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Optimizing conservation strategies for Mexican free-tailed bats: a population viability and ecosystem services approach

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ORIGINAL PAPER

Optimizing conservation strategies for Mexican free-tailed bats: a population viability and ecosystem services approach

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Abstract Conservation planning can be challenging due to the need to balance biological concerns about population viability with social concerns about the benefits biodiversity provide to society, often while operating under a limited budget. Methods and tools that help prioritize conservation actions are critical for the management of at-risk species. Here, we use a multi-attribute utility function to assess the optimal maternity roosts to conserve for maintaining the population viability and the ecosystem services of a single species, the Mexican free-tailed bat

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(*Tadarida brasiliensis mexicana*). Mexican free-tailed bats provide ecosystem services such as insect pest-suppression in agricultural areas and recreational viewing opportunities, and may be threatened by climate change and development of wind energy. We evaluated each roost based on five attributes: the maternity roost's contribution to population viability, the pest suppression ecosystem services to the surrounding area provided by the bats residing in the roost, the ecotourism value of the roost, the risks posed to each roost structure, and the risks posed to the population of bats residing in each roost. We compared several scenarios that prioritized these attributes differently, hypothesizing that the set of roosts with the highest rankings would vary according to the conservation scenario. Our results indicate that placing higher values on different roost attributes (e.g. population importance over ecosystem service value) altered the roost rankings. We determined that the values placed on various conservation objectives are an important determinant of habitat planning.

Keywords Anthropogenic risks · *Tadarida brasiliensis mexicana* · Maternity roosts · Conservation assessment and planning · Ecosystem services · Decision-support tools

Introduction

Conservation planning for migratory species is challenging because not only must one account for multiple factors—anthropogenic risks, species' benefits to society, biological importance and policy, budgetary constraints, and other social considerations—but these issues must be considered across multiple locations and possibly between several countries. Making decisions that aim to balance multiple objectives can be challenging (Kenney 2002). A range of approaches have been developed for prioritizing where, how, when, and why conservation actions should be taken (Wilson et al. 2009). These structured decision analytic approaches can help identify optimal courses of action in a transparent fashion. Further, a decision analytic approach offers the opportunity to learn and explicitly address uncertainty (Nichols et al. 2011). One such structured approach, multi-attribute utility functions, can be used to reconcile tradeoffs among multiple conservation objectives (Ciarleglio et al. 2009). Such tools have been used in a variety of conservation contexts to prioritize land-acquisition decisions (Andelman and Willig 2002; Carwardine et al. 2010; Wilson et al. 2009; Wilson et al. 2007). Similarly, extensive work has been done on the role of ecosystem services in conservation planning (Boykin et al. 2013; Edwards et al. 2010; Egoh et al. 2011; Nelson et al. 2009). However, only a small number of studies have examined the role of ecosystem services in the conservation of migratory species (Dobson 2009; Johnson et al. 2011; Kunz et al. 2011; López-Hoffman et al. 2013; Semmens et al. 2011; Vanoye-Eligio 2012; Whelan et al. 2008). Here we use a multi-attribute utility function to consider population viability, pest suppression services, ecotourism, and anthropogenic risks to prioritize which Mexican free-tailed bat maternity roosts to conserve. To our knowledge, this study, Dobson (2009),

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and Vanoye-Eligio (2012) are the first conservation planning studies to consider threats to population viability and ecosystem services.

Mexican free-tailed bats winter in central and southern Mexico, where they disperse throughout the landscape (Villa and Cockrum 1962). Early each spring, bats migrate north, forming large maternity roosts in the southwestern U.S. and northern Mexico (Davis et al. 1962; Federico et al. 2008; Villa and Cockrum 1962). Ten percent of females and ninety percent of males remain in southern Mexico and do not migrate from the winter habitat to the summer breeding roosts (Federico et al. 2008; McCracken and Gassel 1997). Although most individuals return to the same maternity roost, individuals have been known to change roosts over time (Glass 1982; McCracken 2003).

There is growing concern about threats to Mexican free-tailed bat maternity roosts in North America (Kunz et al. 2011; Mickleburgh et al. 2002). In the U.S. and Mexico, guano mining and the burning or dynamiting of roosts has led to the total loss of several maternity roosts (McCracken 1987; McCracken 1989). Organochlorine pesticides such as DDT may be harmful to insectivorous bats as they can acquire high pesticide loads from their diets (McCracken 1987). Pesticides are thought to have caused a sharp population decline at the roost in Carlsbad Caverns, although there may have been multiple contributing factors (McCracken 1987; McCracken 1989). Protecting maternity bat roosts offsets these threats and helps conserve and sustain bat populations (Medellin 2003).

Mexican free-tailed bats provide several ecosystem services throughout their range (Federico et al. 2008; Gándara Fierro et al. 2006; Villa and Cockrum 1962). For example, bats emerge nightly from their maternity roosts to forage on insects and several major agricultural insect pests up to 50 km away from their roosts (Lee and McCracken 2005; Williams et al. 1973). The total annual cotton pest-suppression services provided by Mexican free-tailed bats across all maternity roosts in the southwestern U.S. and northern Mexico has been valued at \$11.67 million USD (López-Hoffman et al. 2014). Besides reducing the need for regional insecticide use and suppressing pest populations, Mexican free-tailed bats may also hedge against the rise of resistance among pests to transgenically modified Bt *(Bacillus thuringiensis)* crops (Federico et al. 2008; Liu et al. 2014; López-Hoffman et al. 2014). In addition to providing pest suppression services, several large Mexican free-tailed bat maternity roosts in the southwestern U.S. and northern Mexico are important for ecotourism (Bagstad and Wiederholt 2013; Davis et al. 1962; Federico et al. 2008; Villa and Cockrum 1962).

Only one other study has determined conservation priorities for bat roosts taking into account the level of ecosystem services provided (Vanoye-Eligio 2012). This study ranked roosts according to several factors for each site: bat ecosystem services provided, conservation status, bat diversity and number of threatened species, and potential value for education, economic benefit, or ecotourism (Vanoye-Eligio 2012). In contrast to our study focusing on Mexican free-tailed bats across the southwestern U.S. and northern Mexico, this research was conducted in in a more restricted geographic range, northeast Mexico, and considered a range of bat species present at each site. This study did also not consider different conservation scenarios that may alter conservation priorities.

To guide conservation efforts, we have developed a multi-attribute utility function to rank the most important Mexican free-tailed bat maternity roosts in the southwestern U.S. and northern Mexico. We evaluated each roost based on five attributes: the maternity roost's contribution to population viability, the pest suppression ecosystem services to the surrounding area provided by the bats residing the in roost, the ecotourism value of the roost, the risks posed to each roost structure, and the risks posed to the population of bats residing in each roost. We then tested four conservation scenarios to determine how prioritizing different attributes can impact management and conservation strategies.

Methods

We considered all known major maternity roosts with greater than 50,000 individuals in the southwestern U.S. and northern Mexico. We evaluated each roost based on five attributes: the maternity roost's contribution to population viability, the pest suppression ecosystem services to the surrounding area provided by the bats residing the in roost, the ecotourism value of the roost, the risks posed to each roost structure, and the risks posed to the population of bats residing in each roost. To evaluate the biological importance of individual maternity roosts, we used data from a migratory network model which calculated migratory routes from overwintering grounds to maternity roosts and simulated changes in migratory population size associated with the loss of any particular maternity roost (Wiederholt et al. 2013). For the pest suppression ecosystem services of bat maternity roosts, we used data from a valuation study of the cotton pest suppression services of maternity roosts across the southwestern United States (López-Hoffman et al. 2014), expanding the analysis to consider several maternity roosts in northern Mexico. Our assessment of the ecotourism values of the maternity roosts drew upon annual visitation estimates from bat-viewing sites and a wildlife viewing model (Bagstad and Wiederholt 2013; Loomis et al. 2008). We surveyed biologists with expertise in Mexican free-tailed bats to determine the risks to maternity roost structures and to the populations of individuals residing in those roosts.

We tested four conservation scenarios to determine how prioritizing different attributes can impact the management and conservation strategy. In the first scenario, all factors (roost importance, pest suppression, ecotourism, and risks posed to roosts) were equally weighted. In the second scenario, we weighted the biological importance or contribution to population viability of the bat roosts higher than the other attributes. Finally, the third and fourth scenarios prioritized the ecotourism and pest suppression services, respectively, provided by the bats occupying the roost. We hypothesized that the set of maternity roosts with the highest rankings will vary according to the conservation scenario.

Biological importance attribute

We considered all known major maternity roosts of Mexican free-tailed bats in the southwestern U.S. and northern Mexico (Fig. 1). 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). We considered only the largest maternity roosts with greater than 50,000 individuals because these roosts 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 also excluded impermanent structures such as vegetation, nest boxes, sinkholes, and buildings (Lewis 1995). By eliminating the smaller roosts from the model, we have excluded less than 1 % of the overall count total of bats in our database. Because the combined populations of the largest summer colonies are thought to account for most of the migratory population of Mexican free-tailed bats (McCracken 2003), focusing on the dynamics of only the major maternity roosts should provide a reasonable estimate of the conservation needs to the entire bat population. 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 used abundance estimates obtained after 1970. In all, our model dataset consisted of 25 major maternity roosts containing a total estimated population of about 22.8 million individuals (Fig. 1).

To evaluate the biological importance of individual maternity roosts, we used a migratory network approach developed by Taylor & Norris (2010) applied to Mexican free-tailed bats (Wiederholt et al. 2013). This approach allowed us to calculate expected migratory routes based on distance-based mathematical formulations of migration costs, and to simulate changes in migratory population size associated with the loss of any particular maternity roost. The network model simulated migration between four overwintering regions in southern Mexico (in the states of Chiapas, Hidalgo, Querétaro, and Michoacán-Jalisco) and the 25 major summer maternity roosts in northern Mexico and the southwestern U.S. In the overwintering grounds, bats disperse across the landscape rather than aggregate in large roosts as they do in the summer breeding region (Villa 1956). As such, for the purposes of the network model the geographic location of overwintering region was based either on a known major roost or the geographic midpoint of all major roosts in the winter region (Wiederholt et al. 2013).

Each migratory route was weighted with a survival cost derived from its length (Rayfield et al. 2011; Taylor and Norris 2010)—individuals traveling on longer routes were assumed to have lowered survival. This reflected the high mortality rates and poor body conditions reported for bats during migration (Constantine 1967). Longer migrations may increase mortality rates due to increased exposure to inclement weather and predators, and the increased difficulty of locating roosts (Constantine 1967). Mexican free-tailed bats likely use multiple stopover sites during migration. In our model, migratory routes only connected winter habitat to summer roosts. Unfortunately, due to limited data on the *specific* routes bats use when migrating between summer and winter habitats, we were unable to model stopover sites. As such, migratory edges represented the shortest distance between end points, not the actual course traveled.

To examine the entire population's dependence on each roost, we quantified the impact (i.e. population decline) of each roost's removal on the total summer population size (Rayfield et al. 2011; Taylor and Norris 2010; Urban et al. 2009). We simulated the removal of each roost with replacement from the network model; thus only one roost was removed at a time from the model. When removing a given roost from the model, the bats were not "killed," rather the individuals that would have migrated to the removed roost were allowed to disperse to other maternity roosts. Population declines for each roost were standardized on a scale from zero to ten, with zero indicating no decline and ten representing the greatest population decline. Wiederholt et al. (2013) contains more details on our network modeling approach.

Pest suppression ecosystem service attribute

We employed an avoided-cost approach originally used by Cleveland et al. (2006) to estimate the value of bat services in reducing crop damage and pesticide use on cotton. We used data from the López-Hoffman et al. (2014) assessment of cotton pest suppression across the southwestern U.S. and Mexico, which includes all cotton-producing areas near known major maternity roosts of Mexican free-tailed bats.

Estimating the avoided costs of crop damage involved the following steps: (a) estimating the number of bollworms (a major cotton pest) consumed nightly by individual bats, (b) determining the hectares of cotton fields within proximity to bat maternity roosts, which allowed us to estimate (c) the value of the crops that would have been damaged in the absence of bats.

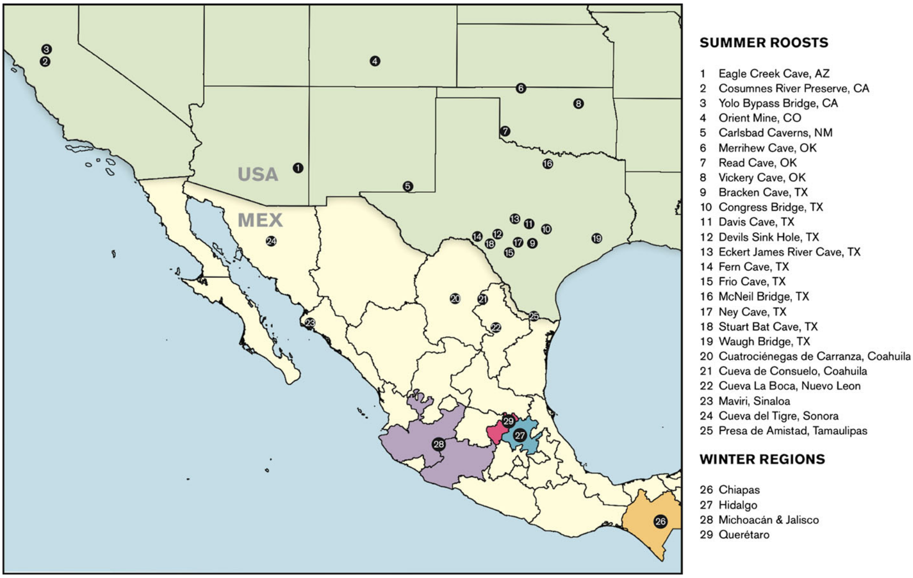

Fig. 1 Major Mexican free-tailed bat maternity roosts and overwintering regions

Conventional and molecular analyses show that moths comprise 30–60 % of the bats' diet and indicate that each reproductively active female bat can consume 5–10 female adult bollworms (*Helicoverpa zea*) per night during periods of peak bollworm infestation (Lee and McCracken 2005). Since bollworms also infest other crops in the area or migrate out of the region, we conservatively estimated that only 10–20 % of the female moths consumed each night (approximately 1.5 individuals per bat) would have dispersed into cotton and laid eggs (Cleveland et al. 2006). Due to high mortality rates during insect development (95–98 %), the nightly consumption of 1.5 adult female moths per bat would prevent five larvae from developing and damaging cotton crops (Cleveland et al. 2006).

We used data from the U.S. Department of Agriculture's National Agricultural Statistics Service (www.usda.nass.gov), the National Cotton Council (www.cotton.org), and the Mexican Department of Agriculture, S.A.G.A.R.P.A (http://www.siap.gob.mx/) on the number of cotton hectares planted per U.S. county or Mexican municipality. We estimated that, conservatively, the bats' nightly foraging distance from their roosts is 50 km (Williams et al. 1973).

To determine the value of reducing insecticide use, we calculated both the reduced private costs to farmers of applying insecticides, and the reduced cost to society of releasing fewer insecticides into the environment (Cornell University's Integrated Pest Management Program 2012; Kovach et al. 1992; Leach and Mumford 2008). Data on private costs of cotton insecticide applications from 1990 through 2008 were obtained from the Mississippi State University Department of Entomology and Plant Pathology's database on cotton losses due to insects (http://www.entomology.msstate.edu/resources/cottoncrop.asp) and S.A.G.A.R.P.A., the Mexican Department of Agriculture (http://www.siap.gob.mx/). We consider only the social costs of only those insecticides that specifically target bollworms (*Helicoverpa zea*) (Leach and Mumford 2008). We used data from Kovach et al. (1992) and from Cornell University's Integrated Pest Management

Program (2012) to estimate the environmental and toxicological impacts of particular cotton insecticides. We then used a pesticide environmental accounting tool (Leach and Mumford 2008) to assign a social-cost value in dollars for each insecticide according to the degree of impact. López-Hoffman et al. (2014) contains more details on our bat pest suppression evaluation. Pest suppression values per roost were standardized on a scale from zero to ten for the analysis, with ten being the highest pest suppression value.

Ecotourism ecosystem service attribute

We estimated the economic value of bat-related tourism for those maternity roosts that support bat viewing (Bagstad and Wiederholt 2013). In this study, we obtained annual visitation estimates through discussions with local resource managers. Although visitation occurs at some sites in Mexico, visitation data are unavailable for those caves (co-author RM, Universidad Nacional Autónoma de México, pers. comm.). We used a wildlife viewing model from the Benefit Transfer and Use Estimating Model Toolkit (Loomis et al. 2008). This model provides a meta-analysis of economic values for wildlife viewing, which we used to estimate consumer surplus for visitors to each site. We calculated the average daily consumer surplus (i.e. for eight hours) from wildlife viewing for each state where Mexican free-tailed bat viewing occurs. We then estimated each roost's distance from the nearest urban center. For roosts located within an urban area, we divided per-visitor consumer surplus by four, assuming the average visitor spends a total of two hours traveling to and engaging in bat viewing. For roosts beyond but less than two hours from an urban area, we assigned four hours of wildlife viewing value per visit, and for roosts greater than two hours from the nearest urban center, we assigned a full day's consumer surplus per visit (Bagstad and Wiederholt 2013). Ecotourism values per roost were standardized on a scale from zero to ten for the analysis, with ten indicating the highest ecotourism value.

Risk to maternity roosts attributes

We assessed two types of risk: (a) to the roost structure itself and (b) to the roost population (i.e. the individual bats residing in the roost). To assess both types of risk, we surveyed 35 bat biologists with expertise in Mexican free-tailed bat research in the region. Survey participants were given a list of 25 maternity roosts and asked to provide information for only those with which they had the most experience. The biologists were asked to score the risk of six different threats. We differentiated between risks to roost structure and risks to individuals because while protecting roost habitat may allay some threats, bats also face other direct threats while foraging outside the roost. The threats considered were development, disturbance (from authorized visitors), climate change, pollution, vandalism, and wind turbines. Respondents were asked to evaluate how these threats could affect the roost structure itself as well as the population of bats residing within the roost. Risk scores per roost were standardized on a scale from zero to ten, with zero representing the lowest risk and ten representing the highest risk.

We pre-tested the survey first with a focus group of five bat biologists. Participants were invited via email to take the survey online using DatStat Illume software. The survey remained open for five weeks. For each roost and each threat, we calculated the mean of participants' response scores. We gave equal weight to each participant's answers because they had been asked to provide information about only those maternity roosts for which they had significant experience. In the U.S., we surveyed biologists representing universities, non-governmental organizations and the Bureau of Land Management (BLM), U.S. Geological Survey (USGS), U.S. Forest Service (USFS), and state natural resource management agencies. Additionally, we surveyed Mexican biologists including researchers from the Universidad Nacional Autónoma de Mexico (UNAM), and the Instituto Politécnico Nacional (IPN). Overall, the bat biologists we surveyed had extensive experience working with bats (mean = 19.3 years) and with *Tadarida* species in particular (mean = 14.5 years).

Multi-attribute utility function

As described above, each maternity roost was given scores for five attributes: (1) biological importance, (2) pest suppression value, (3) ecotourism value, (4) risks to roost structure, and (5) risks to roost population. For each factor, the scores were standardized on a scale of zero to ten.

We developed four scenarios for weighting the attributes. The scenarios were designed to reflect the factors that resource managers and decision-makers might consider when prioritizing conservation actions (Table 1). The first scenario (equal weights scenario) contemplates a situation where a manager might equally value all factors (i.e. all attributes were given equal weights). The second scenario (biological importance scenario) considers a situation where a roost's contribution to the population viability is valued above all. In this case, the biological importance attribute received a value of one (1), and the two ecosystem service attributed received a weight of zero (0). Because continued population viability is a function of the risks faced by the roost structure and the population residing within the roost, we also gave each of the two roost-risk attributes a full weight of one (1). The third and fourth scenarios (pest suppression scenario and ecotourism scenario) prioritize the ecosystem service values that that bat roosts provide. In each of these scenarios, the corresponding ecosystem service attribute (pest suppression or ecotourism) was given a full weight of one (1). In addition, the associated risks with potential to lower service values were also given a weight of one (1). For example, because pest suppression services are a function of numbers of bats foraging each night, risks that could lower the population numbers or compromise the roosting structure were given full weight (see Table 1 for details).

The formula we used to determine each roost's score for each scenario was as follows:

$$U_i = \sum_{j=1}^{4} a_j v_{ij} \tag{1}$$

where U_i is the total score for roost *i*, v_{ij} is the score of roost *i* for attribute *j*, and a_j is the weight for factor *j* (Kangas et al. 2010).

We accommodated uncertainty in our multi-attribute utility analysis using Markov chain Monte Carlo methods calculated in OpenBUGS (Lunn et al. 2009). We calculated total scores (U) given uncertainty in the parameter weights (a) of our four scenarios. We allowed the weighting of attributes to vary according to beta distributions (Wilks 2006:102). In an iterative fashion, we drew weights from prior beta distributions with means μ of the distribution approximately matching the assigned weights previously described in Table 1 (i.e. weight for attribute *j* was $a_j = 1 \approx p/(p + q)$, where p and q are shape parameters and $q \ll 1$). We calculated posterior probabilities for the parameters estimated from 1,000,000 iterations of three sampling chains. We thinned the estimates by 10 (retaining every 10th draw) and removed the first 10,000 iterations.

Table 1 Mean weights applied to each factor for each of four scenarios

Factor	Equal weights	Biological importance	Pest suppression	Ecotourism
Pest suppression	1	0	1	0
Ecotourism	1	0	0	1
Population importance	1	1	0	0
Risk to roost structure	1	1	1	1
Risk to roost population	1	1	1	1

Bayesian approach to estimate missing risk scores

We use a Bayesian approach to address data gaps and uncertainty regarding parameter scores. The following maternity roosts were missing risk scores due to the respondents' lack of adequate experience with these roosts: Presa de Amistad in Tamaulipas, Mexico, Cuatrocienegas and Cueva del Consuelo in Coahuila, Mexico, Devil's Sinkhole, Fern Cave, Stuart Bat Cave, and Waugh Bridge in Texas, Merrihew Cave, Reed Cave, and Vickery Cave in Oklahoma, and Orient Mine in Colorado. As a group, there was no systematic difference between these roosts and the other roosts for which we had risk scores. The roosts for which data was missing covered a wide geographic range, were found in both countries, varied in size from 100,000 to 2 million individuals, represented a variety of structures (bridges, caves and mines), and were located in both urban and agricultural areas. Because there was no systematic bias between the roosts for which we did and did not have risk assessments, we believe a Bayesian approach to be a robust means of estimating the missing risk scores.

We used a Bayesian approach to estimate the risk scores for the roosts which lacked data based on the risk scores of the roosts for which we had data. Our Bayesian prior distributions were normal distributions described by the standard deviation and the mean of the observed risk scores. We calculated total scores (U) given both uncertainty in the parameter weights (a) of our four scenarios and missing data for risk scores (v). We calculated posterior probabilities for the parameters using the procedure described above.

Sensitivity analysis of ranking results to the attribute weights in the scenarios

We evaluated the sensitivity of the roost ranking results to the weighting schemes in the four different scenarios. In the first scenario, which emphasized biological importance, we assessed the sensitivity of the resultant roost rankings to the weights used for both risk factors. We did so by varying the risk weights from zero to one. For the third and fourth scenarios, which prioritized pest suppression and ecotourism, respectively, we assessed the sensitivity of the resultant roost rankings to the weight given to the population importance of the roost. We did so by varying the biological importance attribute from zero to one.

Sensitivity analysis of survey responses to risk

We tested the sensitivity of roost rankings to variability in the respondents' assessment of the risks posed to roosts. For each roost, we assessed the sensitivity of the result to the highest and lowest risk values reported across all respondents. Using the equal weights scenario, we tested high- and low-risk scores for both risk to the roost structure and risk to the bat population.

Results

Biological importance

Our results indicated that the southernmost summering areas are the most important maternity regions for maintaining the bat population (Table 2, Fig. 1; results discussed in detail in Wiederholt et al. 2013). Several maternity roosts in this area (Bracken Cave, Frio Cave, and Devil's Sink Hole Cave in Texas; Cueva La Boca in Nuevo Leon; and Cueva del Tigre in Sonora) had the greatest summer population sizes, and the removal of these large roosts from the network model resulted in the largest overall population declines (Table 2). The declines were not caused by bats being "killed" as the roosts were removed, because the individuals that would have resided in the removed roost were allowed to migrate to other maternity roosts. Rather, removal of these large southern roosts caused individuals to migrate greater distances, which lowered survival, and increased the negative effects of density-dependence in the roosts that subsequently had increased population sizes. Wiederholt et al. (2013) tested the robustness of these results to the migration survival parameter and found that when migration survival was increased, removing these five roosts still caused the largest population declines.

Pest suppression ecosystem services value

The roosts with the largest annual value pest suppression values were Bracken Cave, Texas ($3.42 million), followed by Frio Cave, Texas ($2.42 million). The highest annual values per roost (> $1 million) were all found in Texas (Table 2). The biological importance score of the roost was significantly correlated with the pest suppression value score ($r = 0.67$, p value <0.01).

Ecotourism ecosystem services value

The total annual ecotourism value of 11 viewing sites of Mexican free-tailed bats in the southwestern U.S. was conservatively valued at $6.51 million (Bagstad and Wiederholt 2013). The sites with the highest ecotourism value included the Congress Avenue Bridge, in Austin, Texas, and the Waugh Drive Bridge, in Houston—easily accessible urban areas with established interpretive programs—as well as a more remote national park, Carlsbad Caverns (Table 2). However, population importance score of the roost was unrelated to the ecotourism value score ($r = -0.05$, p value $= 0.82$).

Risks to maternity roosts

The results of the Markov chain Monte Carlo analysis indicated that the highest risks to roost structures were associated with Maviri Cave in Sinaloa, Mexico, followed by Davis and Frio Caves in Texas (Table 2). The roost structures at Frio and Davis Caves are threatened by vandalism, while Maviri Cave is threatened by roost disturbance (from authorized visitors). Our results indicated that the highest risks to bat populations were to

Table 2 Factor scores per Mexican free-tailed bat maternity roosts

Bat roosts	% Population loss from roost removal (%)	Scores[a] for biological importance	Scores[a] for roost structure risk	Scores[a] for bat population risk	Annual pest suppression value	Scores[a] for pest suppression value	Annual ecotourism value	Scores[a] for ecotourism value
Bracken Cave	−10.14	10.000	4.048	10.000	$3,420,256	10.000	$102,320	0.294
Carlsbad Caverns	−0.79	0.650	1.667	4.571	$27,500	0.080	$3,477,072	10.000
Congress Avenue Bridge	−3.51	3.374	3.810	8.286	$2,239,857	6.549	$1,772,694	5.098
Cosumnes River Preserve	−0.14	0.000	2.143	5.571	$7,774	0.023	$2,931	0.008
Cuatrociénegas de Carranza	−2.34	2.197	2.999	4.897	$0	0.000	$0	0.000
Cueva de Consuelo	−2.02	1.876	2.998	4.897	$0	0.000	$0	0.000
Cueva del Tigre	−4.79	4.652	2.857	6.857	$0	0.000	$0	0.000
Cueva La Boca	−5.71	5.564	1.830	1.656	$0	0.000	$0	0.000
Davis Cave	−1.00	0.859	6.429	8.143	$61,981	0.181	$0	0.000
Devil's Sink Hole	−5.17	5.031	3.003	4.904	$0	0.000	$127,900	0.368
Eagle Creek Cave	−0.69	0.554	2.857	3.143	$0	0.000	$0	0.000
Eckert James River Cave	−3.28	3.140	0.714	3.000	$317,973	0.930	$69,066	0.199
Fern Cave	−0.59	0.452	3.000	4.899	$0	0.000	$0	0.000
Frio Cave	−5.68	5.539	4.643	7.500	$2,421,653	7.080	$142,481	0.410
Maviri	−0.23	0.092	10.000	2.571	$0	0.000	$0	0.000
McNeil Bridge	−1.39	1.254	1.429	6.000	$81,077	0.237	$0	0.000
Merrihew Cave	−0.23	0.092	3.005	4.899	$5,605	0.016	$0	0.000
Ney Cave	−0.96	0.818	0.000	0.000	$1,245,623	3.642	$0	0.000
Orient Mine	−0.23	0.092	2.999	4.895	$0	0.000	$82,782	0.238
Presa de Amistad	−2.33	2.194	3.000	4.903	$788,847	2.306	$0	0.000
Reed Cave	−1.20	1.063	3.000	4.905	$524,893	1.535	$0	0.000

Table 2 continued

Bat roosts	% Population loss from roost removal (%)	Scores[a] for biological importance	Scores[a] for roost structure risk	Scores[a] for bat population risk	Annual pest suppression value	Scores[a] for pest suppression value	Annual ecotourism value	Scores[a] for ecotourism value
Stuart Bat Cave	−1.20	1.063	3.003	4.897	$120,438	0.352	$26,808	0.077
Vickery Cave	−2.47	2.331	3.002	4.902	$205,552	0.601	$0	0.000
Waugh Bridge	−0.59	0.452	2.999	4.902	$155,184	0.454	$255,800	0.736
Yolo Bypass Bridge	−0.58	0.443	0.000	1.714	$48,078	0.141	$54,960	0.158

[a] Standardized scores for equal weighting scenario

those populations residing in Bracken Cave, Congress Avenue Bridge, and Davis Cave (Table 2). Our survey participants indicated concern that Bracken Cave's population may be threatened by nearby housing development, wind turbines, and pollution, while bats in the Congress Avenue Bridge and Davis Cave are thought to be threatened by climate change, wind turbines, pollution, and vandalism. Maternity roosts whose populations were more at risk were also more likely to be important for the population ($r = 0.46$, p value $= 0.02$). This indicates that larger roosts were more likely to have threats to their population but not to the roost structure itself ($r = 0.34$, p value $= 0.87$).

Multi-attribute utility function

In the equal-weight scenario of the multi-attribute utility function, Bracken Cave, Congress Avenue Bridge, Frio Cave, and Carlsbad Caverns had the highest overall scores (15.5 to 32.5; Table 3; Fig. 2). In the biological importance scenario (where higher weights were given to the biological importance of the maternity roosts and less to the ecosystem service provision), Bracken Cave, Frio Cave, and Congress Avenue Bridge were also the top three ranked maternity roosts, although the fourth ranked roost was Davis Cave, reflecting its biological importance. The pest suppression scenario maintained the same ranking for the top four maternity roosts as the biological importance scenario. This is because roost population size was correlated with the pest suppression ($r = 0.67$, p value < 0.001). In the ecotourism scenario, the top ranked maternity roosts were, in order, Congress Avenue Bridge, Carlsbad Caverns, Davis Cave, and Bracken Cave. This indicates that the ecotourism values of the Congress Avenue Bridge and Carlsbad Caverns were important components of their overall scores, while the pest suppression services of Frio and Bracken Caves were more significant components of their scores.

There were several unexpected rankings. For example, Davis Cave ranked relatively highly in the ecotourism scenario, and Maviri highly in the pest suppression scenario despite the fact that they do not provide high ecotourism or pest suppression values; this counter-intuitive result arises from their high scores for certain risk attributes that were considered in the scenario (Table 2). In most cases, however, roosts with no ecosystem service values were ranked low in these scenarios. In the ecotourism scenario, 11 out of 14 roosts with no ecotourism values were placed in the lowest 14 ranked roosts, while in the pest suppression scenario seven out of nine roosts with no pest-suppression values were placed in the lowest 13 ranked roosts. Even though five roosts composed the four highest ranked roosts in each scenario, their individual rankings varied between scenarios, as did the rankings of other roosts with lower scores. In sum, our results lend support for our hypothesis that preferentially valuing different attributes (e.g. biological importance over ecosystem service value) will change the roost rankings.

Sensitivity analysis of weights

Our sensitivity analysis revealed that altering the weights of the risk factors in the biological importance scenario did not alter the overall rankings for most maternity roosts (Appendix S1, Table S1). Altering the weight of biological importance attribute in the pest suppression scenario and ecotourism scenario lowered the rankings of the several roosts (Appendix S1, Table S2–3). Some of these maternity roosts had high ecosystem service values, and placing greater weight on their biological importance lowered their overall ranking. Thus, the rankings are sensitive to the weight placed on the biological importance of the roost. However, our scenarios either excluded this factor or gave it full weight (1),

Table 3 Habitat ranking scores for Mexican free-tailed bat roosts

	Total equally weighted scores	Total[a] weighted scores—biological importance scenario	Total[a] weighted scores—pest suppression scenario	Total[a] weighted scores—ecotourism scenario
Weights				
Risks to roost	1	1	1	1
Risks to bat population	1	1	1	1
Pest suppression value	1	0	1	0
Tourism value	1	0	0	1
Bio. importance	1	1	0	0
Bat roosts				
Bracken Cave	32.50	23.81	23.81	14.20
Carlsbad Caverns	15.47	6.82	6.26	16.08
Congress Avenue Bridge	25.22	15.32	18.46	17.02
Cosumnes River Preserve	7.66	7.64	7.66	7.65
Cuatrociénegas de Carranza	9.99	10.07	7.89	7.89
Cueva de Consuelo	9.67	9.74	7.88	7.88
Cueva del Tigre	14.22	14.22	9.62	9.62
Cueva La Boca	8.96	8.96	3.45	3.45
Davis Cave	15.43	15.28	14.61	14.43
Devil's Sink Hole	13.13	12.86	7.87	8.24
Eagle Creek Cave	6.49	6.49	5.94	5.94
Eckert James River Cave	7.74	6.79	4.60	3.87
Fern Cave	8.27	8.33	7.88	7.88
Frio Cave	23.83	17.51	19.03	12.43
Maviri	12.54	12.54	12.45	12.45
McNeil Bridge	8.80	8.60	7.59	7.36
Merrihew Cave	7.93	7.96	7.89	7.87

Table 3 continued

	Total equally weighted scores	Total[a] weighted scores—biological importance scenario	Total[a] weighted scores—pest suppression scenario	Total[a] weighted scores—ecotourism scenario
Ney Cave	3.88	0.81	3.61	0.00
Orient Mine	8.11	7.96	7.87	8.11
Presa de Amistad	11.94	10.06	10.18	7.89
Reed Cave	10.17	8.93	9.39	7.87
Stuart Bat Cave	9.24	8.93	8.22	7.95
Vickery Cave	10.64	10.19	8.48	7.89
Waugh Bridge	9.28	8.32	8.32	8.60
Yolo Bypass Bridge	2.39	2.14	1.84	1.85

[a] The different weighting scenarios represent a biological importance scenario, where the population importance of the roost was emphasized, the pest suppression scenario, where the provisioning of bat pest suppression services was emphasized, or the ecotourism scenario, where the provisioning of bat ecotourism services was emphasized

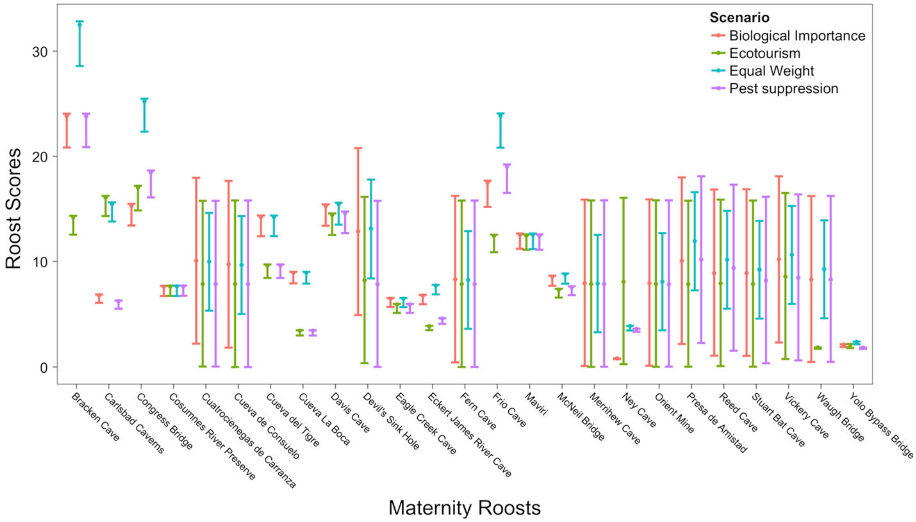

Fig. 2 Overall roost scores for the equal weights scenarios, the biological importance scenario, the pest suppression value scenario, and the ecotourism value scenario

which should reduce the uncertainty associated with this factor. Also, the rankings of the top four maternity roosts were robust to the alterations in the weights.

Sensitivity analysis of survey responses to risk

The sensitivity analysis revealed that altering the survey responses did not greatly alter the roost rankings (Appendix S1, Table S4). Altering the roost structure risk scores to the lowest and highest individual responses shifted the rankings of four and six roosts, respectively. Altering the bat population risk scores to the lowest individual responses shifted the rankings for five roosts, while altering the risk scores to the highest individual responses shifted the rankings of seven roosts.

Discussion

We used a multi-attribute utility function to determine the most critical maternity roosts to protect to maintain the population viability and ecosystem services of Mexican free-tailed bats. Our multi-attribute utility function tool can help prioritize management actions under different conservation scenarios and can be easily adapted to other species and to include additional factors. The results support our hypothesis that preferentially valuing different attributes (e.g. population importance over ecosystem service value) will change the prioritization rankings for roost protection. For example, the results from the weighted scenarios reveal that four out of the following five maternity roosts were ranked highly across all scenarios: Bracken Cave, Congress Avenue Bridge, Frio Cave, and Davis Cave in Texas; Carlsbad Caverns in New Mexico; and Cueva del Tigre in Sonora, Mexico (Table 3, Fig. 2). The preservation of these five roosts would help protect over >10.2 million individuals. However, the individual ranking of these top five roosts varied between scenarios. Beyond these top five roosts, the roost rankings varied greatly between scenarios.

Maternity roosts with high biological importance are more likely to provide high levels of pest suppression and have greater risks posed to their populations. It would be worthwhile for conservation organizations to work with landowners to protect several roosts that are not formally protected, such as Davis and Frio Caves, which survey participants indicated were potentially threatened by vandalism or unauthorized visitors. Even protected roosts face threats. For example, a housing development (composed of 3,800 units, personal comm. Merlin Tuttle) is planned to be sited less than 400 m from Bracken Cave, and there is concern that vandalism and roost disturbance will be inevitable given the proximity of such a large number of residents.

The lack of independence within the scientific expert group we surveyed and our missing risk scores may be a shortcoming of our work. To obtain a reasonable understanding of Mexican free-tailed bat roosts, we conferred with the most prominent members of a very small community familiar with the species. Small science communities can perpetuate complex forms of bias (Baddeley et al. 2004), resulting in a lack of independence (Burgman 2005). It is extremely difficult to guard against these community-wide biases (Kuhn 2012). Finding experts who are independent of one another and who have not worked with or benefited from the science of others within small expert communities is nearly impossible (Doswald et al. 2007). We believe, however, that our assessment of expert opinion provides the best insight possible given the lack of pertinent data on roost risks. We also had missing risk score data for several roosts; we used our Bayesian analysis to obtain estimates of these risks. However, these roosts did not differ systemically in terms of location or size from other roosts for which survey participants provided risk score data. Finally, our sensitivity analysis of survey responses to risk also indicated that the roost rankings were not greatly altered by variation in risk scores. Our Bayesian approach lends itself to updating of roost rankings should new information become available; coupled with the sensitivity analyses, our results point to areas where research would benefit the most from reducing uncertainty in the decision process.

Comprehensive, region-wide management strategies for bats are critical, especially in the face of emerging, large-scale risks posed to their populations (Vanoye-Eligio 2012). For instance, Vanoye-Eligio (2012) found multiple risks posed to bat roosts across northeast Mexico; to ameliorate bat conservation efforts, they suggested several strategies including general public, environmental education programs focused on bats, and measures to prevent vandalism and unauthorized visitors in roosts. Our results reinforce this idea that, although roost protection is an important conservation measure, additional management actions are needed. Even though several of the roosts we identified as priorities for conservation do enjoy formal protection, the bat populations residing in those roosts still have significant threats. Mexican free-tailed bats are exposed to a variety of factors outside these roosts both during migration from overwintering sites in central and southern Mexico, and during their nightly foraging activities. For instance, climate change and wind turbines are emerging threats to bats. The U.S.-Mexico border region is predicted to become warmer and drier, with the potential for increased drought frequency (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). In addition, wind turbines are thought to cause large numbers of fatalities to migrating bats, including Mexican free-tailed bats (Arnett et al. 2008; Cryan and Barclay 2009; Miller 2008; Piorkowski and O'Connell

2010). The deployment of wind turbines for energy production has been increasing in North America and is expected to grow in the future. In 2011, Texas, which contains many important maternity roosts, had the highest production of wind energy of any state in the U.S. according to the U.S. Energy Information Administrations (2012). We note, however, that publically available data on bat fatalities from that state are lacking (Arnett et al. 2008). To effectively tackle such large-scale risks, bat conservation and management planning will undoubtedly benefit from the involvement of a wide variety of stakeholders working across administrative and political boundaries.

In summary, we developed a framework that ranks different habitats to inform management decisions that can be easily adapted to other species. We found that placing higher values on different roost attributes (e.g. biological importance over ecosystem service value) can change the rankings of roosts, although five maternity roosts were among the four highest-ranked roosts across all scenarios. This indicates that the values we place on various conservation objectives can alter which habitats are determined to be optimal for preservation. Conservation strategies focused on landscape-level protection incorporating diverse groups of stakeholders are needed. We suggest that conservation efforts be focused on protecting the most highly ranked maternity roosts while also addressing region-wide factors that may threaten bat populations.

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