

RELATIONSHIP BETWEEN HABITAT AND BARN OWL PREY DELIVERY RATE  
AND COMPOSITION IN A NAPA VALLEY VINEYARD AGROECOSYSTEM

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A Thesis Presented to

The Faculty of Humboldt State University

In Partial Fulfillment of the Requirements for the Degree

Master of Science in Natural Resources: Wildlife

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December 2019

## ABSTRACT

### RELATIONSHIP BETWEEN HABITAT AND BARN OWL PREY DELIVERY RATE AND COMPOSITION IN A NAPA VALLEY VINEYARD AGROECOSYSTEM

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The provision of habitat for natural enemies of agricultural pests is common in integrated pest management approaches globally but has rarely been examined for vertebrate predators controlling vertebrate pests. To mitigate the economic and environmental costs of treating for rodent pests, winegrape producers in Napa Valley, California, have installed nest boxes to attract barn owls (*Tyto alba*) to their properties, but their effectiveness to control rodent pests in vineyards has not been thoroughly tested. A rigorous estimate of the number of rodents barn owls remove from the landscape is a necessary first step, and this study aimed to produce an index of rodent removal and prey composition by using remote nest box cameras. In addition, I tested hypotheses for how habitat may influence prey delivery rates and composition. Results indicate that each barn owl chick received  $191 \pm 10.01$  prey items before dispersing from the nest box. Grassland habitat was an important predictor of prey delivery rate. Prey composition was dominated by voles, gophers, and mice, and their relative proportions were associated with the composition of habitats near a nesting box. Specifically, oak savannah was positively associated with the proportion of gophers, and negatively associated with voles and grassland was positively associated with voles. Further research should focus on the

possible roles of rodent abundance, adult owl quality, and additional metrics of habitat structure on prey delivery rates.

## ACKNOWLEDGEMENTS

Funding for this research was provided by the California State University Agricultural Research Initiative, and Bi-national Agricultural Research & Development. Additional financial support was provided by Ivo Jeramaz of Grgich Hills Estate. This research would also not have been possible without the cooperation of the many producers and vineyard managers who allowed us on their properties in Napa.

Thank you to my advisor, Dr. Matt Johnson, for taking a chance on this east coast transplant that just wanted to study birds. His ambition, problem solving, and support refreshed my perception of ecology and how I communicate science. I greatly appreciate the conceptual and logistic contributions of my committee members, Dr. Barbara Clucas and Dr. Jeff Black.

A thank you to my all of my lab-mates, especially Xerónimo Castañeda and Allison Huysman, who provided invaluable assistance with field work and partook in endless discussions trying to better understand our study system. Thank you Kachina Rowland, Aaron Gottesman, and all of the HSU graduate students who welcomed me into the community and commiserated with me over graduate school woes. I am also grateful for the 20+ undergraduate students who assisted with data review and without, I would still be reviewing footage today.

Finally, an enormous thank you to my parents and soon-to-be wife, Tia Kordell, whose love and support push me every day to leave the world a better place than I found it. Thank you all for your support these past few years, it certainly takes a village.

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## INTRODUCTION

The presence of rodents in agricultural fields imposes economic costs to agricultural producers directly via crop loss and indirectly via treatment expenses (Prakash 1988, Stenseth et al. 2003, Davis et al. 2004). Administration of toxic baits and lethal traps are two of the most common methods to reduce rodent pest populations in agriculture (Tickes et al. 1982, Stenseth et al. 2003, Wood & Fee 2003). From winegrape producer surveys, annual estimates of money spent on trapping and toxic bait application range from \$22 to \$28 per acre (Anderson et al. 2012). Further, Anderson et al. (2012) found that through reduced crop loss and property damage, trapping and toxic baiting resulted in net benefits of \$390 to \$892 per acre per year. While relatively effective (Proulx 1998), the use of rodenticides, particularly second-generation anticoagulant rodenticides (SARs), has been criticized because of ethical concerns and the risk of poisoning non-target wildlife (Mendenhall & Pank 1980, Delfosse 2005, Coeurdassier et al. 2014). To improve their public image and employ economically and environmentally sustainable pest control methods, producers have begun to pursue alternative treatments as part of integrated pest management (IPM) solutions (Lewis et al 1997, Barzman et al. 2015).

Luxury crops such as winegrapes face unique environmental and economic pressures in their pest management solutions (Barber et al. 2010). In addition to responsibly reducing damage by local pest species, especially Botta's pocket gophers (*Thomomys bottae*) and California voles (*Microtus californicus*), the Napa winegrape

industry is further incentivized to adopt sustainable agricultural practices by way of winery tourism and consumer preference for environmentally friendly wine (Barber et al. 2010, Pomarici et al. 2015). California's Napa wine industry is a valuable asset to the United States and California economy with over 300,000 individuals working in production, distribution or sales of Napa wine and an estimated annual impact of \$13.3 billion (Stonebridge 2012). Employing effective IPM solutions to help preserve ecosystem health and longevity may enable producers to satisfy the environmental demands of consumers while providing economic stability for stakeholders.

Ecosystem services are natural conditions or processes that contribute to an ecosystem in a manner that benefits human life and they are often considered as part of IPM solutions (Daily 1997). Biological pest control has long been recognized in agriculture and, through proper land management, it can offer a cost-effective treatment method for producers (DeBach 1964, Wood & Fee 2003, Johnson et al. 2010, Lindell et al. 2018). The primary practice for encouraging biological pest control is to provide habitat for natural enemies of pest species to increase their abundance and occurrence on farmland (Fiedler et al. 2007). The delivery of ecosystem services in agricultural settings is influenced by both local and landscape structure and composition (Tscharntke et al. 2005; Kremen et al. 2007; Benjamin et al. 2014; Kross et al. 2016). With increasing landscape homogeneity and loss of natural habitat, the abundance and diversity of natural enemies diminishes (Tscharntke et al. 2005), dampening the magnitude of ecosystem services delivered (Anderson et al. 2009, Railsback & Johnson 2014, Rusch et al. 2016). In vineyard ecosystems, the conservation of landscape heterogeneity and uncultivated

habitats may favor natural enemies of rodent pests, and possibly alleviate damage to vines.

Due to their expansive global range, foraging behavior, and affinity for open, arid habitat, barn owls (*Tyto alba*) have been considered candidates for biological control agents of rodent pests in agroecosystems (Marti et al. 1979, Wood and Fee 2003, Whelan et al. 2008; Meyrom et al. 2009). Barn owls readily occupy human-made structures, allowing them to persist in agricultural settings better than some other bird species (Kasprzykowski & Golawski 2006). Indeed, nest box occupancy for barn owls is higher in agricultural settings lacking natural nesting sites than in other more intact ecosystems (Meyrom et al. 2009). Barn owls are mostly non-territorial and one km<sup>2</sup> can accommodate several breeding pairs with sufficient numbers of nest boxes (Taylor 1994; Meyrom et al. 2009). These factors, coupled with the ability of barn owls to remove large quantities of rodent prey (Durant et al. 2004, Marti 2010) and the abundance of rodent pests within agroecosystems, make barn owls an attractive option for rodent pest control (Johnson et al. 2019).

In Napa Valley winegrape vineyards, producers have erected nest boxes to attract barn owls, and surveys suggest that producers believe the owls provide some biological services in rodent pest control (Wendt and Johnson 2017, Kross et al. 2018). Various studies have empirically examined biological pest control of arthropods in vineyards and orchards (Landis et al. 2000; Begum et al. 2006; Jedlicka et al. 2011), yet the use of barn owls as pest control agents of rodents in these systems has only been implied and has not

yet been rigorously tested with empirical field data (Byron 2008, Whelan et al. 2008; Browning et al. 2015, Kross et al. 2016).

Understanding and quantifying barn owl foraging behavior is essential to evaluate the potential for barn owls to contribute to rodent pest control. The distribution and foraging habitat selection of barn owls is generally accepted to be dependent on the availability and density of prey (Jaksić & Yáñez 1979; Sutherland 1983; Parker 1988; Taylor 1994), which in turn is influenced by habitat (Preston 1990, Norbury & van Overmeire 2018). Therefore, features of landscape composition such as amount of grassland edge, crop type, and amount of natural habitat may affect barn owl distribution and foraging because of their influence on the density and conspicuousness of prey (Bond et al. 2005; Taylor 1994, Castañeda 2018). Variation in prey composition is also subject to landscape composition; barn owls in California's Central Valley consumed more gophers when their nests were near vineyard or orchard crops (Kross et al. 2016).

The foraging choices that barn owls make while rearing chicks are subject to energy demands of the chicks and likely shape how barn owls use the habitat available to them. To maximize their own individual reproductive success, provisioning parents must offset the cost and benefits of prey type, prey size, and the rate of prey delivery to match the energetic needs of their offspring and maximize the rate of energy delivery (Fagerström et al. 1983, Golet et al. 2000, Steen et al. 2010, Browning et al. 2012). The optimal size and species of prey items depends on the age of nestlings; younger nestlings can only ingest smaller prey whereas older nestlings may be able to handle larger prey items (Steen et al. 2009). However, since barn owl chicks hatch asynchronously, parents

must provision the appropriately sized prey item for each nestling (Slagsvold & Wiebe 2007). Further, if broods are large, parents increase the hunting effort as well as size and/or rate of delivery of prey items to meet the needs of individual nestlings (Daan et al. 1989, Dijkstra et al. 1990). Central place foragers such as the barn owl also exhibit greater search effort per unit area closer to the nest than farther away (Andersson 1981, Rosenberg & McKelvey 1999, Castañeda 2018), therefore, optimal foraging habitat near the box may allow adult barn owls to maximize their foraging efficiency and more easily meet the energetic needs of the chicks.

This study aimed to provide a rigorous estimate of prey delivery rate and prey composition of barn owls breeding in nest boxes in Napa Valley. I addressed the following objectives: 1) Assess the relationship between available habitat to barn owls and prey delivery rate, 2) Test if the species composition of delivered prey (hereafter prey composition) is associated with habitat, 3) Identify patterns between prey composition and prey delivery rate. This study fills a knowledge gap in quantifying the number of prey items taken by barn owls in a vineyard landscape. In addition, elucidating associations between prey delivery rate, prey composition, and habitat will help inform landowners of the capacity of barn owls to remove rodents from the landscape and how the strategic placement of nest boxes may affect rodent removal.

## MATERIALS AND METHODS

### Study Area

Located 100 km north of San Francisco, California, the Napa Valley is a 50 km stretch of land between the Vaca and Mayacamas Mountains (Figure 1). The Mediterranean climate coupled with rich, diverse soils and microclimates make Napa Valley ideal for growing a variety of wine grapes (Elliot-Fisk 1993; Napa Valley Vintners 2014). Vineyards occupy approximately 20,000 ha of the Napa Valley and surrounding foothills, replacing much of the native mixed oak woodlands and oak-grasslands (Napa County 2010, Napa Valley Vintners 2014). Aside from the widespread vineyards and wineries, surrounding landscapes in Napa Valley vary in composition from oak-grassland in the southern extent to mixed oak scrub and conifer forests in the north (Napa County 2010; Wendt 2017). Research started in 2014 by Wendt & Johnson (2017) established affiliations with landowners and provided contacts for 65 collaborating vineyards and access to over 300 barn owl nest boxes throughout Napa Valley.

All nest boxes in my study area were located within or along vineyard edges. Nest boxes installed independently by vineyard managers varied in age, size, structure, orientation, and building materials. Initial contacts established by Wendt (2017) & Johnson were opportunistic; thus, boxes were located haphazardly throughout the valley, with most concentrated in the south. The number of boxes per vineyard ranged from one to 29.



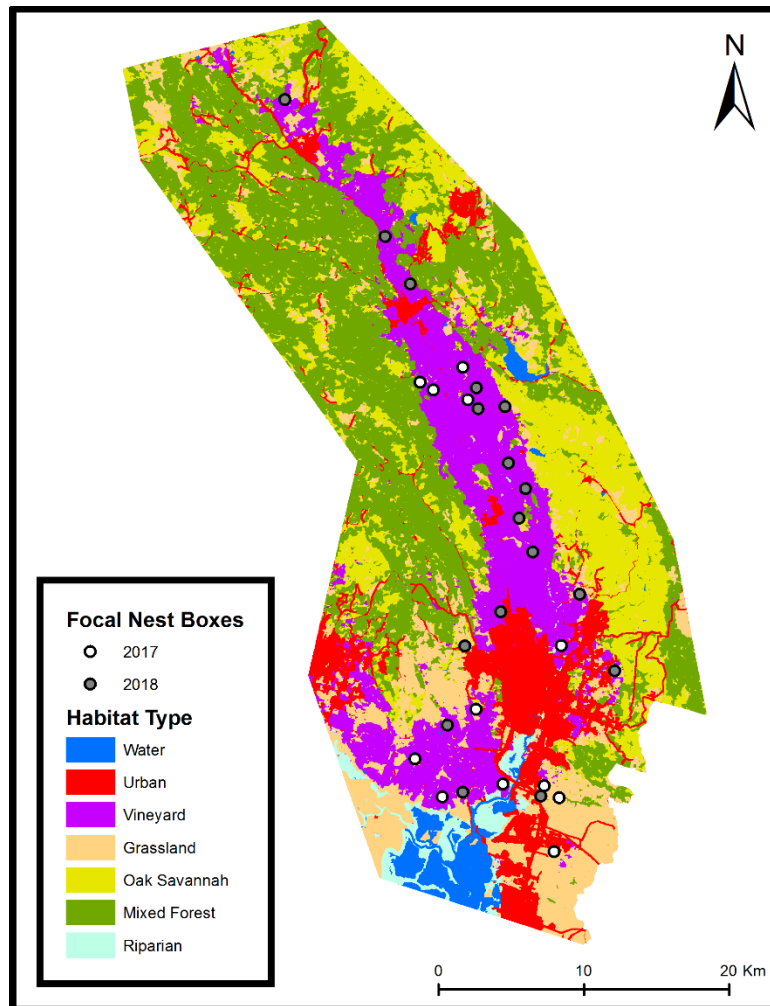


Figure 1: Map showing the study area, Napa Valley, California. Colors indicate the seven delineated habitat types and white and grey circles indicate location of focal nest boxes from 2017 and 2018, respectively.

## Field Methods

### Assessing nest box occupancy

As part of a long-term occupancy study, nest boxes were checked following a protocol developed by Wendt and Johnson (2017). The barn owl breeding season in California begins primarily in January, with most owls laying eggs in February and March and chicks hatching in March through May (Henny 1969, Browning 2014). Beginning February 11, nest boxes were checked for occupancy biweekly through March, and monthly from April through July. I used a GoPro HERO Session camera mounted on an articulating arm at the end of an extendable painter's pole to check nest boxes. By connecting the camera to a smartphone to view a live video stream and using a small light emitting diode (LED) flashlight connected to the camera, I could reliably determine nest box occupancy with minimal disturbance to nesting owls (Wendt 2017).

### Nest box cameras

I used remote video cameras to document prey delivery at 12 nest boxes in 2017 and 17 in 2018 (29 total). I selected nest boxes for camera installation to provide a range of habitat conditions and spread through the nesting season. Habitat composition for the 12 nest boxes in 2017 and 17 in 2018 were similar to the overall composition both within the entire Napa County and within available valley habitat to barn owls, however, habitat surrounding the boxes contained proportionally more vineyard and slightly less oak savannah habitat than the rest of the valley and county (Appendix A).

To reduce spatial and temporal autocorrelation of data, I did not add cameras to nest boxes when more than two cameras had been installed within the previous week or if there was another nest box with a camera within approximately 1000 m, the radius within which barn owls spend most of their time hunting within (Castañeda 2018). Selection of nest boxes for nest cameras was opportunistic so long as they did not violate the space and time constraints aforementioned. Risk of abandonment is high during egg incubation (Marti 1994), so to minimize abandonment while maximizing data collection, cameras were installed in nest boxes only after chicks hatched but before they were three weeks of age. The number of nests with cameras varied throughout the season owing to the variable timing of deployment (week 1-3) and occasional nest failures.

Once a nest box had been determined as occupied and qualified for a camera, the installation process began by approaching the nest box and covering the entrance hole. I positioned a ladder at the access door of the nest box and removed the adult female (and male when applicable). A field assistant would then take the adult(s) away from the nest box to be sexed, measured, and apply a USGS metal leg band while I drilled a 2 cm hole in the upper corner of the nest box opposite the entrance and installed a weatherproof, infrared security camera (ZOSI 720P IP66 CCTV Security Camera) inside the nest box facing the entrance hole. The power and AV cables ran out the back of the nest box down to a weatherproof container at the base of the nest box pole. This container housed the power source (Interstate Deep Cycle Marine Battery – Group 27), AC/DC power conversion cables, and portable digital video recorder (DVR, 1CH MPEG-4 Mini DVR SD Card Video Recorder). To further protect against moisture, the DVR was placed in a

sealed plastic bag with cat litter as a desiccant (see Appendix B for details of camera assembly and installation). I then returned the adult(s) to the nest box and kept the entrance hole covered for five minutes to prevent adults from flying out and allow them to reacclimatize to their nest.

I programmed the DVR to record 15 min videos continuously starting at 30 min before sunset and ending 30 min after sunrise to ensure that all nightly deliveries were captured. I returned to each focal nest box once per week to check and replace batteries and secure digital (SD) cards as needed and to check the number of adults, chicks, and eggs in the boxes using the GoPro camera. The DVRs recorded video throughout the entirety of the nesting period until the chicks dispersed from the nest box, at which point the cameras and electronics were removed.

All research was in accordance with Institutional Animal Care and Use Committee (IACUC) protocol number 15/16.W.43-A.

## Analysis

### Video processing and review

To reduce review time, I converted videos from advanced systems format (ASF) files to Moving Picture Experts Group - 4 (MP4) files and processed them using the MotionMeerkat software (Weinstein 2015). This software takes a video file input and extracts individual frames where “motion” is detected, allowing the user to skip reviewing video with no motion in frame.

For each video file, the images returned from the MotionMeerkat output were reviewed to document when prey deliveries were made and identify prey items. Student volunteers were trained to identify common prey species and assist in footage review. This process entailed documenting when adults arrived to the nest box with prey items, recording the time of delivery, and identifying the prey item. Prey items were identified based on a combination of the following: relative tail length, foot/claw size, overall color, head/mandible shape, ear shape/size, and eye size/orientation. A full description of identified rodent categories is available in Appendix C. Average review time per nest box for 70 data nights was approximately 40 hours.

#### Prey delivery rate and composition

To accommodate for the change in number of chicks throughout the nesting period, I calculated the number of prey deliveries per chick-week. This value was produced by first taking the number of deliveries per night divided by the number of chicks for that night to yield a delivery per chick-night value. Next, the delivery per chick-night values were summed for the calendar week, divided by the number of data nights in that week (accounting for occasional nights of DVR failures), and multiplied by seven to produce an estimate of deliveries per chick-week.

The deliveries per chick-week were combined into three nesting periods for analysis; Period 1 – weeks one through four, Period 2 – weeks five through eight, and Period 3 – weeks nine until dispersal. I selected these three nesting periods to correspond to typical phases of the barn owl nesting cycle (Durant and Handrich 1998, The Barn Owl Trust 2015) and to account for natural fluctuations throughout barn owl development.

Period 1 corresponds to rapid nestling growth, where barn owl limb size, mass, and skull size are increasing and typically peak between week four and five post hatch (Durant and Handrich 1998, Köppl et al. 2005). Period 2 represents the period where physical growth has plateaued, primary feather growth is occurring, and chick mass is slowly decreasing as chicks prepare for dispersal (Durant and Handrich 1998, Köppl et al. 2005). Period 3 is the time that chicks complete the growth of their adult feathers and begin to disperse from the nest box.

The deliveries per chick-week were averaged in each respective period to produce a single deliveries per chick-week estimate for each period. By using weekly estimates, this helps to dampen extreme day-to-day fluctuations in deliveries and simplifies analyses of habitat on overall prey delivery rates. The number of weeks included in a box's estimate of prey delivery rate for each nesting period varied due to the timing of camera deployment. For boxes missing data for week one and/or two due to the variable timing of deployment (week 1-3), I substituted the mean prey delivery per chick-week estimate among all nest boxes with data for those respective weeks. This approach avoided biased-high prey delivery rate estimates for boxes with data from the latter weeks of Period 1 (i.e. weeks where prey delivery rate is expected to increase), and by slightly reducing variation among boxes, was a conservative bias for revealing landscape associations with prey delivery. Of the 29 focal nest boxes, six boxes were missing data from week one, and two boxes were missing data from week one and week two. No boxes were missing entire weeks of data in Period 2 nor Period 3 (for boxes that still had chicks after week 8). If chicks dispersed from the nest box before week nine, no prey delivery rate estimates

were produced in Period 3 and thus, were not included in Period 3 analyses. For nest boxes in which chicks dispersed after week eight but before week ten, only data from week nine was used in determining the Period 3 prey delivery rate.

I calculated descriptive statistics to report prey delivery rates as mean  $\pm$  1 SE and 95% CI as well as overall proportions of prey species and the change in prey composition throughout the breeding season. I compared proportion of prey species between years using means and effect sizes using Cohen's (1988)  $h$  index.

For an overall estimate of the number of rodents delivered per chick over a breeding season, I took a weighted average of the nightly estimates of deliveries per chick using the number of deliveries for each respective night as the weight, multiplied this value by seven to get a deliveries per chick-week estimate, and then summed the weekly estimates through the tenth week to get an estimate for the entire breeding season for an individual nest box. I averaged these values for all nest boxes to produce the overall estimate of deliveries per chick. To yield an estimate of the total number of rodents removed by a nesting pair of owls over the breeding season, I first multiplied the mean number of prey deliveries per chick-week for each period by the average number of chicks fledged in my monitored nests (3.62, see Results). This figure is conservative because in many cases some chicks are fed and only survive a portion of the nesting stage. Second, I added this figure to an estimate of prey removal by adults, which I calculated using published estimates of adult barn owl ingestion and rodent body mass. California voles weigh 36 to 55 g (Verts and Carraway 1998), mice weigh 15 to 52 g (lower range *Mus musculus*, Huminski 1969, upper range *Peromyscus californicus*,

Merritt 1978), and Botta's pocket gophers weigh 89 to 172 g (Vaughn 1967). Bunn et al. (1982) estimated that barn owl daily dietary intake was 100-150 g, which would correspond to 1.8-4.2 voles, 1.9-10.0 mice, or 0.6-1.7 gophers per adult per day. Therefore, I added 155 rodents per adult owl, under the conservative assumption that each adult eats 1.5 rodents per day not captured on the nest video for self-maintenance during the ~103-day breeding season (32 days incubation + 71 days, Browning et al. 2015).

#### Habitat sampling

I used habitat predictors derived from the United States Department of Agriculture (2016) CropScape database following protocols established by Wendt and Johnson (2017). Using ArcMap 10.2, I converted the raster dataset (30 m resolution) into vector data and reclassified the habitat cover types into seven categories; water, urban, vineyard, grassland, oak savannah, mixed forest, and riparian (Figure 2).



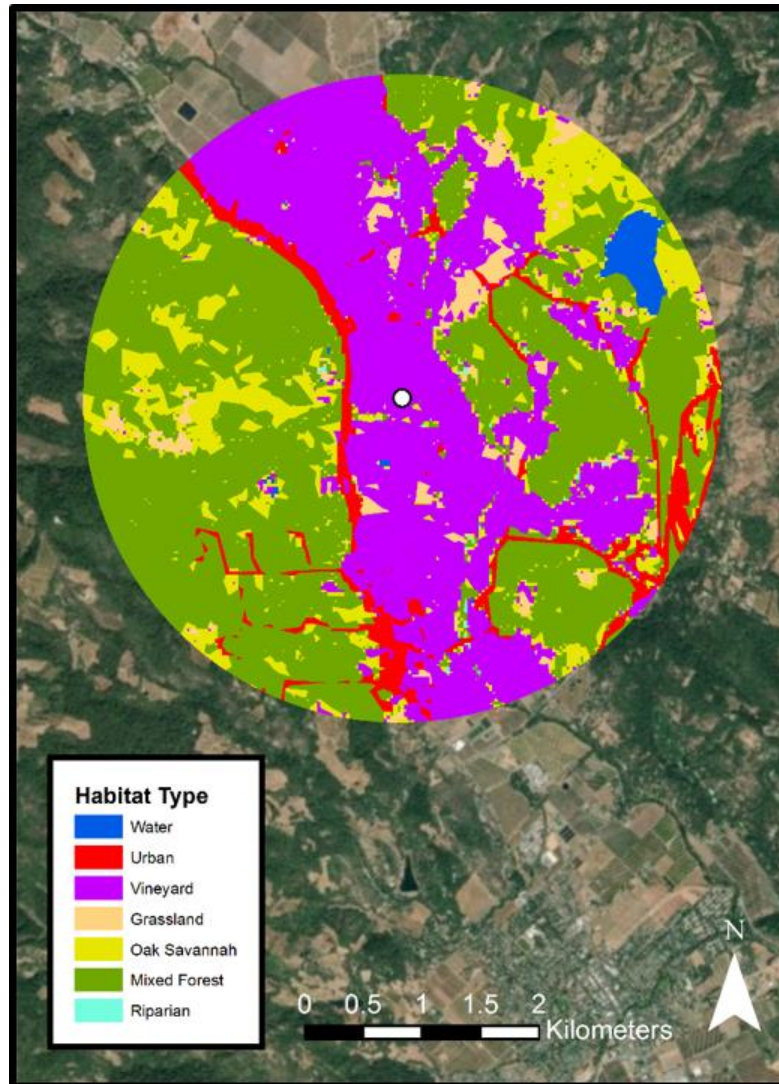


Figure 2: Map showing example of 2.74 km buffer around a nest box used to create habitat cover predictors. The white circle represents the location of the nest box.

In order to have habitat predictors represent the habitat available to barn owls, a 2.74 km buffer was drawn around each nest box, which was the mean furthest distance barn owls in Napa traveled in 2018 as observed by Huysman (2019, unpubl. thesis data). This buffer should encompass most of the expected home range for barn owls, with other studies finding that barn owls hunt primarily within 1-2 km of their nest (Taylor 1994, Castañeda 2018). However, if there is a reliable source of prey far from the nest, it can be more energetically efficient for barn owls to travel to this food-rich area than to expend more energy searching locally (Rosenberg & McKelvey 1999), thus using the 2.74 km buffer distance is a more conservative approach in encompassing the entire home range than limiting the buffer to 1-2 km. The proportion of each habitat cover type within the 2.74 km was calculated using ArcMap 10.3 (Esri 2018) and used as the predictor variables for analysis.

#### Prey delivery rate and prey composition models

I created a candidate model set for multiple linear regression to test the predictive power of habitat and prey composition on prey delivery rates (Response variables: proportion of water, urban, vineyard, grassland, oak savannah, mixed forest, and riparian habitats, distance to nearest grassland and oak savannah habitat, and proportion of voles and gophers in diet, Table 1). Separate models were run on prey delivery rate for each of the three periods. Adding year (2017 or 2018) to models did not significantly improve their fits (unpubl. data), so I pooled both years for analyses. I included a habitat model that consisted of the proportion of the seven habitat cover types to test if the habitat composition solely predicted prey delivery rate. The proportion of vineyards was not

used as a predictor in models that included habitat because of multicollinearity issues associated with using proportions that sum to one as predictors. Thus, the vineyard functioned as the intercept in these models, and coefficients for other habitat predictors can be interpreted as relative to the proportion of vineyard.

Because barn owls disproportionately hunt in natural landscapes (Castañeda 2018), I also included a model that considered the four naturally occurring habitat types, grassland, oak savannah, mixed forest, and riparian, which was calculated by summing the proportion of each habitat type to produce one “Uncultivated” predictor value. Water was not included in this model because many of the water bodies in Napa Valley are human-made irrigation ponds within vineyards, lack extensive riparian habitat, and are unlikely to offer many resources for hunting barn owls. The proportions of voles and gophers delivered to a box were also included as predictors in the prey composition model, since these are two of the most abundant pest species in Napa vineyards, and vary markedly in size, following the hypothesis that prey delivery rate may be lower when larger prey are delivered (Steen et al. 2011). The proportions of gophers and voles did not have a strong correlation with any single habitat variable (all  $r < 0.59$ ), so multicollinearity was not an issue. Lastly, I created a model that used the distance in meters to grassland and oak savannah, two habitats previously demonstrated as important for nest box selection and foraging habitat selection in this system (Wendt 2017, Castañeda 2018). Because the habitat and prey composition predictor variables were proportions and therefore values less than one, I scaled the distance variables to values between zero and one by dividing the respective distances by the farthest distance to any

of the seven habitat types to ease interpretation of coefficients. I used Akaike Information Criterion corrected for small sample size (AICC) to select top models and establish model weights.

While prey composition may operate alone or in concert with habitat to predict prey delivery rate, prey composition itself could also be associated with the composition of habitats around a nest box, and further, may vary throughout the season as a result of energetic requirements. Therefore, I also tested whether habitat (proportion of urban, water, vineyard, grassland, oak savannah, mixed forest, and riparian habitat) could predict prey composition (proportion of voles, gophers, and mice). I used the same candidate model set with the exception of the Prey\_Comp model (Table 1) to model the proportions of deliveries that were voles, gophers, or mice for each of the three nesting periods.

#### Data normality and transformation

I used a Shapiro-Wilk normality test of the assumption of normality for both the response variables (prey delivery rate and prey composition) and predictor variables (habitat) of the linear regression models. To improve homoscedasticity and normality of residuals, I used an arcsine transformation for the habitat predictor variables, which is a common practice for proportion data (Studebaker 1985).

Table 1: Candidate model set for predicting prey deliveries per chick-week and proportion of voles, gophers, and mice for nesting barn owls in Napa, California, 2017 and 2018. The model set was tested using generalized linear models (GLMs). Model 4 – Prey\_Comp was excluded from the proportion of voles, gophers, and mice models.

Model:	Description
1 - Full	Prey delivery <sup>a</sup> ~ Habitat <sup>b</sup> + Prop_Vole <sup>c</sup> + Prop_Gopher <sup>d</sup> + Dist_Grassland <sup>e</sup> + Dist_OakSavannah <sup>f</sup>
2 - All_Habitat	Prey delivery ~ Habitat
3 - Uncultivated	Prey delivery ~ Uncultivated <sup>g</sup>
4 - Prey_Comp	Prey delivery ~ Prop_Vole + Prop_Gopher
5 - Proximity	Prey delivery ~ Dist_Grassland + Dist_OakSavannah
6 - All_Habitat & Prey_Comp	Prey delivery ~ Habitat + Prop_Vole + Prop_Gopher
7 - Uncultivated & Prey_Comp	Prey delivery ~ Uncultivated + Prop_Vole + Prop_Gopher
8 - Proximity & Prey_Comp	Prey delivery ~ Proximity + Prop_Vole + Prop_Gopher
9 - Null	Prey delivery ~ 1

Prey Delivery<sup>a</sup> = Prey deliveries per chick-week for each individual nesting period

Habitat<sup>b</sup> = The proportion of the seven habitat cover types within the buffer: water, urban, grassland, oak savannah, mixed forest, and riparian

Prop\_Vole<sup>c</sup> = Proportion of deliveries that consisted of voles

Prop\_Gopher<sup>d</sup> = Proportion of deliveries that consisted of gophers

Dist\_Grassland<sup>e</sup> = Distance to nearest grassland habitat in meters

Dist\_OakSavannah<sup>f</sup> = Distance to nearest oak savannah habitat in meters

Uncultivated<sup>g</sup> = The summed proportion of uncultivated habitat cover types: grassland, oak savannah, mixed forest, and riparian

## RESULTS

### Overall Prey Delivery and Composition

A total of 29 nest boxes were included in the analyses, with a total 1,781 nights of videography (mean nights per box =  $61.43 \pm 2.55$ ), 20,487 total hours of video, and a total of 11,404 observed prey deliveries. Nightly prey delivery rates within nest boxes fluctuated and was variable amongst all nest boxes with coefficients of variance ranging from 0.32 to 0.69. Weekly prey delivery rate was relatively constant for the first three weeks of the nesting cycle (Period 1), increased from weeks four until six (Period 2), and steadily decreased from seven until dispersal (Period 3, Figure 3). Period 2 had the highest overall delivery per chick-week estimate with  $21.47 \pm 1.15$  deliveries per chick-week (Table 2). Consistent with the energetic demands of chicks, Period 1 had the lowest delivery per chick-week rate (Figure 4). The average dispersal time was  $71 \pm 1.75$  days. By using the mean prey delivery rate per chick week estimate for each calendar week, an individual chick who is in the nest box for 10 weeks will receive on average  $191 \pm 10.01$  prey items. In my study, the mean number of chicks raised to fledging was  $3.62 \pm 1.40$ . With two adult owls (155 rodents consumed per adult) and 3.62 chicks, I estimate 1,001 rodents removed from the landscape during the breeding season per occupied barn owl nest box, not accounting for additional predation by adults and fledged young before and after the nesting season, nor rodents removed for chicks that do not survive to fledging.

Of all prey deliveries, 92.0% were identifiable. Voles made up the majority of the prey items (49.6%), followed by mice (22.0%), and gophers (17.5%, Table 2). The proportion of voles and gophers remained fairly consistent throughout the nesting period, while the proportion of mice decreased from Period 2 to Period 3 (Table 2). However, the proportion of unidentified increased in Period 3, which clouds the certainty of these proportions in later nesting stages. There was a medium effect size for the percentage of voles delivered between the two study years with 62.7% in 2017 and 42.6% in 2018 ( $\mu = 49.6\%$ ,  $h = 0.42$ ). For both gophers and mice, there was a small effect size for the percentage of deliveries between the two study years with 15.0% in 2017 and 25.4% in 2018 for gophers ( $\mu = 17.5\%$ ,  $h = 0.26$ ) and 14.0% in 2017 and 19.7% in 2018 for mice ( $\mu = 22.0\%$ ,  $h = 0.26$ , Figure 5).

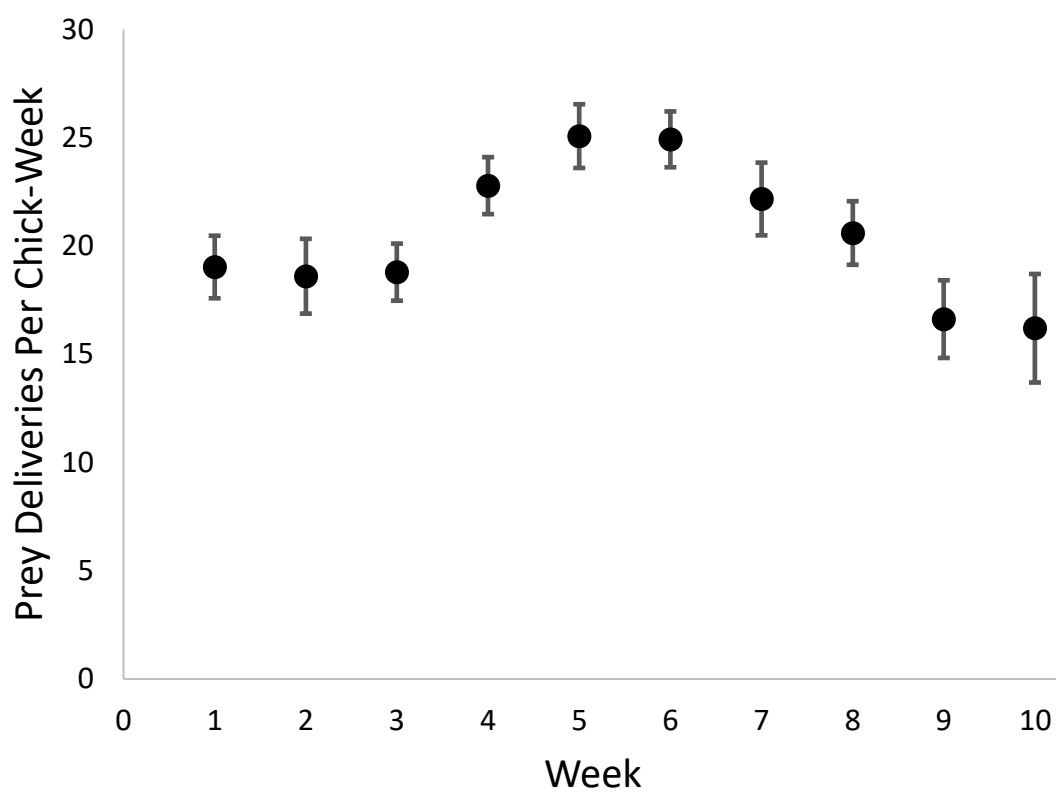


Figure 3: Estimates of prey delivery per chick-week for all focal nest boxes from hatch until the tenth calendar week. Error bars represent standard error.



Table 2: Mean prey deliveries and prey composition for all three nesting periods. SE is the standard error.

<b>Nesting Period</b>	<b>Mean Deliveries Per Chick-Week</b>	<b>SE</b>	<b>CI (95%)</b>	<b>Vole (%)</b>	<b>Mouse (%)</b>	<b>Gopher (%)</b>	<b>Other<sup>a</sup> (%)</b>	<b>Unidentified (%)</b>
Period 1	18.75	0.88	17.00, 20.51	51.65	23.24	16.99	2.68	5.44
Period 2	21.47	1.15	19.16, 23.77	48.49	22.14	18.55	2.70	8.11
Period 3	13.15	1.86	9.43, 16.87	47.68	16.42	14.07	4.20	17.63

<sup>a</sup>The category “Other” includes rabbit, squirrel, rat, frog, bird, and insect.

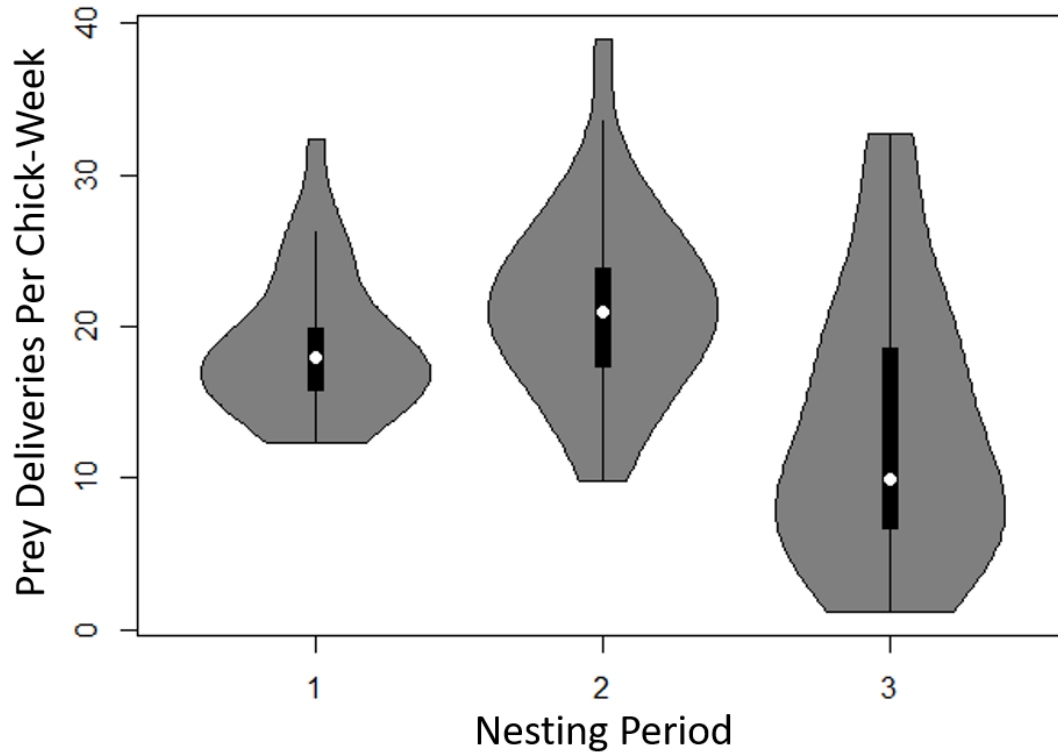


Figure 4:: Violin plots of overall deliveries per chick week estimates for the three nesting periods for all nest boxes. Vertical black lines indicate 95% confidence interval, vertical black rectangles represent the interquartile range, and the white dot represents the median. The width of each period represents the probability density of the data at given values. Nesting Period 1 corresponds to weeks 1-4, Period 2 to weeks 5-8, and Period 3 to weeks 9 until dispersal.

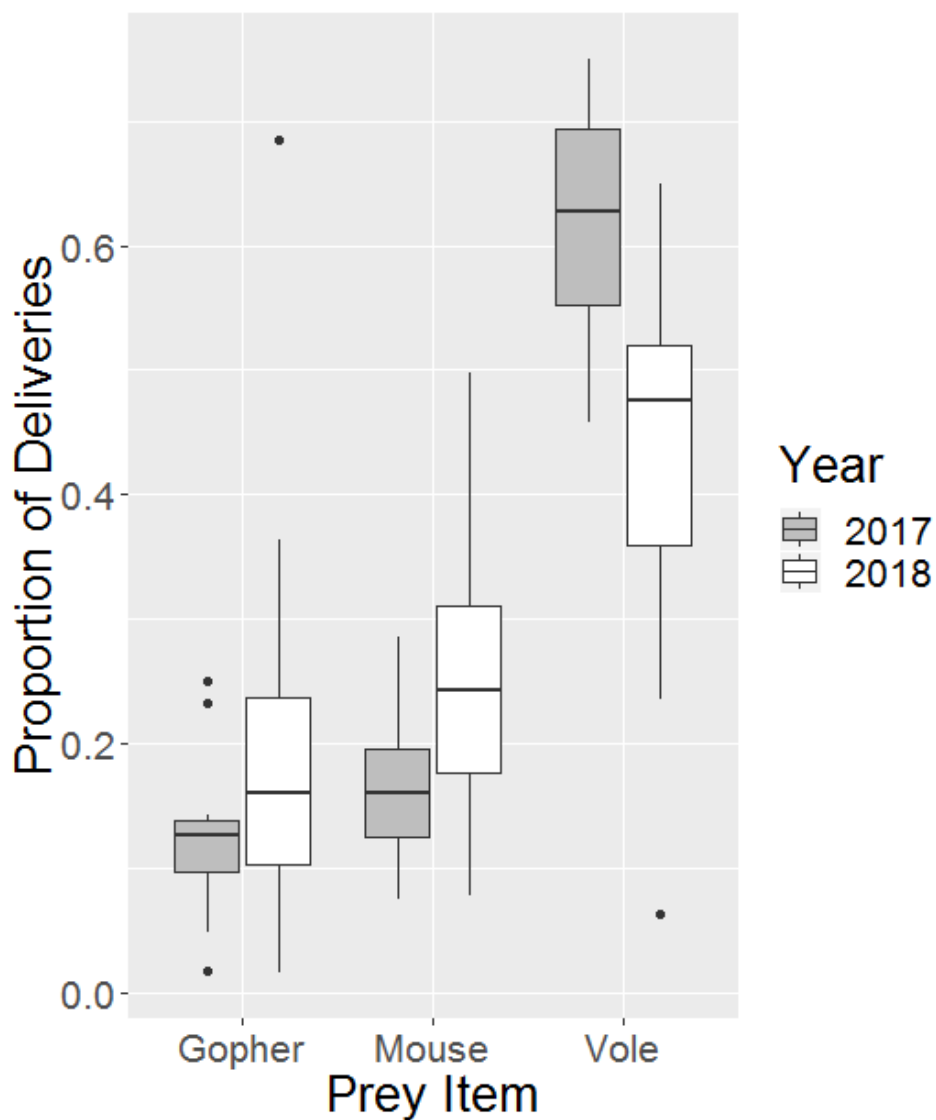


Figure 5: Box plots showing comparison of proportion of prey deliveries for gophers, mice, and voles between 2017 and 2018. Black dots represent outliers based on the 95% interval.

### Prey Delivery Rate Models

The top performing model for predicting prey delivery in Period 1 included prey composition variables (Table 3), with high prey delivery rates associated with slightly higher proportions of voles and lower proportions of gophers ( $\beta = -0.13 \pm 0.09$ ), although confidence intervals of each coefficient overlapped zero (Table 4). The model containing uncultivated habitat and prey composition variable was within 2 AIC<sub>C</sub> and had a model weight  $> 0.3$ . The null model was also competitive ( $\Delta \text{AIC}_C < 2$ ), confirming very weak effects of predictor variables in Period 1. For Period 2, the habitat + prey composition model was the top model with no other models within 2 AIC<sub>C</sub> (Table 3). In this model, prey delivery rate was positively associated with the proportion of grassland and oak savannah habitat (Table 4, Figure 6). Like Period 1, prey delivery was also positively associated with the proportion of voles in the diet and weakly negatively associated with proportion of gophers with the confidence interval for the proportion of voles not overlapping zero and the confidence interval slightly overlapping zero for gophers (Table 4). For Period 3, the uncultivated model was selected as the top model, with the habitat and null models also competitive (Table 3). In this model, uncultivated habitat was positively associated with prey delivery rate, with a confidence interval slightly overlapping zero. Overall, grassland and uncultivated habitat were positively associated with prey delivery rate in the latter nesting periods with a nearly flat relationship seen in Period 1 (Figure 6).

Table 3: Results from candidate model sets for each of the three nesting periods for modelling prey delivery rate. Section (a) corresponds to Period 1, (b) to Period 2, and (c) to Period 3

Period 1

Model	K <sup>a</sup>	Log <sub>e</sub> (L) <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	ΔAIC <sub>c</sub> <sup>d</sup>	W <sup>e</sup>
Prey_Comp	3	-79.86	167.72	0	1
Null	1	-82.23	168.46	0.74	0.69
Uncultivated + Prey_Comp	4	-79.86	169.72	1.99	0.37
Uncultivated	2	-82.15	170.29	2.57	0.28
Proximity	3	-81.19	170.38	2.65	0.27
Proximity + Prey_Comp	5	-79.61	171.22	3.50	0.17
All_Habitat	7	-80.64	177.28	9.56	0.01
All_Habitat + Prey_Comp	9	-79.09	178.19	10.46	0.01
Full	11	-78.84	181.69	13.96	< 0.001

Period 2

Model	K <sup>a</sup>	Log <sub>e</sub> (L) <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	ΔAIC <sub>c</sub> <sup>d</sup>	W <sup>e</sup>
All_Habitat + Prey_Comp	9	-76.75	173.49	0	1
Uncultivated + Prey_Comp	4	-82.91	175.82	2.33	0.31
Full	11	-76.35	176.70	3.21	0.20
Prey_Comp	3	-85.21	178.43	4.93	0.08
Proximity + Prey_Comp	5	-84.28	180.56	7.07	0.03
Uncultivated	2	-88.60	183.21	9.72	0.01
Null	1	-89.81	183.61	10.12	0.01
Proximity	3	-89.54	187.08	13.59	< 0.01
All_Habitat	7	-87.70	191.40	17.91	< 0.001

Period 3

Model	K <sup>a</sup>	Log <sub>e</sub> (L) <sup>b</sup>	AIC <sub>c</sub> <sup>c</sup>	ΔAIC <sub>c</sub> <sup>d</sup>	W <sup>e</sup>
Uncultivated	2	-76.89	159.79	0	1
All_Habitat	7	-72.14	160.29	0.50	0.78
Null	1	-78.37	160.73	0.95	0.62
Prey_Comp	3	-77.31	162.62	2.83	0.24
Proximity	3	-77.31	162.63	2.84	0.24
Uncultivated + Prey_Comp	4	-76.46	162.91	3.13	0.21
All_Habitat + Prey_Comp	9	-72.10	164.19	4.41	0.11
Proximity + Prey_Comp	5	-76.17	164.34	4.55	0.10
Full	11	-71.97	167.93	8.15	0.02

<sup>a</sup>K = Number of parameters

<sup>b</sup>Log<sub>e</sub>(L) = Log-likelihood

<sup>c</sup>AIC<sub>c</sub> = Akaike's Information Criterion correct for small sample size

<sup>d</sup>ΔAIC<sub>c</sub> = Difference in AIC<sub>c</sub> from top model

<sup>e</sup>W = Model weight ( $e^{-0.5 * \Delta AIC_c}$ )

Table 4: Results from top linear models for prey delivery rates for each nesting period. Covariates in which the 95% confidence interval does not overlap zero are bolded.

Period 1 – Prey\_Comp

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	20.39	4.98	10.42, 30.35
Prop_Vole	0.01	0.07	-0.14, 0.16
Prop_Gopher	-0.13	0.09	-0.31, 0.05

Period 2 – All\_Habitat + Prey\_Comp

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	4.76	6.74	-8.72, 18.24
Water	-30.36	20.58	-71.52, 10.80
Urban	-12.68	6.39	-25.47, 0.10
<b>Grassland</b>	<b>11.09</b>	<b>5.42</b>	<b>0.24, 21.94</b>
<b>Oak Savannah</b>	<b>35.00</b>	<b>11.35</b>	<b>12.29, 57.71</b>
Mixed Forest	-9.03	8.27	-25.57, 7.51
Riparian	31.75	16.54	-1.32, 64.83
<b>Prop_Vole</b>	<b>0.21</b>	<b>0.10</b>	<b>0.01, 0.40</b>
Prop_Gopher	-0.19	0.10	-0.40, 0.02

Period 3 – Uncultivated

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	6.56	4.28	-2.01, 15.12
Uncultivated	0.15	0.09	-0.03, 0.33

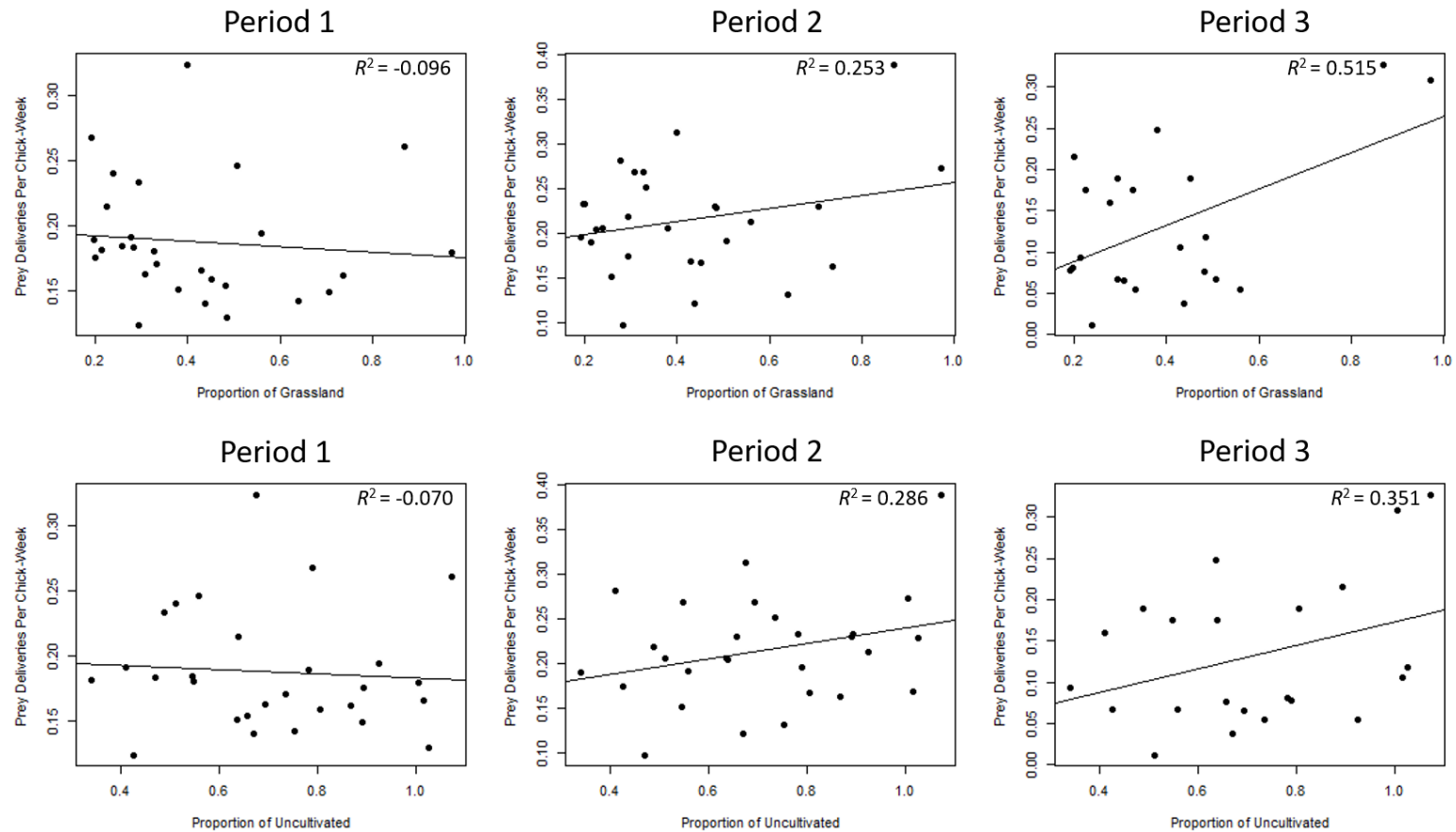


Figure 6: Plots of prey deliveries per chick week averages for each nesting period as they relate to the proportion of grassland and uncultivated habitat.

### Prey Composition Models

Overall, habitat was a relatively weak predictor of variation in prey composition, with the null model competitive in Period 2 for voles (Table 5), Period 1 and 2 for gophers (Table 6), and Period 1 and 3 for mice (Table 7). However, the proportion of oak savannah, grassland and uncultivated habitats emerged as important predictors of prey composition in some nesting periods.

For models predicting the proportion of prey delivered to the nest box that was voles, the top model for Period 1 was the proximity to important habitat (Table 5). In Period 2, the habitat model was the top performing model with the null model and proximity model both competitive. The proportion of oak savannah habitat had a strong negative effect in Period 2 for proportion of voles ( $\beta = -0.68 \pm 0.28$ , Table 8). In Period 3, the proximity model again was the most competitive, with no other models within 2 AIC<sub>C</sub>. Grassland was positively associated with the number of voles in all three periods, with a particularly strong effect in Period 1 ( $\beta = 0.26 \pm 0.10$ ) and Period 3 ( $\beta = 0.25 \pm 0.11$ , Table 8). For the entire breeding season, the proportion of voles was negatively associated with the proportion of oak savannah habitat (Figure 7).

For the proportion of prey that was gophers, the uncultivated habitat model was the top performing model for Period 1 with the proximity and null model both competitive (Table 6). The habitat model and full model performed best in Period 2 and 3, respectively. In Period 1, uncultivated habitat was positively associated with the proportion of gophers and in Period 2, although the effect was weak. Both oak savannah



and riparian habitat were strongly associated with the proportion of gophers ( $\beta = 0.62 \pm 0.23$  and  $\beta = 0.99 \pm 0.42$ , respectively, Table 9). However, both the null and uncultivated models were competitive in Period 2 with both having model weights greater than 0.4 (Table 6). In the top performing full model in Period 3, the proportion of gophers was strongly associated with grassland habitat and distance to oak savannah habitat, somewhat contradicting the results from the top model in Period 2 (Table 9). Overall, the correlation between proportion of gophers and proportion of oak savannah was particularly strong ( $R^2 = 0.448$ , Figure 7).

For models predicting the proportion of prey that was mice, uncultivated habitat was the top model for Period 1 and 2 and was competitive in Period 3 (Table 7). A strong negative association with the proportion of uncultivated habitat was demonstrated for all three nesting periods (Table 10, Figure 7).

Table 5: Results from the candidate model sets for prey composition for the proportion of voles delivered  
Period 1

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b><math>\Delta</math>AIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Proximity	3	12.72	-17.44	0	1
Null	1	9.32	-14.64	2.80	0.25
Uncultivated	2	9.33	-12.66	4.78	0.09
Full	9	16.26	-12.53	4.91	0.09
All_Habitat	7	14.17	-12.33	5.10	0.08

Period 2

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b><math>\Delta</math>AIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
All_Habitat	7	17.94	-19.88	0	1
Null	1	11.71	-19.43	0.45	0.80
Proximity	3	13.70	-19.39	0.49	0.78
Full	9	18.77	-17.54	2.34	0.31
Uncultivated	2	11.76	-17.52	2.36	0.31

Period 3

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b><math>\Delta</math>AIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Proximity	3	8.51	-9.01	0	1
Null	1	5.42	-6.83	2.18	0.34
Uncultivated	2	5.64	-5.28	3.73	0.15
All_Habitat.	7	9.10	-2.21	6.80	0.03
Full	9	10.87	-1.74	7.27	0.03

<sup>a</sup>K = Number of parameters

<sup>b</sup>Log<sub>e</sub>(L) = Log-likelihood

<sup>c</sup>AIC<sub>c</sub> = Akaike's Information Criterion correct for small sample size

<sup>d</sup> $\Delta$ AIC<sub>c</sub> = Difference in AIC<sub>c</sub> from top model

<sup>e</sup>W = Model weight ( $e^{-0.5 * \Delta AIC_c}$ )

Table 6: Results from the candidate model sets for prey composition for the proportion of gophers delivered.

Period 1

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b>ΔAIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Uncultivated	2	11.27	-16.53	0	1
Proximity	3	12.25	-16.51	0.02	0.99
Null	1	10.02	-16.03	0.50	0.78
Full	9	15.95	-11.89	4.64	0.10
All_Habitat	7	13.42	-10.83	5.70	0.06

Period 2

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b>ΔAIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
All_Habitat	7	23.58	-31.15	0	1
Null	1	16.88	-29.75	1.40	0.50
Uncultivated	2	17.85	-29.70	1.45	0.48
Full	9	24.50	-29.00	2.15	0.34
Proximity	3	18.37	-28.75	2.40	0.30

Period 3

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b>ΔAIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Full	9	20.99	-21.97	0	1
Proximity	3	14.69	-21.38	0.60	0.74
Null	1	11.71	-19.43	2.55	0.28
Uncultivated	2	12.23	-18.47	3.50	0.17
All_Habitat	7	14.51	-13.02	8.95	0.01

<sup>a</sup>K = Number of parameters

<sup>b</sup>Log<sub>e</sub>(L) = Log-likelihood

<sup>c</sup>AIC<sub>c</sub> = Akaike's Information Criterion correct for small sample size

<sup>d</sup>ΔAIC<sub>c</sub> = Difference in AIC<sub>c</sub> from top model

<sup>e</sup>W = Model weight ( $e^{-0.5 * \Delta AIC_c}$ )

Table 7: Results from the candidate model sets for prey composition for the proportion of mice delivered.  
Period 1

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b><math>\Delta</math>AIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Uncultivated	2	20.75	-35.51	0	1
Full	9	26.98	-33.96	1.55	0.46
Null	1	18.83	-33.66	1.85	0.40
All_Habitat	7	23.58	-31.16	4.35	0.11
Proximity	3	19.31	-30.61	4.90	0.09

Period 2

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b><math>\Delta</math>AIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Uncultivated	2	25.77	-45.55	0	1
All_Habitat	7	29.98	-43.96	1.59	0.45
Null	1	23.69	-43.38	2.17	0.34
Full	9	31.56	-43.12	2.43	0.30
Proximity	3	23.71	-39.43	6.12	0.05

Period 3

<b>Model</b>	<b>K<sup>a</sup></b>	<b>LL<sup>b</sup></b>	<b>AIC<sub>c</sub><sup>c</sup></b>	<b><math>\Delta</math>AIC<sub>c</sub><sup>d</sup></b>	<b>W<sup>e</sup></b>
Null	1	22.78	-41.56	0	1
Uncultivated	2	23.67	-41.34	0.22	0.89
Proximity	3	22.88	-37.77	3.79	0.15
All_Habitat	7	24.98	-33.95	7.60	0.02
Full	9	25.18	-30.35	11.21	0.00

<sup>a</sup>K = Number of parameters

<sup>b</sup>Log<sub>e</sub>(L) = Log-likelihood

<sup>c</sup>AIC<sub>c</sub> = Akaike's Information Criterion correct for small sample size

<sup>d</sup> $\Delta$ AIC<sub>c</sub> = Difference in AIC<sub>c</sub> from top model

<sup>e</sup>W = Model weight ( $e^{-0.5 * \Delta AIC_c}$ )

Table 8: Results from the top models of the prey composition analysis for proportion of voles delivered in all three nesting periods. Covariates with confidence intervals that did not overlap zero are bolded.

Period 1 – Proximity model

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	0.45	0.05	0.34, 0.55
<b>Dist_Grassland</b>	<b>0.26</b>	<b>0.10</b>	<b>0.06, 0.45</b>
Dist_Oak Savannah	0.01	0.10	-0.18, 0.21

Period 2 – Habitat model

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	0.44	0.14	0.17, 0.72
Water	0.60	0.66	-0.72, 1.91
Urban	0.26	0.21	-0.15, 0.67
Grassland	0.10	0.16	-0.22, 0.42
<b>Oak Savannah</b>	<b>-0.68</b>	<b>0.28</b>	<b>-1.24, -0.12</b>
Mixed Forest	0.35	0.22	-0.09, 0.79
Riparian	-0.25	0.52	-1.29, 0.79

Period 3 – Proximity model

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	0.41	0.07	0.27, 0.54
<b>Dist_Grassland</b>	<b>0.25</b>	<b>0.11</b>	<b>0.03, 0.48</b>
Dist_Oak Savannah	-0.12	0.12	-0.36, 0.12

Table 9: Results from the top models of the prey composition analysis for proportion of gophers delivered in all three nesting periods. Covariates with confidence intervals that did not overlap zero are bolded.

Period 1 – Uncultivated model

Covariate	$\beta$	SE	CI (95%)
Intercept	-0.01	0.12	-0.24, 0.22
Uncultivated	0.25	0.16	-0.07, 0.56

Period 2 – Habitat model

Covariate	$\beta$	SE	CI (95%)
Intercept	0.04	0.11	-0.19, 0.26
Water	-1.05	0.54	-2.12, 0.03
Urban	-0.33	0.17	-0.66, 0.01
Grassland	0.10	0.13	-0.16, 0.36
<b>Oak Savannah</b>	<b>0.62</b>	<b>0.23</b>	<b>0.16, 1.07</b>
Mixed Forest	-0.01	0.18	-0.37, 0.35
<b>Riparian</b>	<b>0.99</b>	<b>0.42</b>	<b>0.14, 1.83</b>

Period 3 – Full model

Covariate	$\beta$	SE	CI (95%)
Intercept	0.02	0.16	-0.30, 0.35
Water	-0.14	0.63	-1.40, 1.11
Urban	-0.15	0.23	-0.62, 0.31
<b>Grassland</b>	<b>0.50</b>	<b>0.17</b>	<b>0.17, 0.84</b>
Oak Savannah	-0.28	0.29	-0.85, 0.30
Mixed Forest	0.28	0.21	-0.14, 0.69
Riparian	0.15	0.49	-0.83, 1.13
Dist_Grassland	-0.30	0.11	-0.51, -0.09
<b>Dist_Oak Savannah</b>	<b>0.22</b>	<b>0.10</b>	<b>0.02, 0.42</b>

Table 10: Results from the top models of the prey composition analysis for proportion of mice delivered in all three nesting periods. Covariates with confidence intervals that did not overlap zero are bolded.

Period 1 – Uncultivated model

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	0.39	0.08	0.22, 0.55
<b>Uncultivated</b>	<b>-0.22</b>	<b>0.11</b>	<b>-0.45, 0.00</b>

Period 2 – Uncultivated model

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	0.35	0.07	0.21, 0.49
<b>Uncultivated</b>	<b>-0.19</b>	<b>0.09</b>	<b>-0.38, 0.00</b>

Period 3 – Uncultivated model\*

<b>Covariate</b>	<b><math>\beta</math></b>	<b>SE</b>	<b>CI (95%)</b>
Intercept	0.22	0.06	0.10, 0.35
Uncultivated	-0.11	0.09	-0.28, 0.06

Uncultivated\* - This model was not the top performing model, but was included as the top model was the null model and the uncultivated model was within <2 AIC<sub>c</sub>

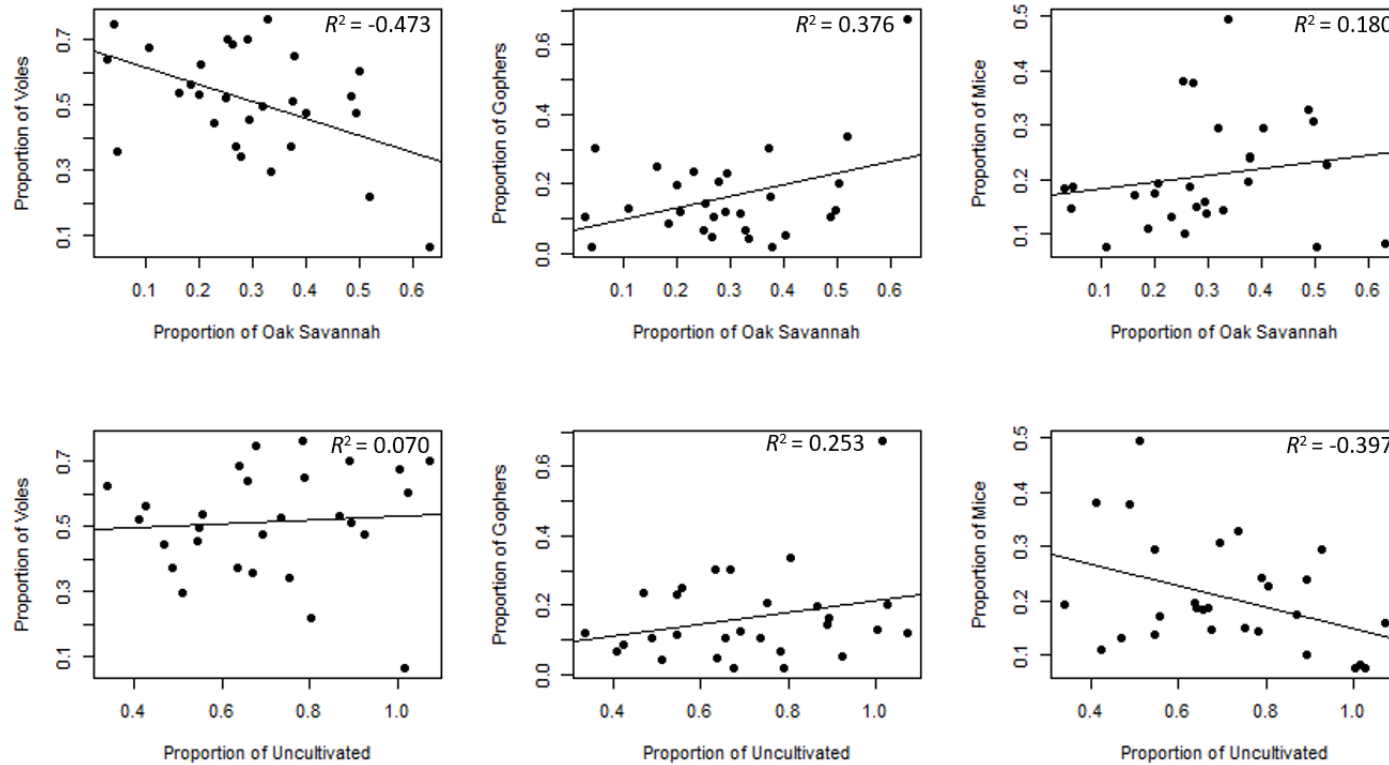


Figure 7: Plots of proportion of voles (first column), gophers (second column), and mice (third column) delivered as they relate to the proportion of oak savannah and uncultivated habitat. Data points represent prey composition pooled from all three nesting periods.



## DISCUSSION

Landscape simplification in agriculture can reduce the abundance and diversity of natural enemies of pest species and in turn diminish the ecosystem services provided by these species (Tscharntke et al. 2005). In the Napa Valley, winegrape producers have erected barn owl nest boxes to attract barn owls to their properties and provide a rodent control service, yet the effectiveness of barn owls and the effect of landscape composition on pest control has yet to be thoroughly tested. Recent studies in the Napa Valley vineyard system have highlighted the importance of natural habitat such as grassland and oak savannah for nest box selection and hunting habitat (Wendt and Johnson 2017, Castañeda 2018), thereby providing further incentive for producers to conserve natural habitats throughout the landscape. Further, better understanding how habitat influences the rate of rodent removal will help quantify the effect size of the ecosystem service provided.

My analyses offer support of the importance of grassland and oak savannah habitats for prey delivery rates to barn owl nest boxes. While habitat did not contribute meaningfully to prey delivery rates in Period 1, the proportion of grassland habitat near a nest box was positively associated with prey delivery rates in Period 2 and Period 3, when energetic demands are high. The proportion of oak savannah was also important in Period 2, but less so in Period 3.

The importance of grassland and oak savannah habitat to a provisioning barn owl is twofold; grassland and oak savannah are the most abundant uncultivated habitats

within range of the nest boxes, and they offer high densities of rodents (Bock et al. 2002). Therefore, having more of these habitats near the nest box may allow barn owls to meet higher energetic demands of chicks by reducing the commute and search time for prey. Central place foragers like barn owls in habitats with patchy resource distribution concentrate foraging activity in areas with higher resource density (Ford 1983). My results suggest the importance of grassland and oak savannah for delivery rate are in accordance with Castañeda (2018), who found that intensity of foraging decreases farther from the nest box, and that grassland and oak savannah habitats are selected for disproportionately to their availability within the landscape.

While habitat was associated with prey delivery in later nesting periods with higher energetic demands, prey composition was a more important predictor of prey delivery rate earlier in the breeding season. This may be due to adult owls' efforts to provide appropriately sized smaller prey such as voles and mice early in the breeding season while the chicks are small, and then relaxing prey selection as chicks get larger, which releases adults from extra handling time to pull prey apart and increases demand for foraging efficiency.

The dominance of voles identified in video of prey deliveries demonstrates their importance in the diet of barn owls in Napa. This may reflect either the availability and abundance of voles or their preferential selection by barn owls, or a combination of both. Charter et al. (2015) found greater reproductive success in barn owls that consumed mostly social voles (*Microtus socialis guentheri*). Depending on the relative abundance of social voles, this could provide support for preferential prey selection by barn owls or

for opportunistic selection of the most accessible prey species. While barn owls are generally viewed as being opportunistic rodent specialists (Taylor 1994, Rifai et al. 2013), Derting and Cranford (1989) found that barn owls preferentially prey on abundant *Microtus* species because this allows them to maintain high energy levels while minimizing foraging time and effort, both of which are important for provisioning parents. However, whether or not barn owl diet reflects the abundance of local rodent species varies regionally (Mikkola 1983, Travaini et al. 1997, Avenant 2005, Bernard et al. 2010). The abundance, activity, and caloric composition of voles near Napa Valley vineyards may make them optimal prey items for barn owls and in concert could explain the prevalence of voles in the diet.

Habitat use by rodent prey may also help explain the proportion of voles and gophers in the diet as well as suggest opportunistic hunting by barn owls. As Castañeda (2018) found, barn owls preferentially forage in grasslands in Napa. Additionally, Castañeda (2018) found that with increasing distance from the nest box, barn owls select for oak savannah habitat. That I found a strong positive association of the proportion gophers brought to the nest box with oak savannah habitat and a strong negative association with the proportion of voles suggests that barn owls may be willing to commute longer distances to obtain larger, energy efficient prey items.

The prominence of voles and gophers, the primary rodent pests in Napa vineyards, in the prey composition is consistent with other diet work on barn owls in California agriculture (Kross et al. 2016) and is good news for producers. Voles and gophers can create significant costs to producers by girdling roots and stalks of vines,

chewing irrigation lines, and damaging vineyard machinery by constructing elaborate burrows (Hueth et al. 1998, Baldwin et al. 2013). Damage directly to vines from voles and gophers can result in reduced crop yield and in newly planted vines, complete crop loss (Marsh 1998). Voles can be particularly problematic in vineyards and cause more girdling when vegetation is allowed to grow beneath vines (Murray and DeFrancesco 2016), which further reiterates the importance of voles in the barn owls' diet. Anderson et al. (2012) found that rodents in vineyards with no form of pest control can incur costs of \$26.40 to \$58.40 per acre via property and crop damage. Whether or not the net economic benefits of barn owls as pest control agents is as significant as lethal trapping and toxic baits is still yet to be determined. My data do not provide evidence that barn owls reduce damage by rodents nor rodent pest abundance, but they do provide substantial support that barn owls are removing large numbers of target pest species from the landscape.

The performance of the uncultivated model in my prey composition analysis suggests that certain prey species may be more likely to occur near vineyards than others. In an agricultural region in Israel, Charter et al. (2009) found varying prey composition across urban and agricultural habitats. In Napa, this may also be true, particularly for mice, which were negatively associated with uncultivated habitats in each of the three nesting periods. House mice are one of the most ubiquitous small mammals in urban settings and California mice have also been found to inhabit urban and peri-urban habitats (Peavey et al. 1997). However, that mice comprise nearly one fourth of the prey

items in my study could speak to the adaptability of barn owls near urban areas (Charter et al. 2007).

Modeling delivery rate as a function of habitat is complicated by other drivers of barn owl foraging and reproductive success. Perhaps the most significant factor is that rodent populations are subject to substantial fluctuations across short time scales (Whitford 1976). Rodent survival and activity are subject to short term weather variation and inter-annual climatic variation (Vickery and Bider 1981). California vole populations are notoriously dynamic, with two- to four-year cycles in abundance (Krebs 1966, Batzli and Pitelka 1971), which may explain the difference in proportion of voles between the first and second year of this study. Starvation and cannibalism of barn owl chicks are common brood reduction events during bouts of unpredictable bad weather (Baudvin 1978). Roulin et al. (1999) found that manipulating brood sizes did not affect physical condition of adult barn owls, indicating that barn owls may prioritize lifetime reproductive success over success of an individual brood under the assumption that adult condition is tied to reproductive success. Therefore, this might suggest that barn owl delivery rate may be influenced more by availability of resources or parenting ability, and less by chick demand or habitat structure. Espie et al. (2004) provided support for the parenting ability hypothesis with merlins (*Falco columbarius*); nest-site quality, and likely the availability of resources, had no significant effect on breeding performance. That is, parental quality may be able to compensate for any variation in prey abundance owing to the quality of surrounding habitats.

Using nest box cameras to document prey deliveries is a cost-effective way to assess the diet of barn owl chicks but is not without its shortcomings. Compared to diet studies of barn owl pellets, cameras allowed me to discern exactly when a prey item was brought to the nest box and was not affected by prey digestibility. However, accuracy regarding proper prey identification is less than that of a pellet analysis, with 92% of delivered prey identifiable using camera footage. For smaller nest boxes, camera footage can be obstructed by chicks once they are preparing to disperse from the nest box, which explains the higher percentage of unidentified prey items for Period 3. Last, collecting, processing, and reviewing camera data is incredibly time intensive and is subject to technological failures.

## CONCLUSIONS

This study is the first to provide a robust estimate of prey delivery rates by barn owls in a vineyard ecosystem. In Napa Valley, California, an individual chick will receive 191 prey deliveries over the course of 10 weeks, and with estimates of adult prey capture, I estimated that a pair of nesting barn owls will remove 1001 rodents from the landscape around a nest box during a single nesting cycle. Extrapolating further, approximately 900,000 rodents will be removed by barn owls during the breeding season (using the 45% occupancy rate from 2017 and 2018 and estimated 2,000 nest boxes in Napa Valley). Their diet consists primarily of voles, mice, and gophers, which are important rodent pests for vineyard managers. I present evidence that grassland and oak savannah habitats are important for parent barn owls in obtaining sufficient resources for chicks. Further, prey composition analyses suggest that gophers may have a strong positive association with oak savannah habitats while voles have a negative association. Further analyses should integrate additional metrics of habitat structure and composition to test the effect of prey composition and prey delivery. Ultimately, it will be necessary to measure abundance of rodents within and surrounding vineyards in conjunction with barn owl monitoring techniques to truly test the impact of barn owls on rodent pest populations. Continuing to elucidate these foraging trends will benefit vineyard managers and help better understand the collective impact of barn owls as rodent pest control agents.

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## APPENDIX A

Appendix A: Comparison of habitats at various scales to justify habitat representativeness of focal nest boxes.

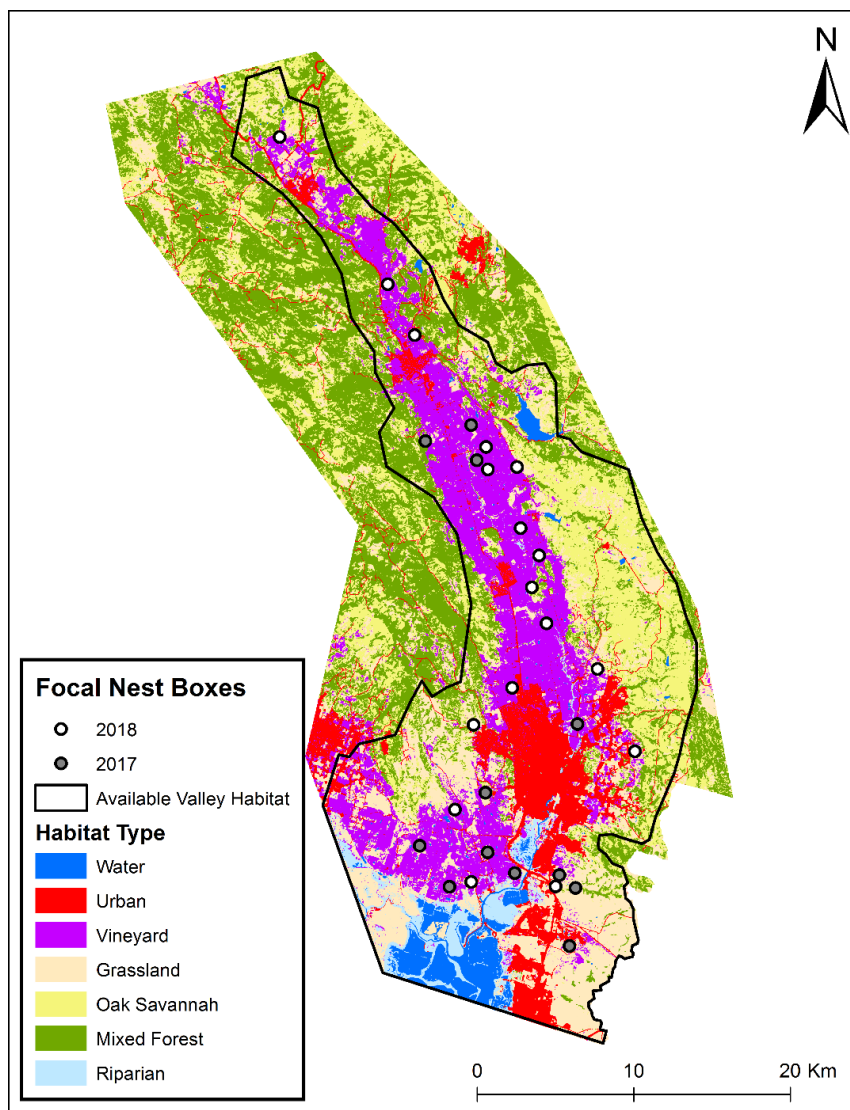


Figure 8: The extent of this map is the entirety of Napa County. Habitat composition is shown for the entire county as well as for a hand-drawn polygon that was delineated to represent available valley habitat. Areas excluded from this polygon to the east and the west contain higher elevation hillsides dominated by mixed forest and were excluded as they are unlikely to contain suitable habitat for barn owls.

## APPENDIX A CONTINUED

Table 11: Percent composition of the seven habitat types to compare the composition of the focal nest boxes, available valley habitat, and habitat of the entire county.

<b>Scale</b>	<b>Water (%)</b>	<b>Urban (%)</b>	<b>Vineyard (%)</b>	<b>Grassland (%)</b>	<b>Oak Savannah (%)</b>	<b>Mixed Forest (%)</b>	<b>Riparian (%)</b>
<b>Napa County</b>	2.73	9.63	15.86	16.24	23.68	29.67	2.20
<b>Available Valley Habitat</b>	4.29	12.86	25.45	20.92	18.73	14.11	3.63
<b>All Boxes</b>	2.03	12.82	36.21	19.75	12.77	13.60	2.81
<b>2017 Boxes</b>	3.00	14.66	38.99	25.59	5.05	7.72	5.00
<b>2018 Boxes</b>	1.79	11.36	38.40	17.39	14.89	13.78	2.40



## APPENDIX B

Appendix B: Details regarding the cost of nest box cameras and commentary on the installation process.

Table 12: Description of nest box camera components and installation notes.

<b>Component</b>	<b>Model</b>	<b>Cost (USD)</b>	<b>Vendor</b>
<b>Camera</b>	ZOSI 720P IP66 CCTV Security Camera	\$15.99	Amazon
<b>Digital Video Recorder (DVR)</b>	1CH MPEG-4 Mini DVR SD Card Video Recorder	\$56.30	Zapals
<b>Memory Card</b>	Sandisk 32 GB Ultra Class 10 SHDC UHS-I Memory Card	\$7.94	Amazon
<b>A/V cable</b>	BNC Video and Power Cable Wire Cord (25 ft)	\$7.99	Amazon
<b>BNC/RCA adapter</b>	BNC/RCA Female and Male Adapter Connector	\$7.99 (x 10)	Amazon
<b>Battery</b>	EverStart Lead Acid Marine/RV Battery, Group 27D C	\$81.67	Wal-Mart
<b>Wire</b>	16/2 Low Voltage Cable	\$0.30/ft	Ace Hardware
<b>AC/DC Power Adapter</b>	2.1 x 5.5 mm Male and Female BNC/DC Power Connector Adapter	\$6.99 (x 10)	Amazon
<b>Power Splitting Cable</b>	Barrel Plug Power Splitter 5.5 x 2.1 mm, 1 Female to 2 Male Jack	\$6.96	Amazon

<b>Component</b>	<b>Model</b>	<b>Cost (USD)</b>	<b>Vendor</b>
<b>Fuse</b>	Slow Blow Glass Cartridge Fuse 250V/5A	\$7.99 (x 6)	Amazon
<b>Protective Box</b>	Hefty 32 qt Hi-rise Latching Container	\$9.23	Wal-Mart
<b>Desiccant</b>	Kitty Litter	\$3.99	Safeway

#### Additional Installation Comments:

There are several benefits for using the ZOSI CCTV security camera, or others with similar specifications; cameras are inexpensive, they are equipped with durable housing that protect against weather and curious chicks, the wide-angle lens is ideal for capturing the entire nest box opening from a short distance, and the cameras can be easily mounted with three screws. Upon connecting the camera to the DVR unit and power source, I secured the exposed connection between the video/power extension cable and the camera cables using duct tape sealed with silicone. When possible, I placed the container where it would have the most shade cover to avoid overheating the electronics. To keep moisture away from the DVR unit, I placed the DVR in a small plastic bag half-filled with kitty litter. I tested recording videos at 30 frames per second (fps) and 15 fps and found no difference in the ability to identify prey items. Further, videos at 15 fps require half the storage as 30 fps videos.

The following link provides a video demonstration of camera assembly and electronic set-up: <https://youtu.be/QrevdJewdwI>

## APPENDIX C

Appendix C: List of potential rodents in Napa County and how rodents were grouped for prey composition analyses.

Table 13: Rodents and small mammals of Napa County, California and the distinctions made for prey composition analyses.

<b>Classification</b>	<b>Common Name</b>	<b>Latin Name</b>
<b>Vole</b>	California Vole	<i>Microtus Californicus</i>
	Sonoma Tree Vole	<i>Arborimus pomo</i>
<b>Gopher</b>	Botta's Pocket Gopher	<i>Thomomys bottae</i>
<b>Mouse</b>	House Mouse	<i>Mus musculus</i>
	California Mouse	<i>Peromyscus californicus</i>
	Brush Mouse	<i>Peromyscus boylii</i>
	Piñon Mouse	<i>Peromyscus truei</i>
	Western Harvest Mouse	<i>Reithrodontomys megalotis</i>
<b>Rat</b>	Roof Rat	<i>Rattus rattus</i>
	Norway Rat	<i>Rattus norvegicus</i>
	Dusky-footed Woodrat	<i>Neotoma fuscipes</i>
<b>Squirrel</b>	Western Gray Squirrel	<i>Sciurus griseus</i>
	California Ground Squirrel	<i>Otospermophilus beecheyi</i>
<b>Rabbit</b>	Black-tailed Jackrabbit	<i>Lepus californicus</i>