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# Multi-scale analysis of barn owl nest box selection on Napa Valley vineyards

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ABSTRACT

Barn owls (*Tyto alba*) have the potential to remove significant numbers of rodent pests in vineyards, which has prompted viticulturists in California to erect artificial nest boxes to attract owls. This study examined the habitat factors influencing barn owl nest box occupancy as well as farmers' perceptions of barn owls in vineyards in Napa Valley, CA. Nest boxes of variable design and placement were distributed across 65 vineyards that varied in local and landscape habitat composition. We monitored 297 nest boxes in 2015 to develop an occupancy model. We evaluated the performance of the 2015 model by revisiting 150 boxes in 2016 and comparing observed occupancy to the predicted probability of occupancy for each nest box. Barn owls occupied approximately one third of the nest boxes we monitored each year. We used variance decomposition to address cross scale correlations among three nested spatial scales and to analyze the variation in nest box occupancy explained uniquely by predictors at each spatial scale. The home range and nest box scales were the most important spatial scales. At the home range scale, barn owls selected nest boxes surrounded by more hectares of grassland, riparian and mixed forest, and fewer hectares of oak scrub within 1 km of the box. Owls were more likely to occupy nest boxes if they were constructed of wood, facing north and positioned higher off the ground. The model developed in 2015 performed well in 2016, correctly classifying 81.3% of the boxes, and the area under the receiver operating characteristic curve was 0.86. In addition, we surveyed farmers to gauge their perceptions of the utility of barn owls as a component of an integrated pest management scheme in winegrape vineyards. The majority of farmers surveyed installed barn owl nest boxes for the perceived pest management services instead of the potential positive public appeal of improving barn owl habitat.

## 1. Introduction

Agricultural expansion and intensification is one of the primary threats to biodiversity worldwide (Green et al., 2005). Agriculture currently covers over 40% of the world's land area (McLaughlin, 2011), resulting in global habitat loss and agrochemical inputs that impact wildlife and surrounding ecosystems (Coeurdassier et al., 2014; Karp et al., 2012). However, several studies have established that wildlife can provide ecosystem services (e.g. pest control and pollination) to farmers in agroecosystems ranging from coffee farms (Johnson et al., 2010) to mixed agricultural systems (Kross et al., 2016; Meyrom et al., 2009) to vineyards (Jedlicka et al., 2011; Kross et al., 2012) and orchards (Klein et al., 2012). Therefore, encouraging and providing for wildlife in agricultural systems may reduce agricultures impact on biodiversity and diminish the need for agrochemical inputs.

With a growing human population and rising middle class, the demand for luxury agricultural goods, such as coffee, chocolate and wine is increasing (Sumner, 2012). Luxury agricultural products are primarily produced in Mediterranean and tropical climates (Jones et al., 2005; Ricketts et al., 2004), which comprise the most sensitive and biologically rich ecosystems on the planet (Myers et al., 2000). From 1988–2010 wine grape cultivation increased approximately 70% worldwide (Viers et al., 2013). As a result, viticulture is one of the top drivers of land conversion in the Mediterranean biome (Viers et al., 2013).

Rodent pests cause significant damage in vineyards (Moore et al., 1998; Ross, 2009). Pocket gophers (*Thomomys bottae*) and voles (*Microtus* spp.) are the most problematic rodent pests in Napa Valley (Salmon and Gorenzel, 2010). They gnaw bark and roots, and girdle vines, which can lead to slowed growth, productivity and vine death (Ross, 2009). Farmers in Napa Valley, California have invested in the potential benefits of barn owls (*Tyto alba*), a rodent predator, as a possible way to reduce pests by installing thousands of barn owl nest boxes throughout Napa vineyards (Hungry Owl Project, 2014; Tillmann, 2012; Walter, 1994). They are often incorporated as part of an integrated pest management (IPM) plan (Bottrell, 1979).

Barn owls have a worldwide distribution that encompasses a range of habitats, from savannas in Africa to rainforests in Australia, as well as

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agricultural landscapes across Europe and North America (Taylor, 1994). They are experiencing worldwide population declines from a loss of hunting and nesting habitat due to land conversion and urbanization (Hindmarch et al., 2014, 2012a; Taylor, 1994). In natural settings, barn owls nest in tree cavities and rock crevices (Taylor, 1994). When natural nest sites are limited they readily occupy open buildings or nest in artificial nest boxes (Taylor, 1994). Therefore, providing nest boxes is a common practice to increase nesting habitat, and thus sustain barn owl populations (Johnson, 1994).

The efficacy of barn owls for reducing pest damage in California's vineyards has not yet been rigorously tested, but several lines of evidence suggest it has promise. First, barn owls in North America mainly feed on small mammals (Charlton et al., 2013; Parker, 1988). Pellet analyses in California vineyards show that barn owls consume over 80% gophers and 15% voles (Browning, 2014; Kross et al., 2016) in this region. Second, barn owls are valuable predators in a variety of other agricultural systems, including rice paddies (Wood and Fee, 2003) and oil palm plantations (Duckett, 1976) in Malaysia, row crops in Israel (Meyrom et al., 2009), and orchards worldwide (Askham, 1990; Taylor, 1994). Third, anecdotal evidence from California suggests, at least in certain settings, that barn owls can reduce gopher abundance (Browning, 2014), and there is currently substantial gray literature on the subject (e.g. nest box producers, cooperative extension specialists, farming magazines), including several documents that recommend using barn owl nets boxes to attract them to vineyards (Browning, 2014; Byron, 2008; Tillmann, 2012; Walter, 1994).

Although using nest boxes in vineyards to attract barn owls is not a novel idea (Walter, 1994), this system has not been thoroughly examined by ecologists (Byron, 2008; Heaton et al., 2008). This has led to considerable speculation by farmers and nest box manufacturers regarding artificial barn owl nest box placement and design (Browning, 2014; Hungry Owl Project, 2014). Nest box manufacturers provide vague placement guidelines with the purchase of nest boxes (Browning, 2014; Ford, 2014; Hungry Owl Project, 2014) and agree that it is difficult to predict the best locations to increase the chances that a box becomes occupied. Many suggest a trial and error approach, moving the boxes if they are not occupied after 2 years. There are few peer-reviewed studies on barn owl nest box placement from which companies can draw information, and none is focused in vineyards (Charter et al., 2010; Marti et al., 1979; Meyrom et al., 2009).

Further, nest box placement may be irrelevant if the box itself is the wrong shape, size, or material. There are several nest box designs on the market. The majority of the pre-constructed boxes are made of wood, but some are molded plastic (Browning, 2014; Ford, 2014). Most homemade box designs are also of wooden construction (Wade et al., 2012). Lambrechts et al. (2012) point out that nest box design is an important factor that is often overlooked when studying cavity-nesting raptors.

Understanding habitat and nest box characteristics that favor occupancy has obvious practical applications for farmers, but it also has relevance for advancing our understanding of the ecology of barn owls in vineyard ecosystems. In theory, natural selection should operate so that birds select nest sites with positive fitness consequences (Martin, 1996). Ecological traps (Battin, 2004), when birds nest in sites with negative fitness consequences, can emerge especially in habitats that are evolutionarily novel (Bock and Jones, 2004; Misenhelter and Rotenberry, 2000) such as intensely managed agricultural systems. In Napa Valley, much of the natural barn owl nesting habitat has been converted to vineyards over the last 100 years (Skinner, 2002), leaving artificial nest boxes on vineyards as the primary resource for nesting sites. Consequently, it is important to examine nest success to shed light on the value of nest boxes for owls in vineyard ecosystems and to contribute to the literature relating habitat selection to fitness consequences in novel habitats. Therefore, we also monitored the fate of occupied nest boxes and tested whether the factors associated with occupancy also predicted nest success and the number of young fledged.

Birds select nest sites over a hierarchy of spatial scales (Hutto, 1985; Kristan, 2006; Mayor et al., 2009). In the case of barn owls in vineyard landscapes, an owl may choose to occupy some boxes over others based on a combination of landscape characteristics, local vineyard conditions, and nest box attributes. Therefore, we examined the hypothesis that nest box occupancy would correlate with habitat characteristics at multiple spatial scales (Hutto, 1985; Lawler and Edwards, 2006). To test this hypothesis, we monitored nest boxes in 2015 that varied in local and landscape scale habitat composition to develop a model for predicting nest box selection. We evaluated the performance of the model by observing occupancy of a subset of nest boxes in the 2016 breeding season.

We also used written surveys to assess farmers' motivations for installing nest boxes and to gain more knowledge about how farmers perceive the biological and economic benefits of barn owl nest boxes in vineyards. This exploratory survey is meant to supplement the growing body of literature reviewing the motivations behind why farmers incorporate wildlife conservation practices on agricultural lands (Kross et al., 2017) and how their motivations may influence conservation efforts.

We addressed three primary questions with this research. (1) Which habitat characteristics, at interacting spatial scales, best predict nest box occupancy? (2) Does nest box design and placement influence nest productivity? (3) Do farmers in Napa perceive barn owls as beneficial predators on vineyards?

## 2. Methods

### 2.1. Study area

We studied barn owls in Napa Valley, California, approximately 100 km north of San Francisco. The Mediterranean climate, characterized by warm, dry summers and cool, wet winters and a diversity of soil orders (Elliott-Fisk, 1993) make Napa Valley ideal for producing complex wine grapes, resulting in a $13 billion a year industry (Stonebridge Research Group, 2012). Approximately 20,000 ha in Napa Valley and the surrounding foothills have been converted from mixed oak woodlands and deciduous oak-grasslands to vineyards and wineries (Carlisle et al., 2006; Grismer and Asato, 2012). Recent vineyard expansion has nearly doubled the number of wineries since 2002, from 240 to over 400 (Skinner, 2002; Wine Institute, 2014). The remaining oak-grassland is primarily south of the city of Napa. North of Napa, the residual natural habitat in the valley floor changes to mixed oak scrub, and going up slope, to mixed oak and conifer forests (Napa County, 2010).

### 2.2. Study sites

We monitored 297 barn owl nest boxes during the 2015 breeding season (March–July) and a subsample of 150 next boxes, proportionally weighted by occupancy status, during the 2016 breeding season. We contacted vineyard owners and management companies in Napa Valley to request participation in the study, and these contacts led to further contacts (Goodman, 1961), yielding a large and representative sample of nest boxes throughout the valley. We included all functioning nest boxes erected on each participating vineyard in the sample. The sample included nest boxes on 65 vineyards owned or managed by 15 different groups. We defined a vineyard as a contiguous block of grapes managed under the same practices and owned or managed by a single entity. Due to this sampling design nest boxes were haphazardly distributed throughout the valley. Nonetheless, the large sample provided a broad range of conditions, habitats, and box designs useful for examining variables associated with nest box occupancy. All nest boxes were located in, or on the edge of vineyards. The number of nest boxes on a vineyard varied from 1 to 27. The highest density of nest boxes was 27 boxes on approximately 70 ha of vineyard.

**Table 1**
Variables included in model selection to predict barn owl nest box occupancy at three spatial scales in Napa Valley, California. Mean ( ± SD) are included for continuous variables. Only variables from the best AICc models were included in the variance decomposition analysis.

| Variable Name | Variable Description | Mean ( ± SD) |
|---|---|---|
| Nest box scale[a] | | |
| bx_type | Nest box construction (plastic or wood) | Categorical |
| bx_orient | Nest box orientation (vertical or horizontal) | Categorical |
| entr_dir | Cardinal direction of the nest box opening | Categorical |
| ht | Distance from the bottom of the nest box to the ground | 3.0 ± 0.674 |
| hole | Size of the entrance opening (large or small) | Categorical |
| Local scale[b] | | |
| cover_crop | Cover crop planted on the vineyard? (Y/N) | Categorical |
| vin_age | Vineyard age (less than 3 years or over 3 years) | Categorical |
| per_vin | Percent vineyard in 75 m circular plot around nest box | 58.35 ± 21.40 |
| per_road | Percent road in 75 m circular plot around nest box | 5.17 ± 5.15 |
| per_gmarg | Percent grassy margin in 75 m circular plot around nest box | 12.12 ± 8.97 |
| per_nathab | Percent natural habitat in 75 m circular plot around nest box | 20.68 ± 20.19 |
| dist_tree | Distance from nest box to nearest tree (m) | 82.45 ± 110.23 |
| dist_build | Distance from nest box to nearest building (m) | 221.95 ± 166.67 |
| Home range scale[c] | | |
| urb1 | Urban land cover in 1 km circular plot (ha) | 25.29 ± 30.07 |
| grass1 | Grassland land cover in 1 km circular plot (ha) | 66.08 ± 68.85 |
| oak1 | Oak-scrub land cover in 1 km circular plot (ha) | 17.97 ± 31.25 |
| mix1 | Mixed forest in 1 km circular plot (ha) | 17.34 ± 16.97 |
| rip1 | Riparian in 1 km circular plot (ha) | 17.98 ± 16.97 |
| vin1 | Vineyard in 1 km circular plot (ha) | 176.30 ± 93.96 |
| dist_occ | Distance to nearest occupied nest box (m) | 1437 ± 1820 |
| dist_nearest | Distance to nearest nest box (m) | 200 ± 150 |
| lat | Latitude of nest box | N/A |
| long | Longitude of nest box | N/A |

[a] The nest box scale was comprised of variables associated with the design and placement of the nest box.
[b] The local scale included a 75 m circular plot surrounding each nest box, the distance to nearest relevant habitat features and the management practices on the vineyard.
[c] The home range scale measured 6 land cover types within 1 km circular plots around each nest box and included the latitude and longitude of the nest box.

### 2.3. Spatial scales

We measured habitat variables at three nested spatial scales considered biologically relevant to barn owl nest box selection: nest box scale, local scale and home range scale (Charter et al., 2010; Lambrechts et al., 2012; Meyrom et al., 2009; Taylor, 1994; Table 1).

#### 2.3.1. Nest box scale

Explanatory predictors at the nest box scale included five characteristics specific to the nest box design and placement (Table 1). Nest box design and placement are often overlooked factors when conducting raptor studies (Lambrechts et al., 2012) and have been shown to influence nest selection. Charter et al. (2010) found that in an arid environment nest boxes with the entrance facing east or north were more likely to be occupied than other directions. Nest box orientation may be important for internal temperature, light and humidity regulation (Butler et al., 2009). The materials used to construct the nest box may also influence nest box thermoregulation which in some cases has been correlated with box use and nestling survivorship (Charter et al., 2010; Johnson, 1994). This study included both plastic and wooden nest boxes (51 plastic nest boxes and 232 wood boxes in 2015 and 26 plastic and 124 wood in 2016).

#### 2.3.2. Local scale

At the local scale, we included eight environmental factors from three sources to predict occupancy (Table 1). Raptors may select nest boxes based on microhabitat composition immediately surrounding the box (Rohrbaugh and Yahner, 1997). Therefore, within the 75-m plots we visually estimated the percent of four relevant habitat categories. We assessed if the nest box was adjacent to young (less than 3 years) or mature vines (greater than 3 years) because vineyard managers consistently expressed that rodents were more destructive to young vines than mature vines (C. Pedemonte, personal communication). In addition, cover crops on vineyards may provide food or increase cover for rodents (Smallwood, 1996). Accordingly, we considered two categorical variables at this scale: the age of the vineyard (older than 3 years or younger than 3 years), and if the vineyard had a cover crop. Taylor (1994) found that trees and human-made structures near the nest site may provide important roosting sites for adult and fledgling barn owls. Therefore, we measured the distance from each box to the nearest tree and building. Barn owls have been shown to be non-territorial during the breeding season (Browning pers. comm.; Smith et al., 1974) therefore we did not include the distance to the nearest nest box at the local scale, but did include this variable at the home range scale to address autocorrelation.

#### 2.3.3. Home range scale

Barn owls primarily hunt within a 1–2 km radius around the nest site (Colvin, 1985; Read and Allsop, 1995; Taylor, 1994). Ongoing research involving GPS trackers on barn owls in Napa showed that the mean distance traveled away from the box was 808 m and 65% of the points were within 1 km of the nest box (Casteñeda and Johnson, unpublished data). Therefore, we used a 1 km radius buffer around each nest box to calculate land cover types at the home range scale. We obtained land cover raster data from the USDA CropScape (2014) database, which categorized major natural land cover types as well as crop specific agricultural land at a 30 m resolution (statewide accuracy = 84.6%, grape accuracy = 91.95%). In ArcMap 10.1, we aggregated and reclassified CropScape land cover classes into the seven primary land cover types in Napa Valley (Fig. 1). We removed water from the analysis because it was correlated with riparian. We calculated the hectares of each land cover class within the 1 km buffers to use as covariates in a model set for predicting nest box occupancy. The elevation of the next box sites was unlikely to influence occupancy because it varied by only 120 m between the highest and lowest sites; therefore we did not include elevation as a covariate in the model set.

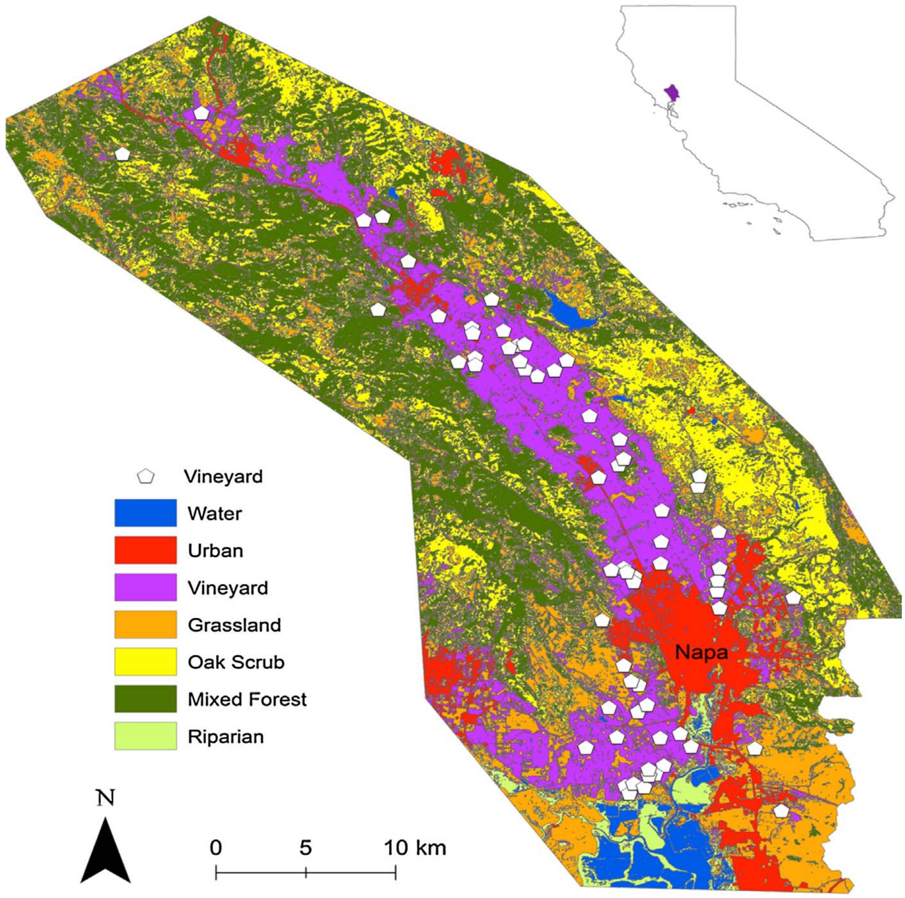


**Fig. 1.** Map of the study area including vineyard locations (n = 65) and the seven reclassified land cover types derived from CropScape data used to inform the home range scale of the nest box occupancy analysis. The inset shows the location of Napa County within California.

Additionally, the home range scale AICc model set included variables to test spatial factors including latitude and longitude of the nest box, distance to the nearest box and distance to the nearest occupied nest box. To assess the degree of spatial autocorrelation for each land cover variable, we calculated Moran's I at 1 km, and we determined the x-intercept of the spline correlogram, which is the distance at which objects are no more similar than that expected by chance alone across the region (Epperson, 1993).

### 2.4. Field techniques

Barn owls in California start selecting nest sites in January and begin laying eggs in mid-February (Browning, 2014). They are sensitive during incubation and may abandon clutches if disturbed (Meyrom et al., 2009; Taylor, 1994, 1991). To minimize disturbance during egg laying and incubation, we checked nest boxes for occupancy from 28 February until 31 March each year (Hoffman, 1999). To monitor nest boxes, we inserted a small camera (IPEVO P2V USB document camera) fitted with an l.e.d. flashlight, mounted on an extendable pole, in through the nest box opening. The camera was connected to a computer showing live stream video. We checked nest boxes every ten days, for a total of three times each during March and considered a nest box occupied if eggs were present (Steenhof, 1987). After 31 March we continued to monitor the occupied nest boxes until they failed or chicks fledged. With this temporal window and nest checking frequency, it is very unlikely that any occupied nest boxes went undetected during this period.

### 2.5. Grower surveys

We created an online survey that was sent to winegrape growers throughout Napa County by the Napa Valley Farm Bureau and Napa Valley Grapegrowers Association (see supplemental data for complete survey). This was an exploratory survey with the purpose of gathering information on farmers' perceptions of barn owls as an effective method of rodent control in vineyards. This was the first known grower survey specifically of barn owls in this region. Results from this survey can be used to direct future research and gauge farmer interest in this research topic. The survey included 14 short answer, multiple choice and rank order questions. The questions addressed four topics, 1) rodent control methods and rodent damage, 2) future barn owl research ideas, 3) current use of barn owl boxes on vineyards, and 4) the value of barn owl boxes as an IMP tool. We collected one survey, filled out by the lead viticulturist or vineyard manager, per vineyard management company or vineyard. The survey was designed to collect information on current and future management practices, not personal opinions of the value of barn owl boxes. We analyzed select questions (Table 2).

We tallied the responses from the survey and calculated the percentage of farmers in each category for select questions. Then used a Chi-squared test to compare the distribution of responses between the two opposing Likert scale questions that explored if growers think the use of barn owl nest boxes has a legitimate IPM value, or whether nest boxes are good for owls and contribute to positive public relations, but have little chance to meaningfully control rodent pests.

### 2.6. Models

#### 2.6.1. Nest box occupancy

We used a variance decomposition analysis (Lawler and Edwards, 2006) to determine the variation in nest box occupancy explained uniquely by each spatial scale, and the cross-scale correlations from the nested spatial scales. This technique involved first fitting and ranking models at each of the three spatial scales, nest box (BX), local (LO), and home range (HR). We then constructed a model for each of the three

**Table 2**
Select questions that were analyzed from the farmer survey.

| Questions From Grower Survey | Responses |
|---|---|
| What methods does this company/vineyard use to control rodents? | Multiple choice: Trapping, Poison Bait, Barn Owls, Burrow Builder, Other |
| How effective are barn owls at reducing rodent damage on your vineyards? | Ordinal scale: Not Effective, Moderately Effective, Very Effective |
| Setting up barn owl nest boxes is good for the owls and contributes to positive public relations, but has little chance to meaningfully control rodent pests. | Likert scale, 1–5, disagree to agree |
| Utilizing barn owl nest boxes has a legitimate value in an integrated pest management plan to help control rodent pests. | Likert scale, 1–5, disagree to agree |

possible combinations of two scales using the variables from the top model at each scale (BX + LO, BX + HR, LO + HR), as well as a full model combining the top variables from each of the three scales (FULL), yielding seven models in all. Before proceeding to model fitting, we tested and removed correlated explanatory variables within each spatial scale ($r > 0.6$). We used Program R (R Core Team, 2013) for all statistical analyses. We constructed model sets for each scale based on biological hypotheses formulated from field observations, data exploration and literature searches. Models were fit using logistic regression and maximum likelihood estimation with the response variable classified as occupied or unoccupied. We used Akaike Information Criterion corrected for small sample size (AICc) model selection to evaluate competing models within each scale (Burnham and Anderson, 2002) and assessed model fit for each selected model using the Pearson chi-squared test.

We used the seven models from the AICc to calculate the deviance explained uniquely by each scale (called pure components of variation) and the deviance explained by two or more scales (called shared components of variation). Using the formulae below, we isolated each element of deviance by subtracting different components from the full model. The p and s terms refer to the pure and shared components of variation and d is the deviance explained by the model. Equations 1–3 computed the three components of pure variation, which were then used to calculate the four components of shared variation (Eqs. (4)–(7)).

$$p(HR) = d(FULL) - d(LO + BX) \tag{1}$$

$$P(LO) = d(FULL) - d(HR + BX) \tag{2}$$

$$p(BX) = d(FULL) - d(HR + LO) \tag{3}$$

$$s(HR + LO) = d(FULL) - d(BX) - p(HR) - p(LO) \tag{4}$$

$$s(LO + BX) = d(FULL) - d(LO) - p(HR) - p(BX) \tag{5}$$

$$s(LO + BX) = d(FULL) - d(HR) - p(LO) - p(BX) \tag{6}$$

$$\begin{aligned} s(HR + LO + BX) = d(FULL) - p(HR) - p(LO) - p(BX) \\ - s(HR + LO) - s(HR + BX) - s(LO + BX) \end{aligned} \tag{7}$$

### 2.6.2. Testing the occupancy model

We used a prospective sampling method (Fielding and Bell, 1997) to evaluate the accuracy and usefulness of the full model developed in 2015. We revisited 150 boxes in 2016 and compared observed occupancy to the predicted probability of occupancy for each nest box with the full model from 2015. We evaluated the performance of the model by calculating the correct classification rate, the kappa statistic (Allouche et al., 2006), and the threshold-independent receiver operating characteristic (ROC) curve. The correct classification rate is an easily calculated and interpretable metric useful for comparisons with other studies. The kappa statistic provides a robust measure of predictive accuracy for cases in which a threshold value is necessary for practical model application (Allouche et al., 2006), and scores $> 0.4$ and $> 0.75$ are considered good and excellent, respectively. For both of these measures we used a threshold of 0.35 based on our observed prevalence in 2015 (i.e., boxes with predicted probabilities of occupancy greater than or equal to this value were considered to be predicted presences for calculation purposes). We constructed the ROC curve using the test data by plotting true positive points (occupied nest boxes) against the false positives (1- specificity) using the PresenceAbsence package in Program R (Fielding and Bell, 1997). An area under the curve (AUC) value of 0.5 indicates a model accuracy of 50% in predicting positives, which is no better than random assignment (Zweig and Campbell, 1993). An AUC value of 1.0 means that the model correctly classified 100% of the points (Zweig and Campbell, 1993). Models with AUC values exceeding 0.7 are considered to have good predictive power (Herrick et al., 2013).

### 2.6.3. Nest success

If evolutionary processes drive nest box selection then barn owls should select nest boxes in habitats that provide sufficient resources to support nest productivity and success (Clark and Shutler, 1999; Martin, 1996). To test this prediction, we fit and ranked two model sets using the explanatory variables derived from the occupancy analysis to predict nest success and productivity. We used GLM logistic regression to determine if the variables associated with occupancy also predict nest success or failure ($n = 90$ boxes monitored for success; response = 1 or 0, with any nest fledging at least 1 chick considered successful) by ranking five models, one for each of the three spatial scales, the full model and a null model, using AICc. We fit and ranked the same set of predictors using linear regression models (response variable = number of chicks fledged) to determine if the variables associated with occupancy also predict the number of chicks fledged from successful nest boxes ($n = 68$).

## 3. Results

Barn owls occupied approximately one third of the nest boxes in each year (2015 barn owls occupied 91/297 nest boxes; 2016 barn owls occupied 53/150 nest boxes). Fourteen of the nest boxes were “new” in 2015 (erected during the previous year) and none became occupied; therefore we excluded them from the occupancy model, for a final sample size of 283 nest boxes. Overall, 66% of the boxes that were occupied in 2016 had also been occupied in 2015; 35 of those occupied in 2015 remained so in 2016, and 86 of those unoccupied in 2015 remained so in 2016. Fifty seven percent of the boxes that were occupied in both years fledged chicks both years. Ten boxes that failed in 2015 successfully fledged chicks in 2016, and 4 boxes that fledged chicks in 2015 failed in 2016.

The average distance from a nest box to the nearest occupied nest box was 1437 ± 1820 m. At 1 km, Moran’s I values averaged 0.52 over all land cover variables, and the average x-intercept in spline correlograms (the distance at which boxes’ land cover surroundings are no more similar than that expected by chance alone) was 4840 m. Of all possible box-pairs distances (39,903), only 6850 (17%) were closer than 4840 m.

**Table 3**
The best models from the AICc model selection, for each spatial scale and combinations of spatial scales, and the percent deviance explained (% DE) of the seven logistic regression models used to explain barn owl nest box selection. Variable names are described in Table 1.

| Model | Variables | AICc | % DE |
|---|---|---|---|
| Full | grass1 + mixed1 + oak1 + rip1 + cover_crop + dist_build + dist_tree + per_gmarg + vin_age + bx_typ + entr_dir + ht | 241.33 | 41 |
| Home range + Local | grass1 + mixed1 + oak1 + rip1 + cover_crop + dist_build + dist_tree + per_gmarg + vin_age | 257.34 | 33 |
| Home range + Box | grass1 + mixed1 + oak1 + rip1 + bx_typ + entr_dir + ht | 232.6 | 40 |
| Local + Box | cover_crop + dist_build + dist_tree + per_gmarg + vin_age + bx_typ + entr_dir + ht | 305.26 | 20 |
| Home range | grass1 + mixed1 + oak1 + rip1 | 256.59 | 31 |
| Local | cover_crop + dist_build + dist_tree + per_gmarg + vin_age | 330.26 | 10 |
| Box | bx_typ + entr_dir + ht | 315.73 | 15 |

### *3.1. Nest box occupancy models*

The full model from the AICc explained 41% of the variation in nest box occupancy (Table 3). At the nest box scale, boxes were more likely to be occupied if they were constructed out of wood, facing north and positioned higher off the ground (max = 5.5 m). At the local scale, the probability of nest box occupancy was positively associated with the percent of grassy margin within the 75 m plot, the presence of a cover crop on the vineyard, and the distance to trees near the nest box. Young vineyard was negatively correlated with occupancy at the local scale. At the home range scale, barn owls selected nest boxes surrounded by more hectares of grassland, riparian and mixed forest, and fewer hectares of oak scrub within 1 km of the box (Table 4). Neither distance to the nearest nest box nor distance to the nearest occupied nest box were included in the top model from the AICc analysis. Likewise, latitude and longitude were not as competitive as the habitat variables, suggesting nest box occupancy was more strongly predicted by habitat than by associations in space caused by simple clumping or spatial autocorrelation.

The variance decomposition analysis examined the deviance explained uniquely by the predictors at the three spatial scales, relative to each other (Table 5). Predictors at the home range scale contributed to the majority of the deviance explained in nest box selection (30% total including pure and shared components). The home range scale uniquely explained almost half (20% out of 42%) of the variation in box occupancy. Nest box scale variables explained 14% of the total variation (combining pure and shared components), and 7% uniquely. The pure components of variation from factors only at the nest box and home range scales explained 65% ((20% + 7%)/41%) of the total explained variation in nest box selection. The pure variation at the local scale did not contribute to the overall variation and the shared deviance explained with combinations including the local scale, were minimal (9%). Overall, cross- scale associations contributed much less to the percent deviance explained than factors at each individual scale.

**Table 4**
Odds ratios and 95% confidence intervals for each variable in the full model, which includes predictors from the top model at each spatial scale (AICc = 241.33, %DE = 41). Variables are ordered from most to least important. Only the significant categories were included for the categorical variables.

| Variable | Odds Ratios | 95% CI |
|---|---|---|
| wood box | 7.133 | (1.425, 64.107) |
| height | 3.378 | (1.798, 6.605) |
| facing north | 1.541 | (0.683, 3.471) |
| riparian (ha) | 1.027 | (1.006, 1.051) |
| grassland (ha) | 1.017 | (1.011, 1.024) |
| mixed forest (ha) | 1.012 | (0.989, 1.032) |
| dist. tree | 1.001 | (0.997, 1.004) |
| dist. building | 1 | (0.998, 1.003) |
| percent grassy margin | 0.999 | (0.959, 1.039) |
| oak scrub (ha) | 0.914 | (0.857, 0.963) |
| facing west | 0.872 | (0.253, 2.908) |
| cover crop (yes) | 0.814 | (0.256, 2.644) |
| young vineyard | 0.554 | (0.151, 0.833) |

**Table 5**
Variation in nest box locations explained by three scales of habitat predictors. Pure components of variation were attributed to factors at a single scale. Shared components of variation were explained by factors at multiple scales due to cross- scale correlations. We algebraically manipulated the deviance explained from seven logistic regression models to calculate the total deviance explained by each of these components.

| Isolated components of variation | % total deviance explained |
|---|---|
| Pure (Box) | 7 |
| Pure (Home range) | 20 |
| Pure (Local) | 0 |
| Shared (Local + Box) | 3 |
| Shared (Home range + Box) | 3 |
| Shared (Home range + Local) | 5 |
| Shared (Home range + Box + Local) | 3 |

### *3.2. Testing the occupancy model*

The occupancy model we developed in 2015 preformed well in 2016. With a threshold of 0.35, the correct classification rate was 0.813 and the kappa statistic was 0.59. The omission error rate (false negatives) was 8%, and the commission error rate (false positives) was 11%. The AUC of the ROC curve for the testing data (2016 occupancy results) was 0.86.

### *3.3. Nest success models*

The same models used to predict nest box occupancy failed to accurately predict nest success or failure. Of the five GLM logistic regression models used to predict nest box success or failure, the null model had the lowest AICc value. Similarly, the null model from the five linear regression models used to predict the number of chicks fledged from successful boxes also had the lowest AICc value.

### *3.4. Grower surveys*

There were a total of 40 responses to the surveys, but not all participants answered every question. Eleven of the respondents participated in the nest box occupancy research. Most of the respondents (82%, $n = 36$) installed barn owl nest boxes to suppress rodents, but all respondents supplemented barn owl boxes with additional rodent control methods such as rodenticide application or trapping. Overall, 93% of vineyard managers surveyed indicated that barn owls are moderately or very effective at reducing rodent pests on their vineyards ($n = 33$). Significantly more respondents strongly agreed that erecting barn owls boxes can provide a viable method for rodent control as part of an integrated pest management plan as opposed to only providing value to barn owls and increasing public appeal, but not meaningfully controlling rodent pests ($\chi^2 = 31.52$, df = 4, $p < 0.001$, Fig. 2).

## 4. Discussion

This study built upon the growing body of literature examining how wildlife uses agricultural habitats. We assessed barn owl habitat use in a

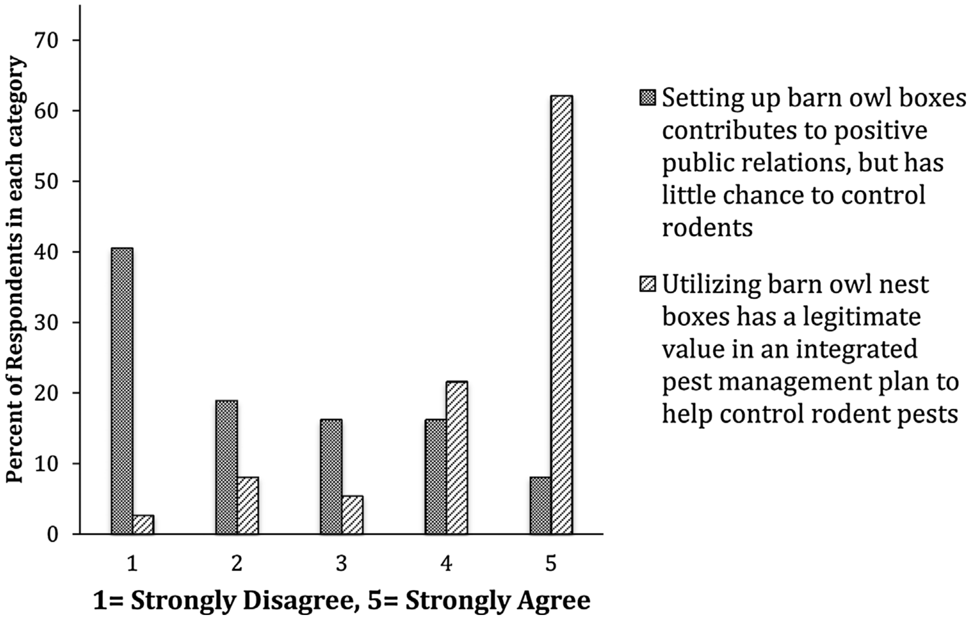


**Fig. 2.** Responses from the grower survey ($n$ = 37) showing the results of two questions designed to gauge the value of barn owls as either a legitimate IPM tool or simply a public relations tool with no pest management applications. The distributions of responses were different between the questions ($\chi^2$ = 31.52, df = 4, p < 0.001). Respondents disproportionately agreed that barn owls have a legitimate value as an IPM tool in vineyards.

vineyard ecosystem and the potential benefits to barn owls and farmers Barn owls selected artificial nest boxes based on landscape characteristics over fine scale local habitat variability surrounding the nest site. Specifically, they tended to occupy nest boxes with more hectares of grassland, mixed forest, and riparian habitat within 1 km. Nest box attributes introduce unique factors not shared with local and home range scale habitat. Specifically, in this system barn owls selected taller, wooden nest boxes that were facing north. The combined importance of these two spatial scales implies that well designed nest boxes must be placed in desirable coarse scale habitats to attract barn owls. The model was also a useful applied predictor that should be tested in other regions and agricultural crops suitable for barn owls.

The strong positive correlation between occupied nest boxes and the hectares of grassland habitat within the home range was not surprising as barn owls are frequently associated with open, grassy and agricultural habitats (Hindmarch et al., 2012a; Read and Allsop, 1995; Taylor, 1994; Wingert, 2015). It is well established that declines in barn owl populations are linked with agricultural intensification and the loss of grassland habitat due to the expansion of cultivated land and urban development (Butler et al., 2015; Colvin, 1985; Hindmarch et al., 2014, 2012b; Taylor, 1994). Growers erect nest boxes hoping that barn owls will hunt on their vineyards, yet occupancy is associated with grassy habitat adjacent to vineyards suggesting that future research should examine the extent to which barn owls nesting in vineyards actually forage for rodents on the vineyards versus surrounding natural habitats. Even if barn owls are not hunting directly in vineyards there may be positive spillover effects if they are reducing the overall abundance of rodents in grasslands adjacent to vineyards. It is estimated that one pair of barn owls and their chicks can consume over 3000 rodents a year (Browning, 2014).

Additionally, barn owls selected boxes based on nest box design and orientation, showing a strong selection for wooden boxes, which were seven times more likely to be occupied than plastic boxes (Table 4; 2 occupied of 51 plastic boxes vs. 89 occupied of 232 wooden boxes). Wood boxes are more similar to natural nesting cavities in trees than plastic nest boxes. Nest box orientation and construction have been correlated with thermoregulation in hot environments. Further research on how nest box orientation influences internal temperatures is warranted. Studies of American kestrels (*Falco sparverius*) nesting in artificial wooden boxes found that nest box design influenced the internal temperature, light levels and humidity of boxes, which in turn impacted chick survivorship (Butler et al., 2009; Charter et al., 2010). In regions with different climates (e.g., the hotter Central Valley of California), variation in internal temperature due to box construction may render some box materials more favorable than others. An examination next box age, as well as nest site fidelity for successful and non-successful individuals, would enhance out understanding of nest box preference.

### 4.1. Nest success

Approximately 75% of the occupied nest boxes in this study successfully fledged young each year. This is comparable to studies in other regions, for example Gubanyi et al. (1992) had a 75% success rate in nest boxes placed in mixed agriculture in Nebraska and Browning (unpublished data) had a 72% success rate in central California vineyards.

Nest survival and reproductive success are products of nest site choice and result in evolutionary selection pressures for nest-site preferences (Clark and Shutler, 1999; Kolbe and Janzen, 2002; Martin, 1998). Variation in habitat, predation and food resources surrounding nest sites produce variation in nest success, allowing for fitness consequences based on nest choice (Martin, 1995). If this variation is persistent and perceptible by birds, then natural selection should operate such that the predictors of nest-site occupancy also correlate with nest success (Clark and Shutler, 1999). The predictors of nest box occupancy in this study did not correlate with nest success or the number of chicks fledged in successful boxes.

Studies on barn owls in other regions (e.g. United Kingdom and British Columbia, Canada) have found similar disconnects between the habitat surrounding nest sites and nest success (Bond et al., 2005; Hindmarch et al., 2012b) Here we provide a few explanations for the misalignment in this study. We evaluated nest success during a single season and patterns may not emerge in short-term nest selection like they would over long-term selection (Clark and Shutler, 1999). An alternative approach would be to measure reproductive success throughout a full year, as barn owls can potentially breed multiple times a year in California. This disconnect is be especially true in stochastic environments such as agricultural systems where prey availability may oscillate more dramatically than in natural environments (Colvin, 1985; Martin et al., 2010). Barn owls may be unable to predict constantly changing vineyard conditions caused by seasonal mowing, tilling and artificial watering that impact the movement and availability of prey. An abundance of rodents early in the season, when barn owls are choosing nest boxes, may prompt farmers to apply rodenticides, depleting the food resource when it is most needed, causing barn owl nests to fail or fewer chicks to fledge. Future research should examine the direct and indirect impact of rodenticides on owls, and demographic work should determine whether nest boxes in vineyards may, in some cases, operate as ecological traps (i.e., selected habitat sinks; Battin, 2004; Klein et al., 2007).

Annual climactic variation impacts nest success and selection in the short term, but may not be indicative of long-term trends. California was experiencing an exceptional drought in 2015 and had been in a moderate to severe drought since 2012 (State of California, 2015) which causes annual fluctuations in rodent populations (Bradley et al., 2006). Barn owls populations decline when rodents decline (Taylor, 1994; Widen, 1994), thus analyzing a single season of nest success data during a drought year may be insufficient for understanding the relationship between nest selection and nest success.

Additionally, nest boxes were usually placed in a way that was convenient for the farmer and farming equipment, often without taking local or landscape scale factors into account. Artificial nest boxes attract owls with limited natural nest sites, and nesting in boxes may influence biological processes such as clutch size, hatching rates, fledgling success, disease vectors and predation rates (Johnson, 1994; Lambrechts et al., 2012), differently than natural nest sites, thus potentially masking natural patterns related to habitat quality (Bock and Jones, 2004).

### 4.2. Grower surveys

Responses from grower surveys indicate that there is strong support for barn owl nest boxes in Napa Valley. The growers we surveyed primarily deployed boxes to exploit the possible IPM benefits barn owls may provide by removing rodent pests, over the benefits to the owls themselves and/or positive public relations. Our exploratory surveys did not distinguish between or measure the relative strength of non-IPM benefits, which may be a fruitful line for future research to better understand farmer motivations for the use of barn owl nest boxes. This may not hold true with farmers in other regions, or for other crops. Most farmers in the survey indicated that barn owls are moderately or very effective at reducing rodent pests in vineyards, even though ecologists are still seeking evidence to support this claim (Kross et al., 2016; Marsh, 1998; Van Vuren et al., 1998). However, even though the majority of respondents use barn owl nest boxes they also indicated that they use additional rodent control methods, suggesting that barn owls alone are not sufficient at reducing rodent pests to an acceptable level. Even if barn owls do not eradicate rodents outright they may reduce populations to a manageable level (Van Vuren et al., 1998) and make other rodent suppression methods more effective. For example, attracting barn owls may reduce the trapping effort needed on vineyards experiencing a rodent outbreak, and therefore reduce costs.

## 5. Conclusion

This study examined the habitat factors associated with barn owl nest box selection on vineyards in Napa County and highlighted the importance of exploring complex ecological systems at multiple spatial scales. In this study individual spatial scales, especially the landscape scale, influenced nest box selection more than the interactions between spatial scales. There needs to be more research on the effectiveness of barn owls at reducing rodent pests; however deploying appropriately designed nest boxes within suitable landscapes may increase the potential for pest removal services. Although vineyard owners do not have control over where established vineyards are located on a landscape scale, they do have control over the nest box design and placement at a local scale, which may improve occupancy rates and therefore increase biological control of rodents. Although the short duration of this study did not show patterns of adaptive nest site selection, providing nest boxes when natural nest sites are limited may benefit barn owl populations in Napa. If the majority of farmers install nest boxes primarily for the biological control of rodents and barn owls are dependent on grasslands surrounding vineyards, there may be an incentive to conserve rapidly disappearing grassland habitat in Napa valley. A growing consumer demand for sustainability produced luxury goods may also lead to financial benefits to vineyard owners who attract barn owls and conserve natural landscapes.

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