ECOSYSTEM SERVICES AFTER A MAJOR ECOLOGICAL DISTURBANCE: DID BARN OWL (TYTO ALBA) NEXT BOX OCCUPANCY AND HUNTING HABITAT SELECTION CHANGE IN RESPONSE TO NAPA VALLEY FIRES?

By

Allison E Huysman

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Committee Membership

Dr. Matthew Johnson, Committee Chair

Dr. William “Tim” Bean, Committee Member

Dr. Daniel Barton, Committee Member

Dr. Erin Kelly, Graduate Coordinator

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ABSTRACT

ECOSYSTEM SERVICES AFTER A MAJOR ECOLOGICAL DISTURBANCE: DOES BARN OWL (TYTO ALBA) NEXT BOX OCCUPANCY AND FORAGING HABITAT SELECTION CHANGE IN RESPONSE TO NAPA VALLEY FIRES?

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Wine producers in Napa Valley, California install barn owl (*Tyto alba*) nest boxes in vineyards with the goal of reducing rodent crop damage. Previous research has shown that the probability of attracting barn owls to nest boxes and encouraging them to hunt in vineyards is strongly influenced by the design of the nest box itself and the composition of the surrounding landscape. In 2017, wildfires in the Napa area burned nearly 60,000 ha, primarily affecting urban areas, which caused human devastation, and uncultivated habitats, which barn owls are known to select. Data collected before the fires on nest box occupancy and hunting habitat selection allowed for a comparative analysis of barn owl behavior before and after the fires. I analyzed four years of occupancy data on 273 nest boxes, finding that nest box occupancy was consistently associated with tall, wooden nest boxes that face away from the sun and have grassland and riparian land cover within the average hunting radius of the nest box. Additionally, wildfires increased nest box occupancy and modeling showed that the probability of a box becoming occupied after the fires was positively associated with the amount of fire edge within the average hunting radius of the nest box. I also analyzed GPS tracking data on 32 birds nesting in

24 individual nest boxes, with data collected before and after the fires. I found that barn owls are most likely to hunt in vineyard, grassland, riparian, and oak savannah land cover types and areas closest to the nest box, and these results were not affected by fire. Barn owls did show some hunting habitat selection for burned edges and low to intermediate severity burned areas, but their land cover type selection was resilient to landscape changes caused by wildfires. The combination of occupancy and hunting habitat selection analysis can be used to provide broad and durable guidance to wine producers who use barn owl nest boxes. With fires increasing in the western United States, the short-term resiliency of barn owls to the landscape changes caused by fires can have positive implications for their ability to provide pest control.

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PREFACE

This thesis is presented as two chapters written for submission for publication in scientific journals. For this reason, there is some unavoidable redundancy between chapters, though this is minimized. Chapter 1 is entitled “Multi-year nest box occupancy and short-term resilience to wildfire disturbance by barn owls in a vineyard agroecosystem” and is written for submission to the journal *The Condor*. Chapter 2 is entitled “Habitat selection by a rodent predator is resilient to wildfire in a vineyard ecosystem” and is written for submission to the journal *Agriculture*, *Ecosystems, and the Environment*

CHAPTER 1: MULTI-YEAR NEST BOX OCCUPANCY AND SHORT-TERM RESILIENCE TO WILDFIRE DISTURBANCE BY BARN OWLS IN A VINEYARD AGROECOSYSTEM

Abstract

In the world-renowned wine growing region of Napa Valley, California, wine producers install nest boxes to attract barn owls (*Tyto alba*) which may reduce rodent crop damage. Annual monitoring of 273 nest boxes began in 2015, and devastating wildfires burned approximately 60,000 ha in the region in 2017, including homes and businesses, as well as some vineyards and uncultivated land. Occupancy surveys before and after these wildfires revealed changes in habitat selection at the nest scale. Occupancy increased during the study, reaching its highest point after the fires. Owls were found breeding in recently burned areas that were previously unoccupied and modeling results showed that nest box occupancy had a positive relationship with burned areas, particularly burned edges. Barn owls also consistently showed a strong preference for taller, wooden nest boxes that faced away from the sun and were near grassland and riparian land cover types, results that can be used by vineyard managers to increase occupancy. These results show that barn owls are resilient in their use of nest boxes as vineyard owners increasingly install nest boxes and as wildfires increase in the western United States.

Introduction

Landscape composition has become a major focus for optimizing ecosystem services in agroecosystems in recent decades (Tscharntke et al. 2005). With threats of climate change and habitat loss, there is increasing interest in optimizing landscapes for both conservation and food production (Kremen and Merenlender 2018). Uncultivated habitat that harbors greater biodiversity has been connected to enhanced delivery of ecosystem services such as pest control in agricultural landscapes (Boesing et al. 2017). Conserving uncultivated habitats can support ecosystem services, but in California, these lands can also increase the area susceptible to wildfires (Westerling et al. 2006). This introduces possible trade-offs in the ability of uncultivated habitat to provide enhanced ecosystem services and greater risk of costly wildfires. Understanding the interactions between landscape composition, ecosystem services, and disturbance is a necessary step to ensure those services can be optimized.

Landscape composition can impact nest site selection by barn owls, a biological control agent, in Napa Valley, which has implications for their potential to deliver rodent pest control (Kross et al. 2016, Wendt and Johnson 2017). One of the main issues for winegrape producers is rodent pests, which can cause millions of dollars in crop damage annually (Baldwin et al. 2014). Vineyard managers often use lethal trapping and chemical rodenticides, but these solutions are labor intensive and cause concern over secondary poisoning to humans and wildlife (Marsh 1992, Baldwin et al. 2015, 2017). The need to control rodent pests has led to an interest in integrated pest management using biological control agents, primarily barn owls (*Tyto alba*; Labuschagne et al. 2016). By installing nest boxes in vineyards, farmers can attract barn owls, which may be able to act as a natural predator and control populations of pocket gophers (*Thomomys bottae*) and voles (*Mictrotus* spp.; Meyrom et al. 2009, Paz et al. 2012, Kan et al. 2013, Browning et al. 2017). However, barn owls are mobile predators and they show a preference for open natural habitats (Taylor 1994), so the effectiveness of nest box installation on pest control delivery may depend on the composition of landscapes surrounding winegrape vineyards. Barn owls were most likely to occupy nest boxes with uncultivated habitats within 1 km, along with preferences for nest boxes constructed of wood, facing away from the sun, and installed at least 3 m above ground (Wendt and Johnson 2017). Barn owls nesting on vineyards also preferentially hunt in uncultivated habitats, selecting them over more closely available vineyards (Castañeda 2018).

After wildfires burned nearly 60,000 ha in Napa Valley in 2017, many uncultivated lands that barn owls prefer were dramatically altered. The fires primarily burned through grasslands, wooded areas, and communities surrounding vineyards (Lapsley and Sumner 2017). Mediterranean biomes, like that of Napa, evolved with fire, though changing climate and fire suppression are increasing the likelihood and severity of fires (Batllori et al. 2013). Additionally, much of California, including Napa, is experiencing conversion of native perennial grasses to non-native annual grasses, which increase the availability of fine fuels and thus increase fire frequency (Jurjavcic et al. 2002, Keeley and Brennan 2012). In the whole western United States, wildfires have increased in both frequency and intensity since the mid-1980s, which is primarily attributed to warming, earlier springs (Westerling et al. 2006), and fuel accumulation (Westerling et al. 2003, Agee and Skinner 2005), making this a critical time to understand the impact of wildfires on landscapes and pest control.

With changes to the landscape caused by wildfires, I hypothesized that barn owls would respond by nesting near recently burned uncultivated land. Because barn owls prefer open habitat and fires have the potential to reduce the structure of denser habitats, the wildfires in Napa Valley could provide more land that is ideal for barn owl hunting, which could lead to greater reproductive success. Additionally, while small mammal responses are variable, rodents can increase in recently burned areas, including in areas similar to my study area (Schwilk and Keeley 1998, Fitzgerald et al. 2001). In other recently burned Mediterranean climates, fires produced edge habitat and open areas that seem to be preferred by rodents (Haim and Izhaki 1994, Torre and Díaz 2004). To my knowledge, this is the first study to address how wildfire may affect the mobile agents of pest control and the resulting impact on ecosystem services.

Barn owl nest site selection in relation to landscape composition is important for both short-term understanding of resiliency to wildfire disturbance and long-term expectations for the potential of barn owls to act as a natural enemy in agriculture. Nest box occupancy is dynamic in nature and fluctuates from year to year. Understanding how barn owls interact with habitat in average years as well as after disturbance is important for management and knowledge of barn owl behavior.

Materials and Methods

Study Area

This project took place on vineyards in Napa Valley, California, where researchers at Humboldt State University have been collecting data since 2015. Napa Valley is about 48 km long and 5-20 km wide and is characterized by a Mediterranean climate ideal for growing grapes (Napa Valley Vintners 2017). Mixed oak woodlands and oak savannahs are spread throughout the region, with grasslands in the south and mixed oak scrub and conifer forests in the north (Napa County 2010, Wendt and Johnson 2017). The unique conditions in Napa Valley have created a wine industry which generates \$3.7 billion in annual revenue and in combination with tourism, employment, and distribution, is estimated to have an annual impact of \$50 billion on the American economy (Stonebridge 2012).

The Atlas, Nuns, and Tubbs fires burned nearly 60,000 ha surrounding Napa Valley in October, 2017 (California Department of Forestry and Fire Protection 2017*a*, *b*, *c*; Figure 1.1). Evidence indicates they were ignited during a spike in fire risk (i.e., low humidity, high temperatures, and unseasonably high warm winds; Martinez et al. 2017), and were extinguished after extensive and costly fire control (Associated Press 2018). Like other western wildfires, they burned in patches of various degrees of fire severity within an irregular fire perimeter, introducing fire-caused vegetation heterogeneity in the following spring and summer. In October, vineyards have lower fuel loads than most surrounding natural vegetation, in many cases are irrigated, and fire suppression activities prioritized human structures. Thus, few vineyards were actually burned (Lapsley and Sumner 2017). The heterogeneity in vegetation after fire did not include conversion of any land cover type to another, but included a mixture of burn severity throughout the burned area, resulting in variability in the state of soils and vegetation (California Department of Forestry and Fire Protection 2017c).

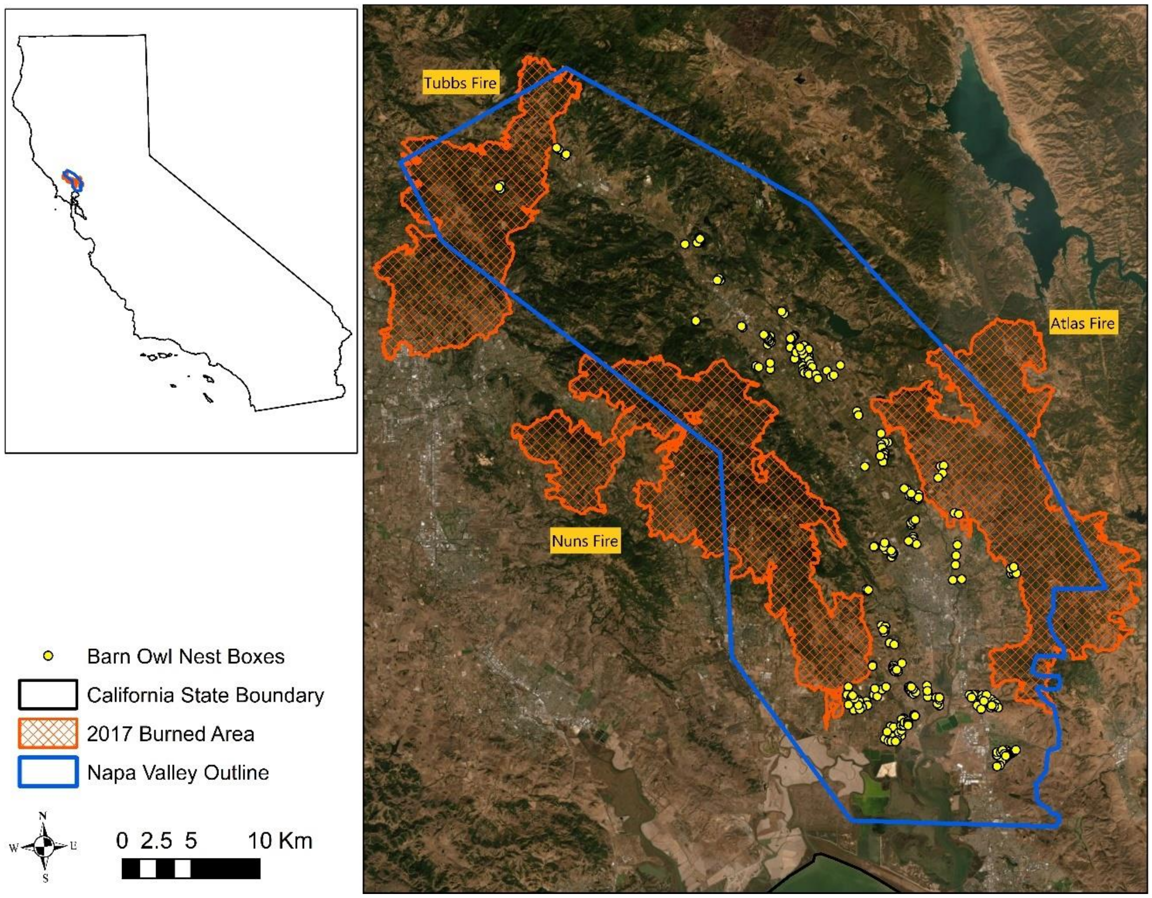

Figure 1.1. Map of Napa Valley, 273 nest boxes, and boundary of 2017 Atlas, Nuns, and Tubbs fires within California.
Service layer credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Field Methods

All methods were approved by the Humboldt State University Institutional Animal Care and Use Committee (IACUC) in Protocol Number 15/16.W.43-A.

Study Species

The barn owl is a widespread raptor species that will readily nest in human-made structures and is adapted to hunt in open grasslands and agricultural fields (Taylor 1994). In Napa Valley, natural nesting cavities are not readily available, as the diameter of most trees are too small (USDA Forest Service 2018) and where larger trees exist, barn owls are subject to predation from great-horned owls (*Bubo virginianus*; Millsap and Millsap 1987). Thus, barn owls in Napa are almost certainly nest-site-limited, and readily make use of nest boxes in vineyards. They are tolerant of their own species and will readily nest in high concentrations (Taylor 1994, Meyrom et al. 2009, Browning et al. 2017). Because of these qualities, barn owls have been used as a means of rodent control for various crops including alfalfa, rice, oil palms, cocoa, and grapes (Labuschagne et al. 2016). Though their ability to meaningfully control rodent populations remains a debated topic (Johnson et al. 2019), over 90% of their diet is composed of rodent pests and the number of rodents they remove is estimated to be substantial (Browning et al. 2017, St. George unpubl.).

Establishing Nest Box Occupancy

After a nest box occupancy study of 297 nest boxes began in 2015 (Wendt and Johnson 2017), a random sample of 150 boxes were monitored in 2016 and 2017. With this study, I monitored the original 297 boxes for a comparative analysis of occupancy after the fires. The methods for the occupancy survey followed those of Wendt and Johnson (2017) and are briefly summarized here.

I visually inspected nest boxes with a GoPro and LED light attached to an extendable pole that I inserted into the opening of the nest box, viewing the contents via a live feed to a handheld smartphone. A nest box was considered occupied if, at any point in a season, it contained barn owl eggs or chicks. Barn owls are known to start courting in January, and in southern California, clutches generally begin in February (Marti et al. 2005). Eggs are laid in intervals of 2-3 days for a mean clutch size of about 5, taking about 10-15 days to complete a clutch, and incubation lasts for 29-34 days (Marti et al. 2005). Nests were checked every 10 days between 28 February and 31 March for breeding occupancy by barn owls. After the initial three checks throughout the month of March, any boxes with evidence of possible occupation were monitored monthly at least three more times to determine occupancy and fate of the nest. Because of this timing and protocol, it is very unlikely that an occupied box went undetected during our timeframe for occupancy checks; using multi-season occupancy modeling, I estimated overall detection probability at over 97% (Huysman unpubl.), so I did not further model detection probability. Though barn owls can double-brood in some locales (Bank et al. 2019), my work focused on first breeding attempts. Like other species of birds, barn owls can be sensitive to disturbance and potentially abandon their nest, but if care is taken there should be no effect on the bird’s nesting productivity (Taylor 1991), and my camera-enabled remote monitoring procedure caused minimal disturbance.

Analysis Methods

Incidence Function Model

Of the original 297 boxes monitored in 2015, 24 were broken (n = 11), removed (n = 8), or burned (n = 5) by 2018 and were excluded from analysis for all years. I used an incidence function model on the final sample of 273 nest boxes to test how alternative combinations of predictor variables affected occupancy, colonization, and extinction of nest boxes. In the context of this study, Ψ (initial occupancy) represented the probability of a box being occupied during 2015, the first year of the study, γ (colonization) represented the probability of an unoccupied nest box becoming occupied each year until 2018, and ε (extinction) represented the probability of an occupied nest box becoming unoccupied each year until 2018. I used the *colext* function from the *unmarked* package (Kéry and Chandler 2016) in program R version 3.5.1, which fits multi-season occupancy models as described by MacKenzie et al. (2003). Because the nature of this study system allowed me to determine with near perfect detection if a nest box is occupied, I fit these models with detection probability fixed equal to one. When this is the case, the model is equivalent to an incidence function model of metapopulation dynamics (Hanski 1998, Kéry and Chandler 2016).

I built my candidate model set using combinations of five predictors of land cover, three predictors of nest box design, and four predictors of wildfire (Table 1.1). The predictors were chosen based on the results of Wendt and Johnson (2017), which revealed that only home range scale and several nest box design predictors were significantly correlated with occupancy. Land cover and wildfire predictors were calculated based on a 2.81 km radius, which is the mean maximum distance moved by GPS tracked barn owls in this population (See Chapter 2). The land cover variables were created using a combination of remote sensing using NAIP (USDA 2009) and LiDAR (NSF 2013) and existing GIS layers (County of Napa 2010, USDA and NASS 2019) to classify land cover into seven categories at 4 m resolution: water/wetland, urban, vineyard, grassland, oak savannah, mixed forest, and riparian. Only five of these land cover categories were used in modeling (Table 1.1). Soil burn severity and fire edge data were obtained from Cal Fire (California Department of Forestry and Fire Protection 2017*a*, *b*, *c*).

Each candidate model represented a different hypothesis about which combination of land cover, nest box design, and wildfire predictors would best explain each parameter in the incidence function model. I began by including all predictors in the formulas for γ and ε and testing various candidate model sets to identify the best combination of predictors of Ψ. Then I used that predictor set in all future models for Ψ and began testing hypotheses for the best combination of predictors for colonization and extinction. My resulting model set consisted of 17 models, which I ranked using Akaike's Information Criterion (AIC; Burnham and Anderson 2002). Models within 4 AIC from the top model were considered to have some support and those within 2 AIC had substantial support (Burnham and Anderson 2004). The models were built on a logit-scale, meaning the presented coefficients are log-odds ratios (Kéry and Chandler 2016).

Table 1.1. Description and justification for inclusion of covariates in incidence function model.

Covariate	**Description**	**Justification**
Home Range Scale		
vineyard	Percent of vineyard within 2.81 km of nest box	Wine producers are interested in maximizing time spent in vineyard
grassland	Percent of grassland within 2.81 km of nest box	Found to be significant predictor of both occupancy[1] and hunting habitat selection[2]
oakSavannah	Percent of oak savannah within 2.81 km of nest box	Found to be significant predictor of both occupancy[1] and hunting habitat selection[2]
mixedForest	Percent of mixed forest within 2.81 km of nest box	Found to be significant predictor of occupancy[1]
riparian	Percent of riparian within 2.81 km of nest box	Found to be significant predictor of occupancy[1]
uncultivated	Percent of vineyard, grassland, oak savannah, and mixed forest within 2.81 km of nest box	Combination of uncultivated habitat has potential to provide a more parsimonious explanation of occupancy
Box Scale		
box_type	Nest box material (plastic or wood)	Found to be significant predictor of occupancy[1]
entr_dir	Binary variable: towards or away from sun	Found to be significant predictor of occupancy[1]
ht	Distance in m from bottom of the nest box to the ground	Found to be significant predictor of occupancy[1]
Fire		
amtBurned	Percent of area burned within 2.81 km of nest box	Represents total area available to the owl for hunting that was impacted by fire
outerFireEdge	Length of fire perimeter (km) within 2.81 km radius of nest box	Owls hypothesized to use edge of fire perimeter because rodents will be recolonizing and tree cover will be less dense in burn
fireSeverityEdge	Length of edge (km) between areas of low severity and higher severity fire within 2.81 km radius of nest box	Edge between different levels of fire severity will likely function similarly to edge between burned and unburned areas
distToFire	Distance from nest box to fire edge	Owls will likely use the fire edge if it is more accessible from the nest box

[1] Wendt and Johnson (2017)
[2] Castañeda (2018)

Results

The proportion of occupied nest boxes increased over the study period, from 30.9% in 2015 to 32.0% in 2016, 40.7% in 2017, and 50.9% in 2018. The increase in occupancy was fairly dynamic, meaning that while some nest boxes became unoccupied, overall more boxes were occupied each year. Occupancy and colonization increased while extinction decreased over the course of the study (Figure 1.2). Of all occupied boxes that were monitored for four years, the mean number of years a box was occupied was 2.5 ± 1.2 ($n = 84$). Several of the nest boxes that were occupied for the first time in 2018 were within 2.81 km of a burned area.

Of 17 incidence function models to test the effects of habitat, box characteristics, time, and fire on initial occupancy, extinction, and colonization, all models with a ΔAIC < 4 had some combination of fire predictors in the formulas for colonization and extinction (Table 1.2). The null model and models that combined all uncultivated habitat into a single predictor carried approximately 0% of the AIC weight (Appendix A).

Effects of the amount of habitat around a box and box characteristics generally followed patterns suggested by prior research (Wendt and Johnson 2017), with similar covariates associated with initial occupancy and colonization, and some of those same covariates showing opposing associations with extinction. The model with the lowest AIC score included uncultivated habitats, box type, entrance direction, and box height as predictors for initial occupancy, colonization, and extinction. For both initial occupancy and colonization, the coefficient estimates with 95% confidence intervals that did not overlap zero included grassland (positive), forest (negative), and plastic box material (negative; Figure 1.3). Initial occupancy additionally included height (positive) and colonization included transition year 2017-2018 (positive) and amount of fire edge (positive). The coefficients with confidence intervals that did not overlap zero for extinction were forest (positive), plastic box material (positive), and fire severity edge (negative; Figure 1.3). The effects of the amount of oak savannah habitat followed the same pattern as forest, but confidence intervals overlapped zero. Box orientation had marginal effects, with confidence intervals overlapping zero. Across all parameters, some of the covariates with the largest coefficient magnitudes were box height, box material, fire severity edge, and year (Figure 1.3).

Wildfire predictors generally had a positive effect on occupancy. Amount of fire edge had a positive effect on colonization of nest boxes between 2017 and 2018 and the confidence interval did not overlap zero (Figure 1.4). Edge between low and high severity fire had a negative relationship with extinction and the confidence interval did not overlap zero (Figure 1.4). Amount of fire was positively associated with extinction and distance to fire edge was negatively associated with extinction, but these effects were weak with confidence intervals overlapping zero (Figure 1.3).

Table 1.2. Model selection table for incidence function model. Symbols for initial occupancy (Ψ), colonization (γ), and extinction (ε) indicate whether each variable was included in the model for that parameter. All fire variables were included in the models as an interaction with year. Only models with a ΔAIC between approximately zero to four are presented here. For all 17 candidate models, see Appendix A.

ΔAIC	**wAIC**	**K**	**Vineyard**	**Grassland**	**Oak Savannah**	**Forest**	**Riparian**	**Uncultivated**	**Box Type**	**Entrance Direction**	**Box Height**	**Amount Burned**	**Outer Fire Edge**	**Fire Severity Edge**	**Distance to Fire Edge**	**Year**
0.00	0.33	33		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ	ε	ε	γ ε
1.82	0.13	34		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ ε	ε	ε	γ ε
2.01	0.12	32		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε		ε	ε	γ ε
2.20	0.11	30		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε		γ			γ ε
2.49	0.10	32		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ	ε		γ ε
3.32	0.06	35		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ ε	γ ε	ε	γ ε
4.12	0.04	31		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ			γ ε

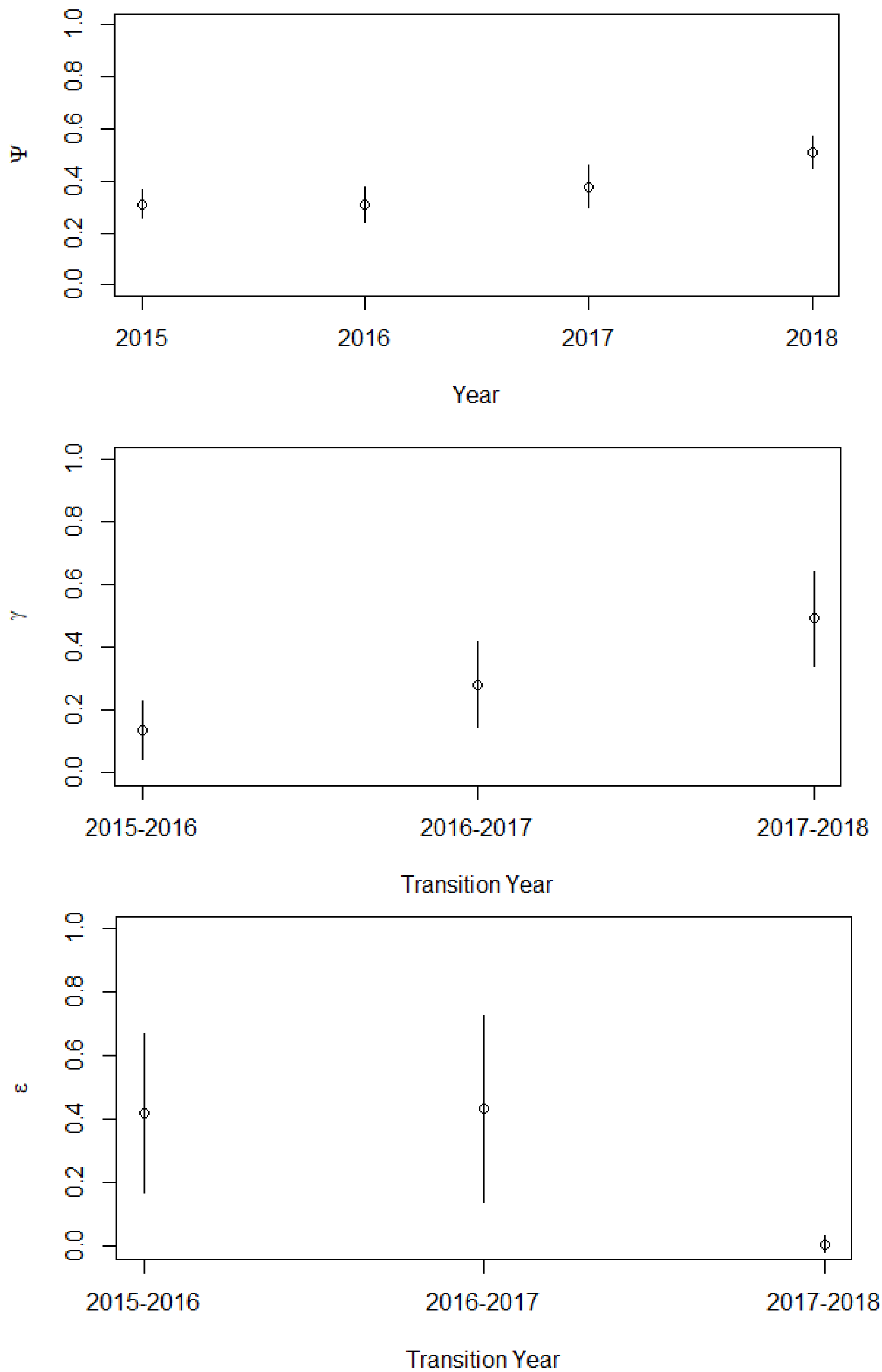

Figure 1.2 Estimated values of Ψ for each year of the study and γ and ε for each transition period between study years with 95% confidence intervals. Parameters were estimated using incidence function model with lowest AIC score and mean yearly values of all covariates in model.

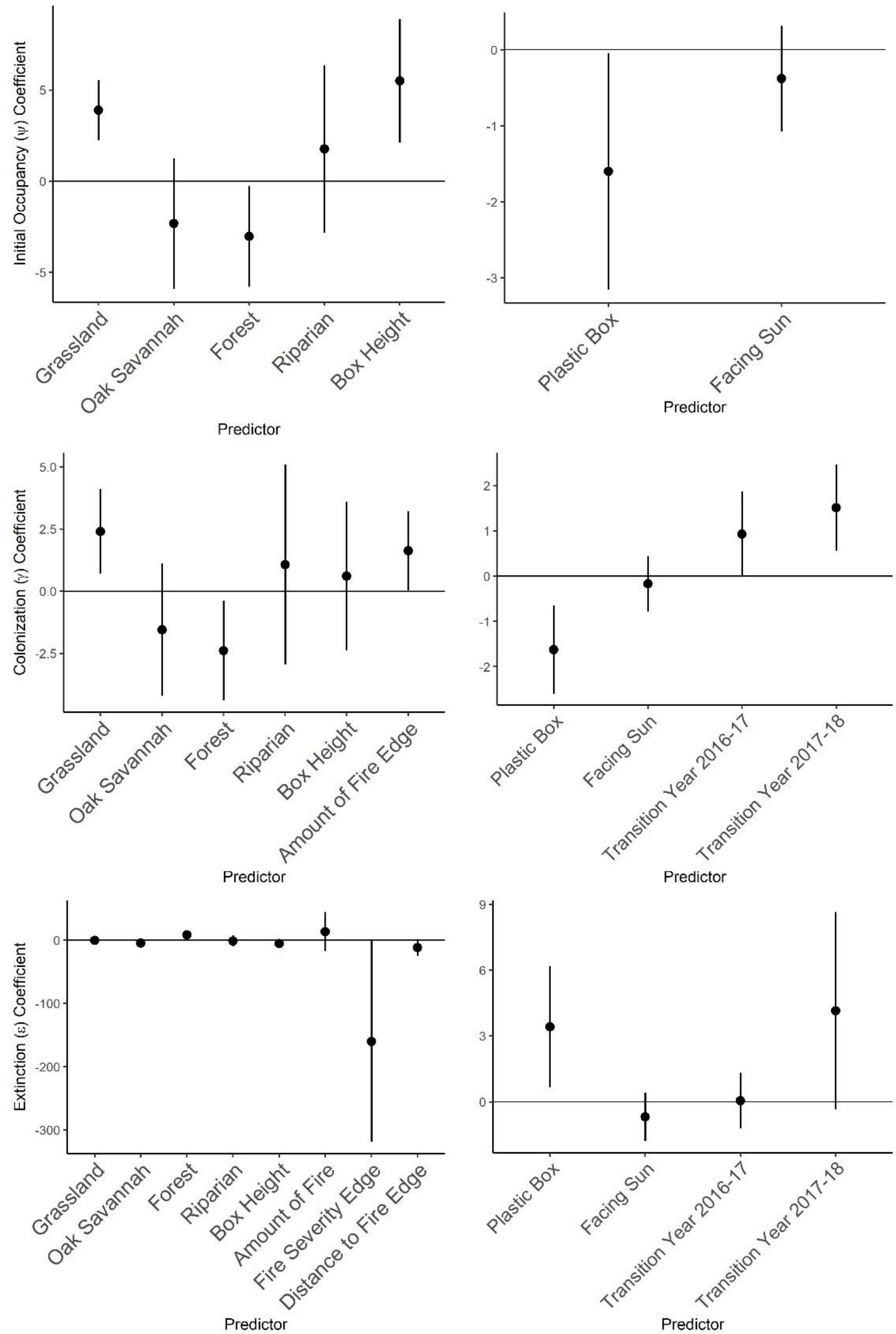

Figure 1.3. Coefficient estimates and 95% confidence intervals for incidence function model with lowest AIC score. Plots on the left show continuous predictors and plots on the right show categorical predictors.

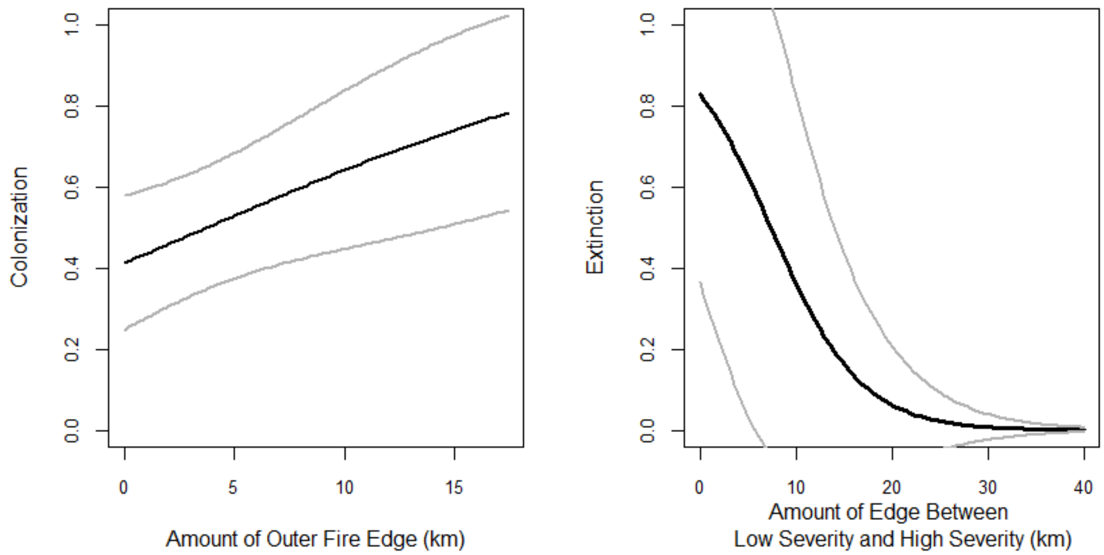

Figure 1.4. Modeled effect of fire covariates in model with lowest AIC score on colonization and extinction with 95% confidence intervals. All other variables in the model were set to their mean values.

Discussion

Through the course of this study, nest box occupancy increased from 30% to 50%, with some nest boxes consistently occupied while others experienced local colonization and extinction. The mechanisms and nest box characteristics behind colonization, extinction, and persistence (the probability of a box remaining occupied) underlie the ability of barn owls to nest in vineyards and provide meaningful pest control. With remaining uncertainty over the ability of barn owls to control rodent damage (Kross and Baldwin 2016, Labuschagne et al. 2016, Johnson et al. 2019), a first step for managing their potential for this ecosystem service is confirming our understanding of their nesting preferences both with and without disturbance.

Among the most broad and durable results for management is the finding that uncultivated land cover types and box material, height, and orientation had consistent effects on initial occupancy, colonization, and extinction. These results are consistent with those of Wendt and Johnson (2017), who concluded that boxes with uncultivated land, and those that are wooden, at least 3 m high, and facing away from the sun are the most likely to be occupied in Napa Valley. Here, I found that barn owls were most likely to colonize and persist in nest boxes with abundant grassland and little forest nearby. The percent of oak savannah and riparian habitat had marginal effects compared to grassland and forest. The importance of uncultivated land on nest box occupancy and persistence suggests that farm conservation should prioritize the habitats that most benefit barn owls. Future work should model changing landscape composition, as well as the effects of habitat loss and restoration on occupancy rates. Barn owl habitat preferences and literature on the positive relationship between landscape heterogeneity and ecosystem services (Tscharntke et al. 2005, Lindell et al. 2018) suggest that changing landscape composition can have significant effects on pest control provided by barn owls.

If we assume nest site selection is adaptive, which is likely given that nest success and survival are important deterministic components of lifetime reproductive success and thus individual fitness, the characteristics associated with increased occupancy should confer some survival or reproductive advantages. Reproduction is likely affected by prey availability, which is likely reflected in land cover variables. Specifically, Botta's pocket gophers and California voles, important pest species and prey of barn owls, are most likely to be found in grassland and can reach high densities in this land cover type (Huntly and Inouye 1988, Fehmi and Bartolome 2002, Ordeñana et al. 2012). Chick survival may be affected by nest box material, direction, and other factors that influence temperature (Charter et al. 2010, 2017; Bank et al. 2019). Future work should test whether reproductive success is associated with the habitat and nest box variables I have found to affect occupancy and persistence.

The conclusion that barn owls are associated with uncultivated land because that is where rodents thrive introduces a potential trade-off in terms of the services and disservices of uncultivated land. Literature on rodent populations shows that landscape heterogeneity increases small mammal abundance in agricultural landscapes (Fischer et al. 2011), suggesting that land cover types such as grassland could be acting as a source for rodent pests to colonize vineyards (Tscharntke et al. 2016). Though this means that barn owls are more likely to occupy nest boxes near uncultivated land, if rodent densities are high enough in vineyards surrounded by preferred rodent habitat, the conservation of this land cover type could be less preferable for wine producers than vineyards that are far away from uncultivated land where they do not have occupied nest boxes, but they also have fewer rodent pest problems. However, this argument assumes that uncultivated land has no other value besides its relationship with rodent pests. In a survey of 30 Napa Valley wine producers, landowners said they left an average of 43% (± 30.5) of their land uncultivated (Estes unpubl.). Though this is arable land, Napa Valley residents choose to conserve (Napa Green 2019) and the local government regulates the amount of land cultivated (Napa County Conservation Devleopment and Planning Department 2005) due to other ecosystem services such as watershed protection (Hannah et al. 2013) and cultural reasons such as the value of *terroir*, or the importance of the surrounding environment in winemaking (Hira and Swartz 2014). Thus, there are several incentives for Napa Valley wine producers to conserve uncultivated land, which benefits rodents, and in turn, barn owls.

In addition to the effects of land cover and box characteristics, there were clear signs that fire played a positive role on nest box use between 2017 and 2018. Fire was important for both colonization and extinction and was in most of the top models. These modeling results align with an observable redistribution of occupied nest boxes the year after the fire. Based on the areas that were newly colonized in 2018, it is likely that the fires altered the habitat in a way that made rodents more available and hunting more accessible. Fire opened canopy in forested areas that made it more similar to the open grasslands and agricultural areas in which barn owls are adapted to hunt (Taylor 1994). In theory, green-up post-fire should also be positive for rodent populations, which heavily use recently burned edges (Haim and Izhaki 1994, Schwilk and Keeley 1998, Parkins et al. 2018), but I was not able to measure these mechanisms. The response of barn owls to landscape heterogeneity induced by wildfires is consistent with their response to heterogeneity in non-fire years, when owls are associated with greater availability of diverse uncultivated habitats (Wendt and Johnson 2017).

Barn owl nest box use is dynamic in nature, but this study revealed that there are characteristics consistently associated with occupancy even after a severe disturbance event. This study provides evidence that fire is positive in the short-term for nest box occupancy, which is a desired result from a pest control and management perspective. However, this assumes that barn owls that choose to nest in vineyards are also hunting there, and previous research indicates that about one third of the hunting by vineyard-nesting barn owls occurs within vineyards (Castañeda 2018). More work is needed to determine if this short-term positive effect on occupancy will persist long-term, and if nest box occupancy is a useful indicator of pest control potential.

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Appendix A

Appendix A: Full model selection table for incidence function model. Symbols for initial occupancy (Ψ), colonization (γ), and extinction (ε) indicate whether each variable was included in the model for that parameter. All fire variables were included in the models as an interaction with year.

Δ AIC	**wAIC**	**K**	**Vineyard**	**Grassland**	**Oak Savannah**	**Forest**	**Riparian**	**Uncultivated**	**Box Type**	**Entrance Direction**	**Box Height**	**Amount Burned**	**Outer Fire Edge**	**Fire Severity Edge**	**Distance to Fire Edge**	**Year**
0.00	0.33	33		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ	ε	ε	γ ε
1.82	0.13	34		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ ε	ε	ε	γ ε
2.01	0.12	32		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε		ε	ε	γ ε
2.20	0.11	30		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε		γ			γ ε
2.49	0.10	32		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ	ε		γ ε
3.32	0.06	35		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ ε	γ ε	ε	γ ε
4.12	0.04	31		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ			γ ε
4.33	0.04	29		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε					γ ε
4.48	0.04	37		Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	γ ε	γ ε	γ ε	γ ε	γ ε
6.15	0.02	37	Ψ	Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ ε	γ ε	γ ε	γ ε

Appendix A (continued from previous page): Full Model selection table for incidence function model. Symbols for initial occupancy (Ψ), colonization (γ), and extinction (ε) indicate whether each variable was included in the model for that parameter. All fire variables were included in the models as an interaction with year.

Δ AIC	**wAIC**	**K**	**Vineyard**	**Grassland**	**Oak Savannah**	**Forest**	**Riparian**	**Uncultivated**	**Box Type**	**Entrance Direction**	**Box Height**	**Amount Burned**	**Outer Fire Edge**	**Fire Severity Edge**	**Distance to Fire Edge**	**Year**
6.52	0.01	32	Ψ	Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		Ψ γ ε	Ψ γ ε	Ψ γ ε					γ ε
73.10	0.00	15		Ψ	Ψ	Ψ	Ψ		Ψ	Ψ	Ψ					γ ε
73.92	0.00	19		Ψ	Ψ	Ψ	Ψ		Ψ	Ψ	Ψ	ε	γ	ε	ε	γ ε
129.17	0.00	24						Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ	ε	ε	γ ε
130.61	0.00	26						Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ ε	ε	ε	γ ε
132.08	0.00	21						Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε		γ			γ ε
132.70	0.00	23						Ψ γ ε	Ψ γ ε	Ψ γ ε	Ψ γ ε	ε	γ	ε		γ ε

CHAPTER 2: HABITAT SELECTION BY A RODENT PREDATOR IS RESILIENT TO WILDFIRE IN A VINEYARD ECOSYSTEM

Abstract

In Napa Valley, California, abundant rodent pests and an interest in integrated pest management have led wine producers to use barn owl (*Tyto alba*) nest boxes to reduce rodent damage. This method of rodent control depends heavily on the amount of time that barn owls spend in vineyards, which is known to be influenced by the amount of uncultivated habitat surrounding the nest box. Wildfires in 2017 burned nearly 60,000 ha of mainly urban and uncultivated lands surrounding Napa Valley in 2017, altering barn owl habitats. I compared GPS tracking data on 32 barn owls nesting in 24 individual nest boxes before and after the fires to analyze their hunting habitat selection. Owls with burned areas available to them after the fires had weak positive selection for burned edges and low to intermediate levels of fire severity. Though there was some affinity for fire edges, selection of land cover types was similar for birds before and after the fires and in burned and unburned areas. The strongest selection was for vineyard, grassland, riparian, oak savannah, and areas closest to the nest box. Overall, habitat selection was resilient to changes caused by wildfires, with some spatial preference for burned areas. These results are important for farmers who use nest boxes as a means of rodent control,

which may be affected after dramatic disturbance events, especially as wildfires increase in the western United States.

Introduction

Recent literature has focused on the link between pest control by natural enemies and the composition of the surrounding landscape (Lindell et al., 2018). Conserving uncultivated habitats and maintaining landscape heterogeneity can increase the potential for ecosystem services, particularly pest control (Grass et al., 2019; Kremen and Merenlender, 2018). The composition of the landscape surrounding agricultural areas is critical when the agents providing pest control are mobile and rely on resources beyond those provided by cultivated habitats. Much of the literature surrounding the relationship between landscape composition and mobile agents that provide ecosystem services has focused on pollinators (Kremen et al., 2007) and insect predators (Boesing et al., 2017; Veres et al., 2013), but this theory also applies to organisms that provide vertebrate pest control.

Barn owl nest boxes are placed in vineyards and other agricultural areas with the hopes of controlling rodent damage, but their ability to deliver pest control depends on how much owls hunt in vineyards. There is increasing interest in maximizing pest control by barn owls, which prey upon pest species such as pocket gophers (*Thomomys bottae*) and voles (*Mictrotus* spp) in California, though the efficacy of this method remains unresolved (Kross and Baldwin, 2016; Labuschagne et al., 2016). Recent research has shown that barn owls in Napa Valley, California preferentially nest near uncultivated lands, particularly grassland (Wendt and Johnson 2017; Chapter 1), and when more of this habitat is available, barn owls spend less time hunting in vineyards (Castañeda, 2018). Thus, the composition of vineyards and uncultivated land throughout the landscape has consequences for the potential of barn owls to both nest and hunt in vineyards, therefore affecting their potential ability to control pests.

The availability of preferred hunting habitat for barn owls in Napa Valley was heavily altered by wildfires in the region in 2017. The Atlas, Nuns, and Tubbs fires burned nearly 60,000 ha around Napa Valley, primarily affecting uncultivated land (Lapsley and Sumner, 2017). Landscape changes caused by these fires also have the potential to change vegetation structure and rodent communities on which barn owls depend. In the western United States, small mammals are likely to have increased populations in recently burned areas (Fitzgerald et al., 2001; Schwilk and Keeley, 1998) and in other recently burned Mediterranean climates, fires produce edge habitat and open areas that seem to be preferred by rodents (Haim and Izhaki, 1994; Torre and Díaz, 2004). With significant changes to rodent communities in the habitats that barn owls prefer, it is likely that barn owls will respond by hunting where prey is more available.

Changes to the landscape caused by wildfires and literature on rodent response to fires led me to hypothesize that owls would hunt near burned edges. Barn owls are central-place foragers that are more likely to hunt near the nest box, but they preferentially choose to hunt on uncultivated land, especially grasslands, when it is available (Castañeda 2018). Other central-place foraging owl species can select for low and moderate-severity burned forests far from their territories (Bond et al., 2009; Eyes et al., 2017). This is likely because of increased rodent populations and easier hunting in burned areas where the tree canopy is made more open by fire. In Napa, I predicted that barn owls would continue to choose their preferred hunting habitats such as grassland, and that much of this selection would occur closer to the fire edge.

An understanding of how owls respond to wildfire is crucial for determining how resilient barn owl pest control is to disturbance and changes to landscape composition. Mediterranean climates such as Napa evolved with fire, though the whole western United States is experiencing increasing fire intensity and frequency due to fire suppression and changing climate conditions (Batllori et al., 2013; Westerling et al., 2006). The increased likelihood of intense fires could affect the ability of mobile predators to provide pest control and aid in habitat recovery after disturbance.

Materials and Methods

Study Area

This project took place on vineyards in Napa Valley, California, where 273 nest boxes have been monitored since 2015. Napa Valley is ~48 kilometers long and 5-20 kilometers wide and is characterized by a Mediterranean climate ideal for growing grapes (Napa Valley Vintners, 2017). Mixed oak woodlands and oak savannahs are spread throughout the region, with more oak-grasslands in the south and more mixed oak scrub and conifer forests in the north (Napa County, 2010; Wendt and Johnson, 2017). The unique conditions in Napa County have created a wine industry that generates $3.7 billion in revenue each year and in combination with tourism, employment, and distribution, is estimated to have an annual impact of $50 billion on the American economy (Stonebridge, 2012). While the Atlas, Nuns, and Tubbs fires of October, 2017 burned over 60,000 hectares surrounding Napa Valley (Cal Fire, 2017), few vineyards were burned (Lapsley and Sumner 2017; Figure 2.1) due to their comparatively low fuel levels and more mesic conditions than surrounding vegetation.

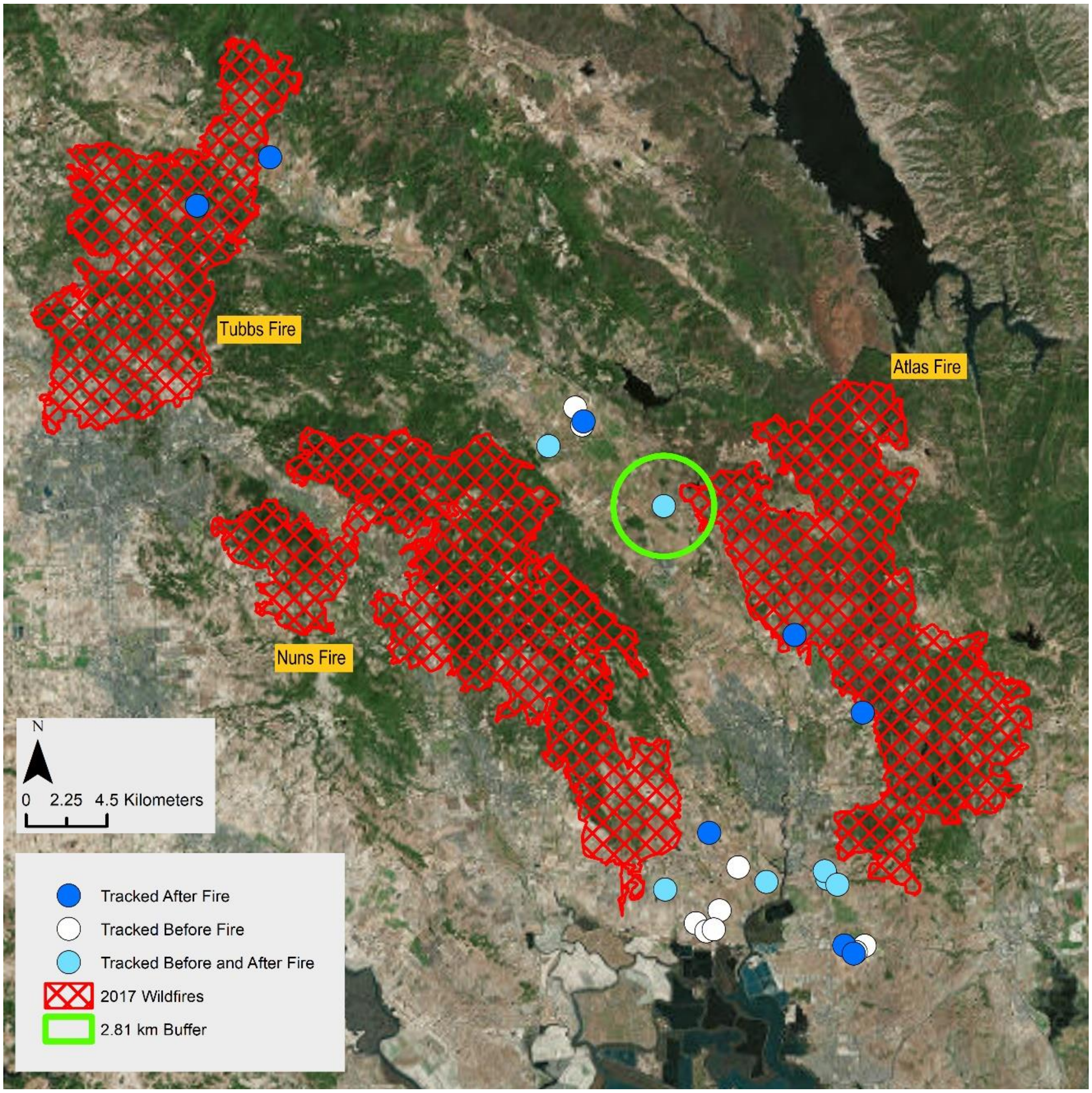

Figure 2.5 Map of Napa Valley, California study area with nest boxes tracked by GPS telemetry and Atlas, Nuns, and Tubbs fires. Green circle represents 2.81 km buffer around nest box, the mean maximum distance recorded for barn owls in this population.
Service layer credits: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

This study focused on owls occupying 24 individual nest boxes, 9 of which were monitored before the Atlas, Nuns, and Tubbs fires of 2017, 7 monitored after the fires, and 8 monitored both before and after the fires (Figure 2.1). The nest boxes were divided into four groups: pre-fire unburned (n = 10), post-fire unburned (n = 4), pre-fire burned (n = 7), and post-fire burned (n = 11), depending on the year(s) the box was studied and whether the nest box was within 2.81 km of the 2017 wildfires (Figure 2.1). This radius was selected because it was the mean maximum distanced moved by all GPS tracked individuals in this study; none of the boxes themselves in this study were burned.

Field Methods

All methods were approved by the Humboldt State University Institutional Animal Care and Use Committee (IACUC) in Protocol Number 15/16.W.43-A.

Study Species

During the breeding season, when barn owls occupy nest boxes, the male and female alternate hunting depending on the stage of raising young. Taylor (1994) observed that the percentage of males that sit beside their females in the nest increases to reach a peak in the two weeks before laying and during laying. After this point, male and then female hunting increase in an effort to meet the varying metabolic requirements of young in the nest, with males doing most of the hunting and provisioning the young and the female in the first couple of weeks, followed by both adults hunting actively to provision the young in weeks 3-10 (Bank et al., 2019; Durant and Handrich, 1998; Taylor, 1994). Adult male owls generally weigh 400-560 g and females weigh 420-700 g (Marti et al., 2005).

GPS Telemetry

I deployed GPS transmitters on 15 barn owls throughout the breeding season in Napa Valley in 2018, adding to a sample of 17 owls which were tagged during the 2016 and 2017 breeding seasons (Castañeda, 2018). Selecting birds to tag depended on occupancy of boxes during tagging occasions, but when feasible, I tagged owls that had extremely high and low amounts of burned area within their home range and prioritized next boxes and individuals previously tagged in 2016 (Castañeda, 2018). All birds tagged were females for consistency with Castañeda (2018) and because females more reliably return to the nest box during the day than the males, which aided retrieval of GPS data and GPS tag recovery. Birds were tagged if there were young at least two weeks old in the nest, as laying and incubation are considered more sensitive stages of the nesting cycle (Meyrom et al., 2009) and because this period coincides with maximum hunting by adults to meet the metabolic requirements of nestlings (Martin et al., 2010; Naim et al., 2010).

Birds were trapped within the next box during the day. I first blocked the entrance to a box with a pillow, then climbed a ladder and removed the owls through a door on the side or top of the box. The owls were placed in a pillowcase to remain calm until processing and then had their eyes covered with a cloth hood during banding and tagging. Each tagged bird was also given a unique U.S. Geological Survey aluminum band. Weight and morphological measurements including wing and bill length were also recorded for each bird. To determine sex, I examined plumage and behavior and looked for a brood patch on each bird. When tagging and data collection were finished, I placed the birds back in the nest box and blocked the entrance for an extra five minutes to allow the birds to calm down before I left the site. Total handling time did not exceed 20 minutes per bird.

GPS tagging followed the protocol of a previous study on the same population (Castañeda, 2018), using the Uria 300 tag developed by Ecotone Telemetry (2015), which weigh 13.5 g each. Tags were attached to birds using a small harness created with a Teflon ribbon that does not interfere with the bird’s movements (Humphrey and Avery, 2014). The Uria 300 can be programmed to record GPS locations at varying times; I programmed my units to record a location every two minutes. Castañeda (2018) collected locations every one minute, so I subsampled the data from those individuals to every two minutes for analytical purposes.

Data from deployed tags were downloaded remotely though a handheld base station left at the nest box. I collected data on each bird for 14 to 21 days, the approximate battery life expectancy with my programmed location frequency, and then attempted to recover the tag so it could be deployed on another owl. If the female was still roosting diurnally in the nest box, I re-trapped the female within this box as described above. When that was not possible because the female was no longer roosting in the nest box, I used a custom trap attached to the nest box (as described by M. Charter, personal comm.) that allowed me to recapture adults at night when they came to deliver prey to nestlings. After recovery of the tag, I removed the trap and returned the adult to the nest box as during diurnal handling.

Analysis Methods

Brownian Bridge Movement Model

I used the package *move* (Smolla and Kranstauber, 2015) in program R version 3.5.1 to build dynamic Brownian Bridge Movement Models (dBBMM) for all 32 tagged birds. I only used GPS locations that were collected more than 30 m from the nest box to exclude locations when the bird was in or very near the box and to account for GPS error. The GPS transmitters were programmed to record three locations at a time, and I removed duplicate timestamps so that only the first of each timestamp was used. I removed duplicate locations rather than averaging duplicates because in many cases, the individual was moving, and an average of the locations could produce a location where the individual was never actually observed. After constructing the dBBMM, I cropped the raster to the 95% utilization distribution for further analysis.

Resource Utilization Function

I used the package *ruf* (Handcock, 2011) in program R to build Resource Utilization Functions (RUF) as described by Marzluff et al. (2004), which allow the use of a utilization distribution as the response variable to estimate resource selection. Depending on when a bird was tracked, I used predictors in RUF models based on rasters for land cover type, soil burn severity, distance to fire edge, and distance to nest box. The land cover raster was created using a combination of remote sensing using NAIP (USDA, 2009) and LiDAR (NSF, 2013) and existing GIS layers (County of Napa, 2010; USDA and NASS, 2019) to classify land cover into seven categories at 4 m resolution: water/wetland, urban, vineyard, grassland, oak savannah, mixed forest, and riparian. Soil burn severity and fire edge data were obtained from Cal Fire (California Department of Forestry and Fire Protection, 2017a, 2017b, 2017c).

For birds that were GPS tagged after the fires and had some burned area within a 2.81 km radius of their nest box (n = 11), I built RUF models using combinations of the predictors: land cover, distance to nest box, distance to fire edge, soil burn severity, and soil burn severity squared, because I hypothesized that barn owls would select for an intermediate level of burn severity (represented mathematically by including a quadratic term). The 2.81 km radius was used to represent available habitat because it was the mean maximum distance recorded from the nest box among all GPS-tagged individuals. I selected the best model based on which one had the lowest AIC score for the most individual birds.

To determine whether the fires affected habitat selection, I constructed RUF models for all 32 birds using the land cover and distance to nest box rasters as predictors. I then ran 2-way ANOVAs for each predictor variable, with each bird as the sample unit, the estimated beta coefficient for each bird as the response variable, and burn group (burn or no burn) and year (pre-fire or post-fire) as the grouping variables, with additive and interactive models for these terms. This design follows a before-after-control-impact (BACI) experimental design, though subjects were obviously not chosen randomly;

rather they were made possible by the availability of previous data (Castañeda 2018) and the distribution of the wildfires and occupied nest boxes.

Results

Between 2016 and 2018, GPS data were collected on 32 birds. After removing locations within 30 m of the nest box and duplicate timestamps, the mean number of locations collected per individual in a year was 851 (range 114-1,876). Throughout the four nest box groups (ten pre-fire unburned, seven pre-fire burned, four post-fire unburned, and eleven post-fire burned), eight nest boxes and three individuals were the same ones studied both before and after the fires (example of data from four nest boxes in Figure 2.2). Hunting locations pooled before and after the fires were composed of approximately 48% in grassland, 29% in vineyard, 10% in oak savannah, and less than 5% in each water, urban, mixed forest, and riparian land cover types.

I evaluated five RUF models for the group of 11 birds that were GPS-tagged near burned areas after the fires (Appendix B). The model with the lowest AIC score for the most birds was UD = land cover + distanceToNestBox + soilBurnSeverity + $(\text{soilBurnSeverity})^2$ + distanceToFireEdge. This model converged for 10 of the 11 birds; one bird did not have enough variation in soil burn severity for the model to converge. I averaged the coefficients from the best model for all birds and used Marzluff et al.'s (2004) recommendation for calculating standard deviation and confidence intervals from averaged coefficients (Figure 2.3). The mean coefficients for grassland, oak savannah, and riparian were positive, though their 95% confidence interval overlapped zero. Selection was negative for distance to fire edge and distance to nest box, meaning intensity of utilization was negatively associated with these variables, though both confidence intervals overlapped zero. Selection was positive for soil burn severity and negative for soil burn severity squared, indicating a humped relationship where intermediate levels of soil burn severity had the highest intensity of utilization, but again their confidence intervals overlapped zero, indicating marked variation among the 10 analyzed birds.

For all 32 tagged birds, the average coefficients for the seven land cover types were all positive, with confidence intervals overlapping zero for most groups (Figure 2.4). The average coefficient for distance to nest box for all groups was negative, with confidence intervals that did not overlap zero. Coefficients for most land cover types were similar among birds tagged before and after the fires, as well as between birds with or without burned area nearby their nest box. I ran a two-way ANOVA on these results to test whether year, burn (and interactive or additive models), or a null model best explained differences in selection for each land cover type and distance from nest box (Appendix C). Multiple models were within 2 ΔAICc of the top model for each response variable, indicating a significant amount of model uncertainty. For all response variables, the burn model and null model were within 1 ΔAICc, making them both competitive as the top model (Appendix C).

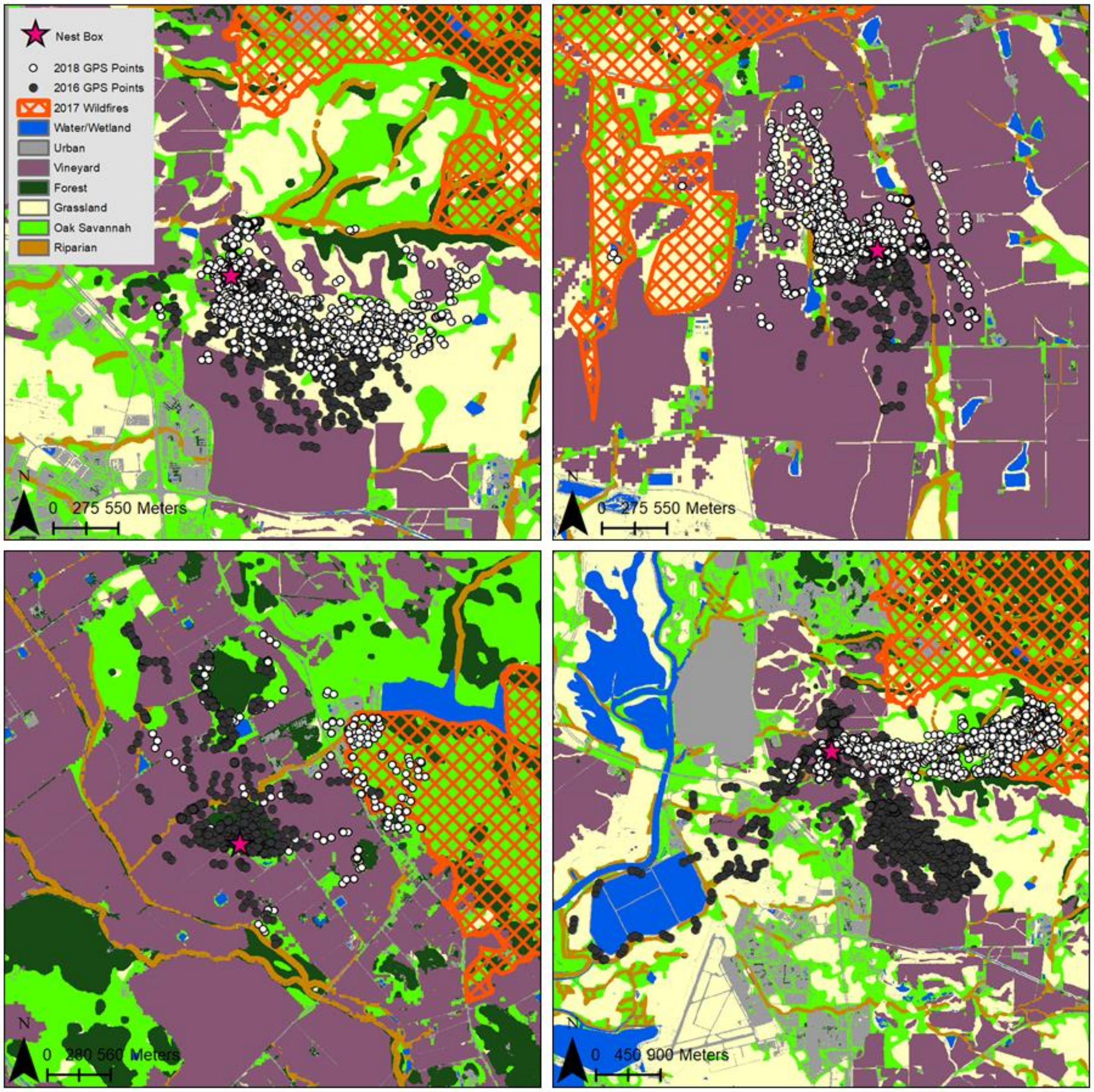

Figure 6.2 Map of Napa Valley land cover classification and GPS telemetry points collected on owls tracked before the fires (2016) and after the fires (2018), with area burned. The top two nest boxes were the same individuals tracked in the depicted nest box before and after the fires. The bottom two nest boxes were different individuals tracked in the depicted nest box before and after the fires.

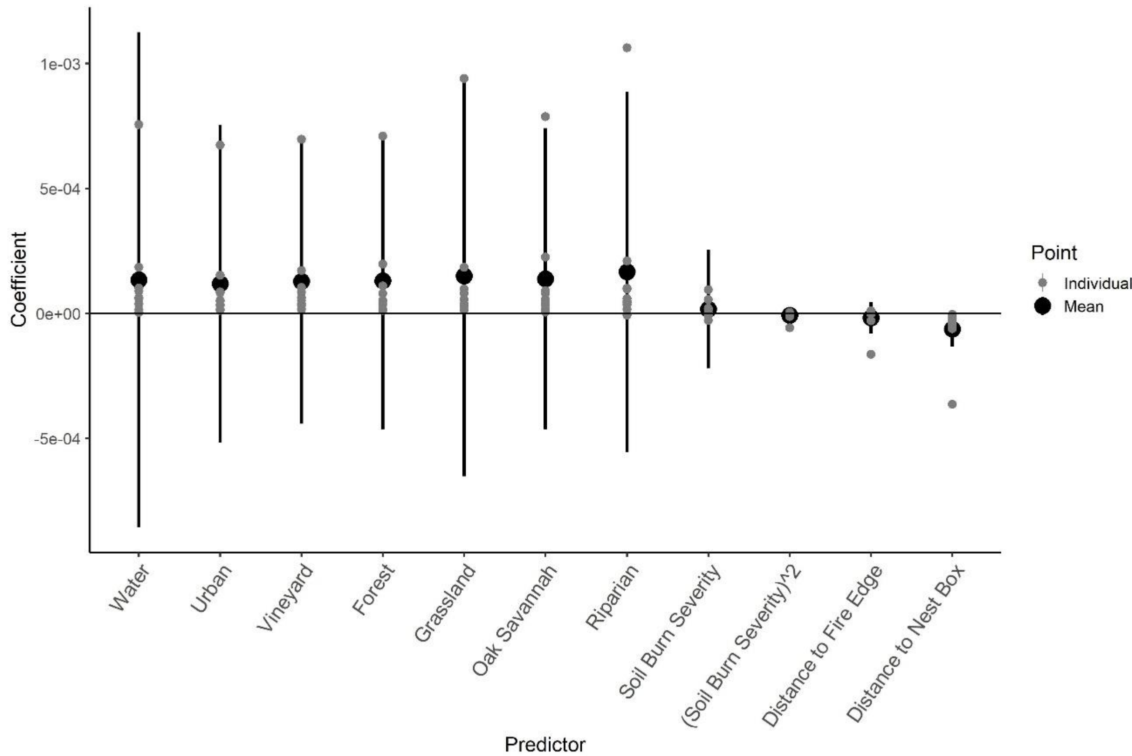

Figure 2.7 Mean selection coefficients and 95% confidence interval for mean of each predictor variable in resource utilization function model, UD = land cover + distanceToNestBox + soilBurnSeverity + $(\text{soilBurnSeverity})^2$ + distanceToFireEdge, calculated for 10 birds that were GPS tagged near burned areas after the fires. Black dots show mean of all coefficients and gray dots show coefficients for each individual.

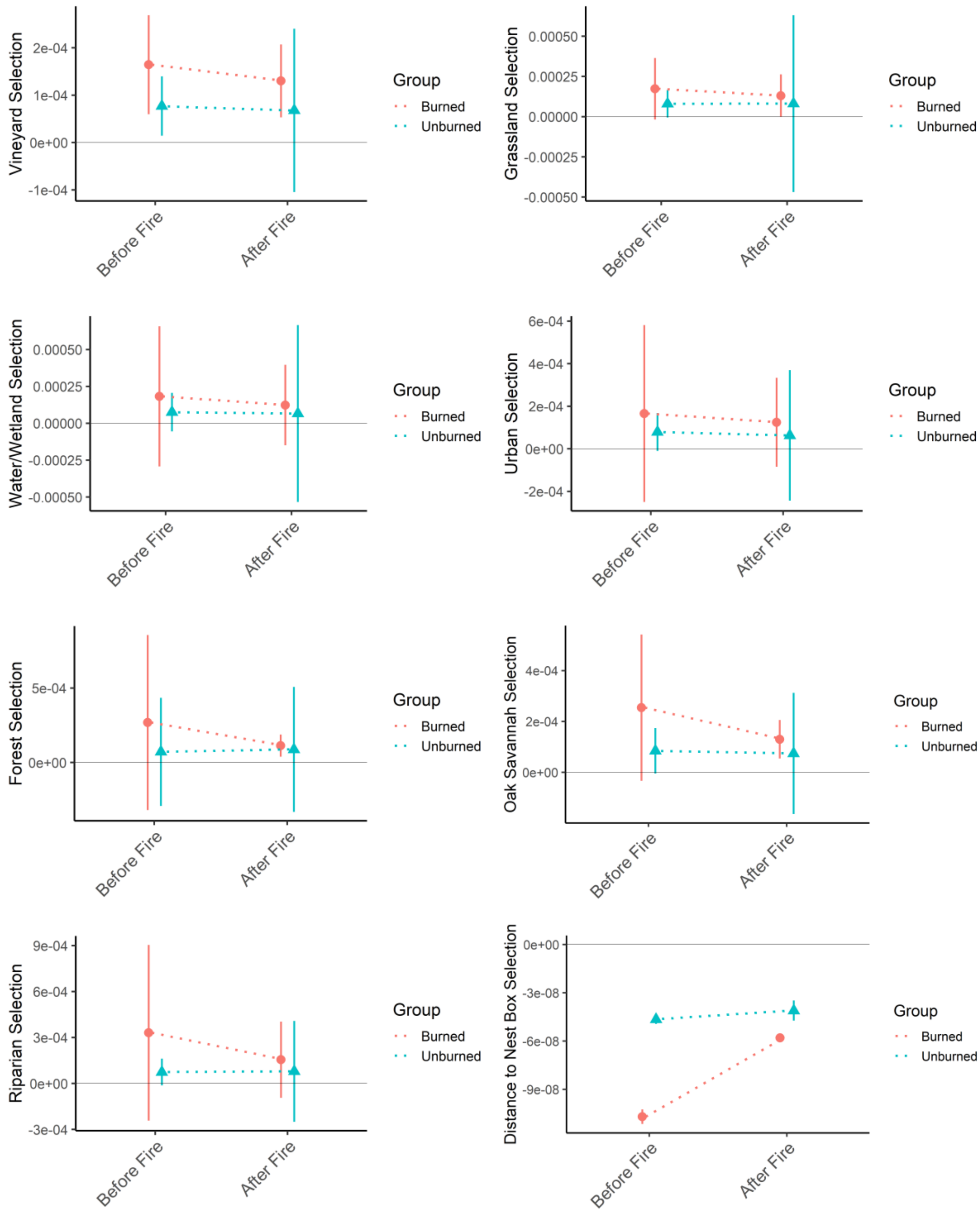

Figure 2.8 Mean selection coefficients and 95% confidence intervals for each predictor variable in resource utilization function model, UD = vineyard + forest + grassland + riparian + oakSavannah + urban + water + distanceToNestBox, calculated for all 32 birds. Colors and symbols indicate whether birds were tracked before or after the 2017 fires, and whether or not their hunting range was near burned habitat.

Discussion

Barn owl habitat selection was resilient to landscape changes caused by wildfires. Specifically, they showed some selection for burned areas, but overall this did not change the land cover types they selected. The selection for burned edges is consistent with edge effects created by fire (Parkins et al., 2018) which cause small mammals to spend time where burned and unburned areas meet (Haim and Izhaki, 1994; Schwilk and Keeley, 1998). Though the effect was weak, barn owls with access to burned areas after fire showed some selection for low to intermediate levels of burn severity, which is also consistent with studies of other owl species post-fire (Bond et al., 2009; Eyes et al., 2017). Ultimately, this sample of barn owls showed some spatial preference for burned edges, but this had minimal effects on their potential for pest control because it did not substantively change their selection of land cover types.

Though barn owls had some affinity for fire edges, overall little change in selection of land cover types could be confidently ascribed to fire. Regardless of the year or proximity to burned area, all owls showed some preference for vineyard, grassland, and oak savannah and areas closest to the nest box. The effect of land cover was weakest for the post-fire unburned group, which may be because the sample size was smallest for this group. Model selection showed that differences in land cover use could be described either by a null model or burn model, so it is not possible to confidently conclude that fire could explain differences in land cover selection among groups. Though RUF coefficients show variation in selection, the number of locations recorded in different land cover types for all birds, regardless of year and proximity to burn, showed a marked preference for uncultivated land.

Previous research has shown that the same land cover variables that are associated with nest box occupancy are also the land cover types that owls select for hunting (Castañeda, 2018; Wendt and Johnson, 2017), a result that is corroborated here. Nest box occupancy before and after fire was positively correlated with amount of grassland and riparian lands, as well as amount of fire edge, and negatively correlated with amount of forest (Chapter 1). Though the patterns are weaker in the RUF results, owls also appear to preferentially hunt in these same land cover types. Due to the hierarchical nature of how habitat selection operates (Mayor et al., 2009), birds may choose nest sites and then foraging areas around them, or select foraging areas first and then the nest sites within them (Lawler and Edwards, 2006). Variance-decomposition analysis has shown that barn owls choose their nest site location primarily based on the characteristics of the landscape at the home range scale (Wendt and Johnson 2017). Since home range foraging habitat availability plays a large role in nest site selection, it is reasonable that many of the same land cover variables are associated with both nest box occupancy and hunting habitat utilization, but nuances around this issue remain unresolved in my study system. In contrast to previous work (Castañeda 2018), the results here also show that barn owls have strong positive selection for vineyards. This is an encouraging result from a pest control perspective, showing that the placement of nest boxes in vineyards means that owls are likely to spend time removing rodents from vineyards. The use of vineyards likely has a relationship with barn owls' central-place foraging tendency, which increases the likelihoood that they will hunt near their nest box (Castañeda, 2018). Furthermore, this result is consistent across all groups, suggesting that it is resilient to landscape changes caused by wildfire.

Though barn owls showed resilience in their selection of land cover types after disturbance, the mechanisms behind this response are difficult to determine. Barn owls are rodent predators, but they are opportunistic when rodent availability changes, so their adaptability may have buffered their response against landscape changes (Kross et al., 2016; Tores et al., 2005). It is unknown if the fires had any long-term effects on fitness and prey availability that could not be detected through occupancy and telemetry monitoring. Rodent monitoring, diet studies, and the combination of diet and telemetry data could help to determine where pest rodents are most available and where they are actually removed (Johnson et al., 2019). It is also possible that barn owls that nested near recently burned areas had different nest success from those that nested away from the fire, so analysis of reproductive success could reveal more short-term and long-term effects of fires on this population. The conclusion that fires did not have a significant short-term impact on barn owl hunting habitat selection suggests a resilience to wildfire, but more work is needed to determine owls' full potential for pest control in years with and without disturbance.

This study reveals that barn owls are resilient to drastic landscape changes caused by wildfires, a finding that is especially significant in California where the threat of wildfire is growing (Batllori et al., 2013; Westerling et al., 2006). Barn owls made opportunistic use of recently burned areas in both nesting (Chapter 1) and hunting habitat selection, but their use of land cover types was not noticeably different as a result of the fires. Considering the known importance of landscape composition for the delivery of pest control (Lindell et al., 2018; Tscharntke et al., 2005), the ability of barn owls to use the landscape in a similar way before and after fire is an encouraging result for wine producers hoping to use barn owls as rodent pest control.

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Appendix B

Appendix B: ΔAIC scores for five resource utilization function models run for all 11 birds GPS tracked in burned areas after fires. Model with lowest AIC score for each nest box is bolded. The model with the lowest AIC score for the most birds was used for further analysis.

Nest Box	Hab + BoxDist	Hab + BoxDist + FireDist + SBS + SBS^2	Hab + BoxDist + FireDist + SBS	Hab + BoxDist + FireDist	Hab + BoxDist + SBS
ben5	279.2	167.8	**0**	258.1	207.9
bos1	**0**	2249.5	3375	1398.3	482.4
huh6	3506.6	2189	2844.7	**0**	2091.9
law2	2845.3	6.5	3911.2	5668.2	**0**
mtg1	2441.6	2068.6	1353.1	737.1	**0**
osr1	526.1	Didn't Converge	Didn't Converge	**0**	Didn't Converge
roy2	2619.4	**0**	1662.5	1541.1	1233.1
scv17	1121.6	**0**	189.1	735	126
scv6	**0**	2551	1230.9	647.7	1924.4
scv9	1054	**0**	1615	2056.8	2724.8
wol2	925.1	1271.6	**0**	305	964.1

Appendix C

Appendix C: ΔAICc scores for six ANOVA models where response variable is the selection coefficient from the resource utilization function model, UD = habitat + distanceToNestBox, calculated for all 32 birds. *year* represents pre or post fire and *burn* indicates whether that nest box ever experienced fire. Model with lowest AICc score for each habitat type is bolded. If the wildfires strongly affected habitat selection, then top models should include additive or interactive models with year and burn as important predictors.

Response Variable	year*burn	year + burn	year	burn	null
Vineyard	5.58	2.82	2.44	0.43	**0.00**
Forest	0.17	0.02	2.66	**0.00**	0.93
Urban	5.66	2.89	2.43	0.65	**0.00**
Riparian	4.20	2.08	2.26	0.40	**0.00**
Savannah	3.28	1.23	2.06	0.10	**0.00**
Grassland	5.54	2.90	2.44	0.52	**0.00**
Water	5.53	2.88	2.40	0.71	**0.00**
Distance to nest box	4.30	2.13	1.96	0.92	**0.00**