LOCALIZED HABITAT USE BY HUMBOLDT'S FLYING SQUIRRELS AND DUSKY-FOOTED WOODRATS IN NORTHERN CALIFORNIA

By

Tessaliz Quiles Delgado

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife - Master of Science

2021

ABSTRACT

LOCALIZED HABITAT USE BY HUMBOLDT'S FLYING SQUIRRELS AND DUSKY-FOOTED WOODRATS IN NORTHERN CALIFORNIA

By

Tessaliz Quiles Delgado

Primary prey for the protected subspecies California spotted owls (Strix occidentalis occidentalis) include dusky-footed woodrats (Neotoma fuscipes) (DFW) and Humboldt's flying squirrels (Glaucomys oregonensis) (HFSQ). The goal of my thesis is to describe fine-scale habitat use of DFW and HFSQ in industrially-managed timberlands in the Sierra Nevada Mountains of California. From 2018 to 2019, I live trapped and tagged 12 HFSQ and 31 DFW. From this sample, I fit five DFW and two HFSQ with radio transmitters (VHF) to assess finescale habitat use. I focused trapping on forest patches with mature and decadent trees, which are common habitat features associated with HFSQ and DFW occurrence. In Chapter One, I describe factors affecting trapping success of DFW and HFSQ. I used trapping success as an index of habitat use by prey, where higher trapping success equated to greater localized use by target species. I found a positive correlation between trap nights and capture probability for HFSQ. For DFW, I found capture probability positively correlated with trap nights and precipitation. In Chapter Two, I describe localized habitat features associated with HFSQ and DFW radio telemetry locations. I compared forest vegetation structure and composition in the immediate vicinity (within 5 m) of daytime locations used by HFSQ and DFW to more distal (>35m) vegetation conditions to determine if micro-forest structures corresponded to HFSQ and DFW use. I found species – level differences in percent ground and basal area where dusky-footed woodrats used areas with significantly more forest litter and shrub cover while Humboldt's flying squirrels used sites with larger diameter trees.

Copyright by TESSALIZ QUILES DELGADO 2021

I would like to dedicate through my education thank you for the supp	. My parents Mrs. Ter	resa Delgado Mora	les and Mr. Edward	pported me Quiles Rivera

ACKNOWLEDGEMENTS

Funding for this research was provided by Sierra Pacific Industries. I express gratitude to my advisor, Mark Rey for the endless guidance, support, and encouragement during this study. Thank you to my committee members Drs. Gary Roloff and Michael Walters for their time, guidance, support, and involvement throughout my research. I am grateful for the help and advice from the biologists and staff of the Stirling District, Sierra Pacific Industries, Chico CA; Matthew A. Reno, Kevin Roberts, and Brian Dotters. An additional thank you for my research assistant Alison Mego for trapping and sampling assistance. A special thank you to Sierra Pacific Industries for hiring me as a wildlife technician before and during my research for their generosity, and for always believing in me. I also appreciate the support of the California Forest Foundation and the College of Agriculture and Natural Resources and Graduate School at Michigan State University during my academic program.

TABLE OF CONTENTS

LIST OF TABLES	vii
LIST OF FIGURES	ix
INTRODUCTION	1
STUDY AREA	3
APPENDIX	5
LITERATURE CITED	7
CHAPTER 1: Capture probability and occurrence of Humboldt's flying squirrels	
and dusky-footed woodrats in the Sierra Nevada Mountains of California	12
1.1 Introduction	
1.2 Methods	14
1.2.1 Data Collection	14
1.2.2 Data Analysis.	16
1.3 Results.	16
1.4 Discussion	18
APPENDIX	21
LITERATURE CITED	34
CHAPTER 2: Localized habitat use by Humboldt's flying squirrels and	
dusky-footed woodrats in the Sierra Nevada Mountains of California	40
2.1 Introduction.	
2.2 Methods	43
2.2.1 Live trapping and telemetry	43
2.2.2 Vegetation Sampling	
2.2.3 Data Analysis.	
2.3 Results.	
2.4 Discussion.	
APPENDIX.	
LITERATURE CITED.	
Conclusion	62
LITERATURE CITED.	65

LIST OF TABLES

Table 1.1. Species, elevation range of captures, trap type (T = Tomahawk (Model 202), S = Sherman (Model LFA)), total captures, and number of trapping grids where species was caught on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 2019.
Table 1.2. Candidate models for estimating nightly capture probability of Humboldt's flying squirrels based on trap nights, average daily maximum temperatures (High Temp), and average daily precipitation (Precipitation), Sierra Nevada mountains, northern California, 2018 - 2019. AIC = Akaike's Information Criterion (AIC), Δ AIC = difference in AIC value from top-ranked model, AIC _{WT} = model weight, and AIC _C = the information score of the model for small sample sizes
Table 1.3. Mixed effects regression model coefficient estimates (standard error), and 95% confidence intervals (UCI, Upper Confidence interval, LCI lower confidence interval) for estimating nightly capture probability of Humboldt flying squirrels, Sierra Nevada Mountains, northern California 2018 - 2019.
Table 1.4. Candidate models for estimating nightly capture probability of dusky-footed woodrats based on trap nights, average daily maximum temperatures (Temperature), average daily precipitation (Precipitation), and bait type (PB = peanut butter, TOM = truffle oil, and VE = vanilla extract) in the Sierra Nevada mountains, northern California, 2018 to 2019. AIC = akaike's information criterion (AIC), Δ AIC = difference in AIC value from top-ranked model, AIC _{WT} = model weight, and AIC _C = the information score of the model for small sample sizes.
Table 1.5. Mixed effects regression model coefficient estimates (standard errors) based on trap nights, average daily maximum temperatures (Temperature), average daily precipitation (Precipitation), and bait type (PB = peanut butter, TOM = truffle oil, and VE = vanilla extract), and 95% confidence intervals (UCI, Upper Confidence Interval, LCI Lower Confidence Interval) for estimating nightly capture probability of dusky-footed woodrats, Sierra Nevada Mountains, northern California 2018 - 2019.
Table 2.1. Mean (standard error) of alive tree counts by species, plot position (proximate [0-5 m], intermediate [10-20 m], and distal [25-35 m]), and multivariate analysis of variance test in localized areas used by dusky-footed woodrat and Humboldt's from 2018 to 2019 in the Sierra Nevada Mountains, California
Table 2.2. Multivariance analysis of variance test comparing alive tree counts among tree species by dusky-footed woodrat and Humboldt's flying squirrel in northern California, USA54

Table 2.3. Mean, standard error, and multivariate analysis of variance significance test for
localized habitat covariates stratified by plot position from 2018 to 2019 in the Sierra Nevada
Mountains, California55
Table 2.4. Mean, standard error, and multivariate analysis of variance significance test localized habitat covariates in sites used by Humboldt's flying squirrel (HFQS) and dusky-footed woodra (DFWR) from 2018 to 2019 in the Sierra Nevada Mountains, California

LIST OF FIGURES

Figure 1.0. Trapping sites for Humboldt's flying squirrels and dusky-footed woodrats from 2018 to 2019 in the Sierra Nevada mountains, California, USA
Figure 1.1. Grid trapping arrangement for small mammals (20 x 40 m) in the Sierra Nevada Mountains, northern California, 2018 -2019
Figure 1.2. Percentage of functional Tomahawk traps placed on trees at breast height on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018-201923
Figure 1.3. Percentage of functional Tomahawk traps placed on the ground on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 201924
Figure 1.4. Percentage of functional Sherman ground traps placed on the ground on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 -201925
Figure 1.5. Total of species captures on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018-2019
Figure 1.6. Capture probability for Humboldt's flying squirrels in relation to trapping nights in the sierra Nevada Mountains, northern California, 2018-201927
Figure 1.7. Capture probability for dusky-footed woodrat in relation to precipitation in the Sierra Nevada Mountains, northern California, 2018 – 2019
Figure 1.8. Captures by trap location in the Sierra Nevada Mountains, northern California, 2018 to 2019. DFWR = dusky-footed woodrat; HFSQ = Humboldt's flying squirrel
Figure 2.1. Plot arrangement used to collect vegetation and forest structure data for each relocation of radio-tagged dusky-footed woodrats and Humboldt's flying squirrels from 2018 to 2019 in the Sierra Nevada Mountains, California
Figure 2.2. Alive tree counts by tree species and plot position (proximal [0-5 m], intermediate [10-20 m], and distal [25-35 m] for sites used by Humboldt's flying squirrel (HFSQ) and dusky-footed woodrat (DFWR) from 2018 to 2019 in the sierra Nevada Mountains California
Figure 2.3. Tree diameter at breast height (dbh) by plot position (proximate [0-5 m], and distal [25-35 m]) for sites used by Humboldt's flying squirrel (HFSQ) and dusky-footed woodrat (DFWR) from 2018 to 2019 in the Sierra Nevada Mountains

INTRODUCTION

Spotted owls (*Strix occidentalis*) are a conservation symbol in North America and include three subspecies: northern spotted owl (NSO; *S. o. caurina*), California spotted owl (CSO; *S. o. occidentalis*), and Mexican spotted owl (*S. o. lucida*) (Verner et al. 1992, Wan et al. 2018). Northern spotted owls occupy areas from the eastern Cascade Range of Washington to northwestern California, California spotted owl occurs from the western Sierra Mountains and southern to central coastal California, and the Mexican spotted owl spans northern Mexico, Arizona, New Mexico, western Texas, southern Utah and southwestern Colorado (Verner et al. 1992, Chutter et al. 2004). Most subpopulations have declined for decades due to habitat loss and fragmentation from logging, wildfires, and more recently by invasion from barred owls (*S. varia*) (Forsman et al. 1996, 2001, Seamans et al. 1999, Franklin et al. 2004, Anthony et al. 2006, Blakesley et al. 2010, Conner et al. 2013, Dugger et al. 2016, Davis et al. 2016, Wan et al. 2018).

Spotted owls occur in a variety of habitat types, but tend to more consistently occupy high density mature and old growth forests. Spotted owls select these forests for foraging, roosting, and nesting (Zabel et al.1995, Franklin et al. 2000, Wan et al. 2019), although some use of younger second growth forests and forest edges has been documented (Zabel et al. 2003, Irwin et al. 2012). One reason spotted owls disproportionately depend on mature and old-growth forest structure is because these areas often support higher prey abundance (Carey et al. 1992, Zabel et al. 1995).

Primary prey of CSO include dusky-footed woodrats (*Neotoma fuscipes*) and northern flying squirrels (Weathers et al. 2001). Prey also include mice (*Peromyscus spp.*), voles (*Microtus spp.*), broad-footed moles (*Scapanus latimanus*), and shrews (*Sorex spp.*) (Marshall 1942, Munton et al. 2002). Nest success and number of fledglings for CSO positively correlate

with prey abundance (Ward et al. 1998, Rosenberg et al. 2003), and diet analyses of NSO and CSO in northern California indicate that focal prey changes across an elevation gradient (Sierra Pacific Industries, unpublished data). Prey biomass in 488 pellets collected at NSO and CSO nest sites in northern California and southern Oregon were dominated (89% of biomass) by northern flying squirrels at higher elevations (> 1,829 m), whereas at lower elevations (762 m - 1828 m) prey biomass was dominated (93% of biomass) by dusky-footed woodrats. Woodrats and flying squirrels are of special conservation concern because of their importance to NSO and CSO diets, and because population declines have been documented in portions of dusky-footed woodrat and northern flying squirrel ranges (Loeb et al. 2001, Matocq 2002).

Northern flying squirrels are a small (30 cm long and ~ 139 g), nocturnal, arboreal rodent inhabiting forests throughout much of northern and western North America (Austin et al. 1990, Jacques et al. 2017). Flying squirrels use tree cavities, mistletoe (*Viscum album*) clumps, and leaf nests for dens, and appear to select older forest structures in mixed conifer and red fir (*A.magnifica*) forests (Rosenberg 1990, Meyer et al. 2007). According to Cowan (1936)₃ two types of flying squirrel dens exist: cavities in trees, and nests on tree branches and boles. Even though nesting sites and food may be more abundant in old forests, these factors do not appear to limit flying squirrel densities in second growth forests (Rosenberg 1990). Dusky-footed woodrats are generally a solitary, semi-territorial rodent that consume leaves, fruits, and nuts of woody plants (Innes et al. 2009). Woodrats inhabit a wide variety of habitats, including chaparral, juniper (*Juniperus occidentali*) woodlands, streamside thickets, and deciduous or mixed forests with well-developed undergrowth (Carey et al.1992, Innes et al. 2007). Woodrats build, maintain, and defend stick structures that are used for nesting, denning, and food storage.

A basic premise of NSO and CSO conservation is to ensure adequate prey for spotted owl survival and reproduction. Given that woodrats and flying squirrels are important prey for CSO, and that these species positively respond to forest structures that can be retained and created in managed forest landscapes (Wilson and Forsman 2013, Tempel et al. 2014), quantifying the importance of these localized habitat features informs land management. The goal of my project was to describe and understand habitat use of flying squirrels and dusky-footed woodrats in the Sierra Nevada Mountains of California. In Chapter 1, I evaluated factors related to trapping success of dusky-footed woodrats, flying squirrels and *Peromyscus* spp. Live trapping is frequently used to characterize small mammal communities (Hoffmann et al. 2010) and has proven effective at capturing spotted owl prey species (Rosenberg and Anthony 1992, Sakai and Noon 1997, Jacques et al. 2017). In Chapter 2, I used radiotelemetry and localized vegetation measurements to compare microsites used by woodrats and flying squirrels to proximate (i.e., within 35 m) vegetation conditions. Results of this work will help inform forest management prescriptions aimed at providing prey for CSO.

STUDY AREA

My study area included forests owned and managed by Sierra Pacific Industries (SPI) in the northern Sierra Nevada and southern Cascade Mountain Ranges of northern California, USA (Figure 1.0). Elevations range from 424 to 2,400 m above sea level and the climate is Mediterranean, with the majority (>85%) of precipitation occurring in late fall and winter as snow (0.05 m to 0.1178 m) and rain (0.762 m; Kauffman 2003, Meyer and Safford 2013). Forests are classified as mixed conifer, with six dominant tree species: ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Douglas fir (*Pseudotsuga menziesii*), and California black oak (*Quercus*)

kelloggii) (Eyre 1980, Beaty and Taylor 2002). Tanoak (*Notholithocarpus densiflorus*) and canyon live oak (*Quercus chrysolepis*) also form dense patches in some locations (Griffin and Critchfield 1972).

The northern Sierra Nevada and southern Cascade Mountain ranges have diverse vegetation, topography, and climate that provide a variety of values and uses to society. Human influence on this landscape has a long history, dating back thousands of years to Native Americans, to more current effects of gold miners, ranchers, loggers, farmers, and recreationists (Helms and Tappeiner 1996, Riegel et al. 2016). Current dominant human impacts include forest management and wildfires. Forest management in this region focuses on sustainable harvesting of conifers including ponderosa pine, Jeffrey pine (*Pinus jeffreyi*), and white fir (Laudenslayer and Darr 1990). Most recently (i.e., since the late 1990s) forestry objectives expanded to include sustaining multiple ecosystem values, including protection of spotted owls and other wildlife species (Helms and Tappeneiner 1996).

APPENDIX

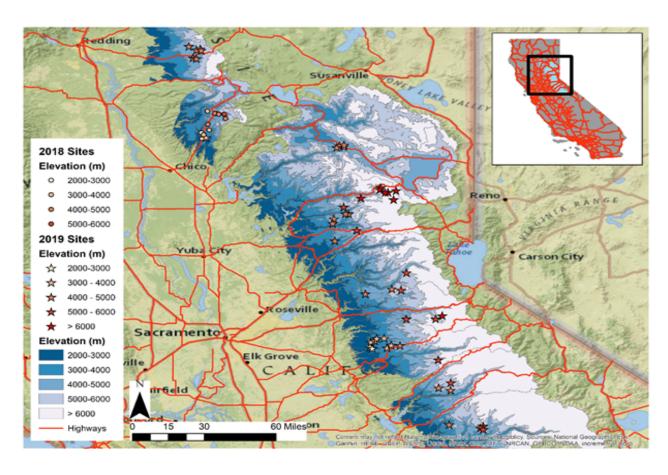


Figure 1.0. Trapping sites for Humboldt's flying squirrels and dusky-footed woodrats from 2018 to 2019 in the Sierra Nevada Mountains, California, USA.

LITERATURE CITED

LITERATURE CITED

- Anthony, R. G., Forsman, E. D., Franklin, A. B., Anderson, D. R., Burnham, K. P., White, G. C., Sovern, S. G. (2006). Status and Trends in Demography of northern Spotted Owls, 1985–2003. *Wildlife Monographs*, 163, 1–48.
- Austin, K., Fies, M., Jacobs, J., Murdock, N., Stihler, C., & Weigl, P. (1990). Appalachian northern Flying Squirrels (*Glaucomys sabrinus fuscus*) (*Glaucomys sabrinus coloratus*) Recovery Plan. *Annapolis Field Office U. S. Fish and Wildlife Service Annapolis, Maryland*, 1-62.
- Beaty, R. M., & Taylor, A. H. (2002). Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. *Journal of Biogeography*, 28 (8), 955-966.
- Blakesley, J. A., Seamans, M. E., Conner, M. M., Franklin, A. B., White, G. C., Gutiérrez, R. J., McDonald, T. L. (2010). Population Dynamics of Spotted Owls in the Sierra Nevada, California. *Wildlife Monographs*, 174(1), 1–36.
- Carey, A. B., Horton, S. P., & Biswell, B. L. (1992). Northern spotted owls: Influence of prey base and landscape character. *Ecological Monographs* 62(2), 223-250.
- Davis, R. J., Ohmann, J. L., Kennedy, R. E., Cohen, W. B., Gregory, M. J., Yang, Z., & Spies, T. A. (2016). Northwest Forest Plan—the first 20 years (1994-2013): status and trends of late-successional and old-growth forests. Gen. Tech. Rep. PNW-GTR-911. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 1-112.
- Dugger, K. M., Forsman, E. D., Franklin, A. B., Davis, R. J., White, G. C., Schwarz, C. J.,
 Burhham, K.P., Nichols, J.D., Hines, J.E., Yackiluc, C.B., Doherty P.F. Jr., Bailey, L.,
 Clark, D.A., Ackers S.H., Andrews. L.S., Augustine, B., Biswell, B.L, Blaskesley, J.,
 Carlson, P.C., Clement, M.J., Diller, L.V., Glenn, E.M., Green, A., Gremel, S.A., Herter,
 D.R., Higley, J.M., Hobson, J., Horn, R.B., Huyvaert, K.P., McCafferty, C., McDonald,
 T., McDonnel, K., Olson, G.S., Reid, J.A., Rockweit J., Ruiz, V., Saenz, J., Sovern, S. G.
 (2016). The effects of habitat, climate, and Barred Owls on long-term demography of
 Northern Spotted Owls. Condor, 118(1), 57–116.
- Eyre, F. H. (1980). Forest Cover Types of the United States and Canada. *Society of American Foresters, Washington, DC,* 1-148.
- Forsman, E. D., DeStefano, S., Raphael, M. G., and Gutiérrez, R. J. (1996). Demography of the northernspotted owl. *Studies in Avian Biology*, 17, 1–122.

- Forsman, E. D., Otto, I. A., Sovern, S. G., Taylor, M., Hays, D. W., Allen, H., Roberts, S.L. Seaman, D. E. (2001). Spatial and temporal variation in diets of Spotted Owls in Washington. *Journal of Raptor Research*, 35(2), 141–150.
- Franklin, A. B., Anderson, D. R., Gutiérrez, R. J., & Burnham, K. P. (2000). Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs*, 70(4), 539–590.
- Franklin, A. B., Gutiérrez, R. J., Nichols, J. D., Seamans, M. E., White, G. C., Zimmerman, G. (2004). Population dynamics of the California spotted owl (*Strix occidentalis occidentalis*): A meta-analysis. *Ornithological Monographs*, 54, 1–54.
- Griffin, J. R., & Critchfield, W. B. (1972). The distribution of forest trees in California. Res. Paper PSW-RP-82. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, 82, 1–124.
- Helms, J.A., & Tappeiner, J.C. (1996). Silviculture in the Sierra. In Sierra Nevada ecosystem project final report to congress status of the Sierra Nevada. Assessment and scientific basis for management options. *Center for water and wildland resources*, 2, 439-476.
- Hoffmann, A., Decher, J., Rovero, F., Schaer, J., Voigt, C., & Wibbelt, G. (2010). Field Methods and Techniques for Monitoring Mammals. Manual on field recording techniques and protocols for All Taxa Biodiversity Inventories and Monitoring. *The Belgian development cooperative*, 482-529.
- Innes, R. J., Van Vuren, D. H., Kelt, D. A., Johnson, M. L., Wilson, J. A., & Stine, P. A. (2007). Habitat associations of dusky-footed woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. *Journal of Mammalogy*, 88(6), 1523–1531.
- Innes, R. J., Van Vuren, D. H., Kelt, D. A., Wilson, J. A., & Johnson, M. L. (2009). Spatial organization of dusky-footed woodrats (*Neotoma fuscipes*). *Journal of Mammalogy*, 90(4), 811–818.
- Irwin, L. L., Rock, D. F., & Rock, S. C. (2012). Habitat selection by northern spotted owls in mixed-coniferous forests. *Journal of Wildlife Management*, 76(1), 200–213.
- Jacques, C. N., Zweep, J. S., Jenkins, S. E., & Klaver, R. W. (2017). Home range use and survival of southern flying squirrels in fragmented forest landscapes. *Journal of Mammalogy*, 98(5), 1479–1488.
- Kauffman, E. (2003). Atlas of the Biodiversity of California. Climate and Topography, 12–15.
- Laudenslayer, W. F., & Darr, H. H. (1990). Historical effects of logging on forests of the Cascade and Sierra Nevada ranges of California. Transactions of the Western Section of the Wildlife Society. *The Wildlife Society*, 12–23.

- Loeb, S. C., Chapman, G. L., & Ridley, T. R. (2001). Sampling small mammals in Southeastern forests: The importance of trapping in trees. *Proceedings of the Southeastern Association of Fish and Wildlife Agencies*, 53, 415-424.
- Marshall, J. T. (1942). Food and Habitat of the Spotted Owl. The Condor, 44(2), 66–67.
- Matocq, M. D. (2002). Phylogeographical structure and regional history of the dusky-footed woodrat, *Neotoma fuscipes*. *Molecular Ecology*, 11(2), 229-42.
- Meyer, M. P. N., Malcolm, P., & Douglas, A. K. (2007). Nest trees of northern flying squirrels in Yosemite National Park, California. *The Southwestern Naturalist*, 52(1), 157–161.
- Meyer, M., & Safford, H. (2013). A summary of current trends and probable future trends in climate and climate driven process in the Sierra National Forest and neighboring Sierra Nevada California. *Trends in Climate Change*, 1-16.
- Munton, T. E., Johnson, K. D., Steger, G. N., & Eberlein, G. P. (2002). Diets of California Spotted Owls in the Sierra National Forest. *USDA Forest Service General Technical Report*, 99-106.
- Riegel, G. M., Miller R. F., Skinner, C. N., & Smith, S. E. (2016). Northeastern plateaus bioregions. *University of California Press*, 225-263.
- Rosenberg, D. K. (1990). Characteristics of northern flying squirrels and Townsend's chipmunk populations in second and old growth forests. *Oregon State University*, 5-156.
- Rosenberg, D. K., & Anthony, R. G. (1992). Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology*, 161-166.
- Rosenberg, D. K., Swindle, K. A., & Anthony, R. G. (2003). Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology*, 81(10), 1715-1725.
- Sakai, H. F., & Noon, B. R. (1997). Between-habitat movement of dusky-footed woodrats and vulnerability to predation. *The Journal of Wildlife Management*, 61(2), 343-350.
- Seamans, M. E., Gutiérrez, R. J., May, C. A., & Perry, M. Z. (1999). Demography of two Mexican spotted owl populations. *Conservation Biology*. 13, 744–754.
- Tempel, D. J., Gutiérrez, R. J., Whitmore, S. A., Reetz, M. J., Stoelting, R. E., Berigan, W. J., & Peery, M. Z. (2014). Effects of forest management on California spotted owls: Implications for reducing wildfire risk in fire-prone forests. *Ecological Applications*, 24(8), 2089-2106.

- Verner, J., Mckelvey, K., Noon, B., Gutierrez, R. J., Gordon, I., Thomas B, W. (1992). "Habitat relations of the California spotted owl," in The California spotted owl: A technical assessment. USDA Forest Service Gen Tech Rep PSW-GTR-I33. Albany, CA: *Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture*, 1-285.
- Wan, H. Y., Cushman, S. A., & Ganey, J. L. (2019). Recent and projected future wildfire trends across the ranges of three spotted owl subspecies under climate change. *Frontiers in Ecology and Evolution*, 7, 1–12.
- Wan, H. Y., Ganey, J. L., Vojta, C. D., & Cushman, S. A. (2018). Managing emerging threats to spotted owls. *Journal of Wildlife Management*, 82(4), 682-697.
- Ward, J. P., Gutiérrez, R. J., & Noon, B. R. (1998). Habitat selection by northern spotted owls: The consequences of prey selection and distribution. *Condor*, 100, 79-82.
- Weathers, W. W., Hodum, P. J., & Blakesley, J. A. (2001). Thermal ecology and ecological energetics of California Spotted Owls. *Condor*.
- Wilson, T. M., & Forsman, E. D. (2013). Thinning effects on spotted owl prey and other forest-dwelling small mammals. In *USDA Forest Service General Technical Report PNW-GTR*, 79-90.
- Zabel, C. J., Dunk, J. R., Stauffer, H. B., Roberts, L. M., Zabel, C. J., Dunk, J. R., & Wright, A. (2003). Northern spotted owl habitat models for research and management application in California (USA). *Ecological Applications*, 13(4), 1027–1040.
- Zabel, C. J., McKelvey, K., & Ward, J. P. (1995). Influence of primary prey on home-range size and habitat-use patterns of northern spotted owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology*, 73(3), 433–439.

CHAPTER 1:

Capture probability and occurrence of Humboldt's flying squirrels and dusky-footed woodrats in the Sierra Nevada Mountains of California

1.1 Introduction

Predator populations directly respond to availability of prey (Carey et al. 1992, Hamer et al. 2001, Wiens et al. 2014, Keane 2017), and availability is dictated by prey life history, abundance, distribution, and habitat associations (Newton 1979, Peery 2000, Rosenberg et al. 2003). Northern spotted owls (NSO) tend to occupy areas containing old forest structures because prey is abundant and accessible (Carey et al. 1992, Ward et al. 1998). Selection of older forest structure by NSO is also related to greater nest availability, and protection from predators (Ward et al. 1998). Forest management reduces old forest structures (Bond et al. 2009, Liira et al. 2011), but opportunities to retain and create old forest elements in support of NSO prey abundance and accessibility can be integrated into forest management prescriptions (Orrock et al. 2000, Innes et al. 2007, Sollman et al. 2015).

Although prey is critical to NSO population viability (Lamberson et al. 1992), robust estimates of prey abundance are often difficult to acquire. A common technique used to assess home range use, seasonal movements, survival, and habitat use is to capture and track animals using radio transmitter tags (Sikes 2016, Jacques et al. 2017, Weldy et al. 2019). Typically, animal capture success is low (<5%; White 1983), with capture probabilities affected by species being targeted, weather, season, type of trap or bait, and trap elements (e.g., size and shape), among others (Llewellyn 1950, Pearson and Ruggiero 2003, Barros et al. 2015). With sufficient captures and recaptures of marked individuals, live trapping can provide robust estimates of local density for species where individual identification is part of the experimental design (Kämmerle

et al. 2018). A critical assumption is that enough individuals can be caught and marked to adequately represent the population of interest (Powell and Gale 2015).

Most capture-based studies on small mammal communities rely on more than one type of trap to obtain species richness and abundance estimates (Santos et al. 2017). A variety of trap types, arrangements, trapping periods, and baits, are used to capture flying squirrels and woodrats (Bond et al. 2009, Ford et al. 2015, Diggins et al. 2016, Jacques et al. 2017). By using a combination of trap types, researchers can maximize detection probability and capture of small mammals (Harkins et al. 2019). In terms of trap arrangement, Pearson, and Ruggiero (2003) compared transect and grid trap designs for assessing small-mammal community composition and relative abundance and found that transects (2,459 captures) produce more captures than grids (1,852 captures), but grids tend to be more commonly used by the scientific community. For small mammal trapping in general, baits often include a combination of peanut butter, oats, raisins, molasses, and bird seed (Anthony 1925, Kumar et al. 2013). For flying squirrels, baits often include a combination of apple and a peanut butter-bacon grease mixture, strawberry jam, vanilla extract, mushrooms, cheese, almonds, and ground meat (Patric 1970, Weigl 1974, Jacques et al. 2017). Baits for dusky-footed woodrats include a mixture of peanut butter, molasses, raisins, and oats (Hooven 1959).

Given that prey accessibility is critical for NSO and CSO conservation, and that part of accessibility depends on prey abundance, the goal of this chapter was to better understand factors affecting trapping success of common CSO prey. I viewed trapping success as an index of prey use, where higher trapping success equates to greater localized use by the focal species. I explored various combinations of traps and trap placement, baits, pre-baiting, and weather variables to identify the most efficient combinations for trapping small mammals in support of

CSO prey assessments in northern California. I hypothesized that capture success would be higher in spring and late fall for flying squirrels, given that populations are lowest in spring, and litters are not produced until early summer (Weigl 2007, Selonen et al. 2020), coinciding with rainy periods and when flying squirrels are more active on the ground (Selonen et al. 2020). I also predicted higher captures in fall for woodrats due to increased activity associated with building up food storage for the winter months (Murphy 1952, Rainey 1955, Monty and Feldhamer, 2002). Furthermore, I predicted that flying squirrel capture success would be higher for traps attached to trees compared to the forest floor, whereas traps on the ground would capture more woodrats.

1.2 Methods

1.2.1 Data Collection

I used a digital elevation model and forest stand layer from SPI in ARCGIS (Esri Inc, 2021) to select forested patches for trapping based on where flying squirrels and woodrats were likely to occur. Forest patches selected for trapping flying squirrels primarily consisted of conifer-dominated and old forests (>100 years). These two forest attributes tend to provide tree cavities for nesting and shelter and are often associated with hypogenous fungi, an important dietary component for flying squirrels (Amaranthus et al. 1994, Carey 1995, Pyare and Longland, 2002, Trudeau et al. 2011). For woodrats I targeted juniper, chaparral, and oak woodland (thick understory) with an approximate stand density of 290 (trees/ha) (Plumb and Pillsbury 1986) and conifer forests, all of which are associated with woodrat nests (Carey et al. 1992, Innes et al. 2007).

I trapped small mammals during the summer (2018 and 2019) and fall (2018), using a combination of Sherman (Model LFA, 7.60 x 8.9 x 22.9 cm H.b. Sherman Traps, Inc.,

Tallahassee, FL) and Tomahawk (Model 202, 48.3 x 15.2 x 15. 2 cm; Tomahawk live Trap Company, Tomahawk, WI) live traps. In each forest patch, I deployed traps in an 800 m² grid with each trap separated by 10 m, resulting in 30 traps per grid (5 rows by 3 columns; Pearson and Ruggiero 2003, Figure 1.1). Trapped patches were distributed throughout different elevation bands to sample the prey gradient (i.e., woodrats at lower elevations, flying squirrels at higher elevations) observed in CSO pellets (Sierra Pacific Industries, Unpublished Data; Figure 1).

I varied trap types across sites, where some sites included a combination of Sherman and Tomahawk traps and others only received Sherman traps. At each trap node within the grid, I placed a live trap on the ground (Sherman) and attached another trap (Tomahawk) at breast height to the nearest tree for sites where I used combinations of both trap types. For sites with only Sherman traps, I placed all traps on the ground. I shaded traps at risk of exposure to direct sunlight (Carey et al. 1991, Gray et al. 2019), and baited traps with a dollop of 12 parts oat, 6 parts birdseed (wild bird seed), 2 parts raisins, 1-part peanut butter, 1- part molasses, 3 drops truffle oil and vanilla extract and included polyester fiber as bedding. I checked traps daily between sunrise and noon. Captured flying squirrels and woodrats were weighed and ear tagged (Monel #1, National Band and Tag Co., Newport NY). Animals were released at the trap location for potential recapture. Capture and handling of animals followed the California Department of Fish and Wildlife collection permit (SC-11963) and was reviewed by the Institutional Animal Care and Use Committee at Michigan State University (IACUC ID PROTO201800011).

1.2.2 Data Analysis

I developed candidate mixed logistic regression models that predicted likelihood of capturing a flying squirrel or woodrat from a trapping grid on a given night based on environmental and sampling covariates. Fixed effects in the model included daily snow amount (cm), daily maximum temperature (°C), daily precipitation (cm), type of bait, and trapping nights, with a grid identification number as a random effect. Weather variables were compiled from the online climate data base from the National Centers for Environmental Information by the National Oceanic and Atmospheric Administration (NOAA). I selected these environmental variables as they have been shown to affect small mammal behavior and hence capture success (Vickery and Bider 1981, Burnham and Anderson 2002, Steinhoff et al. 2012). After I identified the top-ranking and competing models using Akaike Information Criterion (AIC), I evaluated the parameter estimates from the top-ranking model and deemed parameters significant if the 95% confidence intervals (CI) of the parameter estimate did not overlap zero (McQuarrie et al. 1997, Kawakubo and Kubokawa 2014). All statistical analyses were conducted in R and I generated models using the glmer function in the lme4 package (R 4.0.2; Bates et al. 2015).

1.3 Results

I trapped 20 sites for 1-5 nights resulting in 13,028 potential trap nights. I used Tomahawk traps attached to trees and placed on the ground at 17 sites (12,000 potential trap nights) and only Sherman ground traps at 5 sites (1,028 potential trap nights). On average, I found that Tomahawk traps located in trees were functional 93% (SE = 2%, range = 67-100%) of the time (Figure 1.2), and Tomahawk traps on the ground were 94% (SE = 2%, range = 75 – 100%) functional (Figure 1.3). Ground Sherman traps were 81% (SE = 8%, range = 50-100%) functional on average (Figure 1.4). Empty but sprung traps, traps damaged by other wildlife

species (e.g., black bear (*Ursus americanus*), California grey fox (*Urocyon cinereoargenteus*), and Pacific fisher (*Pekania pennanti*)), and malfunctioning traps were counted as disabled traps. I captured dusky-footed woodrats in Tomahawk traps attached to trees, but the majority of were caught on the ground (Figure 1.8). Capture probabilities for both species appeared to increase after 4 nights of trapping, but this finding was inconclusive.

In total, I captured 10 small mammal species from 11 sites including: Allen's or shadow chipmunk (*Tamias senex*), dusky-footed woodrat (*Neotoma fuscipe*), Humboltdt's flying squirrels (*Glaucomys oregonensis*), brush mouse (*Peromyscus boylii*), golden-mantled ground squirrel (*Spermophilus lateralis*), Douglas squirrel (*Tamiasciurus douglasii*), western spotted skunk (*Spilogale gracilis*), deer mouse (*Peromyscus maniculatus*), California ground squirrel (*Otospermophilus beecheyi*), and western gray squirrel (*Sciurus griseus*) (Figure 1.5). Small mammals were captured at 11 of 20 sites, with dusky-footed woodrats captured at 5 sites and flying squirrels at 2 sites (Table 1.1). I had a 1.47% capture success rate for dusky-footed woodrats and Humboldt's flying squirrels based on functional trap nights.

The top-ranked model for flying squirrels only included trap nights (AIC_{wt} = 0.53; Table 1.2); as trap nights increased probability of capture increased (β = 0.580, 95% UCI = 0.77 and LCI = 0.50; Figure 1.3). In addition, I had a competing model (i.e., Δ AIC < 2.0) that included maximum temperatures and trap nights (AIC_{wt} of 0.26; Table 1.2); as maximum temperature (β ₁) and trap nights (β ₂) increased there was a tendency of higher probability of capture (β ₁ = -0.029, 95% UCI = 0.51 and LCI = 0.47; β ₂ = 0.567, UCI = 0.77 and LCI = 0.49; Table 1.3). The top-ranked model estimating the likelihood of capturing a dusky-footed woodrat at a trapping grid on a given night included only precipitation (AIC_{wt} of 0.87) with no other

competing models (Table 1.4). Capture probability increased with increasing precipitation (β = 3.98, 95% UCI = 1.00 and LCI = 0.882; Figure 1.7).

1.4 Discussion

I assessed factors affecting the trapping success of two important prey species of CSO. I found that dusky-footed woodrat capture probability was positively related to precipitation on the day of trapping. Hence, my study indicates that trapping studies on primary prey species of CSO benefit from longer trapping sessions that include precipitation events.

I found daily maximum temperatures and bait type were not significant predictors of capture success, but caution that the range of baits explored was limited to variations in the peanut butter base. Although I used different variations of bait ingredients (oat, birdseed, raisins, molasses, truffle oil and vanilla extract), the base was always peanut butter. Both Humboldt's flying squirrels and dusky-footed woodrats alter behavior to avoid high temperatures. For example, both species are active at night, when temperatures tend to be cooler. Daily maximum temperature tends to correspond to warmer nighttime temperatures, but this phenomenon is moderated by elevation (i.e., more rapid nighttime cooling at higher elevations). Thus, given the activity periods of Humboldt's flying squirrels and dusky-footed woodrats and tendency to occur at higher elevations (i.e., Humboldt's flying squirrels), it is not surprising that daily maximum temperature was a poor predictor of trap success.

Precipitation stimulates small mammal activity (Vickery and Bider 1981, Wróbel and Bogdziewicz 2015), making them more prone to capture. Coupled with lower temperatures, precipitation can stimulate small mammal foraging more intensively during active seasons to balance energetic demands and temperature maintenance (Wróbel and Bogdziewicz 2015).

Based on my results I found a correlation between precipitation and dusky-footed woodrat captures but this pattern was not consistent for Humboldt's flying squirrel.

Though dusky-footed woodrat was the second most frequently captured species in this study (only after shadow chipmunks), capture rates for dusky-footed woodrats and Humboldt's flying squirrels were low overall. Additionally, most Humboldt's flying squirrels were captured from a small number of grids, reinforcing the importance of accounting for grid as a random effect in my models and suggesting that flying squirrels are patchily distributed and that occupied patches are uncommon on industrial forests in northern California. Low capture and recapture rates from a small subset of grids limited model inference. Furthermore, wildfires delayed trapping in some locations resulting in lower than anticipated sample sizes. Nonetheless, my study offers insight into trapping primary prey of CSO in northern California. Although I failed to find a bait effect on capture probability, some recommend using grease for Humboldt's flying squirrel (Weigl 1974, Jacques et al. 2017); a bait option that I did not test. I further recommend that Tomahawk (Model 202) traps be used, and that sites are trapped with both ground and tree based (1-2 m off the ground) traps to promote trapping success. Dusky-footed woodrats were more frequently captured in ground traps, whereas tree-based traps captured more flying squirrels (Risch and Brady 1996, Jacques et al. 2017). Ultimately, using the most efficient trapping methodology will produce capture probabilities that better represent animal abundance and perhaps habitat quality.

Multiple factors affect capture probability and subsequent use of this metric as an index to animal abundance or habitat quality. These factors can be divided into observation (i.e., sampling, like trapping methodology) and ecological factors, like target animal population size, food availability and abundance, weather, elevation, and vegetation characteristics (e.g., ground

cover, tree, canopy; Morris 2016, Santos et al. 2017). Oftentimes, managers are most concerned with ecological factors, and view observation factors as nuisance variables that should be optimized or accounted for in analyses. My study offers insights into some observational factors affecting dusky-footed woodrat and Humboldt's flying squirrel capture success. Although capture probability can serve as an index to population performance, by itself it is best viewed as an index of habitat use unless combined with other, more representative population variables like fecundity or mortality. Further studies should consider grid size, type of bait, and trapping locations to have a higher capture probability.

APPENDIX

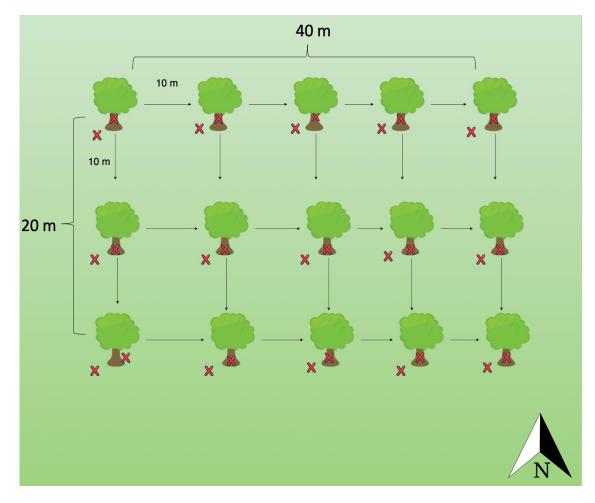


Figure 1.1. Grid trapping arrangement for small mammals (20 x 40 m) in the Sierra Nevada Mountains, northern California, 2018 - 2019.

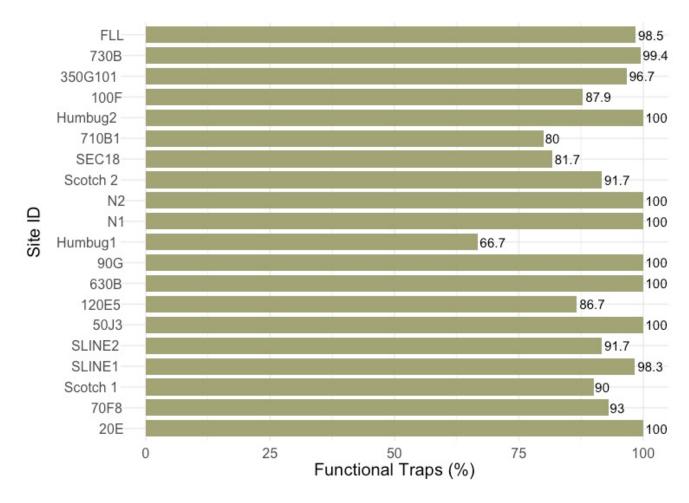


Figure 1.2. Percentage of functional Tomahawk traps placed on trees at breast height on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 2019.

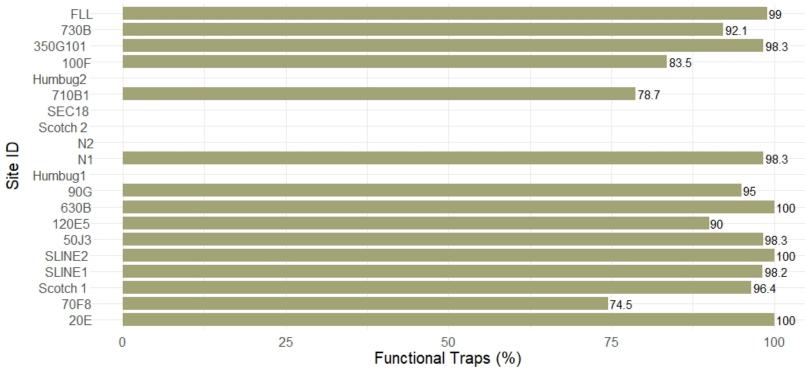


Figure 1.3. Percentage of functional Tomahawk traps placed on the ground on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 2019.

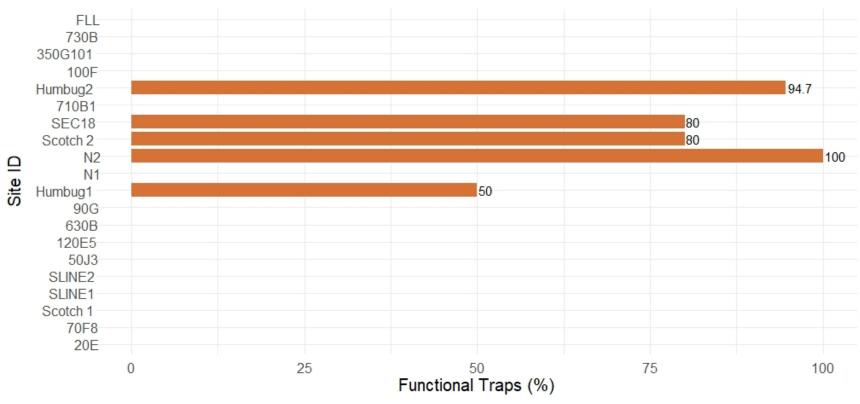


Figure 1.4. Percentage of functional Sherman ground traps placed on the ground on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 2019.

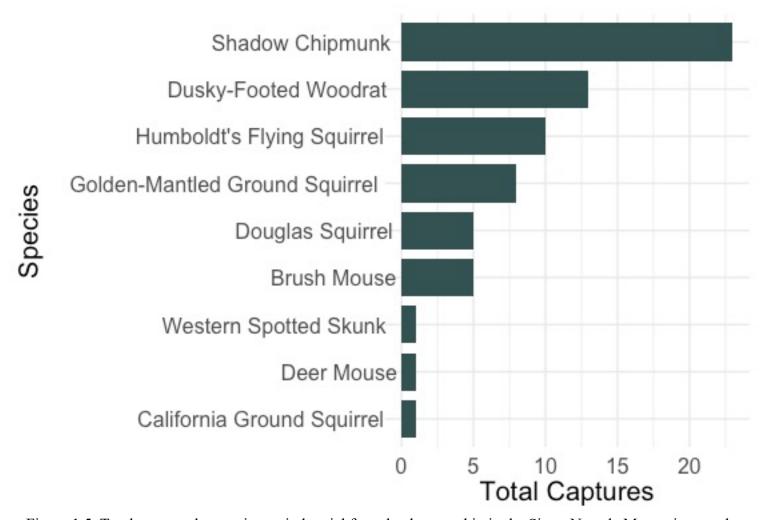


Figure 1.5. Total captures by species on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 2019.

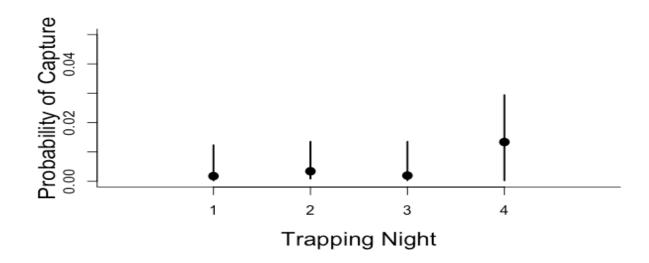


Figure 1.6. Capture probability for Humboldt's flying squirrels in relation to trapping nights in the Sierra Nevada Mountains, northern California, 2018-2019.

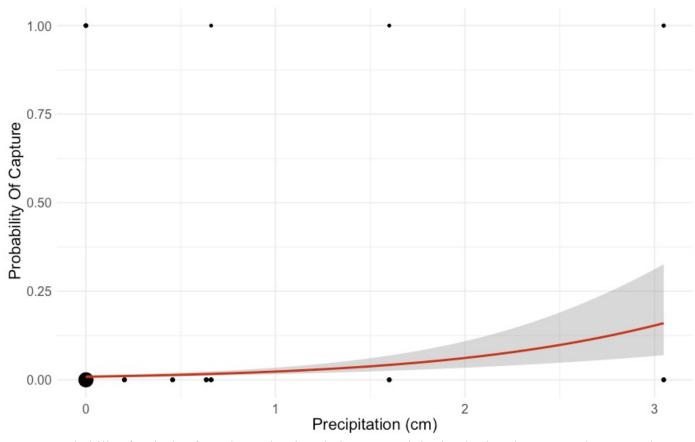


Figure 1.7. Capture probability for dusky-footed woodrat in relation to precipitation in the Sierra Nevada Mountains, northern California, 2018 – 2019.

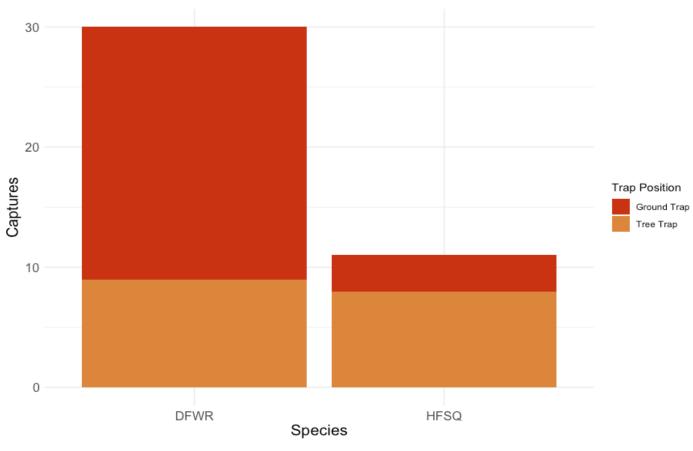


Figure 1.8. Captures by trap location in the Sierra Nevada Mountains, northern California, 2018 to 2019. DFWR = dusky-footed woodrat; HFSQ = Humboldt's flying squirrel.

Table 1.1. Species, elevation range of captures, trap type (T = Tomahawk (Model 202), S = Sherman (Model LFA)), total captures, and number of trapping grids where species was caught on industrial forestland ownership in the Sierra Nevada Mountains, northern California, 2018 - 2019.

	Elevation Range (m)			Number of
Species		Trap Type	Captures	Grids
Shadow chipmunk (Tamias senex)	1,163 – 1,524	T	42	4
Dusky-footed woodrat (Neotoma fuscipes)	969 - 1,314	T, S	31	5
Brush mouse (Peromyscus boylii)	893 - 1,313	T, S	12	5
Humboldt's flying squirrel (Glaucomys oregonensis)	1,224 – 1,318	T	11	2
Golden-mantled ground squirrel (Spermophilus lateralis)	1,524	T	11	2
Douglas squirrel (Tamiasciurus douglasii)	1,164 – 1,481	T	7	2
Western spotted skunk (Spilogale gracilis)	1,312	T	1	1
Deer mouse (Peromyscus maniculatus)	1,934	T, S	1	3
California ground squirrel (Otospermophilus beecheyi)	1,164	T	1	1
Western grey squirrel (Sciurus griseus)	1,524	T	1	1

Table 1.2. Candidate models for estimating nightly capture probability of Humboldt's flying squirrels based on trap nights, average daily maximum temperatures (High Temp), and average daily precipitation (Precipitation), Sierra Nevada Mountains, northern California, 2018 - 2019. AIC = Akaike's Information Criterion (AIC), ΔAIC = difference in AIC value from top-ranked model, AIC_{wt} = model weight, and AICc = the information score of the model for small sample sizes.

Model	AIC	ΔAIC	$AIC_{wt} \\$	AICc
1. Trap Nights	116.5	0.0	0.53	116.6
2. High Temp + Trap Nights	118.0	1.5	0.26	117.9
3. High Temp	119.4	2.9	0.13	119.4
4. Precipitation	120.3	3.8	0.08	120.3

Table 1.3. Mixed effects regression model coefficient estimates (standard error), and 95% confidence intervals (UCI, Upper confidence Interval, LCI Lower Confidence Interval) for estimating nightly capture probability of Humboldt flying squirrels, Sierra Nevada Mountains, northern California 2018 - 2019.

Model	Estimate (Std Error)	95% LCI	95%UCI
1. Trap Nights	0.580 (0.309)	0.50	0.77
2. High Temp	-0.029 (0.041)	0.47	0.51
Trap Nights	0.567 (0.316)	0.49	0.77
3. High Temp	-0.037 (0.401)	0.47	0.51

Table 1.4. Candidate models for estimating nightly capture probability of dusky-footed woodrats based on trap nights, average daily maximum temperatures (Temperature), average daily precipitation (Precipitation), and bait type (PB = peanut butter, TOM = truffle oil, and VE = vanilla extract) in the Sierra Nevada Mountains, northern California, 2018 to 2019. AIC = Akaike's Information Criterion (AIC), ΔAIC = difference in AIC value from top-ranked model, AIC_{wt} = model weight, and AICc = the information score of the model for small sample sizes.

	Model	AIC	ΔAIC	AIC_{wt}	AICc
1.	Precipitation	245.17	0.00	0.87	245.18
2.	Trapping nights +	249.0	3.85	0.13	249.05
	Precipitation +				
	Temperature				
3.	Trap Nights +	267.90	22.73	0.00	267.95
	Temperature +				
	Bait PB +				
	Bait PBTOM +				
	Bait PBVE				

Table 1.5. Mixed effects regression model coefficient estimates (standard errors) based on trap nights, average daily maximum temperatures (Temperature), average daily precipitation (Precipitation), and bait type (PB = peanut butter, TOM = truffle oil, and VE = vanilla extract), and 95% confidence intervals (UCI, Upper confidence Interval, LCI Lower Confidence Interval) for estimating nightly capture probability of dusky-footed woodrats, Sierra Nevada Mountains, northern California 2018 - 2019.

	Model	Estimate (Std Error)	95% LCI	95% UCI
1.	Precipitation	3.98 (1.003)	0.88	1.00
2.	Trap Nights +	-0.001 (0.249)	0.38	0.62
	Precipitation +	3.885 (1.057)	0.86	1.00
	Temperature	-0.011 (0.032)	0.48	0.51
3.	Trap Nights +	0.226 (0.214)	0.45	0.66
	Temperature +	-0.053 (0.027)	0.47	0.49
	Bait BP +	24.762 (33.940)	0.01	1.00
	Bait PBTOM +	22.848 (33.990)	0.00	1.00
	Bait PBVE	21.429 (33.944)	0.00	1.00

- Amaranthus, M., Trappe, J., Bednar, L., & Arthur, D. (1994). Hypogeous fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. *Canadian journal of forest research*, 24, 2157-2165.
- Anthony, H. (1925). The capture and preservation of small mammals for study (2nd ed). New York. *American Museum of Natural History*, 1-60.
- Barros, C. S., Püttker, T., Pinotti, B. T., & Pardini, R. (2015). Determinants of capture-recapture success: An evaluation of trapping methods to estimate population and community parameters for Atlantic forest small mammals. *Zoologia*, 32(5), 334–344.
- Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67 (1), 1-48.
- Bond, M. L., Lee, D. E., Siegel, R. B., & Ward, J. P. (2009). Habitat Use and Selection by California Spotted Owls in a Postfire Landscape. *Journal of Wildlife Management*, 73(7), 1116–11.
- Burnham, K. P., & Anderson, D. R. (2002). Model Selection and Multimodel Inference. A practical Information-Theoretic Approach (2nd ed.). New York. *Springer-Verlag*, 1-512.
- Carey, A. B., Biswell, B. L., & Witt, J. W. (1991). Methods for Measuring Populations of Arboreal Rodents. *Biologist*, 1-22.
- Carey, A. B., Horton, S. P., & Biswell, B. L. (1992). Northern spotted owls: Influence of prey base and landscape character. *Ecological Monographs*, 62 (2), 223-250.
- Carey, A. B. (1995). Sciurids in Pacific Northwest managed and old-growth forests. *Ecological Applications*, 5(3), 648–661.
- Diggins, C. A., Gilley, L. M., Kelly, C. A., & Ford, W. M. (2016). Comparison of survey techniques on detection of northern flying squirrels. *Wildlife Society Bulletin*, 40 (4), 654-662.
- Ford, W. M., Evans, A. M., Odom, R. H., Rodrigue, J. L., Kelly, C. A., Abaid, N., & Newcomb, D. (2015). Predictive habitat models derived from nest-box occupancy for the endangered Carolina northern flying squirrel in the southern Appalachians. *Endangered Species Research*, 67, 131-140.
- Gray, S. M., Roloff, G. J., Dennhardt, A. J., Dotters, B. P., & Engstrom, T. T. (2019). Within-Patch Structures Influence Small Mammal Abundance in Managed Forests of Northern California, USA. *Forest Science*, 65 (6), 796-804.

- Hamer, T. E., Hays, D. L., Senger, C. M., & Forsman, E. D. (2001). Diets of northern barred owls and northern spotted owls in an area of sympatry. *Journal of Raptor Research*, 35(3), 221–227.
- Harkins, K. M., Keinath, D., & Ben-David, M. (2019). It's a trap: Optimizing detection of rare small mammals. *PLOS ONE*, 14(3), 1–20.
- Hooven, E. F. (1959). Dusky-footed woodrat in young Douglas fir. *Oregon Forest Research Center*, 1–24.
- Innes, R. J., Van Vuren, D. H., Kelt, D. A., Johnson, M. L., Wilson, J. A., & Stine, P. A. (2007). Habitat associations of dusky-footed woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. *Journal of Mammalogy*, 88(6), 1523–1531.
- Jacques, C. N., Zweep, J. S., Jenkins, S. E., & Klaver, R. W. (2017). Home range use and survival of southern flying squirrels in fragmented forest landscapes. *Journal of Mammalogy*, 98(5), 1479-1488.
- Kämmerle, J. L., Corlatti, L., Harms, L., & Storch, I. (2018). Methods for assessing small-scale variation in the abundance of a generalist mesopredator. *PLOS One*, 13(11), 1-16.
- Kawakubo, Y., & Kubokawa, T. (2014). Modified conditional AIC in linear mixed models. *Journal of Multivariate Analysis*, 129, 44–56.
- Keane, J. J. (2017). Threats to the viability of California spotted owls. PSW-GTR-254: The California Spotted Owl: A Synthesis of Current Scientific Information, (chapter 5), 185–238.
- Kumar, A. V., Linzey, D. W., & Smith, C. R. (2013). Bait Preferences and Population Status of Small Mammals in Great Smoky Mountains National Park. *Journal of North Carolina Academy of Science*, 129 (2), 44-52.
- Lamberson, R. H., McKelvey, R., Noon, B. R., & Voss, C. (1992). A Dynamic Analysis of northern spotted owl viability in a fragmented forest landscape. *Conservation Biology*, 6(4), 505–512.
- Liira, J., Sepp, T., & Kohv, K. (2011). The ecology of tree regeneration in mature and old forests: Combined knowledge for sustainable forest management. *Journal of Forest Research*, 16, 184-1993.
- Llewellyn, L. M. (1950). Reduction of Mortality in Live-Trapping Mice. *The Journal of Wildlife Management*, 14(1), 84–85.
- McQuarrie, A., Shumway, R., & Tsai, C. L. (1997). The model selection criterion AICu. *Statistics and Probability Letters*, 34 (3), 285-292.

- Monty, A.M., & Feldhamer, G. A. (2002). Conservation Assessment for The Eastern Woodrat, (*Neotoma floridana*) and the Allegheny Woodrat (*Neotoma magister*). *USDA Forest Service*, 1–36.
- Morris, D. W. (2016). Ecological Scale and Habitat Use. *Ecology*, 68(2), 362–369.
- Murphy, M. F. (1952). Ecology and helminths of the osage wood rat, *Neotoma floridana* osagensis, including the description of *Longistriata neotoma* n. sp. (*Trichostrongylidae*). *American Midland Naturalist*, 48 (1), 204-218.
- Newton, I. (1979). Population ecology of raptors. T. & A.D. Poyser. Orrock, J. L., Pagels, J. F., Mcshea, W. J., & Harper, E. K. (2000). Predicting presence and abundance of a small mammal species: The effect of scale and resolution. *Ecological Applications*, 10(5), 1356–1366.
- Orrock, J. L., Pagels, J. F., McShea, W. J., & Harper, E. K. (2000). Predicting presence and abundance of a small mammal species: The effect of scale and resolution. *Ecological Applications*, 10(5), 1356-1366.
- Patric, E. F. (1970). Bait Preference of Small Mammals. *Journal of Mammalogy*, 51(1), 179–182.
- Pearson, D. E., & Ruggiero, L. F. (2003). Transect versus grid trapping arrangements for sampling small-mammal communities. *Wildlife Society Bulletin*, 31(2), 454-459.
- Peery, M. Z. (2000). Factors affecting interspecies variation in home-range size of raptors. *The Auk*, 117(2), 511–517.
- Plumb, T. R., & Pillsbury, N. H. (1986). Origins and Adaptations of California Hardwoods. In Multiple-Use Management of California's Hardwood Resources (pp. 1–22). San Luis Obispo, California: *Pacific Southwest Forest and Range Experiment Station*.
- Powell, L. A., & Gale, G. A. (2015). Estimation of Parameters for Animal Populations: A Primer for the Rest of Us. Nebraska USA: *Caught Napping Publications Lincoln*, 48 (2), 1-239.
- Pyare, S., & Longland, W. S. (2002). Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Canadian Journal of Forest Research*, 32(6), 1016–1024.
- Rainey, D. (1955). Eastern woodrat, *Neotoma floridana*: life history and ecology. *University of Kansas Publications, Museum of Natural History*, 8(10), 535–646.
- Risch, T. S., & Brady, M. J. (1996). Trap height and capture success of arboreal small mammals: Evidence from southern flying squirrels (*Glaucomys volans*). *American Midland Naturalist*, 136(2), 346–351.

- Rosenberg, D. K., Swindle, K. A., & Anthony, R. G. (2003). Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology*, 81, 1715-1725.
- Santos, M. J., Smith, A. B., Thorne, J. H., & Moritz, C. (2017). The relative influence of change in habitat and climate on elevation range limits in small mammals in Yosemite National Park, California, U.S.A. *Climate Change Responses*, 4(7), 1-12.
- Selonen, V., Hongisto, K., Hänninen, M., Turkia, T., & Korpimäki, E. (2020). Weather and biotic interactions as determinants of seasonal shifts in abundance measured through nest-box occupancy in the Siberian flying squirrel. *Scientific Reports*, 10, 1-12.
- Sikes, R. S. (2016). 2016 Guidelines of the American Society of Mammologists for the use of wild mammals in research and education. *Journal of Mammalogy*, 97(3), 663–688.
- Sollmann, R., White, A. M., Gardner, B., & Manley, P. N. (2015). Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations. *Mammalian Biology*, 80(4), 247–254.
- Steinhoff, S. G., Van Deelen, T. R., Martin, K. J., MacFarland, D. M., & Witkowski, K. R. (2012). Nesting patterns of southern flying squirrels in managed northern hardwoods. *Journal of Mammalogy*, 93(2), 532-539.
- Trudeau, C., Imbeau, L., Drapeau, P., & Mazerolle, M. J. (2011). Site occupancy and cavity use by the northern flying squirrel in the boreal forest. *Journal of Wildlife Management*, 75(7), 1646–1656.
- Vickery, W. L., & Bider, J. R. (1981). The Influence of Weather on Rodent Activity. *Journal of Mammalogy*, 62(1), 140-145.
- Ward, J. P., Gutiérrez, R. J., & Noon, B. R. (1998). Habitat selection by northern spotted owls: The consequences of prey selection and distribution. *The Condor*, 100 (1), 79-92.
- Weigl, P. D. (1974). Study of the northern flying Squirrel, *Glaucomys sabrinus*, by temperature telemetry. *The American Midland Naturalist*, 92(2), 482–486.
- Weigl, P. D. (2007). The northern flying squirrel (*Glaucomys sabrinus*): A conservation challenge. *Journal of Mammalogy*, 88(4), 897–907.
- Weldy, M. J., Wilson, T. M., Lesmeister, D. B., & Epps, C. W. (2019). Effects of trapping effort and trap placement on estimating abundance of Humboldt's flying squirrels. *PeerJ*, 1-20.
- White, G. C. (1983). Numerical Estimation of Survival Rates from Band-Recovery and Biotelemetry Data. *The Journal of Wildlife Management*, 47(3), 716-728.

- Wiens, J. D., Anthony, R. G., & Forsman, E. D. (2014). Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. *Wildlife Monographs*, (185), 1–50.
- Wróbel, A., & Bogdziewicz, M. (2015). It is raining mice and voles: which weather conditions influence the activity of *Apodemus flavicollis* and *Myodes glareolus? European Journal of Wildlife Research*, 61(3), 475–478.

CHAPTER 2:

Localized habitat use by Humboldt's flying squirrels and dusky-footed woodrats in the Sierra Nevada Mountains of California

2.1 Introduction

Prey dynamics are critical for understanding the ecology, demography, and viability of spotted owls (*Strix occidentalis*) (Rosenberg et al. 2003). In addition to prey for spotted owls, small mammals functionally affect forest ecosystems through direct impacts on vegetation, soils, and seed dispersal (Coppeto et al. 2006). Some small mammal species (e.g., flying squirrels [*Glaucomys sabrinus*] and woodrats [*Neotoma* spp.] are primary spotted owl prey and the distribution and abundance of these species is affected by localized vegetation structure (DeWalt et al. 2003, Thompson and Gese 2013), patch-level forest structure (Bonham 2016), and landscape variation (Thompson and Gese 2013).

Forest vegetation provides important resources for nesting, foraging, and protection for small mammals (Barnett et al. 1978, DeWalt et al. 2003). Historically, fire and logging have caused considerable variability in forest structure with corresponding impacts on wildlife in the Sierra Nevada mountains of California (Laundenslayer and Fargo 1990, Roberts and North 2012). Additionally, consistent with forest management regulations and practices in northwest California, decades of clear-cutting on private industrial forest lands resulted in a landscape mosaic dominated by early- to mid-rotation forests, with small, interspersed patches of young and old forest (Sakai and Noon 1997). This pattern of forest management often results in abrupt edges between patches of varying ages. The relatively small area immediately impacted by forest management (i.e., cuts are generally <10 ha) undoubtedly affects where woodrats and flying squirrels occur.

The primary prey of California spotted owls (S. o. occidentalis) are dusky-footed woodrats (*N. fuscipes*) and northern flying squirrels (Weathers et al. 2001). Northern flying squirrels are a small, nocturnal, arboreal mammal that inhabit forests throughout much of northern and western North America (Jacques et al. 2017). Northern flying squirrels serve as an older forest indicator species, and are considered a keystone species in forest ecosystems, particularly where dissemination of ectomycorrhizal fungi spores and establishment of mycorrhizal relationships facilitate tree health (Carey 2000, Meyer et al. 2005a Holloway and Malcolm 2007). Flying squirrels use tree cavities and stick or leaf nests and dens, selecting older forest structures in mixed conifer and red fir (Abies. magnifica) forests (Pyare and Longland 2002, Meyer et al. 2005b Smith and Smith 2007), where they consume hypogeous fungi, truffles, and mushrooms. Dusky-footed woodrats are generally a solitary, semi territorial herbivore that eats leaves, fruits, and nuts of woody plants (Lynch et al. 1994). They inhabit a wide variety of habitats, including chaparral, juniper (Juniperus spp.) woodlands, streamside thickets, and deciduous or mixed forests with well-developed undergrowth (Williams et al. 1992, Innes et al. 2007). Dusky-footed woodrats also play an important role in community dynamics, being important prey for many avian and mammalian predators (Sakai and Noon 1997, Innes et al. 2007) and woodrat houses positively affect species richness of small mammals, reptiles, amphibians, and invertebrates (Carey 2000, Cranford 1977, Innes et al. 2007).

Diverse forest macrohabitat characteristics (e.g., logs and soil structure) influence the spatial distribution and pattern of habitat use by many species (Dueser and Shugart 1978, Pyare and Longland 2002). Dead and mature trees are used by birds and mammals for roosting, foraging, and perching (Gibbs et al. 1999, DeWalt et al. 2003). Downed coarse-woody debris provides resources for shelter, nesting, and foraging for many amphibians, reptiles, and small

mammals (DeWalt et al. 2003, Fauteux et al. 2012). For flying squirrels, downed wood and understory cover provide refuge from predators and substrate for food (Meyer et al. 2007). Moreover, presence of decayed logs, coarse woody debris, or perennial creeks may serve as indicators of truffles, a primary food source of flying squirrels (Pyare and Longland 2002, Meyer et al. 2007). Flying squirrels are often impacted by timber harvest given their use of mature (coniferous trees, more than 60 year of age) (Holloway and Smith 2011) trees and snags for food, travel, and nesting (Holloway and Malcolm 2007). Dusky-footed woodrats also rely on forest understory and downed wood to provide key structural elements for denning and food storage (Coppeto et al. 2006) as well as materials for constructing houses (Innes et al. 2007). Changes to these forest structures and microhabitat characteristics through forest management can affect the abundance and distribution of these species.

To reduce potential impacts, forest managers can incorporate prescriptions for protecting wildlife habitat elements during forest management operations, but guidelines on what to protect, where to protect it, and for what specific species are often lacking. For primary prey of California spotted owl (CSO), these prescriptions might include retention of localized canopy cover, snags, and large trees (Carey 2000, Innes et al. 2007, Meyer et al. 2007). Given that industrial forest ownerships in the western US are substantially altered landscapes (Barbour et al. 2002, Coppeto et al. 2006), effective wildlife management strategies should be based in part on understanding localized vegetation composition and structure for focal wildlife species. Here, I examine localized habitat features used by Humboldt's flying squirrels (*G. oregonensis*) and dusky-footed woodrats in industrial forest landscapes of northern California. My objective was to compare forest vegetation structure and composition at locations where flying squirrels and woodrats occurred in comparison to proximate random locations, with the intent of identifying

localized conditions or structures that could potentially be the focus of conservation prescriptions during forest management.

2.2 Methods

2.2.1 Live trapping and telemetry

I trapped small mammals during the summer (2018 and 2019) and fall (2018), using a combination of Sherman (Model LFA, 7.60 x 8.9 x 22.9 cm H.b. Sherman Traps, Inc., Tallahassee, FL) and Tomahawk (Model 202, 48.3 x 15.2 x 15. 2 cm; Tomahawk live Trap Company, Tomahawk, WI) live traps. I deployed traps in an 800 m² grid with each trap separated by 10 m, resulting in 30 traps per grid. I selected grid placement in forest patches thought to support woodrats or flying squirrels (i.e., older forest conditions, riparian zones), and distributed throughout different elevation bands.

I varied trap combinations across sites, where some sites included a combination of Sherman and Tomahawk traps and others only received Sherman traps. I shaded traps at risk of exposure to direct sunlight (Sikes and Gannon 2011), and baited traps with a dollop of 12 parts oat, 6 parts birdseed (wild bird seed), 2 parts raisins, 1-part peanut butter, 1-part molasses, 3 drops truffle oil and vanilla extract, and included polyester fiber as bedding. I checked traps daily between sunrise and noon.

Captured flying squirrels and woodrats were transferred to a handling cone that covered the head but allowed access to the back and ears. Field crews ear tagged each individual and affixed a radio transmitter (TR-2 and TR-3 transmitters, ATS (Advance Telemetry Systems) if the individual was >80g (i.e., transmitter weight <5% of animal weight) with glue (super glue gel). We glued transmitters to the skin between the shoulder blades after shaving the fur. Crews

used a hand-held radio receiver (model R1000, Communication Specialists Inc., Orange County, CA, USA) and 3-element Yagi antenna to locate each tagged animal three times per week during the day and collected habitat information at these diurnal resting locations. Animals were released at the location where they were captured. Capture and handling of animals followed the California Department of Fish and Wildlife collection permit (SC-11963) and was reviewed by the Institutional Animal Care and Use Committee at Michigan State University (IACUC ID PROTO201800011).

2.2.2 Vegetation Sampling

At each telemetered animal location, I sampled ground cover along a 35 m transect oriented in each cardinal direction (Figure 2.1). Canopy cover and percent ground cover (categories: ferns, woody debris, litter, herbs, grass, ever green shrubs and deciduous shrubs, and logs) were collected at each telemetered animal location and in circular plots located every 5 m along transects (Figure 2.1). In this study I distinguished woody debris and logs by certain characteristics. Logs were classified as a bole or piece of wood in contact with the ground. Woody debris was categorized by small twigs, branches, or whole stems in contact with the ground. The difference between these two categories was their dimensions. The minimum size criteria for logs are > 10.0 inches at the large end and ≥ 6 feet length. Ground debris less than this size criteria was counted as woody debris. I binned ground cover percentages in each category from 0-5; where 0 = absent, 1 = 1 to 5%, 2 = 6 to 15%, 3 = 16 to 35%, 4 = 36 to 55%, and 5 = 56 to 100%. For a subset of the locations (i.e., A1 and C1; Figure 2.1) I measured basal area of trees using a 10-factor prism. I measured diameter at breast height (cm), height (using a clinometer; m), and recorded tree species used by animals and whether trees were living or dead (i.e., snag). I also collected height of the understory stems, alive stem counts, and dead stem

counts every 5 meters along the transect. Canopy cover at each used tree, and nest/rest (den) was estimated with a spherical densiometer (Nudds 1973, Meyer et al. 2005b).

2.2.3 Data Analysis

I summarized vegetation data by plot position; proximate (center-A1; 0-5 m), intermediate (A2-B1; 10-20 m), and distal (B2-C2; 25-35 m) to test for localized differences in ground cover and trees (Figure 2.1). I calculated averages for each ground cover category by plot position and used boxplots to detect differences across the 35 m distance (Figure 2.1); some ground cover categories were omitted due to low prevalence in plots. I also used boxplots to compare the distribution of ground cover covariates, average tree height, alive and dead stem count, and canopy cover among plot positions. In addition, I conducted two multivariate analysis of variance (MANOVA) tests to find differences in vegetation and ground cover by comparing means at each plot position. First, I calculated and compared the mean and variation of each covariate by localized habitat areas (proximate, intermediate, and distal) used by both duskyfooted woodrats and Humboldt's flying squirrels (i.e., pooled). For the second MANOVA analysis, I compared means and variance across forest structure and ground cover covariates independently across plots used by each respective species. I used MANOVA over traditional analysis of variance given interest in analyzing more than one continuous response variable (Hand and Taylor 1987, Krzanowski 1988). My goal was to identify differences among plot positions using multiple continuous dependent variables (i.e., ground cover, tree counts by species, canopy cover, and alive and dead stem count). To conform with MANOVA assumptions, data were randomly sampled, and measurements of dependent variables were collected as interval (continuous).

2.3 Results

In the summer (2018 and 2019) and fall (2018), I identified 5 sites used by flying squirrels and 5 for dusky-footed woodrats, with a total of 3 flying squirrels and 6 woodrats radio tagged across the 10 sites. At occupied sites, I documented black oak (Ouercus velutina), incense cedar (Calocedrus decurrens), ponderosa pine (Pinus ponderosa), white fir (Abies concolor), Douglas fir (Pseudotsugs menziesii), bigleaf maple (Acer macrophyllum), and tanoak (Notholithocarpus densiflorus) (Figure 2.2). Among tree species, only incense cedar significantly differed among proximate, intermediate, and distal distances (Table 2.1). I found higher counts of incense cedar in intermediate and distal areas than in proximate areas used by dusky-footed woodrats and Humboldt's flying squirrels combined (Table 2.2). For individual small mammal species, I found that areas used by dusky-footed woodrats had significantly more tanoak and white fir than areas used by flying squirrels (Table 2.2). My MANOVA analyses comparing tree height, alive and dead stem counts, and ground cover did not reveal significant differences by plot position in localized areas used by dusky-footed woodrats and Humboldt's flying squirrels, although there was marginal evidence that deciduous shrub cover was higher in proximate and intermediate locations (Table 2.3). I found species-level differences in ground cover where dusky-footed woodrats used localized areas with significantly greater forest litter and evergreen and deciduous shrub cover than Humboldt's flying squirrels (Table 2.4).

For forest canopy, I did not find any differences by plot position or by species for woodrats and flying squirrels combined (Table 2.3). I also did not find any differences in tree diameter or height in comparing proximate and distal plots (Table 2.3). At the species-level, I found localized areas used by Humboldt's flying squirrel were comprised of trees with

significantly larger diameters than those used by dusky-footed woodrat, and marginal evidence for higher canopy cover and lower stem counts in areas used by flying squirrels (Table 2.4).

2.4 Discussion

In this chapter I examined localized habitat used by Humboldt's flying squirrels and dusky-footed woodrats in industrial forest landscapes of northern California. Most notably, I found species-level differences in percent ground cover and basal area around used sites, with dusky-footed woodrats using sites with higher evergreen and deciduous shrub cover as well as more forest litter, whereas Humboldt's flying squirrels used sites with larger diameter trees. I also noted greater live stem counts of tanoak and white fir in localized areas used by dusky-footed woodrats, while both species tended to use proximate areas with fewer incense cedar relative to intermediate and distal areas. Overall, my study highlights several species-level differences in localized habitat use by common spotted owl prey that can be accounted for during forest management.

Many researchers documented habitat preferences for dusky-footed woodrats and Humboldt's flying squirrels. Both species occupy old-growth forests and forests stands that include younger trees and managed stands (Rosenberg and Anthony 1992, Cranford 1977, Weigl 2007, Ritchie et al. 2009). Sakai and Noon (1997) found that woodrat use spanned different vegetation communities, ground cover, and forest types in northwestern California. Woodrats also persist in different canopy settings, but prefer mixed coniferous stands and areas featuring dense ground cover (Sakai and Noon 1997). Documented use of areas featuring dense shrub cover and forest litter in this study aligns with these findings. In general, dusky footed woodrats tend to use areas with more forest litter, not necessarily relating to plot position or woody debris (McComb 2003). Contrastingly, flying squirrels tend to prefer a variety of ground cover

conditions, such as wet ground, dead, and downed wood and organic substrates (Weigl 2007). These conditions often correspond with the presence of snags, tree cavities, mistletoe brooms, festoons of lichen and moss, and a diverse fungal community (Weigl 2007). Coarse woody debris is important for Humboldt's flying squirrels and dusky- footed woodrats; Humboldt's flying squirrels use the structure mostly for foraging and dusky footed woodrats for nesting, hiding, and as cache site (McComb 2003). In relation to these studies we didn't detect any significant value with coarse woody debris.

Humboldt's flying squirrels and dusky-footed woodrats have microhabitat associations that include, but are not limited to downed logs, shrubs, and downed woody debris (Cranford 1977, Weigl 2007). For dusky-footed woodrats, they have a strong association with downed logs. This may be due to the use of logs and dead wood as support material for building woodrat nests/ houses (Laudenslayer and Fargo 1999, Innes et al. 2007). For flying squirrels, understory shrub cover and downed logs can provide protective cover from aerial predators such as owls (Pyare and Longland 2002, Meyer et al. 2007). In addition, presence of coarse woody debris and litter may be an indicator of truffles, the primary food for Humboldt's flying squirrels. All these features are important for dusky-footed woodrats and flying squirrels, but in this study, I failed to detect significant associations between these small mammal species and downed wood.

Trees are important for the habitat of Humboldt's flying squirrels and dusky-footed woodrats, as they provide food (seeds, fruit, and inner bark) and shelter from aerial predators (Cranford 1977, Innes et al. 2007, Meyer et al. 2007, Weigl 2007). Some studies indicated differences in tree composition in areas used by flying squirrels and dusky-footed woodrats (Sakai and Noon 1993, Waters and Zabel 1995, Bakker and Hastings 2002, Meyer et al. 2005b Innes et al. 2007). In my study, I observed differences in tree species in localized areas used by

dusky-footed woodrats in comparison to Humboldt's flying squirrels. Sites used by woodrats tended to have a higher alive tree counts of tanoak. Previous research found that dusky-footed woodrats had a positive association with ground cover of tanoak, percent tanoak in the shrub and density of understory tanoak (Hamm et al. 2007). Though I did not observe use of individual tree species by Humboldt's flying squirrels, I did find use of sites with larger diameter trees in comparison to dusky-footed woodrats. This aligns with habitat preferences for this species, given that flying squirrels tend to select old-growth, mixed coniferous forests for nesting and resting areas with a preference for large diameter residual snags and mature trees (Meyer et al. 2005a).

There were several limitations to my study. First, I was unable to sample a larger number of sites and capture more individuals for radio-tagging due to wildfires. Second, the short duration of my study limited my ability to sample more sites and subsequently increase species captures. I recommend other researchers expand plot arrangements to cover a broader forest area and facilitate comparisons among species use, forest types, and elevation. In addition, I recommend that future studies consider using spotted owl nesting and resting core areas to assess overlap in habitat features selected by flying squirrels and dusky-footed woodrats. For future forest and wildlife management I recommended the retention of large diameter trees, evergreen and deciduous shrubs that show to be an important vegetation component for Humboldt's flying squirrel and dusky-footed woodrat. This will increase and maintain the habitat site inside the industrial forest.

APPENDIX

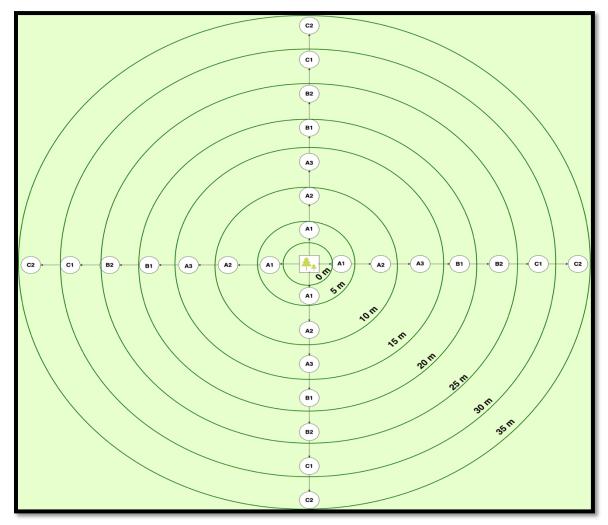


Figure 2.1. Plot arrangement used to collect vegetation and forest structure data for each relocation of radio-tagged dusky-footed woodrats and Humboldt's flying squirrels from 2018 to 2019 in the Sierra Nevada Mountains, California.

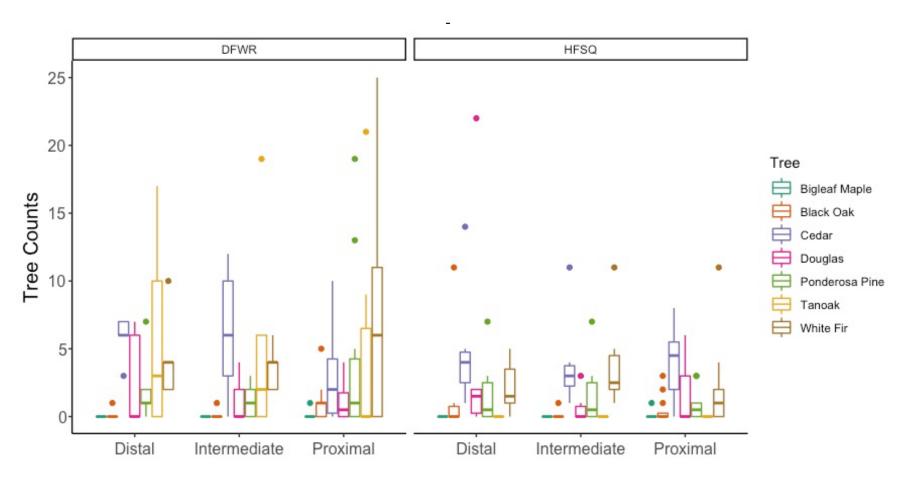


Figure 2.2. Alive tree counts by tree species and plot position (proximate [0-5 m], intermediate [10-20 m], and distal [25-35 m]) for sites used by Humboldt's flying squirrel (HFSQ) and dusky-footed woodrat (DFWR) from 2018 to 2019 in the Sierra Nevada Mountains, California.

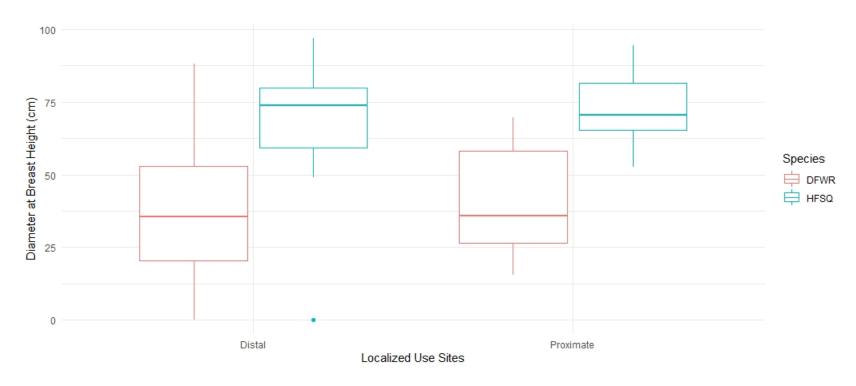


Figure 2.3. Tree diameter at breast height (dbh) by plot position (proximate [0-5 m], and distal [25-35 m]) for sites used by Humboldt's flying squirrel (HFSQ) and dusky-footed woodrat (DFWR) from 2018 to 2019 in the Sierra Nevada Mountains.

Table 2.1. Mean (standard error) of alive tree counts by species, plot position (proximate [0-5 m], intermediate [10-20 m], and distal [25-35 m]), and multivariate analysis of variance test in localized areas used by dusky-footed woodrat and Humboldt's from 2018 to 2019 in the Sierra Nevada Mountains, California.

Tree Species	Mean (SE)			P-value
	Proximate	Intermediate	Distal	
Tanoak (Notholithocarpus densiflorus)	1.00 (0.82)	2.55 (3.71)	2.73 (1.70)	0.68
White Fir (<i>Abies concolor</i>)	3.64 (2.19)	4.59 (2.51)	3.18 (0.83)	0.74
Ponderosa Pine (Pinus ponderosa)	0.64 (0.31)	2.77 (1.90)	2.00 (0.80)	0.30
Douglas Fir (Pseudotsuga menziesii)	0.27(0.19)	1.50 (0.89)	3.64 (1.98)	0.09
Black Oak (Quercus velutina)	0.73 (0.45)	0.50(0.36)	1.18 (0.99)	0.62
Incense Cedar (Calocedrus decurrens)	1.64 (0.62)	5.41 (1.59)	5.36 (1.05)	0.01
Bigleaf Maple (Acer macrophyllum)	0.00(0.00)	0.09(0.12)	0.00(0.00)	0.37

Table 2.2. Multivariate analysis of variance test comparing alive tree counts among tree species by dusky-footed woodrat and Humboldt's flying squirrel in northern California, USA.

Tree Species	Mean (SE)		P-value
	Dusky-footed woodrat	Humboldt's flying squirrel	
Tanoak (Notholithocarpus densiflorus)	4.85 (1.55)	0.00 (0.00)	< 0.01
White Fir (Abies concolor)	5.80 (1.46)	2.50 (0.62)	0.03
Ponderosa Pine (Pinus ponderosa)	2.90 (1.10)	1.33 (0.42)	0.16
Douglas Fir (Pseudotsuga menziesii)	1.45 (0.48)	1.96 (0.93)	0.65
Black Oak (Quercus velutina)	0.65 (0.26)	0.79 (0.47)	0.80
Incense Cedar (Calocedrus decurrens)	4.60 (0.86)	4.33 (0.68)	0.81
Bigleaf Maple (Acer macrophyllum)	0.05 (0.05)	0.04 (0.04)	0.90

Table 2.3. Mean, standard error, and multivariate analysis of variance significance test for localized habitat covariates stratified by plot position from 2018 to 2019 in the Sierra Nevada Mountains, California.

		P-value		
Covariate	Proximate	Intermediate	Distal	
Forest Metrics				
Height for stem count	6.39 (0.80)	7.92 (0.72)	6.42 (0.67)	0.27
(m)				
Alive Stem Count	4.36 (0.90)	4.36 (0.70)	2.93 (0.52)	0.32
Dead Stem Count	0.05 (0.19)	0.68(0.17)	0.34 (0.12)	0.38
Canopy Cover	81.56 (2.36)	77.89 (1.80)	78.09 (1.89)	0.51
Diameter (cm)	56.62 (43.40)	_	53.80 (4.45)	0.62
Tree Height (m)	31.4(0.99)	_	31.1(4.59)	0.95
Ground Cover				
Fern	1.595 (0.69)	2.52 (0.93)	2.99 (1.08)	0.71
Woody Debris	41.60 (4.31)	37.20 (2.84)	40.80 (2.79)	0.63
Litter	43.70 (4.40)	37.40 (2.84)	37.20 (2.83)	0.41
Herb	0.83 (0.28)	1.95 (0.85)	1.27 (0.59)	0.61
Evergreen Shrub	2.46 (0.80)	5.63 (1.56)	2.69 (0.91)	0.15
Deciduous Shrub	9.86 (2.27)	9.70 (1.65)	5.55 (1.09)	0.08
Log	11.00 (2.86)	8.31 (1.48)	12.03 (1.94)	0.28

Table 2.4. Mean, standard error, and multivariate analysis of variance significance test for localized habitat covariates in sites used by Humboldt's flying squirrel (HFQS) and dusky-footed woodrat (DFWR) from 2018 to 2019 in the Sierra Nevada Mountains,

	Camonia.		
Covariate	Mean (S	SE)	P-value
Forest Metrics	DFWR	HFSQ	
Height of stem count(m)	7.56(0.65)	6.30(0.57)	0.14
Alive Stem Count	4.85(0.83)	3.15(0.39)	0.05
Dead Stem Count	0.63(0.16)	0.44(0.11)	0.31
Canopy Cover	76.40(2.00)	80.44(1.29)	0.08
Diameter (cm)	39.50(3.48)	70.92(2.60)	< 0.01
Tree Height (m)	30.20(4.48)	32.30(1.40)	0.65
Ground Cover			
Fern	2.05(0.94)	2.96(0.78)	0.45
Woody Debris	41.80(2.76)	37.00(2.37)	0.18
Litter	42.70(2.83)	35.80(2.35)	0.03
Herb	0.93(0.54)	1.93(0.65)	0.25
Evergreen Shrub	7.36(1.61)	0.95(0.24)	< 0.01
Deciduous Shrub	11.40(1.70)	5.22(0.84)	< 0.01
Log	9.26(1.72)	11.40(1.49)	0.36

- Bakker, V. J., & Hastings, K. (2002). Den trees used by northern flying squirrels (*Glaucomys sabrinus*) in southeastern Alaska. Canadian Journal of Zoology, 80(9) 1623–1633.
- Barbour, M., Kelley, E., Maloney, P., Rizzo, D., Royce, E., & Fites-Kaufmann, J. (2002). Present and past old-growth forests of the Lake Tahoe Basin, Sierra Nevada, US. *Journal of Vegetation Science*, 13(4), 461–472.
- Barnett, J. L., How, R. A., & Humphreys, W. F. (1978). The use of habitat components by small mammals in eastern Australia. *Austral Ecology*, 3(3), 277–285.
- Bonham, C. H. (2016). Report of the Fish and Game Commission a Status review of the northern spotted owl (*Strix Occidentalis caurina*) in California. *State of California Department of Fish and Wildlife*, 118-200.
- Carey, A. B. (2000). Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. In R. L. Goldingay & J. S. Scheibe (Eds.), Biology of Gliding Mammals (pp. 45–61). *Filander Verlag*.
- Coppeto, S. A., Kelt, D. A., Van Vuren, D. H., Wilson, J. A., & Bigelow, S. (2006). Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. *Journal of Mammalogy*, 87(2), 402–413.
- Cranford, J. A. (1977). Home Range and Habitat Utilization by Neotoma fuscipes as Determined by Radiotelemetry. *Journal of Mammalogy*, 58(2), 165–172.
- DeWalt, S. J., Maliakal, S. K., & Denslow, J. S. (2003). Changes in vegetation structure and composition along a tropical forest chrono sequence: Implications for wildlife. *Forest Ecology and Management*, 182(1–3), 139–151.
- Dueser, R. D., & Shugart, H. H. (1978). Microhabitats in a Forest-Floor Small Mammal Fauna. *Ecology*, 59(1), 89–98.
- Fauteux, D., Imbeau, L., Drapeau, P., & Mazerolle, M. J. (2012). Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. *Forest Ecology and Management*, 266(15), 194–205.
- Gibbs, J. P., Hunter, M. L., & Melvin, S. M. (1999). Snag availability and communities of cavity nesting birds in tropical versus temperate forests. *NCASI Technical Bulletin*, 25(2), 236–241.
- Hand, D. J., & Taylor, C. C. (1987) Multivariate analysis of variance and repeated Measures: A practical approach for behavioral scientists. *Chapman and Hall*, 1-304.

- Hamm, K. A., Diller, L. V., & Hughes, K. D. (2007). Abundance and Habitat Associations of Dusky-Footed Woodrats in Managed Redwood and Douglas-fir Forests. In Proceedings of the redwood region forest science symposium: What does the future hold? Albany, CA: Forest service. (235-237).
- Holloway, G. L., & Malcolm, J. R. (2007). Northern and southern flying squirrel use of space within home ranges in central Ontario. *Forest Ecology and Management*, 242(2–3), 747–755.
- Holloway, G. L., & Smith, W. P. (2011). A meta-analysis of forest age and structure effects on northern flying squirrel densities. *The Journal of Wildlife Management*, 75(3), 668-674.
- Innes, R. J., Van Vuren, D. H., Kelt, D. A., Johnson, M. L., Wilson, J. A., & Stine, P. A. (2007). Habitat associations of dusky-footed woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. *Journal of Mammalogy*, 88(6), 1523–1531.
- Jacques, C. N., Zweep, J. S., Scheihing, M. E., Rechkemmer, W. T., Jenkins, S. E., Klaver, R. W., & Dubay, S. A. (2017). Influence of trap modifications and environmental predictors on capture success of southern flying squirrels. *Wildlife Society Bulletin*, 41(2), 313–321.
- Krzanowski, W. J. (1988). Principles of Multivariate Analysis; A User's Perspective. *Oxford Science publications*, *3*,200-563.
- Laudenslayer, W. F., & Fargo, R. (1999). Are house counts reliable estimators of dusky-footed woodrat population size? Transactions of the Western Section of the Wildlife Society, 35, 71–75.
- Lynch, M. F., Fesnock, A. L., & Vuren, D. V. (1994). Home range and social structure of the dusky-footed woodrat (*Neotoma fuscipes*). *Northwestern Naturalist*, 75(2), 73-75.
- McComb, W. C. (2003). Ecology of coarse woody debris and its role as habitat for mammals. In mammal community dynamics: management and conservation in the coniferous forests of western North America. *Cambridge University Press*, 374-404.
- Meyer, M. D., North, M. P., & Kelt, D. A. (2005a). Fungi in the diets of northern flying squirrels and lodgepole chipmunks in the Sierra Nevada. *Canadian Journal of Zoology*, 83(12), 1581–1589.
- Meyer, M. D., Kelt, D. A., & North, M. P. (2005b). Nest trees of northern flying squirrels in the Sierra Nevada. *Journal of Mammalogy*, 86(2), 275–280.
- Meyer, M. D., Kelt, D. A., & North, M. P. (2007). Microhabitat associations of northern flying squirrels in burned and thinned forest stands of the Sierra Nevada. *American Midland Naturalist*, 157(1), 202–211.

- Nudds, T. D. (1973). Quantifying the Vegetative Structure of Wildlife Cover. *Wildlife Society Bulletin*, 5(3), 1973–2006.
- Pyare, S., & Longland, W. S. (2002). Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. *Canadian Journal of Forest Research*, 32(6), 1016–1024.
- Ritchie, L. E., Betts, M. G., Forbes, G., & Vernes, K. (2009). Effects of landscape composition and configuration on northern flying squirrels in a forest mosaic. *Forest Ecology and Management*, 257(9), 1920–1929.
- Roberts, S. L., & North, M. P. (2012). California Spotted Owls. In Managing Sierra Nevada forests (General Te, pp. 225–263). Albany, California: Pacific Southwest Research Station.
- Rosenberg, D. K., & Anthony, R. G. (1992). Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. *Canadian Journal of Zoology*, 70(1), 161–166.
- Rosenberg, D. K., Swindle, K. A., & Anthony, R. G. (2003). Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology*, 81(10), 1715–1725.
- Sakai, H. F., & Noon, B. R. (1993). Dusky-Footed woodrat abundance in Different-Aged forests in Northwestern California. *The Journal of Wildlife Management*, 57(2), 373-375.
- Sakai, H. F., & Noon, B. R. (1997). Between-Habitat Movement of Dusky-Footed Woodrats and Vulnerability to Predation. *The Journal of Wildlife Management*, 61(2), 343–350.
- Sikes, R. S., & Gannon, W. L. (2011). Guidelines of the American Society of Mammologists for the use of wild mammals in research. *Journal of Mammalogy*, 92(1), 235-253.
- Smith, W. P., & Smith, W. P. (2007). Ecology of Glaucomys sabrinus: Habitat, Demography, and Community Relations. *Journal of Mammalogy*, 88(4), 862–881.
- Thompson, C. M., & Gese, E. M. (2013). Influence of vegetation structure on the small mammal community in a shortgrass prairie ecosystem. *Acta Theriol*, 58(1), 55–61.
- Waters, J. R., & Zabel, C. J. (1995). Northern flying Squirrel densities in fir forests of northeastern California. *The Journal of Wildlife Management*, 59(4), 858.
- Weathers, W. W., Hodum, P. J., & Blakesley, J. A. (2001). Thermal ecology and ecological energetics of California Spotted Owls. *Condor*, 103(4), 678–690.
- Weigl, P. D. (2007). The northern flying squirrel (*Glaucomys sabrinus*): A conservation challenge. *Journal of Mammalogy*, 88(4), 897–907.

Williams, D. F., Verner, J., Sakai, H. F., & Waters, J. R. (1992). General biology of major prey species of the California spotted owl. The California spotted owl: A technical assessment of its current status. *U.S Department of Agriculture* 207–221.

Conclusion

My research aimed to identify factors affecting trapping success and examine habitat features used by primary prey of the California spotted owl. In each Chapter, I discussed important components for the conservation and management of dusky-footed woodrats and Humboldt's flying squirrels.

In Chapter 1, I evaluated factors related to trapping success of dusky-footed woodrats and Humboldt's flying squirrels. I used mixed logistic regression models to predict the likelihood of capturing a dusky-footed woodrat or Humboldt's flying squirrel based on environmental and sampling covariates. I found that trap night and environmental conditions, particularly precipitation, play an important role in trapping success. Several studies have reported relatively low numbers of individuals captured during the first night a stand is sampled relative to the subsequent trapping sessions (Carey 2000, Lehmkul et al. 2006, Holloway et al. 2012). In addition, some studies reported fewer captures during the first week of the study in relation with the second week, especially if the location is structurally complex forests (Weldy et al. 2019). Based on the result of chapter one, we can see that there is a correlation between the trap night and trapping success. In addition, weather conditions, particularly precipitation, can affect capture probability by affecting the activity of the animal (e.g the change of encountering a trap). Many studies have shown a positive relationship between temperature and small mammals' activity (Vickery and Bider 1987, Viera et al. 2010, Barros et al. 2015). Part of the results suggest a positive correlation between precipitation and trapping success for dusky-footed woodrats.

In Chapter 2, I explored forest composition and structure differences between duskyfooted woodrat and Humboldt's flying squirrel. I used multivariate analysis of variance
(MANOVA) to test for differences in forest and ground cover metrics between locations used by
flying squirrels and woodrats compared to locations in the immediate (within 35 m) vicinity. For
the tree species that were surveyed, incense cedar was the only one that differed from plot
position. I found that dusky-footed woodrats and Humboldt's flying squirrels often used sites
with a higher presence of deciduous shrub ground cover in proximal and intermediate areas.

Dusky-footed woodrats also used sites with higher forest litter ground cover in proximate areas.
In addition, I found the areas used by Humboldt's flying squirrel had trees with significantly
larger diameters than those used by dusky-footed woodrat.

These results show the importance of accounting for habitat features preferred by Humboldt's flying squirrels and dusky-footed woodrats when conducting forest management across an industrial forest landscape. Given documented decreases in abundance and densities of NSO and CSO prey (Rosenberg et al. 2003), retention of structural forest elements commonly used by prey species can benefit spotted owl conservation. In doing so, negative impacts of simplifying forest structure on spotted owl prey can potentially be mitigated, hopefully with positive effects on spotted owl demography, distribution, reproduction, and survival (Steenhof et al 1997, Brommer et al. 1998, Rosenberg et al. 2003).

My study had several limitations, including low sample sizes and capture successes due to wildfire and logistical challenges. I recommend that further research be conducted on habitat characteristics associated with spotted owl and dusky-footed woodrat and Humboldt's flying squirrels to better understand overlap in space use. Also, further knowledge on the influence of prey availability, abundance, and habitat features can help promote reproductive success of

spotted owls and inform forest management practices in this landscape. In addition, managers can implement silviculture practices that promote the growth and retention of trees, vegetation, and create large logs and stumps within stands to be able to conserve their habitat. Based on the results, forest managers and wildlife personnel should retain some trees with big diameters (e.g, white fir, red fir, sugar pine, Jeffrey pine, and incense cedar). These trees play an important role in Humboldt's flying squirrel habitat. In terms of vegetation and ground cover, the retention of evergreen and deciduous shrubs is recommended since they play an important role in dusky-footed woodrat nest and dens. This will help to maintain a healthy, balanced ecosystem and adequate habitat in the industrial forest.

Conservation practices for Humboldt's flying squirrel and dusky-footed woodrat are important since both species have an ecologically important value to humans and other species. In the case of Humboldt's flying squirrels, they have a positive relationship with fungi, spreading mycorrhizal fungi by excreting fungi spores after feeding on the fruiting bodies (Lehmkuhl et al. 2006, Weigl 2007). These fungi are an important part of the forest ecosystem and contribute to nutrient and water uptake by many coniferous tree species (Smith 2003). Therefore, Humboldt's flying squirrels are considered a keystone species. In the case of dusky footed woodrat, they play an important role in community dynamics in the forest ecosystem. The availability of dusky-footed woodrat houses influences species richness for some mammals, reptiles, amphibians by providing shelter for these species (Innes et al. 2007). In addition, the plant and fecal material from their nest houses help increase soil fertility and moisture, increasing the biodiversity and value in managed forests (Carey et al. 2000).

- Barros, C. S., Püttker, T., Pinotti, B. T., & Pardini, R. (2015). Determinants of capture-recapture success: an evaluation of trapping methods to estimate population and community parameters for Atlantic Forest small mammals. *Zoologia (Curitiba)*, 32(5), 334–344.
- Brommer, J. E., Pietiäinen, H., & Kolunen, H. (1998). The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *Journal of Animal Ecology*, 67(3), 359–369.
- Carey, A. B. (2000). Effects of new forest management strategies on squirrel populations. *Ecological Applications*, 10, 248–257
- Holloway, G. L., Smith, W. P., Halpern, C. B., Gitzen, R. A., Maguire, C. C., & West, S. D. (2012). Influence of forest structure and experimental green-tree retention on northern flying squirrel (Glaucomys sabrinus) abundance. *Forest Ecology and Management*, 285, 187–194.
- Innes, R. J., Van Vuren, D. H., Kelt, D. A., Johnson, M. L., Wilson, J. A., & Stine, P. A. (2007). Habitat associations of dusky-footed woodrats (*Neotoma fuscipes*) in mixed-conifer forest of the northern Sierra Nevada. *Journal of Mammalogy*, 88(6), 1523–1531.
- Lehmkuhl, J. F., Kistler, K. D., Begley, J. S., & Boulanger, J. (2006). Demography of Northern flying squirrels informs ecosystem management of western interior forests. *Ecological Applications*, 16(2), 584–600.
- Rosenberg, D. K., Swindle, K. A., & Anthony, R. G. (2003). Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Canadian Journal of Zoology*, 81(10), 1715–1725.
- Smith, W. P., Anthony, R. G., Waters, J. R., Dodd, N. L., & Zabel, C. J. (2003). Ecology and conservation of arboreal rodents of western coniferous forests. *Mammal Community Dynamics*, 157–206.
- Steenhof, K., Kochert, M. N., & Mcdonald, T. L. (1997). Interactive Effects of Prey and Weather on Golden Eagle Reproduction. *The Journal of Animal Ecology*, 66(3), 350–362.
- Vickery, W. L., & Bider, J. R. (1981). The Influence of Weather on Rodent Activity. *Journal of Mammalogy*, 62(1), 140–145.
- Vieira, E. M., Baumgarten, L. C., Paise, G., & Becker, R. G. (2010). Seasonal patterns and influence of temperature on the daily activity of the diurnal neotropical rodent Necromys lasiurus. *Canadian Journal of Zoology*, 88(3), 259–265.

Weldy, M. J., Clinton, E. W., Lesmeister, D. B., Manning, T., Linnell, M. A., Forsman, E. D. (2019). Effects of trapping effort and trap placement on estimating abundance of Humboldt's flying squirrels. *The Journal of Wildlife Management*, 83, 902–915.