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Abstract. The migration of animals across long distances and between multiple habitats presents a major challenge for conservation. For the migratory Mexican free-tailed bat (*Tadarida brasiliensis mexicana*), these challenges include identifying and protecting migratory routes and critical roosts in two countries, the United States and Mexico. Knowledge and conservation of bat migratory routes is critical in the face of increasing threats from climate change and wind turbines that might decrease migratory survival. We employ a new modeling approach for bat migration, network modeling, to simulate migratory routes between winter habitat in southern Mexico and summer breeding habitat in northern Mexico and the southwestern United States. We use the model to identify key migratory routes and the roosts of greatest conservation value to the overall population. We measure roost importance by the degree to which the overall bat population declined when the roost was removed from the model. The major migratory routes—those with the greatest number of migrants—were between winter habitat in southern Mexico and summer breeding roosts in Texas and the northern Mexican states of Sonora and Nuevo Leon. The summer breeding roosts in Texas, Sonora, and Nuevo Leon were the most important for maintaining population numbers and network structure – these are also the largest roosts. This modeling approach contributes to conservation efforts by identifying the most influential areas for bat populations, and can be used to as a tool to improve our understanding of bat migration for other species. We anticipate this approach will help direct coordination of habitat protection across borders.

Key words: bat conservation; breeding roosts; Mexican free-tailed bats; migratory patterns; network models; *Tadarida brasiliensis mexicana*; U.S.–Mexico cross-border migration routes.

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INTRODUCTION

Species that migrate across long distances and between multiple habitats present a unique challenge for conservation because they require coordinated management of habitats and migratory pathways in multiple locations (Fleming and Eby 2003, Fischman 2011). Migratory bat species are particularly vulnerable because of their tendency to congregate in large numbers at shared roost sites, particularly along migratory routes. This makes the fates of individuals interdependent, limits the capacity of large population sizes to reduce extinction risk, and makes the overall population susceptible to habitat reduction in any part of the migratory range (Davis et al. 1962, Glass 1982, McCracken 2003, Racey and Entwistle 2003). It has been long recognized that pollution, vandalism and urban development pose a threat to bat populations (Mickleburgh et al. 2002, Kunz et al. 2011). In addition, concern is growing about the impacts of climate change and wind turbines on bat migration in North America (Adams and Hayes 2008, Arnett et al. 2008, Cryan and Barclay 2009, Popa-Lisseanu and Voigt 2009). Unfortunately, bat migration is poorly studied (Cryan and Diehl 2009, Holland and Wikelski 2009, Popa-Lisseanu and Voigt 2009), and knowledge of migratory routes used by Mexican free-tailed bats is scant. To address our lack of understanding of bat migration, and to provide tools for tackling the unique conservation challenges of a migratory species, we developed a network model for the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). We use the model to identify key migratory routes and the roosts of greatest conservation value to the overall population.

Attempts to better understand bat migration have been impeded by their life-history traits. The small size, mobility, and nocturnal habits of most bats make tracking individual animals and population-level monitoring difficult, although see (Hayes et al. 2009) for a review of recent progress in this area. While banding has been effective, large-scale programs were abandoned in North America during the 1970s due to concerns about injuries to bats (Ellison 2008, Cryan and Diehl 2009, Popa-Lisseanu and Voigt 2009). As a result, our knowledge of timing, departure points, energetic requirements, and routes followed by bats during migration remains limited (Popa-Lisseanu and Voigt 2009).

Due to the lack of data, there are very few species-specific models of bat migration (Moreno-Valdez et al. 2000, Hedenström 2009), and none on the movement of Mexican free-tailed bats. Traditional meta-population models would require data about vital rates, range-wide abundance estimates, and colonization and extinction rates. With their minimal data requirements, network models are advantageous for studying species' migrations where data are limited. Network models originated in the mathematical field of graph theory and have been adapted to a wide variety of fields (Urban et al. 2009). Network models differ from traditional meta-population models by focusing on the degree of connectivity among multiple seasonal sites that may not contain resident populations, and where each site potentially receives inputs of individuals from several locations (Taylor and Norris 2010). They have been employed in studying bird migration, but have not been used to study bat migration (Weber et al. 1999, Shimazaki et al. 2004, Downs and Horner 2008, Kolzsch and Blasius 2008, Minor and Urban 2008). To our knowledge, we are the first to employ this modeling technique for bat migration.

Female and male Mexican free-tailed bats winter in central and southern Mexico, where they disperse throughout the landscape (Villa and Cockrum 1962). Early each spring, females migrate north, forming large maternity roosts in the southwestern U.S. and northern Mexico (Bernardo and Cockrum 1962, Davis et al. 1962, Federico et al. 2008). Analyses of the genetic structure of migratory and non-migratory populations of bats indicate that the population is well-mixed throughout its range, with no evidence for the genetically distinct sub-populations that would be expected if there were distinct migratory flyways (McCracken et al. 1994, McCracken and Gassel 1997, Russell et al. 2005). Mexican free-tailed bats are thought to have undergone wide-scale population declines since the 1950s; however, definitive evidence is confounded by the likely inaccuracy of historic abundance estimates (McCracken 2003, O'Shea et al. 2003, Betke et al. 2008).

The purpose of our network model is to estimate the degree and pattern of major migratory flows between sites and to determine the most important breeding roosts. The model does not estimate population growth over time. We assume that survival declines with an increase in distance migrated, as high mortality rates and poor body conditions have been reported in bats during migration (Constantine 1967, Cockrum 1973, Tuttle and Stevenson 1977, Tuttle and

Stevenson 1982). As a consequence of the costs of migration, we hypothesize that that the most influential summer breeding roosts should be located closest to the winter regions in central and southern Mexico. The contribution of our work is to help identify the migratory routes and roosts most critical for maintaining bat populations and outline a modeling technique that can be adapted for studying the migratory patterns of other bat species.

METHODS

Overview of modeling approach

We use the approach for modeling networks of winter and breeding sites developed by Taylor and Norris for avian species (Taylor and Norris 2010) to study patterns of connectivity between summer and winter habitats of Mexican free-tailed bats. This approach allows us to calculate expected migratory routes based on simple distance-based mathematical formulations of migration costs, and to simulate changes in network structure and migratory population size associated with the loss of any particular breeding roost. The limited input requirements of the network modeling approach make it well suited to deal with the lack of data and simplifying assumptions needed to model the migratory patterns of species such as Mexican free-tailed bats.

Networks consist of a set of nodes connected via edges. In our model there are a total of 29 nodes, four represent winter habitat and 25 are summer breeding roosts. Edges represent bi-directional migratory routes. Each migratory route is weighted with a survival cost derived from its length (Taylor and Norris 2010, Rayfield et al. 2011)—individuals traveling on longer routes are assumed to have lowered survival. This reflects the high mortality rates and poor body conditions that have been reported in bats during migration (Constantine 1967, Cockrum 1973, Tuttle and Stevenson 1977, Tuttle and Stevenson 1982). Longer migrations may increase mortality rates due to increased exposure to inclement weather and predators, and the increased difficulty of locating roosts (Constantine 1967, Fleming and Eby 2003).

In our model, migratory routes only connect winter habitat to summer roosts (Fig. 1). While bats are known to move between summer roosts after the young have fledged (Genoways et al. 2000), we do not model interconnections between summer roosts, and focus instead on the most demographically important movements between summer and winter habitats. We also do not model the bats that may remain in summer breeding roosts during the winter months, since reported population sizes are relatively small in comparison to their summer population sizes. Most studies have reported fewer than 1000 bats remaining in summer breeding roosts during winter months (Christensen 1947, Constantine 1967). Although Geluso (2008) reported larger numbers of bats in Carlsbad caverns during the early and late winter, those may represent bats that have not yet migrated, or those that have returned early from their winter grounds, respectively (Geluso 2008).

Mexican free-tailed bats likely use multiple stopover sites during migration. Unfortunately, due to limited data on the *specific* routes bats use when migrating between summer and winter habitats, we are unable to model stop-over sites. As such, migratory edges represent the shortest distance between end points, not the actual course traveled.

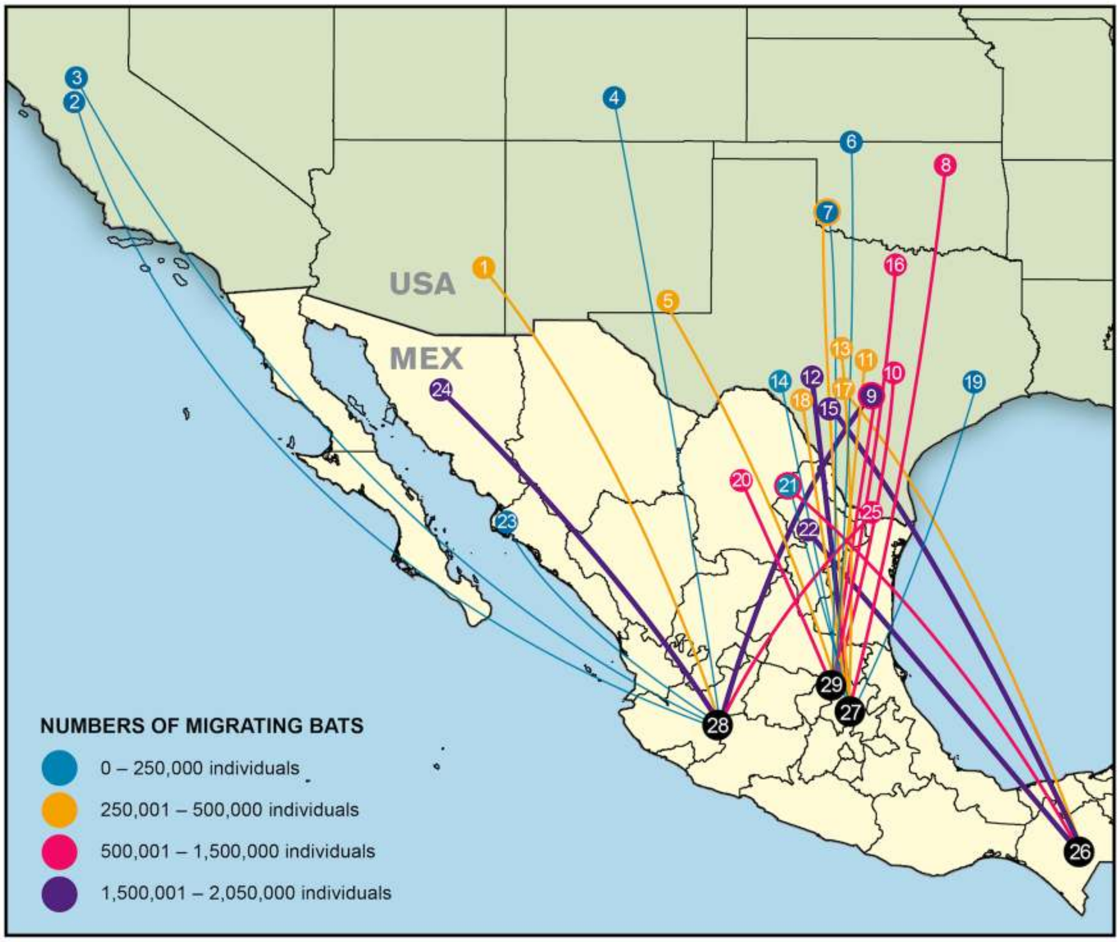
Below we: (1) describe our dataset of the major bat roosts and the criteria used for data inclusion, (2) enumerate the required input and population parameters and justify their selection, (3) describe the model output data, (4) describe the migratory network model, (5) explain the sensitivity analysis we used to address parameter uncertainty, and (6) detail the summer roost removal simulations used to test for roost influence on population size and network connectivity.

Input parameters

Model inputs are: roost locations, abundance estimates for each roost, the ratio of winter-to-summer carrying capacity, and population parameter estimates such as the birth rate, sex ratio, and annual survivorship. We obtained most population parameters from the literature (Table 1); those we derive are described below.

The migratory population

We simulate the migratory dynamics of only those bats that actually migrate to the summer breeding roosts, which is approximately half the



SUMMER ROOSTS

1 Eagle Creek Cave, AZ
2 Cosumnes River Preserve, CA
3 Yolo Bypass Bridge, CA
4 Orient Mine, CO
5 Carlsbad Caverns, NM
6 Merrihew Cave, OK
7 Read Cave, OK
8 Vickery Cave, OK
9 Bracken Cave, TX
10 Congress Bridge, TX
11 Davis Cave, TX
12 Devils Sink Hole, TX
13 Eckert James River Cave, TX
14 Fern Cave, TX
15 Frio Cave, TX
16 McNeil Bridge, TX
17 Ney Cave, TX
18 Stuart Bat Cave, TX
19 Waugh Bridge, TX
20 Cuatrociénegas de Carranza, Coahuila
21 Cueva de Consuelo, Coahuila
22 Cueva La Boca, Nuevo Leon
23 Maviri, Sinaloa
24 Cueva del Tigre, Sonora
25 Presa de Amistad, Tamaulipas

WINTER REGIONS

26 Chiapas
27 Hidalgo
28 Michoacán & Jalisco
29 Querétaro

Fig. 1. Summer breeding roosts and Mexican winter regions for the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). Line colors represent the total number of individual migrant bats. If a summer site was connected to more than one route, the circle representing the summer site was filled and outlined with the colors of the two different routes.

Table 1. Input parameter values.

Parameter	Value	Description	Source
d†	0.72–0.88	intrinsic (i.e., annual) survivorship	Davis et al. 1962
h	0.5	proportion of both males and females in the population	Wilkins 1989
s	0.1	proportion of males that migrate	Federico et al. 2008: Appendix B
f	0.9	number of pups delivered per female	Davis et al. 1962, Federico et al. 2008
M†	5–10	parameter proportional to survival during migration; M determines survival cost per kilometer traveled (see Eq. 4: c_{ij})	
δ	1.41	ratio of winter to summer carrying capacity	winter region has a higher carrying capacity as evidenced by its larger population size, but this is mediated somewhat by the lower energetic demands

† Sensitivity analysis performed on parameter.

population—90% of females and 10% of males. Ten percent of females and 90% of males remain in southern Mexico and do not migrate from the winter habitat to the summer breeding roosts (McCracken and Gassel 1997, Federico et al. 2008).

Summer roost locations and roost abundance estimates

We developed a database of roost locations and population abundances by combining data from a U.S. Geological Survey database (Ellison et al. 2003), our own literature search, and unpublished data from Mexican free-tailed bat experts, co-authors PC, GM, RM, and AR. Due to concerns about the accuracy of some data points given the lack of standardized protocols and estimates of detection probability in older data, the potential that impermanent structures may have disappeared over time, and likelihood of inaccurate locations for small roost sites, we exclude some of the roosts in our database from the model dataset. We consider only the largest roosts ($\geq$50,000 individuals) because they tend to be permanent, long-lasting structures such as caves, bridges, mines, tunnels, dams, and crevices, and are more likely to have reliable location estimates (McCracken 2003, O'Shea et al. 2003). We exclude impermanent structures such as vegetation, nest boxes, sinkholes, and buildings (Lewis 1995). By eliminating the smaller roosts from the model, we exclude less than 1% of the overall bat population in our database. Because the combined populations of the largest summer colonies are thought to account for most of the migratory population of free-tailed bats (McCracken 2003), focusing on the dynamics of only the major roosts should provide a reasonable estimate of migratory linkages. Finally, because of concerns that bat populations may have declined through the decades of the 1950s and 1960s, presumably due to DDT exposure (Betke et al. 2008), we only use abundance estimates obtained after 1970. In all, our model dataset consists of 25 major summer roosts containing a total population of 22,792,105 individuals (Fig. 1; Appendix).

Winter nodes

In the central and southern Mexico winter grounds bats disperse across the landscape rather than aggregate in large roosts as they do in the summer breeding region (Villa 1956). As a result, we are unable to model winter nodes as specific sites. Instead we model four winter nodes, each representing a distinct biogeographic area; we call these nodes "winter regions." The "Chiapas" winter region represents the transitional Nearctic-Neotropical biogeographic area. The "Hidalgo" and "Querétaro" winter regions represent the southeastern and northwestern ranges, respectively, of the Trans-Mexican volcanic belt. The "Michoacán/Jalisco" winter region represents a mosaic of the Trans-Mexican volcanic belt, the Sierra Madre Occidental, and the Michoacán lowlands. For the purposes of the model, the geographic location of each node is based on a known major roost or the geographic midpoint of all major roosts in the winter region (Fig. 1; Appendix).

Calculating carrying capacity

To derive an equilibrium solution for overall network structure, the model requires an estimate of the carrying capacity of each node. For the summer roosts, the carrying capacity is estimated using the roost abundance estimates divided by the product of the intrinsic survival and intrinsic fecundity rate (see Eq. 8). However, due to the lack of abundance estimates and the dispersed nature of the bats in the winter area, we use a different approach for estimating the carrying capacities for the four regions. We base these estimates on the overall ratio of winter-to-summer carrying capacity. The rationale and calculation for the ratio are as follows.

The ecological concept of carrying capacity is based on the maximum number of individuals that can be supported in a particular area (Sharkey 1970). In addition, variation amongst individuals in their energetic needs and resource consumption should also be taken into account when estimating carrying capacities. During winter months, almost the entire bat population is found in the winter region, whereas only half of the population (90% of females and 10% of males) migrates to the summer breeding sites. Further, lactating females in the summer breeding habitat have greater energetic demands (46% higher) than males and non-lactating females (Federico et al. 2008). Our estimated carrying capacity ratio of winter-to-summer population sizes δ is 1.41 and is calculated as follows:

$$\delta = 1/(0.9 \times h \times (1 + l) + 0.1 \times h) \tag{1}$$

where h is 0.5, the proportion of both males and females in the population, and l represents the 46% increase in energetic demands of lactating females, and 0.9 and 0.1 represent the proportion of female and male bats, respectively, that actually migrate (Table 1) (Federico et al. 2008).

To obtain individual carrying-capacity estimates for the four winter nodes, we divide total winter carrying capacity equally between the four regions. Preferably, carrying capacities would have been apportioned according to the number of bats in each area; ideal proxies might have been amount of suitable habitat or habitat quality in each region, but such data are not currently available. Equally dividing the carrying capacity among the four regions is the most conservative approach given the lack of available information.

Output parameters

The model output variables characterize the network structure in terms of: numbers of individuals migrating (traffic) between individual summer roosts and winter regions; estimates of the carrying capacity for each summer roost; the network size (the total number of routes or edges in the network); and the mean degree of connectivity (the mean number of routes that connect to a node). In addition, to assess whether the current bat population is near its maximum potential size, we report the percentage of *summer* carrying capacity reached by the population (Rayfield et al. 2011). We define this as follows:

$$\alpha = \sum_{j=1}^{N_B} \hat{\tau}_{Bj} \Big/ \sum_{j=1}^{N_B} k_{Bj} \tag{2}$$

where $\hat{\tau}_{Bj}$ is the model estimate of the peak population of summer roost j, N_B is the number of summer breeding roosts, and k_{Bj} is the carrying capacity for summer roost j.

Network model description

Our model uses a number of derived parameters (Table 2) and input abundance estimates for summer roosts (Appendix) to compute an equilibrium solution for traffic along each migratory route, $A_{ij(t)}$. In the model, the number of individuals traveling between winter region i and summer roost j is based on annual probabilities of fecundity, migration survival, and overwintering survival. The number of individuals traveling between winter region i and summer roost j between year t and year $t + 1$ is

$$A_{ij(t+1)} = (c_{ij})^2 F_{ij} S_i A_{ij(t)} \tag{3}$$

where c_{ij} is the survival rate per kilometer traveled for individuals migrating between winter region i and summer roost j (squared to account for migration in both directions); F_{ij} is the fecundity (number of pups produced) of individuals overwintering in region i and breeding at roost j; and S_i is the survival of individuals overwintering in region i (Taylor and Norris 2010).

The overall survival rate for migrating individuals (c_{ij}) is distance-dependent, decreasing with increasing distance traveled, and is calculated as follows:

Table 2. Network model parameter values (adapted from Taylor and Norris 2010).

Parameter	Value	Description
$\boldsymbol{N}_B$	variable	number of breeding (summer) roosts
N_W	variable	number of nonbreeding winter regions
G_{ij}	distance between region *i* and roost *j*	geodetic distance between region *i* and roost *j* in km
b'_{ij}	$\exp(-0.02 \times (r_{ij} - 1)$	relative breeding (summer) disadvantage of bats; r_{ij} is the rank of roost *j* with respect to closeness of roost *j* from region *i*
f_f	$f \times h \times (1 - s)$	winter region to summer roost migratory female pups produced per female
f_m	$f \times h \times s$	winter region to summer roost migratory male pups produced per female
b†	$1 + (f_f + f_m) \times (1 - s)$	intrinsic fecundity, number of offspring produced per migrant individual
k_{Bj}	roost-specific for all *j*	carrying capacity for breeding (summer) roost *j*
k_{Wi}	region-specific for all *i*	carrying capacity for nonbreeding winter region *i*
τ_B, peak population	variable	list of peak summer roost populations

† Sensitivity analysis performed on parameter.

$$c_{ij} = \exp(-10^{-M} \times G_{ij}) \tag{4}$$

where G_{ij} is distance between winter region *i* and summer roost *j* in km (Table 2); and *M* is survival during migration (survival cost per kilometer traveled; Table 1).

Fecundity represents a per capita breeding rate across both males and females and is determined by:

$$F_{ij} = b \exp\left(-\frac{b^{\prime}_{\prime ij}\sum_{i=1}^{N_W} A_{ij}}{k_j}\right). \tag{5}$$

The fecundity (number of pups produced) of both males and females overwintering in region *i* and breeding at roost *j* (F_{ij}; Eq. 5) depends on three factors. First, it depends on the intrinsic fecundity per migrant individual (*b*). Second, it is density dependent based on the individual carrying capacity of summer breeding roost *j*, k_j, and declines with an increasing roost population. The population size of summer roost *j* is calculated by summing the flows of individuals from all winter regions to summer roost *j*, $\sum_{i=1}^{N_W} A_{ij}$, where N_W is the number of winter regions. The third and last component of fecundity is the relative breeding disadvantage b_{ij}' experienced by individuals overwintering in region *i* and breeding in roost *j*. This disadvantage arises from the assumption that individuals migrating longer distances from winter habitat to summer breeding sites will have lowered reproductive rates. This is in addition to lowered survival rates experienced during long-distance migration determined by c_{ij} (Eq. 4).

The overwintering survival of individuals in winter region *i* is given by:

$$S_i = d \exp\left(-\frac{2 \times \sum_{j=1}^{N_B} A_{ij}}{k_i}\right). \tag{6}$$

Overwintering survival depends on two factors: an intrinsic survival rate *d* and a density-dependent component that is based on the winter region's carrying capacity, k_i, that declines as the roost population increases. Abundance for a given winter region *i* is calculated by summing the total flows of individuals from all summer roosts to winter region *i*, $2 \times \sum_{j=1}^{N_B} A_{ij}$, where N_B is the number of summer roosts. To account for the (non-migratory) winter population, we multiplied the total sum by 2 as the migratory population composes only half of the total population size. Because in Eq. 5 the model assumes that the survival rate during migration, c_{ij}, decreases with distance migrated, we do not apply an additional disadvantage in overwintering survival.

The total number of migratory individuals is the sum of migrants along all migratory routes and is given by:

$$N_{\text{global}} = \sum_{i=1}^{N_W} \sum_{j=1}^{N_B} A_{ij}. \tag{7}$$

The model is solved by using the input

abundance estimates for each summer roost to estimate that roost's carrying capacity, assuming that its peak population was at a stable equilibrium. The model iteratively calculates the number of individuals traveling between winter region i and summer roost j, $A_{ij(t+1)}$ until the difference between the modeled population size estimates for each summer roost and input abundance estimates for each roost is below a specified error threshold of 10^{-6}. In the first step of this process, we set the initial carrying capacity for summer roost j as

$$k_{Bj} = \frac{\tau_{Bj}}{\ln(bd)} \tag{8}$$

where τ_{Bj} is the input peak population estimate of summer roost j, b is the intrinsic fecundity per migrant individual, and d is the intrinsic survival rate. We set the initial carrying capacity for winter region i as

$$k_{wi} = \frac{\delta \sum_{j=1}^{N_B} k_{Bj}}{N_W}$$

where N_W is the number of winter regions and δ is the ratio of winter-to-summer population sizes (see Eq. 1). Initially, all flows from the four winter regions to summer roost j are set equal. Next, we solve Eqs. 2, 3, and 4 numerically, and compare $\hat{\tau}_{Bj} = \sum_{i=1}^{N_W} A_{ij}$, the model estimate of the peak population of summer roost j, with τ_{Bj}, our inputted population value. When the desired level of precision, $||\hat{\tau}_{Bj} - \tau_{Bj}||/||\tau_{Bj}|| < \varepsilon = 10^{-6}$, is reached, the model stops iterating. Otherwise, we define a new equilibrium population

$$\tau_{BEj} = \tau_{Bj} bd \exp\left(-\frac{\tau_{Bj}}{k_{Bj}}\right),$$

update our estimates of

$$k_{Bj} = \frac{\tau_{Bj}}{\ln(bd \frac{\tau_{Bj}}{\tau_{BEj}})},$$

and repeat the first step.

Baseline scenario and sensitivity analysis

For our baseline model scenario, values for intrinsic (annual) survival (d) and the intrinsic fecundity (b) were 0.8 and 1.4, respectively. Empirical estimates of annual survival of Mexican free-tailed bats range from 0.7–0.8 (Davis et al. 1962); because the corresponding parameter in our model represents density-independent survival, we use the upper value of this range. The parameter M, survival during migration, is a component of the overall survival rate for migrating individuals (c_{ij}, Eq. 4), and estimates the survival cost per kilometer traveled. Estimates of survival during migration are not available, so for the baseline scenario, we use the greatest, most conservative, migration cost ($M = 5$) that still results in summer roosts having non-zero carrying capacities. This value also results in a survival rate c_{ij} per kilometer of 0.99 which is consistent with the known annual survival rates for Mexican free-tailed bats (Davis et al. 1962, Glass 1982).

We tested the model's sensitivity to uncertainty in 3 input parameters: migration survival (M), intrinsic fecundity (b), and intrinsic survival (d). For the sensitivity analyses, we altered d and b by ±10% of their baseline values. We also tested model sensitivity to values of M from 6 to 10, which correspond to increases of 20 to 100% in M relative to the baseline of 5 (note that because M is a negative exponent in Eq. 4, increased values of M lower migration costs and increase migratory survival).

Roost removal experiments for roost importance

To test how the hypothetical loss of a roost site would impact the overall bat population, we iteratively remove each roost from the model, with replacement, and rerun the model to obtain the updated network structure. This approach is used in network modeling to understand the impact of losing a node on network structure (Urban et al. 2009, Taylor and Norris 2010, Rayfield et al. 2011). For the roost removal experiments, we use the baseline input parameters of $d = 0.8$, $b = 1.4$, and $M = 5$ and the carrying capacities for each node that had been previously solved in the baseline model. When removing a given roost from the model, the bats are not "killed," rather the individuals that would have migrated to the removed roost are allowed to disperse to other summer roosts. Upon each iteration, the individuals are initially assigned in equal numbers to the remaining migratory routes, and the model is resolved using Eqs. 3–7 to obtain the updated network structure. To further examine the robustness of the model to variation in survival during migration, we conducted roost-removal simulations at both the baseline migration survival value of $M = 5$, and at $M = 10$. The assumption that individuals move to other roosts when a roost is damaged or destroyed is reasonable given that individuals are known to change roosts over time (Glass 1982, Genoways et al. 2000, McCracken 2003).

RESULTS

Network model results

The network size, the total number of routes in the network, was 28 (Fig. 1). The mean degree of connectivity (i.e., the mean number of routes that connect to a node) was 1.93. The summer roosts had at most two connections to the winter regions. The winter regions with the most connections to summer roosts were the most centrally located (Querétaro, Hidalgo and Michoacán/Jalisco). All flows with greater than one million migrants were to summer roosts in southern Texas or northern Mexico. The greatest migratory flow (2.05 million individuals) occurred between the Michoacán/Jalisco winter region and Bracken Cave in Texas (Fig. 1). Large flows (greater than 2 million) also occurred between the routes of Michoacán/Jalisco → Cueva del Tigre, Hidalgo → Devil's Sink Hole, Chiapas → Cueva La Boca, and Chiapas → Frio Cave. In fact, the majority of the summer migratory population was contained in northern Mexico (30%) and Texas (58%), as opposed to more distant summer roosts in Arizona, New Mexico, Colorado, Oklahoma and California.

In the baseline scenario, the mean percentage of the carrying capacity (α; Eq. 2) reached by the summer roost populations was 7.1% (SD = 1.1%) across the 25 roosts. This suggests that the summer population may be less than 10% of its potential maximum size. The populations in two distant northern California roosts, Cosumnes River Preserve and Yolo Bypass Bridge, reached a particularly low percentage (3.4%) of their summer carrying capacity.

Sensitivity analysis

The model was fairly robust to the input parameter value alterations according to the sensitivity analysis (Fig. 2). Increasing the survival during migration parameter M, which increased the survival rate per kilometer traveled (c_{ij}) for migrating individuals, had little effect on the percentage of summer carrying capacity reached by the population (Fig. 2A). In addition, increasing the migration survival M augmented the mean degree of connectivity of the network, up to a maximum of 43% higher than the baseline value (Fig. 2B). Even with greater values of M, the route with greatest migratory flow was always Michoacán/Jalisco → Bracken Cave. This indicates that the model was not very sensitive to alterations in migration survival. Further, the analyses suggest that $M = 5$ was a reasonable value for the baseline scenario.

Increasing survival (d) and fecundity (b) increased the percent of summer carrying capacity reached by the population α. Likewise, decreasing survival and fecundity decreased the percent of carrying capacity reached and lowered the mean degree of network connectivity, whereas increased fecundity augmented connectivity (Fig. 2B). However, increasing survival decreased the mean degree of network connectivity by 3.6% and resulted in elimination of the migratory route Hidalgo → Cueva de Consuelo (Fig. 2B). Under this scenario, the flow of individuals from Hidalgo stopped, while flows increased from other winter regions, especially from the more distant region of Chiapas. Thus, higher survival increased migration from more distant sites. In summary, the sensitivity analyses indicated that while variations in survival (d) and breeding (b) success affected summer carrying capacity, network connectivity was robust to these changes.

Roost removal simulations

The roost-removal simulations (which tested the hypothetical destruction of a roost site while allowing the bat population to disperse to other roosts) indicated that summer roosts in southern Texas and northern Mexico had the most significant impact on the migratory population. When roosts in these areas were removed, both summer population size and network connectivity decreased. In addition, there was a marginally significant negative correlation ($r = -0.338$, p-value $= 0.098$) between the number of connections a summer roost has and the population loss caused by its removal. This suggests that well-connected roosts may have more influence on the

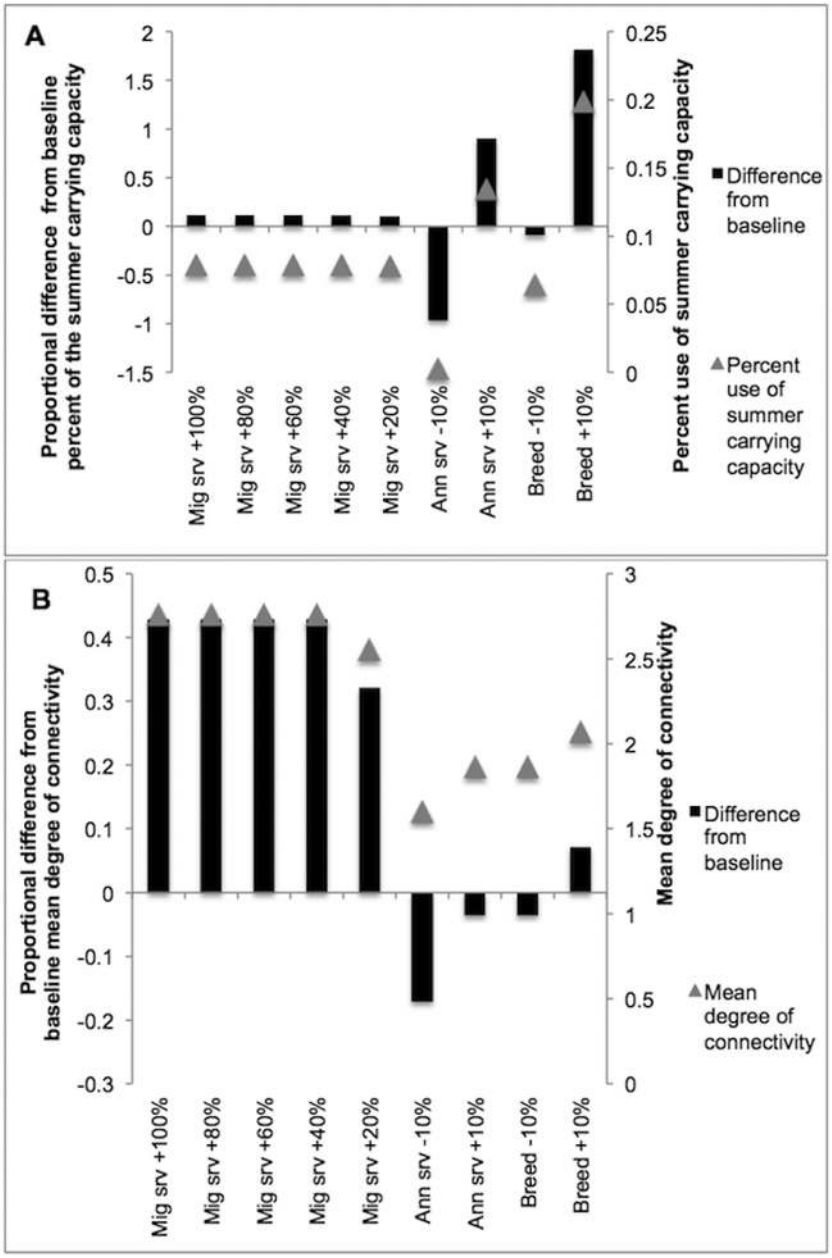


Fig. 2. Sensitivity analysis results for percent of summer carrying capacity and the mean degree of connectivity. Results are expressed as the proportional difference from the baseline values for the percent of the summer carrying capacity reached by the population (α) (A) and proportional difference from the baseline values for the mean degree of connectivity and total number of routes in the migratory network (B). Codes are as follows: Mig srv = survival during migration parameter (M), Ann srv = intrinsic survival (d), Breed = intrinsic fecundity (b).

migratory network.

In the baseline scenario, removing the Bracken Cave, Frio Cave, or Devil's Sink Hole roosts in Texas, or the Cueva La Boca or Cueva del Tigre roosts in northern Mexico, reduced the total summer population size the most. Depending on which roost was removed from the network, the total decline in summer population ranged from

1.1 to 2.3 million individuals or approximately 4.8–10.1% (Fig. 3A). Further, increasing survival during migration (M) did not change the impact of removing these five roosts; they still had the largest impact on the summer population size. We also found that there was a highly significant negative correlation between the population loss caused by a particular roost's removal and that roost's population size ($r = -0.996$, $p < 0.0001$), while the latitude of the roost had a nearly significant positive correlation with the population loss caused by a particular roost's removal ($r = 0.386$, $p < 0.057$).

Under the baseline scenario ($M = 5$), the removal of any of the 25 summer roosts resulted in decreased network connectivity, with the removal of Bracken Cave having the greatest impact (decrease of 7.5%; Fig. 3B). When migration survival was increased ($M = 10$), removing Bracken Cave and two additional roosts, Congress Bridge and Presa de Amistad decreased network connectivity the most. Overall, in the baseline scenario the summer roosts whose removal most affected connectivity were all centrally located in Texas, Oklahoma, and northern Mexico (Fig. 3B).

DISCUSSION

Network structure and importance of breeding regions

As hypothesized, the most important summer breeding areas for maintaining the population were the most southerly-located; the ranked importance of these roosts was robust to alterations in network structure. Several of the most southern breeding roosts (Bracken Cave, Frio Cave, Devil's Sink Hole, in Texas; Cueva La Boca, in Nuevo Leon, Mexico; and Cueva del Tigre, in Sonora, Mexico) had the greatest summer population sizes. Removing these large southern breeding roost sites from the model forced bats to migrate farther north and greater distances, reducing their survival rates (Fig. 3A). Removal of these sites also increased the negative effects of density-dependence in the remaining roosts. As a consequence, the overall population size declined.

The major migratory routes—those with the greatest number of migrants—were between centrally-located winter habitat and the most southern breeding roosts in Texas, Sonora and Nuevo Leon. The greatest reduction in network connectivity was also caused by removing breeding roosts in northern Mexico and Texas, emphasizing the importance of this region for the conservation of Mexican free-tailed bats (Fig. 3B).

Conservation threats

Several of the roosts we identified as being crucial for the population maintenance of Mexican free-tailed bats are facing threats from disturbance, pollution, development and vandalism. Populations in Bracken Cave, Frio Cave, and Cueva La Boca are thought to have declined possibly due to DDT exposure or disturbance from guano mining (Cockrum 1970, Bat Conservation International 1991, Clark 2001, Betke et al. 2008). Both Bracken Cave and Devil's Sink Hole are protected. However, Bracken Cave is located in the outskirts of San Antonio; the area immediately adjacent to the roost is being considered for a 3,800-unit housing development (M. Tuttle, *personal communication*). Proximity to such a large development could potentially reduce food sources for the bats and increase roost vandalism. Frio Cave is situated on a private ranch and is not under a formal conservation arrangement (F. Hutchins, *personal communication*).

Two new threats to Mexican free-tailed bats are emerging—climate change and wind turbines—that are likely to affect migration survival and network structure (Arnett et al. 2008, Cryan and Barclay 2009, Popa-Lisseanu and Voigt 2009). The U.S.–Mexico border region is predicted to become warmer and drier under climate change (Intergovernmental Panel on Climate Change 2007). It is thought that under warmer and drier conditions, bats will experience increased water stress, which will compound the already high rates of water loss occurring during migration and potentially reduce survival (Adams and Hayes 2008, Popa-Lisseanu and Voigt 2009).

A number of studies suggest that wind turbines might cause Mexican free-tailed mortalities and decrease survival rates (Arnett et al. 2008, Cryan and Barclay 2009). The deployment of wind turbines for energy production has been increasing in North America and is expected to continue to grow in the future. Many wind facilities have been built near the summer

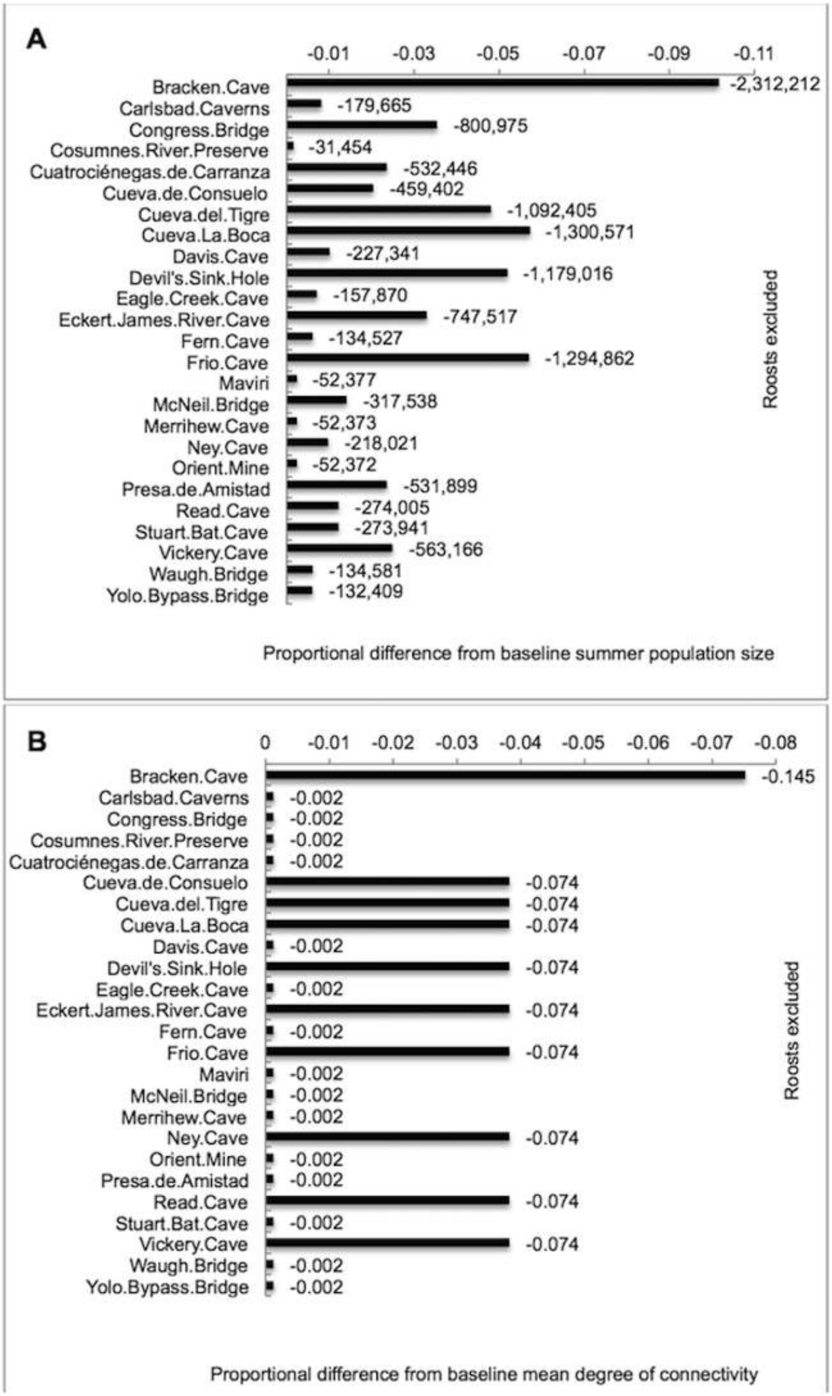


Fig. 3. Roost removal experiment results. Changes in summer population size (A) and mean degree of connectivity (B) with eliminated summer roosts are expressed as proportional difference from the baseline scenario. Labels indicate the overall decrease in summer population size (A) and the decrease in the mean degree of connectivity (B). The baseline scenario (which included all roosts) was 22.8 million individuals for the total summer population size and 1.93 for the mean degree of connectivity.

breeding areas we have identified as critical. Several roosts in Texas are of particular concern, as the state had the highest production of wind energy of any state in the U.S. in 2011 (U.S. Energy Information Adminstration; http://www.eia.doe.gov).

In our model, decreased migration survival, as might be expected under scenarios of climate change and wind turbine development, decreases network connectivity, suggesting that migration over shorter distances may be favored in the future. Improved knowledge of Mexican free-tailed bat mortality rates caused by wind turbines, the physiological effects of hotter and drier climatic conditions, and the ability of Mexican free-tailed bats to colonize new sites, is needed to better assess the effects of these factors on the population and network structure.

Bi-national conservation agreements

By illustrating the importance of transboundary habitat connectivity between countries, our results emphasize the necessity of conservation efforts focused on critical roosts in Texas and northern Mexico. Cross-border coordinated management and population-level monitoring is critical as bats may switch roosts overtime and the population's viability depends on breeding habitat in both countries (Glass 1982, Genoways et al. 2000, McCracken 2003). North American conservation agreements already exist, such as the Program for the Conservation of Migratory Bats, between the U.S. and Mexico, and the North American Bat Conservation Partnership, between Canada, the U.S., and Mexico (Keeley et al. 2003, Medellin 2003). Our model results, by identifying important breeding roosts and major migratory routes, can help focus conservation efforts on crucial habitat. The need for effective conservation strategies in the transboundary region is compounded by the fact that Mexican free-tailed bats are just one of the 34 bat species found in the region that provide important ecosystem services such as pest control and pollination (Medellin 2009).

Conclusions

A major challenge for bat conservation is the migration of species across international borders and between habitats with varying levels of protection. An understanding of the relative importance of individual roosts and identification of migratory routes is critical for targeting conservation efforts, especially under the threats of climate change and wind turbine development. In accordance with our hypothesis, we found that southernmost breeding roosts, located in northern Mexico and Texas, were particularly important. Our results suggest that conservation efforts for Mexican free-tailed bats should focus on these areas, particularly on large breeding roosts. Further, our results suggest that additional declines in survival during migration from potential threats such as climate change or wind turbines could cause a restructuring of the migratory network. The network modeling approach, as of yet underemployed, shows promise in furthering our understanding of bat migration; we suggest that network modeling, with its ability to simulate migratory patterns with scarce data, can be an effective method for studying migration for other bat species.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Summer (S) breeding roosts and winter (W) regions for Mexican free-tailed bats.

Site/Region	Country	State	Type	Abundance estimate	Source
Eagle Creek Cave	USA	AZ	S	300,000	Mohr 1972, Reidinger 1972
Cosumnes River Preserve	USA	CA	S	60,000	NorCal bats, *unpublished data*
Yolo Bypass Bridge	USA	CA	S	250,000	NorCal bats, *unpublished data*
Orient Mine	USA	CO	S	100,000	Freeman and Wunder 1988
Carlsbad Caverns	USA	NM	S	341,026	Betke et al. 2008
Merrihew Cave	USA	OK	S	100,000	Arganbright 1989
Read Cave	USA	OK	S	500,000	Elliot 1994
Vickery Cave	USA	OK	S	1,000,000	Humphrey 1971
Bracken Cave	USA	TX	S	4,000,000	GM, *unpublished data*
Congress Bridge	USA	TX	S	1,500,000	Wahl 1993, Keeley and Tuttle 1999
Davis Cave	USA	TX	S	431,205	Betke et al. 2008
Devil's Sink Hole	USA	TX	S	2,000,000	GM, *unpublished data*
Eckert James River Cave	USA	TX	S	1,312,027	Betke et al. 2008
Fern Cave	USA	TX	S	250,000	Bat Conservation International 2003
Frio Cave	USA	TX	S	2,000,000	GM, *unpublished data*
McNeil Bridge	USA	TX	S	600,000	Allen et al. 2010
Ney Cave	USA	TX	S	397,846	Betke et al. 2008
Stuart Bat Cave	USA	TX	S	500,000	Texas Parks Wildlife 2007
Waugh Bridge	USA	TX	S	250,000	Texas Parks Wildlife 2007
Cuatrociénegas de Carranza	Mexico	Coahuila	S	1,000,000	MaNIS 2011
Cueva de Consuelo	Mexico	Coahuila	S	800,000	Bat Conservation International 2003
Cueva La Boca	Mexico	Nuevo Leon	S	2,000,000	Lopez-Damian 2009
Maviri	Mexico	Sinaloa	S	100,000	RAM and Ejido Juan Aldama, *unpublished data*
Cueva del Tigre	Mexico	Sonora	S	2,000,000	RAM, *unpublished data*
Presa de Amistad	Mexico	Tamaulipas	S	1,000,000	RAM, *unpublished data*
Chiapas	Mexico	Chiapas	W	1,000,000	Lopez-Damian 2009
Hildago	Mexico	Hildago	W	20000	MaNIS 2011
Michoacán/Jalisco	Mexico	Michoacán/Jalisco	W	20000	Clark et al. 1995
Querétaro	Mexico	Querétaro	W	10000	RAM, *unpublished data*