RESEARCH ARTICLE

Barn Owls select uncultivated habitats for hunting in a winegrape growing region of California

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ABSTRACT

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 furcata*) to nest on farms for pest management has been implemented worldwide but has not been evaluated in vineyard agroecosystems. Napa Valley, California, is a renowned winegrape growing region, and viticulturists encourage Barn Owl occupancy to help minimize damage from Botta's pocket gophers (*Thomomys bottae*) and voles (*Microtus* spp.). This study modeled the use of habitats in space and time by hunting Barn Owls, providing information about their potential to provide the critical ecosystem service of pest consumption. We used global positioning system tags to track hunting owls and used a resource selection function to compare used and available habitats. We constructed the intensity of use and home range-movement maps using a time local convex hull analysis from location data. We found that Barn Owls selected uncultivated habitats when hunting, some of which were relatively rare on the landscape. Approximately, one-third of Barn Owl hunting locations occurred in vineyards, but this use was out of proportion to the availability of vineyards, which comprised 50% of the area around nest boxes. The owls' use of vineyards increased with decreasing amount of selected uncultivated habitat in the landscape. However, as reported by a previous study, the 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. A true test of pest management by Barn Owls awaits experimentation coupled with monitoring rodent populations.

Keywords: ecosystem service, habitat heterogeneity, habitat selection, habitat use, pest management, *Tyto furcata*, vineyard

LAY SUMMARY

- Agricultural landscapes are composed of a variety of habitats, both cultivated and uncultivated, and it is vital to understand how wildlife use these areas, especially for predatory birds that may help control agricultural pests.
- We used Global Positioning System telemetry to examine the selection of habitats for hunting by Barn Owls breeding in nest boxes in winegrape vineyards.
- Barn Owls selected uncultivated habitats, such as oak savanna, riparian forest, and grasslands for hunting, some of which were relatively rare on the landscape.
- Nonetheless, approximately, one-third of Barn Owl hunting locations occurred in vineyards, suggesting their predation of rodent pests could be useful for farmers.

Tyto furcata selecciona hábitats no cultivados para cazar en una región vitivinícola de California

RESUMEN

La conversión a gran escala de tierra no cultivada a agricultura amenaza la vida silvestre y puede disminuir los servicios ecosistémicos brindados por la naturaleza. Entender cómo la vida silvestre brinda servicios ecosistémicos puede incentivar su conservación en los paisajes agrícolas. Atraer individuos de *Tyto furcata* a que aniden en granjas para el manejo de plagas ha sido implementado en todo el mundo, pero no ha sido evaluado en agro-ecosistemas de viñedos. El Valle de Napa en California es una región vitivinícola famosa, y los vitivinicultores alientan la ocupación de *T. furcata* para ayudar a minimizar los daños de los topos de la especie *Thomomys bottae* y de los campañoles del género *Microtus* spp. Este estudio modeló el uso de hábitat en espacio y tiempo por parte de individuos de *T. furcata* que cazan, brindando

información sobre su potencial para ofrecer el servicio ecosistémico crítico de consumo de plagas. Usamos marcadores en un sistema de posicionamiento global para seguir a los individuos que cazan, y usamos una función de selección de recursos para comparar a los hábitats usados vs. los disponibles. Elaboramos mapas de intensidad de uso y de movimiento en los rangos de hogar mediante un análisis de Envoltura Convexa Local de Tiempo (t-LoCoH, por sus siglas en inglés) a partir de datos de localización. Encontramos que *T. furcata* seleccionó hábitats no cultivados cuando caza, algunos de los cuáles fueron relativamente raros en el paisaje. Aproximadamente un tercio de las localizaciones de caza de *T. furcata* se ubicaron en viñedos, pero este uso fue desproporcionado con relación a la disponibilidad de viñedos, que representó el 50% del área alrededor de las cajas nido. El uso de viñedos por parte de *T. furcata* aumentó con una cantidad seleccionada decreciente de hábitat no cultivado en el paisaje. Sin embargo, como se reportó en un estudio anterior, la ocupación de las cajas nido en los viñedos aumentó con los hábitats no cultivados cercanos. Investigaciones futuras deberían modelar la composición del paisaje para determinar la cantidad de hábitat preferido necesaria para promover la ocupación así como la caza en los viñedos. Se necesita un verdadero test experimental de manejo de plagas por parte de *T. furcata* junto con un monitoreo de las poblaciones de roedores.

Palabrasclave: función de selección de recursos, heterogeneidad de hábitat, manejo de plagas, selección de hábitat, servicio ecosistémico, telemetría, *Tyto furcata*, uso de hábitat, viñedo

INTRODUCTION

Increasing human population sizes and rising per capita consumption accelerate the conversion of uncultivated lands to agriculture (Tanentzap et al. 2015), resulting in drastic declines in habitat quantity and quality that are primary threats to biodiversity (Green et al. 2005, McLaughlin 2011, Balmford et al. 2012). Expansion and intensification of agriculture not only diminish habitat quality for many species; increased use of agrochemical inputs (Matson et al. 1997, Grismer and Asato 2012) can impair the ability of agroecosystems to provide nonmarketed services, such as water purification, pollination, and pest control (Swinton et al. 2007). These concerns have stimulated research in alternative management practices to alleviate detrimental impacts on ecosystems while also promoting factors that support nonmarket services (e.g., wildlife; Power 2010, Hannah et al. 2013). Many of the studies have shown that wildlife can benefit agroecosystems by enhancing pest control or pollination (Kremen and Merenlender 2018), including services delivered by birds (Sekercioglu et al. 2016). 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, Lindell et al. 2018).

In regions with unique and sensitive habitats, land-use conversion continues to be the greatest threat to ecosystems (Myers et al. 2000, Wood et al. 2013). The Mediterranean biome, which includes portions of California, is home to some of the highest concentrations of endemism on the planet but remains minimally protected (Myers et al. 2000, 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 to agriculture within the Mediterranean biome, particularly for the production of winegrapes (Viers et al. 2013). California vineyards account for over 90 percent of all winegrapes grown

in the United States, an industry valued at nearly $3 billion in 2014 (CDFA 2019). 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).

Integrated pest management is critical for improving sustainability in agricultural industries. In Napa Valley, Botta's pocket gophers (*Thomomys bottae*) and voles (*Microtus* spp.) are rodents that reduce farm functionality, threaten the health of the vines, and cause significant economic losses (Ross 2009, Salmon and Baldwin 2009, Salmon and Gorenzel 2010). Anderson et al. (2012) estimated a 4% yield loss due to rodents and costs of $22 to $27 per acre for rodent control. By cutting roots and gnawing bark, rodents can slow the growth and productivity of vines and, in extreme cases, kill the plants (Ross 2009). Traditional rodent control techniques include trapping and rodenticides, which must be evaluated with respect to efficacy, cost, and safety to workers and the environment (Baldwin et al. 2014).

Integrating the use of natural predators with more traditional techniques can produce effective management of vertebrate pests (Bottrell 1979, Kogan 1998, Kross et al. 2012, Baldwin et al. 2014, Coeurdassier et al. 2014). Life history attributes of Barn Owls (*Tyto furcata*) suggest they could be part of such pest management systems (Labuschagne et al. 2016, Johnson et al. 2018). Nesting Barn Owls are central place foragers, meaning their use of space centers on a nest site to which they frequently return (Rosenberg and McKelvey 1999). They 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. 2016). Barn Owls

are cosmopolitan, found in habitats ranging from dry savannas to rainforests, and adjust well to human settlements and farms throughout North America and Europe (Johnsgrad 1988, Taylor 1994). Despite their widespread distribution, Barn Owl populations still face significant loss of nest sites and hunting habitats in some places as well as threats from rodenticides and roadway mortality (Colvin 1985, Taylor 1994, Bond et al. 2005, Hindmarch et al. 2012). In unaltered habitats, Barn Owls nest in cavities found in trees or rock faces or create cavities through excavation (Martin 1973, Taylor 1994). Where natural nest sites are limited, Barn Owls use 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 management practices that attract and sustain wildlife (Labuschagne et al. 2016).

The practice of attracting Barn Owls to nest on farms for pest management has been implemented in rice and oil palm fields in Malaysia (Duckett 1976, Wood and Fee 2003), alfalfa production in Israel (Meyrom et al. 2009, Kan et al. 2014), row crops in Utah (Marti 2010), and sugarcane fields in Florida (Martin 2009). However, the use of Barn Owls for pest management in vineyards has only been recommended and not robustly evaluated (Byron 2008, Tillmann 2012, but see Browning et al. 2016), and further examination of this system is warranted (Johnson et al. 2018). 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, Arlettaz et al. 2010, Hindmarch et al. 2017), likely because of high rodent abundance and accessibility (Taylor 1994). Barn Owls have also demonstrated the ability to hunt successfully in lightly wooded environments as well as along urban edges (Fast and Ambrose 1976).

In a heterogeneous landscape, predators must balance costs and benefits when selecting habitats for hunting (Rosenberg and McKelvey 1999). Highly mobile predators such as Barn Owls can target hunting efforts in productive habitats within broad landscapes (Pyke et al. 1977). During the breeding season when provisioning prey to young, a Barn Owl must balance costs of prey depletion and travel to determine whether hunting close to a nest may be more cost effective than traveling further to a more productive hunting area (Rosenberg and McKelvey 1999). In Napa Valley, these balances may influence the likelihood of a Barn Owl hunting on a vineyard where its nest box is located. Identifying habitat composition across the landscape and evaluating the hunting range and habitat preference of Barn Owls can provide useful information to farmers for directing management practices that promote and sustain Barn Owl hunting in and around their farms (sensu Lindell et al. 2018).

In this study, we 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 to the 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. This study provides practical information to farmers on how to attract Barn Owls, and it advances our understanding of how landscape composition affects the delivery of regulating services such as pest management by a highly mobile predator.

METHODS

Study Area

Napa Valley is ~100 km north of San Francisco, California (Figure 1). The valley sits between the Vaca Mountains to the east and the Mayacamas 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 and grasslands 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 the region ideal for growing a variety of winegrape cultivars (Napa Valley Vintners 2015). Total acreage in winegrape production has increased from 12,345 ha in 1999 to 17,891 ha in 2019 (45% increase; Napa County Agricultural Commissioner's Office 2019).

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).

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 as early as mid-February (Browning et al. 2016). Nest boxes were checked for occupancy from 28 February until 31 March, 2016. Nest monitoring was done using a GoPro HERO Session camera, Riverside, California that was mounted with an LED flashlight to the end of an extendable pole, allowing access to the nest box opening with minimal disturbance. The camera was connected wirelessly to a smartphone and showed a live feed of nest box contents.
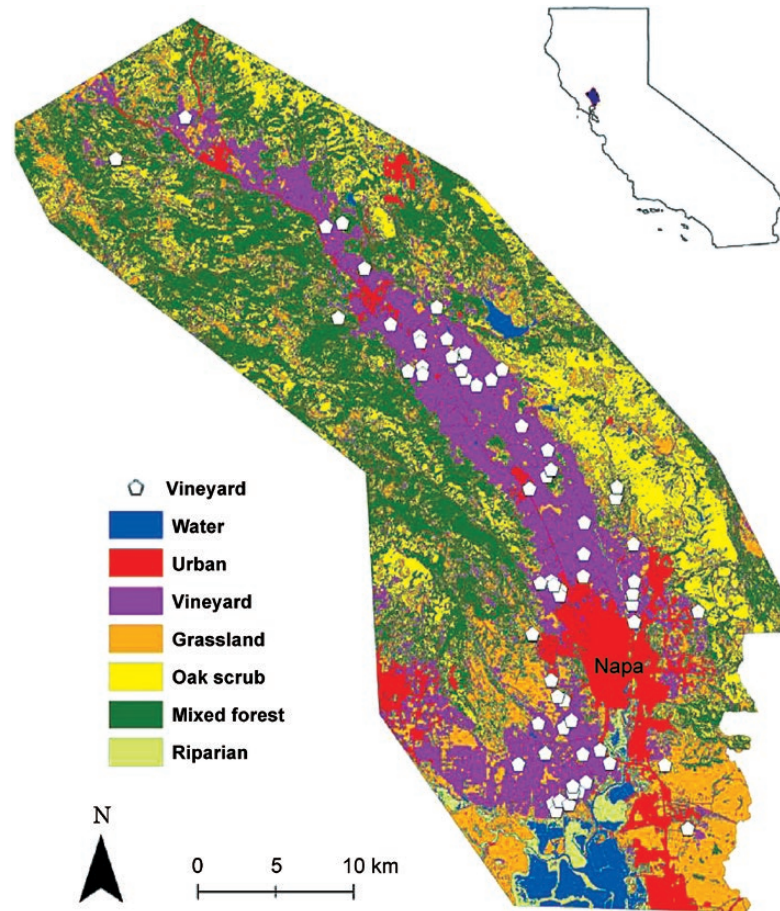
FIGURE 1. Location of Napa Valley within California, ~161 km northeast of San Francisco (inset). Distribution of vineyards (white polygons) that were surveyed for the presence of Barn Owls in spring 2016 (from Wendt and Johnson 2017).

Quantifying Habitat Use

During the 2016 breeding season, March through August 2016, 24 individual female nesting Barn Owls were fitted with Uria 300 Global Positioning System (GPS) units (Gdynia, Poland). 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 a 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, which weighed 13.5 g including harness, did not exceed 3% of the owls' mass (Fair et al. 2010). Transmitters were attached via a small backpack harness constructed of Teflon ribbon that was designed not to impede the bird's natural mobility (Humphrey and Avery 2014). After the transmitter was attached, the owl was placed back in the nest box and the entrance blocked for 10 min to reduce the risk of the owl flushing from the box. Total handling time did not exceed 20 min per bird. Telemetry tracking began the night after

attaching the transmitter, 8–12 hr after handling. All monitoring and handling were approved by Humboldt State University's Institutional Animal Care and Use Committee (IACUC No.15/16.W.43-A; see Acknowledgments).

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. Each telemetry tag was set to record a location once per minute to provide fine temporal 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, we experimented with deployment and programming details to optimize battery life and data retrieval. Battery life was shorter than initially expected but was optimized by programming tags to not record locations when within range (~40 m) of a handheld base station placed directly at the nest box. This also increased the likelihood that all location data were retrieved.

Tags were deployed on females known to have chicks due to sensitivity to disturbance in earlier stages of nesting (i.e. laying and incubation). Barn Owl's sex was determined

by the presence of a brood patch. Birds were selected if their oldest young were ~10–15 days old at the beginning of tag deployment. This stage was selected because it is after brooding when females are actively hunting to provision the chicks, but when chicks are still young enough to increase the likelihood the tagged female would still be using the nest box for diurnal roosting 3 to 8 days later. This allowed for tag retrieval after the battery on the tag had drained and was no longer collecting locations. A total of 24 females were tagged; all but 3 tags were retrieved. The age of young was determined via plumage development using an aging guide developed by The Barn Owl Trust (2015).

Habitat Sampling

Using high-resolution (<1 m) National Agriculture Imagery Data provided by the US Department of Agriculture (2015) and fine-scale elevation LiDAR (Light Detection and Ranging) data from the National Center for Airborne Laser Mapping (NCALM), vegetation and habitat were classified into 7 dominant categories: water/wetland, urban, vineyard, grassland, oak savanna, mixed forest, and riparian (see Appendix A for a detailed description of each habitat category). Non-vineyard row crops were virtually absent (<0.5% of the landscape) and were small plots adjacent to urban areas with which they were lumped. Managed pastures (<2%) were combined with grasslands. A 100% minimum convex polygon (MCP) was constructed around each bird's hunting locations (Figure 2). We defined available habitat within each bird's MCP, rather than within a fixed kernel home range estimate, because MCPs may more accurately represent the area available to hunting owls (Comfort et al. 2016, Eyes et al. 2017). All habitat analysis was conducted using R 3.5.1 (R Core Team 2019).

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 MCP. Due to a limited number of birds sampled, competing models were assessed using the Akaike information criterion corrected for a small sample size (AIC_c) (Burnham et al. 2011). Models for all analyses were run through the R Package *lme4* (Bates et al. 2015), using a no-intercept model (aka deviation coding). Models run with deviation coding yield a coefficient for each habitat category, so that the effect of each category is contrasted against the overall mean effect of the habitat variable rather than against an arbitrary reference class (Johnson et al. 2004). Model selection was determined using R package *AICcmodavg* (Mazerolle 2017). We report the coefficients

and their standard errors ($\beta \pm 1$ SE) for each covariate in the top models.

Determining 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 points) to available locations randomly distributed within each animal's home range (i.e. third order habitat selection, Johnson 1980). Because the objective of the study was to understand habitat selected for hunting specifically, telemetry locations were filtered based on criteria that best identified hunting behavior. 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 10 m s^{-1} and were not stationary (i.e. roosting) for > 10 min at a time. These criteria were used to exclude resting periods as well as longer nonhunting flights (i.e. commuting) and were based on field observations as well as natural history observations of foraging behavior (Taylor 1994) and recent telemetry studies in Switzerland showing that barn owls hunt at flying speeds < 5 m s^{-1} and commute at speeds > 7 m s^{-1} (Roulin 2020). 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 analyzed Barn Owls. The result was a spread of hunting locations over each bird's tracking period (mean of 6.27 ± 0.73 days). An equal number of available locations ($n = 260$ per bird) were distributed randomly within each tagged bird's MCP.

Telemetry locations taken very frequently raise the complicating issue of spatial autocorrelation and non-independence of successive points (Cushman 2010). Our intent was to examine fine temporal 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. However, subsampling data to achieve statistical independence often incurs heavy costs in terms of lost information for fine-resolution habitat selection, and many of the 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 the intensity of habitat use and quantification of fine-scale behavioral decisions may be to use the
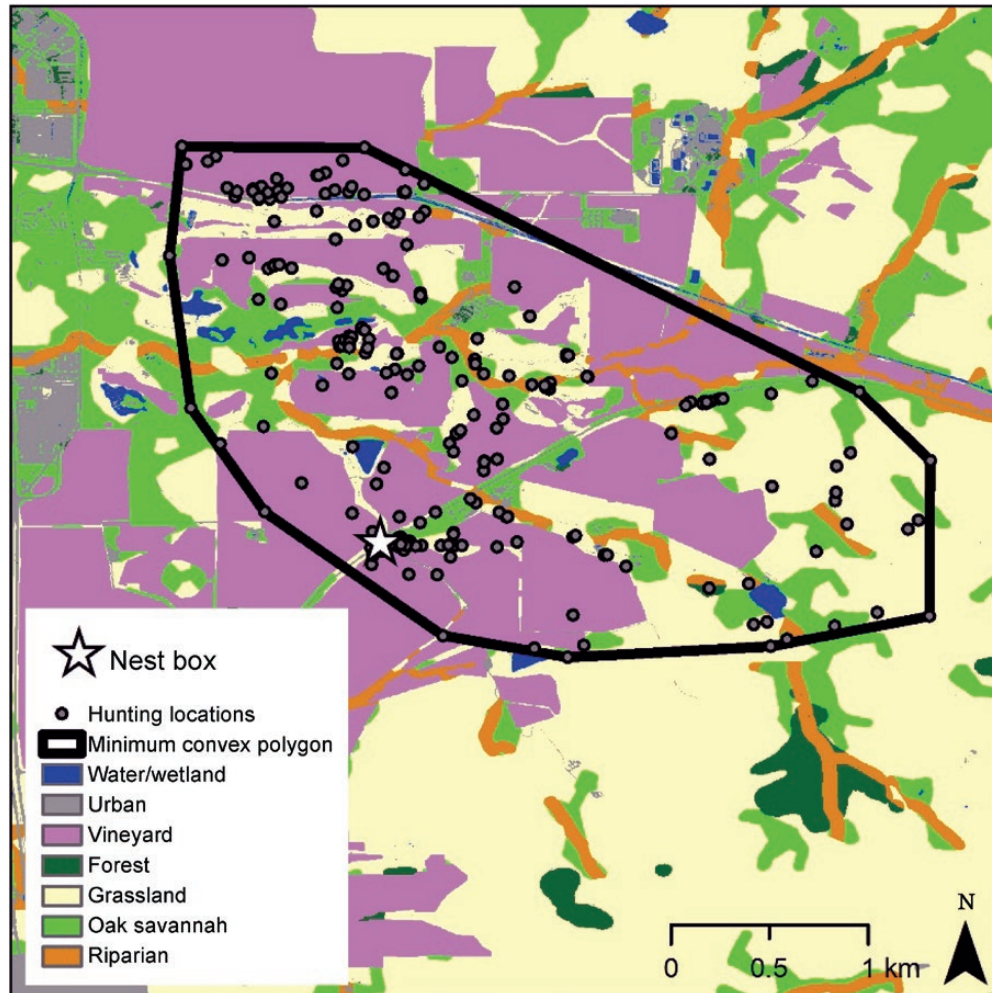
FIGURE 2. An example of habitat classification within and surrounding the MCP created using 260 randomly sampled hunting locations from a nesting female Barn Owl in Napa Valley, CA, spring 2016. Gray circles represent GPS locations and the white star represents the nest box for this individual owl.

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).

We conducted 4 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, we 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, we 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, we calculated the proportion of locations that remained in the same habitat category after the location time lag. Third, we 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, we calculated the duration of time between habitat changes and plotted frequency distributions. Fourth, we calculated Moran's I on the residuals of the top-performing habitat selection model (see below for model section methods).

These analyses showed that while the data were spatially autocorrelated (e.g., Moran's I of model residuals = 0.283), the mode time to change habitats was only 1 min, and > 50% of all hunting habitat changes occurred within 4 min (Appendix B). These patterns, combined with suggestions to use the shortest possible sampling interval over the longest possible period, led us to retain all locations after randomly subsampling down to 260 locations per owl, yielding a total of 2,860 telemetry locations used in the RSF. The points ranged over a sampling period of $6.00 ± 0.71$ days per owl, which was the most possible

given battery life and logistics, and 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).

Our primary intent for this model set was to examine the effect of habitat and proximity to resources on the owls' space use. Recognizing that 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 (m). We took a tiered model selection approach to determine which habitat was the best predictor of use. First, we created a competing model set with each distance to habitat as a unique model. From this approach, we determined distance to oak savanna was the best distance variable as a predictor of use (see Results). Next, we included all additive combinations of habitat category, distance from the nest box, and distance to oak savanna habitat as predictor variables in candidate model sets. All distances were scaled to a range of 0 to 1 for these analyses, as is commonly practiced in RSF analyses (Manly et al. 2002), then back scaled for a clearer interpretation of the effects of distance on habitat selection. Individual bird identity was included as a random effect in the models.

Habitat selection model evaluation. The top model in the candidate set, as determined by the lowest AIC_c score, was evaluated following Boyce et al. (2002) and Johnson et al. (2006). More specifically, the predicted probability of use for each used and the available location was calculated, then sorted, and divided into 10 equal bins. The mean predicted probability of use for each bin was determined and regressed against the proportion of used locations for each bin. A strongly predictive model should yield a Pearson's correlation coefficient near one and a positive slope significantly different from zero (Johnson et al. 2006).

Modeling the intensity of use of habitat categories within their hunting range. Use vs. available analyses examine habitat selection, but they reveal little about the intensity of space use (i.e. some areas may be visited rarely but used for longer durations or used for vital purposes; Carey and Peeler 1995, Gervais et al. 2003). Therefore, time local convex hull (t-LoCoH) analyses were used to reveal more information about Barn Owl hunting habitat use (Getz et al. 2007, Lyons et al. 2013). Specifically, we used the mean number of locations per visit (mnlv), which is defined as the mean number of sequential telemetry locations in a given hull before the bird moved to another hull, as a metric for the duration of patch use generated from the t-LoCoH analysis (Getz et al. 2007, Lyons et al. 2013). 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 oak savanna habitat, based on predictors from the RSF described above.

Examining the effect of landscape composition 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 uncultivated habitats (riparian, oak savanna, grassland, and mixed forest) within the bird's hunting range. Competing models were again compared with a tiered approach. First, we determined whether each 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, we tested a priori hypothesized combinations of these variables based on the previous habitat selection results and Barn Owl natural history (Taylor 1994) while not including collinear ($r \geq 0.6$) predictor variables. Coefficients are reports ± 1 SE.

RESULTS

A total of 9,526 GPS telemetry locations were obtained from 20 owls (locations per owl: 476.3 ± 95.8). Of all locations, 26% were within grassland habitat, 26% within vineyard, 25% within oak savanna, 12% within riparian habitat, and the remaining 11% were spread between urban, mixed forest, and water/wetland 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 2 nights ($n = 4$), but once we optimized the deployment strategy (see Methods), the tag's batteries lasted about 8 nights. Due to these complications, 9 birds did not have enough location points (<200) to be useful and, thus, were excluded from all subsequent habitat selection analyses. Of the remaining locations, 3,348 (35%) were classified as hunting locations (mean number per owl ± SE: 304.37 ± 33.11). Of these hunting locations, 32% were within vineyard, 35% within grassland habitat, 19.5% within oak savanna, 4% within mixed forest, 7% within riparian habitat, and the remaining 1.5% spread between urban and water/wetland environments. For comparison, the average overall composition of habitat categories within the 11 owls' hunting ranges used (MCP around 260 hunting locations) was 50% vineyard, 25% grassland, 9% oak savanna, 2% mixed forest, 4% riparian, 6% water/wetland, and 3% urban.

Resource Selection Function

The top model in the RSF analysis included additive effects of habitat, distance to nest, and distance to oak savanna (Table 1). Barn owls are central place foragers and this was reflected by a strong negative effect of distance from nest on habitat selection ($\beta = -4.07 \pm 0.23$; Figure 3). Although we recorded locations up to 9 km from a nest, most of the locations were far closer, with 73% of hunting locations within

TABLE 1. Results of the model set for an RSF predicted hunting habitat of Barn Owls in Napa Valley, CA, spring 2016. The response variable was used/available locations, and predictor variables included habitat category, distance to nest, and distance to oak savanna, with owl identity as a random effect. Models were run using a generalized mixed model with random effect.

Model[a]	k[b]	$Log_e(L)$[c]	ΔAIC_c[d]	w_i[e]
Habitat + D_{Nest} + D_{sav} + (1|owl_id)[f]	10	−3,456.45	0.00	0.88
Habitat + D_{Nest} + (1|owl_id)	9	−3,459.43	3.95	0.12
Habitat + D_{sav} + (1|owl_id)	9	−3,633.67	352.43	0.00
Habitat + (1|owl_id)	8	−3,654.22	391.53	0.00
D_{Nest} + (1|owl_id)	3	−3,768.25	609.57	0.00
D_{sav} + (1|owl_id)	3	−3,882.42	837.90	0.00
1 + (1|owl_id)	2	−3,964.80	1,000.66	0.00

[a]D_{nest} is the distance from nest; D_{sav} is the distance from oak savanna; habitat is the 7 categories of identified habitat within hunting range (see Methods).
[b]Number of parameters.
[c]Log_e(likelihood).
[d]Difference between model AIC_c and top model AIC_c.
[e]AIC_c weight.
[f]Lowest AIC_c: 6,932.94.

1,000 m and 50% within 500 m of a birds' nest box. Among the 7 habitat categories, the strongest positive predictors of use were for the uncultivated habitats (Table 2): riparian (β = 1.98 ± 0.17), oak savanna (β = 1.85 ± 0.12), mixed forest (β = 1.55 ± 0.18), and grassland (β = 1.43 ± 0.12; Figure 3), and each had coefficient estimates well above the overall average coefficient for all habitat categories (0.87). Distance to oak savanna habitat also showed a negative relationship (β = −0.55 ± 0.22), suggesting locations close to oak savanna were selected for hunting.

Model evaluation indicated the top model was a strong predictor of used locations. The linear relationship between the mean predicted probabilities and the proportion of use within each bin yielded a Pearson's correlation coefficient of 0.968, and the slope of the regression line was significantly different from zero ($F_{1,8}$ = 118.9, P < 0.01) with an adjusted R^2 of 0.93. The high Pearson's coefficient suggests that the model explained significant variation in hunting habitat use by Barn Owls in this system.

Intensity of Habitat Use
Model selection using AIC_c indicated that a model with habitat, distance to nest, and distance to oak savanna was the best for explaining the intensity of habitat use by hunting Barn Owls (Table 3). Oak savanna and water/wetland habitats had the largest positive coefficients (β = 9.22 ± 1.29 and β = 8.68 ± 1.94, respectively; Table 4), suggesting that when owls used these habitats, they did so for longer durations than the other habitats. Distance from nest and distance to oak savanna each had a positive, although comparatively weaker, association with intensity of habitat use

TABLE 2. Coefficients, SEs, and CIs from the top RSF model of Barn Owl habitat use in the Napa Valley, CA, spring 2016.[a]

Covariate[b]	Coefficient	SE	95% CI LL[c]	95% CI UL[d]
Urban	0.22[e]	0.23	−0.23	0.67
Vineyard	0.35	0.11	0.13	0.57
Grassland	1.43	0.12	1.19	1.67
Oak savanna	1.85	0.12	1.61	2.09
Mixed forest	1.55	0.18	1.20	1.90
Riparian	1.98	0.17	1.65	2.31
Water/wetland	−1.34	0.30	−1.93	−0.75
D_{nest}	−4.07	0.23	−4.52	−3.62
D_{sav}	−0.55	0.22	−0.98	−0.12

[a]Use ~ Habitat + D_{Nest} + D_{sav} + (1\|owl_id); see Table 1 for more details and abbreviations.
[b]Nine covariates included in the top model.
[c]LL, lower limit.
[d]UL, upper limit.
[e]Coefficients for habitat categories should be evaluated with respect to the mean among all 7 categories (0.87) to infer relative selection.
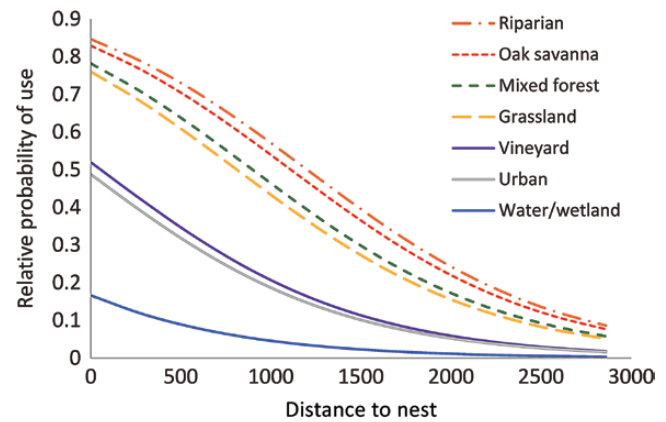

FIGURE 3. An RSF model using locations (i.e. Barn Owl hunting locations within Napa Valley, CA, spring 2016) as a function of habitat and distance to nest; distance to oak savanna habitat, which also appeared in the top model, was held constant (at its overall mean). Farthest distance traveled was limited to within mean maximum hunting range of all owls, 2.86 km. Uncultivated habitats (dashed) were the most strongly selected.

(β = 7.72 ± 0.79 and β = 1.14 ± 0.75, respectively), suggesting the owls spent relatively more time hunting once arriving to locations farther from these resources (Table 4).

Habitat Composition Effects on Vineyard Use
Model selection revealed that the proportion of an owl's hunting locations that were in vineyard was best explained by the relative proportion of riparian and oak savanna habitats within an owl's hunting range (Table 5). As the log of the proportion of an owl's hunting range comprised of oak savanna increased, the proportion of hunting locations within vineyard declined, and this confidence interval (CI) for the coefficient did not overlap zero

TABLE 3. Results of the competing model set for the intensity of habitat use by hunting Barn Owls in Napa Valley, CA, spring 2016. The response variable was the mean number of locations to a hull per visit (mnlv; see Methods), and predictor variables included habitat category, distance to nest, and distance to oak savanna, with owl identity as a random effect. The models were run using a generalized mixed model with a random effect.

Model[a]	k[b]	$\text{Log}_e(L)$[c]	ΔAIC_c[d]	w_i[e]
Habitat + D_{Nest} + D_{sav} + (1|owl_id)[f]	11	−13,303.82	0.00	1
Habitat + D_{sav} + (1|owl_id)	10	−13,331.56	53.48	0
D_{Nest} + (1|owl_id)	4	−13,413.05	204.43	0
Habitat + D_{sav} + (1|owl_id)	10	−13,570.16	530.67	0
Habitat + (1|owl_id)	9	−13,608.42	605.18	0
1 + (1|owl_id)	2	−13,683.73	745.79	0
D_{sav} + (1|owl_id)	4	−13,728.31	832.95	0

[a]D_{nest} is the distance from nest; D_{sav} is the distance from oak savanna; habitat is the 7 categories of identified habitat within hunting range (see Methods).
[b]Number of parameters.
[c]Log_e(likelihood).
[d]Difference between model AIC_c and top model AIC_c.
[e]AIC_c weight.
[f]Lowest AIC_c: 26,627.68

TABLE 4. Coefficients, SEs, and CIs from the top model of the intensity of habitat use by hunting Barn Owls in Napa Valley, CA, spring 2016.[a]

Covariate[b]	Coefficient	SE	95% CI LL[c]	95% CI UL[d]
Urban	7.47[e]	1.59	4.71	10.58
Vineyard	7.65	1.29	5.11	10.18
Grassland	7.50	1.30	4.96	10.05
Oak savanna	9.22	1.29	6.68	11.75
Mixed forest	7.78	1.35	5.13	10.44
Riparian	7.64	1.34	5.00	10.27
Water/wetland	8.68	1.94	4.88	12.48
DNest[f]	7.72	0.79	6.17	9.27
DSav[g]	1.14	0.75	−0.33	2.62

[a]mnlv ~ Habitat + D_{Nest} + D_{Sav} + (1\|owl_id); see Table 3 for more details and abbreviations.
[b]Nine covariates that were included in the top model.
[c]LL, lower limit.
[d]UL, upper limit.
[e]Coefficients for habitat categories should be evaluated with respect to the mean among all 7 categories (7.99) to infer relative effect.
[f]Distance to nest.
[g]Distance to savanna habitat.

($\beta = -0.22 \pm 0.03$). The proportion of riparian had a positive coefficient ($\beta = 8.20 \pm 1.04$), suggesting that vineyard use increased with increasing riparian habitat, and this CI did not overlap zero.

DISCUSSION

Our results indicated that riparian, oak savanna, mixed forest, and grassland habitats were strongly selected

TABLE 5. AIC_c comparison of a competing model set predicting the proportion of Barn Owl hunting locations located within vineyards in Napa Valley, CA, spring 2016. The model set included the proportion of riparian, oak savanna, grassland, and mixed forest habitats as predictors; models were run using a generalized linear model.

Model	k[a]	$\text{Log}_e(L)$[b]	ΔAIC_c[c]	w_i[d]
PRiparian + log(POakS)[e]	4	16.00	0.00	1
PRiparian + POakS + log(PGrass) + log(PMixedF)	6	21.73	12.53	0
PRiparian + log(PGrass)	4	8.27	15.45	0
PRiparian + log(PMixedF)	5	5.59	20.81	0

[a]Number of parameters.
[b]Log_e(likelihood).
[c]Difference between model AIC_c and top model AIC_c.
[d]AIC_c weight.
[e]Lowest AIC_c: −15.99.

for hunting by Barn Owls nesting in boxes located in a winegrape vineyard ecosystem. Water/wetland habitats were strongly avoided, while vineyard and urban habitats were less strongly avoided. That Barn Owls actively selected uncultivated habitats in the landscape, including rare riparian habitats, suggests that these habitats provide important resources for the owls, such as prey and staging or perch sites that Barn Owls use while hunting (Askham 1990, Taylor 1994). Conversely, although vineyard habitat was not selected as strongly as other habitat types for hunting, most of the birds' home ranges were dominated by vineyard (50% of random points, overall), so a substantial portion of the owls' hunting occurred within vineyards (32% of hunting locations, overall). Preferred habitat for Barn Owls is often considered to be open, grassy areas (Evans and Emlen 1947, Hindmarch et al. 2017, Roulin 2020), likely because of high rodent abundance and accessibility (Taylor 1994, Arlettaz et al. 2010). In Napa Valley, these habitats are associated with increased nest box occupancy by Barn Owls (Wendt and Johnson 2017), and our telemetry results also indicate these habitats are selected for hunting. While urban habitats were rarely used, their use is important to note because of possible increased exposure risk to second-generation anticoagulant rodenticides (Hindmarch et al. 2017), which are prohibited by the State of California in crop areas but permitted around houses and structures.

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 recorded within 1 km of an owl's nest box. The top model included this effect for all habitats (Figure 3). It should be noted, however, that we only tracked females, who could have a stronger association with the nest box than do males, whose hunting habitat selection has not yet been examined. Distance from oak savanna habitat

had a weak negative relationship in predicting used locations, suggesting Barn Owls selected hunting areas close to oak savanna habitat. Whether this is because of favorable roosting opportunities, prey abundance, or other factors associated with oak savanna is unknown. 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. The role of predators may also be important, as Great Horned Owls (*Bubo virginianus*) are known predators and can be found in more forested habitat, which could reduce Barn Owls' use of forested areas (Millsap and Millsap 1987).

Conversely, the intensity of use (as measured with a metric for duration of patch use the t-LoCoH analysis) was positively associated with distance to nest, indicating that areas far from nests were used for longer hunting bouts. This finding may appear at first to be at odds with the negative effect of distance to nest on selection probability. However, both findings are consistent with optimal foraging theory for a central place forager, as hunting time in a patch should offset travel costs to a more distant location (Pyke et al. 1977). Surprisingly, the intensity of use was also high for water/wetland habitats, suggesting that, although this habitat was rarely used (see Figure 3 for selection results), when barn owls did use patches of water/wetland, they tended to do so for longer durations than for some other habitat categories. Barn Owls will occasionally prey on amphibians (Roulin and Dubey 2013, St. George 2019), but additional research is needed to better understand this result. The intensity of use was also high for oak savannah habitats, suggesting that owls had longer hunting bouts in this habitat.

It is important to note that while our results reveal hunting habitat preferences in this vineyard landscape, much remains unresolved about the foraging ecology of Barn Owls in this system. That uncultivated habitats were most selected does not necessarily mean they are the highest in quality for Barn Owls (Johnson 2007). Also, there may be different prey in different habitats, and Barn Owls may prefer certain prey items over others at certain times of the nesting cycle (St. George 2019). Lastly, perches can be important foraging structures for Barn Owls (Roulin 2020), and some habitats may be preferred for hunting because of perches located close to potential prey.

The 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. Specifically, all non-cultivated habitats were selected (Table 2), and owls lingered longer in oak savanna habitat than in other habitats (Table 4). 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, uncultivated habitats are dominated by expansive grassland (~30% of total area) and oak savanna (~7% of total area) with relatively few riparian habitats. Farther north, uncultivated 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. The coverage of vineyard also varies, increasing by more than 20% in the northern part of valley.

This gradient in habitat composition and landscape complexity from south to north in Napa Valley could affect pest control services by Barn Owls, and resolving this pattern could advance our understanding of the role of landscape heterogeneity in the delivery of ecosystem services by mobile predators (Bianchi et al. 2006, Lindell et al. 2018). For example, some of the results suggest that pest removal could be strongest in the southern part of the valley. Although there is an increase in relative landscape complexity to the north, the decline in grassland may not be ideal to support occupancy (Wendt and Johnson 2017) or extensive hunting (this study) 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).

Alternatively, theory suggests that owl hunting and pest removal may be strongest in the more heterogeneous north. A major review by Bianchi et al. (2006) on the effects of landscape complexity on natural pest control services suggested that complex landscapes support greater pest regulation than simple landscapes, because they can provide favorable conditions and meet all the requirements for the establishment and maintenance of natural predators. As highly mobile predators, Barn Owls have the ability to evaluate conditions across large spatial extents to determine where hunting efforts may be the most cost effective (Pyke et al. 1977). 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. With nest boxes placed within the vineyards and Barn Owls showing strong central place foraging, the owls in the north may have been constrained to use more vineyard habitat. Perhaps this explains why the 3 Barn Owls tracked in this study from the northern part of the valley traveled less distance from the nest when hunting than those in the south (mean distance traveled: north = 1,675 m, south = 3,137 m) and thus may be providing a greater service to the farms around their nest boxes. Our analysis did not examine any effect of landscape configuration; that is, the spatial arrangement of habitat categories, their sizes, or contagion. This may be a fruitful area for additional research. In particular, the role of riparian habitats

in vineyard ecosystems as corridors has been previously recognized (Hilty and Merenlender 2004); these habitats may facilitate owl movement across simpler agricultural landscapes.

The effect of landscape heterogeneity and uncultivated habitat on habitat selection in this study may be related to prey availability. Voles and Botta's pocket gophers, specifically, are commonly found in grassland (Huntly and Inouye 1988, Fehmi and Bartolome 2002), which we observed to be a preferred hunting habitat for Barn Owls. Additionally, literature shows that small mammal abundance is higher as landscape heterogeneity increases in agricultural areas (Fischer et al. 2011). Thus, landscape heterogeneity may influence rodent pests in farms (Tscharntke et al. 2016), which would in turn affect the number of Barn Owls using nest boxes and hunting in vineyards. Additionally, because rodent populations are high in grasslands surrounding vineyards, this introduces the possibility that Barn Owls hunting away from vineyards may still be providing a pest control service by reducing rodent populations in surrounding uncultivated land. 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. Available evidence indicates that over 90% of Barn Owl diets are comprised of rodent pests in California agricultural habitats (Kross et al. 2016, St. George 2019), and modeling suggests they could be helpful in non-outbreak years (Kross and Baldwin 2016), but a true test of the capacity for Barn Owls to reduce rodent pests in vineyard awaits experimentation (Johnson et al. 2018).

Our results showed that the overall composition of the landscape can affect how much hunting occurs in farmland; in this case, owls hunted less on vineyards where nearby riparian and oak savanna habitats were available (Table 5). This result underscores the importance of uncultivated habitats to the delivery of pest control in agriculture (Tscharntke et al. 2016, Lindell et al. 2018). Although grassland, riparian, mixed forest, and oak savanna were the most selected habitats, oak savanna and riparian were among those most intensively used, and the final analysis showed that as these habitats increased across the landscape, hunting in vineyard habitat diminished. Studies of land-use change clearly indicate that the expansion of winegrape vineyards is coming at the cost of these important habitats, especially oak savanna and grassland. As a result, owls nesting in boxes located on vineyards may need to travel farther to reach their preferred uncultivated habitats. To some degree, this could concentrate hunting by owls in vineyards, but at some point, the loss of uncultivated habitats will likely diminish nest box occupancy altogether (Wendt and Johnson 2017), resulting in fewer owls on the landscape. Thus, there may be a tradeoff in that preferred uncultivated habitats enhance occupancy but diminish proportional hunting in vineyards by Barn Owls. Spatial modeling will be required to more fully explore the nuances of this possible tradeoff in habitat allocation, bird numbers, and the delivery of an ecosystem service (sensu Railsback and Johnson 2014). Likewise, the delivery of desired ecosystem services could be influenced by not only the amount but also the distribution of preferred habitats (Railsback and Johnson 2014, Mitchell et al. 2015, Tscharntke et al. 2016). The use of Barn Owl nest boxes for possible rodent management is also practiced in the Central Valley of California, where farm sizes are larger and there is less uncultivated habitat. In Israel, where nest boxes are also used in agricultural landscapes with large fields (e.g., alfalfa), Barn Owls also travel farther from the nest for hunting (Motti Charter, personal communication). Future work examining hunting habitat selection in populations in landscapes with varying levels of heterogeneity and patch sizes could help inform the role of landscape composition on delivery of rodent pest management by highly mobile avian predators.

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APPENDIX A

Description of Each Habitat Category within a Barn Owls Hunting Range in Napa Valley, Ca, Spring 2016
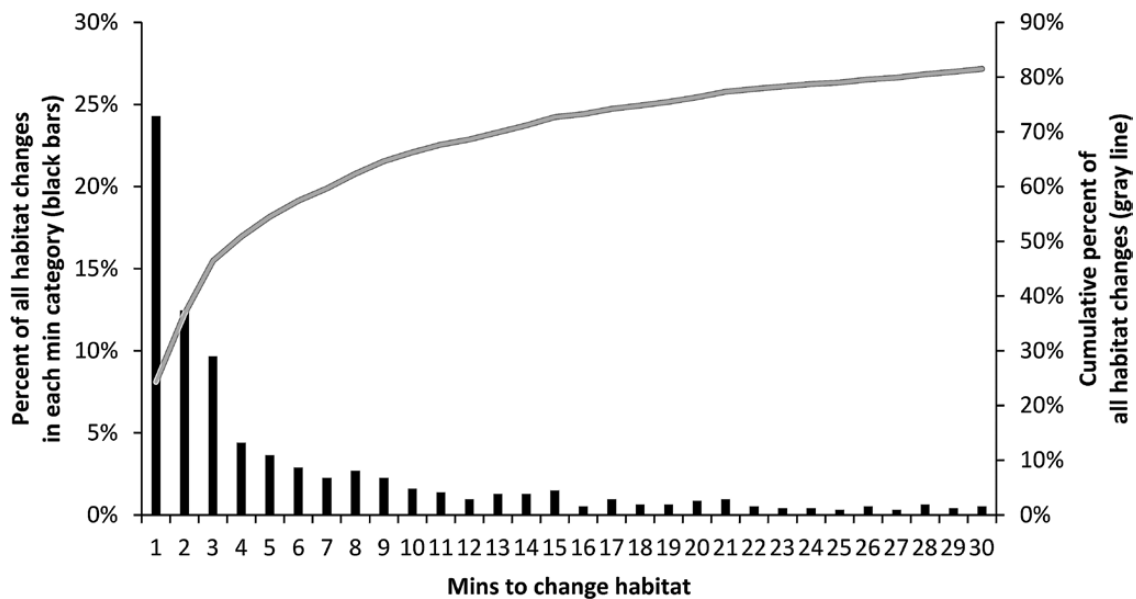
Water/wetland consists of irrigation ponds, lakes, rivers, and tidal mudflats. Urban areas consist of all structural development, including but not limited to buildings, roads, work sites, and heavily maintained landscaped areas. Vineyard was classified as any land that has been or currently is in use for the production of winegrapes 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; dominant species included wild oat (*Avena* sp.), bromes (*Bromus* sp.), ryegrass (*Lolium multiflorum*), wild barley (*Hordeum* sp.), and squirreltail (*Elymus multisetus*). Oak savanna was a mix of grassland and patchy oak forest, with characteristic tree species being coastal live oak (*Quercus agrifolia*), blue oak (*Q. douglasii*), interior live oak (*Q. wislizenii*), and valley oak (*Q. lobata*). The mixed forest consisted of any continuous forest or dense shrub cover that limits access of Barn Owls to the ground and included the same tree species as in oak savanna as well as Doulas-fir (*Pseudotsuga menziesii*), tanoak (*Notholithocarpus densiflorus*), California black oak (*Q. kelloggii*), and California bay (*Umbellularia californica*), and in drier areas madrone (*Arbutus menziesii*), ceanothus (*Ceanothus* sp.), manzanita (*Arctostaphylos* sp.), chamise (*Adenostoma fasciculatum*), and coffee berry (*Frangula californica*). Lastly, riparian was classified as habitat surrounding streams, rivers, and large lakes and ponds as well as high marsh, with characteristic species, including Oregon ash (*Fraxinus latifolia*), bigleaf maple (*Acer macrophyllum*) willows (*Salix* sp.), and mulefat (*Baccharis salicifolia*) among many others.

APPENDIX B

Autocorrelation Results of Barn Owl Hunting Locations Collected in Napa Valley, CA, Spring 2016

Autocorrelation analyses indicated that true statistical independence of sequential telemetry locations was not obtained until they were from 400 to over 5,000 m apart. Likewise, even up to a time lag of 30 locations, most of the variables showed a statistically significant autocorrelation. However, the sample size and statistical power to detect even a weak correlation were large, and a sharp drop in autocorrelation coefficients of most of the variables was seen for sequential locations that were 100 m and 5 min apart. The time to change hunting habitat ranged from 1 to 297 min, with an average of 23 min. The frequency distribution was strongly non-normal (skewed right), the mode time to change habitats was only 1 min, and the median was only 4 min, with over 50% of all hunting habitat changes occurring within 4 min (Appendix Figure 4).

APPENDIX FIGURE 4. Frequency distribution of all times to change habitats based on Barn Owl hunting telemetry locations (*n* = 930 habitat changes) among 1-min bins. All bins over 30 min contained 10 or fewer habitat changes (<1%). Black bars indicate the percent of habitat changes in a minute bin; the gray 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.