | 0.4626 |
| Leptonycteris yerbabuenae | Summer | 3.2     | H, L, Q  | 0.8266 | 0.7581 | 0.6958 | 0.4539 |
| Leptonycteris yerbabuenae | Fall   | 3.0     | H, L, Q  | 0.8872 | 0.7931 | 0.8674 | 0.6605 |
| Variable | Contribution (%) |
|----------|-----------------|
| Bat SDMs |                 |
| **Choeronycteris mexicana** |            |
| Pilosocereus leucocephalus | 46.5 |
| Species richness of food plants | 32.4 |
| Agave palmeri | 12.1 |
| Temperature seasonality (Bio 4) | 9.0 |
| **Leptonycteris nivalis** |            |
| Agave scabra | 42.0 |
| Elevation | 31.4 |
| Species richness of food plants | 26.6 |
| **Leptonycteris yerbabuenae** |            |
| Species richness of food plants | 78.3 |
| Precipitation seasonality (Bio 15) | 21.7 |

| Variable | Contribution (%) |
|----------|-----------------|
| **Choeronycteris mexicana** seasonal models |            |
| Winter |        |
| Stenocereus beneckei | 38.1 |
| Psuedobombax ellipticum | 31.4 |
| Agave horrida | 20.4 |
| Precipitation of the driest quarter (Bio 17) | 10.2 |
| Spring |        |
| Agave xylonacantha | 49.8 |
| Species richness of spring food plants | 42.5 |
| Precipitation of the driest quarter (Bio 17) | 7.6 |
| Summer |        |
| Pilosocereus chrysacanthus | 28.8 |
| Species richness of summer food plants | 24.2 |
| Agave palmeri | 16.0 |
| Agave havardiana | 11.0 |
| Fall |        |
| Agave xylonacantha | 48.5 |
| Species richness of fall food plants | 26.2 |
| Stenocereus stellatus | 25.3 |
| **Leptonycteris yerbabuenae** seasonal models |            |
| Winter |        |
| Stenocereus pruinosus | 35.5 |
| Bauhinia pauletia | 26.3 |
| Ipomoea ampullacea | 13.9 |
| Precipitation seasonality (Bio 15) | 12.6 |
| Species richness of winter food plants | 11.8 |
| Spring |        |
| Species richness of spring food plants | 100 |

(Continues)
seasonal models for *L. nivalis*. However, our sample sizes for *C. mexicana* and *L. yerbabuenae* were adequate for each season of the year (see Table 1).

We generated seasonally dynamic models (Hayes, Cryan, et al., 2015) for *C. mexicana* and *L. yerbabuenae* following the same model tuning and model evaluation methods as for the SDMs. However, we only used predictor layers of food plants that would be available to a nectarivorous bat in the season being modelled. We considered a plant available if it flowered in the given season. We also considered cacti to be available if the species produced fruit in the season being modelled, given the importance of cactus fruit to migratory nectarivorous bats (Hernández & Herrera, 2016; Valiente-Banuet et al., 1996). We used herbarium records and the literature to determine seasonal availability (see Appendix S1). We also included a plant richness layer of seasonally available food plants, rather than overall plant richness. We evaluated seasonal models using block-partitioned AUC metrics, along with TSS, sensitivity and specificity.

### 2.7 | Predicting migratory corridors

We used CIRCUITSCAPE, a software which utilizes circuit theory (McRae, Dickson, Keitt, & Shah, 2008; McRae, Shah, & Mohapatra, 2013), to predict movement corridors for *C. mexicana* and *L. yerbabuenae*, using the MAXENT-derived seasonal models of *C. mexicana* and *L. yerbabuenae* as conductance rasters (Algeo et al., 2017; Poor, Loucks, Jakes, & Urban, 2012). Because we wanted to model connectivity between specific seasonal habitats rather than overall landscape connectivity, we averaged seasonal models for two seasons to represent the conductance of the landscape between those seasons. For example, if we wanted to estimate landscape conductance between spring and summer habitats, we averaged the spring and summer seasonal models. We then used spatially rarefied presence locations for the given seasons to use as focal nodes. Using resistance or conductance values of grid cells surrounding the focal nodes, CIRCUITSCAPE then produces a series of networks by which the species may travel between seasonal habitats based on its likelihood of crossing a given grid cell. We used the logistically transformed cumulative current map to denote potential migratory pathways for *C. mexicana* and *L. yerbabuenae*, with higher values representing more likely travel corridors.

### 3 | RESULTS

#### 3.1 | Bat SDMs

We generated SDMs with satisfactory performance based on their block-partitioned AUC evaluation metrics all >0.8 and TSS values of all moderate or substantial (see Table 2). Tuned β values were higher than MAXENT’s default value of 1 (see Table 2). Variables in the final bat SDMs consisted of a mix of food, bioclimatic and topographic variables, with individual food plant variables and/or food plant richness variables having high contribution compared to other variables overall (see Table 3). The influence of food plants on the distribution of nectarivorous bats was strongly positive (see Appendix S2). The distribution of *C. mexicana* was predominately explained by the distribution of food plants. The columnar cacti, *Pilosocereus leucocephalus*, accounted for almost half of the contribution to the model for *C. mexicana*. This was followed by species richness of food plants, the paniculate agave, *Agave palmeri* and a negative influence of temperature seasonality (Bio 4). For *L. nivalis*, the paniculate agave, *Agave scabra*, explained 42% of the contribution to the model. This was followed by

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**FIGURE 1** Species distribution model for *Choeronycteris mexicana* (top), *Leptonycteris nivalis* (centre) and *Leptonycteris yerbabuenae* (bottom)
a strongly positive influence of elevation and species richness of food plants (see Appendix S2). Lastly, for *L. yerbabuenae* species richness of food plants explained 78% of the model, which was followed by a positive influence of precipitation seasonality (Bio 15).

The output of the SDM is a relative occurrence rate (ROR), which can be interpreted as the likelihood of occurrence or as environmental suitability. Given our use of potential food plant distribution as predictor variables, we interpret higher ROR values as reflecting a higher environmental suitability (Elith et al., 2010). In the SDMs for all three species of bats, there is high environmental suitability throughout south-central Mexico that varies with increasing latitude (see Figure 1). In the SDM for *C. mexicana*, there is high environmental suitability in the Madrean Archipelago, as well as throughout south-central Mexico, and along the east and west coasts of Mexico. In the SDM for *L. nivalis*, the highest environmental suitability values are only about 78%, which occur throughout south-central Mexico, with the highest values occurring more inland than for the other two species. Low-to-moderate environmental suitability values for *L. nivalis* occur throughout the Chihuahuan Desert of northern Mexico, western Texas and southern New Mexico, with lower values in the Sky Island region of Arizona. Similar to the SDM for *C. mexicana*, that for *L. yerbabuenae* reveals strong coastal affiliations in south-central Mexico, with moderate-to-high suitability south of about 20° latitude. The SDM for *L. yerbabuenae* indicates moderate environmental suitability in the Sonoran Desert, with lower values in the Chihuahuan Desert than for *C. mexicana* or *L. nivalis*.

3.2 | Seasonal models

Results of the seasonal models for *C. mexicana* and *L. yerbabuenae* were more nuanced than the overall SDMs (see Table 3), with climatic variables and seasonally available food plants shaping the distribution of *C. mexicana* and *L. yerbabuenae* differently each season (see Figures 2 and 3). Block-partitioned AUC values were generally...
over 0.8 for seasonal distribution models, with TSS values moderate to substantial (see Table 2).

The winter distribution model for *C. mexicana* was mostly influenced by food plants (*Stenocereus beneccki*, *Psuedobomax ellipticum* and *Agave horrida*), with minimal but strongly negative influence by the climatic variable, precipitation of the driest quarter (Bio 17). Spring distribution of *C. mexicana* was mostly influenced by food plants, including *Agave xylonacantha* and species richness of spring food plants, and with minimal but strongly negative influence by precipitation of the driest quarter (Bio 17). Summer distribution of *C. mexicana* was explained solely by food plants, including the columnar cactus *Pilosocereus chrysacanthus*, species richness of summer food plants, *Agave palmeri* and *Agave havardiana*. Fall distribution of *C. mexicana* was influenced by food plants, including *Agave xylonacantha*, species richness of fall food plants and the columnar cactus *Stenocereus stellatus*.

The winter distribution model for *L. yerbabuenae* also was mostly influenced by food plants, with the columnar cactus, *Stenocereus pruinosus*, as the most influential variable, followed by *Bauhinia pauletia* (Fabaceae), *Ipomoea ampullacea* (Convolvulaceae), a positive influence by precipitation seasonality (Bio 15) and species richness of winter food plants. Spring distribution of *L. yerbabuenae* was explained solely by species richness of spring food plants. Summer distribution of *L. yerbabuenae* was predominantly explained by species richness of summer food plants, followed by the columnar cactus *Isolatocereus dumortieri*. Fall distribution of *L. yerbabuenae* was mostly influenced by food plants including *Crescentia alata* (Bignoniaceae), species richness of fall food plants, *Agave palmeri*, and then positively by precipitation seasonality (Bio 15).

### 3.3 Migration models

The migration models for *C. mexicana* and *L. yerbabuenae* indicated divergent migratory pathways between seasons (see Figures 4 and
Pathways are similar for both species along the western flank of the Sierra Madre Occidental, with weaker pulses along the Sierra Madre Oriental overall. The winter to spring migration models indicated movement throughout southern Mexico, with strong connectivity up to the Pacific Coast and western flank of the Sierra Madre Occidental, and weaker connectivity along the eastern flank into the Chihuahuan Desert. The spring to summer models portrayed similar movement, with stronger connectivity into the northern Sonoran and Chihuahuan deserts. For the summer to fall model, connectivity remained strong along the western flank of the Sierra Madre Occidental, with additional connectivity eastward into the Chihuahuan Desert. The fall to winter model for L. yerbabuenae indicated more narrow corridors returning from the Sonoran and Chihuahuan deserts back to wintering grounds in southern Mexico, with broader corridors exemplified by C. mexicana. Consistent short-distance connectivity is shown in each migration model throughout the southern portion of the range of both species.

### 3.4 Post hoc analysis

Given the importance of species richness of food plants in the SDMs for all three species of bats, we ran a post hoc analysis to test the relative importance of the components to this richness: agave richness, cactus richness and C3 plant richness. We did this by creating SDMs for each bat species using only these three richness variables (see Appendix S2). Each species exhibited varying reliance on the richness of these three plant groups, especially the agaves and cacti. The distribution of L. nivalis was only influenced by the richness of agaves. The distribution of Choeronycteris mexicana also was strongly influenced by the richness of agaves (63% contribution), but also moderately influenced by the richness of cacti (37% contribution). In contrast, the distribution of L. yerbabuenae was primarily influenced by the richness of cacti (85.8% contribution) with small influences by the richness of agave (7.7% contribution) and C3 plants (6.5% contribution).
Overall, our results support the hypothesis that nectarivorous bat distribution is explained by the distribution of individual food plants and/or the overall richness of their food plants. Species richness of food plants was a final variable in the SDMs for *C. mexicana*, *L. nivalis* and *L. yerbabuenae*, and was a final variable in all but one seasonal model for these bats. Relationships between nectarivorous bat distribution and species richness of food plants were always strongly positive, indicating that these bats likely select for regions with higher food plant diversity throughout their ranges (see variable response curves in Appendix S2). Elevation was also a strong contributor to the *L. nivalis* SDM, supporting the hypothesis that *L. nivalis* and *L. yerbabuenae* are separated by elevation (Arita, 1991; Baker & Cockrum, 1966). Seasonal models for *C. mexicana* and *L. yerbabuenae* indicate shifts in the relative importance of specific food plants throughout the year, supporting the theory that nectarivorous bats undergo seasonal shifts in habitat selection based on available food sources. This, in conjunction with the migration corridor models, adds independent support to the theory of latitudinal migration based on the seasonal availability of food sources.

The relative importance of food plant and bioclimatic variables to the distribution of *C. mexicana* and *L. yerbabuenae* varied by season, highlighting the importance of accounting for temporal variation in resource needs when dealing with animals with seasonal habitats across a wide geographic range. Winter models for both species highlight the importance of *Stenocereus* cacti, as well as C3 plants and winter-blooming *Agave* species. Species richness of available food plants became increasingly important for both species in spring and summer, particularly for *Leptonycteris yerbabuenae*, and potentially reflecting increased energetic demands due to migration.
towards maternity roosts and eventual lactation (Fleming, Hooper, & Wilson, 1972; Hernández & Herrera, 2016). Similar to the findings of Hayes, Cryan, et al. (2015) with respect to continental scale bat migration, our models indicate that the distribution of migratory nectarivorous bats is the most uncertain and widespread during migration periods in spring and fall, especially for *C. mexicana*, highlighting the potential for increased vulnerability during these time periods, as well as the need for a better understanding of migratory corridors.

The migration models support the theory of latitudinal migration along a corridor of shifting food resources and show divergent western and eastern migratory pathways for *C. mexicana* and *L. yerbabuenae*, with strong connectivity along the western coast of Mexico and moderately strong connectivity inland throughout the Sierra Madre Occidental. Local connectivity is also displayed in south-central Mexico based on the region’s consistently high suitability throughout the year, further supporting the findings of Rojas-Martínez et al. (1999) that populations around 21° are likely resident or undergo short-distance migrations. These are the first spatially explicit models to substantiate *L. yerbabuenae* migration theories derived from stable isotope and mitochondrial DNA analyses, as they show both a reliance on seasonally available resources and two main divergent pathways. These are the first spatial models to predict migratory corridors for the lesser studied *C. mexicana*. These models demonstrate that migration strategies can be derived from presence-only data and be used to investigate migratory strategies in animals that are difficult to study in the field.

The post hoc tests highlight several important issues and suggest we broaden the conversation with respect to habitat conservation for migratory nectarivorous bats. Our results add support to the findings of Gómez-Ruiz and Lacher (2016) that show the distribution of *L. nivalis* is positively associated with the richness of Agave species. However, our results also indicate that the richness of food plants in general may be the ultimate driver of the distribution of migratory nectarivorous bats, and the relative importance of plant groups varies for each species of bat. Our results suggest that both *Leptonycteris* species are narrow specialists; *L. nivalis* is a specialist on agaves and *L. yerbabuenae* is a specialist on columnar cacti, while *Choeronycteris mexicana* is more of a generalist in its diet. The narrative for the conservation of these bats is often focused on Agave spp. (U.S. Fish and Wildlife Service, 2018). Our results indicate a need to shift conservation efforts towards the preservation of biodiverse ecosystems rich in chiropterophilic plants throughout the range of each species that will render these bats resilient to landscape change. The consistent importance of food plant richness and predicted bat distributions throughout south-central Mexico and the Pacific Coast of the Sierra Madre Occidental highlights the need to preserve imperiled tropical dry forest ecosystems (Janzen, 1988; Quesada et al., 2009). Sustained plant richness in this ecosystem depends on the ability to preserve remaining tropical dry forest fragments via coordinated conservation efforts across the region (Banda et al., 2016). Important food plants for each bat species face threats from rapid deforestation of tropical dry forests (Janzen, 1988; Trejo & Dirzo, 2000), overutilization (Nabhan & Fleming, 1993), altered fire-return intervals from invasive species introductions (McDonald & McPherson, 2013) and climate change (Dávila, Téllez, & Lira, 2013); columnar cacti are especially susceptible to these threats. Given the strong importance of columnar cacti richness to *L. yerbabuenae*, mitigation of these threats may be especially important for the full recovery of this recently delisted species.

The SDMs and migration models from this study can be overlaid with protected lands databases to identify potential gaps in landscape connectivity, allowing researchers and land managers to prioritize landscape preservation and restoration efforts. The SDMs can also be used to allocate survey efforts to obtain more occurrence records for these species. Using the existing SDMs to target monitoring efforts could lead to new detections (Rebelo and Jones, 2010), allowing seasonal and migration models to be generated for *L. nivalis* and to be continually improved for *C. mexicana* and *L. yerbabuenae*. The ability to target conservation efforts along migratory corridors for *L. nivalis* could be invaluable to the conservation and recovery of this species. Generating seasonal models for *L. nivalis* would allow us to more fully understand shifting habitat needs. A better understanding of migratory pathways for this species can help researchers identify stopover habitat, prioritize conservation of roosts and foraging grounds, inform restoration of food plants throughout migratory corridors and seasonal habitats, and identify flyways that could be impacted by human development. We recommend the use of these models to promote an overall transboundary approach to monitoring these species throughout their predicted ranges to enhance the conservation of these nectarivores and their habitats.

**ACKNOWLEDGEMENTS**

Funding for this project came from T&E Inc., New Mexico Native Plant Society Otero Chapter, the U.S. Bureau of Land Management and New Mexico State University. Additional academic funding was received via a career development grant from the American Association of University Women. We thank Paul M. Cryan, Lois Balin, Randy D. Jennings, Bonnie Mayes and Patricia Gegick for providing additional presence records to support this study. Also, we thank Melanie Bucci and the University of Arizona Museum of Natural History Mammalogy Collection, Jonathan L. Dunnnum and the Museum of Southwestern Biology Division of Mammals, Heath Garner and the Natural Science Research Laboratory at the Museum of Texas Tech University, Robert D. Fisher and Suzanne Peuruch at the Smithsonian National Museum of Natural History Division of Mammals, Jessica E. Light and Emma P. Ruiz-Gómez at the Biodiversity Research and Teaching Collections of Texas A&M, and Arthur H. Harris and the University of Texas El Paso Biodiversity Collections for hosting us at museum collections during this project. We thank two anonymous referees for helpful comments that improved the paper.

**DATA ACCESSIBILITY**

Environmental layers used as predictor layers in this study are publicly available and sourced in the main text of this paper. All occurrence
records used to generate the SDMs in this study (plant and bat SDMs) are publicly available via museum collections, publications or reports. The authors can provide raster grids or kmz files of SDMs or migration models generated in this study to land managers if requested, but due to the sensitive nature of these species, the models generated in this study have not been made publicly available.

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[Correction statement added on 03 July 2019 after first online publication: This reference was previously omitted and has been added in this version]