

# The importance of natural habitats to Brazilian free-tailed bats in intensive agricultural landscapes in the Winter Garden region of Texas, United States



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## ARTICLE INFO

### Article history:

Received 8 September 2014

Received in revised form 17 May 2015

Accepted 24 May 2015

### Keywords:

Conservation of threatened species

Land use change

Ecosystem services

Landscape management

Agricultural systems

Bats

## ABSTRACT

The conversion of natural lands to agriculture is a leading cause of the worldwide loss of biodiversity. In particular, cropland monocultures alter insect abundance and diversity compared to adjacent natural habitats. While agricultural lands can provide large numbers of insect pests as prey items to predators such as bats, insect pest population size vary greatly throughout growing seasons. This study assesses the importance of land use and corn earworm moth availability as spatial and temporal drivers of bat activity. We quantified spatial variation in land use patterns at fifteen sites located within the Winter Garden region in south central Texas and used bat detectors and insect pheromone traps to monitor nightly bat activity and corn earworm moth abundance across the landscape and throughout most of the year. Our temporal analyses show that bat activity was positively correlated with moth abundance, but only early in the growing season when moth abundance is at its peak. The key result from this study is a positive relationship between bat activity and natural habitat cover during late summer months, corresponding to periods of low moth abundance and a peak in bat activity. During the late summer period, bats were more active at sites containing a larger percentage of natural habitats than those containing a larger percentage of agricultural land. Our results strongly suggest that intensive agricultural practices create systems providing bats with inconsistent resource supply, but the persistence of natural habitats provides consistency in food supply through time. Taken together, these findings illustrate the importance of protecting and restoring natural habitats for the conservation for bats and the pest-suppression services they provide in agricultural ecosystems.

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## 1. Introduction

Agricultural landscapes exist as mosaics of monocultural croplands and remaining fragments of variously intact natural habitat. The conversion of natural habitats into agricultural land alters the abundance and interactions of native species, and land conversion,

largely for agriculture, is recognized as the most important threat to biodiversity worldwide (Dale et al., 1994; Myers et al., 2000; Foley et al., 2005; Morton et al., 2006). Bats are predators of insects in agricultural landscapes and are known to contribute valuable economic services through consumption of insect pests (Kunz et al., 2011). However, many studies to date on bat habitat use within agricultural landscapes demonstrate that bats prefer remaining woodland, corridor and riparian habitats and avoid arable and agricultural lands (e.g. Walsh and Harris, 1996; Vaughan et al., 1997; Razgour et al., 2011). Studies also indicate that the abundance, diversity and activity of bats decline in parallel with the intensity of agricultural development (Russo and Jones, 2003; Wickramasinghe et al., 2003).

Apart from their intrinsic conservation value, the loss of bats is of concern because they provide several crucial

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ecosystem services worldwide, including pollination (Bumrungsri et al., 2008; Cox et al., 1991) and seed dispersal (Cox et al., 1991; Moran et al., 2009). Insectivorous bats can act as biological control agents and significantly reduce populations of agricultural insect pests (Cleveland et al., 2006; Federico et al., 2008).

Agricultural habitats alter the insect resource base available to bats. Reductions in plant diversity as occurs in agricultural landscapes is associated with a parallel decrease in insect diversity (Crutsinger et al., 2006; Haddad et al., 2009; Genung et al., 2010), and prey availability (Krebs et al., 1999; Benton et al., 2003; Racey and Entwistle, 2003; Tsitsilas et al., 2006). In addition, observations that bat activity and insect abundance are significantly higher on organic farms than on conventional farms (Wickramasinghe et al., 2004, 2003), provides further support for the idea that preservation of natural and semi-natural habitats within agricultural landscapes is important for the conservation of bat populations. Further, non-crop habitat becomes even more crucial in periods of decreased quality of crop habitat; i.e. when crops are in senescence and no longer provide an ample insect source (Wickramasinghe et al., 2004).

In what is naturally a semi-arid ecosystem, the irrigated croplands of the Winter Garden agricultural region in southwest Texas annually produce billions of noctuid moths (*Lepidoptera: Noctuidae*) and other crop pests (Wolf et al., 1990; Westbrook et al., 1997). These insects provide valuable resources to the large numbers of Brazilian free-tailed bats (*Tadarida brasiliensis*) that inhabit the region (Kunz et al., 2011; Lee and McCracken, 2002, 2005; McWilliams, 2005). The insects infesting the region's crops, including adult corn earworms (*Helicoverpa zea*), fall armyworms (*Spodoptera frugiperda*) and other members of the noctuid pest clade are among the most abundant pests in the region and an important part of the bats' diet (Lee and McCracken, 2005; McCracken et al., 2012). Corn earworm are among the world's most destructive agricultural pests (King and Rogers, 1986; Williams, 2014) and by consuming them, bats perform valuable ecosystem services such as decreasing damage to crops and reducing the need for pesticide use (Cleveland et al., 2006; Federico et al., 2008; Lopez-Hoffman et al., 2014).

Populations of Brazilian free-tailed bats roosting in the caves of south-central Texas may be the largest, densest aggregations of mammals on earth (McCracken, 2003), and the activity levels of foraging bats in the Winter Garden region are among the highest recorded in the literature (McCracken et al., 2008). Because of the substantial resource base that is needed to sustain these large bat populations (Kunz et al., 2011), and because croplands provide a breeding ground for insect pests (Wolf et al., 1990; Westbrook et al., 1997), it has been speculated that these huge bat populations may exist because of the insects made available by intensive agriculture (Russell et al., 2011). However, this hypothesis remains largely untested.

Land development could affect bat populations directly by altering habitats and indirectly through effects on insect prey populations. Some studies suggest that bats avoid agricultural lands. Specifically, agricultural and human developments have the greatest impacts on bats with lower wing-loading and more specialized habitat requirements. Woodland and riparian species are most affected (Walsh and Harris, 1996; Wickramasinghe et al., 2004; Duchamp and Swihart, 2008; Razgour et al., 2011), whereas more generalist species with typically higher wing-loading appear to be less at risk from anthropogenic impacts, including agricultural intensification (Duchamp and Swihart, 2008). Species with higher wing-loading typically forage in uncluttered habitats above canopy and exploit a higher diversity of insect prey than species with lower wing-loading. These traits define Brazilian free-tailed bats which

have among the most diverse diets reported for any insectivorous bat species (Lee and McCracken, 2002, 2005) and are known to forage from ground level to several 1000 m above the ground where they opportunistically exploit swarms of insects and localized insect emergences (McCracken et al., 2008). When assessing extinction risks for bats, studies concur that species with the constellation of traits possessed by Brazilian free-tailed bats are less vulnerable to human impacts (Duchamp and Swihart, 2008).

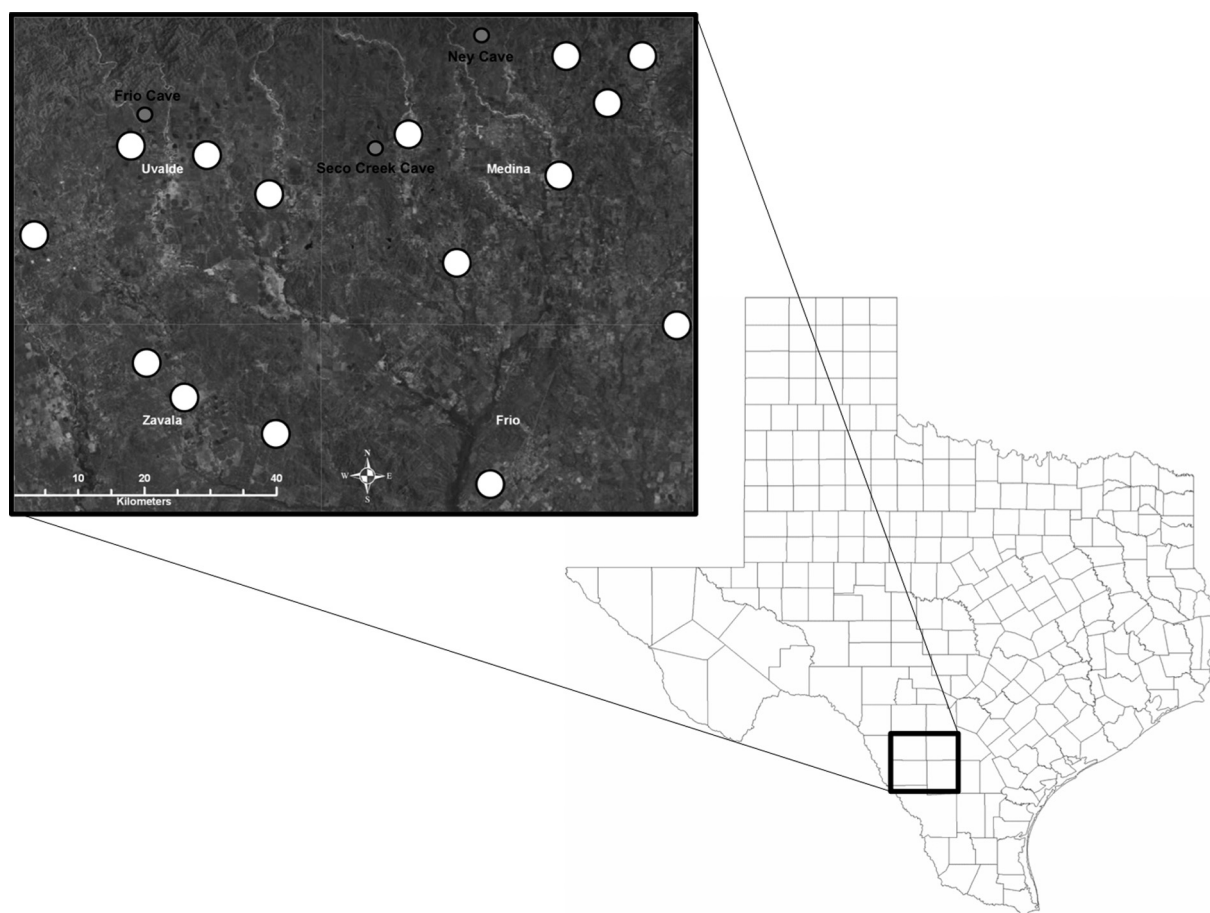
We tested the hypothesis that the abundance of insect pests was a better predictor of spatial variation in Brazilian free-tailed bats' foraging activity than land use type. First, we examined how land-use type relates to bat activity by relating the proportion of man-altered versus natural habitats to spatial variation in the number of recorded bat calls across sites. Then, we examined the relationship between the abundance of agricultural insect pests (adult moths) detected in pheromone traps and the number of bat calls. Finally, we monitored bats and insects pests over a period of nine months to assess temporal variability in those spatial associations. Based on previous studies (McCracken et al., 2012), we predicted that insect pests would be the main predictor of bat activity patterns across sites and throughout the study period.

## 2. Methods

### 2.1. Study area

We monitored bat activity nightly from March until November 2007 at fifteen sites within the Winter Garden agricultural region in south central Texas. At least 8 km, usually more, separated monitoring sites. The four-county study region (Uvalde, Frio, Zavala and Medina) covers approximately 2500 km<sup>2</sup> (Fig. 1) with land use dominated by agriculture and ranching. Whereas, croplands are cultivated annually for corn, cotton and sorghum (USDA-NASS, 2002), what we term here as "natural habitats" are not cultivated and include native oak trees, brush, forbs and grasses, as well as invasives (Stevens and Richmond, 1976). The presence of ranches and small towns result in interspersed buildings and light sources in and around the study sites. Within the study region, there are three known major bat roosts, Frio Cave, Ney Cave, and Seco Creek Bridge (Fig. 1). The colonies of Brazilian free-tailed bats in Frio and Ney Caves are among the largest in North America (McCracken, 2003; Cleveland et al., 2006). Although historical counts estimated peak summer populations to be around ten million bats in each of these caves (Davis et al., 1962), more recent estimates show present colony sizes to be approximately one million bats per cave (Betke et al., 2008). Colony size at Seco Creek Bridge is estimated to be around 250,000 bats (Kunz, personal communication). Although other species of bats forage over this landscape, Brazilian free-tailed bats are by far the most abundant species, and earlier analyses of echolocation call characteristics showed that the calls of Brazilian free-tailed bats comprise >95% of bat calls recorded in the vicinity at ground level (Gillam and McCracken, 2007).

Monitoring sites were located 5–100 km from the three major bat roosts in the region and within the over 100 km nightly foraging range of the Brazilian free-tailed bats roosting at one or more of these sites (Best and Geluso, 2003; G.F. McCracken, unpublished). To assess the effects of habitat type on bat activity, sites were selected to encompass surrounding vegetation ranging from full cropland to full natural habitat. Sites also were selected based on distance to the roosts to ensure a range of distances that include monitoring sites both near and far from the three major bat roosts (Best and Geluso, 2003).



**Fig. 1.** Study area in the Winter Garden region of Texas, which includes Uvalde, Frio, Zavala, and Medina counties. White dots indicate the fifteen monitoring sites. Grey dots indicate the location of three large Brazilian free-tailed bat colonies: Frio Cave, Ney Cave, and Seco Creek Bridge.

## 2.2. Monitoring bat activity

Foraging activity was assessed using a single broadband Anabat II ultrasonic bat detector (Titely Electronics, Ballina, New South Wales, Australia) placed at the center of each monitoring site. These ultrasonic detectors transform the echolocation signals of bats into audible frequencies (Fenton, 1988), and their use has become increasingly common for surveying bat habitat use (e.g. Vaughan et al., 1997; Lee and McCracken, 2002; Rydell et al., 2002; Duchamp and Swihart, 2008; Razgour et al., 2011). Bat detectors are especially valuable for the detection and identification of bats that fly above canopy, such as the Brazilian free-tailed bat (Corben and Fellers, 2001), which can be missed completely in capture studies (O'Farrell and Gannon, 1999).

We recorded echolocation calls nightly at each of the fifteen sites, with all detectors programmed to record simultaneously for four hours each night, beginning at sundown (i.e. between 17:00 and 20:00 h depending on time of year). This satisfies the recommended three-hour time minimum and includes the peak activity time for bats (Milne et al., 2004). Using an omnidirectional ultrasonic speaker broadcasting previously recorded echolocation calls at 100 dB (Avisoft 60401, Avisoft Bioacoustics, Berlin, Germany), we estimated the average detection range of Brazilian free-tailed bat calls at  $16.0 \pm 1.8$  m. We quantified bat activity using the AnaLookW software (version 3.3q, Titely Electronics) with a custom-designed filter that recognized characteristics specific to the bats' echolocation calls. The AnaLookW software outputs include (i) the number of recorded files (i.e. number of fifteen-second segments during a single night that contained at

least one bat call), and (ii) the total number of bat calls counted during a night of monitoring. Both of these measures have been employed in previous studies using Anabat detectors to measure activity of insectivorous bats (Britzke et al., 1999; Tibbels and Kurta, 2003). Numbers of calls are a measure of bats searching for food and have been demonstrated to increase in an area with local foraging success (Gillam, 2007).

## 2.3. Quantifying proportion of landscape cover

We used spatial analysis techniques in a Geographic Information Systems (GIS) to determine the percentage of different habitat types around each of the fifteen monitoring sites. We geo-referenced seven habitat types (crop types: (1) corn, (2) cotton, (3) sorghum, (4) other crop; (5) natural habitat; (6) water bodies; and (7) buildings) by ground-truthing the corners and edges of each habitat type within a 0.5-km radius of each site using a hand-held Global Positioning System (GPS). Using the ArcGIS program (ESRI 2006), we then defined a 0.5-km radius circular buffer area around each of the fifteen study sites, within which we determined the proportion of each of the seven habitat types (see Appendices A–C).

Natural habitat comprised 10–100% of the habitat within the 0.5 km radius around all monitoring sites, with an average of about 40%, (Appendix A). Sites dominated by natural habitat are Batesville north, Batesville east, Devine, Quihi, Uvalde west, and Yancey. During the 2007 growing season, sorghum was the dominant crop around the sites (Appendix B). Corn and cotton also were prevalent with the areas of corn exceeding those of cotton. Other

crops in the region, of lesser and varied coverage, included wheat, onions, watermelon, peanuts, and potatoes. Most of these crops are not known to be significant host plants of *H. zea* and were not examined individually.

Areas containing buildings and other man-made structures made up less than 1% of the area around all sites. Bodies of water, including lakes, ponds, watering holes, and large streams comprised approximately 1.5% of the area around the sites.

#### 2.4. Quantifying moth abundance

We estimated the abundance of *H. zea* moths at each site using Hartstack cone type pheromone traps (Westbrook et al., 1997; Parajulee et al., 1998) baited with a Zealure sex pheromone (Hercon Environmental, Emigsville, PA). These traps have an attraction range of about 20 ha or 0.2 km<sup>2</sup> (Schneider, 1999). Because the pheromone only attracts male moths searching for mates, they underestimate populations that are emerging and dispersing long distances (Raulston et al., 1990). We installed one pheromone trap within 3 m of each bat detector. Traps were emptied and counted once a week at each site throughout the study, from March until October 2007.

#### 2.5. Statistical analysis

To standardize the temporal scale of the different variables, we summarized all data into a weekly format. Because pairwise correlation (using Pearson's coefficient) between weekly bat file (i.e. number of call sequences) and weekly bat call (i.e. number of calls) data showed the two to be highly correlated ( $r = 0.85$ ), we use only the weekly bat file data for our analyses to assess bat activity. Additionally, we log-transformed both bat activity and moth counts to achieve normality and reduce heteroscedasticity (referred to as bat activity and moth counts).

##### 2.5.1. Determinants of spatial variation in bat activity

We estimated bat activity by month (March–November 2007) for each site by summing nightly counts of bat files and then calculating a monthly average. Previous studies have used linear models to establish a functional relationship between bat activity and habitat variables (Walsh and Harris, 1996; Duchamp and Swihart, 2008). Here, first ran a stepwise regression model to reduce the number of variables to be included in our global model relating spatial variation in bat calls to moth abundance and the proportion of landcover for several landcover types (Ganas and Robbins, 2005). Because spatial variation in bat calls might be influenced by proximity to large roosts, we further added a variable representing the distance of each study site from the nearest bat roost in the stepwise regression. Using a forward variable selection procedure and minimum BIC as a stopping rule, the proportion of landscape representing natural habitat, water bodies and uncharacterized crops were retained (BIC = 1239.57).

Our global model was thus a linear mixed model including these three environmental variables and month as fixed factors, and sample location as a random factor. We added month of the year as fixed factor in the global model because bat calls vary greatly through time. We added the sample location as a random factor (using REML to estimate parameters) in the model to account for the non-independence of the repeated observations. Because the proportion of natural habitats was significant in the global model and a variable of particular interest, we built a second mixed model aiming more specifically at testing the time-dependency of the relationship between bat activity and the proportion of natural habitats. As such, we implemented a model with proportion of natural habitat, month of the year and the interaction of these variables as fixed factors. Sample location was again

included as a random factor in this model. All analyses were performed in JMP (JMP®, Version 11. SAS Institute Inc., Cary, NC, 2013).

##### 2.5.2. Bat activity and moth abundance through time

To assess whether bat activity tracks moth abundance through time, we used a pairwise correlation testing the correlation (using Pearson's coefficient) between bat activity and moth counts across the entire sampling period. To test whether temporal estimates of bat activity and moth abundance co-vary, we calculated the mean of bat activity and moth counts across all of the sampled sites, and for each week. Since moths are most abundant in the system during the early part of the season (early March through late May), we ran an additional pairwise correlation to test for a co-variance between weekly bat activity and moth counts during this time of high moth availability.

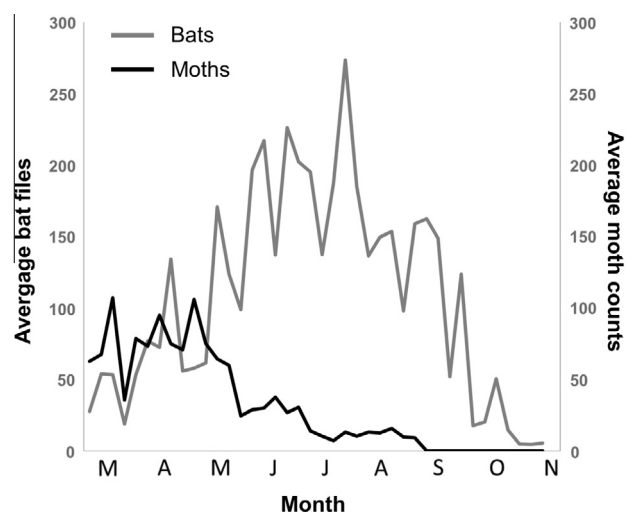
### 3. Results

#### 3.1. Bat activity

We analyzed a total of 9552 h of recordings during 243 nights from the fifteen monitoring sites. The data include a total of 2 914 172 calls attributed to Brazilian free-tailed bats with a range of 20–129 056 calls per week (mean  $\pm$  SE of  $1376.91 \pm 139.46$  and median of 471.02). These calls were collected in a total of 278 906 files with a range of 9–7377 files per week (mean  $\pm$  SE of  $131.68 \pm 9.35$  and median of 51.2). Bat activity (calls per nightly recording session per site) was relatively low in March with a mean bat activity of  $49.37 \pm 10.40$ , increasing to a peak in August with a mean bat activity of  $195.31 \pm 32.28$ , and steadily decreasing through November with a mean bat activity of  $18.57 \pm 4.79$  (Fig. 2).

#### 3.2. Moth abundance

A total of 99,107 moths, ranging from 0 to 1583 moths per week per site, were captured during the study (mean  $\pm$  SE of  $34.73 \pm 2.41$



**Fig. 2.** Weekly averages of bat activity (number of Anabat files; grey line) and moth abundance (black line) averaged across all sites from March through November 2007. Data show an increase to a peak in bat activity around mid to late summer, corresponding to the time when juvenile bats begin to forage independently. A decrease in activity is then seen as the bats migrate out of the region. Moth captures are high during the late-spring into early-summer, corresponding to the times moths migrate into the region and emerge from corn crops. Local moth captures drop as the moths migrate northward and the region sees a shift from corn to cotton crops.

**Table 1**  
Tests of fixed effects on bat activity (i.e. average number of bat files).

Model	Source	Num DF	Den DF	F	P
Global	Month	7	75.15	1.21	0.310
	Prop. natural habitat	1	10.16	12.64	0.005*
	Prop. water	1	10.53	5.81	0.036*
	Prop. other	1	7.67	3.64	0.094
Time-dependent	Month	1	11.58	3.60	0.083
	Prop. natural habitat	7	68.45	1.60	0.151
	Month × prop. natural habitat	7	69.70	2.92	0.010*
	habitat				

\* Indicate values that are significant at  $P < 0.05$ .

and a median of 19.36). Moth abundances fluctuated but were highest from March through May. Moth numbers dropped beginning in July and remained low for the remainder of the sampling period (Fig. 2).

### 3.3. Relationship between bat activity and landscape cover

Our global model ( $R^2 = 0.29$ , adjusted  $R^2 = 0.21$ ,  $P < 0.0001$ ) showed that only the proportion of natural habitats and water bodies surrounding our study sites were significant predictors of spatial variation in bat activity (Tables 1 and 2). All other habitat features, as well as month and distance from the roost were not significant.

Our second model ( $R^2 = 0.46$ , adjusted  $R^2 = 0.36$ ,  $P < 0.0001$ ) aimed to test whether the relationship between bat activity and proportion of natural habitat was time-dependent (Tables 1 and 2). The proportion of habitat cover by month interaction term was significant (Table 1), suggesting that the relationship between bat activity and proportion of natural habitat is indeed time-dependent. Specifically, this relationship was significant only for the months of July ( $t_{ratio} = 2.90$ ,  $P = 0.005$ ) and August ( $t_{ratio} = 2.95$ ,  $P = 0.004$ ), as shown in Fig. 3.

### 3.4. Bat activity and moth abundance through time

We found a negative correlation between bat and moth activity across the entire sampling period ( $r = -0.05$ ,  $P < 0.001$ ). However, if the analysis is restricted to the early part of the season, during weeks 8–19 (early March to late May), an additional pairwise correlation test shows a near-significant positive correlation between bat activity and moth counts ( $r = 0.03$ ,  $P = 0.01$ ; Bonferroni corrected  $P = 0.025$ ). Admittedly, correlations were weak in both cases.

## 4. Discussion

Our results show that within an intensive agricultural landscape, the proportion of natural habitats is the best predictor of Brazilian free-tailed bat activity. These results are consistent with earlier studies showing that land use is an important predictor of

bat activity (Walsh and Harris, 1996; Vaughan et al., 1997; Razgour et al., 2011) and that bats select for the presence of natural or semi-natural habitats (Walsh and Harris, 1996; Duchamp and Swihart, 2008; Razgour et al., 2011). However, remaining natural habitat was the best predictor of bat activity only during the months of July and August (Fig. 3). It is during this time period that female bats are lactating and bat pups begin to forage independently. The bats' energetic requirements are therefore at a maximum and foraging activity is at its peak. It is also at this time that pest moth abundance declines, and areas consisting of a large proportion of crop habitat mostly show a reduction of bat activity. In the Winter Garden region in mid- to late-summer months, most crops are harvested or are in senescence, with the exception of cotton in which insect populations are suppressed with pesticides (Texas Crop Reports 2007, internal report). Thus, most crop lands are no longer productive for insect reproduction. We conclude that during these summer months, areas of natural habitat become a remaining viable source of insect prey and are crucial for sustaining bat populations. We interpret these results as likely resulting from a more consistent and, perhaps, higher diversity and abundance of available prey items than provided by more homogeneous agricultural landscapes.

Our results also highlight the positive influence of water bodies on bat activity. The importance of water features as a source of prey items for foraging bats is well documented, and previous studies show that among all habitat types, sites with water, when available, are most highly preferred by foraging insectivorous bats (Walsh and Harris, 1996; Vaughan et al., 1997; Russo and Jones, 2003; Razgour et al., 2011). Our study provides further support for this. With seasonal *H. zea* populations as well as populations of other agricultural pests numbering in the billions (Wolf et al., 1990; Westbrook et al., 1997), crops should provide abundant insect prey for bats during the periods that the crops are attractive to insects. However, we found no relationship between bat activity and the proportion of major crops.

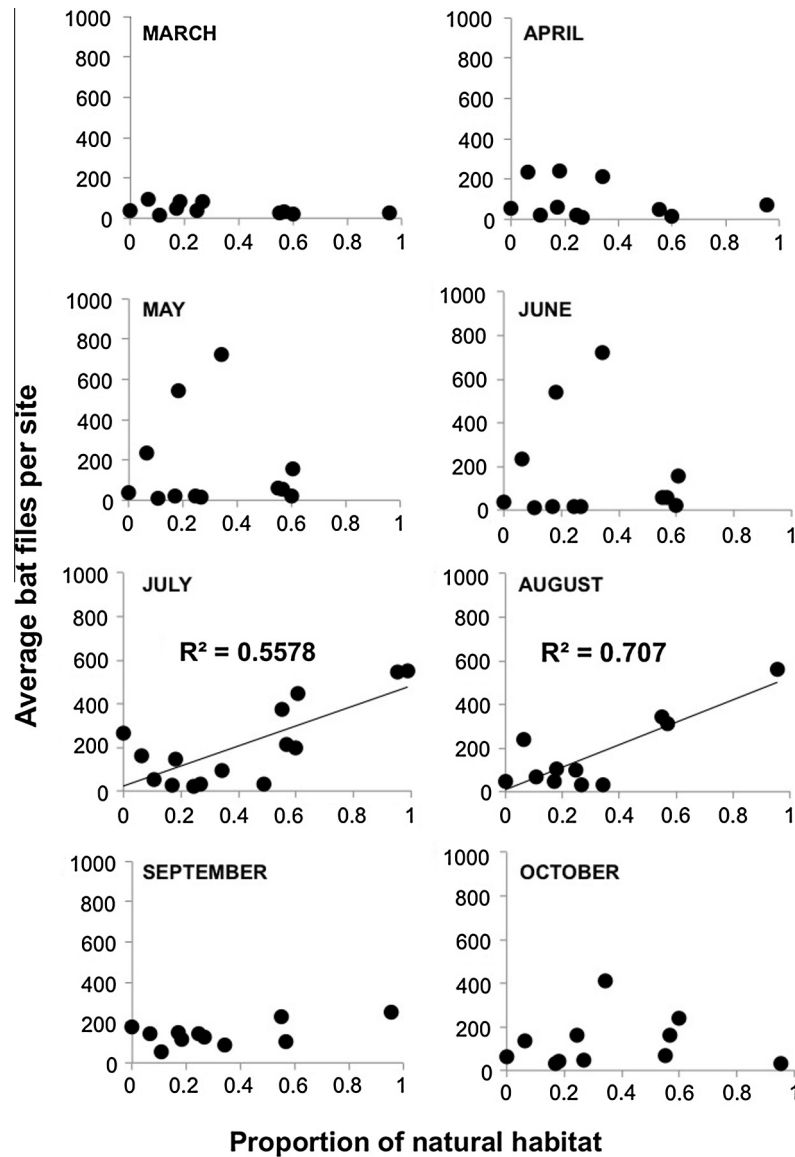
Previous studies in the region have shown a positive correlation between Brazilian free-tailed bat activity and the abundance of insect pests (Lee and McCracken, 2002, 2005; McCracken et al., 2008); however, these studies were all on finer temporal scales of nightly or even hourly observations. This study, which examined spatial and temporal patterns over several months, showed an overall negative temporal relationship between bat activity and *H. zea* moth abundance, and no positive spatial relationship among local sites. While moths are plentiful in crop habitat in the region during late spring to early summer, their abundance varies throughout the season and across landscape types (Lingren et al., 1993; Lopez et al., 1995). At the larger scale of this study, temporal patterns of bat foraging activity were positively associated with moth abundance only during the early weeks of the season.

### 4.1. Conservation implications

Our study documenting the importance of natural habitats within agricultural landscape of Texas is consistent with results documented for other bat species in regions throughout much of

**Table 2**  
Estimates of covariance parameters for random effect on bat activity (i.e. average number of bat files). We used REML to estimate parameters.

Model	Random effect	Estimate	Std. Error	Lower 95%	Upper 95%
Global	Sample location	654.78	1774.45	-2823.07	4132.63
	Residual	18648.54	3087.56	13817.43	26557.87
	Total	19303.32	3023.09	14519.43	26926.24
Time-dependent	Sample location	2297.26	2120.80	-1859.43	6453.95
	Residual	15927.30	2760.82	11649.21	23098.14
	Total	18224.56	3036.64	13479.42	26018.07



**Fig. 3.** Association between bat activity (number of Anabat files), averaged across each month during the sampling period, and the proportion of natural habitat at each site. A trendline and  $R^2$  value is shown only for significant relationships (as indicated in our global model). Results from November are excluded from this figure owing to the presence of bats at only 4 of the 15 sites.

the world including Europe (Walsh and Harris, 1996; Russo and Jones, 2003; Wickramasinghe et al., 2004), Australia (Tsitilias et al., 2006) and South America (Dale et al., 1994). As agricultural intensification is expanding across the globe, we are only beginning to appreciate the value of the services of bats within these systems (Bumrungsi et al., 2008; Duchamp and Swihart, 2008).

Within the Winter Garden region, Brazilian free-tailed bats provide valuable ecosystem services by reducing the damage caused by these insects to crops and by suppressing pest numbers on crops below economic thresholds, thereby reducing pesticide applications (Cleveland et al., 2006; Federico et al., 2008; Lopez-Hoffman et al., 2014). The economic value of the pest control services provided by the Brazilian free-tailed bats in a 9-county region of Texas alone, is estimated to be \$741,000 per year (Cleveland et al., 2006). The bats consume enormous numbers of insects, including noctuid moths (Lepidoptera: Noctuidae) (Lee and McCracken, 2005; McCracken et al., 2012), and reduce the use of pesticides in the system by one or two applications per year (Cleveland et al., 2006), ultimately delaying the need for new

pesticides (Federico et al., 2008). However, for these services to be sustained, the bats must persist in the landscape on alternative prey during periods when pest numbers are low. Our results strongly suggest that the remaining fragments of natural habitats sustain bats during these periods and are essential for the continued presence and maintenance of the ecosystem services that the bats provide within the agricultural landscape.

Within the agricultural landscape of southern Texas, Brazilian free-tailed bats make preferential use of remaining fragments of native habitats during periods when the bats' energetic needs are great and insect pest populations are at their nadir. This association of bat activity with natural habitats supports the need to maintain alternative habitat features within agricultural landscapes, such as intact habitat patches comprising shrubs and trees. The persistence of natural habitats may provide consistency in food supply through time. Farmland strategies that maximize landscape complexity, with interspersed natural habitats, might further provide a variety of habitats thereby increasing prey density and diversity. We conclude that the protection and maintenance of

natural habitat within agricultural landscapes is essential for the conservation of bat populations and ecosystem services amid the ongoing biodiversity crisis.

## Acknowledgments

We thank Mariano Rodríguez-Cabal and Aaron Gove for providing comments on early draft of the manuscript. Rodney Sams, Seth Walker and Thomas Maslen provided valuable assistance with the fieldwork. We thank three anonymous reviewers for their comments, which significantly improved previous versions of the manuscript. We also thank the numerous agricultural landowners who provided us access to field sites. Noa Davidai was supported by the Department of Ecology and Evolutionary Biology at the University of Tennessee, a Bat Conservation International Student Research Scholarship, and NSF Grant EIA-0326483 (TH Kunz, PI, M Betke, GF McCracken, P Morton, and JK Westbrook, CoPI's).

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.05.015>.

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