HUNTING HABITAT USE AND SELECTION PATTERNS OF BARN OWL (*TYTO ALBA*) IN THE URBAN-AGRICULTURAL SETTING OF A PROMINENT WINE GRAPE GROWING REGION OF CALIFORNIA

By

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ABSTRACT

HUNTING HABITAT USE AND SELECTION PATTERNS OF BARN OWL (*TYTO ALBA*) IN THE URBAN-AGRICULTURAL SETTING OF A PROMINENT WINE GRAPE GROWING REGION OF CALIFORNIA

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Large scale conversion of uncultivated land to agriculture threatens wildlife and can diminish ecosystem services provided by nature. Understanding how wildlife provision ecosystem services may incentivize wildlife conservation in agricultural landscapes. Attracting barn owls (*Tyto alba*) to nest on farms for pest management has been documented worldwide, but has not been thoroughly evaluated in vineyard agroecosystems. Napa Valley, California is a renowned winegrape growing region, and viticulturists encourage barn owl occupancy to help minimize plant damage from pocket gophers (*Thomomys bottae*) and voles (*Microtus* spp.). This study aimed to establish a basis for revealing the abilities of a predator to provide an ecosystem service to farmers by modelling space and time use of selected habitats. I constructed intensity of use and home range-movement maps using a Time Local Convex Hull (T-LoCoH) analysis from location data obtained from nesting owls. I found that barn owls selected uncultivated habitats when hunting, some of which were relatively rare on the landscape. Though owls did not use them in proportion to their availability, approximately one third of barn owl hunting locations occurred in vineyards. A final analysis showed that the owls' use of vineyards increased with decreasing amount of preferred uncultivated habitat in the landscape. However, as reported by a previous study, occupancy of nest boxes in vineyards increases with uncultivated habitats nearby. Future research should model landscape composition to determine the amount of preferred habitat necessary to support occupancy as well as hunting in vineyards.

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food, connecting me to where that food comes from and showing me the importance of a balanced farm ecosystem.

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INTRODUCTION

The conversion of uncultivated lands to agriculture has resulted in drastic declines in habitat quantity and quality and has become a primary threat to biodiversity (Green et al. 2005, McLaughlin 2011). Steady global population growth, expansion and intensification of agriculture not only degrades land, it often coincides with increased use of expensive agrochemical inputs (Matson et al. 1997, Tillman et al. 2011, Grismer and Asato 2012). This commonly impairs the ability of agroecosystems to provide non-marketed services such as water purification, pollination and pest control (Swinton et al. 2007). This has stimulated interest in research and alternative management practices devoted to alleviating detrimental impacts to ecosystems while also promoting factors that support non-market services (e.g., wildlife; Power 2010, Hannah et al. 2013). Many studies have shown that wildlife can benefit agroecosystems (tropical coffee farms, Johnson et al. 2010; semi-arid mixed agricultural systems, Meyrom et al. 2009; vineyards, Jedlicka et al. 2011, Kross et al. 2012; orchards, Klein et al. 2012; field crops, Kremen et al. 2002). Thus, managing for wildlife that provide beneficial services may be valuable to farmers and contribute to reducing negative impacts caused by expansion and intensification of agriculture across the globe (Ricketts et al. 2004, Green et al. 2005).

In regions with unique and sensitive habitats, land use conversion continues to be the greatest threat to loss and disruption of uncultivated environments (Myers et al. 2000, Wood et al. 2013). The Mediterranean biome, which includes portions of California, is known to have some of the highest concentrations of biodiversity and endemism on the planet, but remains minimally protected (Myers et al. 2002, Viers et al. 2013). Despite this biome's sensitivity and recognized importance to biodiversity, there has been a worldwide increase in the conversion of land within the Mediterranean biome, particularly for the production of winegrapes (Viers et al. 2013). California vineyards account for over 90 percent of all wine grapes grown in the United States, an industry valued at nearly 3 billion dollars in 2014 (CDFA 2014). Within California, Napa Valley wine and associated tourism have proven to be a dominant contributor to both state and national economies, and show no signs of slowing down (Stonebridge Research Group 2012). Due to California viticulture's heightened visibility in the public eye, its economic importance, and its impacts on wildlife, growers are seeking ways to promote more environmentally sustainable practices while maintaining profitability (Poitras and Getz 2006, Viers et al. 2013).

Integrative pest management development is critical for improving sustainability in agricultural industries. In Napa Valley, pocket gophers (*Thomomys bottae*) and voles (*Microtus* spp.) are rodents that pose the greatest nuisance to farm functionality, threaten the health of the vines, and can cause significant economic losses (Ross 2009, Salmon and Baldwin 2009, Salmon and Gorenzel 2010). By cutting roots and gnawing bark, rodents can slow the growth and productivity of vines, and in extreme cases can kill the plants (Ross 2009).

Implementing integrated pest management programs that utilize natural predators along with more traditional techniques can prove to be useful in effectively managing rodent pests (Bottrell 1979, Kogan 1998, Baldwin et al. 2014, Coeurdassier et al. 2014).

Life history attributes of barn owls (*Tyto alba*) suggest they could be part of such pest management systems in vineyards (Labushagne et al. 2016). Barn owls when nesting act as central place foragers, produce large numbers of young, nest in close proximity to each other, are easily attracted to nest boxes, and feed primarily on rodents (Lyman 2012, Browning et al. 2017). Barn owls are widely distributed globally, being found in a diverse number of habitats ranging from dry savannas to rainforests and adjust well to live near human settlements and farms, especially throughout North America and Europe (Johnsgrad 1988, Taylor 1994). Despite their near cosmopolitan distribution, barn owl populations still face significant negative pressures due to loss of nesting habitat and hunting areas as a result of increased land conversion from uncultivated environments (Colvin 1985, Taylor 1994, Bond et al. 2005, Hindmarch et al. 2014). In unaltered habitats, barn owls nest in cavities found in trees, rock faces, or create cavities through excavation (Martin 1973, Taylor 1994). Where natural nest sites are limited, barn owls are known to utilize human-made structures such as barns or artificial nest boxes (Marti et al. 1979, Taylor 1994). The potential for natural predators, such as barn owls, to help control rodent pests may be an incentive for farmers to adapt integrated pest control practices that attract and sustain wildlife, specifically barn owls, on their farms (Labushagne et al. 2016). In doing so, farmers could meet their need for reduced costs in pest management, all while reducing impacts on a heavily stressed, sensitive environment (Viers et al. 2013).

The practice of attracting barn owls to nest on farms for pest management has been documented in various agricultural settings, from rice and oil palm fields in

Malyasia (Duckett 1976, Wood and Fee 2003), to alfalfa in Israel (Meyrom 2009, Kan et al. 2014), to row crops in Utah (Marti 2010), to sugarcane in Florida (Martin 2009). However, the use of barn owls for pest control in vineyards has only been recommended, not robustly evaluated (Byron 2008, Tillmann 2012), and further examination of this system is warranted. A recent study in Napa Valley vineyards revealed that barn owls select nest boxes with nearby grassland, mixed-forest, and riparian habitats (Wendt and Johnson 2017). Open, grass-dominated habitat is also preferred when hunting (Evans and Emlen 1947, Fast and Ambrose 1976). Barn owls have also demonstrated the ability to hunt successfully in lightly wooded environments as well as along urban edges (Evans and Emlen 1947, Fast and Ambrose 1976).

In a heterogeneous landscape, predators must balance costs and benefits when selecting habitats for hunting (Rosenberg et al. 1999). Mobile predators, such as barn owls, have the ability to evaluate conditions across large spatial scales to determine where hunting efforts may be most cost effective (Pyke et al. 1977). During the breeding season when provisioning prey to young, an optimally hunting barn owl must balance costs of prey depletion and travel to determine whether hunting close to a nest may be more cost effective than travelling further to a more bountiful hunting area (Rosenberg et al. 1999). In Napa Valley, these balances may influence the likelihood of a barn owl hunting on a vineyard where its nest is located. Identifying habitat composition across the landscape and evaluating the hunting range and habitat preference of barn owls can provide useful knowledge to famers for directing management practices that promote and sustain barn owl hunting in and around their farms.

This study sought to document hunting habitats of barn owls in Napa’s winegrape vineyards by addressing the following objectives: 1) Determine hunting habitat selection by comparing habitats used while hunting to overall habitat availability, 2) Model the intensity of use of different habitats within the owls' hunting range, and 3) Examine the effect of landscape composition on barn owl use of vineyards when hunting. The study aims to identify habitats that support barn owls hunting in and around vineyards. Data gathered from this study can provide important information to farmers for attracting barn owls to farms, and aid to reveal the role of landscape composition on the delivery of regulating services such as rodent pest removal by a highly mobile predator.

MATERIALS AND METHODS

Study Area

Napa Valley is approximately 100 km north of San Francisco California (Figure 1). The Valley sits between two mountain ranges, the Vaca Mountains to the east and the Mayacama Mountains to the west (Napa Valley Vintners 2015). The Valley stretches for 80 km from the flats near San Pablo Bay in the south to the peak of Mount Saint Helena at 1,323 m in the north (Napa Valley Vintners 2015). A mild Mediterranean climate hosts native vegetation consisting of coastal scrub near the bay to oak woodlands, oak savannas, and mixed forests in the north (Warner 2007). Numerous microclimates created by elevation and coastal gradients throughout the Valley make this region ideal for growing a variety of wine grape cultivars (Napa Valley Vintners 2015). Recent vineyard expansion has shown an approximate 50% increase in acreage of new vineyards over the past thirteen years (Skinner 2002; Napa Valley Vintners 2015).

The vineyards in this study have been part of ongoing research started in spring 2014 by Wendt and Johnson (2017). Vineyards included in the study were distributed throughout Napa Valley and varied in size, surrounding habitat, urban densities, growing techniques, and nest box densities (Wendt and Johnson 2017).

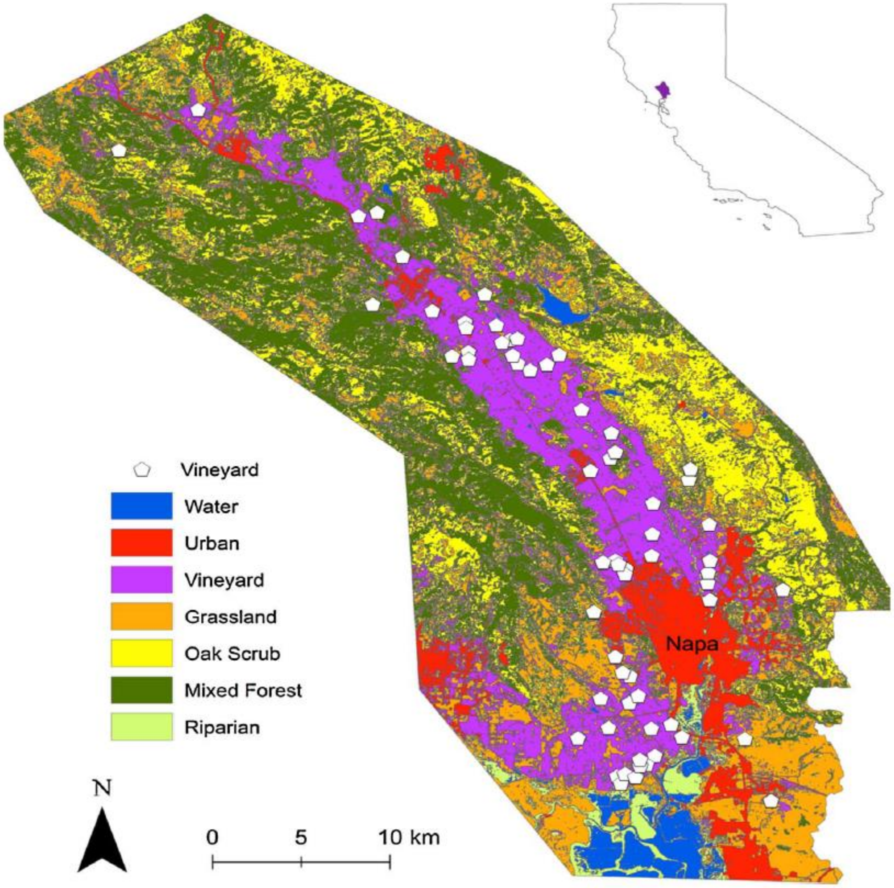


Figure 1. Location of Napa Valley within California, Approximately 161 kilometers NE of San Francisco (inset). The distribution of vineyards (white polygons) that were surveyed for the presence of barn owls in spring 2016 (Wendt and Johnson 2017).

Field Methods

Establishing Occupancy and Nest Box Monitoring

Protocols established by Wendt and Johnson (2017) were used to determine nest box occupancy and subsequent monitoring for this study. In California, barn owls begin nest site selection as early as January with first eggs being laid by mid-February (Browning 2014). Nest boxes were checked for occupancy from 28 February until 31 March, 2016. Nest monitoring was done using a GoPro HERO Session camera that was mounted with an l.e.d. flashlight to the end of an extendable pole, allowing me to reach into the nest box opening with minimal amounts of disturbance. The camera was connected wirelessly to a smartphone and showed a live feed of nest box contents.

Quantifying Habitat Use

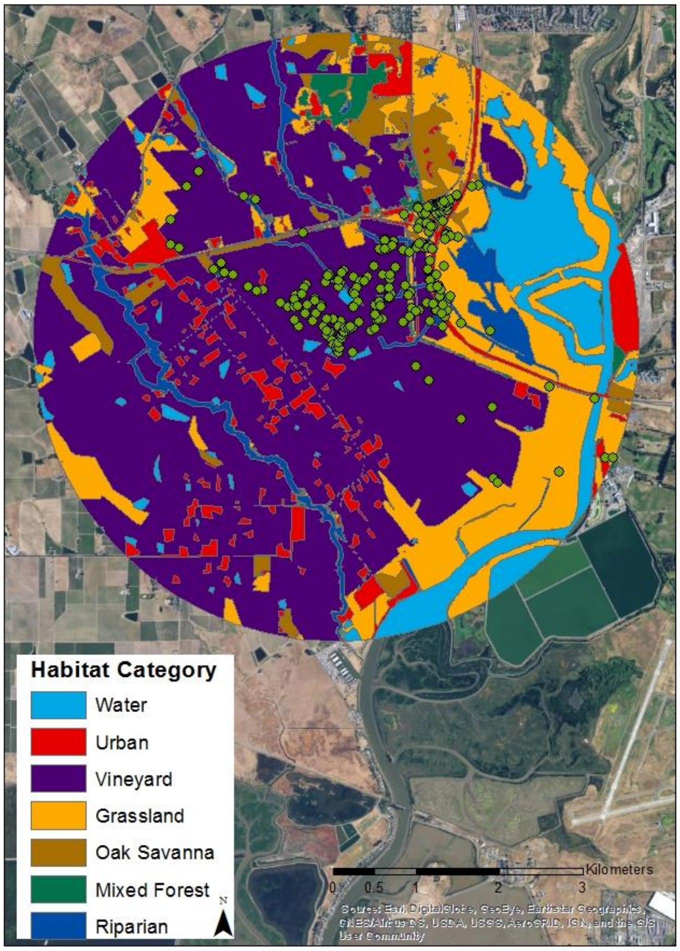
During the 2016 breeding season, March through August 2016, 21 individual female nesting barn owls were fitted with Uria 320 Global Positioning System (GPS) units (Ecotone Telemetry 2015). Only females were tagged because they roost diurnally in the nest box for several weeks after the chicks hatch, increasing the likelihood of retrieving the transmitter at a later time. Transmitters were attached via a small harness constructed of Teflon ribbon that was designed not to impede the bird’s natural mobility (Humphrey and Avery 2014). Each unit was set to record locations once per minute to provide fine-scale data on hunting habitat use. As this study was among the first to use GPS tags on a bird of this size, and with locations taken so frequently to examine fine-scale habitat selection, I experimented with deployment and programming details to optimize battery life and data retrieval. I determined the battery life was shorter than expected for this fine-scale data collection. However, by programming tags to not record locations when within range of a handheld base station (about 40 m) placed directly at the nest box I was able to optimize battery life. This also increased the likelihood that all location data was retrieved.

Because there is no definitive sexual dimorphism in barn owls, sex was determined by the presence of a brood patch (Pyle 1995). Due to sensitivity of barn owls in early stages of nesting (i.e. laying and incubation), GPS tags were deployed at nests known to have chicks. Birds were selected if their oldest young were approximately 10 to 15 days old at the beginning of tag deployment. This stage was selected to increase likelihood the tagged female would still be using the nest box for diurnal roosting three to eight days later, which allowed tag retrieval after the battery on the tag had drained and was no longer collecting location points. In all, 24 females were tagged and in all but three occasions tags were retrieved. Age of young was determined via plumage development using an ageing guide developed by The Barn Owl Trust (www.barnowltrust.org.uk).

Barn owls were captured in their nest box by covering the exit with a flat piece of wood on a pole, climbing a ladder to gain access, removing the owls (usually through the side door of the box), calming them by covering their heads with cloth or placing them in a cloth bag, and lowering them to the ground from a ladder for processing. Each owl was weighed to ensure they met the minimum weight requirement and that the GPS unit did not exceed 3% of the owls' mass (USFW 2016). When the transmitters were attached, the owls were placed back in the nest box and the entrance blocked for ten minutes to allow birds to calm down and reduce risk of flushing from the box. Total handling time did not exceed 20 minutes per bird. All monitoring and handling was approved by Humboldt State University's Institutional Animal Care and Use Committee (IACUC No. 15/16.W.43-A).

Habitat Sampling

Using National Agriculture Imagery Data provided by the United States Department of Agriculture (2016), habitat composition was reclassified into seven dominant habitat categories: water, urban, vineyard, grassland, oak-savanna, mixed-forest, and riparian (Appendix 1). Taylor (1994) reports the home range of a barn owl to be one to three kilometers, in this study owls were seen travelling as far as nine kilometers away. Though owls can travel great distances when away from the nest, during the nesting season they are central place foragers and these longer distance forays are not frequent. To standardize home range among all owls in this study the mean furthest location of the owls was calculated to reflect the home range of barn owls in this system. The calculated 2.86 km fell between the previously reported home range of one to three kilometers and thus was used as the home range distance in this study. Percent coverage of each habitat category was calculated in this buffer for each owl. All habitat sampling was conducted in ArcGIS 10.2 (ESRI 2016).



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 2. An example of habitat classification within a 2.86 km hunting range for a nesting female barn owl in Napa Valley, CA, spring 2016. Green circles represent GPS locations for this individual owl.

Analysis

Analysis involved descriptive statistics as well as the use of competing models of habitat use and selection to identify variables associated with hunting locations. Descriptive statistics were calculated to determine the composition of habitats used and available to each of the owls within its hunting buffer (2.86 km). Due to a limited number of birds sampled, competing models were assessed using the corrected Akaike information criterion (AIC_c) (Burnham et al. 2011). Models for all analysis were run through the R Package 'lme4' (Bates et al. 2015). In addition, model selection was determined using R package 'AICcmodavg' (Mazerolle 2017).

Determine Hunting Habitat Selection by Comparing Used to Available Areas

A resource selection function (RSF - logistic model; Manly et al. 2002) was used to compare used locations (GPS locations) to available locations randomly distributed within each animal's home range (i.e., 3rd order habitat selection, Johnson 1980). Because the objective of the study was to understand habitat selected for hunting, I sub-sampled from all telemetry locations based on criteria that I determined to best explain hunting behavior. Through field observations of barn owl movements away from the nest as well as a thorough examination of time signatures, velocities, and spatial relation within the raw data I determined these best criteria to yield hunting locations only; these points were used for all subsequent analysis. For each location, the GPS tags provided a rate of speed in meters per second. Locations were considered hunting locations if they did not exceed a maximum speed threshold of ten meters per second and were not stationary (i.e., roosting) for more than ten minutes at a time. These criteria were used to exclude resting periods as well as longer non-hunting flights (i.e., commuting), and were based on field observations as well as natural history observations of foraging behavior (Taylor 1994). To ensure that no single owl's locations weighted the model disproportionately, an equal number of hunting locations (*n* = 260) were randomly selected for each of the eleven barn owls' their respective sampling periods. The result was a spread of hunting locations over each birds tracking period (mean of 6.27 ± 0.73 days). The sub-sample was analyzed in the RSF and all subsequent analysis. Available locations were distributed randomly within each 2.86 km buffer of each box with an equal number of available locations as hunting locations for each barn owl (*n* = 260).

Telemetry locations taken very frequently raise the complicating issue of spatial autocorrelation and non-independence of successive points (Cushman 2010). My intent was to examine fine scale habitat selection using point data, which demands frequent locations, creating challenges to balance time between locations with issues of independence. Mantel correlograms (Cushman et al. 2005) have been recommended to illustrate the structure and duration of autocorrelation, and some have suggested sub-sampling data accordingly. However, sub-sampling data to achieve statistical independence often incurs heavy costs in terms of lost information for fine-resolution habitat selection, and many researchers have argued that such filtering may not be necessary (Swihart and Slade 1997, Rooney et al. 1998, Cushman 2010). For example, Rooney et al. (1998) argue that strict attempts to achieve statistical independence can obliterate fine-scale patterns in habitat use that may be present in the data (Rooney et al. 1998), and Swihart and Slade (1997) argue that regular sampling intervals resulting in autocorrelated data will not invalidate many estimates of habitat selection so long as the study time frame is adequate (Cushman 2010). The best strategy for estimating intensity of habitat use and quantification of fine-scale behavioral decisions may be to use the shortest possible sampling interval over the longest possible period (Rooney et al. 1998) appropriate for the study question, and to restrict inferences to the temporal and spatial scope justified by that time frame (Otis and White 1999).

I conducted three analyses to examine autocorrelation and spatial dependence of variables used in the RSF habitat selection analysis, using all telemetry locations classified as hunting locations (*n* = 5,042; see below). First, I calculated spatial (cross-) Mantel correlograms for all continuous variables (i.e., "distance to" variables; see below) using the correlog function in the ncf package of R (Bjørnstad 2005). Second, I performed a data series autocorrelation (time lag) analysis, shifting telemetry locations by 1-30 sequential positions and calculating the Pearson's autocorrelation for continuous variables. For the categorical habitat variable, I calculated the proportion of locations that remained in the same habitat category after the location time lag. Third, I identified all habitat changes, defined as when a bird moved from one hunting habitat to another, excluding when this occurred between the last location on one day and the first location on the next (*n* = 930 total habitat changes). Then I calculated the duration of time between habitat changes and plotted frequency distributions.

These analyses (see Appendix 2 for details) showed that while the data were spatially autocorrelated, the mode time to change habitats was only one minute, and the median was only four minutes, with more than 50% of all hunting habitat changes occurring within four minutes. These patterns, combined with recent suggestions to use the shortest possible sampling interval over the longest possible period, led me to retain most locations, randomly subsampling all analyzed owls' locations down to 260 locations per owl to ensure each contributed an equal number of locations to analyses. This yielded a total of 2860 telemetry locations used in the RSF, ranging over a sampling period of 6.00 ± 0.71 days per owl, which was the most possible given battery life and logistics. The time between sequential analyzed locations for the same owl on the same day ranged from 1 to 321 min (mean = 9.71 ± 0.60 min).

My primary intent for this model set was to examine the effect of habitat and proximity to resources on space use, and as nesting owls are central place foragers, predictor variables used in the RSF were habitat category (7 categories), distance from nest box (m), and distance to each habitat category. I took a tiered model selection approach to determine which habitat was the best predictor of use. I created a competing model set with each distance to habitat as a unique model. This allowed me to determine which distance to habitat was the best predictor of use and available locations. From this approach I determined distance to riparian was the best predictor of use (see Results). I then included habitat category, distance from nest box and distance from riparian habitat as the predictor variables in my final model set (Table

1). All distances were scaled to a range of 0 to 1 for this analysis, and all subsequent analysis, then back scaled for more clear interpretation of the effects of distance on habitat selection. Individual bird identity was included as a random effect when running the models.

Table 1. Candidate model set for the Resource Selection Function (RSF) of barn owl hunting habitat selection in Napa Valley, CA, spring 2016. Used/available locations were the response variable, habitat category, distance to nest, and distance to riparian were fixed-effects, with owl identity as a random-effect. The models were run using a generalized mixed model.

Models[a]	
Null	Use ~ 1 + (1|owl_id)
Model 1	Use ~ DNest + (1|owl_id)
Model 2	Use ~ DRip+ (1|owl_id)
Model 3	Use ~ Habitat + (1|owl_id)
Model 4	Use ~ Habitat + DNest + (1|owl_id)
Model 5	Use ~ Habitat + DRip + (1|owl_id)
Model 6	Use ~ Habitat + DNest + DRip + (1|owl_id)

[a] Habitat = seven categories of identified habitat within hunting range (see Field Methods), Dnest = distance from nest, and Drip = distance from riparian.

Habitat Selection Model Evaluation

The top model in the candidate set, as determined by the lowest AICc score, was evaluated following Boyce et al. (2002) and Johnson et al. (2006). More specifically I calculated the predicted probability of use for each used and available location, then divided these scores into 10 equal bins. I then calculated mean prediction probabilities for each bin as well as the proportion of used locations for each bin. I used the Pearson's correlation coefficient to evaluate the relationship between the predicted probabilities and the proportion of used locations, with a strongly predictive model yielding a coefficient near one and a poor model having a coefficient closer to zero. Linear regression was used to find if the slope of the resulting line was significantly different from zero and to yield the R^2 value (Johnson et al. 2006).

Model the intensity of use of habitat categories within their hunting range

Use versus available analyses examine habitat selection, but they reveal little about the intensity of space use; i.e., some areas are used more often or intensively than others (Carey and Peeler 1995, Gervais et al. 2003). Therefore, I used Time Local Convex Hull (t-LoCoH) analyses to reveal more information about barn owl hunting habitat use (Getz et al. 2007, Lyons et al. 2013). Specifically, I calculated the mean number of locations per visit (mnlv), which is a metric for duration of use of a hull generated from the t-LoCoH analysis (Getz et al. 2007, Lyons et al. 2013) and was used as an index of intensity of habitat use. This variable served as the response variable in general linear models, again with bird identity as a random effect. Predictor variables were again habitat category (7), distance from nest box, and distance from riparian habitat, based on predictors from the RSF in part one (Table 2).

Table 2. Candidate model set for predicting duration of visit (response variable) by hunting barn owls in Napa Valley, CA, spring 2016. Habitat, distance to nest and distance to riparian, with owl identity as a random-effect, using a generalized mixed model with random effect (GLMER).

Models:	
Null	MNLV ~ 1 + (1|owl_id)
Model 1	MNLV ~ DNest + (1|owl_id)
Model 2	MNLV ~ DRip + (1|owl_id)
Model 3	MNLV ~ Habitat + (1|owl_id)
Model 4	MNLV ~ Habitat + DNest + (1|owl_id)
Model 5	MNLV ~ Habitat + DRip + (1|owl_id)
Model 6	MNLV ~ Habitat + DNest + DRip + (1|owl_id)

[a] MNLV = mean number of visits as an index of intensity of use, Habitat = seven categories of identified habitat within hunting range (see Field Methods), Dnest = distance from nest and Drip = distance from riparian habitat.

Examine the effect landscape composition has on the amount of time barn owls spend hunting in vineyards

To examine the potential importance of landscape composition on the delivery of regulating services such as rodent pest removal, the proportion of each owl's hunting points that were within vineyard habitat was modeled, using linear regression, against the proportion of non-crop habitats (riparian, oak savanna, grassland, and mixed forest) within the bird's hunting range. I built competing models again with a tiered approach. First, I determined whether each predictor variable best predicted proportion of hunting locations in vineyard with a linear or pseudo-threshold function form (i.e., logarithmic functional form, Franklin et al. 2000). Then, I tested *a priori* hypothesized combinations of these variables based on the previous habitat selection results and barn owl natural history (Taylor 1994).

RESULTS

A total of 9,196 GPS telemetry locations were obtained from the 21 owls tracked (locations per owl: 517.2 ± 94.7). Of all locations, 27% were within grassland habitat, 36% within vineyard, 12% within oak-savanna, 10% within riparian habitat, and the remaining 15% were spread between urban, mixed-forest, and water environments. However, with GPS tags programmed to record locations at every minute, the batteries drained much faster than initially expected. Some of the tags first deployed only lasted about two nights, but once I optimized the deployment strategy (see Methods), the tag's batteries lasted about 8 nights. Due to these complications, ten birds did not have a large enough number of location points (< 200) to be useful and thus were excluded from all subsequent habitat selection analyses. Of the remaining locations, 5,042 (55%) were classified as hunting locations (mean number per owl: 458, S.E. ± 177), with 34% of hunting locations within vineyard, 36% within grassland habitat, 15% within oak-savanna, 1% within mixed forest, 11% within riparian habitat, and the remaining 3% spread between urban and water environments. For comparison, the overall composition of habitat categories within the 11 owls' hunting ranges used (2.86 km buffer of nest box) was 10% urban, 43% vineyard, 22% grassland, 8% oak-savanna, 6% mixed-forest, 3% riparian, and 8% water.

Resource Selection Function (RSF)

Barn owls are central place foragers and this was reflected in the RSF results which showed a strong negative effect of distance from nest on habitat selection (Figure 3). Although I recorded locations up to nine km from a nest, most locations were far closer, with 73% of hunting locations within 1000 m and 50% within 500 m of a birds' nest box. The top model in the candidate set included habitat, distance to nest, and distance to riparian (i.e. full model; Table 4). In this analysis the predictor variables competed against a true intercept for more meaningful interpretation. Unsurprisingly, an often cited habitat of preference for barn owls in other systems (Hindmarch et al. 2014, Taylor 1994) was positive and had the greatest beta value ($\beta = 0.64$ C.I. ± 0.09). (Table 4). Among the other habitat categories, this model showed oak savanna ($\beta = 0.36$ C.I.

±.11) and to a lesser extent riparian (β = 0.51 C.I. ± 0.13) to be habitats most favored when comparing used to available locations (Figure 3).

Both distance from nest (β = -1.41 C.I. ± 0.03) and distance from riparian habitat (β = -0.13 ± 0.03) were negatively associated with hunting habitat location and neither confidence interval overlapped zero (Table 4). Distance from nest had an especially strong negative relationship, indicating that selection probability declined for locations further from the nest, consistent with the behavior of a central place forager. Distance to riparian habitat also showed a negative relationship, albeit weaker, suggesting locations close to riparian were favored for hunting.

Evaluation of RSF

Testing the linear relationship between the mean predicted probabilities to the proportion of use within each bin yielded a Pearson's correlation coefficient of 0.76. The slope of the regression line was significantly different from zero (F = 8.10, df = 1 and 8, $P = 0.02$) with an adjusted-R^2 of 0.44. The high Pearson's coefficient suggests that the model explained significant variation in hunting habitat use by barn owls in this system, though there is considerable unresolved variation and there are likely additional factors that contribute to selection of hunting sites within their hunting ranges.

Table 3. AICc results of the model set which predicted hunting habitat selection of barn owls in Napa Valley, CA, spring 2016. The model set inluded habitat, distance to nest and distance to riparian habitat.

Model	K^a	$Log_e(L)^b$	$AIC_c{}^c$	$\Delta AIC_c{}^d$	$W_i{}^e$
Habitat + DNest + Drip + (1|owl_id)	**10**	**-1970.81**	**3961.65**	**0.00**	**1**
Habitat + DNest + (1|owl_id)	10	-1977.91	3973.86	12.21	0
DNest + (1|owl_id)	10	-2303.47	4610.94	649.29	0
Habitat + DRip+ (1|owl_id)	9	-3476.70	6971.43	3009.78	0
Habitat+ (1|owl_id)	3	-3554.05	7124.12	3162.47	0
DRip + (1|owl_id)	9	-3861.72	7727.44	3765.80	0
1 + (1|owl_id)	9	-3964.80	7931.60	3969.96	0

[a] Number of parameters

[b] Log_e(likelihood)

[c] Akaike's Information Criterion corrected for small sample size

[d] Difference between AIC_c and top model AIC_c

[e] AIC_c weight

Table 4. Coefficients, standard errors and confidence intervals from the top logistic regression model of barn owl habitat use in the Napa Valley, CA, spring 2016.

Habitat + DNest + DRip + (1|owl_id)

Covariate[a]	Coefficient	SE	95% CI LL	95% CI UL
Urban	**-0.86**	**0.14**	**-1.15**	**-0.38**
Vineyard	**-0.72**	**0.09**	**-0.90**	**-0.54**
Grassland	**0.64**	**0.09**	**0.46**	**0.83**
Oak Savanna	**0.36**	**0.11**	**0.15**	**0.58**
Mixed Forest	-0.28	0.17	-0.61	0.05
Riparian	**0.51**	**0.13**	**0.26**	**0.76**
Water	**-0.71**	**0.17**	**-1.03**	**-0.38**
Dnest	**-1.41**	**0.03**	**-1.47**	**-1.34**
DRip	**-0.13**	**0.03**	**-0.20**	**-0.06**

[a] Habitat = seven dominant habitats across the landscape, Dnest = distance from nest, DRip = distance from riparian. Bolded rows show confidence intervals that do not overlap zero.

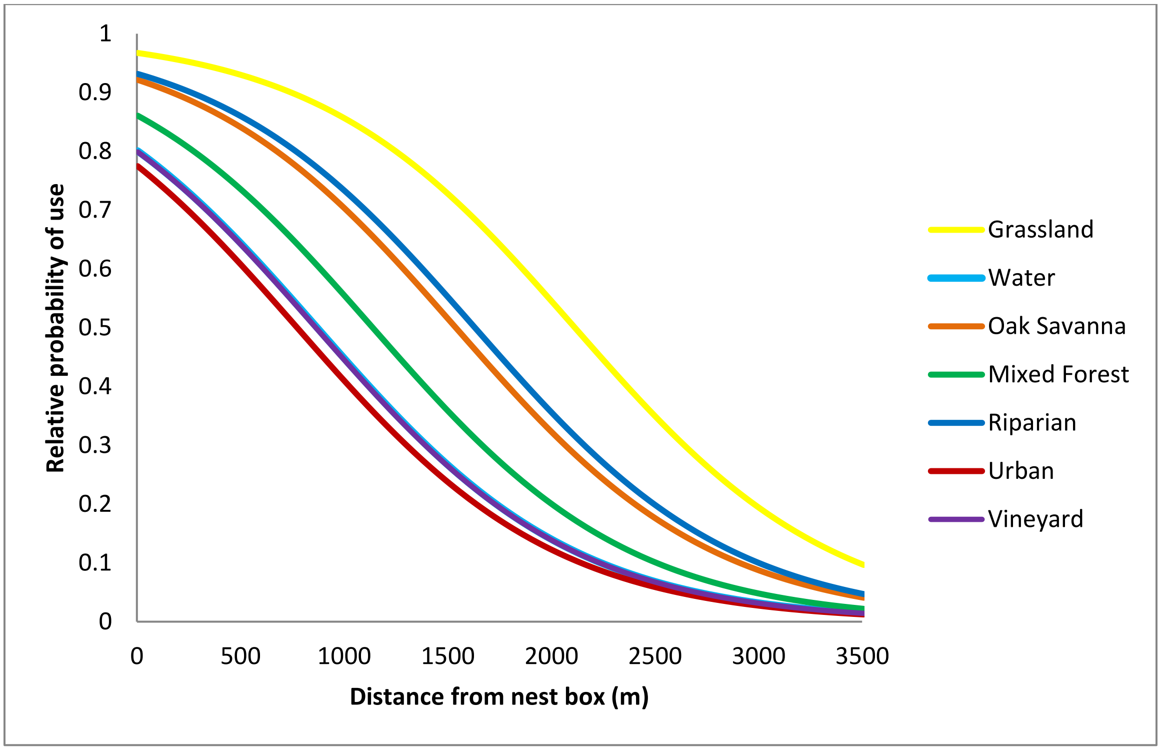


Figure 3. A resource selection function model using locations (i.e. barn owl hunting locations within Napa Valley, CA, spring 2016) as a function of habitat and distance to nest. Farthest distance travelled was limited to within mean hunting range of all owls, 2.86 km. Vineyard and water overlap.

Intensity of Habitat Use

Model selection using AICc indicated that a model with habitat, distance to nest, and distance to riparian was the best for explaining intensity of habitat use by hunting barn owls (Table 6). All betas were positive, however Oak-savanna and mixed forest habitats had the largest positive betas, β = 2.25 (CI ± 0.05) and β = 2.25 (CI ± 0.06), respectively. Having confidence intervals that did not overlap zero suggest oak-savanna and mixed forest were the most significant predictors of the duration of a visit (i.e., intensity of use) when hunting. Vineyard habitat also had a significant relationship with intensity of use but not as strong as for other habitats, β = 2.05 (CI ± 0.05) (Table 7). Distance from nest and distance from riparian each had coefficients significant in affecting duration of a visit. Distance from nest and riparian had a positive, though weak, association with duration of visit to a given area, with β = 0.13 (C.I. ± 0.01) and β = 0.08 (C.I. ± 0.01), respectively.

Table 5. AICc results of the competing model set which included habitat, distance to nest and distance to riparian as predictors of the intensity of habitat use by hunting barn owls in Napa Valley, CA, spring 2016.

Model	K^a	$Log_e(L)^b$	AIC_c^c	ΔAIC_c^d	W_i^e
Habitat + DNest + DRip + (1|owl_id)	**10**	**-13303.82**	**26627.68**	**0.00**	**1**
Habitat + DNest + (1|owl_id)	9	-13331.56	26681.16	53.48	0
DNest+ (1|owl_id)	3	-13413.05	26832.11	204.43	0
Habitat + DRip + (1|owl_id)	9	-13570.16	27158.35	530.67	0
Habitat + (1|owl_id)	8	-13608.42	27232.86	605.18	0
DRip + (1|owl_id)	3	-13683.73	27373.47	745.79	0
1 + (1|owl_id)	2	-13728.31	27460.63	832.95	0

[a] Number of parameters

[b] Log_e(likelihood)

[c] Akaike's Information Criterion corrected for small sample size

[d] Difference between AIC_c and top model AIC_c

[e] AIC_c weight

Table 6. Coefficients, standard errors and confidence intervals from the top logistic regression model of the intensity of habitat use by hunting barn owls in Napa Valley, CA, spring 2016.

Habitat + DNest + Drip + (1|owl_id)

Covariate[a]	Coefficient	SE	95% CI LL	95% CI UL
Urban	**2.06**	**0.06**	**1.94**	**2.17**
Vineyard	**2.05**	**0.05**	**1.96**	**2.14**
Grassland	**2.11**	**0.05**	**2.02**	**2.21**
Oak Savanna	**2.25**	**0.05**	**2.16**	**2.34**
Mixed Forest	**2.25**	**0.06**	**2.14**	**2.37**
Riparian	**2.09**	**0.05**	**1.99**	**2.18**
Water	**2.14**	**0.07**	**1.99**	**2.28**
Dnest	**0.13**	**0.01**	**0.12**	**0.14**
DRip	**0.08**	**0.01**	**0.06**	**0.10**

[a] Dnest=distance from nest, and DRip=distance from riparian. Bolded rows show confidence intervals not overlapping zero.

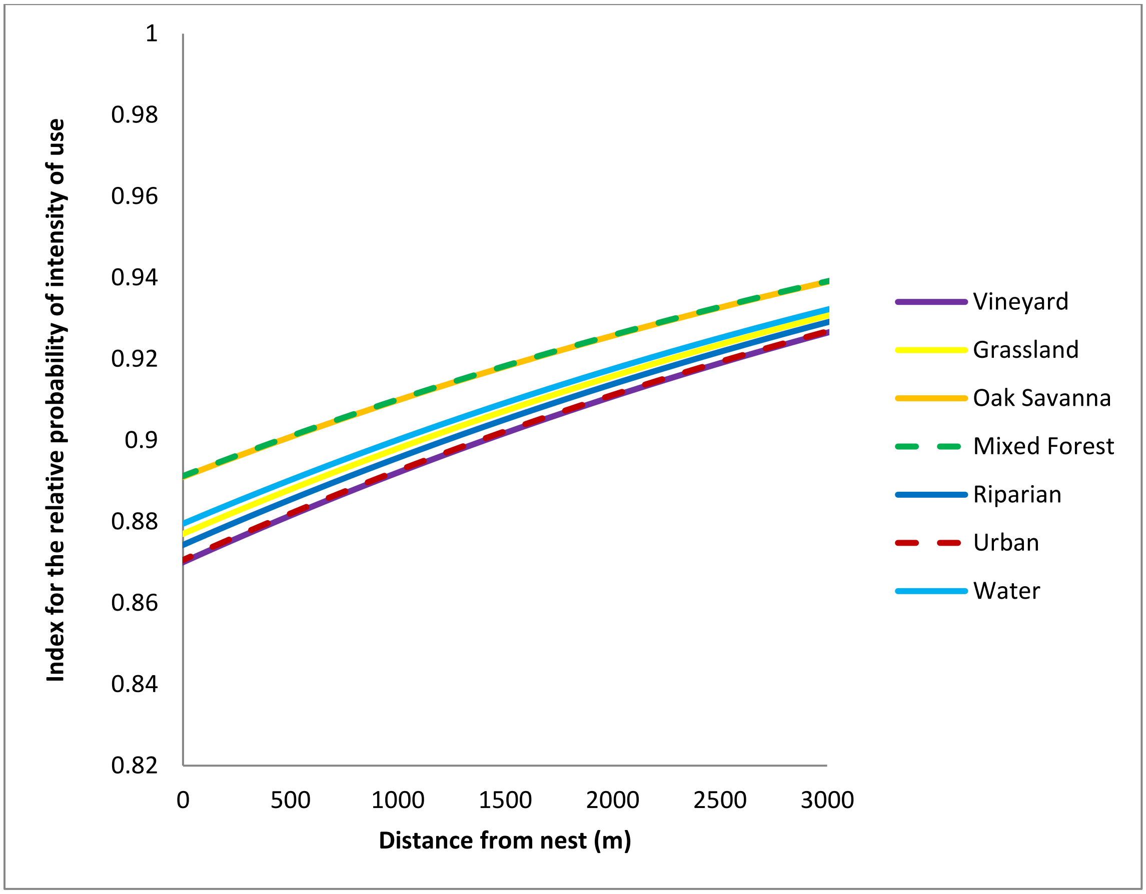


Figure 4. Model output of duration as an index of intensity of habitat use by hunting barn owls in Napa Valley, CA, spring 2016. Duration of visit was derived from a Time-Local Convex Hull (t-LoCoH) analysis and used as an index of intensity of use. Mixed forest and Oak Savanna overlap. Urban and vineyard probabilities overlap.

Habitat Composition Effects on Vineyard Use

As the proportion of an owl’s hunting range comprised of oak savanna increased, the proportion of hunting location within vineyard declined (Figure 5). Model selection revealed that proportion of an owl’s hunting location that was in vineyard was best explained by the relative proportion of riparian and oak savanna habitat within an owl’s hunting range (Table 8). Proportion of riparian had a positive beta, $\beta = 624.29$ (CI ± 328.92). Proportion of oak savanna had a negative beta, $\beta =-184.97$ (CI ± 67.44). The proportion of oak savanna had a confidence interval that did not overlap zero, suggesting it was the most important predictor of the proportion of an owl’s hunting locations within a vineyard.

Table 7. AICc comparison of a competing model set predicting the proportion of barn owl hunting locations within vineyards in Napa Valley, CA, spring 2016. The model set included proportion of riparian, oak savanna, grassland, and mixed forest habitats as predictors of the proportion of barn owl hunting locations within vineyards.

Model	K^a	$Log_e(L)^b$	$AIC_c{}^c$	$\Delta AIC_c{}^d$	$W_i{}^e$
PRiparian + POakS	**4**	**-44.91**	**104.49**	**0.00**	**0.88**
PRiparian + PGrass	4	-47.23	109.13	4.64	0.09
PRiparian + PMixedF	4	-48.07	110.81	6.33	0.04
PRiparian + POakS + PGrass + PMixedF	6	-42.69	118.38	13.90	0.00

[a] Number of parameters

[b] Log_e(likelihood)

[c] Akaike's Information Criterion corrected for small sample size

[d] Difference between AIC_c and top model AIC_c

[e] AIC_c weight

Table 8. Coefficients, standard errors and confidence intervals from the top generalized linear model for predicting barn owl hunting locations within vineyards of Napa Valley, CA, spring 2016.

PRiparian + POakS				
Covariate[a]	Coefficient	SE	95% CI LL	95% CI UL
Intercept	**31.16**	**13.15**	**5.38**	**56.94**
PRiparian	624.29	328.92	-20.38	1268.95
POakS	**-184.97**	**67.44**	**-317.14**	**-52.79**

[a] PRiparian = proportion of available riparian habitat, POakS = proportion of available oak savanna habitat. Bolded rows show confidence intervals not overlapping zero.

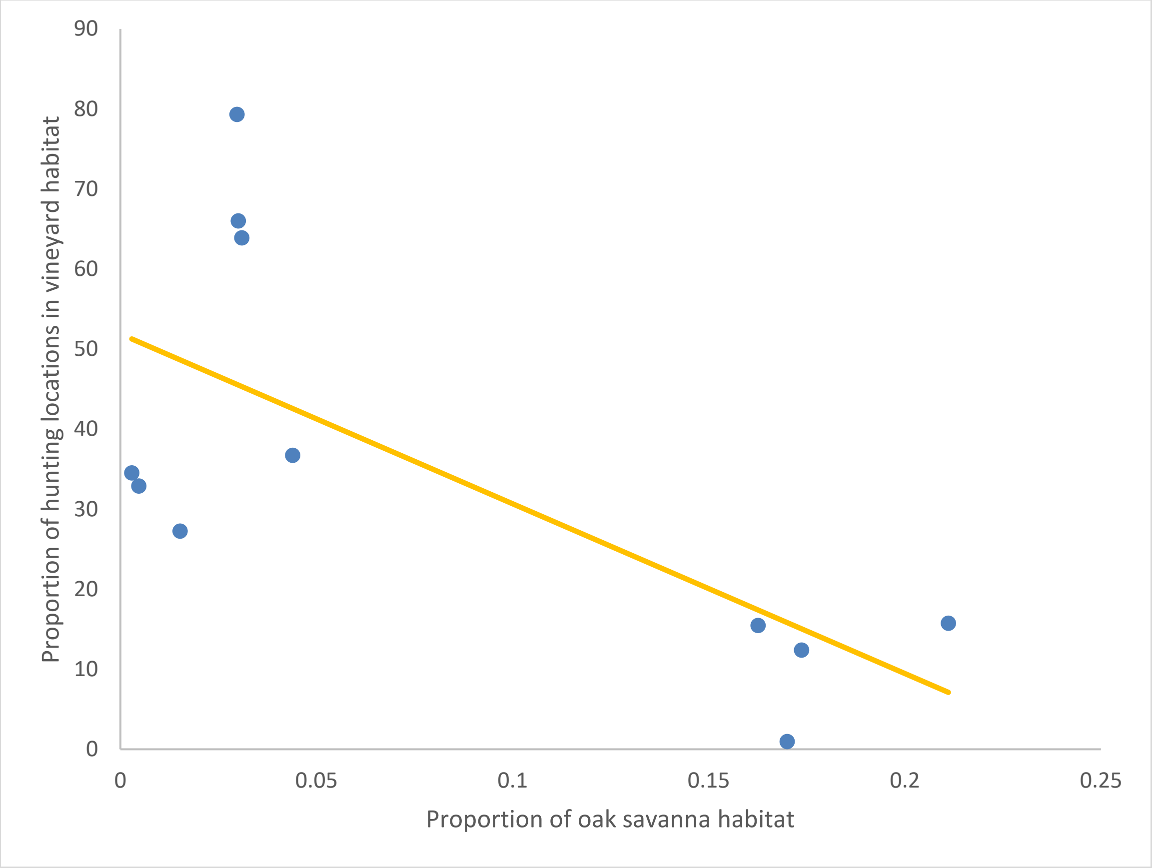


Figure 5. Comparison of proportion of locations in vineyards and the proportion of oak-savanna within the hunting area of barn owls (2.86 km buffer) in Napa Valley, CA, spring 2016, adj-R2 = 0.42.

DISCUSSION

My analysis of hunting locations indicated that grasslands along with riparian habitat were selected for hunting. Urban, vineyard, water, and mixed forest habitats were avoided, while the selection of oak savanna fell in between these extremes (Table 5). That barn owls actively selected relatively rare habitats in the landscape suggest these habitats provide important resources for the owls, such as staging areas and perch sites which barn owls routinely utilize while hunting (Askham 1990, Taylor 1994). Conversely, although vineyard habitat was not strongly selected for hunting, most birds' home ranges were dominated by vineyard (43% of random points, overall), so a substantial portion of the owls' hunting occurred within vineyards (34% of hunting locations, overall). Preferred habitat for barn owls is often considered to be open, grassy areas (Evans and Emlen 1947, Fast and Ambrose 1976, Taylor 1994) and in Napa Valley these habitats are associated with increased nest box occupancy by barn owls (Wendt and Johnson 2017).

As expected for a central place forager, distance from the nest had a significant negative effect on barn owl habitat selection, with almost three fourths of the hunting locations within 1 km of an owl's nest box. Distance from riparian habitat had a weak negative relationship in predicting used locations, suggesting proximity to riparian habitat also influenced where barn owls chose to hunt. Whether this is because of favorable roosting opportunities, prey abundance, or other factors is unknown, and future work should evaluate rodent abundance in different habitats, as well as the favored roosting sites for male and female barn owls once they forgo roosting with the chicks in the nesting box.

Conversely, the intensity of use as measured with a metric for duration of use of a hull in the t-LoCoH analysis showed a positive effect of distance to nest, indicating that areas far from nest were used for longer hunting bouts. This finding is also consistent with optimal foraging theory for a central place forager, as hunting time should offset travels costs to a more distant location (Pyke et al. 1977). As in the RSF, the model for intensity of use also showed that grassland is an especially important habitat for hunting barn owls (Figure 4).

Results of this study suggest that the composition of vineyard and non-cultivated habitats in a landscape affects where and for how long barn owls hunt, and this has important implications for the delivery of possible pest control services. In Napa Valley, habitats selected for hunting are unevenly distributed. In the southern portion of the valley, non-vineyard habitats are dominated by large tracts of expansive grassland 30% of total area and oak-savanna 7% of total area with relatively few riparian habitats. Farther north, non-vineyard habitat becomes scrub-dominated, transitioning to oak-savanna 11% of total area and mixed forest 15% of total area at the most northern extent of the Valley. Also, the coverage of vineyard increases by more than 20% in the north. It must be noted that there are still patches of fallow agriculture fields, pastures, and undeveloped open grassland, 1% of total area, throughout the middle to northern regions of the Valley and overall the landscape has greater heterogeneity.

This gradient in habitat composition and landscape complexity from south to north in Napa Valley could affect pest control services by barn owls. For example, some results suggest that pest removal could be strongest in the south. Although barn owls do demonstrate some resiliency to changes in landscape (Hindmarch et al. 2012) and can make behavioral shifts based on what resources are available to them (Marti 1974, Jaksic et al. 1982, Bose` and Guidali 2001), a recent study of nest box occupancy in Napa Valley revealed occupancy rates declined from south to north (Wendt and Johnson 2017). Though there is an increase in relative landscape complexity to the north, the decline in grassland and the proximity, composition, or configuration of the other available non-crop habitats may not be ideal to support occupancy or effective hunting, and as a result may substantially limit provisioning of ecosystem services (Tscharntke et al. 2016). In addition, a highly fragmented landscape can contribute to limited movement and constricted home ranges and decrease provisioning rates to young, as seen in other owls (Hinam and St. Clair 2008). The disproportionate landscape cover dominated by vineyard may thus minimize the accessibility of barn owls to preferred habitats affecting the provisioning of regulating ecosystem services in this system.

Alternatively, results could suggest that owl hunting and pest removal may be strongest in the north. As highly mobile predators, barn owls have the ability to evaluate conditions across large spatial scales to determine where hunting efforts may be most cost effective (Pyke et al. 1977). In a heterogeneous landscape, more profitable hunting habitat may be several kilometers away, thus limiting options for hunting. A major review by Bianchi et al. (2006) on the effects of landscape complexity on natural pest control services showed that complex landscapes support greater pest regulation than simple landscapes, because they can provide favorable conditions and balanced requirements for the establishment and maintenance of natural predators. The more complex landscape structure in the northern part of Napa Valley may thus promote greater provisioning of regulating ecosystem services to farmers. For example, during the breeding season when partitioning prey to young, an optimally hunting barn owl must balance costs of prey depletion and travel to determine whether hunting close to a nest may be more cost effective than travelling further to a more bountiful hunting area (Rosenberg et al. 1999). Where they occupy areas with a more heterogeneous habitat composition, owls may have limited access to preferential hunting grounds and thus be forced to more heavily hunt on vineyards, potentially providing greater pest removal services to farmers. The northern portion of the Valley has proportionately more vineyard, and preferred uncultivated habitats are spaced at greater distances apart than they are in the south. Perhaps this explains why the three barn owls tracked in this study from the northern part travelled less distance from the nest when hunting than those in the southern part of the Valley (mean distance travelled: North = 1675m, South = 3137m) and thus may be providing a greater service to the farms around their nest boxes. Additional research is necessary to better understand the effect of landscape composition on the delivery of pest removal services, either by examining prey delivery rates to nests located in different landscapes (i.e., via remote videography) or by rodent sampling along a habitat/landscape gradient.

When considering the overall composition of the landscape, results show that as oak-savanna increases across the landscape, barn owl use of vineyards for hunting diminishes. Not all uncultivated habitat is created equally (Tscharntke et al. 2016), and this result demonstrates that there is preference when it comes to hunting. Though grassland, riparian, and oak-savanna were selected habitats, oak savanna and riparian were most intensively used, the final analysis showed that as oak savanna increased across the landscape hunting in vineyard habitat diminished. Studies of land use change clearly indicate that expansion of winegrape vineyards is coming at the cost of the loss of these important habitats, especially oak savanna. As a result, owls may need to travel farther to reach this preferred habitat. To some degree, this could actually increase the hunting by owls in vineyards, but at some point the habitat loss of preferred habitat will likely diminish nest box occupancy altogether (Wendt and Johnson 2017), resulting in fewer owls across the landscape. Thus, there may be a trade-off in which vineyard expansion could diminish the delivery of an ecosystem service by barn owls. Spatial modeling will be required to more fully explore the nuances of this possible trade-off in habitat allocation, bird numbers, and the delivery of an ecosystem service (sensu Railsback and Johnson 2014). By reframing the way we look at how landscape affects these services we can see that not only do we need the preferred habitat but it needs to be partitioned in a particular way to optimize the delivery of desired ecosystem services (Tscharntke et al. 2016, Mitchel et al. 2015, Railsback and Johnson 2014).

Results from our study and a recent occupancy study (Wendt and Johnson 2017), suggest it may be crucial to maintain heterogeneity with appropriate amounts of preferred habitats across the landscape to ensure barn owls are present and can provision themselves throughout the breeding season. In addition, a heterogeneous landscape with patches of uncultivated habitat, embedded within an agricultural matrix can provide refugia, favorable conditions facilitating owl establishment, and access to hunting habitats when vineyard hunting may be unsuccessful. Also, a mixed landscape ensures abundant edges between vineyards and uncultivated habitats, where owls may have better access to additional resources (Frey et al. 2011). The use of barn nest boxes for possible rodent control is also practiced in the Central Valley of California, where farm sizes are larger and there is less uncultivated habitat (Browning et al. 2017). In Israel barn owls also travel farther from the nest for hunting (Motti Charter, pers. Comm.). Future work should then examine hunting habitat selection in populations were barn owls are known to travel further when hunting.

CONCLUSIONS

This study provides additional support that barn owls are closely associated with grassland habitats, and it also brings to light that barn owls readily utilize more forested habitats such as riparian and oak-savanna areas for hunting purposes. Furthermore, these partially forested land cover types may be more important than expected considering our study took place when adults were provisioning young. Ultimately, in the framework of ecosystem services, there appears to be a trade-off from the farmer’s perspective: uncultivated habitats near nest boxes appear to increase the likelihood a box is occupied

(Wendt and Johnson 2017), but results of this study show that increased uncultivated habitat nearby were associated with less hunting within vineyards. To understand this trade-off, future modeling should examine whether there is an “optimal” landscape composition that balances nest occupancy as well as vineyard use while hunting. In addition, many studies suggest that barn owls can consume large numbers of rodents, but the capacity for barn owls to actually reduce rodent pests on vineyards remains unknown (but see Browning et al. 2017). Future work could examine this by linking hunting locations, prey deliveries, and provisioning rates to the nest. Multi-year before-after-control-impact studies involving rodent monitoring and nest box deployment may be needed to confirm or refute that barn owls can meaningfully suppress prey in winegrape vineyards. Ensuring appropriate amounts of preferred habitat types across the landscape are present may help a common species stay common and can continue to provide regulating pest control services to farmers.

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APPENDIX A

Appendix A: Description of each habitat category within a barn owls hunting range in Napa Valley, CA, spring 2016.

As described in the introduction Napa Valley, CA, is described as being part of the Mediterranean biome. Though land cover can vary significantly across the valley there are some habitats that dominate the landscape. For simplification of analysis, I classified landscape composition into seven dominant categories: Water, urban, vineyard, grassland, oak savanna, mixed forest, and riparian habitats, respectively. Each habitat is described as follows: Water consists of irrigation ponds, lakes, rivers and tidal mudflats. Urban areas consist of all structural development including but not limited to buildings, roads, work sites, and heavily maintained landscaped areas. Vineyard was classified as any land that has been or currently is in use for the production of wine grapes along with any infrastructure that is used in viticulture i.e. dirt roads and field margins. Grassland can be described as any expansive area covered with grass, forbs or other vegetation that gives the effect of open unobstructed landscape. Oak savanna is a mix of grassland and patchy oak forest. Mixed forest consists of any continuous forest or dense shrub cover that limits access of barn owls to the ground. Lastly, riparian is classified as habitat surrounding streams, rivers, large lakes and ponds as well as high marsh.

APPENDIX B

Appendix B: Autocorrelation analysis of barn owl hunting locations collected in Napa Valley, CA, spring 2016.

I conducted three analyses to examine autocorrelation and spatial dependence of variables used in the RSF habitat selection analysis, using all telemetry locations classified as hunting locations (see Methods, *n* = 5,042). First, I calculated spatial (cross-) Mantel correlograms for all continuous variables (i.e., “distance to” variables) using the correlog function in the ncf package of R (Bjørnstad 2005). Second, I performed a data series autocorrelation (time lag) analysis, shifting telemetry locations by 1-30 sequential positions and calculating the Pearson’s autocorrelation for continuous variables. For the categorical variable habitat (7 levels), I calculated the proportion of locations that remained in the same habitat category after the location lag. Third, I identified all habitat changes, defined as when a bird moved from one hunting habitat to another, excluding when this occurred between the last location on one day and the first location on the next (*n* = 930 total habitat changes). Then I calculated the duration of time between habitat changes, and plotted frequency distributions.

These analyses indicated that true statistical independence of sequential telemetry locations was not obtained until they were from 400 to over 5000 m apart (Figures 1-6). Likewise, even up to a time lag of 30 locations, most variables showed a statistically significant autocorrelation (Figure 7). However, the sample size and statistical power to detect even a weak correlation was large, and a sharp drop in autocorrelation coefficients of most variables was seen for sequential locations that were 100 m and 5 mins apart. The time to change hunting habitat ranged from 1 to 297 mins, with an average of 23 mins. The frequency distribution was strongly non-normal (skewed right), and the mode time to change habitats was only 1 minute, and the median was only 4 mins, with over 50% of all hunting habitat changes occurring within 4 mins (Figure 8).

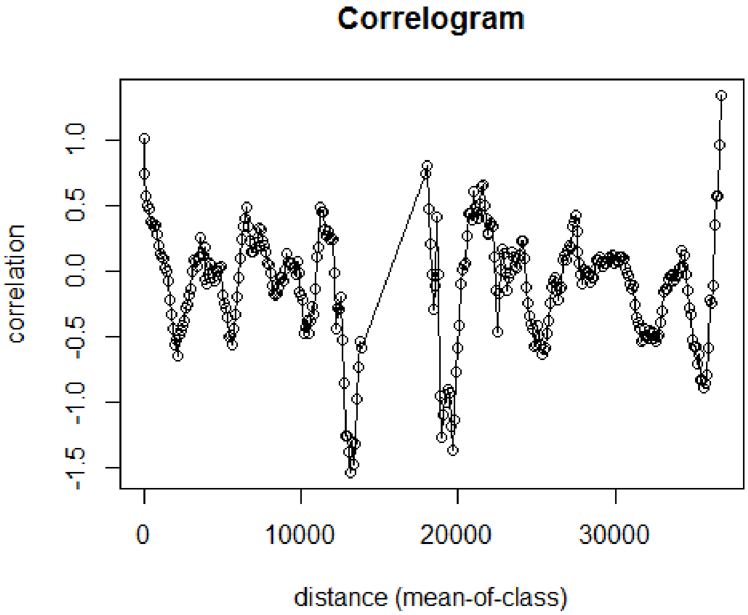

Figure 6. Correlogram for barn owl hunting locations from distance to nest; distance is in meters. Napa Valley, CA, spring 2016.

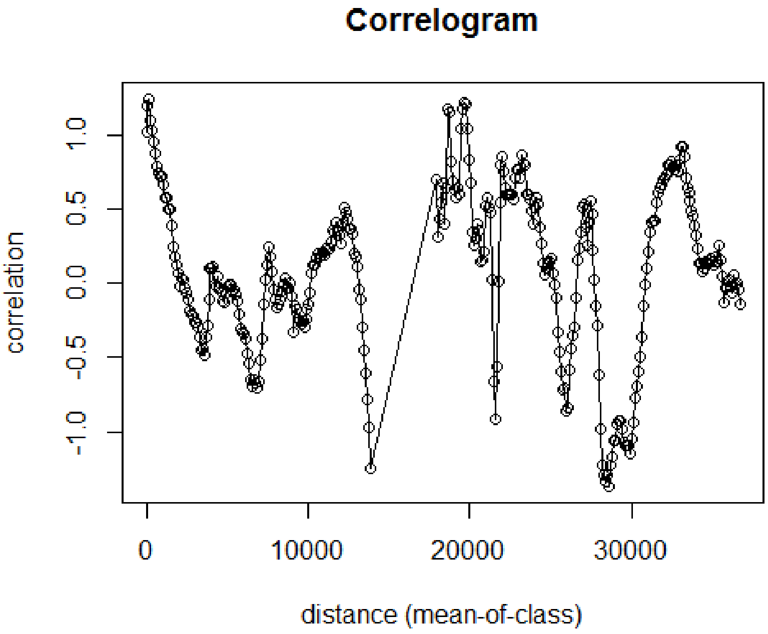

Figure 7. Correlogram for barn owl hunting locations from distance to oak savannah; distance is in meters. Napa Valley, CA, spring 2016.

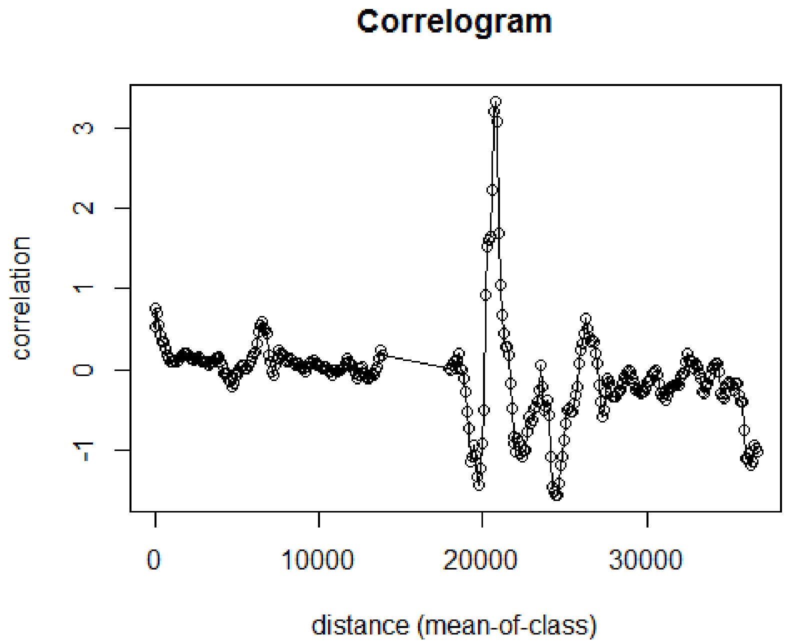

Figure 8. Correlogram for barn owl hunting locations from distance to grassland; distance is in meters. Napa Valley, CA, spring 2016.

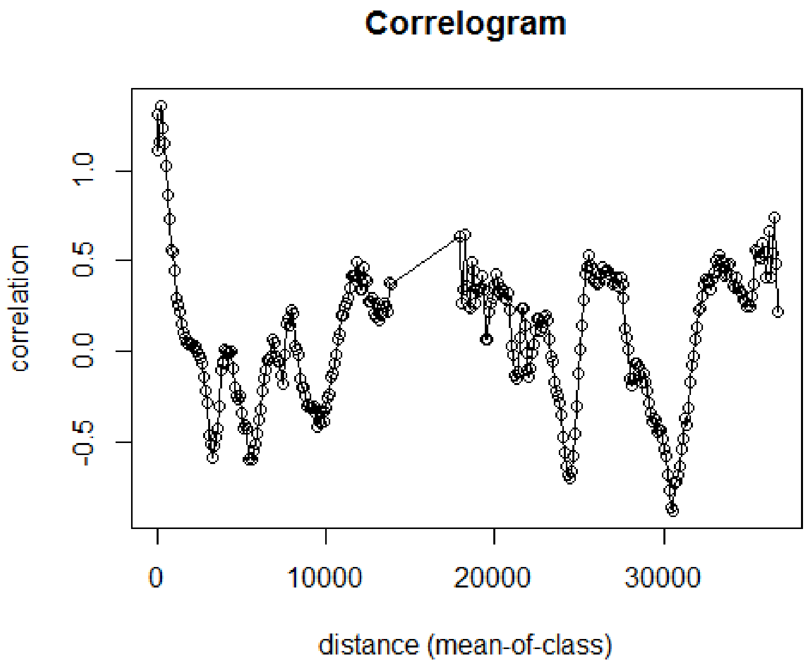

Figure 9. Correlogram for barn owl hunting locations from distance to riparian; distance is in meters. Napa Valley, CA, spring 2016.

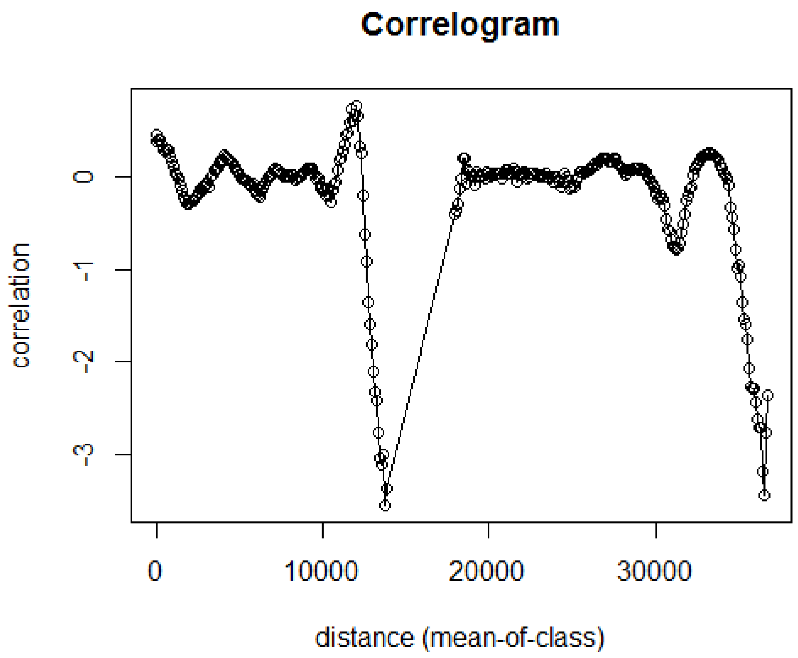

Figure 10. Correlogram for barn owl hunting locations from distance to vineyard; distance is in meters. Napa Valley, CA, spring 2016.

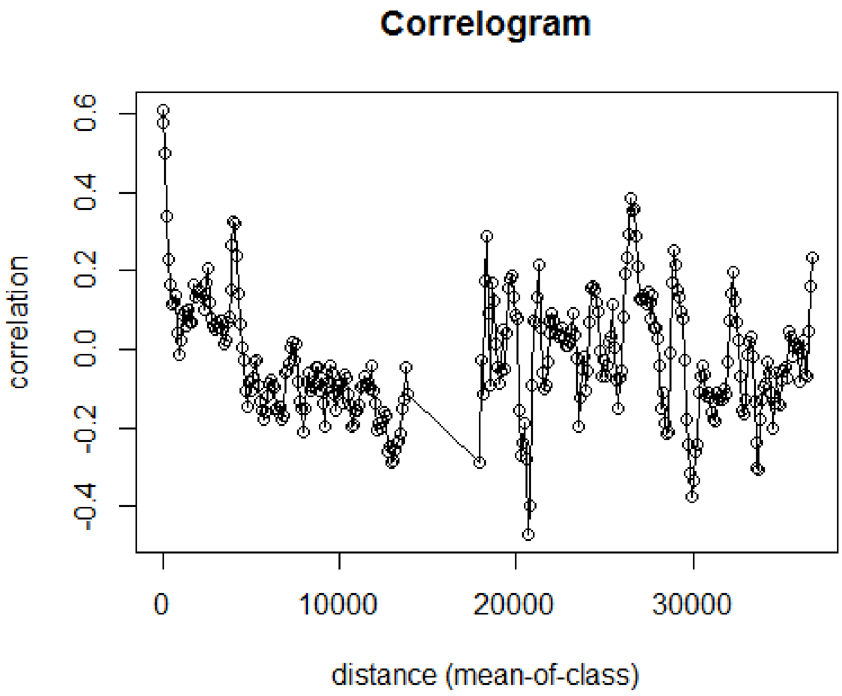

Figure 11. Correlogram for barn owl hunting locations from distance to (any) uncultivated habitat; distance is in meters. Napa Valley, CA, spring 2016.

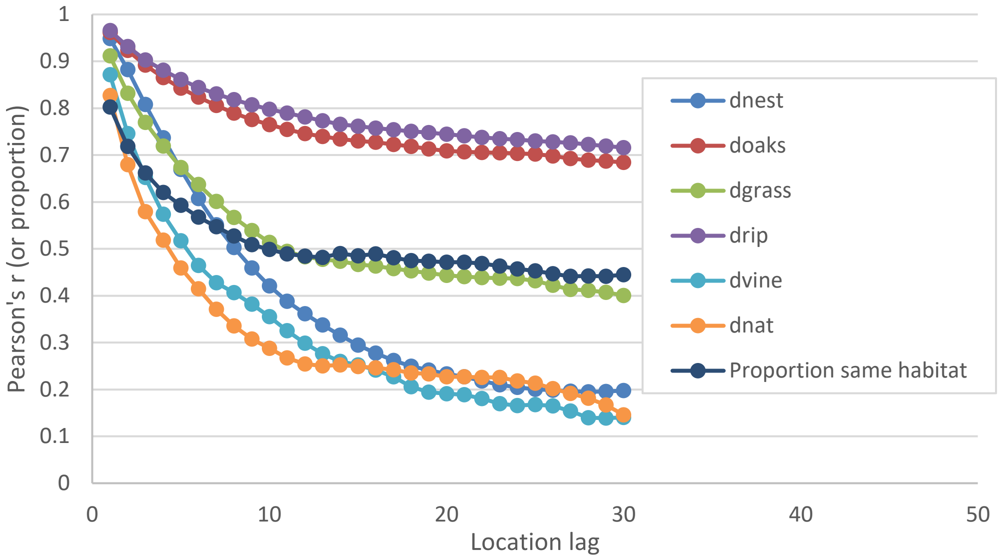

Figure 12. Temporal autocorrelation plotted against an increase in lag of telemetry series locations, from a lag of 1-30 locations. The y-axis is Pearson's correlation coefficient for all "distance to habitat" variables, which were continuous. For the categorical habitat variable, the y-axis is the proportion of barn owl hunting locations that remained in the same habitat after the location lag. Napa Valley, CA, spring 2016.

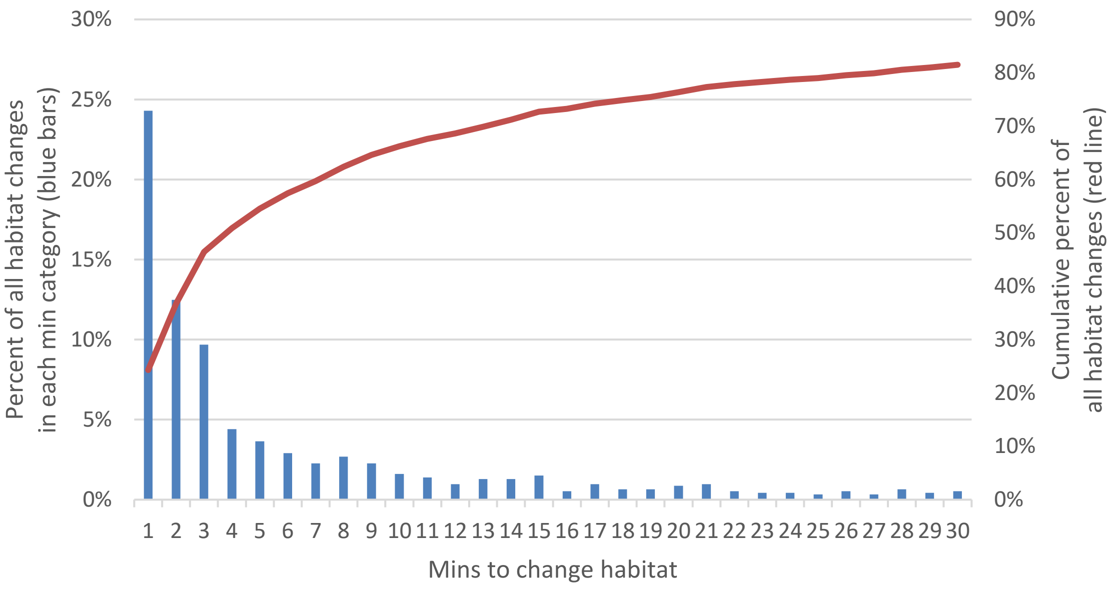

Figure 13. Frequency distribution of all times to change habitats based on barn owl hunting telemetry locations (n = 930 habitat changes) among minute bins. All bins over 30 mins contained 10 or fewer habitat changes (<1%). Blue bars indicate the percent of habitat changes in a minute bin; the orange line depicts the cumulative percent of all hunting habitat changes that occurred in the up to and including a given minute. Napa Valley, CA, spring 2016.