Bat Activity at Remnant Oak Trees in California Central Coast Vineyards[1]

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Abstract

During 1990 to 2013, the area planted with wine grapes increased nearly 4.5 times in San Luis Obispo County. Much of this development occurred on open oak savanna with scattered oak (*Quercus* spp.) trees. Remnant trees are retained in some vineyards, but their value to biodiversity retention has not been quantified. During April to September 2014, at six vineyards in San Luis Obispo County, we compared echolocation activity of bats and the abundance of insects at remnant trees to locations without trees in the vineyards. The mean number of insects per night was over two times greater at vineyard trees. We recorded 3,677 bat calls at vineyard trees compared to 1,070 bat calls at open vineyard sites. Calls characteristic of bats that forage around trees were almost exclusive to trees (97 percent of high frequency calls), compared to calls of open-space bats, which were similar at both site types (57 percent of low frequency calls at trees vs. 43 percent in open vineyard). These findings indicate that large remnant oak trees in vineyards not only support higher levels of bat activity, but also increase the diversity of bats that occur and forage in the vineyard. This small-scale study lays the framework for addressing larger, more complex questions surrounding the benefits of remnant trees for bats and the ecosystem services they provide to grape growers.

Key words: bats, California, ecosystem services, echolocation, oak woodland, remnant tree, vineyard

Introduction

Over the past two decades, vineyards have become a predominant feature on the California Central Coast landscape. During 1990 to 2013, the area in vineyards increased from 3300 ha to 14 675 ha in San Luis Obispo County alone (San Luis Obispo County Annual Crop Reports 1990-2013), a 4.5-times increase. Much of this land conversion has occurred, and continues today, on former oak savanna with scattered oak trees. Despite lower production levels, many grape growers choose to retain these trees. However, we know of only one study that has examined the contribution of remnant trees in vineyards toward the maintenance of ecological functions and biodiversity of the native oak savanna. Michael and Tietje (2008) concluded that passerine bird diversity and numbers were similar at large valley oak (*Quercus lobata*) trees in vineyards and valley oak trees of similar architecture in adjacent oak savanna. However, the habitat value of these trees in vineyards to biodiversity more generally remains unquantified.

In other settings, large remnant trees are considered keystone structures, providing a wide range of ecosystem services (Lumsden and Bennett 2005, Manning and others 2006, Tews and others 2004). It is becoming increasingly clear that managing and

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maintaining these structures may be an economically and ecologically prudent way to retain many of the ecological functions of the native woodland habitat and thereby maintain biodiversity in the agricultural matrix. The trees may also provide important ecosystem services and economic benefits that may not be apparent to grape growers, land managers, or the public (Kunz and others 2011).

Insectivorous bats (*Microchiropteran* spp.) are of increasing importance because of their role in the provision of ecosystem services in the agricultural matrix. Nationwide, bats are credited with saving the agricultural industry nearly 24 billion dollars annually in chemical pest control services (Boyles and others 2011). Recent studies demonstrate that the maintenance of even scattered trees in highly modified landscapes makes a major difference in the use of an area by bats. For example, bat activity and richness increased significantly with the presence of only one to several scattered trees compared to bat activity in treeless areas. (Fischer and Law 2010, Lumsden and Bennett 2000). Where there are scattered trees, bat foraging areas tend to be centered on the trees (Lumsden and Bennett 2000, Threlfall and others 2012). Furthermore, Lumsden and Bennett (2000) observed that not only did bat activity drop off appreciably in the treeless areas of their study, but the community composition of bats was different. Arthropod abundance also increased with the presence of scattered trees and had a positive relationship with foraging activity of insectivorous bats (Lumsden and Bennett 2005, Threlfall and others 2012).

Hence, we predicted increased bat activity around remnant trees in vineyards. Remnant trees in vineyards may provide the heterogeneity and resources needed to meet the roosting and foraging requirements of bats adapted for foraging in woodland. To our knowledge, no study has documented the effect remnant trees within a vineyard setting have on the occurrence and foraging activity of bats.

Study objective

Our objective was to evaluate use of remnant trees by bats in vineyards of central-coastal California. We compared bat activity and insect abundance at trees within vineyards to paired locations without trees in the same vineyard. We evaluated the null hypotheses of no difference in bat activity or insect abundance between the tree and the paired location without a tree.

Methods

Study area

We conducted our study in the Central Coast region of California within the northern half of San Luis Obispo County, east of the Highway 101 corridor. The area is characterized by a Mediterranean climate with hot summers and mild-to-cool winters. Nearly all rainfall occurs between October and May, and average annual rainfall varies widely by geographic location in the study area, from as little as 13 cm to 97 cm.

Tree site and no-tree site selection

We created a list of potential sites using Google Earth, and then selected study sites based on land owner access permission and on-the-ground evaluations. Our six study vineyards were more than 3 years old (in other words, producing fruit), ≥50 ha in area, and had at least one widely separated oak tree. Candidate trees were either valley oak or blue oak (*Q. douglasii*), >50 cm diameter at 1.37 m above ground (DBH) with large spreading canopy, and at least 100 m from another tree, vineyard edge, and anthropogenic features such as a building, open water, or highway. The same spatial criteria were used to select the non-tree site, which we placed 100 m from the paired tree and >100 m from any other tree or anthropogenic feature. We chose to study single remnant trees rather than small groups of trees to reduce ambiguity in our assessment of a tree effect. We selected the 100 m distance between tree sites and no-tree sites to balance the need to be close enough such that habitat, aspect, topography, and microclimate were similar, but far enough apart to minimize recording the same individual bats using both sites sequentially. This distance (100 m) was also used by Frey-Ehrenbold and others (2013) to define control areas for their study of bat activity around habitat structures. Finally, we measured tree DBH (cm), tree height (m), and canopy radius as the mean of four distances (m) in the N, S, E, W directions from the base of the trunk to the drip line (outermost edge of the tree's canopy).

Bat sampling

We recorded echolocation activity during the summer active season (April to 21 September 2014) using Anabat II echolocation detector microphones (Titley Electronics Ballina, NSW, Australia) that were housed in weatherproof casings ('bat hats'; EME System, Berkeley, California) and directed straight down (fig 1). Polycarbonate sound reflector plates on the microphone enclosures were positioned at 45 degrees below horizontal so that the angle of call reception was upward at 45 degrees. All microphones were placed at the top of 3-m-long by 1.9 cm diameter conduit. Detectors were connected via Canare LE5-C microphone cable to bat detectors and ANABAT storage Zero-Crossings Analysis Interface Modules (Z-CAIMs) housed in weather proof and dust proof containers which we hung from a carabiner attached to the conduit. We affixed a 10 watt, 30 cm by 40 cm, solar panel to the conduit between the microphone and dust proof container. Because the echolocation recorders were operated using solar power, we attached the conduit by hand clamps to a vine post on the south side of the remnant tree and oriented the echolocation recorder system south. This location provided both maximum solar exposure during the daytime and unobstructed vertical exposure to bat calls at night. At the no-tree site, in the same manner as at the tree, we secured an echolocation recorder system to a vine post and oriented the recorder south.

Figure 1—Echolocation recording system clamped to a vine post at one of our tree sites. The photograph shows an Anabat II detector echolocation microphone with a polycarbonate sound reflector plate mounted at the top of a 3-m conduit, a 10 watt solar panel that charges a 9-volt battery housed with an Anabat recorder and Z-CAIM (see text) in the weather proof and dust proof container. (Photo: S. Giordano)

Echolocation recorders were activated from sunset to sunrise. To control for night-to-night variation in bat activity (Hayes 1997) resulting from factors such as weather or insect emergences, we used a paired design. That is, we deployed echolocation detection systems concurrently and for equal time at the tree site and no-tree site within a vineyard. During April to mid-July, we sampled at only one vineyard. After mid-July and until the end of fieldwork on 21 September, we moved our echolocation detection systems every 5 to 9 days and repeated paired sampling among six replicate vineyards. During the study (1 April to 21 September 2014), we accumulated 122 nights of paired sampling.

Insect sampling

During August to 21 September, 2014, we sampled flying insects at the tree and no-tree sites with 15 cm by 30 cm insect trap cards (yellow sticky card; Gempler's, Inc.). We adhered a card to a 20 cm by 35 cm piece of cardboard and then clamped a card along a telescoping fiberglass painter's pole at each of 2 m and 5 m heights. We then clamped the pole to the same vineyard post that supported an echolocation recorder system. Insect cards were deployed and collected on the same schedule as were the bat echolocation recorders (5 to 9 days). During this time, the four insect trap cards in a vineyard were up day and night. We therefore designated each full day (24 hr) a 'trap day' for each of the four cards; therefore, four insect trap card days were accumulated for one 24-hr day.

Using a home photo lab and camera stand, we photographed each card with a Nikon D3200 SLR camera. Jeffrey T. Drake, an independent researcher, counted the insects using computer image processing. The insect trap card photographs were processed on a PC using algorithms to separate possible insects from background and other non-insect material (Drake 2009).

Data summary and analyses

We viewed time vs. frequency displays of recordings using the program ANALOOKW (version 3.8c). Potential bat echolocations were separated from non-bat ultrasound via use of two filters. The first filter identified sounds with frequencies ≥20 kHz and durations >2 ms (millisecond). The second filter identified sounds ≥7 kHz and duration ≥5 ms. This second filter was designed to identify potential echolocation calls of California bat species (in the family Mollosidae) that echolocate at low frequencies as they fly in open space. Each file that passed either filter was visually inspected to determine whether it was a bat call. We defined a bat call as either a series of ≥2 echolocation calls each with duration ≥2 ms or a single echolocation call with duration ≥5 ms. Bat calls were then categorized as to whether they were produced by high frequency (≥35 kHz; hereafter HiF) or low frequency (<35 kHz; LoF) echolocating bats, based on minimum frequency. Finally, we used a set of filters designed for use with the Anabat system to identify echolocation calls of species of bats in California (C. Corben, personal communication). Because one bat can produce multiple call records during one night, we could not equate number of calls to the number of bats at a particular site. Instead, we let the number of bat calls be an index of bat activity at the site, as typically done by others (Hayes 1997). Due to an unusually high number of bat calls on several nights, the distributions of bat activity recordings per night were heavily skewed. To achieve normality, we transformed the data using a square root function.

To compare the number of echolocation recordings between tree sites and no-tree sites, we used paired t-tests, one for HiF calls and one for LoF calls. We tested insect counts with ANOVA. For all statistical analyses we used SAS JMP, Version 11 (JMP® Pro 11, SAS Institute Inc., Cary, NC). Differences were considered significant at $\alpha = 0.05$.

Results

Trees

Mean measurements of the six vineyard trees (five valley oak and one blue oak): DBH, 104.7 cm (83.8 to 142.2 cm); height, 19.5 m (12.2 to 29.3 m); canopy radius, 9.8 m (8.1 to 16.0 m).

Bat Activity

During 122 nights, we recorded 4,747 bat calls, 3,677 at tree sites and 1,070 at no-tree sites. Of the bat calls recorded at trees, 2,449 were HiF and 1,228 were LoF. Of the bat calls in open vineyard (no-tree sites), 119 were HiF and 951 were LoF. We recorded significantly more HiF bat calls at trees than in the open vineyard ($t = 5.113$, $p < 0.0001$). In contrast, the number of recordings of LoF bat calls was similar at trees and in the open vineyard ($t = 1.026$, $p = 0.3063$; fig. 2).

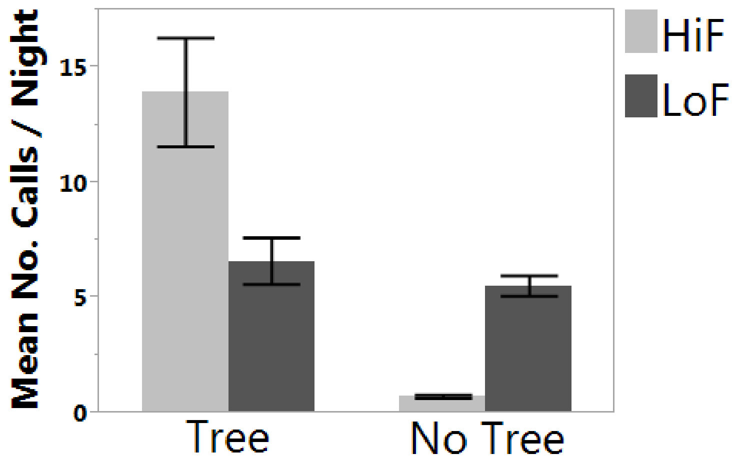

Figure 2—Mean number of bat calls per night that were high frequency (HiF) and low frequency (LoF) calls at vineyard tree sites and no-tree sites in six vineyards in San Luis Obispo County, California.

Bat species

Of the 2,568 HiF recordings at the tree sites (2,449 HiF calls) and no-tree sites (119 HiF calls), 1,213 were assigned to the 50 kHz frequency class and 53 were assigned to the 40 kHz frequency class. The remainder, based on the filters we used, was not assigned to a frequency class. Species comprising the 50 kHz frequency class likely included the California myotis (*Myotis californicus*), Yuma myotis (*Myotis yumanensis*), canyon bat (*Parastrellus hesperus*), and possibly the Western red bat (*Lasiurus blossevillii*). Among these species, it is likely that the majority of the 50 kHz activity was produced by California myotis, as they specialize on foraging near the canopy of trees (Simpson 1993). Other species that may have contributed to HiF bat activity include long-legged myotis (*M. Volans*), little brown bat (*M. lucifugus*), and western small-footed myotis (*M. ciliolabrum*). Of the LoF echolocating species, we were able to identify the Mexican free-tailed bat (*Tadarida brasiliensis*) and the hoary bat (*Lasiurus cinereus*). LoF bat species could also have been pallid bat (*Antrozous pallidus*), big brown bat (*Eptesicus fuscus*), silver-haired bat (*Lasionycteris noctivagans*), fringed myotis (*M. thysanodes*), and Townsend's big-eared bat (*Corynorhinus townsendii*). Mexican free-tailed bats and hoary bats are open-space bats (*sensu* Schnitzler and Kalko 2001) and were identified from similar numbers of calls recorded at tree sites and no-tree sites.

Insects

Over an accumulation of 180 trap card days, we captured 393 insects on 24 insect trap cards, 273 at tree sites and 120 at the no-tree sites. More than twice as many insects were captured in vineyards at trees than at no-tree sites (mean = 3.0 insects/trap day at trees vs. 1.3 insects/trap day at no-tree sites, a significant difference ($t = –2.9$, $p < 0.01$; fig. 3). At the 2-m card height, 2.7 insects per trap day and 1.4 insects per trap day were collected at tree and no tree sites, respectively, and

3.4 insects and 1.2 insects, respectively, at 5 m. There was no difference in number of insects captured between the 2 m card and 5 m card heights (t = –0.35, p = 0.73). Furthermore, similar proportions of insects were collected at both heights at tree sites and no-tree sites; that is, card height did not interact with the presence of the tree (t = 0.83, p = 0.42).

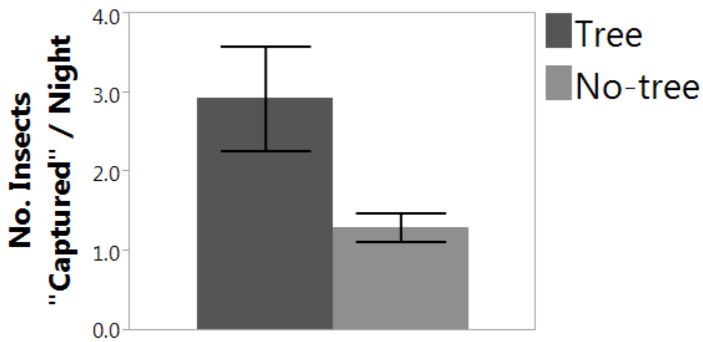

Figure 3—Histogram showing the average number of insects per night collected at tree sites and no-tree sites in six vineyards in San Luis Obispo County, California, 2014.

Discussion

Our study results support our alternative hypothesis that large remnant trees enhance biodiversity within vineyards. We recorded more bat activity and higher insect abundance at trees than at the no-tree locations within vineyards. We found that large-bodied, low-frequency echolocating bats (25 kHz, Mexican free-tailed bats and hoary bats) dominate activity in those areas of the vineyard that lack trees. By contrast, the majority of bat activity we recorded around trees was produced by small-bodied, high frequency echolocators in the 50 kHz frequency group. We expect that most of this activity was by California myotis. This provides compelling evidence that the habitat heterogeneity created by large remnant oak trees may create foraging opportunities in the producing vineyard for another guild of bats. Bats may have been using the oak trees as roosting habitat or foraging habitat, but we strongly suspect the latter. Large oak trees provide rugose bark, hollows, and foliage surfaces that the open vineyard cannot provide to the woodland-dependent suite of bats. The trees also create a microhabitat and wind break that may allow insect prey to move beyond the tree canopy where they become available to open-space (aerial hawking) bats. We do not mean to suggest that the vineyard with trees provides a suitable surrogate for the native oak savanna it perhaps replaced. Our results indicate only that scattered large oak trees may add the structural diversity and prey necessary to support a broader community of bats than would be supported by the comparatively homogenous structure of a treeless vineyard.

Our results are not particularly surprising. Recent studies conducted in other landscape contexts and other parts of the world acknowledge the importance to foraging bats of legacy trees and large remnant trees. For example, Mazurek and

Zielinski (2004) recorded more bat activity at individual old growth legacy trees (*Sequoia sempervirens*), especially those with basal hollows used by the bats for roosting, than at nearby commercially-mature trees. Fuentes-Montemayor and others (2013) working in agricultural areas in Scotland and Lumsden and Bennett (2005) in Australia, showed that, although bat foraging activity was notably higher in more heavily treed habitats, the occurrence of foraging bats in areas with only scattered trees was much greater than in non-treed locations. Fischer and others (2010) reported that with the addition of one or two trees, bat species richness more than doubled and bat activity increased by as much as 10 times. Our study results provide evidence that the large remnant oak tree within a vineyard serves bats' habitat needs in like manner as the scattered tree has been shown to do in other landscape contexts.

Oak trees in vineyards may become increasingly important as vineyard size increases. DeMars and others (2010) concluded that this was the situation for passerine birds in crop fields in the agricultural matrix of the Willamette Valley, Oregon. Those Oregon white oak (*Quercus garryana*) trees that were most isolated had more visits and more species of birds than did trees that occurred in groups. A commercial vineyard on the California Central Coast may be >240 ha in size and devoid of trees. It is likely that use of such a vineyard will be limited to large-bodied, low-frequency echolocating bats. While these bats are voracious predators, particularly where they occur in large numbers (Boyles and others 2011), their prey is limited to large-bodied insects. Lumsden and Bennett (2000) surmised that those bats in the open treeless parts of their study area were only passing through en route to foraging areas. Maintenance of a broader suite of bat species within vineyards may lead to a more diverse set of ecosystem services provided, particularly in the form of insect reduction.

In the Okanagan Valley, British Columbia, open vineyard does not replace the habitat value for bats of nearby native habitat (Rambaldini and Brigham 2011), at least not for the pallid bat (*Antrozous pallidus*). Is it possible that by the retention and maintenance of remnant oak trees within the vineyard, many of the ecological functions of the native oak savanna can be retained? If so, might there be unrecognized benefits to the grape grower? The retention and maintenance of oak trees in the vineyard incur a cost to the grape grower: pruning, water uptake, irrigation system modification, additional end posts, altering of tractor passes, less land in production. Without value to the grower, many of the trees will likely be lost. If bats can be shown to benefit their operations, grape growers may be more willing to maintain oak trees within their vineyards.

To document the ecosystem services provided by bats in vineyards, some important questions need to be answered. Do the bats benefit the grower? For example, do bats eat Lepidopteran grape pests such as cutworm (*Agrotis* spp.) moths and nocturnal leafhoppers (family Cicadellidae) in great enough quantity to make a difference in grape production? Do they prey on the recently introduced light brown apple moth (*Epiphyas postvittana*) and orange tortrix moth (*Argyrotaenia franciscana*)? If these two grape pests become well-established in Central Coast vineyards, could bats make a difference? If so, can grape growers reap the benefits in terms of lower pest loads or reduced use of pesticides? Perhaps, yes. The two most frequently identified bat species in this study, hoary bat and Mexican free-tailed bat, prey on moths. In walnut orchards in the California Central Valley, codling moths (*Cydia pomonella*) parasitize the walnut kernel, causing millions of dollars of damage annually in lost crop and the cost of increased application of insecticides. Long and others (2014) concluded that Mexican free-tailed bats consume enough codling moths to save more than $17,000 in crop loss at an average-sized walnut orchard. If bats can provide similar benefits in vineyards, grape growers will have greater incentive to maintain the remnant trees.

The value of this small-scale study is twofold. It demonstrates that remnant oak trees within the vineyard provide foraging foci for insectivorous bats, due perhaps in part to the larger number of insects that occur at the trees than in the open vineyard. Second, it lays a framework to address larger, more complex questions. How do we conserve biodiversity in the agricultural matrix and how do we document the economic benefits that can accrue to the grape grower? For the scientist, the concern is whether trees in a vineyard enhance the distribution, abundance, survival, reproductive success and diversity of bats in the agricultural matrix. For the grape grower, a foremost concern is whether trees and bats help to provide an integrated pest management program without excessive cost to operations. Addressing these concerns is necessary to inform management guidelines that not only maintain the trees, but that also advance the livelihood of the grape farmer.

Many of the oak trees in vineyards are aging. If not valued in the eyes of the grape grower, most of these trees will be lost. The ecological and economic values of remnant oak trees for insectivorous bats, and for the ecosystem services the bats provide, need to be further documented and, importantly, articulated to growers.

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References

Boyles, J.G.; Cryan, P.M.; McCracken, G.F.; Kunz, T.H. 2011. **Economic importance of bats in agriculture.** Science 332 (6025): 41–42.

DeMars, C.A.; Rosenberg, D.K.; Fontaine, J.B. 2010. **Multi-scale factors affecting bird use of isolated remnant oak trees in agro-ecosystems.** Biological Conservation 143: 1485–1492.

Drake, J. 2009. **Robotic automated pest identification.** In: Safeguarding through science: 2008 accomplishments. Misc. Pub. 1605. Beltsville, MD: U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Center for Plant Health Science and Technology: 28–29. http://www.aphis.usda.gov/publications/plant_health/content/printable_version/CPHST_report_2008.pdf. (12 February 2015).

Fischer, J.; Stott, J.; Law, B.S. 2010. **The disproportionate value of scattered trees.** Biological Conservation 143: 1564–1567.

Frey-Ehrenbold, A.; Bontadina, F.; Arlettaz, R.; Obrist, M.K. 2013. **Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices.** Journal of Applied Ecology 50: 252–261.

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. Agriculture, Ecosystems and Environment 172: 6–15.

Hayes, J.P. 1997. **Temporal variation in activity of bats and the design of echolocation-monitoring studies.** Journal of Mammalogy 78: 514–524.

JMP®, Version Pro 11. SAS Institute Inc., Cary, NC, 1989-2015.

Kunz, T.H.; Braun de Torrez, E.; Bauer, D.; Lobova, T.; Fleming, T.H. 2011. **Ecosystem services provided by bats.** Annuals New York Academy of Sciences 1223(1): 1–38.

Long, R.F.; Bayless, M.M.; Unruh, T.; Ingram, K. 2014. **What's a bat worth to a walnut orchard?** Bats Conservation International. BATS Newsletter 32(1).

Lumsden, L.F.; Bennett, A.F. 2000. **Bats in rural landscapes: a significant but largely unknown faunal component.** In: Barlow, T.; Thorburn, R., eds. Proceedings of the bushcare grassy landscapes conference, Balancing Conservation and Production in Grassy Landscapes. Clare, South Australia: Environment Australia, Canberra: 42–50.

Lumsden, L.F.; Bennett, A.F. 2005. **Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia.** Biological Conservation 122: 205–222.

Manning, A.D.; Fischer, J.; Lindenmayer, D.B. 2006. **Scattered trees are keystone structures—implications for conservation.** Biological Conservation 132: 311–321.

Mazurek,M.J.; Zielinski, W.J. 2004. **Individual legacy trees influence vertebrae wildlife diversity in commercial forests.** Forest Ecology and Management 193: 321–334.

Michael, J.; Tietje, W. 2008. **Bird use of lone oak trees in vineyard vs. savanna in central-coastal California oak woodland—a pilot study.** Transactions of the Western Section, The Wildlife Society 44: 37–42.

Rambaldini, D.A.; Brigham, R.M. 2011. **Pallid bat (*Antrozous pallidus*) foraging over native and vineyard habitats in British Columbia, Canada.** Canadian Journal Zoology 89: 816–822.

San Luis Obispo County Annual Crop Reports. 1990-2013. San Luis Obispo County Department of Agriculture, Weights and Measures. http://www.slocounty.ca.gov/agcomm/Crop_Reports.htm. (12 February 2015).

Schnitzler, H-U.; Kalko, E.K.V. 2001. **Echolocation by insect-eating bats.** BioScience 51(7): 557–569.

Simpson, M.R. 1993. ***Myotis californicus*.** Mammalian Species 428: 1–4.

Tews, J.; Brose, U.; Grimm, V.; Tielborger, K.; Wichmann, M.C.; Schwager, M.; Jeltsch, F. 2004. **Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures.** Journal of Biogeography 31: 79–92.

Threlfall, C.G; Law, B.; Banks, P.B. 2012. **Influence of landscape structure and human modifications on insect biomass and bat forging activity in an urban landscape.** PLoS ONE 7(6) DOI: 10.1371/journal.pone.0038800.