



Habitat diversity promotes bat activity in a vineyard landscape



Rochelle Marie Kelly^{a,b,*}, Justin Kitzes^c, Houston Wilson^a, Adina Merenlender^a

^a Department of Environmental Resources Policy and Management, University of California, 130 Mulford Hall, Berkeley, CA 94720-3114, USA

^b Department of Biology and Burke Museum of Natural History and Culture, University of Washington, 24 Kincaid Hall, Seattle, WA 98195-1800, USA

^c Energy and Resources Group, University of California, 310 Barrows Hall, Berkeley, CA 94720, USA

ARTICLE INFO

Article history:

Received 23 October 2015

Received in revised form 3 March 2016

Accepted 5 March 2016

Available online xxx

Keywords:

Chiroptera

Acoustics

Songmeter

Agriculture

Vineyard

Ecosystem services

ABSTRACT

Intensification of agricultural production has greatly limited the capacity of agricultural land to support other species. Maintaining landscape heterogeneity in and around agricultural landscapes can help conserve biodiversity and potentially natural pest control. Whereas bats (order: Chiroptera) are highly valued as natural predators of agricultural pests, little is known about the distribution and abundance of bat species across different types of agricultural landscapes. The objective of our study was to assess how local remnant habitat and surrounding natural areas influence bat activity levels within a vineyard landscape. To accomplish this, we conducted acoustic surveys at 21 vineyards within the North Coast wine-grape growing region of California. Using generalized linear mixed-models, we assessed the influence of local remnant habitat and surrounding natural areas to predict overall and species-specific activity patterns. A total of 14,613 bat passes were recorded, of which 80% were identified by a random forest classifier as either *Tadarida brasiliensis* the Brazilian free-tailed bat (25%), *Myotis yumanensis* the Yuma Myotis (24%), or *Eptesicus fuscus* the big brown bat (23%). The results of our models indicate that total bat activity, and the activity of each of the common bat species, was higher adjacent to remnant vegetation along the edges of vineyards as compared to within the vineyard, but that the effect of landscape-scale characteristics on bat activity was weak. This suggests that natural trees and shrubs should be conserved and restored throughout the vineyard landscape to enhance bat abundance for a win-win agricultural production and conservation solution.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Intensification of agricultural production has greatly limited the capacity of agricultural land to support other species (Benton et al., 2003). Recent studies focused on quantifying the extent to which wildlife use agricultural landscapes have revealed that structurally simple agricultural systems support a limited numbers of species (Aue et al., 2014; Caudill et al., 2015). Retaining heterogeneous vegetation structure within the agricultural matrix, however, can increase species diversity (Frey-Ehrenbold et al., 2013; Medina et al., 2007; Mendenhall et al., 2014; Muñoz et al., 2013) as well as ecological services such as biological pest control (Veres et al., 2013).

Bats provide an important example of biological pest control, valued at 3.7 billion dollars in the United States alone (Boyles et al., 2012). Yet bats face myriad threats ranging from habitat loss and fragmentation, deforestation, environmental contaminants, to roost disturbance across the globe (Jones et al., 2009; Kunz et al., 2011; Weller et al., 2009). In light of the particularly widespread threat posed by habitat modification, several studies have examined the factors that serve to support bat populations in managed landscapes (Gert and Chelstvig, 2004; Lentini et al., 2012; Morris et al., 2010). Within managed landscapes, numerous features have been implicated to influence bat activity, from forested edges (Duff and Morrell, 2007; Ethier and Fahrig, 2011), tree lines (Fuentes-Montemayor et al., 2013; Kalda et al., 2015; Verboom and Spoelstra, 1999), and riparian buffers (Akasaka et al., 2012; Law and Chidel, 2002). Small local habitat remnants and linear landscape features, such as forested edges and riparian buffers provide a number of benefits to commuting and foraging bats, including greater insect abundance (Morris et al., 2010), protection from wind (Verboom and Spoelstra, 1999), potential

* Corresponding author at: Department of Biology, University of Washington, 24 Kincaid Hall, Seattle, WA 98195-1800, USA.

E-mail addresses: rmkelly@uw.edu, cellardoor428@gmail.com (R.M. Kelly).

cover from predators, and navigational landmarks (Verboom and Spoelstra 1999). Heterogeneity in urban areas is also related to bat activity rates; a lack of heterogeneity resulted in low activity in Illinois' agricultural lands (Gert and Chelsvig, 2004).

While agricultural expansion in particular is generally perceived as negatively affecting the distribution, abundance, and diversity of bats (Duchamp and Swihart, 2008; Gert and Chelsvig, 2004; Weller et al., 2009), individual species' abilities to exploit agricultural ecosystems (Wickramasinghe et al., 2003) vary significantly (Coleman and Barclay, 2011; Estrada and Coates-Estrada, 2002; Kalda et al., 2015). Characteristics of both individual farms (Wickramasinghe et al., 2003) as well as the larger agricultural landscape (Lentini et al., 2012) may influence on farm bat activity. Structural features such as remnant vegetation, hedgerows, and windbreaks have been shown to support increased bat activity within agricultural landscapes in Europe (Frey-Ehrenbold et al., 2013; Kalda et al., 2015; Wickramasinghe et al., 2003) and Australia (Lentini et al., 2012), arguing that heterogeneity in agricultural lands can enhance bat occupancy.

In new world Mediterranean-climate regions such as Chile and Northern California, the growth of the wine industry has led to extensive conversion of land to vineyard acreage (Viers et al., 2013). Given the importance of wine-grapes to regional economies, and the potential for continued expansion of viticulture, it is essential to integrate ecological and viticultural practices to produce landscapes that will sustain wine-grape production and species and habitat protection. Maintaining bat diversity in and around the vineyard landscape presents the possibility for a win-win solution for wine production and bat conservation.

There is little information about the diversity or activity of bats within California's agricultural landscapes (Long et al., 1996). While Long et al. (1996) confirmed agricultural pests in the diets of two common bat species; the extent to which these or other species use various agricultural landscapes remains poorly understood. The growth of the wine industry along the north coast of California has created a mosaic landscape, with much of the valley floor dominated by vineyard acreage. Despite vineyard expansion, riparian setbacks persist (Merenlender, 2000), and may serve to promote bat activity in this agricultural landscape, as well as promote connectivity between the remnant oak woodlands, grasslands, and hardwood forests that persist along hillsides and mountains (Hilty and Merenlender, 2004).

This study was designed to answer three questions regarding bat activity and distribution within these vineyard landscapes in northern California. Firstly, what is the relative activity and species composition in these landscapes? Secondly, how does maintaining natural vegetation that increases structural heterogeneity in and around individual vineyards affect bat activity within vineyards? Thirdly, to what extent do larger landscape-scale land cover patterns affect bat activity at specific sites?

To answer these questions, we conducted acoustic surveys within the North Coast wine-growing region along a gradient of natural land cover and compared bat activity in the middle of vineyards to sites immediately adjacent to remnant vegetation. We hypothesized that local and landscape scale habitat diversity influence bat activity within vineyards, and predicted that overall and species-specific bat activity patterns would be positively

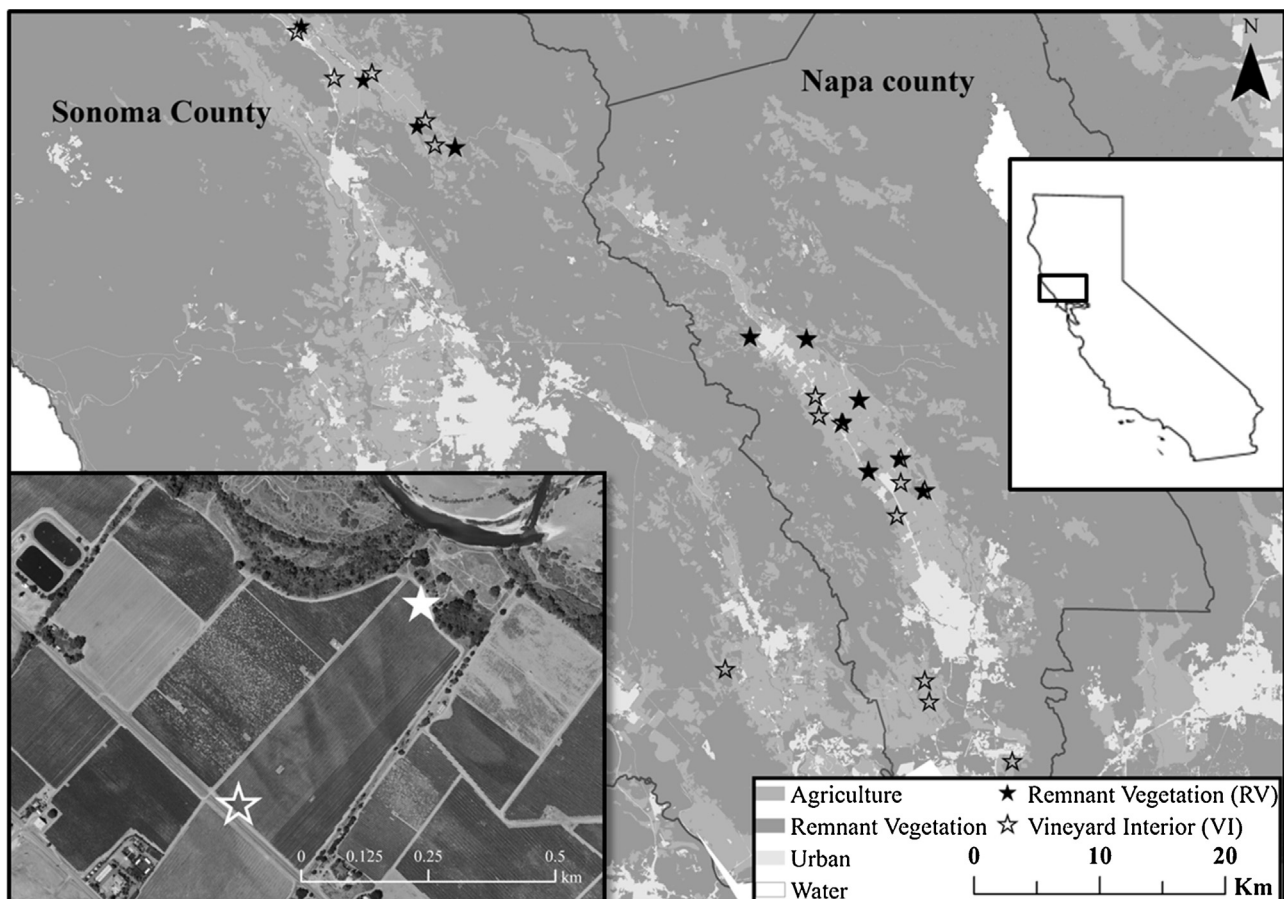


Fig. 1. Study area. "VI" indicates sites with 1 sampling point ($n = 10$). "RV" sites indicate the sites that had 2 nested sampling points, one in the vineyard interior (minimum of 70 m into vine rows), and vineyard edge (maximum of 35 m from edge of vineyard), adjacent to remnant natural vegetation ($n = 11$).

influenced by (1) proximity to natural habitat within vineyards and (2) the proportion natural land cover at the landscape level.

2. Methods

2.1. Study area

We carried out acoustic surveys within a 6,610 km² area of the wine-growing region of the North Coast of California (Fig. 1), 60 km Northeast of San Francisco in adjacent valleys situated on either side of the Mayacamas Mountains. The region is characterized by a Mediterranean climate zone, and patches of natural habitat surrounding vineyards predominately consist of riparian habitat and oak forest and woodland (Merenlender, 2000). As of 2014, Napa and Sonoma Counties reported 62,650 and 45,380 acres of vineyards (Napa County Agricultural Crop Report, 2014; Sonoma County Agricultural Crop Report, 2014), and vineyard expansion is has been implicated as the key driver of habitat conversion in the region (Merenlender, 2000).

2.2. Acoustic sampling

Acoustic surveys were conducted at twenty-one vineyards ranging from 3.3 – 80.6 acres, with a mean area of 15.7 ± 3.4 acres.; five located in Sonoma County and seventeen located in Napa County (Fig. 1a). We selected the vineyards in our study from a subset of vineyards participating in a larger study examining the role of local and landscape level heterogeneity on conservation biological control of vineyard pests (Miles et al., 2012; Wilson et al., 2015). Surrounding remnant vegetation around the vineyards ranged from natural (e.g., intact riparian setback, oak woodland) to semi-natural (e.g., eucalyptus grove); both of which will be subsequently referred to as “remnant vegetation”. Within eleven vineyards, paired survey points were established at the edge of the vineyard, adjacent to remnant vegetation (RV) and within the vineyard interior (VI) (Fig. 1b.). At all paired sites, the ‘VI’ sampling point was a minimum of 70 m from the edge of the vineyard block into the vine rows, while ‘RV’ points, were placed a maximum distance of 35 m from the remnant vegetation. Paired survey points were >75 m apart, with the exception of two vineyards, where the width of the vine row was <100 m.

We surveyed each site for consecutive 3–4 night periods, twice per year, between July and August in 2011 and between June and July in 2012. We monitored bat activity acoustically using Songmeter SM2BAT 192 Hz full-spectrum bat detectors (Wildlife Acoustics Inc., Concord, MA). Omnidirectional microphones were mounted to 2 m poles to minimize ground and leaf noise and to prevent the recording of call reflections from the ground. Acoustic sampling took place between sunset and sunrise, and the detectors were programmed to record ambient temperature at 15-minute intervals each night.

2.3. Call identification

We first converted call data to 8-division zero-crossing format using wac2wav 3.3.0. Passes were split by a minimum spacing of five seconds between calls. Call data were then filtered with AnalookW 3.8s to extract high quality calls consisting of a characteristic frequency between 5 and 60 kHz, a duration between 2 and 50 milliseconds, a body over 1 millisecond, and a Qual index less than 0.3 (Armitage and Ober, 2010). Only passes containing at least 1 high quality call were included in the analysis (Kitzes and Merenlender, 2014). The number of recorded passes per night was used to describe bat activity. To allow for statistical analysis of individual species, the open source software BatID version 1.1 (<http://jkitzes.github.io/batid>) was used to identify passes to the species level (BatID). Using a random forest classifier, BatID assigns each call to a given species based on a hierarchical classification of 12 parameters of each call. The probabilities that a given species made the call are then summed across all calls in a pass sequence, and the species with the highest probability is assigned. This classifier has been fit to species found in the San Francisco Bay region, and has a mean accuracy of $84 \pm 0.13\%$ of correctly identifying calls to the species level (see Kitzes and Merenlender, 2014, for further details). To analyze species richness, the call classification settings within BatID 1.1 were adjusted to minimize false positive species identification. We required a minimum of 4 calls with at least 85% certainty of being that species for any pass to be classified to species level.

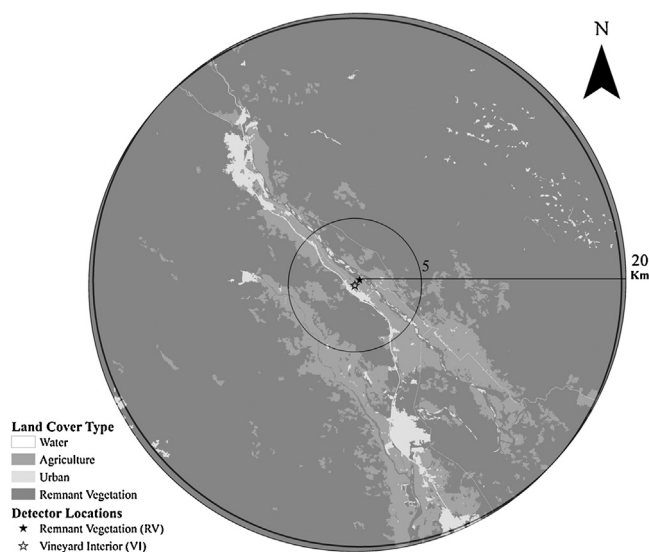


Fig. 2. Surrounding land use analysis using CalVEG land cover data. Ring buffers were created at 0.2, 5, and 20 km. The percent coverage of agriculture, urban, and remnant vegetation were determined from the SRM_COVER_TYPE class.

2.4. Landscape data

To analyze the relationship between bat activity within vineyards and surrounding landscape, we obtained land cover data from the USDA forest Service CALVEG classification system. All spatial data were analyzed using ArcGIS 10.1 (ESRI, Redlands, USA).

Among temperate bat species, home range sizes vary significantly between species (Duchamp et al., 2004; Evelyn, 2004; Fellers and Pierson, 2002), thus individual species may perceive changes in habitat differently at various spatial scales. In order to assess the relationship between surrounding land use and bat activity for individual species, we classified land use at multiple spatial scales. Concentric ring-buffers were defined around each sampling point to characterize the local landscape (200 m and 1000 m) and the broader landscape (5 km and 20 km). Using the 'SRM Rangeland Cover Type' class, which classifies existing vegetation, we distilled these cover types into three categories: natural habitat, agricultural habitat, and urban cover (Fig. 2). We then calculated the proportional area of agricultural, urban, and natural land cover within each buffer. Since we were interested in the influence of habitat conservation, the proportion of natural habitat at each scale was used in subsequent analysis. In addition to land use, proximity to water can influence bat activity (Duff and Morrell, 2007), and riparian corridors and water holding ponds are common features throughout the study area. Using aerial LANDSAT imagery, we determined the presence of any natural or artificial water source within 200 m of the sampling location to include in subsequent analyses.

2.5. Statistical analysis

Statistical analyses were conducted using R 2.15.2 (R Core Team, 2012), with the packages lme4 0.999999-0 (Bates et al., 2014) and MuMIn 1.9.0 (Bartoń, 2015) used for modeling and model selection.

To avoid extrapolating patterns from rare occurrences that could have potentially resulted from misclassified calls, we only performed analyses on the three species that each constituted more than 20% of identified individuals (see Section 3). Modeling was not performed for the remaining species identified by BatID, none of which exceeded 7% of total recorded activity. We analyzed bat activity patterns using the number of bat passes per night from all species combined as well as for each of the three most commonly recorded species individually.

As appropriate for count data, Poisson generalized linear mixed models with a log link function were used to model the relationship between bat activity and predictor variables (Burnham and Anderson, 2002). Preliminary analyses suggested that nightly count data were overdispersed (ratio of summed Pearson residuals to residual degrees of freedom equal to 9.1 for total nightly activity, and 3.1–4.4 for individual species models). To account for this overdispersion, an individual level random effect (*indiv*) was also included, to achieve a lognormal Poisson error structure (Elston et al., 2001). We first generated a global model that included six main variables of interest that could potentially influence bat activity: proximity to remnant vegetation 'RV' vs. vineyard interior 'VI' (RV, two levels: False, True), the presence of water within 200 m (*wtr_200*, two levels: False, True), minimum nightly temperature (*min_temp*, continuous), and the proportion of natural habitat within 200 m (*natural_0.2 km*, continuous), 5 km (*natural_5 km*, continuous), and 20 km (*natural_20 km*, continuous) concentric rings. The proportion of natural habitat at 1000 m was excluded from analyses due to the high correlation (>0.6) with the 200 m and 5 km buffers. In addition to these variables, year (*year*, two levels: 2011 and 2012), site (*site*, random effect), and night (*night*, random effect) were also included in subsequent models. Sum contrasts were applied to the year variable, such that model

estimates reflect an average year. For each global model, we plotted the log transformed fitted values against the fitted residuals, to confirm that there were no violations of homogeneity, as recommended by Zuur et al. (2007).

From the global model, which contained all variables of interest, we used all subset selection to generate a candidate set of models using the *dredge* command of the MuMIn package. We then ranked each model using Akaike's Information Criterion (AIC). Incorporating the surrounding land use variables produced a large number of top ranking models for each species (Table S1), and no clear top model ($\Delta AIC > 2$) was identified (Burnham and Anderson, 2002) (see Section 3). Therefore, we used a model averaging approach to obtain estimated coefficients, unconditional standard errors, and to assess the relative importance of predictor variables from the top model set ($\Delta AIC < 2$). To allow for comparison of effect sizes between explanatory variables in model averaged estimated coefficients, input variables were first standardized to a mean of 0 and SD of 1 for continuous variables. The results for all individual models with a $\Delta AIC < 2$, indicating substantial support (Burnham and Anderson, 2002), are shown in the Supporting Information (Table S1).

3. Results

A total of 14,613 bat passes containing at least one high quality call were recorded over 442 detector-nights. The random forest classifier, BatID, classified 80% of recorded passes as either *Tadarida brasiliensis* the Brazilian free-tailed bat, *Myotis yumanensis* the Yuma Myotis, or *Eptesicus fuscus* the big brown bat, with other species classified at lower levels (Table 1).

Results from our model averaging indicate that for all species combined, activity was 2.3 times higher adjacent to RV, relative to the interior ($\beta = 0.85$ $P < 0.001$) (Table 2). This positive effect of local habitat was also significant for *M. yumanensis* ($\beta = 0.58$, $P < 0.001$), and *E. fuscus* ($\beta = 1.55$, $P < 0.001$), however RV had no significant influence on the activity of *T. brasiliensis*. Given the log-link function and standardized model structure, on an average night we would expect that, relative to the interior, activity adjacent to RV would be nearly four times as high for *E. fuscus* and almost twice as high for *M. yumanensis* (Fig. 3). Temperature had no observable effect on the activity of *T. brasiliensis* or *M. yumanensis*. However, there was a positive effect of temperature on overall species activity and that of *E. fuscus* ($\beta = 0.13$, $P = 0.01$; and $\beta = 0.29$, $P < 0.01$ respectively) (Table 2).

There was a significant year effect for all species combined and for each individual species (Table 2), with greater activity of all species in 2011 than 2012. However, the effect of year is confounded by the seasonal effect of sampling later in the summer in 2011 (July–August), than in 2012 (June–July) (see Section 2.2). While nightly minimum temperatures were higher, on average in 2011 ($17.7 \pm 0.2^\circ\text{C}$) than in 2012 ($15.3 \pm 0.4^\circ\text{C}$), given the structure of our models, the significant year coefficient indicates that year was significant independent of temperature.

None of the surrounding land use variables (natural_0.2 km, 5 km, 20 km) had a statistically significant impact on bat activity in our averaged model, and estimated effect coefficients were small

Table 1

Counts of nightly passes recorded during acoustic surveys in Napa and Sonoma county vineyards, and percent activity of the most common species identified using the random forest classifier BatID (see Section 2).

Species	Percent	Total
All spp.		14613
<i>T. brasiliensis</i>	25.4%	3708
<i>M. yumanensis</i>	24.6%	3591
<i>E. fuscus</i>	23.3%	3407

Table 2

Results from model averaging: Model variable and coefficient estimates from Poisson regression of counts of nightly activity in North Coast vineyards (see Section 2). Coefficients were estimated with a bias toward zero (with shrinkage). Model coefficients reflect a log link such that multiplicative effects are equal to exp (β). Estimates are provided for overall bat activity, and the three most common vineyard species: the Brazilian free-tailed bat (*T. brasiliensis*), Yuma myotis (*M. yumanensis*), and the Big brown bat (*E. fuscus*). (***) $P < 0.001$, (**) $P < 0.01$, (*) $P < 0.05$.

Coefficient ^a	All spp.	<i>T. brasiliensis</i>	<i>M. yumanensis</i>	<i>E. fuscus</i>
(Intercept)	2.57***	.87***	1.01***	0.23
RV	0.85***	0.082	0.58***	1.55***
Year	0.37***	0.38***	0.39***	0.20**
Temp	0.11*	0	0.06	0.26**
Temp:RV	-0.06	-0.036	-0.04	-0.09
Natural_0.2 km	-0.04	-0.22	-0.01	0
Natural_5 km	-0.06	-0.27	-0.18	0
Natural_20 km	0.02	0.03	-0.01	0.19
Wtr_200m	-0.02	0.67*	-0.01	0.05

^a RV = binary variable, adjacent to remnant vegetation vs. vineyard interior (see Section 2).

compared to the effects of RV and year. The model-averaged results for *T. brasiliensis* indicate that the presence of water within a 200 m radius had a significant effect ($\beta = 0.66$, $P = 0.03$) on activity (Table 2). However this variable was highly negatively correlated with the natural_0.2 km variable (-0.74), and when natural_0.2 km was dropped from the model the water variable became insignificant. While land use variables were often incorporated into individual models with AIC support (Table S1), the pattern of inclusion of these variables was inconsistent and effect sizes were similarly weak.

4. Discussion

Using acoustic surveys, we assessed the relationship between bat activity and local and landscape level habitat characteristics in California North Coast vineyards. The most common species acoustically detected in this vineyard landscape are *T. brasiliensis*, *M. yumanensis*, and *E. fuscus*. The results of our models indicate that overall bat activity, and the activity of two of the three most common species, was up to nearly four times higher adjacent to remnant vegetation 'RV' within a vineyard landscape (Fig. 3). This finding is consistent with previous studies of North American bats in other managed landscapes (Avila-flores and Fenton, 2005; Dixon, 2011; Ethier and Fahrig, 2011; Morris et al., 2010), demonstrating the importance of habitat heterogeneity and the advantages of maintaining remnant habitat patches for bat species within managed and heavily altered ecosystems. Our finding that the activity of *T. brasiliensis* was unaffected by remnant vegetation within vineyards is consistent with this species' wing morphology and echolocation features, which suggest that this species is well adapted to rapid flight in open areas. We find little evidence, however, that larger-scale landscape characteristics are a major determinant of vineyard-scale bat activity levels.

The lack of an association between *M. yumanensis* activity and the presence of water contrasts with previous studies (Bringham et al., 1992). Proximity to water is frequently identified as a predictor of *M. yumanensis* roosting and foraging activity (Duff and Morrell, 2007; Evelyn, 2004). If *M. yumanensis* were foraging directly over the water surface, then acoustic monitoring adjacent to water sources may be necessary to detect a difference in activity patterns (Ober and Hayes, 2008; Stahlschmidt et al., 2012). For

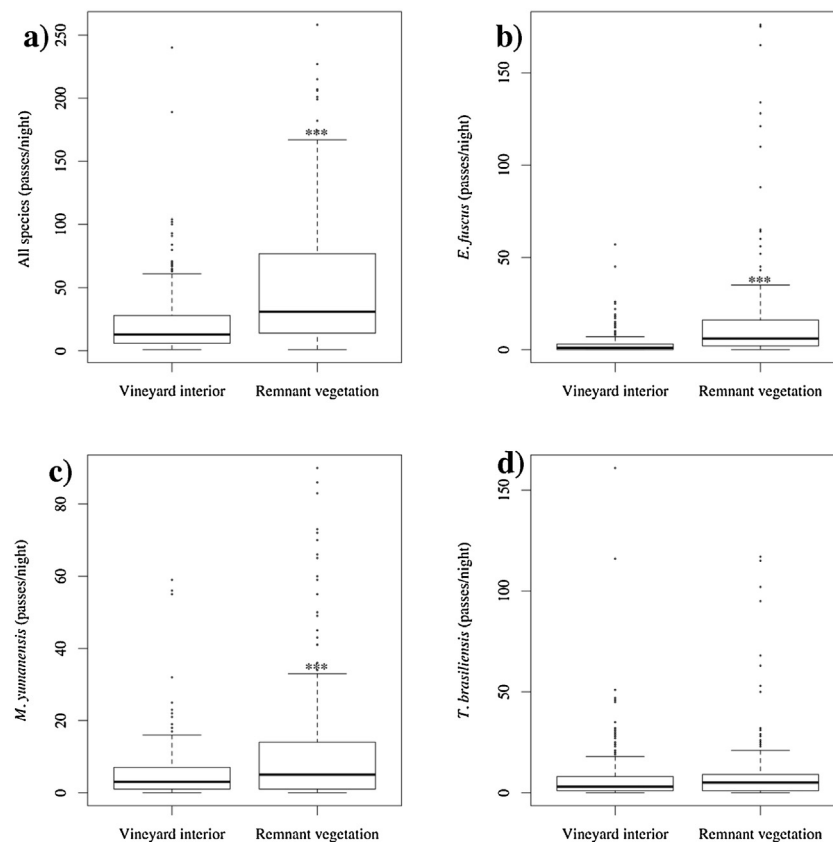


Fig. 3. Nightly recorded activity (passes per night) of bats in North Coast Vineyards within the vineyard interior and adjacent to remnant vegetation for: (a) all species combined (b) *E. fuscus* (c) *M. yumanensis* and (d) *T. brasiliensis*. The middle line is equal to the median nightly passes, boxes indicate interquartile range, the whiskers extend to 1.5 times the interquartile range, and values beyond this range are indicated by (°). Differences in overall and species-specific relative activity patterns were assessed by fitting generalized linear mixed effects models (see Section 2), and are indicated by (***) at $P < 0.001$.

example, acoustic studies in a German vineyard landscape found significantly higher bat activity at constructed wetlands as compared with paired vineyard recording stations 80 meters away (Stahlschmidt et al., 2012). In our study area, both natural and artificial water sources are abundant and potentially not a limiting factor in *M. yumanensis* activity patterns. Moreover, foraging observations of *M. yumanensis* suggest they also forage extensively along forested edges (Bringham et al., 1992). The 'edge' habitat provided by remnant vegetation within and among vineyards may serve as habitat for foraging, commuting or both although we cannot distinguish among these with our acoustic sampling design.

In contrast with site level habitat features, there was no clear trend in the activity of any species with the relative extent of surrounding upland natural habitat. At the 5 and 20 km scale, surrounding natural vegetation ranged between 40–70% and 59–85%, respectively, and our results suggest that this level of habitat variation is not sufficient to cause significant variation in bat activity. This analysis cannot rule out the possibility that more extreme loss of surrounding oak woodland habitat may have an influence on bat activity in vineyards.

The large differences in detections between 2011 and 2012 may be a result of two factors: naturally high levels of inter-annual variation and/or sampling time. Inter-annual variation is frequently observed in acoustic bat surveys (Ober et al., 2008; Seidman and Zabel, 2001). However, it is likely that seasonal variation influenced the observed detection differences. This would support the results of Seidman and Zabel (2001) who observed a seasonal increase in bat activity over the course of the summer (June–September) in a multi-year study. They suggest this could be the result of increasing population size (due to juveniles, greater insect abundance, and/or increasing temperatures).

While acoustic sampling techniques have permitted researchers to study the activity patterns of cryptic mammals, it is important to recognize the bias with such techniques. Echolocation calls are highly variable among species, and not all species are equally detectable acoustically. Additionally, the choice of acoustic detector also influences detection rates (Adams et al., 2012). Using the classifier BatID allowed us to analyze the activity of the most commonly identified species as well as overall bat activity, but prevented us from drawing conclusions about rare species. The numerous factors that influence intraspecific variability in echolocation calls (O'Farrell et al., 2000; Sun et al., 2013) as well as interspecific overlap (Teeling, 2009; Weller et al., 2007) make identifying echolocation calls of bats problematic. Therefore it is generally not advised to rely on acoustic surveys alone to confirm the presence of rare species unless additional survey methods (e.g., mist-netting) are employed (Clement et al., 2014). In order to assess the distribution of rare species, additional sampling methods would need to be employed, which was unfortunately beyond the scope of this study.

All of the common bat species present within North Coast vineyards have previously been documented to consume agricultural pests (Cleveland et al., 2006; Duchamp et al., 2004; Long et al., 1996). Our results suggest that remnant vegetation generally increase overall bat activity in our study area. This underscores the importance of well-maintained remnant natural habitat corridors for regional biodiversity within this vineyard dominated landscape (Hilty and Merenlender, 2004). However, activity was highly variable within and between sites, with total activity ranging from just 1 pass to 258 passes per night adjacent to remnant vegetation and from 1–240 passes per night in the vineyard interior. The non-negligible activity levels within the vineyard interior suggest that bats do use this habitat for commuting, foraging, or both. Since vineyard development will likely continue in the future, it is critical to gain a better understanding not only of the factors influencing

bat activity, but also the negative impacts of agricultural practices (e.g., pesticides) on bats and other wildlife (Boyles et al., 2012; Frick et al., 2007).

While surrounding land use does not appear to explain the observed variation in activity levels, microhabitat characteristics (Estrada-Villegas et al., 2012; Ober et al., 2008) may be a better indicator for bat activity patterns (Gehrt et al., 2003). In addition to remnant vegetation, roost availability, and/or insect abundance (Avila-flores and Fenton, 2005; Fuentes-Montemayor et al., 2013; Rambaldini and Brigham, 2011) may be influencing bat activity patterns within North Coast vineyards. Behavioral observations within Canadian vineyards confirmed bats foraging within viticultural landscapes, however the authors suggests that preferred prey availability may influence foraging activity (Rambaldini and Brigham, 2011). Therefore future research should attempt to quantify pest regulatory services, in order promote the adoption of on farm conservation practices. Such efforts have the potential to contribute to ecosystem services as well to conservation.

5. Conclusions

Using non-invasive acoustic sampling, we were able to characterize the activity of common bat species and overall activity within a major wine-growing region of California. The strong influence of remnant habitat patches on the observed bat activity argues for retaining local structural heterogeneity in and around the vineyard matrix for a win-win solution for bat conservation and potential pest control. Promoting biodiversity in agricultural landscapes has the potential to benefit bat conservation and growers alike (Muñoz et al., 2013; Viers et al., 2013).

Acknowledgments

We thank the growers who participated in this study and allowed us access to their ranches. We would also like to thank the anonymous reviewers for their suggestions.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2016.03.010>.

References

- Adams, A.M., Jantzen, M.K., Hamilton, R.M., Fenton, M.B., 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods Ecol. Evol.* 3, 992–998. doi:<http://dx.doi.org/10.1111/j.2041-210X.2012.00244.x>.
- Akasaka, T., Akasaka, M., Nakamura, F., 2012. Scale-independent significance of river and riparian zones on three sympatric *Myotis* species in an agricultural landscape. *Biol. Conserv.* 145, 15–23. doi:<http://dx.doi.org/10.1016/j.biocon.2011.08.017>.
- Armitage, D.W., Ober, H.K., 2010. A comparison of supervised learning techniques in the classification of bat echolocation calls. *Ecol. Inform.* 5, 465–473. doi:<http://dx.doi.org/10.1016/j.ecoinf.2010.08.001>.
- Aue, B., Diekötter, T., Gottschalk, T.K., Wolters, V., Hotes, S., 2014. How high nature value (HNV) farmland is related to bird diversity in agro-ecosystems—towards a versatile tool for biodiversity monitoring and conservation planning. *Agric. Ecosyst. Environ.* 194, 58–64. doi:<http://dx.doi.org/10.1016/j.agee.2014.04.012>.
- Avila-flores, R., Fenton, M.B., 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* 86, 1193–1204.
- Bartoni, Barton-Kamil, 2015. MuMIn: Multi-Model Inference. R package version 1.9.0. <http://CRAN.R-project.org/package=MuMIn>.
- Bates D., Maechler M., Bolker B., Walker S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1, 1–7.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18, 182–188. doi:[http://dx.doi.org/10.1016/S0169-5347\(03\)00011-9](http://dx.doi.org/10.1016/S0169-5347(03)00011-9).
- Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2012. Economic importance of bats in agriculture. *Science* 332, 41–42.
- Bringham, R.M., Aldridge, H.D.J.N., Mackey, R.L., 1992. Variation in habitat use and prey selection by Yuma bats, *Myotis yumanensis*. *J. Mammal.* 73, 640–645.

- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.
- Caudill, S.A., DeClerck, F.J.A., Husband, T.P., 2015. Connecting sustainable agriculture and wildlife conservation: does shade coffee provide habitat for mammals? *Agric. Ecosyst. Environ.* 199, 85–93. doi:http://dx.doi.org/10.1016/j.agee.2014.08.023.
- Clement, M.J., Rodhouse, T.J., Ormsbee, P.C., Szwczak, J.M., Nichols, J.D., 2014. Accounting for false-positive acoustic detections of bats using occupancy models. *J. Appl. Ecol.* 51 (5), 1460–1467. doi:http://dx.doi.org/10.1111/1365-2664.12303.
- Cleveland, C.J., Betke, M., Federico, P., Frank, J.D., Thomas, G., Horn, J., Jr, J.D.L., Mccracken, G.F., Medellín, R.A., Sansone, C.G., Westbrook, J.K., Kunz, T.H., Hallam, T.G., Jr, J.D.L., Medellín, R.A., 2006. Economic value of the pest control services provided by Brazilian free-tailed bats in south-central Texas. *Front. Ecol. Environ.* 4, 238–243.
- Coleman, J.L., Barclay, R.M.R., 2011. Urbanization and the abundance and diversity of Prairie bats. *Urban Ecosyst.* 15, 87–102. doi:http://dx.doi.org/10.1007/s11252-011-0181-8.
- Dixon, M.D., 2011. Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosyst.* 15, 683–695. doi:http://dx.doi.org/10.1007/s11252-011-0219-y.
- Duchamp, J.E., Sparks, D.W., Whitaker, J.O., 2004. Foraging-habitat selection by bats at an urban–rural interface: comparison between a successful and a less successful species. *Can. J. Zool.* 82, 1157–1164. doi:http://dx.doi.org/10.1139/Z04-095.
- Duchamp, J.E., Swihart, R.K., 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landsc. Ecol.* 23, 849–860. doi:http://dx.doi.org/10.1007/s10980-008-9241-8.
- Duff, A.A., Morrell, T.E., 2007. Predictive occurrence models for bat species in California. *J. Wildl. Manag.* 71, 693–700. doi:http://dx.doi.org/10.2193/2005-692.
- Elston, D.A., Moss, R., Boulinier, T., Arrowsmith, C., Lambin, X., 2001. Analysis of aggregation, a worked example: numbers of ticks on red grouse chicks. *Parasitology* 122, 563–569.
- Estrada, A., Coates-Estrada, R., 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biol. Conserv.* 103, 237–245. doi:http://dx.doi.org/10.1016/S0006-3207(01)00135-5.
- Estrada-Villegas, S., McGill, B.J., Kalko, E.K.V., 2012. Climate, habitat, and species interactions at different scales determine the structure of a Neotropical bat community. *Ecology* 93, 1183–1193.
- Ethier, K., Fahrig, L., 2011. Positive effects of forest fragmentation, independent of forest amount, on bat abundance in eastern Ontario, Canada. *Landsc. Ecol.* 26, 865–876. doi:http://dx.doi.org/10.1007/s10980-011-9614-2.
- Evelyn, M., 2004. Conservation of bats in suburban landscapes: roost selection by *Myotis yumanensis* in a residential area in California. *Biol. Conserv.* 115, 463–473. doi:http://dx.doi.org/10.1016/S0006-3207(03)00163-0.
- Fellers, G.M., Pierson, E.D., 2002. Habitat use and foraging behavior of Townsend's Big-Eared Bat (*Corynorhinus townsendii*) in Coastal California. *J. Mammal.* 83, 167–177.
- Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R., Obrist, M.K., 2013. Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *J. Appl. Ecol.* 50, 252–261. doi:http://dx.doi.org/10.1111/1365-2664.12034.
- Frick, W.F., Rainey, W.E., Pierson, E.D., 2007. Potential effects of environmental contamination on Yuma *Myotis* demography and population growth. *Ecol. Appl.* 17, 1213–1222.
- Fuentes-Montemayor, E., Goulson, D., Cavin, L., Wallace, J.M., Park, K.J., 2013. Fragmented woodlands in agricultural landscapes: The influence of woodland character and landscape context on bats and their insect prey. *Agric. Ecosyst. Environ.* 172, 6–15. doi:http://dx.doi.org/10.1016/j.agee.2013.03.019.
- Gehrt, S.D., Chelvig, J.E., Applications, S.E., Aug, N., 2003. Bat Activity in an Urban Landscape: Patterns at the Landscape and Microhabitat Scale. *Ecol. Appl.* 13, 939–950.
- Gert, S.D., Chelvig, J.E., 2004. Species-Specific Patterns of Bat Activity in an Urban Landscape. *Ecol. Appl.* 14, 625–635.
- Hilty, J.A., Merenlender, A.M., 2004. Use of Riparian Corridors and Vineyards by Mammalian Predators in Northern California. *Conserv. Biol.* 18, 126–135. doi: http://dx.doi.org/10.1111/j.1523-1739.2004.00225.x.
- Jones, G., Jacobs, D., Kunz, T., Willig, M., Racey, P., 2009. Carpe noctem: the importance of bats as bioindicators. *Endanger. Species Res.* 8, 93–115. doi: http://dx.doi.org/10.3354/esr00182.
- Kalda, O., Kalda, R., Liira, J., 2015. Multi-scale ecology of insectivorous bats in agricultural landscapes. *Agric. Ecosyst. Environ.* 199, 105–113. doi:http://dx.doi.org/10.1016/j.agee.2014.08.028.
- Kitzes, J., Merenlender, A., 2014. Large roads reduce bat activity across multiple species. *PLoS One* 9, e96341. doi:http://dx.doi.org/10.1371/journal.pone.0096341.
- Kunz, T.H., Torrez, E.B., De Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* 1223, 1–38. doi:http://dx.doi.org/10.1111/j.1749-6632.2011.06004.x.
- Law, B., Chidel, M., 2002. Tracks and riparian zones facilitate the use of Australian regrowth forest by insectivorous bats. *J. Appl. Ecol.* 39, 605–617. doi:http://dx.doi.org/10.1046/j.1365-2664.2002.00739.x.
- Lentini, P.E., Gibbons, P., Fischer, J., Law, B., Hanspach, J., Martin, T.G., 2012. Bats in a farming landscape benefit from linear remnants and unimproved pastures. *PLoS One* 7, e48201. doi:http://dx.doi.org/10.1371/journal.pone.0048201.
- Long, R.F., Simpson, T., Ding, T.-S., Heydon, S., Reil, W., 1996. Bats feed on crop pests in Sacramento valley. *Calif. Agric.* 52, 8–10.
- Medina, A., Harvey, C.A., Merlo, D.S., Vilchez, S., Merlo, D.S., Vilchez, S., Hernandez, B., Rica, C., 2007. Bat Diversity and Movement in an Agricultural Landscape in Matiguas. *Nicaragua.Biotropica* 39, 120–128.
- Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* 1 doi:http://dx.doi.org/10.1038/nature13139.
- Merenlender, A.M., 2000. Mapping vineyard expansion provides information on agriculture and the environment. *Calif. Agric.* 7–12.
- Miles, A., Daane, K., Altieri, M.A., Wilson, H., Miles, A.F., Daane, K.M., Altieri, M.A., 2012. Effect of vineyard proximity to riparian habitat on biological control of the western grape leafhopper (*Erythroneura elegantula*) in northern California wine grape vineyards.
- Morris, A.D., Miller, D. a., Kalcounis-Rueppell, M.C., 2010. Use of Forest Edges by Bats in a Managed Pine Forest Landscape. *J. Wildl. Manag.* 74, 26–34. doi:http://dx.doi.org/10.2193/2008-471.
- Muñoz, J.C., Aerts, R., Thijs, K.W., Stevenson, P.R., Muys, B., Sekercioglu, C.H., 2013. Contribution of woody habitat islands to the conservation of birds and their potential ecosystem services in an extensive Colombian rangeland. *Agric. Ecosyst. Environ.* 173, 13–19. doi:http://dx.doi.org/10.1016/j.agee.2013.04.006.
- Napa County Agricultural Crop Report, 2014. <http://www.countyofnapa.org/agcommissioner/cropreport/> (accessed 05.03.15).
- O'Farrell, M.J., Corben, C., Gannon, W.L., 2000. Geographic variation in the echolocation calls of the hoary bat (*Lasius cinereus*). *Acta Chiropterol.* doi:http://dx.doi.org/10.1139/cjz-77-4-530.
- Ober, H.K., Hayes, J.P., 2008. Prey selection by bats in forests of Western Oregon. *J. Mammal.* 89, 1191–1200.
- Ober, H.K., Hayes, J.P., Press, A., Hall, R., 2008. Influence of vegetation on bat use of riparian areas at multiple spatial scales. *J. Wildl. Manag.* 72, 396–404.
- R Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
- Rambaldini, D.A., Brigham, R.M., 2011. Pallid bat (*Antrozous pallidus*) foraging over native and vineyard habitats in British Columbia, Canada. *Can. J. Zool.* 89, 816–822. doi:http://dx.doi.org/10.1139/Z11-053.
- Seidman, V.M., Zabel, C.J., 2001. Bat activity along intermittent streams in Northwestern California. *J. Mammal.* 82, 738–747.
- Sonoma County Agricultural Crop Report, 2014. http://www.sonoma-county.org/agcomm/crop_report.htm (accessed 05.03.15).
- Stahlschmidt, P., Pätzold, A., Ressler, L., Schulz, R., Brühl, C.A., 2012. Constructed wetlands support bats in agricultural landscapes. *Basic Appl. Ecol.* 13, 196–203. doi:http://dx.doi.org/10.1016/j.baae.2012.02.001.
- Sun, K., Luo, L., Kimball, R.T., Wei, X., Jin, L., Jiang, T., Li, G., Feng, J., 2013. Geographic variation in the acoustic traits of greater horseshoe bats: testing the importance of drift and ecological selection in evolutionary processes. *PLoS One* 8, e70368. doi:http://dx.doi.org/10.1371/journal.pone.0070368.
- Teeling, E.C., 2009. Hear, hear: the convergent evolution of echolocation in bats? *Trends Ecol. Evol.* 24, 351–354. doi:http://dx.doi.org/10.1016/j.tree.2009.02.012.
- Verboom, B., Spoelstra, K., 1999. Effects of food abundance and wind on the use of tree lines by an insectivorous bat, *Pipistrellus pipistrellus*. *Can. J. Zool.* 77, 1393–1401. doi:http://dx.doi.org/10.1139/z99-116.
- Veres, A., Petit, S., Conord, C., Lavigne, C., 2013. Does landscape composition affect pest abundance and their control by natural enemies? A review. *Agric. Ecosyst. Environ.* 166, 110–117. doi:http://dx.doi.org/10.1016/j.agee.2011.05.027.
- Viers, J.H., Williams, J.N., Nicholas, K.A., Barbosa, O., Kotzé, I., Spence, L., Webb, L.B., Merenlender, A., Reynolds, M., 2013. Vinecology: pairing wine with nature. *Conserv. Lett.* 6 (5), 287–299. doi:http://dx.doi.org/10.1111/conl.12011.
- Weller, T.J., Scott, S.A., Rodhouse, T.J., Ormsbee, P.C., Zinck, J.M., 2007. Field identification of the cryptic vespertilionid bats: *Myotis lucifugus* and *M. yumanensis*. *Acta Chiropterol.* 9, 133–147.
- Weller, T.J., Cryan, P.M., Shea, T.J.O., 2009. Broadening the focus of bat conservation and research in the USA for the 21st century. *Endanger. Species Res.* 8, 129–145. doi:http://dx.doi.org/10.3354/esr00149.
- Wickramasinghe, L.P., Harris, S., Jones, G., Vaughan, N., 2003. Bat activity and species richness on organic and farms: impact of agricultural intensification. *J. Appl. Ecol.* 40, 984–993.
- Wilson, H., Miles, A.F., Daane, K.M., Altieri, M.A., 2015. Vineyard proximity to riparian habitat influences Western grape leafhopper (*Erythroneura elegantula* Osborn) populations. *Agric. Ecosyst. Environ.* 211, 43–50. doi:http://dx.doi.org/10.1016/j.agee.2015.04.021.
- Zuur, A., Ieno, E.N., Smith, G.M., 2007. *Analysing Ecological Data*. Springer Science & Business Media.