AN ABSTRACT OF THE THESIS OF

<u>Matt Weldy</u> for the degree of <u>Master of Science</u> in <u>Wildlife Science</u> presented on <u>March</u> 9, 2018.

Title: <u>Spatiotemporal Associations of Abundance and Vital Rates of Co-occurring</u> <u>Small Mammals in a Late Successional Forest.</u>

Abstract approved:

Clinton W. Epps

Informed conservation of small mammals, ecosystems, and predators requires a detailed understanding of how small mammals species and communities vary in both space and time, as well as the relative cyclicity and synchrony of this variation. This variation can be especially informative to land managers interested in manipulating the abundance or density of populations, as it often provides inference into the habitat and weather factors to which species and communities are sensitive. While this inference is often informed by spatial or temporal variation in speciesspecific abundance or density, in some cases, species-specific metapopulation and sink-source dynamics can confound the interpretation of this variation. Thus, more informed inference is based not only on the spatiotemporal variation in abundance or density, but also on the spatiotemporal variability on species-specific vital rates. Here, in Chapter 2, I estimated the abundance, temporal synchrony, and spatiotemporal associations of small mammal populations in a late-successional forest in western Oregon. In Chapter 3, I estimated the vital rates (apparent annual survival, population growth rate, and recruitment) of Humboldt's flying squirrels (Glaucomys

oregonensis) and Townsend's chipmunks (*Neotamias townsendii*). For both analyses, I used live-trapping data collected on 9 sites from 2011–2016, in a late successional forest.

In Chapter 2, I used Huggins closed-capture models to estimate site-specific abundance of Humboldt's flying squirrels, Townsend's chipmunks, western redbacked voles (Myodes californicus), and deer mice (Peromyscus maniculatus). Additionally, I used generalized linear mixed effects models to investigate effects of 4 spatial and 3 temporal covariates on species-specific mean abundance estimates. I then estimated the linear correlation between individual counts of the 8 most commonly-caught species of small mammals using Pearson's correlation coefficients. Lastly, I assessed spatial variation in sex ratios and body mass of focal species among grids. Focal species abundances varied by as much as 4-fold among years and 6-fold among sites, with only slight evidence of linear correlation between species. Humboldt's flying squirrel abundance was positively autocorrelated at 1 and 5-year intervals, whereas western red-backed vole abundance was negatively autocorrelated at 4 and 5-year intervals. Sex ratios and body masses did not vary widely across grids. Humboldt's flying squirrels were more abundant on low elevation sites with high berry producing plant cover than on high elevation sites with low berry producing plant cover. Townsend's chipmunks and western red-backed voles were more abundant on high elevation, open canopy sites than on low elevation, closed canopy sites. Deer mice were slightly more abundant on sites with high berry producing plant cover than on sites with low berry producing plant cover. Minimum winter temperature was positively related to the mean abundance of Humboldt's flying

squirrels and Townsends chipmunks and negatively related to the mean abundance of western red-backed voles and deer mice, while western red-backed voles and deer mice were less abundant after periods of drought. Counts of the 8 most commonly captured species were only weakly correlated.

In Chapter 3, I used robust design Pradel models to estimate site-specific apparent annual survival, population growth rate, and recruitment for Humboldt's flying squirrels and Townsend's chipmunks. I then used Pearson's correlation coefficients to estimate the species-specific linear correlations among population growth rate, abundance, apparent annual survival, and recruitment. My estimates were generally intermediate to previous estimates of vital rates. I was able to link abundance-associated covariates with the vital processes most associated with population growth rate. Changes in Humboldt's flying squirrel population growth rate were strongly correlated with apparent annual survival, while the population growth of Townsend's chipmunks was strongly correlated with both apparent annual survival and recruitment. But, for both species, abundance was only moderately correlated with vital rates. Apparent annual survival was nearly constant among years and grids for Humboldt's flying squirrels, but was consistently lower and highly variable among years for Townsend's chipmunks. Recruitment and population growth rates for both species were similar and variable among years.

Taken together, the results of this study further our understanding of the spatial and temporal variation of small mammal population attributes and vital processes in late-successional forests in Oregon's western Cascades. Co-occurring species abundance varied independently even when exposed to similar spatial and temporal drivers, and 2 of the 4-focal species abundances exhibited cyclical population dynamics. There has been considerable debate about the usefulness of abundance variability in determining habitat quality, but these results suggest that in this study system, inference based on abundance variation and inference based on vital rate variation are consistent. ©Copyright by Matt Weldy March 9, 2018 All Rights Reserved

Spatiotemporal Associations of Abundance and Vital Rates of Co-occurring Small Mammals in a Late Successional Forest

by Matt Weldy

A THESIS

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Master of Science

Presented March 9, 2018 Commencement June 2018 Master of Science thesis of Matt Weldy presented on March 9th, 2018

APPROVED:

Major Professor, representing Wildlife Science

Selina S. Heppell of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Matt Weldy, Author

ACKNOWLEDGEMENTS

I'd like to start by thanking my advisor Clint Epps. I am incredibly grateful for the opportunity to work with Clint on this project. He has been a great mentor and has provided a great example of how to be a responsible scientific practitioner. He has offered great feedback that improved my critical scientific thinking and the quality of my research.

I'd also like to thank my committee members. Damon Lesmeister was generous with his time and made a point of taking the time, when I was new to the study, to come into the field and discuss my research plan and help me think through research problems. In addition, I'd like to thank Damon for his continued support of this project and for providing both vegetation sampling equipment and vehicles. Lisa Ganio, always accommodated meetings, sometimes on short notice, and had a patient ear to make sure I really understood the questions being asked. Katie Dugger, was also generous with her time and helped me develop my analysis approach and answered many specific questions along the way.

I would also like to thank Tom Manning and Eric Forsman. Tom truly runs a well-oiled, small mammal trapping crew. I have never worked as part of a wildlife crew that ran so smoothly. Also, thank you Tom for sharing so much of your small mammal knowledge. I think I would have been hard pressed to find anyone else with as much experience working with these communities in the Pacific Northwest. I would like to thank Eric for his role in developing this project and continuing to support it, even after retirement. I would also like to acknowledge and thank the other current and former members of the Epps research group for their support, good spirits, and willingness to help. These include Rob Spaan, Rachel Crowhurst, Doni Schwalm, Page Minton-Edison, Mark Linnell, and Katie Moriarty. Specifically, thanks to Rob for humoring many tangential discussions that helped me grow as both a scientist and a person. Rob has a genuine interest in biological questions and is a great reminder to focus on the specific question on hand. Also, thanks go to Mark for his instrumental work in getting this intended long-term experiment off the ground.

Thanks to my family for providing a wonderful support network. Kelsea, I want to thank you for your unconditional love, for the gift of our amazing child, and for keeping me grounded. To my parents, thank you for making a point of bringing me out into the woods as a child. Countless camping, hunting, and fishing trips helped solidify my love of the outdoors. Lastly, little Rosemary, I hope to foster in you a curious spirit and a kindred respect and love of the outdoors.

Lastly, I would like to thank the many field assistants who have participated in this study, especially to those who returned for multiple seasons. Small mammal trapping is a lot of work, and is often made more exhausting on this project by the reliable Pacific Northwest rain and fog: Mark Linnell, Nick Bromen, Shalyn Pack, Angela Hsiung, Ashley Bies, Nathan Alexander, Hattie Oswald, Paige Kannor, Marinda Cokeley, Jay Winiarski, April Bartelt, Derek Arnold, Chelsea Hutton, Tim Mayer, Sarah Ward, Stephanie Bishir, Chris Gray, David Tange, Lorraine Carver, Lindsey Howard, Lynn Hodnett, Brie Kerfoot, DeAnne Jacobsma, Brittany Nahorney, and Katelyn (Keke) Ray. Specifically, I would like to thank Nathan Alexander for your engaging scientific discussions and for your comments on both chapter drafts.

Funding for small mammal trapping and analysis was provided by the USDA Forest Service Pacific Northwest Research station. Spatial data and facilities were provided by the HJ Andrews Experimental Forest and Long-Term Ecological Research program, administered cooperatively by the USDA Forest Service Pacific Northwest Research Station, Oregon State University, and the Willamette National Forest.

CONTRIBUTION OF AUTHORS

Matt Weldy developed the research questions presented here, conducted the analysis, performed field work, and drafted this manuscript. Dr. Clinton W. Epps and Dr. Eric Forsman conceived the study and with the help of Mark Linnell developed the study design. Mark Linnell also performed field work. Dr. Clinton W. Epps also provided data, assisted in developing research questions, and assisted in writing both manuscripts. Dr. Damon Lesmeister, assisted in developing research questions.

TABLE OF CONTENTS

	<u>1 450</u>
Chapter 1. GENERAL INTRODUCTION	1
BACKGROUND	2
STUDY SPECIES	8
Humboldt's flying squirrel	8
Townsend's chipmunk	9
Western red-backed vole	10
Deer mouse	10
STUDY LOCATION	12
RESEARCH APPROACH	12
LITERATURE CITED	15
Chapter 2. ABUNDANCE, COMMUNITY CORRELATIONS AND ECOLOGICAL ASSOCIATIONS OF FOUR SMALL MAMMAL SPECIES IN LATE SUCCESSIONAL FORESTS	23
ABSTRACT	24
INTRODUCTION	25
STUDY AREA	29
METHODS	30
Trapping design	30
Development of covariates	32
Detection and abundance analysis	35
Spatial and temporal intraspecific and community correlations	36
Population structure	37

TABLE OF CONTENTS (Continued)

	<u>Page</u>
Habitat relationships	38
RESULTS	41
DISCUSSION	46
MANAGEMENT IMPLICATIONS	52
LITERATURE CITED	54
Chapter 3. VITAL RATES AND SPATIOTEMPORAL ASSOCIATIONS OF HUMBOLDT'S FLYING SQUIRRELS AND TOWNSEND'S CHIPMUNKS IN WESTERN CASCADES LATE SUCCESSIONAL FORESTS	82
ABSTRACT	83
INTRODUCTION	84
MATERIALS AND METHODS	87
Study area and trapping sites	87
Live trapping	88
Study species	89
Development of covariates	90
Analysis	92
Correlations among vital rates and abundance	95
RESULTS	95
DISCUSSION	99
LITERATURE CITED	105
Chapter 4. GENERAL CONCLUSION	124
RESEARCH GOALS	125

TABLE OF CONTENTS (Continued)

PRIMARY FINDINGS125	
FUTURE ANALYSIS128	
LITERATURE CITED131	
BIBLOGRAPHY	
APPENDIX 1. Supplemental information providing Pearson's correlation coefficients of considered and selected model covariates, species-specific counts of captured individuals, species and year specific sex-ratios, and sex, year and species specific average individual weights (g)148	
APPENDIX 2. Negative binomial generalized linear mixed-effects model description	
APPENDIX 3. Model selection results testing for behavioral effects, AIC _c combined Pradel model selection table and grid- and year-specific real estimates from robust design Pradel models	

Page

LIST OF FIGURES

<u>Figure</u>

 2.1 Location of our study sites in the H. J. Andrews Experimental Forest, in central Oregon. We collected mark-recapture data for small mammals on 9 sites, represented by the black squares, in late-successional forests from 2011–2016
 2.2 Fall abundance from 2011–2016 of Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>, 7.84 ha), Townsend's chipmunks (<i>Neotamias townsendii</i>, 7.84 ha), western red-backed voles (<i>Myodes californicus</i>, 1 ha), and deer mice (<i>Peromyscus maniculatus</i>, 1 ha) estimated using Huggins models and live capture data collected in a late successional forest within the H. J. Andrews Experimental Forest from 2011–2016
 2.3 Intraspecific abundance temporal autocorrelation for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>), and western red-backed voles (<i>Myodes californicus</i>) captured in a natural successional forest from 2011–2016
 2.4 Correlograms of pairwise Pearson's correlation coefficients for pairwise estimates of abundance between 9 sites (indicated on the x- and y-axis) from 2011–2016 for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) captured in the H. J. Andrews Experimental Forest
 2.5 Correlograms of the pairwise Pearson's correlation coefficients of abundance between years (indicated on the x- and y-axis) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) captured in the H. J. Andrews Experimental Forest from 2011–2016
2.6 The estimated effect size and 95% CIs on mean abundance across the sampled range of spatiotemporal covariates for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>), and western red-backed voles (<i>Myodes californicus</i>) captured in a late successional forest from 2011–2016

LIST OF FIGURES (Continued)

Figure	Page
3.1 Location of our study sites in the H. J. Andrews Experimental Forest, in central Oregon. We collected mark-recapture data for small mammals on 9 sites, represented by the black squares, in late-successional forests from 2011–2016.	120
3.2 Apparent annual survival of Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) from all open-population trapping intervals from 2011–2016 in the H. J. Andrews Experimental Forest in Oregon	121
3.3 Recruitment of Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) from all open-population trapping intervals from 2011–2016 in the H. J. Andrews Experimental Forest in Oregon.	.122
3.4 Annual population growth of Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) from all open-population trapping intervals from 2011–2016 in the H. J. Andrews Experimental Forest in Oregon.	123

LIST OF TABLES

<u>Table</u> <u>Pag</u>	<u>e</u>
2.1 Description of variables considered in model construction of detection probability (p), recapture probability (c), and abundance (N) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>)	.65
2.2 <i>A priori</i> predictions of variable effects in models of detection probability (<i>p</i>), recapture probability (<i>c</i>), and abundance (\hat{N}) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>), and western red-backed voles (<i>Myodes californicus</i>)	.67
2.3 Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), western red-backed voles (<i>Myodes californicus</i>), and deer mice (<i>Peromyscus maniculatus</i>) sex ratios of total captures and individuals from all years and sites on the H. J. Andrews Experimental Forest in Oregon from 2011–2016	.69
2.4 Top 5 ranking models used to estimate recapture probability (<i>c</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011– 2016.	.70
2.5 Top 5 ranking models used to estimate capture probability (<i>p</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011-2016.	.72
2.6 Pairwise Pearson's correlation coefficients between species-specific number of known individuals (Appendix 1.3) for the 8 most commonly captured species captured in a natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016	.74

LIST OF TABLES (Continued)

<u>Table</u>

2.7	Pairwise Pearson's correlation coefficients between Humboldt's flying squirrel (<i>Glaucomys oregonensis</i>), Townsend's chipmunk (<i>Neotamias townsendii</i>), deer mouse (<i>Peromyscus maniculatus</i>), and western red-backed vole (<i>Myodes californicus</i>) abundance estimates in a natural successional forest in the H. J. Andrews Experimental Forest from 2011–201675
3.1	Description of variables considered in model construction of detection probability (p), recapture probability (c), apparent survival (ϕ) and recruitment (f) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) using mark-recapture data recorded in late-successional forests in the central Oregon Cascades from 2011–2016
3.2	A priori predictions of variable effects in models of detection probability (p) , recapture probability (c) , apparent annual survival (ϕ) , and recruitment (f) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>)
3.3	Estimates, from a previous study, of Humboldt's flying squirrel (<i>Glaucomys oregonensis</i>) and Townsend's chipmunk (<i>Neotamias townsendii</i>) abundance from Huggins closed population models
3.4	Top 5 ranking models used to estimate recapture probability (<i>c</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016115
3.5	Top 5 ranking models used to estimate capture probability (<i>p</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.6	Top 5 ranking models used to estimate apparent survival (φ) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016

LIST OF TABLES (Continued)

Table

3.7	Top 5 ranking models used to estimate recruitment (<i>f</i>) for Humboldt's	
	flying squirrels (Glaucomys oregonensis) and Townsend's chipmunks	
	(Neotamias townsendii) in natural successional forest in the H. J.	
	Andrews Experimental Forest from 2011–2016	118
3.8	Pairwise Pearson's correlation coefficients for a comparison of estimated vital rates and fall abundance of Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) from all years and sites on the H. J. Andrews Experimental Forest in Oregon from 2011–2016	119

LIST OF APPENDIX FIGURES

<u>Figure</u>

Page

58

LIST OF APPENDIX TABLES

<u>Table</u> Page	,
1.1 Pearson's correlation coefficients for a priori spatial variables estimated once during 2016 on our sites across the H. J. Andrews Experimental Forest149	
1.2 Pearson's correlation coefficients for a priori temporal variables150	
 1.3 Number of captured individuals across all grids for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016	
 1.4 Year and grid-specific proportion of males to females for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>), and western red-backed voles (<i>Myodes californicus</i>) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016	
1.5 Grid- and species-specific counts of trees collected at 9 research sites in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016	
 1.6 Spatial variable models ranked using Akaike's Information Criterion corrected for small sample sizes for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016	
 1.7 Temporal variable models ranked using Akaike's Information Criterion corrected for small sample sizes for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>), Townsend's chipmunks (<i>Neotamias townsendii</i>), deer mice (<i>Peromyscus maniculatus</i>) and western red-backed voles (<i>Myodes californicus</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. 	

LIST OF APPENDIX TABLES (Continued)

Table

3.1	Model selection results used to test for a behavioral effect between capture probability (<i>p</i>) and recapture probability (<i>c</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) in a natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.2	All models used to estimate apparent survival (φ) and recruitment (f) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.3	Estimates of recapture probability (c) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.4	Estimates of first capture probability (<i>p</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.5	Estimates of apparent annual survival (φ) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.6	Estimates of recruitment (<i>f</i>) for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016
3.7	Model averaged estimates of population growth for Humboldt's flying squirrels (<i>Glaucomys oregonensis</i>) and Townsend's chipmunks (<i>Neotamias townsendii</i>) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016213

Chapter 1

GENERAL INTRODUCTION

Matt Weldy

BACKGROUND

The spatial and temporal variation of population attributes (abundance, density) and vital rates (recruitment, survival, and population growth) are primary areas of research interest in the field of population ecology. Land managers and wildlife biologists are also interested in these population attributes and vital rates because they are central to the management of wildlife populations (Williams et al. 2002). Capture-recapture models are important tools for estimating these population attributes and vital processes (Seber 1982), and these tools are routinely used by managers and population ecologists to monitor the size and performance of populations (Dugger et al. 2016), to estimate species-specific habitat associations (Coppeto et al. 2006), or to estimate population-specific responses to management actions (Sullivan et al. 2017). Capture-recapture studies are time and labor intensive, and as a result inferences based on these studies are often limited in space or time. However, these estimates can vary quite dramatically in both space and time (Hansson 1977). Thus, for such limited estimates to be useful to managers, it is important to understand how population attributes and vital rates interact to limit or regulate populations in space and time.

Often management goals include the maintenance, alteration, or prediction of a population attribute in space or time. For example, management goals seek to maintain the abundance of harvested species (Conn et al. 2004, Ciuti et al. 2015, DeVivo et al. 2016), decrease the abundance of pest species (Moon et al. 2015, Jones et al. 2016), or increase the abundance of rare species or their prey (Karanth and Nichols 2015). However, to influence population attributes in space or time, land managers need to manipulate at least one vital process that, in turn, is associated with the targeted-species' abundance. Northern spotted owls (*Strix occidentalis caurina*) are a good illustration of ongoing efforts to manipulate species-specific vital rates to increase the abundance of a threatened species (Forsman et al. 2011, Dugger et al. 2016). The northern spotted owl was listed as a threatened subspecies in 1990 under the United States Endangered Species Act, and the Northwest Forest Plan was initiated in 1994 to slow the decline of old forest habitat, which is strongly associated with adult survival and reproduction (U.S. Fish and Wildlife Service 1990, USDA and USDI 1994, Forsman et al. 2011). The protections this legislation enacted are ongoing, and both land managers and researchers continue to monitor the population trends of the northern spotted owl (Dugger et al. 2016).

Previous studies have presented many hypotheses about the regulation of population attributes and processes (Chitty 1960, Lidicker 1978, Krebs 2013, Prevedello et al. 2013, Wang et al. 2013). These hypotheses broadly fit into two groups: populations regulated by extrinsic factors or populations regulated by intrinsic factors (Krebs 2002). Extrinsic factors are biological, spatial, or temporal variables that are not inherently caused by the species itself and that affect population attributes and processes through external actions. Intrinsic factors are not dependent on external species or spatiotemporal variables. Much of the population regulation research has focused on bottom-up and top-down extrinsic factors that affect food supply and predation pressure (Ernest et al. 2000, Prevedello et al. 2013, Lobo 2014). Bottom-up factors affect resource availability and can cause spatial and temporal demographic heterogeneity at multiple scales (Ransome and Sullivan 1997, Hernández et al. 2011). Top-down factors affect population attributes and vital processes through predation (Hanski et al. 2001, Terborgh et al. 2001, Eagan et al. 2011). However, additional extrinsic factors such as disease, parasites, weather, and landscape are growing in importance (Krebs 2013). Competition is a commonly explored intrinsic factor that relates to parallel dynamics among co-occurring species often competing for limited resources, but agonistic social behaviors, physiological effects, and genetic structure are also potentially important intrinsic factors (Oli and Dobson 1999, Ernest et al. 2008, Selva et al. 2012, Creel et al. 2013, Krebs 2013). The relative influence of these factors on population attributes and population regulation is still unclear and realistic regulation models most likely include complex interactions of multiple factors, sometimes non-linear, operating on multiple scales (Coppeto et al. 2006, Krebs 2013).

Small mammal population attributes and vital processes are thought to be strongly regulated by resource availability (Batzli 1992, Prevedello et al. 2013). For example, a number of studies have observed demographic changes in small mammal populations in response to supplemental food treatments (Gilbert and Krebs 1981, Krebs et al. 1986, Ransome and Sullivan 1997), forest age (Carey 1995), vegetation cover (Smith et al. 2004), and coarse woody debris volumes (Butts and McComb 2000, Fauteux et al. 2012). Beyond resource availability, a number of studies have demonstrated the regulating effects of both predation (Hanski et al. 2001, Terborgh et al. 2001), competition (Porter and Dueser 1982, Galindo and Krebs 1985), social behavior, and stress. Stress-induced population regulation in small mammals was largely disregarded after early studies failed to detect an effect; however, improved sampling and analysis techniques suggest that the delayed effects of stress might be a cause of population cycling in some small mammal populations (Boonstra et al. 1998, Sheriff et al. 2009).

In the forests of the Pacific Northwest (hereafter PNW), small mammals are particularly important to ecosystem management because of their importance as a prey-base for both avian and mammalian predators (Wilson and Carey 1996, Fryxell et al. 1999, Bull 2000, Forsman et al. 2001, Rosenberg et al. 2003), and their influence on plant and fungal community dynamics through the consumption and dispersal of berries, seeds, and hypogenous fungi (Maser et al. 1978, Bowers and Dooley Jr 1993). Following the release of the Northwest Forest Plan, a large amount of research has focused on the population dynamics and habitat associations of small mammals in the PNW. However, much this research has focused on the effects of timber management, and it largely consists of abundance or density contrasts between managed and unmanaged forests (Rosenberg and Anthony 1992, 1993, Anthony et al. 1994, Carey 1995, Butts and McComb 2000, Lehmkuhl et al. 2006, Holloway and Malcolm 2007, USDA and USDI 1994), or on key prey species for northern spotted owls such as the northern flying squirrel (Glaucomys sabrinus) and bushy-tailed woodrat (*Neotoma cinera*; Waters and Zabel 1995, Wilson et al. 1999, Pyare and Longland 2001, Smith et al. 2005, Lehmkuhl et al. 2006, Smith 2007). Less is known about the population attributes and vital rates of co-occurring species. Additionally, even for the well-studied northern flying squirrel, little is known about the mechanisms driving spatial and temporal variation in population attributes, an active criticism in studies of other taxa (Cushman 2006, Todd and Rothermel 2006).

I used 6 years of small mammal live-trapping data collected in a late successional forest in western Oregon from 2011–2016. Live-trapping was conducted on 9 study sites arranged across elevation and canopy openness gradients. I selected the four most commonly captured species during the study's first six years as the focal species for demographic analysis. Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*) occur sympatrically in a broad range of forested habitat throughout Western Oregon. Beyond being the 4 most commonly captured species, the focal species exhibit a wide range of life history traits that facilitate potential niche overlap and niche differentiation. Broad similarities in diet and common predators suggests potential similarities in bottom-up and top-down influences. However, fine scale dietary separation, differences in daily activity patterns, and vertical partitioning of habitat might suggest potential niche partitioning.

Many habitat and environmental features have been used to explain the focal species' spatial and temporal abundance patterns. In general, previous studies have shown the focal species to increase abundance in response to increased precipitation, which affects food availability, and to decrease abundance in response to increasing winter severity and elevation both of which are associated with winter survival (Aubry et al. 1991, Ernest et al. 2000, Lehmkuhl et al. 2004). The focal species diet preferences are broadly similar; however, some studies have demonstrated niche partitioning based on food resources (Ure and Maser 1982, Maser and Maser 1988, North et al. 1997, Lehmkuhl et al. 2004). For example, the focal species all

demonstrate a high occurrence of hypogenous fungi in their digestive track, but the species-level composition of fungal species varies (Maser et al. 1978). Specifically, *Rhizopogon* and *Gauteria* fungi are commonly detected in the scats of these scurids (northern flying squirrel and Townsend's chipmunks) and western red back voles (Jacobs and Luoma 2008). Deer mice also consume a wider range of fungi species, but fungi make up less of their total stomach contents than the other focal species (North et al. 1997). In addition to fungi, Townsend's chipmunks, western red-backed voles, and deer mice consume both seeds and berries (Ure and Maser 1982, Tallmon et al. 2003). Specifically, the density of Townsend's chipmunks is positively associated with the cover of salal (*Gaultheria shallon*), which may be an important food source (Hayes et al. 1995).

High diversity and abundance of prey in PNW forests support a large suite of co-occurring mammalian and avian predators. Patterns of competition resulting from overlapping prey niches or the presence of generalist predators likely stabilize small mammal population dynamics. Specialist predators, although not a necessary component of small mammal population cycles, can both amplify the size of population cycles and contribute to spatiotemporal patterns of demographic heterogeneity in prey species (Reynolds and Meslow 1984, Hansson 1987, Oli 2003). northern spotted owls are prey specialists that are largely dependent on northern flying squirrels, deer mice, and western red-backed voles (Forsman et al. 2001, 2004, Rosenberg et al. 2003, Wiens et al. 2014). In some regions, northern spotted owl prey species have shown periodic temporally autocorrelated population cycles typical of top-down specialist predation (Fryxell et al. 1998). The growing presence of barred owls (*Strix varia*) in PNW forests, a generalist avian predator, has likely already caused changes in prey behavior and abundance (Wiens et al. 2014) and could stabilize the population dynamics of some prey species that have historically had cyclical dynamics (Hanski et al. 1991).

STUDY SPECIES

Humboldt's flying squirrel

The northern flying squirrel, a nocturnal, arboreal mammal, has been proposed as both a management indicator species and a keystone species in the PNW because of its important role as a prey source for northern spotted owls and the ecosystems service provided by the dispersal of fungal spores (Smith et al. 2005, Holloway and Smith 2011). Populations of northern flying squirrel in the PNW were recently described as a separate species, now designated as the Humboldt's flying squirrel (Arbogast et al. 2017). Hereafter, I assume that previous studies conducted on northern flying squirrels across much of the PNW pertained to Humboldt's flying squirrels. Unlike the northern flying squirrel, the Humboldt's flying squirrel's range is restricted to west of the Cascades Range in the PNW. In the PNW, Humboldt's flying squirrels occupy Douglas-fir and western hemlock mixed-conifer forests. Humboldt's flying squirrels have previously shown strong associations between density, understory structural richness, coarse woody debris, and hypogenous fungi biomass (Carey et al. 1999, Smith 2007). The diet of Humboldt's flying squirrels is strongly dependent on the sporocarps of hypogenous fungi (Maser et al. 1978). They are the primary prey item for northern spotted owls and are a significant prey source

for barred owls and mammalian carnivores (Carey et al. 1992, Wiens et al. 2014, Wilson and Carey 1996).

Townsend's chipmunk

Townsend's chipmunks are the most commonly captured species on this project; however, little is known about their ecological role in the PNW (Rosenberg and Anthony 1993). Townsend's chipmunks make up a small proportion of the biomass consumed by northern spotted owls and barred owls, probably due to temporal differences in activity periods (Wiens et al. 2014). However, they may be an important prey source for mammalian and avian carnivores that are more active during the day, such as ermines (Mustela erminea) and Accipiters including the Coopers hawk (Accipiter cooperi; Reynolds and Meslow 1984, Wilson and Carey 1996). Hayes et al. (1995) and Rosenberg and Anothony (1993) both observed higher densities of Townsend's chipmunks in old or mature forests relative to young forests, but it is still unclear if this is consistent across the PNW (Hayes et al. 1995). Additionally, Waldien et al. (2006) observed an association of Townsend's chipmunks with downed woody debris and understory structural richness. Townsend's chipmunks are another important mycophagist in the PNW and are believed to play an important role in the dispersal of mycorrhizal fungal spores (Carey et al. 1999, Maser et al. 1978). However, they also consume seeds and berries; for example, the percentage cover of salal (*Gaultheria shallon*) is positively associated with Townsend's chipmunk densities suggesting that salal berries may be an important food source (Hayes et al. 1995).

Western red-backed vole

The western red-backed vole is a conifer-dependent species that is endemic to northern California and western Oregon (Thompson et al. 2009). The diet of western red-backed voles consists primarily of fungi, with seasonal lichen and seed supplementation (Ure and Maser 1982). Thompson et al. (2009) and Anthony et al. (1994) have demonstrated the spatial variability of western red-backed vole populations, especially in response to land management strategies. However, there is still uncertainty about their response. For example, Doyle (1987) and Anthony et al. (1994) found higher western red-backed vole abundance in mature and old forests when compared to young forests, while Aubry et al. (1991) were unable to detect a difference in abundance among old, mature, and young forests. There is some evidence for cyclical dynamics in other similar vole populations; however, other factors associated with temporal variability in western red-backed vole abundance are uncertain (Fryxell et al. 1998, Sullivan et al. 2017). For example, Sullivan et al. (2017) provide evidence for 6-8-year population cycles. At a fine scale, western redbacked voles have been associated with both highly decayed logs and rich organic forest soil types (Anthony et al. 1994, Gomez 1992). Western red-backed voles are a prey source for both northern spotted owls and barred owls; however, they make up a small proportion of the total consumed biomass for both species (Wiens et al. 2014). **Deer mouse**

The deer mouse is a wide-ranging nocturnal mammal that occupies many types of habitats. Deer mice have a broad dietary niche that includes arthropods, fruit, fungus, vegetation, and seeds (Jameson 1952, Maser et al. 1978, Van Horne 1981, Falls et al. 2007, Lobo et al. 2009, 2013). However, the dietary niche of deer mice varies in different habitat types. For example, Van Horne (1982) observed differences in the diets of deer mice in old forests and harvested stands; deer mice in old forests consumed more relatively more inflorescences, while those in harvested stands consumed relatively more seeds and fruit. Multiple food supplementation studies have demonstrated increases in deer mouse abundance on food supplemented sites (Gilbert and Krebs 1981, Taitt 1981). Yet, Dracup et al. (2016) did not observe demographic or physiological deer mouse response in a food supplementation study using dried fruit. These generalist qualities likely make spatial habitat associations difficult to detect. In addition, adult deer mice are aggressive towards juvenile deer mice (Fairbairn 1978, Van Horne 1982), and these aggressive intraspecific interactions might bias the interpretation of deer mouse habitat associations because juvenile deer mice might occur in high densities in suboptimal habitats due to competitive exclusion (Van Horne 1982).

While deer mice show little variation in abundance across spatial gradients they do show strong variation across time (Fryxell et al. 1998). However, little is known about the specific temporal drivers of deer mouse abundance in the PNW. Rosenberg et al. (2003) observed some correlation between the breeding success of northern spotted owls and the abundance of deer mice, which might affect the temporal patterning of deer mouse abundance in the PNW. But, there has been no experimental test of this effect.

STUDY LOCATION

We conducted this study in the H. J. Andrews Experimental Forest (hereafter HJA) near Blue River, OR (Figure 2.1). The HJA is part of the larger Willamette National Forest and covers the entire 6,400-ha Lookout Creek drainage basin. The HJA forest is one of National Science Foundation's (NSFs) 26 Long-Term Ecological Research sites and one of 81 United States Department of Agriculture (USDA) experimental forests. It is a site of ongoing concentrated research exploring the interconnections of ecosystems, watersheds, and biodiversity in old-growth and mountainous communities.

RESEARCH APPROACH

The research presented in Chapter 2 and Chapter 3 marks the first analysis of data from this ongoing small mammal live-trapping project. I used mark-recapture data collected from 2011–2016 on 9 sites that span all combinations of 3-elevation classes (<800m, 800-1,000m, >1,000m) and 3-canopy openness classes (0-15%, 15-30%, 30-40%). In two research chapters, I developed 7 research objectives to understand the patterns of spatiotemporal variation of small mammal population attributes and vital rates in late successional forests in Oregon's western Cascades. In Chapter 2, I 1) estimated site and year-specific abundances of the focal species, 2) sought to estimate the temporal autocorrelation of species-specific abundances, 3) investigated the patterns of spatial associations averaged over years and temporal associations averaged across sites, and 4) estimated the patterns of co-occurrence among the 8 most commonly captured species. In Chapter 3, 1) I estimated the vital rates of two co-occurring small mammals, 2) sought to clarify the link between mean

abundance-associated covariates and vital processes, and 3) estimated the correlation among vital rates.

In Chapter 2, using Huggins' closed capture models implemented in Program MARK, I estimated the annual fall abundance of Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), western red-backed voles (*Myodes californicus*), and deer mice (*Peromyscus maniculatus*; Huggins 1989, White and Burnham 1999). I also investigated autocorrelation patterns of focal species abundance among years. I investigated the effects of habitat, regional climate variation, and local weather on the mean abundance of the focal species using generalized linear mixed effects models with negative binomial distributions (Zurr et al. 2009). Lastly, I explored patterns of community composition and pairwise interspecific correlations of using Pearson's correlation among individual counts of the 8 co-occurring species of small mammals, including the four focal species abundance estimates.

In Chapter 3, I estimated the apparent annual survival (φ), population growth rate (λ), and recruitment (f) of Humboldt's flying squirrels and Townsend's chipmunks, two co-occurring small mammals. I estimated the effects of mean abundance-associated covariates identified in Chapter 2 on apparent annual survival and recruitment. In addition, I used pairwise Pearson's correlation coefficients to estimate the linear correlations between site and year-specific abundance, apparent annual survival, population growth rate, and recruitment.

13
The results of this study further our understanding of the spatial and temporal variation of small mammal population attributes and vital processes in latesuccessional forests in Oregon's western Cascades. Additionally, I provide precise estimates of small mammal population attributes on a long-term ecological research site, which will contribute to our understanding of small mammal population dynamics and to our understanding of population regulation of both mammalian and avian carnivores.

LITERATURE CITED

- Anthony, R. G., D. K. Rosenberg, and K. A. Swindle. 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. Northwest Science 68:266–272.
- Aubry, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Batzli, G. O. 1992. Dynamics of small mammal populations: a review. Pp. 831–850 in Wildlife 2001: populations. Springer.
- Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs 68:371–394.
- Bowers, M. A., and J. L. Dooley Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia 94:247–254.
- Bull, E. 2000. Seasonal and sexual differences in American marten diet in northeastern Oregon. Northwest Science 74:186–191.
- Butts, S. R., and W. C. McComb. 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. The Journal of Wildlife Management 64:95–104.
- Carey, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications 5:648–661.
- Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. Ecological Monographs 62:223–250.
- Carey, A. B., J. Kershner, B. Biswell, and L. D. de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142:3–71.
- Chitty, D. 1960. Population processes in the vole and their relevance to general theory. Canadian Journal of Zoology 38:99–113.
- Ciuti, S., W. F. Jensen, S. E. Nielsen, and M. S. Boyce. 2015. Predicting mule deer recruitment from climate oscillations for harvest management on the northern Great Plains: predicting deer recruitment from climate indices. The Journal of Wildlife Management 79:1226–1238.

- Conn, P. B., W. L. Kendall, and M. D. Samuel. 2004. A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. Biometrics 60:900–909.
- Coppeto, S. A., D. A. Kelt, D. H. Van Vuren, J. A. Wilson, and S. Bigelow. 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. Journal of Mammalogy 87:402–413.
- Creel, S., B. Dantzer, W. Goymann, and D. R. Rubenstein. 2013. The ecology of stress: effects of the social environment. Functional Ecology 27:66–80.
- Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128:231–240.
- DeVivo, M. T. et al. 2017. Endemic chronic wasting disease causes mule deer population decline in Wyoming. PloS one 12:e0186512.
- Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus, Microtus oregoni* and *M. richardsoni*. American Midland Naturalist 118:258.
- Dracup, E. C., D. M. Keppie, and G. J. Forbes. 2016. The short-term impact of abundant fruit upon deer mouse (*Peromyscus maniculatus*), southern red-backed vole (*Myodes gapperi*), and woodland jumping mouse (*Napaeozapus insignis*) populations. Canadian Journal of Zoology 94:555–563.
- Dugger, K. M. et al. 2016. The effects of habitat, climate, and Barred Owls on longterm demography of Northern Spotted Owls. The Condor 118:57–116.
- Eagan, T. S., J. C. Beasley, Z. H. Olson, and O. E. Rhodes. 2011. Impacts of generalist mesopredators on the demography of small-mammal populations in fragmented landscapes. Canadian Journal of Zoology 89:724–731.
- Ernest, S. K., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.
- Ernest, S. K. M., J. H. Brown, K. M. Thibault, E. P. White, and J. R. Goheen. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. The American Naturalist 172:E257–E269.
- Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*. Oecologia 32:171–193.
- Falls, J. B., E. Falls, and J. M. Fryxell. 2007. Fluctuations of deer mice in Ontario in relation to seed crops. Ecological Monographs 77:19–32.

- Fauteux, D., L. Imbeau, P. Drapeau, and M. J. Mazerolle. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. Forest Ecology and Management 266:194–205.
- Forsman, E. D. et al. 2001. Spatial and temporal variation in diets of Spotted Owls in Washington. Journal of Raptor Research 35:141–150.
- Forsman, E. D., R. G. Anthony, E. C. Meslow, and C. J. Zabel. 2004. Diets and foraging behavior of Northern Spotted Owls in Oregon. Journal of Raptor Research 38:214–230.
- Forsman, E. D. et al. 2011. Population demography of Northern Spotted Owls. Studies in Avian Biology 40.
- Fryxell, J. M., J. B. Falls, E. A. Falls, and R. J. Brooks. 1998. Long-term dynamics of small-mammal populations in Ontario. Ecology 79:213–225.
- Fryxell, J. M., J. B. Falls, E. A. Falls, R. J. Brooks, L. Dix, and M. A. Strickland. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. Ecology 80:1311–1321.
- Galindo, C., and C. J. Krebs. 1985. Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. Canadian Journal of Zoology 63:1870–1879.
- Gilbert, B. S., and C. J. Krebs. 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. Oecologia 51:326–331.
- Gomez, D. M. 1992. Small-mammal herpetofauna abundance in riparian and upslope areas of five forest conditions.
- Hansson, L. 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. Oikos 29:539–544.
- Hansson, L. 1987. An interpretation of rodent dynamics as due to trophic interactions. Oikos 50:308–318.
- Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist Predators, Generalist Predators, and the Microtine Rodent Cycle. The Journal of Animal Ecology 60:353-367.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Smallrodent dynamics and predation. Ecology 82:1505–1520.

- Hayes, J. P., S. P. Cross, and P. W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in southwestern Oregon. Northwest Science 60:250–257.
- Hayes, J. P., E. G. Horvath, and P. Hounihan. 1995. Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range. Canadian Journal of Zoology 73:67–73.
- Hernández, L., J. W. Laundré, A. González-Romero, J. López-Portillo, and K. M. Grajales. 2011. Tale of two metrics: density and biomass in a desert rodent community. Journal of Mammalogy 92:840–851.
- Holloway, G. L., and J. R. Malcolm. 2007. Northern and southern flying squirrel use of space within home ranges in central Ontario. Forest Ecology and Management 242:747–755.
- Holloway, G. L., and W. P. Smith. 2011. A meta-analysis of forest age and structure effects on northern flying squirrel densities. The Journal of Wildlife Management 75:668–674.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.
- Jameson, E. W. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada, California. Journal of Mammalogy 33:50.
- Karanth, K. U., and J. D. Nichols. 2011. Estimating tiger abundance from camera trap data: field surveys and analytical issues. Pp. 97–117 in Camera Traps in Animal Ecology (A. F. O'Connell, J. D. Nichols & K. U. Karanth, eds.). Springer Japan.
- Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986. Population biology of snowshoe hares. I. demography of food-supplemented populations in the southern Yukon, 1976-84. The Journal of Animal Ecology 55:963.
- Krebs, C. J. 2002. Two complementary paradigms for analyzing population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1211–1219.
- Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Illinois.
- Lehmkuhl, J. F., L. E. Gould, E. Cázares, and D. R. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200:49–65.

- Lehmkuhl, J. F., K. D. Kistler, J. S. Begley, and J. Boulanger. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16:584–600.
- Lidicher, W. Z. J. 1978. Regulation of numbers in small mammal populations: historical reflections and a synthesis. Pp. 122–166 in Populations of Small Mammals under Natural Conditions. University of Pittsburgh, United States.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: a review of the patterns, implications and limitations of top-down and bottom-up interactions. Forest Ecology and Management 328:45–54.
- Lobo, N., M. Duong, and J. S. Millar. 2009. Conifer-seed preferences of small mammals. Canadian Journal of Zoology 87:773–780.
- Lobo, N., D. J. Green, and J. S. Millar. 2013. Effects of seed quality and abundance on the foraging behavior of deer mice. Journal of Mammalogy 94:1449–1459.
- Jacobs, K. M., and D. L. Luoma. 2008. Small mammal mycophagy response to variations in green-tree retention. Journal of Wildlife Management 72:1747–1755.
- Jones, H. P. et al. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.
- Maser, C., and Z. Maser. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. The Great Basin Naturalist 48:358–369.
- Moon, K., D. A. Blackman, and T. D. Brewer. 2015. Understanding and integrating knowledge to improve invasive species management. Biological Invasions 17:2675–2689.
- North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78:1543–1554.
- Oli, M. K. 2003. Population cycles of small rodents are caused by specialist predators: or are they? Trends in Ecology & Evolution 18:105–107.
- Oli, M. K., and F. S. Dobson. 1999. Population cycles in small mammals: the role of age at sexual maturity. Oikos 86:557–565.

- Porter, J. H., and R. D. Dueser. 1982. Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. Oikos 39:228.
- Prevedello, J. A., C. R. Dickman, M. V. Vieira, and E. M. Vieira. 2013. Population responses of small mammals to food supply and predators: a global metaanalysis. Journal of Animal Ecology 82:927–936.
- Pyare, S., and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681–689.
- Ransome, D. B., and T. P. Sullivan. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. Journal of Mammalogy 78:538–549.
- Reynolds, R. T., and E. C. Meslow. 1984. Partitioning of food and niche characteristics of coexisting accipiter during breeding. The Auk 101:761–779.
- Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology 70:161–166.
- Rosenberg, D. K., and R. G. Anthony. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. The Journal of Wildlife Management 57:365–373.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. Canadian Journal of Zoology 81:1715–1725.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. MacMillian, New York.
- Selva, N., K. A. Hobson, A. Cortés-Avizanda, A. Zalewski, and J. A. Donázar. 2012. Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. PLoS ONE 7:e51267.
- Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78:1249–1258.
- Smith, W. P., S. M. Gende, and J. V. Nichols. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. Journal of Mammalogy 85:663–674.

- Smith, W. P., S. M. Gende, and J. V. Nichols. 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. Ecological Applications 15:689–700.
- Smith, W. P. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. Journal of Mammalogy 88:862–881.
- Sullivan, T. P., D. B. Ransome, D. S. Sullivan, P. M. F. Lindgren, and W. Klenner. 2017. Tree squirrel abundance and demography in managed coniferous forests of British Columbia are within the range of natural fluctuations of old-growth stands. Canadian Journal of Forest Research 47:565–582.
- Sullivan, T. P., D. S. Sullivan, R. Boonstra, C. J. Krebs, and A. Vyse. 2017. Mechanisms of population limitation in the southern red-backed vole in conifer forests of western North America: insights from a long-term study. Journal of Mammalogy 98:1367–1378.
- Taitt, M. J. 1981. The effect of extra food on small rodent populations: I. deermice (*Peromyscus maniculatus*). The Journal of Animal Ecology 50:111.
- Tallmon, D. A., E. S. Jules, N. J. Radke, and L. S. Mills. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. Ecological Applications 13:1193–1203.
- Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1925.
- Thompson, R. L., C. L. Chambers, and B. C. McComb. 2009. Home range and habitat of western red-backed voles in the Oregon Cascades. Northwest Science 83:46–56.
- Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). Biological Conservation 133:178–185.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.
- U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. Federal Register 55:26114–26194.
- USDA, and USDI. 1994. Northwest Forest Plan record of decision for amendments for forest service and bureau of land management planning documents within the range of the Northern Spotted Owl.

- Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. Canadian Journal of Zoology 59:1045–1061.
- Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus Maniculatus*) in seral stages of coniferous forest. Ecology 63:992–1003.
- Waldien, D. L., J. P. Hayes, and M. M. P. Huso. 2006. Use of downed wood by Townsend's chipmunks (*Tamias townsendii*) in western Oregon. Journal of Mammalogy 87:454–460.
- Wang, G. M. et al. 2013. Comparative population dynamics of large and small mammals in the Northern Hemisphere: deterministic and stochastic forces. Ecography 36:439–446.
- Waters, J. R., and C. J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. The Journal of Wildlife Management 59:858–866.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.
- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. Wildlife Monographs 185:1–50.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press.
- Wilson, T. M., and A. B. Carey. 1996. Observations of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. Northwestern Naturalist 77:35.
- Wilson, T. M., C. C. Maguire, A. B. Carey, and B. L. Biswell. 1999. Distribution and abundance of Neotoma in western Oregon and Washington.
- Zurr, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. no date. Mixed effects models and extensions in ecology with R. Springer Science Business Media, New York.

Chapter 2

ABUNDANCE, COMMUNITY CORRELATIONS AND ECOLOGICAL ASSOCIATIONS OF FOUR SMALL MAMMAL SPECIES IN LATE SUCCESSIONAL FORESTS

Matt Weldy, Clinton W. Epps, Damon Lesmeister

ABSTRACT

Effective conservation and management of small mammals requires knowledge of the dynamic nature of population demographics across co-occuring species. We estimated the abundance, temporal synchrony, and spatiotemporal associations of small mammal populations in old forest habitat in western Oregon from 2011–2016 using live-trapping mark-recapture methods at 9 sites across elevation and canopy-openness gradients. We used Huggins closed-capture models to estimate site-specific abundance of Humboldt's flying squirrels (Glaucomys oregonensis), Townsend's chipmunks (Neotamias townsendii), western red-backed voles (*Myodes californicus*), and deer mice (*Peromyscus maniculatus*). Additionally, we used generalized linear mixed effects models to investigate effects of 4 spatial and 3 temporal covariates on species-specific abundance estimates, we estimated the linear correlation between individual counts of the 8 most commonly-caught species of small mammals using Pearson's correlation coefficients, and we assessed spatial variation in sex ratios and body mass of focal species among grids. Abundance estimates varied by as much as 4-fold among years and 6-fold among sites, with only slight evidence of linear correlation between species. We observed positive autocorrelations of Humboldt's flying squirrel abundance at 1 and 5-year intervals, and negative autocorrelations of western red-backed vole abundance at 4 and 5-year intervals. Species-specific sex ratios and body masses did not vary widely across grids. Humboldt's flying squirrels were more abundant on low elevation sites with high cover of berry-producing plants, than on high elevation sites with low cover of berry-producing plants. Townsend's chipmunks and western red-backed voles were

more abundant on high elevation and open canopy sites. Deer mice were slightly more abundant on sites with high berry producing plant cover. Minimum winter temperature was positively related to the mean abundance of Humboldt's flying squirrels and Townsends chipmunks and negatively related to the mean abundance of western red-backed voles and deer mice, while western red-backed voles and deer mice were less abundant after periods of drought. Counts of the 8 most commonly captured species were only weakly correlated. Thus, even when exposed to similar spatial and temporal drivers, the focal species abundances varied independently, and 2 species exhibited cyclical population dynamics that were non-synchronous. Our findings suggest that future studies concerned with prey abundance use prey-specific temporal covariates as indices of prey abundance.

INTRODUCTION

Forests in the Pacific Northwest (hereafter PNW) have declined since the start of the 19th century primarily due to harvest for forest products until only approximately 14% of the historical old forest remains (Strittholt et al. 2006). Following the 1990 federal listing of the northern spotted owl (*Strix occidentalis caurina*) as threatened by the U. S. Fish and Wildlife Service under the Endangered Species Act, and the 1994 release of the Northwest Forest, concerns over declines in old-forest associated species led to changes in PNW forest management practices during the last 27-years (USDA and USDI 1994). In some areas, forest management practices have changed to reflect ecological values such as biodiversity, conservation, and sustainability (Christensen 1996, Holloway et al. 2012). Often, management strategies developed to foster biodiversity have used indicator species, which were

hypothesized to have correlated abundances with other species that occur in similar vegetation types (Lindenmayer et al. 2000, Smith et al. 2005, Shanley et al. 2013). Multi-species strategies are increasingly used because effective conservation requires detailed knowledge of spatiotemporal and interspecific associations within communities, guild-level contributions to ecosystem functions, and temporal synchrony of sympatric populations (Pyare and Longland 2002, Weigl 2007, White et al. 2013). Moreover, studies that explore the demographic associations and ecosystem function of species in old forests establish important comparisons of managed and disturbed ecosystems (Sinclair 1998).

Small mammals are particularly important in the PNW because they are a large component of the prey-base for both avian and mammalian predators (Wilson and Carey 1996, Fryxell et al. 1999, Bull 2000, Forsman et al. 2001, 2004, Rosenberg et al. 2003), and they improve forest health through the consumption and subsequent dispersal of hypogenous fungi, berries, and seeds (Maser et al. 1978, Bowers and Dooley Jr 1993). Small mammal research in the PNW has focused primarily on abundance or density in managed and unmanaged forests (Rosenberg and Anthony 1992, Anthony et al. 1994, Butts and McComb 2000, Holloway and Malcolm 2007), and on important northern spotted owl prey species such as the northern flying squirrel (*Glaucomys sabrinus*) and bushy-tailed woodrat (*Neotoma cinera*; Waters and Zabel 1995, Wilson et al. 1999, Pyare and Longland 2001, Smith et al. 2005, Smith 2007). Relatively few studies have quantified the spatiotemporal variability and the associations of small mammal abundance within heterogenous old forests while simultaneously exploring patterns of community structure and composition, or

while estimating the correlation in abundance of co-occurring species (Hayes et al. 1986, Aubry et al. 1991, Rosenberg and Anthony 1993, Anthony et al. 1994).

Decomposing the causes of small mammal population cycles has been an ongoing global area of research (Batzli 1996, Oli 2003, Krebs 2013). However, site specific drivers of population cycles vary widely, from patterns driven by specialist or generalist predators (Eagan et al. 2011), to patterns of food cycling (Sullivan et al. 2017b), and these patterns are often contradictory. Fryxell et al. (1998) provided evidence of population cycling for northern flying squirrels and southern red-backed voles (*Myodes gapperi*) in conifer forests in Ontario, Canada with broad similarities to the PNW small mammal community. But, similar patterns have not been observed in the PNW, despite potential influences of pulses in conifer seed resources and longterm research focus on northern spotted owl prey. In particular, the degree to which different small mammal species abundance varies, the inter and intra-specific synchronicity of that variation, and the site characteristics that influence abundance in PNW old forests are poorly understood. Yet, such variation has potential to influence forest health and exert significant pressure on species in higher trophic levels.

Here, we evaluate spatio-temporal variation and correlation in abundance for 4 focal species of small mammals from 2011–2016 in late-successional forests, as well as assessing correlation of counts of individuals for a broader community of 8 species. The objectives of our study were to 1) estimate site and year-specific capture probability (*p*), recapture probability (*c*), and fall abundance from 2011–2016 for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), western red-backed voles (*Myodes californicus*), and deer

mice (*Peromyscus maniculatus*), 2) investigate temporal autocorrelations in the abundance of focal species, 3) investigate the effects of habitat, regional climate variation, and local weather on abundance of focal species along with patterns of community composition (Table 2.1), and 4) investigate interspecific correlations of individual counts among 8 co-occurring species of small mammals.

We hypothesized that the autocorrelation patterns of Humboldt's flying squirrel, and western red-backed vole fall abundance, would show evidence for population cycling. In addition, we hypothesized that the abundances of old-forestassociated focal species would be correlated due to the synchronized effects of climate and weather on common food sources such as berry-producing shrubs and fungi. We hypothesized that spatial and temporal covariates related to forest complexity, food availability, and winter severity would be associated with the abundance of the focal species, and that trapping effort, forest canopy structure and understory composition would affect the focal species capture and recapture probabilities due to differences in trap availability and predation exposure (Table 2.2). We predicted that the abundance of Humboldt's flying squirrels, western redbacked voles and deer mice would have at least 1 significant temporal autocorrelation of abundance. We predicted that the abundances of old forest associated species such as Humboldt's flying squirrels, Townsend's chipmunks, and western red-backed voles would be positively correlated. We predicted a positive association between the fall abundance of the focal species and covariates that are related to primary food sources (coarse woody debris, berry-producing plants, conifer seed production, Palmer Drought Severity Index), and forest structural complexity (understory cover,

shrubs, canopy cover; Table 2.2). We also predicted a negative association between the fall abundance of the focal species and covariates related to winter severity (elevation, minimum winter temperature, number of days below 0 °C; Table 2.2).

STUDY AREA

We conducted this study in the H. J. Andrews Experimental Forest (hereafter HJA), on the west slope of the Oregon Cascades, near Blue River, OR (Figure 2.1). The forest completely encompasses the 6,400 ha Lookout Creek drainage basin and is part of the Willamette National Forest that is administered by Oregon State University, the Willamette National Forest and the USDA Forest Service's Pacific Northwest Research Station. The HJA is a National Science Foundation Long-Term Ecological Research site, a United States Department of Agriculture (USDA) experimental forest, and part of the Central Cascades Adaptive Management Unit delineated under the Northwest Forest Plan (USDA and USDI 1994).

The study area is representative of late-successional forests in mountainous terrain, and the dominant vegetative communities are Douglas-fir (*Pseudotsuga mensiesii*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabalis*; Cissel et al. 1999). There is a wide range of documented avian and mammalian predators including 4 species of *Accipitridae*, 6 of *Strigidae*, and 12 carnivores (Garman and Anthony 2001, Garman and McKee 2001). Elevation ranges from 636–1,288 m and the climate is marine temperate with cool, wet winters and hot, dry summers (Swanson and Jones 2001). Approximately 80% of the annual precipitation falls during the winter (October to April), and consists of rain at low elevations and snow above 1,000 m. Mean average annual precipitation during a 38-

year interval (1958–1996) on the HJA was 2,259 mm (Swanson and Jones 2001). During the study period (September to November), the mean average daily temperature was 9.3 ± 0.55 °C (\pm SE), and the mean average daily rainfall was $6.4 \pm$ 0.40 mm (\pm SE).

METHODS

Trapping design

Our grid layout and trapping procedures were in accordance with the protocols described by Carey et al. (1991). We selected 9 (10 ha) sites from a larger pool of suitable sites located in old (>400 years old) late-successional forest stands, with large trees (>81.21 cm diameter; Schulze and Lienkaemper 2015). The sites span all combinations of 3-elevation (<800m, 800–1,000m, >1,000m) classes and 3- canopy openness classes (0–15%, 15–30%, 30–40%). The elevation and canopy openness classes were classified using the Geospatial Modelling Environment (GME) tools (Version GME 0.7.4, Spatial Ecology, LLC., http://www.spatialecology.com). The average inter-site distance was 2,963 m (range = 1,078-5,940m).

On each site, we established 2 nested trapping grids to sample small mammals with a range of body sizes. The larger of the nested grids (7.84 ha) consisted of 128 Tomahawk Model 201 live traps (Tomahawk Live Trap, WI, USA) placed at 64 trap stations arranged in an 8 x 8 array with a slope adjusted 40 m inter-trap distance. We deployed two Tomahawk traps < 5 m from each trap station center. One trap was attached approximately 1.5 m from the ground to a suitable tree bole and the other was placed on the ground (Risch and Brady 1996). We placed both traps on the ground if there was not a suitable tree bole within 5 m of the trap station center. The smaller of the nested grids (1 ha), intended to target the smaller-bodied mammals, consisted of 100 Sherman model LFATDG live traps (H. B. Sherman Traps, FL, USA) placed within 2 m of 100 trap station centers. We arranged the trap stations in a 10 x 10 grid array with 10 m inter-trap distances corrected for slope. We standardized the position of the small trapping grids relative to the larger trapping grid to avoid spatial sampling bias. To increase the probability of a small mammal encountering a trap, we placed Sherman and Tomahawk ground traps near habitat features (Carey et al. 1991). It rained consistently during the study period, thus, to reduce trapping related mortalities, we set traps in waxed cardboard cartons and each was supplied with a nest a box stuffed and dry cotton batting. Traps were baited with a mixture of peanut butter, molasses, oats, and sunflower seeds (Carey et al. 1991).

We randomly determined the site trapping order, once in 2011, with priority given to higher elevation sites to reduce the impact of snow and rain as fall temperatures decrease. Each fall (September to November) from 2011–2016, we trapped each Tomahawk grid for 3 consecutive trapping weeks, and each Sherman grid for one trapping week. However, in 2011 we did not trap 3 of the Sherman grids due to time constraints. A trapping week consisted of 4 trap nights; traps were opened on Monday, closed on Fridays and checked once per day. We marked each animal with a unique ear tag and recorded individual condition, species, sex, and body weight (g). In addition, we recorded the tail width (mm), reproductive condition, and individual age class of Humboldt's flying squirrels (Villa et al. 1999). At the end of each season, we necropsied all trap-related mortalities to validate field identification of species, sex, and reproductive condition. Although we captured 21 species of

mammals during the study, many of the species were uncommon. We therefore chose the 4 most commonly captured species as focal species for a mark-recapture estimation of annual fall abundance and habitat association: Humboldt's flying squirrels, Townsend's chipmunks, western red-backed voles, and deer mice. Our protocols were approved by Oregon State Universities Institutional Animal Care and Use Committee (ACUP #4191, 2011-2013; #4590, 2014-2016), and are in accordance with the standard animal care principles of the American Society of Mammalogists (Sikes and Gannon 2011).

Development of covariates

We developed 6 covariates related to forest complexity and food availability to examine spatial variation in abundance, capture probability, and recapture probability (Table 2.1). We estimated average study site elevation and canopy openness using 2008 LiDAR data in ArcGIS version 10.3.1 (Spies 2016). To estimate study site canopy openness, we first classified each square meter of our sites into 2 vegetation height classes (0 – 10 m and >10 m), and then used the proportion of the 2 vegetation height classes as an estimate of site-level canopy openness. During the summer of 2016, we measured understory vegetation at 18 Tomahawk sampling stations across each study site. We assumed that study-site understory characteristics were stable during the 6-year time study because there were no disturbance events to change forest structural characteristics and the dominant tree community on each study site did not change. We measured all coarse woody debris >10 cm in diameter that intersected 2 perpendicular 18 x 3 m transects centered on each vegetation sampling station. We estimated coarse woody debris volume by summing all

individual log volumes (multiplied the length of each measured log by the diameter at one-half the intersecting length; Harmon and Sexton 1996, Smith 2007). We visually estimated berry-producing plant, shrub cover, and subcanopy cover as the percentage of ground covered by each understory characteristic of interest (to the nearest 5%) in 2 m diameter subplots at the center of each habitat sampling station. The cover of berry-producing plant species overlapped at some of the habitat sampling stations. Thus, the berry-producing plant cover covariate was the sum of sampling-site percentage of ground covered by *Rubus spp.*, huckleberry (*Vaccinium spp.*), salal (Gaultheria shallon), and Oregon grape (Mahonia aquifolium). Therefore, the berryproducing plant cover could exceed 100%. We estimated shrub cover as the percentage of ground covered by woody shrubs <1.5 m tall. Subcanopy cover was the amount of canopy or sky within 2 m of the habitat sampling station center occluded by shrubs >1.5 m tall and <6 m tall. The habitat measurements for each of the sampled understory characteristics were averaged across the 18 habitat sampling stations on each study-site. We tested the understory characteristics for linear correlation using the Pearson's correlation coefficient and we tested for differences in understory characteristics between sites using a separate means model (Appendix 1.1). We corrected the pairwise test using the Bonferroni multiple test correction. We retained only understory characteristics with a Pearson's correlation coefficient <0.80 that also had at least one significant difference between sites after the multiple test correction.

We developed 3 trapping, 1 inter-annual, 4 weather, and 3 climate covariates to examine temporal variation in abundance, capture probability or recapture probability. The 12 covariates were either found to be associated with the parameters of interest in previous studies or were considered relevant given the biology of the focal species (Table 2.1). The three trapping covariates tested the effect of trapping methodology on the parameters of interest. Trapping trend was a count of trapping days, that tested for a change in the parameter of interest during trapping. The season covariate was a linear trend from the start of the trapping season until the last day of trapping. The trapping effort and Townsend's chipmunk covariates tested for an effect of trap availability on the probability of capture. Minimum daily air temperature (°C), the number of days below zero (°C), total winter precipitation (mm) from October 1 to April 1, and the maximum snow depth from October 1 to April 1 were recorded by the H. J. Andrews Central Meteorological Station, which is within the study site elevation range and is just east of the project's center (Daly and McKee 2016). However, from 2011–2016 two pairs of estimates were highly correlated (pairwise Pearson's correlation coefficients >0.8): minimum daily air temperature and maximum snow depth as well as the number of days below zero and winter precipitation. Therefore, we only considered minimum daily air temperature (°C) and the number of days below zero (°C), which were uncorrelated (Appendix 1.2). Palmer's Drought Severity Index (PDSI), Pacific Decadal Ossiclation (PDO) and Southern Oscillation Index (SOI) were highly correlated in our study region from 2011–2016 so we retained only the PDSI (Appendix 1.2). PDSI is a monthly estimate of the regional deviations from average moisture conditions and is an index of net primary productivity (NOAA 2017). PDSI values range from -6-6 and describe a range of moisture conditions from drought to wet respectively. We used an 18-month

average of the Oregon PDSI estimate because net primary productivity in the Northern hemisphere is associated with cumulative droughts, longer than one year (Huang et al. 2016).

Detection and abundance analyses

We used Huggins' closed capture models implemented in Program MARK to estimate the annual site-specific fall abundance for the focal species (Huggins 1989, White and Burnham 1999). Huggins' closed capture and recapture models are used to estimate capture probability (p) and recapture probability (c) in terms of observable characteristics. Capture probability is defined as the the probability of capturing an animal for the first time. Recapture probability is defined as the probability of recapturing an individual that has been captured before. The Huggins model likelihood was conditioned only on captured individuals, and abundance (N) was a derived parameter that was a function of the number of individuals caught and the probability that individuals are captured at least once during the study (Huggins 1991). We used a sequential modeling strategy to develop and identify the most supported model(s). The data were insufficient to accommodate interactions, so we considered only single and 2-factor additive models for capture and recapture probability. Furthermore, each model was limited to one spatial and one temporal covariate. First, we tested each of the focal species for behavioral effects using models that tested for differences in the capture and recapture probability that might indicate an effect of trapping (trap attraction or trap aversion). Next, we modeled recapture probability while maintaining a time-varying capture probability model structure. We then modeled capture probability using the best model structure for

recapture probability identified in the previous step. After the sequential modeling, we used model averaging to obtain our best site and year-specific estimates of abundance.

We used Akaike's Information Criterion, corrected for small sample sizes (AIC_c) and cumulative AIC_c weights (w_i) , to select the best supported model in each sequential modelling step (Burnham and Anderson 2002). We selected the model with the lowest AIC_c and highest w_i as our best supported model (Burnham and Anderson 2002). In addition, we used the relative change in AIC_c (Δ AIC_c) to evaluate each model relative to the top-ranking model. We used w_i and the degree to which the 95% confidence interval (hereafter CI) for the slope coefficients overlapped 0 to evaluate the strength of evidence for single parameters.

Spatial and temporal intraspecific and community correlations

We estimated intra-species autocorrelation of grid- and year-specific abundances to assess the correlation between the species-specific abundance estimates as a function of the time separating them (lag). We considered the first 5 annual lags and we assumed the abundance estimates of each grid were independent spatial replicates. We evaluated the first 5 lags on all nine sites and computed the species-specific range of correlation values that could be obtained if the correlation was actually 0. The magnitude of each estimated annual lag indicates the correlation between abundance estimates at an interval of the lag coefficient. The direction of each estimated lag indicates the direction of the correlation relationship between two abundance estimates. We considered the magnitude of the annual lags meaningful, if they were larger than the range of sample correlations that could be obtained if the true correlation really was 0.

To assess the relationships among MNKA and the relationships among the estimated abundances, we performed a year- and site-specific pairwise assessment of the Pearson's correlation coefficient between species counts (minimum number known alive, MNKA) for the 8 most commonly captured species and the abundance estimates of the focal species. The 8 most commonly captured species were Humboldt's flying squirrels, Townsend's chipmunks, western red-backed voles, deer mice, bushy-tailed woodrats (*Neotoma cinerea*), creeping voles (*Microtus oregoni*), Douglas' squirrels (*Tamiasciurus douglasii*), snowshoe hares (*Lepus americanus*), and American pikas (Ochotona princeps). We also estimated the intra-specific spatial and temporal correlation of the focal species abundance estimates using the Pearson's correlation coefficient. We interpreted the strength of the relationship according to the absolute value of the estimated correlation coefficient and the sign of the correlation coefficient as the direction of the relationship. Specifically, we considered pairwise correlation coefficients with an absolute value >0.7 to be strongly correlated, pairwise correlation coefficients with an absolute value between 0.5–0.7 to be moderately correlated, pairwise correlation coefficients with an absolute value between 0.3-0.5 to be weakly correlated, and pairwise correlation coefficients <0.3 to have negligible correlation (Hinkle et al. 2003).

Population structure

Abundance is not always a good indicator of habitat quality, because suboptimal or sink habitats can sometimes have high animal abundance as a result of

37

emigration (Robertson and Hutto 2006, Van Horne 1983). Suboptimal or sink habitat may harbor populations composed primarily of the subordinate sex (for species with sex-segregated habitat use patterns), or poor-quality individuals, or reflect the upswing phase of larger magnitude temporal variations in abundance (Ecke et al. 2002, Robertson and Hutto 2006). Thus, to examine relative differences in habitat quality between our sites, we estimated year and site-specific sex ratios and sexspecific average body weight (Greenberg et al. 2006, Sollmann et al. 2015). We considered a site- and species-specific departure among all years from the mean species-specific sex ratio, where a site might have either the highest or lowest sex ratio among all years, as evidence for abnormal species sex structuring, which might be related to habitat quality (Robertson and Hutto 2006). Species-specific sex-ratios were estimated as the number of known males divided by the number of known females caught at each site within a year. Average body weight estimates were calculated by averaging the individual body weights of all captured individuals on a grid.

Habitat relationships

We used generalized linear mixed effects models (GLMM) with negative binomial distributions to examine the relationships between the mean abundance of the focal species and the main effects of spatial (4) and temporal (3) covariates (Zurr et al. 2009, Bates et al. 2014, See Appendix 2 for a model description). The site and year-specific Huggins abundance estimates were the dependent response variables, and the spatial and temporal covariates were the independent variables. All models included one random effect: spatial models included a year-specific random effect to compensate for unmodeled temporal variability and temporal models included a sitespecific random effect to compensate for unmodeled spatial variability. We assessed average stand elevation, stand canopy openness, berry-producing plant cover, coarse woody debris volume, the number of winter days below 0°C, minimum winter temperature, and PDSI as fixed effects for each of the focal species.

We assessed model assumptions graphically. We checked plots of the fitted values against the residual values from the fitted model, to check for patterning. In addition, we checked each fitted model for over dispersion by comparing the sum of the squared Pearson residuals to the residual degrees of freedom from the model. Overdispersion estimates for all fitted models were assessed by dividing the Pearson's residuals by the residual degrees of freedom.

We assessed the strength of evidence for each variable in the GLMM's by comparing the estimated changes in mean abundance, and 95% CI, across the sampled range, to species-specific *a priori* biologically meaningful values. We used average site-level temporal change in abundance as our biologically significant value. We chose this because we assumed that in late-successional forests there is no longterm trend in the average abundance of the focal species and that average site level temporal change in abundance would adequately describe naturally occurring variability that reflects stochastic noise around a constant long-term mean abundance (Fryxell et al. 1998). The biologically significant value is likely conservative, because the average site-level annual change in abundance also incorporates variation associated with the effect being tested and the sampled range for each effect does not describe the full biologically potential range for each considered variable (Sullivan et al. 2017a). We considered a covariate to be strongly associated with abundance if the absolute value of the estimated change in mean abundance across the range of the sampled covariate was larger than the biologically meaningful value and the 95% CIs for the estimated change in mean across the range of sampled covariate also did not contain 0 or the biologically meaningful value. If the 95% CIs for the prediction did not contain 0 but included values less than the biologically meaningful value, the covariate was considered weakly associated with mean abundance. The sign of the estimated change in mean abundance indicated the direction of the effects. This comparison was used as general evidence of a biological effect, and not a strict null hypothesis test.

We used bootstrapping (n=5,000) to estimate the variance for the estimated effect sizes. Individual bootstrap samples estimated the difference in average abundance at the maximum and minimum values of the sampled variable using the fitted GLMMs. We then estimated the 95% CI using the 0.025 and 0.975 quantiles of the bootstrapped samples.

We estimated all correlations, and fit all GLMMSs using R (R Version 3.4.1, www.r-project.org, accessed 1 Aug 2017). The GLMMs were fit using the lme4 package (lme4 version 1.1-13, https://cran.r-project.org/web/package=lme4, accessed 1, Aug 2017). GLMMs were then ranked according to AIC using the AICcmodavg package (AICcmodavg version 2.1-1, https://cran.r-project.org/package=AICcmodavg, accessed 1, Aug 2017). We estimated response predictions and 95% CIs using the merTools package version 0.3.0 (merTools version 0.3.0, https://CRAN.R-project.org/package=merTools, accessed 1 Aug 2017).

RESULTS

Over the 6-year study period, we captured 45,683 small mammals of 21 species, with an average of 1,261 individuals caught per year. From 2011–2016, we live-trapped a total of 62,217 Tomahawk and 15,130 Sherman trap nights (adjusted for stuck or sprung traps). We individually marked 1,076 Humboldt's flying squirrels, 3,464 Townsend's chipmunks, 757 deer mice, and 635 western red-backed voles (Appendix 1.3). Average grid- and year-specific captures of individuals were 30.7 (4–56) Humboldt's flying squirrels, 73.8 (25–176) Townsend's chipmunks, 15.5 (4–42) deer mice, and 13.1 (0–44) western red-backed voles.

Townsend's chipmunks were captured more frequently than Humboldt's flying squirrels on the Tomahawk trapping grids and deer mice were captured more frequently than western red-backed voles on the Sherman grids during the first 4 years of the study (Appendix 1.3). However, captures of western red-backed voles increased each year of the study on all trapping sites eventually surpassing deer mice on some study-sites during 2016. Sex ratios based on the numbers of individuals captured were male-biased for both Townsend's chipmunks and deer mice, femalebiased for western red-backed voles and nearly unbiased for Humboldt's flying squirrels (Table 2.3). The site and year-specific male to female ratios did not indicate a consistent bias for any of the species among all years (Appendix 1.4). However, the site-specific male to female ratio for Humboldt's flying squirrels on low elevation sites was consistently closer to the observed average ratio than on higher elevation grids. Average sex-specific body weight comparisons between sites did not reveal any consistent pattern (Appendix 1.8). We observed slight evidence for spatial variation in focal species abundance among grids, but there was no evidence of a consistent significant between-site difference in temporal change in abundance (Figure 2.2, Appendix 1.3). Thus, we concluded that there was no evidence for any of our trapping sites being marginal or sink habitat.

Recapture probabilities were higher than capture probability for all of the focal species. Recapture probability of the focal species was negatively associated with the trapping session (Humboldt's flying squirrels: β_{Trapping Trend}: -0.05 95% CI: -0.07 to -0.04, Townsend's chipmunks: $\beta_{\text{Trapping Trend}}$: -0.53 95% CI: -0.54 to -0.52, deer mice: β_{Trapping Trend}: -0.37 95% CI: -0.52 to -0.22, western red-backed vole: $\beta_{\text{Trapping Trend}}$: -0.11 95% CI: -0.27 to 0.03; Table 2.4). Elevation was positively associated with the recapture probability of Humboldt's flying squirrels ($\beta_{\text{Elevation}}$: 0.05 95% CI: -0.23 to 0.33) and deer mice ($\beta_{\text{Elevation}}$: 0.13 95% CI: -0.73 to 0.98), and negatively associated with recapture probability for Townsend's chipmunks ($\beta_{Elevation}$: -0.89 95% CI: -1.07 to -0.72) and western red-backed voles (β_{Elevation}: -0.82 95% CI: -1.60 to -0.04). Year-specific effects were associated most with Humboldt's flying squirrel and Townsend's chipmunk capture probability (Table 2.5). Humboldt's flying squirrel capture probability ranged from 15% (95 % CI: 13% to 19%) in 2013 to 33% (95% CI: 29% to 38%) in 2015. Townsend's chipmunk capture probability ranged from 24% (95% CI: 22% to 27%) in 2011 to 44% (95% CI: 41% to 48%) in 2015. The day of the trapping session was positively associated with western redbacked vole ($\beta_{\text{Trapping Trend}}$: 0.19 95% CI: 0.03 to 0.35) and deer mouse ($\beta_{\text{Trapping Trend}}$: 0.19 95% CI: 0.03 to 0.35) capture probability. Canopy openness was positively associated with Humboldt's flying squirrel (β_{Canopy} : 0.19 95% CI: 0.03 to 0.35) and

deer mouse (β_{Canopy} : 0.04 95% CI: -0.03 to 0.12) capture probability (Table 2.5). Shrub cover (β_{Shrub} : 0.007 95% CI: 0.003 to 0.01) was positively associated with Townsend's chipmunks capture probability.

Humboldt's flying squirrel and Townsend's chipmunk abundance significantly increased on moderate to high canopy openness sites from 2011–2013, and then decreased in 2014, 2015, 2016 (Figure 2.2). Western red-backed vole abundance significantly increased on every study site during the study (Figure 2.2), except the low elevation/high canopy openness study site. Western red-backed vole abundance was higher on high elevation sites especially in 2013, 2014, 2015 and 2016. However, there were few detectable differences in western red-backed vole abundance across the range of canopy openness (Figure 2.2). We did not observe a consistent pattern in deer mouse abundance changes during the study, but every grid had at least 1 significant change (Figure 2.2).

Counts of the 8 considered species were not strongly correlated (Table 2.6). Bushy-tailed woodrats were moderately positively correlated with American pikas, but MKNA was low for both species. Humboldt's flying squirrel counts were negatively correlated with western red-backed vole counts and positively correlated with deer mouse counts, but the correlation was weak. Townsend's chipmunk and western red-backed vole counts were negatively weakly correlated with bushy-tailed woodrat counts, but the correlation was weak. Western red-backed vole and creeping vole counts were also weakly correlated with snowshoe hare counts. We found multiple autocorrelation lags of focal species fall abundance that were statistically different from zero: lags 1 and 5 for Humboldt's flying squirrels, lags 1–4 for Townsend's chipmunks, lags 1, 2, 4 and 5 for western red-backed voles, and lag 1 for deer mice (Figure 2.3). Humboldt's flying squirrels, western red-backed vole (negative) and deer mouse (positive) abundance estimates were weakly correlated (Table 2.7). Spatial correlations of abundance between sites for Humboldt's flying squirrels, Townsend's chipmunks, and western red-backed vole's abundance estimates were moderate to strong, while the spatial correlations of deer mice were weak to negligible (Figure 2.4). Temporal correlations of abundance between for Humboldt's flying squirrels were strong, Townsend's chipmunks and western red-backed vole between for Humboldt's flying squirrels were strong, Townsend's chipmunks and western red-backed voles were moderate, and deer mice were weak (Figure 2.5).

We found no graphical evidence that the assumptions of our negative binomial generalized linear mixed effects models were not met. We did not observe any patterning of the residual values when plotted against the fitted values. Estimates of overdispersion for all negative binomial generalized linear mixed effects models ranged between 0.76–1.02, which indicates no overdispersion.

We observed a positive association between Humboldt's flying squirrel mean abundance, minimum winter temperature ($\beta_{Min. Temp.}$: 0.34 95% CI: 0.04 to 0.65), and berry-producing plant cover (β_{Berry} : 1.89 95% CI: 1.31 to 2.56), and a negative association between Humboldt's flying squirrel mean abundance and elevation ($\beta_{Elevation}$: -0.81 95% CI: -1.23 to -0.47; Figure 2.6). A change in berry-producing plant cover from 12.1–51.2% resulted in a estimated increase of 23.72 squirrels (95% CI: 22.24 to 41.34) per 7.84 ha site, which was a biologically meaningful effect (Figure 2.6). Canopy openness, coarse woody debris, the number of days below 0°C in the preceding winter and PDSI did not have a detectable effect on Humboldt's flying squirrel mean abundance (Figure 2.6).

Townsend's chipmunk mean abundance was positively associated with elevation ($\beta_{Elevation}$: 1.00 95% CI: 0.60 to 1.42), canopy openness (β_{Canopy} : 2.17 95% CI: 1.26 to 2.99), and minimum winter temperature ($\beta_{Min. Temp.}$: 0.22 95% CI: 0.01 to 0.43), and negatively associated with berry-producing plant cover (β_{Berry} : -1.07 95% CI: -1.90 to -0.21). A change in average site elevation from 683–1,244 m resulted in an estimated increase of 46.13 chipmunks (95% CI: 45.72 to 69.39) per (7.84 ha) site and a change in site canopy openness from 9–38% resulted in an estimated increase of 48.14 chipmunks (95% CI: 47.66 to 73.23) per (7.84 ha) site, both effects were biologically meaningful (Figure 2.6). Coarse woody debris, the number of winter days below 0 °C and PDSI did not have a detectable effect on Townsend's chipmunk mean abundance (Figure 2.6).

Western red-backed vole mean abundance was positively associated with elevation ($\beta_{Elevation}$: 1.77 95% CI: 1.02 to 2.51) and canopy openness (β_{Canopy} : 3.06 95% CI: 0.91 to 4.95), and negatively associated with berry-producing plant cover (β_{Berry} : -1.78 95% CI: -3.39 to -0.20), minimum winter temperature ($\beta_{Min. Temp.}$: -0.87 95% CI: -1.50 to -0.19), and PDSI (β_{PDSI} : -0.45 95% CI: -0.54 to -0.38. A change in PDSI from -2.67–2.25 resulted in biologically meaningful decrease of 27.32 voles (95% CI: 25.11 to 12.09) per (1 ha) site (Figure 2.6). Canopy openness, coarse woody debris volume, and the number of winter days below 0°C did not have a detectable effect on western red-backed vole mean abundance (Figure 2.6).

Deer mouse mean abundance was positively associated with berry-producing plant cover (β_{Berry} : 1.48 95% CI: 0.11 to 2.91), and negatively associated with minimum winter temperature ($\beta_{Min. Temp.}$: -0.87 95% CI: -1.59 to -0.15), and PDSI (β_{PDSI} : -0.14 95% CI: -0.24 to -0.06). These observed effects were all weak and were not biologically meaningful (Figure 2.6). Elevation, canopy openness, coarse woody debris, and the number of days below 0°C in the preceding winter did not have detectable effects on deer mouse mean abundance (Figure 2.6).

DISCUSSION

We observed considerable temporal variation in fall abundance that was larger than spatial variation in fall abundance. We also observed variable responses to the same spatiotemporal predictors among 4 co-occurring small mammal species from 2011–2016. In general, focal species mean abundances were associated with elevation, berry-producing plant cover and minimum winter temperature, but both the magnitude and direction of the effects varied. Spatial and temporal associations of mean abundance were most similar for Humboldt's flying squirrels and deer mice, and for Townsend's chipmunks and western red-backed voles. We identified at least 1 biologically meaningful association for each of the three old forest-associated species, with no overlap between species. In contrast, we did not observe any biologically meaningful associations for the generalist deer mouse.

Many previous studies of PNW small mammal demography have explored the effects of forest management practices on 2 or fewer co-occurring small mammals with an emphasis on Humboldt's flying squirrels (Rosenberg and Anthony 1992, Anthony et al. 1994, Carey 1995, Butts and McComb 2000, Lehmkuhl et al. 2006).

Few studies have concurrently explored natural variability in late-successional forests or the demographics of more than 2 co-occurring species (Aubry et al. 1991, Anthony et al. 1994, Songer et al. 1997, Pyare and Longland 2002, Smith and Nichols 2003, Shanley et al. 2013). If co-occurring species compete for resources, we might expect a negative linear pairwise correlation of abundance or counts, although negative linear correlations can also indicate differences in species habitat associations (Porter and Dueser 1982). Conversely, we would expect positive linear associations between species that rely on similar food resources or were similarly affected by temporal variation in local weather or regional climate. We found little evidence of strong correlations between the counts of the 8 most commonly captured species or the abundance estimates of the focal species. We did not observe a positive correlation between deer mouse and western red-backed vole abundance, which has been previously observed (Galindo and Krebs 1985). However, contrary to our predictions, we did observe a weak negative correlation between Humboldt's flying squirrels and western red-backed voles, which have similar food habits and activity patterns (Ure and Maser 1982, Maser et al. 1985); moreover, the counts of other old-forestassociated species were not correlated.

Humboldt's flying squirrel's 3-year negative and 5-year positive autocorrelations suggests that populations on our study sites might exhibit population cycles at least every 5 years, which is slightly shorter than previous estimates of Fryxell et al. (1998), but in general agreement. Our observed 4–5-year negative autocorrelations for western red-backed voles are similar to evidence found for 6–8year population cycles for southern red-backed voles (*Myodes gapperi*) in southern British Columbia, Canada, but approximated half of the cycle time for southern redbacked voles observed in Algonquin Provincial Park, Ontario, Canada (Fryxell et al. 1998, Sullivan et al. 2017). Additionally, we found evidence for positive autocorrelation among Townsend's chipmunk abundance that diminished as the number of years between estimates increased, similar to patterns observed by Fryxell et al. (1998).

Small mammal populations in the PNW are likely resource limited (Sullivan and Sullivan 1982, Carey and Johnson 1995, Waters and Zabel 1995), but little is known about the effects of predation and interspecific competition among small mammals in the PNW (Smith et al. 2003). If resource limitations are driving the differences between species, the limiting resource for each species is different. We observed peak abundances of Humboldt's flying squirrels and Townsend's chipmunks during 2013; yet, differences in the spatiotemporal associations of the focal species suggests little temporal synchrony of small mammal abundances on our study sites. Thus, we emphasize the differences in abundance and spatiotemporal associations between co-occurring small mammal species and we suggest that single species management strategies might not facilitate biodiversity management goals.

Much of the previous work in the PNW exploring variation in abundance of these focal species has focused on spatial relationships, especially for the Humboldt's flying squirrel (Lehmkuhl et al. 2006, Holloway and Malcolm 2007*b*, Holloway and Smith 2011, Shanley et al. 2013). We observed considerable variability in the focal species' response to spatial environmental covariates, but the species-specific responses were generally in agreement with the findings of previous studies or with our predictions. The spatial associations of Humboldt's flying squirrels were least similar to other focal species. The generalist deer mouse was only weakly associated with any of our predictor variables, which is consistent with other studies where habitat generalists have little change in abundance between study sites (Martell 1983, Klenner and Sullivan 2009, Lehmkuhl et al. 1999).

Previous work exploring the diets of northern flying squirrels have primarily consisted of a microscopic examination of fecal pellets and subsequent identification of fungal genera (Maser et al. 1985, Cazares et al. 1999, Lehmkuhl et al. 2004). As a result, differences in the digestibility of food items have likely resulted in an underestimation of the regional variation in the diet of Humboldt's flying squirrels and northern flying squirrels (Smith 2007). Humboldt's flying squirrel mean fall abundance was associated most strongly with berry-producing plant cover. Thysell et al. (1978) reported observations of northern flying squirrels foraging on salal berries in western Washington. Smith et al. (2004) reported a slight significant positive correlation between the abundance of *Vaccinium* plants and northern flying squirrel habitat use. The ecological link between northern and Humboldt's flying squirrel abundance and berry-producing plants is poorly understood (Smith et al. 2004). We were unable to further develop our understanding of the ecological link, so future studies will be needed to test this relationship.

We hypothesize that the strong positive association we observed between Townsend's chipmunk mean abundance, elevation, and canopy openness, as well as the weak positive association between western red-backed vole mean abundance, elevation, and canopy openness, were related to efficient consumption of seeds or

49
spatial variability in conifer seed production. Conifer cone crops are associated with mean abundance of mice (Muridae and Cricetidae), voles, and squirrels (Falls et al. 2007, LaMontagne et al. 2013, Lobo 2014, Ogawa et al. 2017). Douglas-fir (2–7 years between peaks) seed production is known to vary annually and can fail, which can have strong demographic consequences for seed foragers (Allen and Owens 1972, Fowells 1965, Smith 1970). Western hemlocks (3–4 years between peaks) produce some seed every year, which might stabilize populations of seed predators on sites with relatively high western hemlock densities (Fowells 1965). Although we predicted that western red-backed voles would be more abundant in closed canopy stands because more overstory trees would contribute to litter depth, as observed by Anthony et al. (1994) and Thompson et al. (2009), we only observed a weak positive association. Doyle (1987) observed a positive relationship between western redbacked vole abundance and western hemlock canopy coverage, but we did not estimate canopy openness for individual tree species. Western hemlock needles decay more slowly than Douglas-fir needles and may disproportionately contribute to an increase in forest floor litter depth (Edmonds 1990). As predicted, the abundance of western red-backed voles increased as study site elevation increased. On our study sites, changes in elevation might reflect an increase in western hemlock density, because western hemlocks were slightly more numerous on our mid to high elevation sites (with the exception of our highest elevation site; Appendix 1.5).

The focal species in this study contribute to the diet of many PNW predators, and previous studies have identified multiple hypotheses about how forest structural components influence the ability of small mammals to escape from predation (Carey 2000, Holloway and Malcom 2006). For example, Manning and Edge (2004) suggested that nonlinear association between deer mouse apparent survival understory characteristics, might be related to an association between understory density and predation rates. However, the demographic consequences of predation for small mammals in the PNW remain unknown, and we were unable to estimate the potential effects of predators during this study.

Few previous studies in the PNW have examined effects of temporal covariates on small mammal abundance (Tallmon et al. 2003, Lehmkuhl et al. 2006). We observed similarities in temporal associations that were structured by animal size. Humboldt's flying squirrels and Townsend's chipmunks, the two larger focal species, were both most associated with minimum winter temperature, but the effect for both species was weak despite considerable temporal variation in abundance. However, despite differences in winter torpor strategies, the direction and magnitude of the association between these two species was similar. Because northern flying squirrels do not hibernate, while Townsend's chipmunks are true hibernators (Wells-Gosling and Heaney 1984, Levesque and Tattersall 2009), we expected that minimum winter temperature could have a stronger effect on Humboldt's flying squirrels (Turbill and Prior 2015). Western red-backed voles and deer mice abundances were both associated strongly with PDSI. While they also were both weakly associated with minimum winter temperature, the relationship was opposite to that of the largerbodied Humboldt's flying squirrels and Townsend's chipmunks.

In summary, the spatial and temporal drivers of abundance for these focal species varied in both their strength and direction. Previous research did little to

51

explore the drivers of PNW small mammal community assembly beyond speciesspecific habitat associations and niche descriptions, especially in natural forests (Smith and Balda 1979, Galindo and Krebs 1985). In our system, overlap in speciesspecific associations with spatial and temporal covariates indicate the potential for intraspecific competition driven by resource limitation. We did not observe evidence for interspecific competition between our focal species based on correlations in species-specific abundance estimates on our sites. Instead, the focal species might effectively partition resources by size, space or time to minimize competitive overlap in a potential food limited system.

MANAGEMENT IMPLICATIONS

Assessing population size in harvested forests relative to natural variability in old forests is an informative method to compare effects of disturbance on small mammal populations (Sullivan et al. 2017a). This long-term data for small mammal populations provides an effective baseline estimate of demographic response to spatial and temporal covariates in late-successional forests, which can be used to compare with populations in disturbed landscapes. Previous, short-term studies indicated that Humboldt's flying squirrels, Townsend's chipmunks and western redbacked voles were more abundant in old forests when compared to younger forests, and our estimates were intermediate to these where methods were comparable (Carey 2000, Doyle 1987, Rosenberg and Anthony 1993, Holloway and Smith 2011). Multiple studies have explored the effects of management strategies designed to create old forest conditions in managed stands (Butts and McComb 2000, Holloway and Malcom 2007*a*, Loeb 1999, Sinclair 1998), and this study indicated that

managers might positively influence the abundance of Humboldt's flying squirrels by increasing the cover of berry producing plants.

Prey abundance has been suggested as an influential variable affecting the population parameters of multiple forest carnivores including the northern spotted owl (Wiens et al. 2014). Few studies have used prey-specific demographic estimates or surrogates for abundance. Previous northern spotted owl demographic studies have used PDSI as a surrogate variable for prey abundance, which, might have been a poor predictor of prey abundance during this study, as it would have predicted only a small component of the spotted owl's diet (Forsman et al. 2004, Glenn et al. 2010, Forsman et al. 2011, Dugger et al. 2016). Thus, we suggest future studies use prey-specific temporal covariates as indices of prey abundance. Specifically, we suggest that minimum winter temperature was a better overall predictor of the focal species abundance and a better predictor of Humboldt's flying squirrel and Townsend's chipmunk's abundance. While PDSI would be an effective predictor for studies that consider the abundance of western red-backed voles and deer mice.

LITERATURE CITED

- Allen, G. S., and J. N. Owens. 1972. The life history of Douglas-fir. Forest Service, Ottawa, Canada.
- Anthony, R. G., D. K. Rosenberg, and K. A. Swindle. 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. Northwest Science 68:266–272.
- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. GutiéRrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs 163:1–48.
- Aubry, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Bowers, M. A., and J. L. Dooley Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia 94:247–254.
- Bates, D., M. M\u00e4chler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.
- Bull, E. 2000. Seasonal and sexual differences in American marten diet in northeastern Oregon. Northwest Science 74:186–191.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- Butts, S. R., and W. C. McComb. 2000. Associations of forest-floor vertebrates with coarse woody debris in Managed forests of western Oregon. The Journal of Wildlife Management 64:95–104.
- Carey, A. B., B. L. Biswell, and J. W. Witt. 1991. Methods for measuring populations of arboreal rodents. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Carey, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications 5:648–661.

- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological applications 5:336–352.
- Carey, A. B., J. Kershner, B. Biswell, and L. D. de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142:3–71.
- Cazares, E., D. L. Luoma, M. P. Amaranthus, C. L. Chambers, and J. F. Lehmkuhl. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade Range. Northwest Science 73:64–76.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, and others. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications 6:665–691.
- Cissel, J. H., F. J. Swanson, and P. J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9:1217–1231.
- Cotton, C. L., and K. L. Parker. 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. Canadian Journal of Zoology 78:1896–1901.
- Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus, Microtus oregoni* and *M. richardsoni*. American Midland Naturalist 118:258–265.
- Daly, C., and W. McKee. 2016. Meteorological data from benchmark stations at the Andrews Experimental Forest, 1957 to present. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MS001 Accessed 18 March 2018.
- Dracup, E. C., D. M. Keppie, and G. J. Forbes. 2016. The short-term impact of abundant fruit upon deer mouse (*Peromyscus maniculatus*), southern red-backed vole (*Myodes gapperi*), and woodland jumping mouse (*Napaeozapus insignis*) populations. Canadian Journal of Zoology 94:555–563.
- Dugger, K. M., E. D. Forsman, A. B. Franklin, R. J. Davis, G. C. White, C. J.
 Schwarz, K. P. Burnham, J. D. Nichols, J. E. Hines, C. B. Yackulic, P. F.
 Doherty, L. Bailey, D. A. Clark, S. H. Ackers, L. S. Andrews, B. Augustine, B.
 L. Biswell, J. Blakesley, P. C. Carlson, M. J. Clement, L. V. Diller, E. M. Glenn,
 A. Green, S. A. Gremel, D. R. Herter, J. M. Higley, J. Hobson, R. B. Horn, K. P.
 Huyvaert, C. McCafferty, T. McDonald, K. McDonnell, G. S. Olson, J. A. Reid,
 J. Rockweit, V. Ruiz, J. Saenz, and S. G. Sovern. 2016. The effects of habitat,

climate, and barred owls on long-term demography of northern spotted owls. The Condor 118:57–116.

- Ecke, F., O. Löfgren, and D. Sörlin. 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. Journal of Applied Ecology 39:781–792.
- Edmonds, R. L. 1990. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and pacific silver fir ecosystems in western Washington. Canadian Journal of Forest Research 10:327–337.
- Ernest, S. K., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.
- Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*. Oecologia 32:171–193.
- Falls, J. B., E. Falls, and J. M. Fryxell. 2007. Fluctuations of deer mice in Ontario in relation to seed crops. Ecological Monographs 77:19–32.
- Forsman, E. D., I. A. Otto, S. G. Sovern, M. Taylor, D. W. Hays, H. Allen, S. L. Roberts, and D. E. Seaman. 2001. Spatial and temporal variation in diets of spotted owls in Washington. Journal of Raptor Research 35:141–150.
- Forsman, E. D., R. G. Anthony, E. C. Meslow, and C. J. Zabel. 2004. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research 38:214–230.
- Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, J. E. Hines, J. B. Lint, R. J. Davis, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, S. A. Gremel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. P. Schaberl, T. J. Snetsinger, and S. G. Sovern. 2011. Population demography of northern spotted owls. Studies in Avian Biology 40.
- Fowells, H. A. 1965. The silvics of forest trees in the United States. Agriculture Handbook 271, U. S. Department of Agriculture, Washington, D. C.
- Fryxell, J. M., J. B. Falls, E. A. Falls, and R. J. Brooks. 1998. Long-term dynamics of small-mammal populations in Ontario. Ecology 79:213–225.
- Fryxell, J. M., J. B. Falls, E. A. Falls, R. J. Brooks, L. Dix, and M. A. Strickland. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. Ecology 80:1311–1321.

- Garman, S., R. Anthony. 2001. Mammal species list of the Andrews Experimental Forest, 1971 to 1976. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=SA005 Accessed 4 January 2018.
- Garman, S., W. McKee. 2001. Bird species list for the Andrews Experimental Forest and Upper McKenzie River Basin, 1975 to 1995. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=SA003 Accessed 4 January 2018.
- Galindo, C., and C. J. Krebs. 1985. Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. Canadian Journal of Zoology 63:1870–1879.
- Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51:1018–1026.
- Gilbert, B. S., and C. J. Krebs. 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. Oecologia 51:326–331.
- Glenn, E. M., R. G. Anothny, and E. D. Forsman. 2010. Population trends in northern spotted owls: Associations with climate in the Pacific Northwest. Biological Conservation 143:2543–2552.
- Greenberg, C. H., D. L. Otis, and T. A. Waldrop. 2006. Response of white-footed mice (*Peromyscus leucopus*) to fire and fire surrogate fuel reduction treatments in a southern Appalachian hardwood forest. Forest Ecology and Management 234:355–362.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Volume 20. US LTER Network Office Seattle (WA).
- Hayes, J. P., S. P. Cross, and P. W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in Southwestern Oregon. Northwest Science 60:250–257.
- Hayes, J. P., E. G. Horvath, and P. Hounihan. 1995. Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range. Canadian Journal of Zoology 73:67–73.
- Hinkle, D. E., W. Wiersma, and S. G. Jurs. 2003. Applied statistics for the behavioral sciences. 5th ed. Houghton Mifflin, Boston.
- Holloway, G. L., and J. R. Malcolm. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. Journal of Wildlife Management' 70:1735–1745.

- Holloway, G. L., and J. R. Malcolm. 2007*a*. Northern and southern flying squirrel use of space within home ranges in central Ontario. Forest Ecology and Management 242:747–755.
- Holloway, G. L., and J. R. Malcolm. 2007b. Nest-tree use by northern and southern flying squirrels in central Ontario. Journal of Mammalogy 88:226–233.
- Holloway, G. L., and W. P. Smith. 2011. A meta-analysis of forest age and structure effects on northern flying squirrel densities. The Journal of Wildlife Management 75:668–674.
- Holloway, G. L., W. P. Smith, C. B. Halpern, R. A. Gitzen, C. C. Maguire, and S. D. West. 2012. Influence of forest structure and experimental green-tree retention on northern flying squirrel (*Glaucomys sabrinus*) abundance. Forest Ecology and Management 285:187–194.
- Huang, L., B. He, A. Chen, H. Wang, J. Liu, A. Lű, and Z. Chen. 2016. Drought dominates the interannual variability in global terrestrial net primary production by controlling semi-arid ecosystems. Scientific Reports 6.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725-732.
- Jameson, E. W. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada, California. Journal of Mammalogy 33:50-60.
- Klenner, W., and T. P. Sullivan. 2009. Partial and clearcut harvesting of dry Douglasfir forests: implications for small mammal communities. Forest Ecology and Management 257:1078–1086.
- Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Illinois.
- LaMontagne, J. M., C. T. Williams, J. L. Donald, M. M. Humphries, A. G. McAdam, and S. Boutin. 2013. Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels. Journal of Mammalogy 94:1048–1058.
- Lehmkuhl, J. F., S. D. West, C. L. Chambers, W. C. McComb, D. Manuwal, K. B. Aubry, J. Erikson, R. A. Gitzen, and M. Leu. 1999. An experiment for assessing vertebrate response to varying levels and patterns of green-tree retention. Northwest Science 73:45–63.

- Lehmkuhl, J. F., L. E. Gould, E. Cázares, and D. R. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200:49–65.
- Lehmkuhl, J. F., K. D. Kistler, J. S. Begley, and J. Boulanger. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16:584–600.
- Lobo, N., M. Duong, and J. S. Millar. 2009. Conifer-seed preferences of small mammals. Canadian Journal of Zoology 87:773–780.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: a review of the patterns, implications and limitations of top-down and bottom-up interactions. Forest Ecology and Management 328:45–54.
- Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy 80:460–471.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. Journal of Mammalogy 85:87–96.
- Martell, A. M. 1983. Demography of southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) after logging in north-central Ontario. Canadian Journal of Zoology 61:958–969.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.
- Maser, Z., C. Maser, and J. M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084–1088.
- Miller, D. H., and L. L. Getz. 1977. Factors influencing local distribution and species diversity of forest small mammals in New England. Canadian Journal of Zoology 55:806–814.
- National Oceanic and Atmospheric Administration [NOAA]. 2017. Palmer Drought Severity Index (PDSI) < https://www.ncdc.noaa.gov/temp-andprecip/climatologicalrankings/index.php?periods%5B%5D=18¶meter=pdsi&state=35&div=0& month=8&year=2016#ranks-form>. Accessed 6 Aug 2017.

- North, M. P. 2002. Seasonality and abundance of truffles from oak woodlands to red fir forests. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Southwest Research Station.
- Ogawa, R., A. Mortelliti, J. W. Witham, and M. L. Hunter. 2017. Demographic mechanisms linking tree seeds and rodent population fluctuations: insights from a 33-year study. Journal of Mammalogy 98:419–427.
- Porter, J. H., and R. D. Dueser. 1982. Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. Oikos 39:228-236.
- Pyare, S., and W. S. Longland. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. Canadian Journal of Forest Research 32:1016–1024.
- Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.
- Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology 70:161–166.
- Rosenberg, D. K., and R. G. Anthony. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. The Journal of Wildlife Management 57:365–373.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. Canadian Journal of Zoology 81:1715–1725.
- Risch, T. S., and M. J. Brady. 1996. Trap height and capture success of arboreal small mammals: evidence from southern flying squirrels (*Glaucomys volans*). American Midland Naturalist 136:346.
- Schulze, M., G. Lienkaemper. 2015. Vegetation classification database. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TV061. Accessed 4 January 2018.
- Shanley, C. S., S. Pyare, and W. P. Smith. 2013. Response of an ecological indicator to landscape composition and structure: implications for functional units of temperate rainforest ecosystems. Ecological Indicators 24:68–74.
- Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildlife Society Bulletin 399–409.

- Smith, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. Ecological Monographs 38:31–64.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349–371.
- Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. American Zoology 19:1065–1083.
- Smith, W. P., and J. V. Nichols. 2003. Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. Journal of Mammalogy 84:1044–1058.
- Smith, W. P., R. G. Anthony, J. R. Waters, N. L. Dodd, and C. J. Zabel. 2003. Ecology and conservation of arboreal rodents of western coniferous forests. Mammal community dynamics. Management and conservation in the coniferous forests of Western North America. Cambridge University Press, Cambridge, United Kingdom 157–206.
- Smith, W. P., S. M. Gende, and J. V. Nichols. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. Journal of Mammalogy 85:663–674.
- Smith, W. P., S. M. Gende, and J. V. Nichols. 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. Ecological Applications 15:689–700.
- Smith, W. P. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. Journal of Mammalogy 88:862–881.
- Sollmann, R., A. M. White, B. Gardner, and P. N. Manley. 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 80:247–254.
- Songer, M. A., M. V. Lomolino, and D. R. Perault. 1997. Niche dynamics of deer mice in a fragmented, old-growth-forest landscape. Journal of Mammalogy 78:1027–1039.
- Spies, T. 2016. LiDAR data (August 2008) for the Andrews Experimental Forest and Willamette National Forest study areas. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=GI010 Accessed 23 March 2018.
- Strittholt, J. R., D. A. Dellasala, and H. Jiang. 2006. Status of mature and old-growth forests in the Pacific Northwest. Conservation Biology 20:363–374.

- Sullivan, T. P., and D. S. Sullivan. 1982. Population dynamics and regulation of the Douglas squirrel (*Tamiasciurus douglasii*) with supplemental food. Oecologia 53:264–270.
- Sullivan, T. P., D. S. Sullivan, and C. J. Krebs. 1983. Demographic responses of a chipmunk (*Eutamias townsendii*) population with supplemental food. The Journal of Animal Ecology 52:743-755.
- Sullivan, T. P., D. B. Ransome, D. S. Sullivan, P. M. F. Lindgren, and W. Klenner. 2017a. Tree squirrel abundance and demography in managed coniferous forests of British Columbia are within the range of natural fluctuations of old-growth stands. Canadian Journal of Forest Research 47:565–582.
- Sullivan, T. P., D. S. Sullivan, R. Boonstra, C. J. Krebs, and A. Vyse. 2017b. Mechanisms of population limitation in the southern red-backed vole in conifer forests of western North America: insights from a long-term study. Journal of Mammalogy 98:1367–1378.
- Swanson, F. J., and J. A. Jones. 2002. Geomorphology and Hydrology of the H. J. Andrews Experimental Forest, Blue River, Oregon. Field Guide to Geologic Processes in Cascadia:289–313.
- Taitt, M. J. 1981. The effect of extra food on small rodent populations: deer mice (*Peromyscus maniculatus*). The Journal of Animal Ecology 50:111-124.
- Tallmon, D. A., E. S. Jules, N. J. Radke, and L. S. Mills. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. Ecological Applications 13:1193–1203.
- Thompson, R. L., C. L. Chambers, and B. C. McComb. 2009. Home range and habitat of western red-backed voles in the Oregon Cascades. Northwest Science 83:46–56.
- Thysell, D. R., L. J. Villa, and A. B. Carey. 1997. Observations of northern flying squirrel feeding behavior: use of non-truffle food items. Northwestern Naturalist 78:87–92.
- Trappe, J. M., R. Molina, D. L. Luoma, E. Cazares, D. Pilz, J. E. Smith, M. A. Castellano, S. L. Miller, and M. J. Trappe. 2009. Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).

- Turbill, C., and S. Prior. 2016. Thermal climate-linked variation in annual survival rate of hibernating rodents: shorter winter dormancy and lower survival in warmer climates. Functional Ecology 30:1366–1372.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.
- United States Department of Agriculture [USDA], and United States Department of the Interior [USDI]. 1994. Northwest Forest Plan - Record of Decision for amendments for Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl.
- Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. Canadian Journal of Zoology 59:1045–1061.
- Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63:992–1003.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893-901.
- Villa, L. J., A. B. Carey, T. M. Wilson, and K. E. Glos. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).

Watersheds and Gauging Stations. <https://andrewsforest.oregonstate.edu/research/infrastructure/watersheds>. Accessed 8 Jul 2017.

- Waters, J. R., and C. J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. The Journal of Wildlife Management 59:858–866.
- Weigl, P. D. 2007. The northern flying squirrel (*Glaucomys sabrinus*): a conservation challenge. Journal of Mammalogy 88:897–907.
- Wells-Gosling, N., and L. R. Heaney. 1984. *Glaucomys sabrinus*. Mammalian Species 229:1–8.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.
- White, A. M., E. F. Zipkin, P. N. Manley, and M. D. Schlesinger. 2013. Conservation of avian diversity in the Sierra Nevada: moving beyond a single-species management focus. PLoS ONE 8:e63088.

- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. Wildlife Monographs 185:1–50.
- Wilson, T. M., and A. B. Carey. 1996. Observations of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. Northwestern Naturalist 77:35-39.
- Zurr, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science Business Media, New York.

Variables	Description	Range
Spatial		
Elevation	Average study site elevation, estimated using	683 - 1,244 m
	2008 lidar data.	
Canopy	Study site proportion of $0 - 10$ m canopy	9 - 38%
	openness to 10 + m canopy openness,	
	estimated using 2008 lidar data.	
Shrub	Mean percentage cover of all woody shrubs	10.3 - 58.3%
	between 0.5 m and 1.5 m in height.	
Berry	Mean percentage cover of berry-producing	12.1- 51.2%
	plants.	
CWD	Study site sum of coarse woody debris	77.274 -
	volumes on 18 habitat sampling station for all	218.186 m ³
	CWD > 10 cm in diameter.	
Temporal		
Year	A year specific effect for each trapping	2011 - 2016
	occasion from 2011 to 2016.	
Season	Trend from the first to the last day of the	1 – 36
	trapping.	
Trapping	Trend from the first to the last day for each	1 – 12 days
Trend	trapping occasion.	

Table 2.1. – Description of variables considered in models of detection probability(p), recapture probability (c), and abundance (\hat{N}) for Humboldt's flying squirrels(Glaucomys oregonensis), Townsend's chipmunks (*Neotamias townsendii*), deer mice(Peromyscus maniculatus), and western red-backed voles (*Myodes californicus*).

Julian date	Trend from the first to the last day of the	11269 -
	project across the first 6 years of data	16323
	collection.	

Min. Temp. Minimum winter ^c daily mean temperature	-13 – -3.9 °C
---------------------------------------------------------------	---------------

Days Below	The number of days in the winter with a mean	11 – 34 days
0°C	daily temperature below 0°C.	
PDSI	18-month average of Palmer drought severity	-2.67 – 2.25
	index values preceding each trapping occasion.	

Spatiotemporal

Effort	Trap type specific trapping effort, adjusted for	945 - 1498.5
	stuck and sprung traps.	trap-nights
Chipmunks	The effect of year and site specific TC ^b	189 - 941
	captures on trap availability of nocturnal	captures
	species.	

a- Winter is defined as October 1 through April 1.b- Townsend's chipmunk (*Neotamias townsendii*)

Table 2.2. – A priori predictions of variable effects in models of detection probability (p), recapture probability (c), and abundance (\hat{N}) for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*). Habitat covariates were measured once during the summer of 2016 at 18 standardized trap stations per study site in the H. J Andrews Experimental Forest, near Blue River, OR. + indicates a positive prediction, - indicates a negative prediction, / indicates no effect, and empty box indicates direction prediction not feasible or no prediction made.

					Exp	ected	Resu	lts				
		HF	S		TC		V	VRE	3V		DN	Л
Covariate	р	С	Ń	р	С	Ń	р	С	Ń	р	С	Ń
Spatial												
Elevation	-	+	-	-	+	+	-	+	+	-	+	-
Canopy	-	-	-	+	-	+	-	+	-	-	+	-
Shrub	+	+		+	+		+	+		+	+	
Berry			+			+			+			+
CWD			+			+			+			+
Temporal												
Year												
JDate	+	+		+	+		/	/		/	/	
Season	-	+		+	+		+	+		+	+	
Trapping Trend	-	+		-	+		-	+		-	+	
Effort	+	+		+	+		+	+		+	+	
Chipmunks ^b	+	+										
Min. Temp.			-			-			-			-
Days Below 0°C			-			_			_			-

PDSI	+	+	+	+

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*)

Table 2.3. –Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), western red-backed voles (*Myodes californicus*), and deer mice (*Peromyscus maniculatus*) total capture and individual sex ratios from all years and sites on the H. J. Andrews Experimental Forest in Oregon from 2011–2016.

	Total Captures			Total Individuals			
Species	Males	Females	Males:Females	Males	Females	Males:Females	
HFS	2,337	2,159	1:1.08	504	477	1.06:1	
TC	8,707	6,028	1.44:1	1,773	1,252	1.41:1	
WRBV	305	468	1:1.53	155	225	1:1.45	
DM	945	631	1.50:1	366	250	1.46:1	

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*) **Table 2.4.** – Top 5 ranking models used to estimate recapture probability (*c*) of Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western redbacked voles (*Myodes californicus*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model ^a	AICc	ΔAICc	W	K
HFS	Trapping Trend	21448.54	0.00	0.70	14
	Trapping Trend + Elevation	21450.32	1.78	0.29	15
	Year	21457.58	9.04	0.01	18
	Year + Elevation	21459.58	11.04	0.00	19
	Chipmunks	21488.53	40.00	0.00	14
TC	Trapping Trend + Elevation	47029.71	0.00	1.00	15
	Trapping Trend + Canopy	47100.01	70.30	0.00	15
	Trapping Trend	47131.37	101.66	0.00	14
	Season + Canopy	58745.50	11715.78	0.00	15
	Season + Elevation	58861.67	11831.96	0.00	15
WRBV	Year + Elevation	2939.88	0.00	0.27	19
	Trapping Trend + Elevation	2940.44	0.56	0.20	15
	Elevation	2940.78	0.91	0.17	14
	Year	2941.79	1.91	0.10	18
	Effort + Elevation	2942.14	2.26	0.09	15
DM	Trapping Trend	3652.95	0.00	0.72	14
	Trapping Trend + Elevation	3654.88	1.93	0.27	15

Year + Shrub	3664.13	11.17	0.00	19
Year	3665.22	12.26	0.00	18
Year + Elevation	3669.24	16.29	0.00	19

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*) a- Model structure for initial capture probability (*p*) was held to a year by trapping trend model structure (Year*Trapping Trend). **Table 2.5.** – Top 5 ranking models used to estimate capture probability (p) of Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*) and western redbacked voles (*Myodes californicus*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011-2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the topranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model	AICc	ΔAICc	W	K
HFS ^a	Year + Canopy	21484.64	0.00	0.79	10
	Year + Elevation	21487.80	3.16	0.16	10
	Year	21490.97	6.33	0.03	9
	Year + Shrub	21492.91	8.26	0.01	10
	Julian Date + Canopy	21604.13	119.49	0.00	5
TC ^b	Year + Shrub	47087.58	0.00	1.00	10
	Year + Elevation	47103.26	15.69	0.00	10
	Trapping Trend + Shrub	47103.78	16.20	0.00	6
	Year + Canopy	47104.06	16.49	0.00	10
	Year	47105.02	17.44	0.00	9
WRBV ^c	Trapping Trend + Elevation	2921.40	0.00	0.38	10
	Trapping Trend	2922.04	0.64	0.28	9
	Trapping Trend + Shrub	2923.85	2.46	0.11	10
	Trapping Trend + Canopy	2923.95	2.55	0.11	10
	Effort + Elevation	2926.05	4.65	0.04	10
$\mathbf{D}\mathbf{M}^{\mathrm{d}}$	Trapping Trend + Canopy	3632.24	0.00	0.30	5
	Trapping Trend	3632.92	0.68	0.21	4

Season + Canopy	3634.56	2.32	0.09	5
Trapping Trend + Elevation	3634.90	2.66	0.08	5
Trapping Trend + Shrub	3634.93	2.68	0.08	5

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*) a- Model structure for recapture probability c(Trapping Trend). b- Model structure for recapture probability c(Trapping Trend + Elevation).

c- Model structure for recapture probability c(Year + Elevation).

d- Model structure for recapture probability *c*(Trapping Trend).

	HFS	TC	WRBV	DM	BW	CV	DS	SH
TC	0.12							
WRBV	-0.39	0.06						
DM	0.4	0.21	-0.01					
BW	-0.28	0.33	0.42	-0.11				
CV	0.01	-0.25	0.26	0.07	-0.13			
DS	0.11	-0.2	-0.05	-0.12	0.08	-0.04		
SH	-0.12	0.24	-0.26	-0.19	-0.03	-0.24	-0.06	
AP	-0.24	0.34	0.24	-0.17	0.73	-0.19	0.1	0.07

Table 2.6. – Pairwise Pearson's correlation coefficients between species-specific number of known individuals (Appendix 1.3) for the 8 most commonly captured species captured in a natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016.

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*); BW – bushytailed woodrat (*Neotoma cinerea*); CV – creeping vole (*Microtus oregoni*); DS – Douglas' squirrel (*Tamiasciurus douglasii*); SH – snowshoe hare (*Lepus americanus*); AP – American pika (*Ochotona princeps*).

Table 2.7. – Pairwise Pearson's correlation coefficients between Humboldt's flying squirrel (*Glaucomys oregonensis*), Townsend's chipmunk (*Neotamias townsendii*), deer mouse (*Peromyscus maniculatus*), and western red-backed vole (*Myodes californicus*) abundance estimates in a natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016.

	HFS	TC	WRBV
TC	0.15		
WRBV	-0.39	0.09	
DM	0.34	0.12	0.03

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*)



Figure 2.1. – Location the H. J. Andrews Experimental Forest, in Central Oregon. We collected mark-recapture data for small mammals on 9 sites, represented by the black squares, in late-successional forests from 2011–2016.



Figure 2.2. – Fall abundance from 2011–2016 of Humboldt's flying squirrels (*Glaucomys oregonensis*, 7.84 ha), Townsend's chipmunks (*Neotamias townsendii*, 7.84 ha), western red-backed voles (*Myodes californicus*, 1 ha), and deer mice (*Peromyscus maniculatus*, 1 ha) estimated using Huggins models and live capture data collected in a late successional forest within the H. J. Andrews Experimental Forest from 2011–2016.



Figure 2.3. – Intraspecific abundance temporal autocorrelation for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*) captured in a natural successional forest from 2011–2016. The autocorrelation for each lag represents the Pearson's correlation between annual fall abundance estimates in years as far apart as the lag. The height of bars indicates the strength of the autocorrelation and the area between the dark grey horizontal lines represents values of correlation that we would likely conclude are not statistically different from 0.



Figure 2.4. – Correlograms of pairwise Pearson's correlation coefficient estimates of abundance between 9 sites (indicated on the x- and y-axis) from 2011–2016 for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western redbacked voles (*Myodes californicus*) captured in the H. J. Andrews Experimental Forest.



Figure 2.5. – Correlograms of pairwise Pearson's correlation coefficient estimates of abundance between years (indicated on the x- and y-axis) for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*) captured in the H. J. Andrews Experimental Forest from 2011–2016.



Figure 2.6 – The estimated effect size and 95% CIs on mean abundance across the sampled range of spatiotemporal covariates for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*) captured in a late successional forest from 2011–2016. The horizontal dark area indicates the range of values that do not achieve the *a priori* biological significance value, where biological significance is defined as the average site- and species-specific temporal change in abundance.

Chapter 3

VITAL RATES AND SPATIOTEMPORAL ASSOCIATIONS OF HUMBOLDT'S FLYING SQUIRRELS AND TOWNSEND'S CHIPMUNKS IN WESTERN CASCADES LATE SUCCESSIONAL FORESTS

Matt Weldy, Clinton W. Epps, Damon Lesmeister

ABSTRACT

Managing population abundance requires understanding spatial and temporal variability in species abundance and vital rates. While abundance of small mammal species has been estimated frequently, few studies have examined spatial and temporal variability of vital rates and covariance among species in late successional forests of the Pacific Northwest. Here we sought to develop precise estimates of vital rates for Humboldt's flying squirrels (Glaucomys oregonensis) and Townsend's chipmunks (*Neotamias townsendii*), test whether rates vary with spatial and temporal abundance-associated covariates, and test intraspecific correlations among those rates. We collected live-trapping data from 2011–2016 on 9 sites arranged across an elevation and canopy-openness gradient. We used robust design Pradel models to estimate site-specific apparent annual survival, population growth rate, and recruitment. We used Pearson's correlation coefficient to estimate the species-specific linear correlations among population growth rate, abundance, apparent annual survival, and recruitment. Our estimates were generally intermediate to previous estimates of vital rates. We found that abundance-associated covariates from a previous study were associated with the vital processes most associated with population growth rate. Population growth of Humboldt's flying squirrels was strongly correlated with apparent annual survival, while the population growth of Townsend's chipmunks was strongly correlated with both apparent annual survival and recruitment. The abundance of both species was only moderately correlated with the vital rates. Apparent annual survival was nearly constant among years and grids for Humboldt's flying squirrels but was consistently lower and highly variable among years for Townsend's chipmunks. Recruitment and population growth rates for both species were similar and variable among years. We observed slight evidence for spatial variation in the vital rates of both species, but temporal variation was much larger, which highlights the importance of temporal variability in vital rates especially when comparing habitat quality. The usefulness of abundance as a proxy for habitat quality has been debated considerably, but our results suggest that inferences based on abundance are consistent with inferences based on vital rates in our study system.

INTRODUCTION

The effective management of animal populations relies on an understanding of the spatial and temporal variability of population attributes (abundance or density) and vital rates (survival, population growth, recruitment). Spatial and temporal variability in abundance, density, or species-specific counts have been used to assess the regulating influence of specific habitat or temporal characteristics (Coppeto et al. 2006, Fauteux et al. 2011). However, estimates of abundance, density, or count indices can be poor indicators of habitat associations, if detection probability or habitat quality are quite variable (Van Horne 1983, Todd and Rothermel 2006). Thus, managers should consider the demographic mechanisms driving spatiotemporal variation in population size by decomposing estimates of abundance or density into their contributing vital rates and associated density-dependent mechanisms (Williams et al. 2002, Cushman 2006). Managers may need to also consider potential for temporal variability causing confounded inference in short-term studies of habitat quality and population regulation, especially in populations that exhibit strong temporal variation.

Much of the previous work in the Pacific Northwest (hereafter PNW) has focused on spatial comparisons of population density to explore the effects of forest management practices on Humboldt's flying squirrels (Glaucomys oregonensis) and northern flying squirrels (*Glaucomys sabrinus*; see studies reviewed in Holloway and Smith 2011). Few studies have estimated the vital rates of northern flying squirrels, and the two that we are aware of were north of our study area and either conducted on managed timber lands (Ransome and Sullivan 2002) or in dry ponderosa pine (Pinus ponderosa) forests east of the Cascades Mountains (Lehmkuhl et al. 2006). As a result, the current understanding of flying squirrel habitat associations and the mechanisms resulting in population change are primarily based on studies demonstrating spatiotemporal associations between population attributes and environmental covariates (Coppeto et al. 2006), rather than vital rates like survival or reproduction. Moreover, because of this research focus on northern flying squirrels, few studies have estimated the population attributes and habitat associations of other sympatric small mammals (but see Rosenberg and Anthony (1993) for estimates of Townsend's chipmunk chipmunks (Neotamias townsendii) densities in old- and second-growth stands).

Detailed estimates of Humboldt's flying squirrels and Townsend's chipmunks population attributes and habitat associates are particularly important, because of the importance of these species to the ecology of PNW forests. The focal species are both an important component of the preybase for avian and mammalian predators (Fryxell et al. 1999, Bull 2000, Forsman et al. 2001, Rosenberg et al. 2003), and consume and disperse hypogenous fungi, berries, and seeds (Maser et al. 1978, Bowers and Dooley
Jr 1993). Taken together these effects help shape the structure of food webs through interactions with primary producers and predator communities in the PNW.

Until recently, flying squirrels in the PNW and west of the Cascades were considered northern flying squirrels (*Glaucomys sabrinus*), but Arbogast et al. (2017) described these populations as a separate species, the Humboldt's flying squirrel, in 2017. Hereafter, we assume that previous studies conducted on northern flying squirrels across much of the PNW pertained to Humboldt's flying squirrels. Both Humboldt's flying squirrels and Townsend's chipmunks are similar in weight, have broadly similar diets including fungi, and occur more abundantly in old forests (Maser et al. 1978, Rosenberg and Anthony 1993, Holloway and Smith 2011). However, percieved differences in dietary niches, as well as differences in activity patterns, hibernation strategies, and dominant predators might drive differences in life history strategies that manifest as differences in the drivers of population growth and the associations among vital rates and abundance (Carey et al. 1999, Bull 2000, Forsman et al. 2004, Reynolds and Meslow 1984).

In this study, we estimate the vital rates of Humboldt's flying squirrels and Townsend's chipmunks, two co-occurring small mammals across a late-successional forest in the central Oregon Cascades. Our study had two primary objectives: 1) to develop estimates of apparent annual survival, recruitment and per-capita rate of population change, and 2) to evaluate the effects of species-specific abundanceassociated covariates on the apparent annual survival and recruitment (Weldy, *Chapter 2*). We hypothesized that covariates previously identified as abundanceassociated would also be associated with the vital rate most affecting to population growth rate and we developed a set of a priori hypotheses for the effect of each covariate (Table 3.1, Table 3.2).

MATERIALS AND METHODS

Study area and trapping grids

We conducted live-trapping for this study on 9 grids in the H. J. Andrews Experimental Forest (hereafter HJA) near Blue River, OR (44°N, 112°W; Figure 3.1). The HJA encompasses the 6,400-ha Lookout Creek drainage basin and is part of the Willamette National Forest. We used grid layout and trapping procedures that were in general accordance with the protocols described by Carey et al. (1991). Our protocols were approved by OSU's IACUC (ACUP #4191, 2011-2013; #4590, 2014-2016), and were in accordance with the standard animal care principles of the American Society of Mammalogists (Sikes and Gannon 2011).

The 9 grids spanned all combinations of 3 elevation (<800m, 800-1,000m, >1,000m) and 3 canopy openness classes (0–15%, 15–30%, 30–40%), classified using the Geospatial Modelling Environment (GME) tools (Version GME 0.7.4, Spatial Ecology, LLC., http://www.spatialecology.com). All of our study grids were in old forests >400 years old with trees >81.21 cm, that were dominated by Douglas-fir (*Pseudotsuga mensiesii*), western hemlock (*Tsuga heterophylla*) and Pacific silver fir (*Abies amabalis*) vegetative communities (Cissel et al. 1999, Schulze and Lienkaemper 2015). Annual precipitation occurs primarily during the winter as rain at low elevations and snow at elevations above 1,000 m (Swanson and Jones 2001). Average grid elevations ranged from 683–1,244 m, and canopy openness ranged from 9–38%. The average inter-grid distance was 2,963 m, but pair-wise intergrid distances varied from 5,940 m (grids 3 and 8)–1,078 m (grids 2 and 4). Average daily temperature from 2011–2016 during the fall trapping season was 9.3 ± 0.55 °C (± SE), and the average daily rainfall was 6.4 ± 0.40 mm (± SE).

Live Trapping

We live-trapped Humboldt's flying squirrels and Townsend's chipmunks on each grid from 2011–2016. Each year we trapped each grid for 3 consecutive weeks during the fall. On each grid, we established 64 trap stations arranged in an 8 x 8 grid (7.84 ha) with a slope-corrected inter-trap distance of 40 m. Each grid consisted of 128 Tomahawk Model 201 live traps (Tomahawk Live Trap, WI, USA). We placed two Tomahawk traps at each trap station within 5 m of the trap station center. We attached one Tomahawk trap approximately 1.5 m from the ground to a suitable tree bole and the second trap on the ground (Risch and Brady 1996). We placed both traps on the ground if no suitable tree bole was within 5 m of the trap station center. Ground traps were placed near habitat features that might increase the probability of a small mammal encountering the trap (Carey et al. 1991). Each trap was placed in a waxed cardboard carton and supplied with a nest box stuffed and dry cotton batting to reduce trapping related mortalities. Traps were baited with a mixture of peanut butter, molasses, oats, and sunflower seeds (Carey et al. 1991).

We initially randomly determined the grid trapping order at the start of the study and repeated that trapping order each following year. However, trapping order for higher elevation grids were prioritized in the trapping order, to reduce the impact of fall snow and rain on survival of animals in traps as temperatures decreased. A trapping week consisted of 4 trap nights; traps are opened on Monday, closed on Fridays and checked once per day. We marked each animal with a unique ear tag and recorded individual condition, species, sex, and body weight (g). In addition, we recorded the tail width (mm), reproductive condition, and individual age class of Humboldt's flying squirrels (Villa et al. 1999). At the end of each season, we necropsied all trap related mortalities to validate field identification of species, sex, and reproductive condition. From 2011–2016, we captured 21 species of mammals. **Study species**

Humboldt's flying squirrels and Townsend's chipmunks co-occur in a broad range of forested habitat throughout western Oregon, and were the most commonly captured species at the HJA study grids. Many habitat and environmental features have been used to explain the focal species' spatial and temporal patterns of abundance. In general, previous studies showed an association between abundance and precipitation which affects forest productivity and food availability, and a negative association between winter survival and winter severity as well as elevation (Aubry et al. 1991, Ernest et al. 2000, Lehmkuhl et al. 2004). Humboldt's flying squirrel density is associated with understory structural richness and coarse woody debris volumes (Carey et al. 1999, Smith 2007), while Townsend's chipmunks are associated with downed woody debris and understory structural richness (Waldien et al. 2006). The focal species' abundances exhibited spatiotemporal variation on our study grids from 2011–2016 (Weldy, *Chapter 2*). Fall abundance of Humboldt's flying squirrels was negatively associated with elevation, and positively associated with berry producing plant cover and minimum average daily temperature (Weldy, Chapter 2). Townsend's chipmunks were positively associated with elevation, canopy openness, and minimum winter temperature and negatively associated with berry producing plant cover (Weldy, *Chapter 2*). Diet preferences of the focal species are broadly similar; however, some studies have demonstrated niche partitioning based on food resources (Maser and Maser 1988, North et al. 1997, Lehmkuhl et al. 2004). For example, both northern flying squirrels and Townsend's chipmunks demonstrate a high occurrence of hypogenous fungi in their digestive tract (Maser et al. 1978). Specifically, *Rhizopogon* and *Gauteria* fungi are commonly detected in the scats of northern flying squirrels and Townsend's chipmunks. In addition to fungi, Townsend's chipmunks are positively associated with salal groundcover and consume its seeds (Ure and Maser 1982, Hayes et al. 1995, Tallmon et al. 2003).

Development of covariates

We used 4 spatial covariates and 9 temporal covariates that previously were determined to be associated with the focal species abundance (Weldy, *Chapter 2*). The spatial covariates characterized forest complexity and food availability and were used to examine the spatial variability of capture, recapture, recruitment, and survival probabilities (Table 3.1). We estimated average grid elevation and canopy openness using ArcGIS version 10.3.1 and 2008 LiDAR data (Spies 2016). We estimated average grid level canopy openness as the proportion of vegetation <10 m compared to vegetation >10 m. During the summer of 2016 we visually estimated the percentage of ground covered by sampled berry-producing plant cover and shrub cover to the nearest 5% in 2 m diameter circles at 18 habitat sampling stations per study grid. Habitat sampling stations were each centered on a Tomahawk trapping station and were evenly spaced in a regular pattern across each study grid, with 3

habitat sampling stations along each grid edge and 2 habitat sampling stations on each interior row of the trapping grid. The percentage cover of berry-producing plants was a grid level average of the sum of the percentage cover of *Rubus spp.*, huckleberry (Vaccinium spp.), salal (Gaultheria shallon) and Oregon grape (Mahonia aquifolium) at each habitat sampling station. Thus, the total percentage cover of berry-producing plants could exceed 100%. Similarly, we estimated shrub cover by estimated the amount of ground covered by woody shrubs < 1.5 m tall. We averaged the 18 measurements on each grid. In a previous study, we tested for differences in understory characteristics between grids using a separate means model (Weldy, *Chapter 2*). We corrected pairwise tests using the Bonferroni multiple test correction and retained only understory characteristics with at least one significant difference after correction for multiple tests. The temporal covariates described annual temporal change (n = 2), within and multiseason trends (n = 3), and grid specific temporal patterns (n = 4; Table 3.1; Weldy, *Chapter 2*). Specifically, we used an estimate of minimum daily air temperature (°C) and a year-specific covariate to describe annual temporal change. We used minimum daily air temperature measurements recorded by the HJA Central Meteorological Station, which is within the study grid elevation range and is just east of the project's center (Daly, C. and W. McKee 2016). We used 3 covariates to describe both within season and multi-season trends. We used the Julian Date to describe temporal variation within and across seasons. We used a trend from the first to last day of the fall trapping season to describe potential variation related to seasonal weather changes during the fall that were consistent among years. We used a trapping trend from the first to last day of each grid trapping window to

describe potential behavioral changes that were related to our trapping protocol. We used 4 spatiotemporal covariates that captured temporal patterns that were specific to each grid (Table 3.1). We characterized potential variation in trap availability, which might affect capture and recapture probability, with 2 covariates: effort and number of chipmunk captures. The effort covariate was used to describe the grid and year-specific adjusted trapping effort. Both effort and number of chipmunk captures were used to describe grid and year-specific trap availability. We used grid- and year-specific estimates of Humboldt's flying squirrel abundance and Townsends chipmunk abundance to characterize potential density-dependence and competition effects on the vital rates of both species (Weldy, *Chapter 2*).

Analysis

We used a robust design Pradel parameterization of the Jolly-Seber capturerecapture models implemented in Program MARK to estimate annual capture probability (*c*), recapture probability (*p*), recruitment (*f*), survival (φ) and population growth (λ) of the focal species across 6 primary trapping periods and 9 grids (Pradel 1996, White and Burnham 1999). Within each primary trapping period 12 daily secondary periods were trapped for Humboldt's flying squirrels and 8 daily secondary periods were trapped for Townsend's chipmunks; the primary trapping periods contained fewer secondary trapping occasions for Townsend's chipmunks because we released chipmunks during the third week of live-trapping due to high capture rates. The robust design Pradel models implemented in Program MARK estimate the probability of first capture and recapture using a Huggins closed population capturerecapture model, and then estimate apparent survival, recruitment and per-capita rate of population change across the open population intervals (Huggins 1989, 1991, Pradel 1996). Pradel models decompose realized population growth (λ) into two pieces that are linearly related: apparent survival (φ) and recruitment (f). We chose the model structure that allowed for modeling of covariates on apparent survival and recruitment. This model structure does not allow the direct modelling of population growth rate; however, population growth rate can be derived. In our study, apparent survival reflects individual annual survival between the fall primary trapping periods and grid fidelity. Recruitment is the per capita number of animals added to the population between primary fall trapping periods, and reflects the number of births, juvenile survival, adult immigration, and juvenile emmigration. The primary assumptions of constant survey effort and sampled area during each sampling period are both satisfied with this data set. Because the first estimates of recruitment and population growth are often unreliable or confounded, we discarded both the first and last estimates of recruitment and population growth.

We used a sequential modeling strategy to develop and select the most parsimonious model(s). The data were insufficient to accommodate interactions, so we considered only single and 2-factor additive models for each parameter. Furthermore, each model was limited to one spatial and one temporal covariate. We began by testing each of the focal species for behavioral effects using models that tested all captures for differences in the probability of the first capture and recapture. Then, we modeled recapture probability while maintaining a time-varying capture probability model structure. Next, we modeled capture probability using the best recapture probability model structure identified in the second step. Per-capita population growth, apparent annual survival, and recruitment are linearly related, and a linear constraint placed on any one of the two modeled parameters will directly affect the estimation of the other parameter, biasing the parameter interpretation. To avoid bias in the estimation of apparent survival and recruitment we modeled apparent survival while holding recruitment to a time-varying structure and both capture and recapture probability to the best structure. Similarly, we then modeled recruitment while holding apparent survival to a time-varying structure and both capture and recapture probability to the best structure. We then used model averaging to obtain the best estimate for each of the parameters of interest. We estimated modelaveraged apparent annual survival and recruitment by averaging the parameter of interest over the candidate model set from the corresponding model set. We estimated the derived annual rate of population change by averaging the parameter of interest over a combined model set containing all models that were used to estimate apparent annual survival and recruitment.

For covariate inference, we used Akaike's Information Criterion, corrected for small sample sizes (AIC_c), and AIC_c weights (*w*) to select the best-supported model in each sequential modeling step (Burnham and Anderson 2002). We selected the model with the lowest AIC_c and highest *w* as our best-supported model (Burnham and Anderson 2002). However, models within 2 AIC_c of the top-ranking model were considered competitive (Stanley and Burnham 1998). In addition, we used the relative change in AIC_c (Δ AIC_c) to evaluate models relative to the top-ranking model. We used *w*_i and the degree to which the 95% confidence interval for the slope coefficients

overlapped 0 to evaluate the strength of evidence for single parameters (Anthony et al. 2006, Forsman et al. 2011, Dugger et al. 2016).

Correlations among vital rates and abundance

We interpreted the strength of the relationship between apparent annual survival, population growth, recruitment, and estimates of abundance according to the absolute value of the estimated Pearson's correlation coefficient. We interpreted the sign of the Pearson's correlation coefficient as the direction of the relationship. We considered pairwise correlation coefficients with an absolute value >0.7 to be strongly correlated, pairwise correlation coefficients with an absolute value between 0.5–0.7 to be moderately correlated, pairwise correlation coefficients with an absolute value between 0.5–0.7 to be moderately correlated, pairwise correlated and pairwise correlation coefficients of the absolute value between 0.3–0.5 to be weakly correlated and pairwise correlation coefficients <0.3 to have negligible correlation (Hinkle et al. 2003).

RESULTS

From 2011–2016 we captured and processed 45,683 small mammals of 21 species during 62,217 adjusted Tomahawk trap nights. We individually marked 1,076 Humboldt's flying squirrels and 3,464 Townsend's chipmunks, and yearly grid-level captures ranged from 4–56 Humboldt's flying squirrels and 25–176 Townsend's chipmunks.

Behavioral models for both species accounted for 100% of the cumulative model weight, and the highest-ranking model without a behavioral effect ranked substantially lower than the top-ranking model (Humboldt's flying squirrel $\Delta AIC_c =$ 174.75; and Townsend's chipmunks $\Delta AIC_c = 2,431.58$; Table 3.4). Elevation was positively associated with Humboldt's flying squirrel ($\beta_{Elevation}$: 0.47 95% CI: 0.15 to 0.80) recapture probability and negatively associated Townsend's chipmunk ($\beta_{Elevation}$: -0.95 95% CI: -1.13 to -0.77) recapture probability. Townsend's chipmunks recapture probability decreased during the trapping session ($\beta_{Trapping Trend}$: -0.16 95% CI: -0.18 to -0.15). Humboldt's flying squirrel recapture probability (c_{2016} : 23.02% 95% CI 21.97% to 24.10%) was slightly lower than capture probability (p_{2016} : 24.86% 95% CI 20.62% to 29.65%), while on high elevation sites, recapture probability (c_{2016} : 26.57% 95% CI 24.54% to 28.70%) was higher than capture probability (p_{2016} : 20.12% 95% CI 16.31% to 24.57%; Appendix 3.3, Appendix 3.4). Townsend's chipmunks recapture probability (c_{2016} Day 2 Low Elevation: 76.51% 95% CI 75.17% to 77.80%) was much higher than capture probability (p_{2016} Day 2 Low Elevation: 20.55% 95% CI 18.39% to 22.90%) on all sites.

Capture probability of Humboldt's flying squirrels was most strongly associated with year-specific effects and elevation, while the capture probability of Townsend's chipmunks was most strongly associated with the trapping session day and shrub cover (Table 3.5). The year-specific effects on Humboldt's flying squirrel capture probability varied, but only the negative effect of 2011 was detecatable (β_{2011} : -2.61 95% CI: -2.90 to -2.32). Townsend's chipmunk capture probability was positively associated with shrub cover (β_{Shrub} : 0.016 95% CI: 0.01 to -0.02) and negatively associated with the day of the trapping session ($\beta_{Trapping Trend}$: -0.22 95% CI: -0.25 to -0.19; Table 3.5).

We detected individual Humboldt's flying squirrels and Townsend's chipmunks that were capture in both 2011 and 2016 and were at least 6 years old. Model-averaged apparent annual survival of Humboldt's flying squirrels ranged from 0.47 (95% CI: 0.43–0.51)–0.51 (95% CI: 0.45–0.57) and was nearly constant on each grid among years (Figure 3.2, Appendix 3.5). Elevation ($\beta_{Elevation}$: 0.54 95% CI: -0.07 to 1.16) and Humboldt's flying squirrel apparent annual survival had a weak positive association (Table 3.6). Apparent survival of Townsend's chipmunks ranged from 0.13 (95% CI: 0.11–0.16)–0.31 (95% CI: 0.27–0.36) and was highest during 2013–2014 (Figure 3.2). Minimum winter temperatures ($\beta_{Min. Temp.}$: -0.11 95% CI: -0.14 to -0.08) were negatively associated with Townsend's chipmunk apparent annual survival (Table 3.6). While, canopy openness (β_{Canopy} : 0.68 95% CI: -0.20 to 1.56) had a weak positive association with Townsend's chipmunk apparent annual survival (Table 3.6).

Model-averaged recruitment of Humboldt's flying squirrels ranged from 0.23 (95% CI: 0.18–0.29)–0.86 (95% CI: 0.54–0.97; Figure 3.3, Appendix 3.6). We observed strong support for a 3-fold decrease in recruitment on all grids from the 2012–2013 to the 2013–2014 trapping interval and subsequent increase on most grids, during the following 2014–2015 interval (Figure 3.3). Relatively high minimum winter temperatures during the winter of 2011 and 2012 were associated with higher recruitment for both Humboldt's flying squirrel ($\beta_{Min. Temp.}$: 0.12 95% CI: 0.08 to 0.16) and Townsend's chipmunks ($\beta_{Min. Temp.}$: 0.11 95% CI: 0.09 to 0.13; Table 3.7). High elevation ($\beta_{Elevation}$: 0.57 95% CI: 0.11 to 1.02) sites with low berry-producing plant cover (β_{Berry} : -0.008 95% CI: -0.013 to 0.002) were associated with higher Humboldt's flying squirrel recruitment rates; however, the model selection support for the two effects was similar (Δ AICc Berry to Elevation= 0.51; Table 3.7). Open canopy

forests (β_{Canopy} : 0.24 95% CI: -0.04 to 0.52) and Townsend's chipmunk recruitment were positively association, but the effect was weak (Table 3.7).

Humboldt's flying squirrel annual realized population growth ranged from 0.82 (95% CI: 0.73 to 0.88)–1.48 (95% CI: 1.30 to 1.66; Figure 3.4, Appendix 3.7). Townsend's chipmunks realized annual population growth ranged from 0.68 (95% CI: 0.63 to 0.73)–1.25 (95% CI: 1.14 to 1.35; Appendix 3.7). The pattern of realized population growth rate among years was similar for both species. Realized population growth of both Humboldt's flying squirrels and Townsend's chipmunks was highest on all grids during the 2012–2013 interval and then decreased during the two later intervals (2013–2014 and 2014–2015; Figure 3.4).

We observed a weak negative correlation between Humboldt's flying squirrel abundance and apparent annual survival, and we observed a strong positive association between population growth of Humboldt's flying squirrels and recruitment (Table 3.8). Apparent annual survival of Humboldt's flying squirrels and population growth were nearly uncorrelated. In contrast, we observed a weak positive correlation between Townsend's chipmunk abundance and apparent annual survival, as well as a weak negative correlation between Townsend's chipmunk abundance and population growth rate (Table 3.8). We also observed strong correlations between Townsend's chipmunk population growth rate, apparent annual survival, and recruitment. Similarly, to Humboldt's flying squirrels, Townsend's chipmunk recruitment was positively correlated with population growth rate. However, apparent annual survival of Townsend's chipmunks was negatively correlated with apparent annual survival.

DISCUSSION

We observed stark differences in the patterns of apparent annual survival between Humboldt's flying squirrels and Townsend's chipmunks, two co-occurring species, in an old forest study site in the Oregon Cascades. From 2011–2016, apparent survival of Humboldt's flying squirrels was nearly constant among years and grids, with only slight evidence for spatial variation. In contrast, the apparent survival of Townsend's chipmunks was lower than Humboldt's flying squirrels during each interval and varied among years. In particular, from 2012–2014, we observed a 1.2-fold increase in mean Townsend's chipmunk apparent survival. The apparent annual survival of Humboldt's flying squirrels and Townsend's chipmunks were correlated weakly with population abundance (Weldy, *Chapter 2*), with the same magnitude; however, the direction of the effect differed. In addition, the apparent annual survival of Humboldt's flying squirrels was not correlated with recruitment or realized population growth rate, while the apparent annual survival of Townsend's chipmunks was strongly correlated with both recruitment and realized population growth rate. These differences suggest different life history strategies and potential for co-occurrence patterns regulated by niche partitioning of resources, predator associations, or time.

Temporal variation was larger than spatial variation in all of the estimated parameters except the apparent annual survival of Humboldt's flying squirrels. We observed an increase of more than 2-fold in the apparent annual survival of Townsend's chipmunks in the interval just before our peak abundance estimate. Moreover, we observed an approximately 3-fold decrease in recruitment and a 2-fold decrease in population growth of Humboldt's flying squirrels and Townsend's chipmunks in the interval before peak abundance when compared to the interval after peak abundance. Previous studies have noted strong differences in vital rates across years (Ozgul et al. 2004, Lehmkuhl et al. 2006), yet the striking difference we observed is especially salient when assessing habitat quality for species. Single estimates of population change could result in different classifications of habitat suitability. For example, on the same sites, from 2012–2013 estimated population growth was much higher than from 2013–2014 and from 2014–2015. Thus, single estimates of population growth from different years might categorize these study sites as sink or source habitat.

For both species, we were able to identify an associative link between abundance-associated covariates and vital processes (Weldy, *Chapter 2*). Moreover, the directions of covariate effects on abundance were similar to their effects on vital rates. For example, high elevation sites had fewer Humboldt's flying squirrels and higher apparent annual survival, which was associated negatively with population growth (Weldy, *Chapter 2*). In addition, the top-ranking model for the vital process most associated with species-specific population growth included the covariates identified as having a biologically meaningful (i.e., biologically meaningful was defined as an effect size larger than average grid and year-specific temporal change in abundance) effect on abundance. Specifically, canopy openness was included in the top-ranking models for annual apparent survival and recruitment of Townsend's chipmunks (Weldy, *Chapter 2*), and berry-producing plant cover was included in the top-ranking model estimating Humboldt's flying squirrel recruitment (Weldy, *Chapter 2*). Previous studies have highlighted potential biases that might affect inference in habitat quality studies that rely primarily on spatial or temporal changes in abundance to describe specific spatiotemporal associations (Armstrong 2005, Todd and Rothermel 2006). For example, spatial variation in movement and individual behavior might affect abundance estimates (Bailey et al. 2004) and in sink habitats abundance might remain high despite low individual survival due to immigration (Todd and Rothermel 2006). We observed little spatial variation in vital rates. Instead, temporal variation was a much better indicator of vital rate fluctuations. However, these results support the habitat associations proposed by Weldy (*Chapter* 2) based on variation in abundance and properties of community composition.

Villa et al. (1999) proposed that Humboldt's flying squirrels can exhibit different r- and K-selection survival strategies in different forests. Humboldt's flying squirrels exhibit K-selected strategies in stable environments with stable food and nest resources, and r- selected strategies in less suitable environments (Wilson and Bossert 1971, Villa et al. 1999). We are unaware of any studies that have assessed the survival strategy of Humboldt's flying squirrels in the Oregon Cascades. Our estimates of apparent survival are only slightly less than previous proportional estimates of survival (not accounting for detection probability) presented by Villa et al. (1999) for K-selected northern flying squirrels in the Oregon Coast Range, and we observed little temporal or spatial variability in the apparent annual survival of Humboldt's flying squirrels. But, population growth rates were primarily driven by recruitment. Thus, we suggest that Humboldt's flying squirrels were intermediate to the r- and K-selection strategies on our sites. Townsend's chipmunks are much less studied, and we are unaware of their association with multiple selection strategies. Our apparent annual survival estimates for Townsend's chipmunks were 1.5–3-fold lower than our estimates for Humboldt's flying squirrel apparent annual survival in all years and more variable. In addition, population growth rates were being driven by both recruitment, apparent annual survival, suggesting that Townsend's chipmunks were r-selected.

Contrary to predictions, none of our covariates were associated strongly with the apparent annual survival of Humboldt's flying squirrels. Our estimates of Humboldt's flying squirrel apparent annual survival are intermediate to the estimates of previous studies (Ransome and Sullivan 2002, Gomez 2005, Lehmkuhl 2006). However, we did not estimate age-specific apparent survival, which might have lowered our overall group estimates. For example, heavy predation of young Humboldt's flying squirrels could lower the estimate of overall survival (Carey 2002). We are aware of only one other study that estimated apparent survival of Townsend's chipmunk (Sullivan et al. 1983), but that study's estimates of 14 and 21day survival are not comparable to our annual survival estimates. However, our estimates were within the range of estimated apparent survival for yellow-pine chipmunks (*Tamias amoenus*) in the Front Range of the Rocky Mountains. Contrary to prediction, minimum winter temperature had a negative effect on the apparent survival of Townsend's chipmunks, where lower minimum winter temperatures resulted in higher apparent survival. Differences in winter torpor strategies might explain the differences in response to minimum winter temperature. Tamias spp. are

true hibernators, while *Glaucomys* spp. do not enter true winter torpor (Levesque and Tattersall 2009, Olson et al. 2017).

Our estimates of Humboldt's flying squirrel recruitment largely were intermediate to previous annual estimates by Lehmkuhl et al. (2006) in more dry pine forests dominated by ponderosa pine (*Pinus ponderosa*), Douglas-fir, and grand fir (Abies grandis). The exception was our recruitment estimates during the 2012-2013 interval, which both our additional recruitment estimates and those given by Lehmkuhl et al. (2006). Our estimates were also intermediate to previous estimates of recruitment derived using the ratios of juveniles to adults (Rosenberg and Anthony 1992, Smith and Nicols 2003), but substantially smaller than the Smith et al. (2007) estimate. While the difference may have been methodological in part, our study highlights the potential for strong temporal variation in Humboldt's flying squirrel recruitment. Thus, much of the variability presented as differences across forest types and ages might instead largely reflect inter-annual variation. We are unaware of any studies estimating recruitment of Townsend's chipmunks. However, Sullivan et al. (1983) did observe large recruitment pulses that corresponded with large periods of population growth. As predicted, low minimum winter temperature strongly reduced recruitment of Humboldt's flying squirrels and Townsend's chipmunks. Spatial associations with recruitment varied between Townsend's chipmunks and Humboldt's flying squirrels. Spatial variation in Humboldt's flying squirrel recruitment was associated most with berry producing plant cover and elevation, which were moderately correlated during this study. Townsend's chipmunk recruitment was associated most with canopy cover, but the effect was small and not

significant. Carey et al. (1999) previously identified the importance of canopy stratification in explaining variance in chipmunk carrying capacity.

Our results highlight the similarities and differences in the life-history strategies of two co-occurring small mammals and clarifies the link between abundance associated habitat features and the vital processes of the species (Van Horne 1983, Weldy, Chapter 2). In particular, we emphasize the importance of temporal variation in vital rate estimation, especially when comparing habitat quality. We were able to identify mechanistic links between the vital rates of both species and habitat covariates previously identified as influential to abundance (Weldy, *Chapter* 2). Humboldt's flying squirrels on our study sites were intermediate between r- and K-selection life history strategies, while Townsend's chipmunks, despite their hypothesized ability for true winter hibernation, followed an r-selected life history strategy. In addition, we provide precise estimates of Humboldt's flying squirrel and Townsend's chipmunk's vital rates in the foothills of the Oregon Cascades, on the site of a long-term northern spotted owl research site. Further research is needed to explore variation in abundance of co-occurring small mammals in old forests as well as the relative contribution of vital rates to observed changes in abundance. Fully understanding the relationship between these small mammal demographics and forest-adapted predator vital rates remains an important information need.

LITERATURE CITED

- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. GutiéRrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and Trends in Demography of Northern Spotted Owls, 1985–2003. Wildlife Monographs 163:1–48.
- Anthony, R. G., D. K. Rosenberg, and K. A. Swindle. 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. Northwest Science 68:266–272.
- Arbogast, B. S., K. I. Schumacher, N. J. Kerhoulas, A. L. Bidlack, J. A. Cook, and G. J. Kenagy. 2017. Genetic data reveal a cryptic species of New World flying squirrel: *Glaucomys oregonensis*. Journal of Mammalogy 1-15.
- Aubry, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Beyer, H. 2012. Geospatial Modelling Environment. Spatial Ecology.
- Bowers, M. A., and J. L. Dooley Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia 94:247–254.
- Bull, E. 2000. Seasonal and sexual differences in American marten diet in northeastern Oregon. Northwest Science 74:186–191.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- Carey, A. B. 2002. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. Furth, Germany. http://www.treesearch.fs.fed.us/pubs/5528 Accessed 16 February 2016.
- Carey, A. B., B. L. Biswell, and J. W. Witt. 1991. Methods for measuring populations of arboreal rodents. USDA Forest Service, General Technical Report, Pacific Northwest Research Station (USA).
- Carey, A. B., J. Kershner, B. Biswell, and L. D. de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142(1):3–71.

- Cissel, J. H., F. J. Swanson, and P. J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9:1217–1231.
- Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biological Conservation 128:231–240.
- Daly, C., and W. McKee. 2016. Meteorological data from benchmark stations at the Andrews Experimental Forest, 1957 to present. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MS001 Accessed 18 March 2018.
- Dugger, K. M. et al. 2016. The effects of habitat, climate, and Barred Owls on long-term demography of Northern Spotted Owls. The Condor 118:57–116.
- Ernest, S. K., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.
- ESRI. 2011. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.
- Forsman, E. D. et al. 2001. Spatial and temporal variation in diets of Spotted Owls in Washington. Journal of Raptor Research 35:141–150.
- Forsman, E. D. et al. 2011. Population demography of Northern Spotted Owls. Studies in Avian Biology 40.
- Forsman, E. D., R. G. Anthony, E. C. Meslow, and C. J. Zabel. 2004. Diets and foraging behavior of Northern Spotted Owls in Oregon. Journal of Raptor Research 38:214–230.
- Fryxell, J. M., J. B. Falls, E. A. Falls, R. J. Brooks, L. Dix, and M. A. Strickland. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. Ecology 80:1311–1321.
- Gomez, D. M., R. G. Anthony, and J. P. Hayes. 2005. Influence of thinning of Douglas-fir forests on population parameters and diet of northern flying squirrels. The Journal of Wildlife Management 69:1670–1682.
- Hansson, L. 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. Oikos 29:539–544.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. US LTER Network Office Seattle (WA).

- Hinkle, D. E., W. Wiersma, and S. G. Jurs. 2003. Applied statistics for the behavioral sciences. 5th ed. Houghton Mifflin, Boston.
- Holloway, G. L., and W. P. Smith. 2011. A meta-analysis of forest age and structure effects on northern flying squirrel densities. The Journal of Wildlife Management 75:668–674.
- Huang, L. et al. 2016. Drought dominates the interannual variability in global terrestrial net primary production by controlling semi-arid ecosystems. Scientific Reports 6:24639.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725–732.
- Lehmkuhl, J. F., L. E. Gould, E. Cázares, and D. R. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200:49–65.
- Lehmkuhl, J. F., K. D. Kistler, J. S. Begley, and J. Boulanger. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16:584–600.
- Levesque, D. L., and G. J. Tattersall. 2010. Seasonal torpor and normothermic energy metabolism in the eastern chipmunk (*Tamias striatus*). Journal of Comparative Physiology B 180:279–292.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. Journal of Mammalogy 85:87–96.
- Maser, C., and Z. Maser. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. The Great Basin Naturalist 48:358–369.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.
- North, M., J. Trappe, and J. Franklin. 1997. Standing crop and animal consumption of fungal sporocarps in Pacific Northwest forests. Ecology 78:1543–1554.
- Olson, M. N., J. Bowman, and G. Burness. 2017. Seasonal energetics and torpor use in North American flying squirrels. Journal of Thermal Biology 70:46–53.

- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.
- Pyare, S., and W. S. Longland. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. Canadian Journal of Forest Research 32:1016–1024.
- Ransome, D. B., and T. B. Sullivan. 2002. Short-term population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in commercially thinned and unthinned stands of coastal coniferous forest. Canadian Journal of Forest Research 32:2043–2050.
- Reynolds, R. T., and E. C. Meslow. 1984. Partitioning of food and niche characteristics of coexisting accipiter during breeding. The Auk 101:761–779.
- Risch, T. S., and M. J. Brady. 1996. Trap height and capture success of arboreal small mammals: evidence from southern flying squirrels (*Glaucomys volans*). American Midland Naturalist 136:346–351.
- Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology. Canadian Journal of Zoology 70:161–166.
- Rosenberg, D. K., and R. G. Anthony. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. The Journal of Wildlife Management 57:365–373.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. Canadian Journal of Zoology 81:1715–1725.
- Schulze, M., and G. Lienkaemper. 2015. Vegetation classification, Andrews Experimental Forest and vicinity (1988,1993,1996,1997,2002, 2008). http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TV061 Accessed 13 February 2018.
- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. MacMillian, New York.
- Sikes, R. S., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.
- Smith, W. P. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. Journal of Mammalogy 88:862–881.

- Smith, W. P., and J. V. Nichols. 2003. Demography of the prince of wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. Journal of Mammalogy 84:1044–1058.
- Spies, T. 2016. LiDAR data (August 2008) for the Andrews Experimental Forest and Willamette National Forest study areas. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=GI010 Accessed 23 March 2018.
- Stanley, T. R., and K. P. Burnham. 1998. Information-theoretic model selection and model averaging for closed-population capture-recapture studies. Biometrical Journal 40:475–494.
- Sullivan, T. P., D. S. Sullivan, and C. J. Krebs. 1983. Demographic responses of a chipmunk (*Eutamias townsendii*) population with supplemental food. The Journal of Animal Ecology 52:743–755.
- Swanson, F. J., and J. A. Jones. 2002. Geomorphology and hydrology of the H. J. Andrews Experimental Forest, Blue River, Oregon. Field Guide to Geologic Processes in Cascadia:289–313.
- Tallmon, D. A., E. S. Jules, N. J. Radke, and L. S. Mills. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. Ecological Applications 13:1193–1203.
- Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). Biological Conservation 133:178–185.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893-901.
- Villa, L. J., A. B. Carey, T. M. Wilson, and K. E. Glos. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. USDA Forest Service, General Technical Report PNW-GTR-444:1-59.
- Waldien, D. L., J. P. Hayes, and M. M. P. Huso. 2006. Use of downed wood by Townsend's chipmunks (*Tamias townsendii*) in western Oregon. Journal of Mammalogy 87:454–460.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Wilson, E. O., and W. H. Bossert. 1971. A primer of population biology. Sinauer Associates Sunderland, MA.

Table 3.1. – Description of variables considered in models of detection probability (p), recapture probability (c), apparent survival (φ) , and recruitment (f) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) using mark-recapture data recorded in late-successional forests in the central Oregon Cascades from 2011–2016.

Variables	Description	Range
Elevation	Average study site elevation, estimated using 2008 lidar	683 - 1,244 m
	data.	
Canopy	Study site proportion of $0 - 10$ m canopy openness to $10 +$	9 - 38%
	m canopy openness, estimated using 2008 lidar data.	
Shrub	Mean percentage cover of all woody shrubs between 0.5	10.3 - 58.3%
	m and 1.5 m in height.	
Berry	Mean percentage cover of berry-producing plants.	12.1- 51.2%
Year	A year specific effect for each trapping occasion from	2011 - 2016
	2011–2016.	
Season	Trend from the first to the last day of the trapping.	1 – 36
Trapping	Trapping Trend is a linear trend from the first to the last	1 – 12 days
Trend	day of trapping. The trend is the same across all grids and	
	describes a protocol related effect independent of	
	seasonality.	
Julian date	Trend from the first to the last day of the project across	11269 – 16323
	the first 6 years of data collection.	
Min.	Minimum daily mean temperature during the winter.	-13 – -3.9 °C
Temp.		

Effort	Trap type specific trapping effort, adjusted for stuck and	945 - 1498.5			
	sprung traps.	trap nights			
TC ^c	The effect of TC ^c captures on trap availability for HFS ^b .	189 - 941			
Captured		captures/trappin			
		g period			
TC ^c	The effect of TC ^c abundance, which was estimated using	25.06 - 172.84			
Abundance	Huggins' closed capture models (Weldy, Chapter 2).	TC ^c			
HFS ^b	The effect of HFS ^b abundance, which was estimated using	5.71 - 62.50			
Abundance	Huggins' closed capture models (Weldy, Chapter 2).	HFS ^b			
a. Winter is defined as October 1 through April 1					

a- Winter is defined as October 1 through April 1.b- Humboldt's flying squirrel (*Glaucomys oregonensis*)

c- Townsend's chipmunk (Neotamias townsendii)

Table 3.2. – A priori predictions of variable effects in models of detection probability (p), recapture probability (c), apparent survival (φ) , and recruitment (f) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*). Habitat covariates were measured once during the summer of 2016 at 18 standardized trap stations per study site in the H. J Andrews Experimental Forest, near Blue River, OR. p indicates detection probability, c indicates recapture probability, φ indicates apparent annual survival, f indicates recruitment, + indicates a positive prediction, - indicates a negative prediction, / indicates no effect, and empty box indicates no prediction made.

	HFS ^a			TC ^b				
Covariate	p	С	φ	f	p	С	φ	f
Elevation	-	+	-	+	-	+	-	+
Canopy	-	-	-	+	+	-	-	+
Shrub	+	+			+	+		
Berry			+	+			+	+
Year								
JDate	+	+			+	+		
Effort	+	+			+	+		
Season	-	+			+	+		
Trapping Trend	-	+			-	+		
TC ^b Captured	-	-						
Min. Temp.			+	+			+	+
TC ^b abundance			-	-			-	-
HFS ^a abundance			-	-			/	/

Expected Results

a- Humboldt's flying squirrel (Glaucomys oregonensis)

b- Townsend's chipmunk (Neotamias townsendii)

Table 3.3. – Estimates, from a previous study, of Humboldt's flying squirrel (*Glaucomys oregonensis*) and Townsend's chipmunk (*Neotamias townsendii*) abundance from Huggins closed population models. The abundance estimates are site and year-specific. Estimates were derived on 9 sites arranged across elevation and canopy openness gradients in a late successional forest within the H. J Andrews Experimental Forest, near Blue River, OR.

Experimental Forest, near Di	ue River,	OR.					
Site	Species	2011	2012	2013	2014	2015	2016
1,060-1,080 m, <15% Openness	HFS	15.85	34.11	24.34	22.35	21.17	12.33
	TC	91.31	48.29	108.26	79.55	60.28	34.35
1,090-1,210 m, 15-30% Openness	HFS	17.13	45.62	60.43	48.49	27.48	33.65
	TC	108.18	102.26	172.84	129.39	103.20	73.34
1,210-1,280 m, 30-45% Openness	HFS	5.71	15.35	32.16	25.29	11.35	19.49
	TC	78.93	100.12	130.76	114.17	89.08	74.17
630-710 m, <15% Openness	HFS	38.43	47.79	55.45	40.75	31.31	24.78
	TC	36.85	44.14	41.52	31.11	25.06	54.30
650-730 m, 30-45% Openness	HFS	20.24	42.82	56.74	41.50	20.43	21.20
	TC	64.52	67.22	83.06	63.24	56.14	62.36
680-740 m, 15-30% Openness	HFS	36.97	53.47	55.11	37.90	34.45	11.45
	TC	85.28	53.09	110.85	66.13	47.06	64.21
810-910 m, 30-45% Openness	HFS	27.14	45.07	62.50	42.60	34.77	23.37
	TC	52.33	81.29	90.26	81.34	75.21	90.58
850-950 m, <15% Openness	HFS	30.33	38.19	53.86	38.58	26.20	27.72
	TC	50.41	45.19	61.96	41.20	31.10	54.39
890-920 m, 15-30% Openness	HFS	19.33	30.52	48.89	30.80	29.43	10.44
	TC	99.13	72.20	130.50	80.26	66.14	57.29

HFS-Humboldt's flying squirrel (Glaucomys oregonensis)

TC- Townsend's chipmunk (Neotamias townsendii)

Table 3.4. – Top 5 ranking models used to estimate recapture probability (*c*) of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in a late successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model ^a	AICc	ΔAICc	W	K
HFS ^b	Chipmunk + Elevation	28421.77	0.00	0.97	25
	Chipmunk	28428.57	6.80	0.03	24
	Year	28435.21	13.44	0.00	28
	Year + Elevation	28437.23	15.46	0.00	29
	Trapping Trend ^d	28440.26	18.50	0.00	24
TC ^c	Trapping Trend ^d + Elevation	56041.37	0.00	1.00	25
	Trapping Trend ^d + Canopy	56111.14	69.77	0.00	25
	Trapping Trend ^d	56146.74	105.37	0.00	24
	Year + Elevation	56246.46	205.09	0.00	29
	Effort + Elevation	56292.48	251.12	0.00	25

a- $\varphi(t) f(t) p(YR*T)$

b- Humboldt's flying squirrel (Glaucomys oregonensis)

c- Townsend's chipmunk (Neotamias townsendii)

d- Trapping Trend is a linear trend from the first to the last day of trapping. The trend is the same across all grids and describes a protocol related effect independent of seasonality.

Table 3.5. – Top 5 ranking models used to estimate capture probability (p) of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in a late successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (w), and the number of parameters (K).

Species	Model	AICc	ΔAICc	W	K
HFS ^{a c}	Year + Elevation	28472.22	0.00	0.71	20
	Year + Canopy	28474.77	2.55	0.20	20
	Year	28476.82	4.61	0.07	19
	Year + Shrub	28478.77	6.56	0.03	20
	Julian Date + Canopy	28589.28	117.06	0.00	16
$TC^{b d}$	Trapping Trend ^e + Shrub	56104.46	0.00	1.00	16
	Trapping Trend ^e + Elevation	56125.51	21.06	0.00	16
	Trapping Trend ^e	56127.74	23.28	0.00	15
	Trapping Trend + Canopy	56127.76	23.30	0.00	16
	Year + Shrub	56254.35	149.89	0.00	20

- a- Model structure for initial recapture probability (*c*) for Humboldt's flying squirrels was held to the top-ranking model structure from step 2 of the sequential modeling strategy. Model structure for was $\varphi(t)$ f(t)*c*(Chipmunk + Elevation).
- b- Model structure for initial recapture probability (*c*) for Townsend's Chipmunks was held to the top-ranking model structure from step 2 of the sequential modeling strategy. Model structure for was $\varphi(t) f(t)c$ (Trapping Trend + Elevation).
- c- Humboldt's flying squirrel (Glaucomys oregonensis)
- d- Townsend's chipmunk (Neotamias townsendii)
- e- Trapping Trend is a linear trend from the first to the last day of trapping. The trend is the same across all grids and describes a protocol related effect independent of seasonality.

Table 3.6. – Top 5 ranking models used to estimate apparent survival (φ) of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in a late successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the topranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model	AICc	ΔAICc	W	K
HFS ^{a c}	Elevation	28486.62	0.00	0.25	17
	Chipmunk Abundance	28487.09	0.47	0.20	17
		28487.51	0.89	0.16	16
	Berry	28488.20	1.58	0.11	17
	Min. Temp.+ Elevation	28488.38	1.76	0.10	18
TC ^{b d}	Min. Temp. + Canopy	56283.56	0.00	0.34	14
	Min. Temp.	56283.87	0.31	0.29	13
	Min. Temp. + Elevation	56284.15	0.59	0.25	14
	Min. Temp. + Berry	56285.51	1.94	0.13	14
	HFS Abundance	56334.79	51.23	0.00	13

a- Model structure used to estimate apparent annual survival $\varphi(t)$ was held to f(t)p(Year + Elevation)c(Trapping Trend + Elevation).

b- Model structure used to estimate apparent annual survival $\varphi(t)$ was held to f(t)p(Trapping Trend + Shrub)c(Trapping Trend + Elevation).

c- Humboldt's flying squirrel (Glaucomys oregonensis)

d- Townsend's chipmunk (Neotamias townsendii)

Table 3.7. – Top 5 ranking models used to estimate recruitment (*f*) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model	AICc	ΔAICc	W	Κ
HFS ^{a c}	Min. Temp. + Berry	28503.94	0.00	0.53	18
	Min. Temp. + Elevation	28504.45	0.51	0.41	18
	Min. Temp.	28508.37	4.42	0.06	17
	Berry	28542.89	38.94	0.00	17
	Elevation	28543.32	39.37	0.00	17
$TC^{b d}$	Min. Temp. + Canopy	56159.95	0.00	0.47	14
	Min. Temp.	56160.82	0.87	0.30	13
	Min. Temp. + Berry	56162.77	2.82	0.11	14
	Min. Temp. + Elevation	56162.82	2.87	0.11	14
	TC Abundance	56322.49	162.54	0.00	13

a- Model structure used to estimate apparent annual survival f(t) was held to $\varphi(t)p(\text{Year} + \text{Elevation})c(\text{Trapping Trend} + \text{Elevation}).$

b- Model structure used to estimate apparent annual survival f(t) was held to $\varphi(t)p(\text{Trapping Trend} + \text{Shrub})c(\text{Trapping Trend} + \text{Elevation}).$

c- Humboldt's flying squirrel (Glaucomys oregonensis)

d- Townsend's chipmunk (Neotamias townsendii)

Table 3.8. – Pairwise Pearson's correlation coefficients for a comparison of estimated vital rates and fall abundance of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) from all years and sites on the H. J. Andrews Experimental Forest in Oregon from 2011–2016. We used grid- and year-specific abundance estimates from Huggins closed-capture models (Weldy, *Chapter 2*). We present correlations between year- and site-specific abundance; λ - population growth; *f*- recruitment; φ - apparent annual survival. Humboldt's Flying Squirrel Townsend's Chipmunk

						r
	λ	f	φ	λ	f	φ
Abundance	-0.17	-0.31	-0.44	-0.41	-0.37	0.44
λ		0.98	0.08		0.97	-0.99
f			0.18			-0.97



Figure 3.1. – Location the H. J. Andrews Experimental Forest, in Central Oregon. We collected mark-recapture data for small mammals on 9 sites, represented by the black squares, in late-successional forests from 2011–2016.



Figure 3.2. – Apparent annual survival of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) from all open-population trapping intervals from 2011–2016 in the H. J. Andrews Experimental Forest in Oregon. Here we present only the estimates from one study site with a range of elevation of 890 to 920 m, and a canopy openness of 15-30%. There was some support for spatial variation in apparent annual survival; however, the effect was small and there was no detectable (overlapping confidence intervals) for a difference between sites.


Figure 3.3. – Annual recruitment of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) from all open-population trapping intervals from 2011–2016 in the H. J. Andrews Experimental Forest in Oregon. Here we present only the estimates from one study site with a range of elevation of 890 to 920 m, and a canopy openness of 15-30%. There was some support for spatial variation in recruitment; however, the effect was small and there was no detectable (overlapping confidence intervals) for a difference between sites.



Figure 3.4. – Annual population growth of Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) from all open-population trapping intervals from 2011–2016 in the H. J. Andrews Experimental Forest in Oregon. Here we present only the estimates from one study site with a range of elevation of 890 to 920 m, and a canopy openness of 15-30%. There was some support for spatial variation in recruitment; however, the effect was small and there was no detectable (overlapping confidence intervals) for a difference between sites.

Chapter 4

GENERAL CONCLUSION

Matt Weldy

RESEARCH GOALS

In this study, I explored 7 research objectives focused on the spatiotemporal variation in small mammal population attributes and vital rates within late successional forests in Oregon's western Cascades. Specifically, I sought to estimate the year and site-specific abundance of 4 co-occurring species, and apparent annual survival, population growth, and recruitment for 2 of those species. I also sought to clarify the patterns of co-occurrence, species-specific abundance autocorrelation. In addition, I sought to identify a link between abundance-associated covariates and species-specific vital rates, and identify correlations among vital rates.

PRIMARY FINDINGS

I presented the results from the analysis of the first 6 years of data collected on an ongoing small mammal mark-recapture study. The experimental design of the study was observational and we performed no strict experimental tests. Thus, the scope of inference should only be conservatively applicable beyond the marked population of small mammals on our sites. In cases where I retested previously established hypotheses, the results should provide reasonable support or retraction to the generalization of these hypothesis. However, where I tested new hypotheses relevant to species-specific biology, inference based on my results should be reevaluated in other systems to test their spatial and temporal generalizability. Due to limitations of the data I only tested linear relationships; however, quadratic relationships between abundance and some of the tested covariates are biologically feasible (Manning and Edge 2004). Thus, future studies with more robust datasets should test for quadratic or phase-specific (in species exhibiting population cycles) relationships between abundance, covariates, and vital rates.

In Chapter 2, I estimated year- and site-specific abundance of Humboldt's flying squirrels (Glaucomys oregonensis), Townsend's chipmunks (Neotamias townsendii), western red-backed voles (Myodes californicus), and deer mice (*Peromyscus maniculatus*). I observed variable abundance responses to the same spatiotemporal predictors among these co-occurring small mammals, and at least 1 biologically meaningful association between abundance and a spatiotemporal predictor. I defined biologically meaningful as an effect size that was larger than average year- and site-specific change in species-specific abundance. In addition, I observed evidence for both spatial and temporal variation in year- and site-specific abundance estimates. However, temporal variation was much stronger than spatial variation for each of these species, which resulted in apparent spatial synchrony in species-specific abundance among our sites. I observed little evidence of linear correlation among the abundance estimates (4 species) and counts (8 species), except for a weak negative correlation between the abundance of Humboldt's flying squirrels and western red-backed voles. Lastly, I found moderate evidence, despite a short time series, of cyclical population dynamics for Humboldt's flying squirrels (5-year positive autocorrelation) and western red-backed voles (4-5-year negative autocorrelation); however, these estimates should be revisited in future years of this study.

In Chapter 3, I estimated annual apparent survival, population growth and recruitment of Humboldt's flying squirrels and Townsend's chipmunks. Similarly, to

126

my Chapter 2 results, temporal variation was much stronger then spatial variation. We observed clear differences between the two species in their patterns of apparent annual survival. Apparent annual survival of Humboldt's flying squirrels was relatively high and nearly constant among years and grids, whereas the apparent annual survival of Townsend's chipmunks was consistently lower and exhibited significant temporal variation. Annual population growth rate and recruitment of Humboldt's flying squirrels and Townsend's chipmunks varied similarly among years. For both species, population growth rate and recruitment peaked just prior to peak species-specific abundance estimates (during the 2012–2013 interval) and declined significantly as abundance decreased (Weldy, *Chapter 2*). Annual population growth rate of Humboldt's flying squirrels was strongly correlated with annual recruitment, whereas annual population growth rate of Townsend's chipmunks was strongly correlated with both apparent annual survival and recruitment. Population growth rate was density independent for both species. Lastly, I identified an associative link between abundance-associated covariates and vital processes (Weldy, *Chapter 2*). For both species, abundance-associated covariates were associated with the vital rate most correlated with population growth rate.

In summary, my results provide insight into the life-history strategies and patterns of association for co-occurring small mammals, which might inform management of these species and their predators. At the spatial scale of my study I observed some evidence of spatial variability, but temporal variability was much larger. This result is especially important when assessing habitat quality. Previous studies have suggested that density or abundance can be a misleading indicator of habitat quality and that vital rates should be used instead (Van Horne 1983, Todd and Rothermel 2006). However, the temporal variability of vital rates might further confound habitat quality inference, especially in short-term studies. Moreover, while density and abundance might be misleading indicators of habitat quality in some studies, during this study inference regarding habitat quality based on abundance and on vital rates was strikingly consistent.

FUTURE ANALYSIS

As stated previously, this work represents the first analysis of small mammal data for this intended long-term study. Future analyses should revisit the analysis of cyclical population dynamics and test specific predictions about population cycling based on this initial analysis. Hayes et al. (2017) noted that long-term studies on rodents conducted across a wide range of environments have contributed much to the current understanding of social processes, community dynamics, and population regulation; however, the authors noted a need to include manipulative experiments as part of long-term studies to further our understanding of population dynamics. Thus, future analysis should consider experimental manipulations of habitat features to test casual relationships between the abundance and vital rates of the focal species.

The experimental focus on annual estimates might not align well with the biological factors regulating populations on these study sites. While Humboldt's flying squirrels typically only have one litter in the spring (Smith 2007), western red-backed voles and deer mice can have multiple litters per year (Galindo and Krebs 1985). Instead, temporal covariates might be more closely correlated with the phases (increasing, peak, decreasing, trough) of population cycles, which might occur on

monthly or multiyear time scales depending on the species (Krebs 2013). If the continued dataset confirms that Humboldt's flying squirrels and western red-backed voles do fluctuate cyclically in our study area as they do in Ontario (Fryxell et al. 1998) and British Columbia (Sullivan et al. 2017), future analyses should evaluate the effects of temporal covariates on population cycle phases.

Seed production has been strongly associated with temporal fluctuations of many small mammal species (Smith 1970, Falls et al. 2007, Lobo et al. 2013, Lobo 2014, Ogawa et al. 2017), but few studies have evaluated this effect in the Pacific Northwest (Sullivan et al. 2017). Development of a temporal species-specific seed production covariate would allow for a detailed comparison of co-occurring small mammal responses to pulsed food resources and might highlight potential sources of competition. In addition, previous studies have demonstrated the importance of fungi in the diet of many small mammals in the PNW (Maser et al. 1978, Ure and Maser 1982, Pyare and Longland 2001). I was unable to estimate the relative occurrence of fungi during this study, but future analysis should consider fungal sampling methodologies that do not disturb the *in situ* ecology of the study sites, such as the use of eDNA.

In summary, this intended long-term study of the ecology of co-occurring small mammals across heterogenous late successional forests, will likely continue to contribute to our understanding of Pacific Northwest small mammal population dynamics, life history, and patterns of co-occurrence. In addition, this study will help establish an important baseline for studies designed to explore the effects of habitat disturbance. Lastly, this study will contribute to the rich small mammal literature by serving as an additional long-term (5-10 years) dataset (Krebs 2013, Hayes et al. 2017).

LITERATURE CITED

- Falls, J. B., E. Falls, and J. M. Fryxell. 2007. Fluctuations of deer mice in Ontario in relation to seed crops. Ecological Monographs 77:19–32.
- Fryxell, J. M., J. B. Falls, E. A. Falls, and R. J. Brooks. 1998. Long-term dynamics of small-mammal populations in Ontario. Ecology 79:213–225.
- Hayes, L. D., L. A. Ebensperger, D. A. Kelt, P. L. Meserve, N. Pillay, V. A. Viblanc, and C. Schradin. 2017. Long-term field studies on rodents. Journal of Mammalogy 98:642–651.
- Galindo, C., and C. J. Krebs. 1985. Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. Canadian Journal of Zoology 63:1870–1879.
- Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Illinois.
- Lobo, N., D. J. Green, and J. S. Millar. 2013. Effects of seed quality and abundance on the foraging behavior of deer mice. Journal of Mammalogy 94:1449–1459.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: A review of the patterns, implications and limitations of top-down and bottom-up interactions. Forest Ecology and Management 328:45–54.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. Journal of Mammalogy 85:87–96.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.
- Ogawa, R., A. Mortelliti, J. W. Witham, and M. L. Hunter. 2017. Demographic mechanisms linking tree seeds and rodent population fluctuations: insights from a 33-year study. Journal of Mammalogy 98:419–427.
- Pyare, S., and W. S. Longland. 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. Journal of Mammalogy 82:681–689.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349–371.
- Smith, W. P. 2007. Ecology of *Glaucomys sabrinus*: Habitat, Demography, and Community Relations. Journal of Mammalogy 88:862–881.

- Sullivan, T. P., D. S. Sullivan, R. Boonstra, C. J. Krebs, and A. Vyse. 2017. Mechanisms of population limitation in the southern red-backed vole in conifer forests of western North America: insights from a long-term study. Journal of Mammalogy 98:1367–1378.
- Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: Effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). Biological Conservation 133:178–185.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893–901.

BIBLIOGRAPHY

- Allen, G. S., and J. N. Owens. 1972. The life history of Douglas-fir. Forest Service, Ottawa, Canada.
- Anthony, R. G., D. K. Rosenberg, and K. A. Swindle. 1994. Habitat associations of California red-backed voles in young and old-growth forests in western Oregon. Northwest Science 68:266–272.
- Anthony, R. G., E. D. Forsman, A. B. Franklin, D. R. Anderson, K. P. Burnham, G. C. White, C. J. Schwarz, J. D. Nichols, J. E. Hines, G. S. Olson, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, K. M. Dugger, K. E. Fehring, T. L. Fleming, R. P. Gerhardt, S. A. Gremel, R. J. GutiéRrez, P. J. Happe, D. R. Herter, J. M. Higley, R. B. Horn, L. L. Irwin, P. J. Loschl, J. A. Reid, and S. G. Sovern. 2006. Status and trends in demography of northern spotted owls, 1985–2003. Wildlife Monographs 163:1–48.
- Arbogast, B. S., K. I. Schumacher, N. J. Kerhoulas, A. L. Bidlack, J. A. Cook, and G. J. Kenagy. 2017. Genetic data reveal a cryptic species of New World flying squirrel: *Glaucomys oregonensis*. Journal of Mammalogy 1-15.
- Aubry, K. B., M. J. Crites, and S. D. West. 1991. Regional patterns of small mammal abundance and community composition in Oregon and Washington. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Bates, D., M. M\u00e4chler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.
- Batzli, G. O. 1992. Dynamics of small mammal populations: a review. Pp. 831–850 in Wildlife 2001: populations. Springer.
- Beyer, H. 2012. Geospatial Modelling Environment. Spatial Ecology.
- Boonstra, R., D. Hik, G. R. Singleton, and A. Tinnikov. 1998. The impact of predator-induced stress on the snowshoe hare cycle. Ecological Monographs 68:371–394.
- Bowers, M. A., and J. L. Dooley Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. Oecologia 94:247–254.
- Bull, E. 2000. Seasonal and sexual differences in American marten diet in northeastern Oregon. Northwest Science 74:186–191.

- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer, New York.
- Butts, S. R., and W. C. McComb. 2000. Associations of forest-floor vertebrates with coarse woody debris in Managed forests of western Oregon. The Journal of Wildlife Management 64:95–104.
- Carey, A. B. 1995. Sciurids in Pacific Northwest managed and old-growth forests. Ecological Applications 5:648–661.
- Carey, A. B. 2002. Ecology of northern flying squirrels: implications for ecosystem management in the Pacific Northwest, USA. Furth, Germany. http://www.treesearch.fs.fed.us/pubs/5528> Accessed 16 February 2016.
- Carey, A. B., B. L. Biswell, and J. W. Witt. 1991. Methods for measuring populations of arboreal rodents. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Carey, A. B., S. P. Horton, and B. L. Biswell. 1992. Northern spotted owls: influence of prey base and landscape character. Ecological Monographs 62:223–250.
- Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old-growth forests. Ecological applications 5:336–352.
- Carey, A. B., J. Kershner, B. Biswell, and L. D. de Toledo. 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. Wildlife Monographs 142:3–71.
- Cazares, E., D. L. Luoma, M. P. Amaranthus, C. L. Chambers, and J. F. Lehmkuhl. 1999. Interaction of fungal sporocarp production with small mammal abundance and diet in Douglas-fir stands of the southern Cascade Range. Northwest Science 73:64–76.
- Chitty, D. 1960. Population processes in the vole and their relevance to general theory. Canadian Journal of Zoology 38:99–113.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, D. J. Parsons, and others. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications 6:665–691.
- Cissel, J. H., F. J. Swanson, and P. J. Weisberg. 1999. Landscape management using historical fire regimes: Blue River, Oregon. Ecological Applications 9:1217–1231.

- Ciuti, S., W. F. Jensen, S. E. Nielsen, and M. S. Boyce. 2015. Predicting mule deer recruitment from climate oscillations for harvest management on the northern Great Plains: predicting deer recruitment from climate indices. The Journal of Wildlife Management 79:1226–1238.
- Conn, P. B., W. L. Kendall, and M. D. Samuel. 2004. A general model for the analysis of mark-resight, mark-recapture, and band-recovery data under tag loss. Biometrics 60:900–909.
- Coppeto, S. A., D. A. Kelt, D. H. Van Vuren, J. A. Wilson, and S. Bigelow. 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. Journal of Mammalogy 87:402–413.
- Cotton, C. L., and K. L. Parker. 2000. Winter activity patterns of northern flying squirrels in sub-boreal forests. Canadian Journal of Zoology 78:1896–1901.
- Creel, S., B. Dantzer, W. Goymann, and D. R. Rubenstein. 2013. The ecology of stress: effects of the social environment. Functional Ecology 27:66–80.
- Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation 128:231–240.
- Daly, C., and W. McKee. 2016. Meteorological data from benchmark stations at the Andrews Experimental Forest, 1957 to present. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=MS001 Accessed 18 March 2018.
- DeVivo, M. T. et al. 2017. Endemic chronic wasting disease causes mule deer population decline in Wyoming. PloS one 12:e0186512.
- Doyle, A. T. 1987. Microhabitat separation among sympatric microtines, *Clethrionomys californicus, Microtus oregoni* and *M. richardsoni*. American Midland Naturalist 118:258–265.
- Dracup, E. C., D. M. Keppie, and G. J. Forbes. 2016. The short-term impact of abundant fruit upon deer mouse (*Peromyscus maniculatus*), southern red-backed vole (*Myodes gapperi*), and woodland jumping mouse (*Napaeozapus insignis*) populations. Canadian Journal of Zoology 94:555–563.
- Dugger, K. M., E. D. Forsman, A. B. Franklin, R. J. Davis, G. C. White, C. J.
 Schwarz, K. P. Burnham, J. D. Nichols, J. E. Hines, C. B. Yackulic, P. F.
 Doherty, L. Bailey, D. A. Clark, S. H. Ackers, L. S. Andrews, B. Augustine, B.
 L. Biswell, J. Blakesley, P. C. Carlson, M. J. Clement, L. V. Diller, E. M. Glenn,
 A. Green, S. A. Gremel, D. R. Herter, J. M. Higley, J. Hobson, R. B. Horn, K. P.
 Huyvaert, C. McCafferty, T. McDonald, K. McDonnell, G. S. Olson, J. A. Reid,

J. Rockweit, V. Ruiz, J. Saenz, and S. G. Sovern. 2016. The effects of habitat, climate, and barred owls on long-term demography of northern spotted owls. The Condor 118:57–116.

- Eagan, T. S., J. C. Beasley, Z. H. Olson, and O. E. Rhodes. 2011. Impacts of generalist mesopredators on the demography of small-mammal populations in fragmented landscapes. Canadian Journal of Zoology 89:724–731.
- Ecke, F., O. Löfgren, and D. Sörlin. 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. Journal of Applied Ecology 39:781–792.
- Edmonds, R. L. 1990. Litter decomposition and nutrient release in Douglas-fir, red alder, western hemlock, and pacific silver fir ecosystems in western Washington. Canadian Journal of Forest Research 10:327–337.
- Ernest, S. K., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.
- Ernest, S. K. M., J. H. Brown, K. M. Thibault, E. P. White, and J. R. Goheen. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. The American Naturalist 172:E257–E269.
- ESRI. 2011. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.
- Fairbairn, D. J. 1978. Dispersal of deer mice, *Peromyscus maniculatus*. Oecologia 32:171–193.
- Falls, J. B., E. Falls, and J. M. Fryxell. 2007. Fluctuations of deer mice in Ontario in relation to seed crops. Ecological Monographs 77:19–32.
- Fauteux, D., L. Imbeau, P. Drapeau, and M. J. Mazerolle. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. Forest Ecology and Management 266:194–205.
- Forsman, E. D., I. A. Otto, S. G. Sovern, M. Taylor, D. W. Hays, H. Allen, S. L. Roberts, and D. E. Seaman. 2001. Spatial and temporal variation in diets of spotted owls in Washington. Journal of Raptor Research 35:141–150.
- Forsman, E. D., R. G. Anthony, E. C. Meslow, and C. J. Zabel. 2004. Diets and foraging behavior of northern spotted owls in Oregon. Journal of Raptor Research 38:214–230.

- Forsman, E. D., R. G. Anthony, K. M. Dugger, E. M. Glenn, A. B. Franklin, G. C. White, C. J. Schwarz, K. P. Burnham, D. R. Anderson, J. D. Nichols, J. E. Hines, J. B. Lint, R. J. Davis, S. H. Ackers, L. S. Andrews, B. L. Biswell, P. C. Carlson, L. V. Diller, S. A. Gremel, D. R. Herter, J. M. Higley, R. B. Horn, J. A. Reid, J. Rockweit, J. P. Schaberl, T. J. Snetsinger, and S. G. Sovern. 2011. Population demography of northern spotted owls. Studies in Avian Biology 40.
- Fowells, H. A. 1965. The silvics of forest trees in the United States. Agriculture Handbook 271, U. S. Department of Agriculture, Washington, D. C.
- Fryxell, J. M., J. B. Falls, E. A. Falls, and R. J. Brooks. 1998. Long-term dynamics of small-mammal populations in Ontario. Ecology 79:213–225.
- Fryxell, J. M., J. B. Falls, E. A. Falls, R. J. Brooks, L. Dix, and M. A. Strickland. 1999. Density dependence, prey dependence, and population dynamics of martens in Ontario. Ecology 80:1311–1321.
- Galindo, C., and C. J. Krebs. 1985. Habitat use and abundance of deer mice: interactions with meadow voles and red-backed voles. Canadian Journal of Zoology 63:1870–1879.
- Garman, S., R. Anthony. 2001. Mammal species list of the Andrews Experimental Forest, 1971 to 1976. Accessed 4 January 2018">http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=SA005>Accessed 4 January 2018.
- Garman, S., W. McKee. 2001. Bird species list for the Andrews Experimental Forest and Upper McKenzie River Basin, 1975 to 1995. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=SA003 Accessed 4 January 2018.
- Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51:1018–1026.
- Gilbert, B. S., and C. J. Krebs. 1981. Effects of extra food on *Peromyscus* and *Clethrionomys* populations in the southern Yukon. Oecologia 51:326–331.
- Glenn, E. M., R. G. Anothny, and E. D. Forsman. 2010. Population trends in northern spotted owls: Associations with climate in the Pacific Northwest. Biological Conservation 143:2543–2552.
- Gomez, D. M. 1992. Small-mammal herpetofauna abundance in riparian and upslope areas of five forest conditions.
- Greenberg, C. H., D. L. Otis, and T. A. Waldrop. 2006. Response of white-footed mice (*Peromyscus leucopus*) to fire and fire surrogate fuel reduction treatments

in a southern Appalachian hardwood forest. Forest Ecology and Management 234:355–362.

- Hansson, L. 1977. Spatial dynamics of field voles *Microtus agrestis* in heterogeneous landscapes. Oikos 29:539–544.
- Hansson, L. 1987. An interpretation of rodent dynamics as due to trophic interactions. Oikos 50:308–318.
- Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen, and P. Turchin. 2001. Smallrodent dynamics and predation. Ecology 82:1505–1520.
- Harmon, M. E., and J. Sexton. 1996. Guidelines for measurements of woody detritus in forest ecosystems. Volume 20. US LTER Network Office Seattle (WA).
- Hayes, J. P., S. P. Cross, and P. W. McIntire. 1986. Seasonal variation in mycophagy by the western red-backed vole, *Clethrionomys californicus*, in Southwestern Oregon. Northwest Science 60:250–257.
- Hayes, J. P., E. G. Horvath, and P. Hounihan. 1995. Townsend's chipmunk populations in Douglas-fir plantations and mature forests in the Oregon Coast Range. Canadian Journal of Zoology 73:67–73.
- Hayes, L. D., L. A. Ebensperger, D. A. Kelt, P. L. Meserve, N. Pillay, V. A. Viblanc, and C. Schradin. 2017. Long-term field studies on rodents. Journal of Mammalogy 98:642–651.
- Hernández, L., J. W. Laundré, A. González-Romero, J. López-Portillo, and K. M. Grajales. 2011. Tale of two metrics: density and biomass in a desert rodent community. Journal of Mammalogy 92:840–851.
- Hinkle, D. E., W. Wiersma, and S. G. Jurs. 2003. Applied statistics for the behavioral sciences. 5th ed. Houghton Mifflin, Boston.
- Holloway, G. L., and J. R. Malcolm. 2006. Sciurid habitat relationships in forests managed under selection and shelterwood silviculture in Ontario. Journal of Wildlife Management' 70:1735–1745.
- Holloway, G. L., and J. R. Malcolm. 2007*a*. Northern and southern flying squirrel use of space within home ranges in central Ontario. Forest Ecology and Management 242:747–755.
- Holloway, G. L., and J. R. Malcolm. 2007b. Nest-tree use by northern and southern flying squirrels in central Ontario. Journal of Mammalogy 88:226–233.

- Holloway, G. L., and W. P. Smith. 2011. A meta-analysis of forest age and structure effects on northern flying squirrel densities. The Journal of Wildlife Management 75:668–674.
- Holloway, G. L., W. P. Smith, C. B. Halpern, R. A. Gitzen, C. C. Maguire, and S. D. West. 2012. Influence of forest structure and experimental green-tree retention on northern flying squirrel (*Glaucomys sabrinus*) abundance. Forest Ecology and Management 285:187–194.
- Huang, L., B. He, A. Chen, H. Wang, J. Liu, A. Lű, and Z. Chen. 2016. Drought dominates the interannual variability in global terrestrial net primary production by controlling semi-arid ecosystems. Scientific Reports 6.
- Huggins, R. M. 1989. On the statistical analysis of capture experiments. Biometrika 76:133–140.
- Huggins, R. M. 1991. Some practical aspects of a conditional likelihood approach to capture experiments. Biometrics 47:725-732.
- Jacobs, K. M., and D. L. Luoma. 2008. Small mammal mycophagy response to variations in green-tree retention. Journal of Wildlife Management 72:1747–1755.
- Jameson, E. W. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada, California. Journal of Mammalogy 33:50-60.
- Jones, H. P. et al. 2016. Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences 113:4033–4038.
- Karanth, K. U., and J. D. Nichols. 2011. Estimating tiger abundance from camera trap data: field surveys and analytical issues. Pp. 97–117 in Camera Traps in Animal Ecology (A. F. O'Connell, J. D. Nichols & K. U. Karanth, eds.). Springer Japan.
- Klenner, W., and T. P. Sullivan. 2009. Partial and clearcut harvesting of dry Douglasfir forests: implications for small mammal communities. Forest Ecology and Management 257:1078–1086.
- Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986. Population biology of snowshoe hares. I. demography of food-supplemented populations in the southern Yukon, 1976-84. The Journal of Animal Ecology 55:963.
- Krebs, C. J. 2002. Two complementary paradigms for analyzing population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 357:1211–1219.

- Krebs, C. J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Illinois.
- LaMontagne, J. M., C. T. Williams, J. L. Donald, M. M. Humphries, A. G. McAdam, and S. Boutin. 2013. Linking intraspecific variation in territory size, cone supply, and survival of North American red squirrels. Journal of Mammalogy 94:1048–1058.
- Lehmkuhl, J. F., S. D. West, C. L. Chambers, W. C. McComb, D. Manuwal, K. B. Aubry, J. Erikson, R. A. Gitzen, and M. Leu. 1999. An experiment for assessing vertebrate response to varying levels and patterns of green-tree retention. Northwest Science 73:45–63.
- Lehmkuhl, J. F., L. E. Gould, E. Cázares, and D. R. Hosford. 2004. Truffle abundance and mycophagy by northern flying squirrels in eastern Washington forests. Forest Ecology and Management 200:49–65.
- Lehmkuhl, J. F., K. D. Kistler, J. S. Begley, and J. Boulanger. 2006. Demography of northern flying squirrels informs ecosystem management of western interior forests. Ecological Applications 16:584–600.
- Levesque, D. L., and G. J. Tattersall. 2010. Seasonal torpor and normothermic energy metabolism in the eastern chipmunk (*Tamias striatus*). Journal of Comparative Physiology B 180:279–292.
- Lidicher, W. Z. J. 1978. Regulation of numbers in small mammal populations: historical reflections and a synthesis. Pp. 122–166 in Populations of Small Mammals under Natural Conditions. University of Pittsburgh, United States.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: a review of the patterns, implications and limitations of top-down and bottom-up interactions. Forest Ecology and Management 328:45–54.
- Lobo, N., M. Duong, and J. S. Millar. 2009. Conifer-seed preferences of small mammals. Canadian Journal of Zoology 87:773–780.
- Lobo, N., D. J. Green, and J. S. Millar. 2013. Effects of seed quality and abundance on the foraging behavior of deer mice. Journal of Mammalogy 94:1449–1459.
- Loeb, S. C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. Journal of Mammalogy 80:460–471.
- Manning, J. A., and W. D. Edge. 2004. Small mammal survival and downed wood at multiple scales in managed forests. Journal of Mammalogy 85:87–96.

- Martell, A. M. 1983. Demography of southern red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) after logging in north-central Ontario. Canadian Journal of Zoology 61:958–969.
- Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59:799–809.
- Maser, Z., C. Maser, and J. M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084–1088.
- Miller, D. H., and L. L. Getz. 1977. Factors influencing local distribution and species diversity of forest small mammals in New England. Canadian Journal of Zoology 55:806–814.
- Moon, K., D. A. Blackman, and T. D. Brewer. 2015. Understanding and integrating knowledge to improve invasive species management. Biological Invasions 17:2675–2689.

National Oceanic and Atmospheric Administration [NOAA]. 2017. Palmer Drought Severity Index (PDSI) < https://www.ncdc.noaa.gov/temp-andprecip/climatologicalrankings/index.php?periods%5B%5D=18¶meter=pdsi&state=35&div=0& month=8&year=2016#ranks-form>. Accessed 6 Aug 2017.

- North, M. P. 2002. Seasonality and abundance of truffles from oak woodlands to red fir forests. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Southwest Research Station.
- Ogawa, R., A. Mortelliti, J. W. Witham, and M. L. Hunter. 2017. Demographic mechanisms linking tree seeds and rodent population fluctuations: insights from a 33-year study. Journal of Mammalogy 98:419–427.
- Oli, M. K. 2003. Population cycles of small rodents are caused by specialist predators: or are they? Trends in Ecology & Evolution 18:105–107.
- Oli, M. K., and F. S. Dobson. 1999. Population cycles in small mammals: the role of age at sexual maturity. Oikos 86:557–565.
- Olson, M. N., J. Bowman, and G. Burness. 2017. Seasonal energetics and torpor use in North American flying squirrels. Journal of Thermal Biology 70:46–53.
- Porter, J. H., and R. D. Dueser. 1982. Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. Oikos 39:228-236.

- Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.
- Prevedello, J. A., C. R. Dickman, M. V. Vieira, and E. M. Vieira. 2013. Population responses of small mammals to food supply and predators: a global metaanalysis. Journal of Animal Ecology 82:927–936.
- Pyare, S., and W. S. Longland. 2002. Interrelationships among northern flying squirrels, truffles, and microhabitat structure in Sierra Nevada old-growth habitat. Canadian Journal of Forest Research 32:1016–1024.
- Ransome, D. B., and T. P. Sullivan. 1997. Food limitation and habitat preference of *Glaucomys sabrinus* and *Tamiasciurus hudsonicus*. Journal of Mammalogy 78:538–549.
- Ransome, D. B., and T. B. Sullivan. 2002. Short-term population dynamics of *Glaucomys sabrinus* and *Tamiasciurus douglasii* in commercially thinned and unthinned stands of coastal coniferous forest. Canadian Journal of Forest Research 32:2043–2050.
- Reynolds, R. T., and E. C. Meslow. 1984. Partitioning of food and niche characteristics of coexisting accipiter during breeding. The Auk 101:761–779.
- Risch, T. S., and M. J. Brady. 1996. Trap height and capture success of arboreal small mammals: evidence from southern flying squirrels (*Glaucomys volans*). American Midland Naturalist 136:346.
- Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. Ecology 87:1075–1085.
- Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology 70:161–166.
- Rosenberg, D. K., and R. G. Anthony. 1993. Differences in Townsend's chipmunk populations between second- and old-growth forests in western Oregon. The Journal of Wildlife Management 57:365–373.
- Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. 2003. Influence of prey abundance on northern spotted owl reproductive success in western Oregon. Canadian Journal of Zoology 81:1715–1725.
- Schulze, M., G. Lienkaemper. 2015. Vegetation classification database. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=TV061. Accessed 4 January 2018.

- Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. MacMillian, New York.
- Selva, N., K. A. Hobson, A. Cortés-Avizanda, A. Zalewski, and J. A. Donázar. 2012. Mast pulses shape trophic interactions between fluctuating rodent populations in a primeval forest. PLoS ONE 7:e51267.
- Shanley, C. S., S. Pyare, and W. P. Smith. 2013. Response of an ecological indicator to landscape composition and structure: implications for functional units of temperate rainforest ecosystems. Ecological Indicators 24:68–74.
- Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2009. The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. Journal of Animal Ecology 78:1249–1258.
- Sikes, R. S., and W. L. Gannon. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.
- Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. Wildlife Society Bulletin 399–409.
- Smith, C. C. 1968. The adaptive nature of social organization in the genus of three squirrels *Tamiasciurus*. Ecological Monographs 38:31–64.
- Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecological Monographs 40:349–371.
- Smith, C. C., and R. P. Balda. 1979. Competition among insects, birds and mammals for conifer seeds. American Zoology 19:1065–1083.
- Smith, W. P., and J. V. Nichols. 2003. Demography of the Prince of Wales flying squirrel, an endemic of southeastern Alaska temperate rain forest. Journal of Mammalogy 84:1044–1058.
- Smith, W. P., R. G. Anthony, J. R. Waters, N. L. Dodd, and C. J. Zabel. 2003. Ecology and conservation of arboreal rodents of western coniferous forests. Mammal community dynamics. Management and conservation in the coniferous forests of Western North America. Cambridge University Press, Cambridge, United Kingdom 157–206.
- Smith, W. P., S. M. Gende, and J. V. Nichols. 2004. Ecological correlates of flying squirrel microhabitat use and density in temperate rainforests of southeastern Alaska. Journal of Mammalogy 85:663–674.

- Smith, W. P., S. M. Gende, and J. V. Nichols. 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. Ecological Applications 15:689–700.
- Smith, W. P. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. Journal of Mammalogy 88:862–881.
- Sollmann, R., A. M. White, B. Gardner, and P. N. Manley. 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 80:247–254.
- Songer, M. A., M. V. Lomolino, and D. R. Perault. 1997. Niche dynamics of deer mice in a fragmented, old-growth-forest landscape. Journal of Mammalogy 78:1027–1039.
- Spies, T. 2016. LiDAR data (August 2008) for the Andrews Experimental Forest and Willamette National Forest study areas. http://andlter.forestry.oregonstate.edu/data/abstract.aspx?dbcode=GI010> Accessed 23 March 2018.
- Stanley, T. R., and K. P. Burnham. 1998. Information-theoretic model selection and model averaging for closed-population capture-recapture studies. Biometrical Journal 40:475–494.
- Strittholt, J. R., D. A. Dellasala, and H. Jiang. 2006. Status of mature and old-growth forests in the Pacific Northwest. Conservation Biology 20:363–374.
- Sullivan, T. P., and D. S. Sullivan. 1982. Population dynamics and regulation of the Douglas squirrel (*Tamiasciurus douglasii*) with supplemental food. Oecologia 53:264–270.
- Sullivan, T. P., D. S. Sullivan, and C. J. Krebs. 1983. Demographic responses of a chipmunk (*Eutamias townsendii*) population with supplemental food. The Journal of Animal Ecology 52:743-755.
- Sullivan, T. P., D. B. Ransome, D. S. Sullivan, P. M. F. Lindgren, and W. Klenner. 2017a. Tree squirrel abundance and demography in managed coniferous forests of British Columbia are within the range of natural fluctuations of old-growth stands. Canadian Journal of Forest Research 47:565–582.
- Sullivan, T. P., D. S. Sullivan, R. Boonstra, C. J. Krebs, and A. Vyse. 2017b. Mechanisms of population limitation in the southern red-backed vole in conifer forests of western North America: insights from a long-term study. Journal of Mammalogy 98:1367–1378.

- Swanson, F. J., and J. A. Jones. 2002. Geomorphology and Hydrology of the H. J. Andrews Experimental Forest, Blue River, Oregon. Field Guide to Geologic Processes in Cascadia:289–313.
- Taitt, M. J. 1981. The effect of extra food on small rodent populations: deer mice (*Peromyscus maniculatus*). The Journal of Animal Ecology 50:111-124.
- Tallmon, D. A., E. S. Jules, N. J. Radke, and L. S. Mills. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. Ecological Applications 13:1193–1203.
- Terborgh, J. et al. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1925.
- Thompson, R. L., C. L. Chambers, and B. C. McComb. 2009. Home range and habitat of western red-backed voles in the Oregon Cascades. Northwest Science 83:46–56.
- Thysell, D. R., L. J. Villa, and A. B. Carey. 1997. Observations of northern flying squirrel feeding behavior: use of non-truffle food items. Northwestern Naturalist 78:87–92.
- Todd, B. D., and B. B. Rothermel. 2006. Assessing quality of clearcut habitats for amphibians: effects on abundances versus vital rates in the southern toad (*Bufo terrestris*). Biological Conservation 133:178–185.
- Trappe, J. M., R. Molina, D. L. Luoma, E. Cazares, D. Pilz, J. E. Smith, M. A. Castellano, S. L. Miller, and M. J. Trappe. 2009. Diversity, ecology, and conservation of truffle fungi in forests of the Pacific Northwest. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Turbill, C., and S. Prior. 2016. Thermal climate-linked variation in annual survival rate of hibernating rodents: shorter winter dormancy and lower survival in warmer climates. Functional Ecology 30:1366–1372.
- Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.
- U.S. Fish and Wildlife Service. 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Northern Spotted Owl. Federal Register 55:26114–26194.
- United States Department of Agriculture [USDA], and United States Department of the Interior [USDI]. 1994. Northwest Forest Plan Record of Decision for

amendments for Forest Service and Bureau of Land Management planning documents within the range of the Northern Spotted Owl.

- Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. Canadian Journal of Zoology 59:1045–1061.
- Van Horne, B. 1982. Niches of adult and juvenile deer mice (*Peromyscus maniculatus*) in seral stages of coniferous forest. Ecology 63:992–1003.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:893-901.
- Villa, L. J., A. B. Carey, T. M. Wilson, and K. E. Glos. 1999. Maturation and reproduction of northern flying squirrels in Pacific Northwest forests. USDA Forest Service General Technical Report, USDA Forest Service General Technical Report, Pacific Northwest Research Station (USA).
- Watersheds and Gauging Stations. <https://andrewsforest.oregonstate.edu/research/infrastructure/watersheds>. Accessed 8 Jul 2017.
- Waldien, D. L., J. P. Hayes, and M. M. P. Huso. 2006. Use of downed wood by Townsend's chipmunks (*Tamias townsendii*) in western Oregon. Journal of Mammalogy 87:454–460.
- Wang, G. M. et al. 2013. Comparative population dynamics of large and small mammals in the Northern Hemisphere: deterministic and stochastic forces. Ecography 36:439–446.
- Waters, J. R., and C. J. Zabel. 1995. Northern flying squirrel densities in fir forests of northeastern California. The Journal of Wildlife Management 59:858–866.
- Weigl, P. D. 2007. The northern flying squirrel (*Glaucomys sabrinus*): a conservation challenge. Journal of Mammalogy 88:897–907.
- Wells-Gosling, N., and L. R. Heaney. 1984. *Glaucomys sabrinus*. Mammalian Species 229:1–8.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.
- White, A. M., E. F. Zipkin, P. N. Manley, and M. D. Schlesinger. 2013. Conservation of avian diversity in the Sierra Nevada: moving beyond a single-species management focus. PLoS ONE 8:e63088.

- Wiens, J. D., R. G. Anthony, and E. D. Forsman. 2014. Competitive interactions and resource partitioning between northern spotted owls and barred owls in western Oregon. Wildlife Monographs 185:1–50.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press.
- Wilson, E. O., and W. H. Bossert. 1971. A primer of population biology. Sinauer Associates Sunderland, MA.
- Wilson, T. M., and A. B. Carey. 1996. Observations of weasels in second-growth Douglas-fir forests in the Puget Trough, Washington. Northwestern Naturalist 77:35-39.
- Zurr, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer Science Business Media, New York.

Appendix 1. – Supplemental information providing Pearson's correlation coefficients of considered and selected model covariates, species-specific counts of captured individuals, species and year specific sex-ratios, and sex, year and species specific average individual weights (g).

Table 1.1. – Pearson's correlation coefficients for a priori spatial variables estimated once during 2016 on our sites across the H. J. Andrews Experimental Forest. We removed variables with Pearson's correlation coefficients from consideration for the same demographic parameter if the correlation coefficient was greater than 0.8 or less than -0.8.

	Subcanopy	Shrub	Berry	CWD ^a	Elevation
Shrub	0.37				
Berry	0.57	-0.09			
CWD ^a	0.38	-0.31	0.38		
Elevation	-0.58	0.18	-0.73	-0.26	
Canopy	0.36	0.65	-0.36	0.01	0.29

a- Site-level average coarse woody debris volume.

Table 1.2. – Pearson's correlation coefficients for a priori temporal variables. Weather-related variables were recorded at the Central Meteorological station on the H. J. Andrews Experimental Forest. We removed variables with Pearson's correlation coefficients from consideration for the same demographic parameter if the correlation coefficient was greater than 0.8 or less than -0.8.

	Min.	Days	Winter	Max Snow	18 mo	
	Temp.	below 0 °C	Precip.	Depth	PDSI	PDO
Days below 0 °C	0.35					
Winter Precip.	0.4	0.85				
Max Snow Depth	0.81	0.08	0.23			
18 mo PDSI	0.28	0.38	0.45	0.1		
PDO	0.04	0.56	0.68	-0.13	0.89	
SOI	0.04	0.43	0.37	-0.14	0.94	-0.86

Species	To	Total Individuals Caught Per Year						
	2011	2012	2013	2014	2015	2016		
HFS	172	337	420	323	234	178		
TC	647	610	926	683	557	566		
DM	48	89	178	198	124	156		
WRBV	17	36	77	147	188	199		
BW	6	3	3	9	5	3		
CV	2	3	3	5	14	14		
DS	4	16	5	15	11	3		
SH	10	10	5	5	3	4		
AP	0	6	2	5	2	1		

Table 1.3. – Number of captured individuals across all grids for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016.

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*); BW – bushytailed woodrat (*Neotoma cinerea*); CV – creeping vole (*Microtus oregoni*); DS – douglas' squirrel (*Tamiasciurus douglasii*); SH – snowshoe hare (*Lepus americanus*); AP – American pika (*Ochotona princeps*).

Table 1.4. – Year and grid-specific proportion of males to females for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. *- Indicates species-specific within year high estimate, `- Indicates species-specific within year low estimate, M- Indicates only males captured, F-Indicates only females captured.

								Site	Species
Species	Grid	2011	2012	2013	2014	2015	2016	Average	Average
HFS	1	1.07	1.30	0.86	0.82	1.38	1.18	1.10	1.04
	2	1.23	0.96	1.04	0.76	1.06	0.57	0.94	
	3	0.67	0.83	1.43	1.05	1.00	1.00	1.00	
	4	0.67	0.95	0.89	0.95	1.70	2.11`	1.21	
	5	1.14	1.23	0.59*	1.00	0.71	1.50	1.03	
	6	0.54	0.62*	1.19	0.95	1.43`	0.69	0.90	
	7	1.80`	1.75`	2.29`	2.67`	1.10	1.40	1.83	
	8	0.18	0.79	0.87	0.69*	1.00	0.33*	0.64	
	9	0.33*	0.75	1.33	1.00	0.38*	0.64	0.74	
TC	1	1.47	1.75	2.73`	2.88`	2.13`	1.08	2.00	1.53
	2	1.35	1.21	1.29	1.43	1.00	0.97*	1.21	
	3	0.97*	1.16	1.00	1.74	1.95	1.58	1.40	
	4	1.13	2.21`	1.90	2.73	1.38	1.84	1.87	
	5	1.04	0.74	1.08	1.16*	0.89*	1.15	1.01	
	6	1.60	1.36	1.54	2.00	1.34	1.14	1.50	
	7	1.79`	1.33	2.18	2.59	1.44	2.00`	1.89	
	8	1.74	0.73*	0.92*	1.36	1.19	1.35	1.22	

	9	1.36	1.83	1.32	2.00	2.07	1.64	1.71	
WRBV	1	M`	NA	1.00	1.00`	0.40*	0.78	0.79	1.05
	2	0.67	0.75	0.60	0.14	1.13	0.62	0.65	
	3	NA	NA	0.50	F*	1.75`	0.40*	0.88	
	4	F*	3.00	0.50	0.20	1.22	1.50`	1.28	
	5	0.25	3.00	2.00	0.83	0.78	1.17	1.34	
	6	NA	M`	2.00	0.35	1.30	1.23	1.22	
	7	1.00	M`	1.33	0.23	0.62	0.71	0.78	
	8	NA	0.33*	7.00`	0.63	0.50	0.55	1.80	
	9	NA	1.00	0.21*	0.52	1.14	0.50	0.68	
DM	1	3.00	1.50	1.25	1.22	1.50	2.14	1.77	2.05
	2	1.25*	1.50	1.50	2.70`	0.50*	1.67	1.52	
	3	NA	1.00	0.90	1.50	2.00	1.25*	1.33	
	4	14.00	1.50	0.83	1.20	1.00	1.70	3.37	
	5	2.50	1.00	2.63`	1.31	2.33	2.40	2.03	
	6	NA	1.50	1.35	2.40	1.00	3.00	1.85	
	7	M`	M`	1.80	2.00	1.50	Μ	1.77	
	8	5.00	0.70	0.93	1.00	2.63`	1.56	1.97	
	9	NA	F*	0.50*	0.75*	1.14	9.00`	2.85	

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*) **Table 1.5.** – Grid- and species-specific counts of trees collected at 9 research sites in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. The 9 research sites are arranged across in a 3 x 3 crossed design of 3 elevation and 3 canopy openness classes. The counts were collected at 18 habitat sampling stations per grid and each count indicates the total number of each tree species per grid identified from the center of each habitat sampling station by a basal area prism (size 10).

Site	TSUHET	PSEMEN	ACECIR	ACEMAC	ABIAMA	ABIGRA	ABIPRO	Total
1	105	232	12	2	0	0	0	419
2	136	153	2	0	0	0	0	385
3	163	139	3	0	0	0	0	336
4	195	307	5	0	0	0	0	548
5	184	151	11	1	0	0	0	466
6	99	129	12	0	0	0	0	334
7	240	263	3	0	1	0	0	508
8	190	215	1	0	55	0	0	461
9	35	234	1	0	20	15	21	327

Species: TSUHEY – western hemlock (*Tsuga heterophylla*); PSEMEN – Douglas-fir (*Pseudotsuga menziesii*); ACECIR – vine maple (*Acer circinatum*); ACEMAC – bigleaf maple (*Acer macrophyllum*); ABIAMA – Pacific silver fir (*Abies amabilis*); ABIGRA – grand fir (*Abies grandis*); ABIPRO – noble fir (*Abies procera*).

Table 1.6. – Spatial variable models ranked using Akaike's Information Criterion corrected for small sample sizes for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*) and western red-backed voles (*Myodes californicus*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model ^{a b}	AICc	ΔAICc	W	K
HFS	Berry	402.14	0	1	4
	Elevation	415.74	13.61	0	4
	Canopy	427.6	25.46	0	4
	CWD ^c	427.86	25.72	0	4
TC	Elevation	499.00	0.00	0.69	4
	Canopy	500.62	1.62	0.31	4
	Berry	512.58	13.58	0.00	4
	CWD ^c	517.02	18.02	0.00	4
WRBV	Elevation	360.69	0.00	0.99	4
	Berry	374.93	14.24	8.10E-04	4
	Canopy	379.24	18.55	9.37E-05	4
	CWD ^c	380.20	19.50	5.82E-05	4
DM	Berry	409.93	0.00	0.53	4
	Elevation	412.02	2.09	0.19	4
	Canopy	412.53	2.60	0.14	4
	CWD ^c	412.54	2.60	0.14	4

Species: HFS – Humboldt's flying squirrel (*Glaucomys oregonensis*); TC – Townsend's chipmunk (*Neotamias townsendii*); WRBV – western red-backed vole (*Myodes californicus*); DM – deer mouse (*Peromyscus maniculatus*)

- a- All models included a random effect (1|Year) to compensate for temporal variation while testing spatial fixed effects.
- b- Y_i ~ Negative Binomial(mean= μ_i , var= $\mu_t + \frac{\mu t^2}{\theta}$), log(μ_i) = $\alpha_0 + \alpha_1$ I.Covariate(t or r) + b(t or r), t = 6 years, r = 9 grids
- c- Site-level average coarse woody debris volume.

Table 1.7. – Temporal variable models ranked using Akaike's Information Criterion corrected for small sample sizes for Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*) and western red-backed voles (*Myodes californicus*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model ^{a b}	AICc	ΔAICc	W	K
HFS	Min. Temp.	438.66	0.00	0.73	4
	PDSI	441.73	3.07	0.16	4
	Days Below 0°C	442.40	3.74	0.11	4
TC	Min. Temp.	494.62	0.00	0.63	4
	PDSI	496.16	1.53	0.29	4
	Days Below 0°C	498.87	4.24	0.08	4
WRBV	PDSI	346.42	0.00	1	4
	Min. Temp.	395.29	48.88	2.44E-11	4
	Days Below 0°C	398.91	52.49	3.99E-12	4
DM	PDSI	408.10	0.00	0.92	4
	Min. Temp.	414.44	6.34	0.04	4
	Days Below 0°C	414.51	6.41	0.04	4

Species: HFS – Humboldt's flying squirrel (<i>Glaucomys oregonensis</i>); TC –
Townsend's chipmunk (Neotamias townsendii); WRBV - western red-backed vole
(Myodes californicus); DM – deer mouse (Peromyscus maniculatus)

- a- All models included a random effect (1|Grid) to compensate for spatial variation while testing temporal fixed effects.
- b- Y_i ~ Negative Binomial(mean= μ_i , var= $\mu_t + \frac{\mu t^2}{\theta}$), log(μ_i) = $\alpha_0 + \alpha_1$ I.Covariate_{(t} or r) + b_(t or r), t = 6 years, r = 9 grids


Figure 1.8. – Average sex-specific mean body weight for Humboldt's flying squirrels (A. *Glaucomys oregonensis*), Townsend's chipmunks (B. *Neotamias townsendii*), deer mice (D. *Peromyscus maniculatus*), and western red-backed voles (C. *Myodes californicus*) captured in the H. J. Andrews Experimental Forest from 2011–2016.

Appendix 2. – Negative binomial generalized linear mixed-effects model description.

The following statistical model describes the generalized linear mixed effects model:

Y_i ~ Negative Binomial(mean=
$$\mu_i$$
, var= $\mu_t + \frac{\mu t^2}{\theta}$)
log(μ_i) = $\alpha_0 + \alpha_1$ I.Covariate(t or r) + b(t or r)

$$t = 6$$
 years, $r = 9$ grids

- Y_{ti} is the grid and year specific estimate of abundance for focal species i, α_0 is the logarithm of the mean estimate of abundance for focal species i,
- α₁ is the incremental effect of the habitat variable, on the mean estimateof abundance of focal species i,

I.Covariate_(t or r) is equal to the sampled value of the j^{th} spatial or temporal variable.,

 b_t is the random intercept effect of the r^{th} grid or t^{th} year on the mean estimate of abundance for focal species i, $b_r \sim N(0,\sigma_b^2)$ and b_r and $b_{r'}$ are independent. **Appendix 3.** – Model selection results testing for behavioral effects, AIC_c combined Pradel model selection table and grid- and year-specific real estimates from robust design Pradel models.

Table 3.1. – Model selection results used to test for a behavioral effect between capture probability (*p*) and recapture probability (*c*) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in a natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (*w*), and the number of parameters (K).

Species	Model ^a	AICc	ΔAICc	W	Κ
HFS ^b	p(t) c(t)	28490.25	0.00	1.00	22
	<i>p</i> (t) <i>c</i> (.)	28509.20	18.95	0.00	16
	p(t)=c(t)	28665.00	174.76	0.00	16
	<i>p</i> (.) <i>c</i> (t)	28697.65	207.40	0.00	17
	<i>p</i> (.) <i>c</i> (.)	28718.64	228.39	0.00	12
	<i>p</i> (.)= <i>c</i> (.)	28752.88	262.63	0.00	11
TC ^c	p(t) c(t)	56604.82	0.00	1.00	22
	<i>p</i> (.) <i>c</i> (t)	56670.46	65.64	0.00	17
	<i>p</i> (t) <i>c</i> (.)	56837.84	233.02	0.00	17
	<i>p</i> (.) <i>c</i> (.)	56903.49	298.67	0.00	12
	p(t)=c(t)	59036.40	2431.58	0.00	16
	<i>p</i> (.)= <i>c</i> (.)	59161.85	2557.03	0.00	11

a- $\varphi(t) f(t)$

b- Humboldt's flying squirrel (Glaucomys oregonensis)

c- Townsend's chipmunk (Neotamias townsendii)

Table 3.2. – All models used to estimate apparent survival (φ) and recruitment (f) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We model averaged across this full model set to estimate population growth for both species. Here, we present model structure, Akaike's Information Criterion adjusted for sample size (AICc), change in AICc from the top-ranking model (Δ AICc), AICc weight of evidence (w), and the number of parameters (K).

Species	Model	AICc	ΔAICc	W	K
HFS ^{a c}	φ (Elevation) $f(t)$	28486.62	0.00	0.25	17
	$\varphi(\text{TC Abundance}) f(t)$	28487.09	0.47	0.20	17
	$\varphi(.) f(t)$	28487.51	0.89	0.16	16
	$\varphi(\text{Berry}) f(t)$	28488.20	1.58	0.11	17
	φ (Min. Temp. + Elevation) f (t)	28488.38	1.76	0.10	18
	$\varphi(Min. Temp.) f(t)$	28489.31	2.70	0.07	17
	$\varphi(HFS Abundance) f(t)$	28489.51	2.90	0.06	17
	φ (Min. Temp. + Berry) f (t)	28489.97	3.35	0.05	18
	$\varphi(t) f(Min. Temp. + Berry)$	28503.94	17.33	0.00	18
	$\varphi(t)$ <i>f</i> (Min. Temp. + Elevation)	28504.45	17.83	0.00	18
	$\varphi(t) f(Min. Temp.)$	28508.37	21.75	0.00	17
	$\varphi(t) f(Berry)$	28542.89	56.27	0.00	17
	$\varphi(t) f$ (Elevation)	28543.32	56.70	0.00	17
	$\varphi(t) f(.)$	28546.36	59.74	0.00	16
	$\varphi(t) f(HFS Abundance)$	28547.18	60.56	0.00	17
	$\varphi(t) f(Chipmunk Abundance)$	28547.94	61.32	0.00	17
TC ^{b d}	$\varphi(t) f(Min. Temp. + Canopy)$	56159.95	0.00	0.47	14
	$\varphi(t) f(Min. Temp.)$	56160.82	0.87	0.30	13

$\varphi(t) f(Min. Temp. + Berry)$	56162.77	2.82	0.11	14
$\varphi(t) f(Min. Temp. + Elevation)$	56162.82	2.87	0.11	14
φ (Min. Temp. + Canopy) f (t)	56283.56	123.62	0.00	14
$\varphi(Min. Temp.) f(t)$	56283.87	123.93	0.00	13
φ (Min. Temp. + Elevation) $f(t)$	56284.15	124.20	0.00	14
φ (Min. Temp. + Berry) f (t)	56285.51	125.56	0.00	14
$\varphi(t) f(TC Abundance)$	56322.49	162.54	0.00	13
$\varphi(t) f(Canopy)$	56327.67	167.72	0.00	13
$\varphi(t) f(.)$	56327.81	167.87	0.00	12
$\varphi(t) f(HFS Abundance)$	56329.57	169.62	0.00	13
$\varphi(t) f(Berry)$	56329.73	169.79	0.00	13
$\varphi(t) f$ (Elevation)	56329.81	169.86	0.00	13
$\varphi(\text{HFS Abundance}) f(t)$	56334.79	174.84	0.00	13
φ (Elevation) $f(t)$	56337.24	177.30	0.00	13
$\varphi(\text{Canopy}) f(t)$	56337.67	177.73	0.00	13
$\varphi(.) f(t)$	56337.80	177.86	0.00	12
$\varphi(\text{TC Abundance}) f(t)$	56339.26	179.31	0.00	13

a- Model structure for was held to *p*(Year + Elevation)*c*(Trapping Trend + Elevation).

b- Model structure for was held to *p*(Trapping Trend + Shrub)*c*(Trapping Trend + Elevation).

c- Humboldt's flying squirrel (Glaucomys oregonensis)

d- Townsend's chipmunk (Neotamias townsendii)

Table 3.3. – Estimates of recapture probability (*c*) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present species, grid characteristics, year, trapping day (Day), the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Species	Label	Year	Day	Estimate	LCI	UCI
HFS ^a	630-710 m, <15% Openness	2011	2-12	0.24	0.23	0.25
	680-740 m, 15-30% Openness		2-12	0.20	0.19	0.22
	650-730 m, 30-45% Openness		2-12	0.22	0.21	0.23
	850-950 m, <15% Openness		2-12	0.25	0.24	0.26
	890-920 m, 15-30% Openness		2-12	0.22	0.21	0.23
	810-910 m, 30-45% Openness		2-12	0.25	0.24	0.26
	1,060-1,080 m, <15% Openness		2-12	0.25	0.23	0.26
	1,090-1,210 m, 15-30% Opennes	SS	2-12	0.23	0.22	0.24
	1,210-1,280 m, 30-45% Opennes	SS	2-12	0.24	0.23	0.26
	630-710 m, <15% Openness	2012	2-12	0.24	0.23	0.25
	680-740 m, 15-30% Openness		2-12	0.23	0.22	0.24
	650-730 m, 30-45% Openness		2-12	0.22	0.21	0.24
	850-950 m, <15% Openness		2-12	0.26	0.25	0.27
	890-920 m, 15-30% Openness		2-12	0.23	0.22	0.23
	810-910 m, 30-45% Openness		2-12	0.23	0.22	0.24
	1,060-1,080 m, <15% Openness		2-12	0.26	0.25	0.28
	1,090-1,210 m, 15-30% Opennes	SS	2-12	0.21	0.20	0.22
	1,210-1,280 m, 30-45% Opennes	SS	2-12	0.28	0.26	0.31
	630-710 m, <15% Openness	2013	2-12	0.24	0.23	0.26

680-740 m, 15-30% Openness		2-12	0.18	0.17	0.20
650-730 m, 30-45% Openness		2-12	0.20	0.18	0.21
850-950 m, <15% Openness		2-12	0.24	0.23	0.25
890-920 m, 15-30% Openness		2-12	0.20	0.18	0.21
810-910 m, 30-45% Openness		2-12	0.21	0.20	0.22
1,060-1,080 m, <15% Openness		2-12	0.22	0.21	0.23
1,090-1,210 m, 15-30% Openness		2-12	0.19	0.17	0.20
1,210-1,280 m, 30-45% Openness		2-12	0.22	0.20	0.23
630-710 m, <15% Openness	2014	2-12	0.25	0.24	0.27
680-740 m, 15-30% Openness		2-12	0.21	0.20	0.23
650-730 m, 30-45% Openness		2-12	0.22	0.21	0.23
850-950 m, <15% Openness		2-12	0.27	0.25	0.28
890-920 m, 15-30% Openness		2-12	0.23	0.22	0.24
810-910 m, 30-45% Openness		2-12	0.23	0.22	0.23
1,060-1,080 m, <15% Openness		2-12	0.25	0.23	0.26
1,090-1,210 m, 15-30% Openness		2-12	0.20	0.19	0.22
1,210-1,280 m, 30-45% Openness		2-12	0.22	0.21	0.24
630-710 m, <15% Openness	2015	2-12	0.26	0.24	0.27
680-740 m, 15-30% Openness		2-12	0.24	0.23	0.25
650-730 m, 30-45% Openness		2-12	0.23	0.22	0.24
850-950 m, <15% Openness		2-12	0.26	0.25	0.28
890-920 m, 15-30% Openness		2-12	0.24	0.23	0.24
810-910 m, 30-45% Openness		2-12	0.21	0.20	0.22

1,060-1,080 m, <15% Openness		2-12	0.25	0.24	0.27
1,090-1,210 m, 15-30% Openness		2-12	0.21	0.20	0.22
1,210-1,280 m, 30-45% Openness		2-12	0.23	0.22	0.25
630-710 m, <15% Openness	2016	2-12	0.23	0.22	0.24
680-740 m, 15-30% Openness		2-12	0.24	0.23	0.25
650-730 m, 30-45% Openness		2-12	0.23	0.22	0.24
850-950 m, <15% Openness		2-12	0.26	0.25	0.28
890-920 m, 15-30% Openness		2-12	0.26	0.25	0.27
810-910 m, 30-45% Openness		2-12	0.22	0.21	0.23
1,060-1,080 m, <15% Openness		2-12	0.28	0.26	0.30
1,090-1,210 m, 15-30% Openness		2-12	0.26	0.24	0.27
1,210-1,280 m, 30-45% Openness		2-12	0.27	0.25	0.29
630-710 m, <15% Openness	2011	2	0.77	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.66	0.68
		6	0.63	0.62	0.64
		7	0.59	0.58	0.60
		8	0.55	0.54	0.57
680-740 m, 15-30% Openness		2	0.76	0.75	0.77
		3	0.73	0.72	0.74
		4	0.70	0.68	0.71
		5	0.66	0.65	0.67

TC^b

	6	0.62	0.61	0.63
	7	0.58	0.57	0.60
	8	0.54	0.53	0.56
650-730 m, 30-45% Openness	2	0.76	0.75	0.78
	3	0.73	0.72	0.75
	4	0.70	0.69	0.71
	5	0.67	0.65	0.68
	6	0.63	0.62	0.64
	7	0.59	0.58	0.60
	8	0.55	0.54	0.56
850-950 m, <15% Openness	2	0.73	0.72	0.75
	3	0.70	0.69	0.71
	4	0.67	0.66	0.67
	5	0.63	0.62	0.64
	6	0.59	0.58	0.60
	7	0.55	0.54	0.56
	8	0.51	0.50	0.52
890-920 m, 15-30% Openness	2	0.73	0.72	0.74
	3	0.70	0.69	0.71
	4	0.66	0.65	0.67
	5	0.63	0.62	0.63
	6	0.59	0.58	0.59
	7	0.55	0.54	0.56

	8	0.51	0.49	0.52
810-910 m, 30-45% Openness	2	0.74	0.73	0.75
	3	0.71	0.70	0.72
	4	0.67	0.67	0.68
	5	0.64	0.63	0.64
	6	0.60	0.59	0.61
	7	0.56	0.55	0.57
	8	0.52	0.51	0.53
1,060-1,080 m, <15% Openness	2	0.71	0.69	0.72
	3	0.67	0.66	0.68
	4	0.64	0.63	0.65
	5	0.60	0.59	0.61
	6	0.56	0.55	0.57
	7	0.52	0.51	0.53
	8	0.48	0.46	0.49
1,090-1,210 m, 15-30% Openness	2	0.70	0.68	0.71
	3	0.66	0.65	0.68
	4	0.63	0.62	0.64
	5	0.59	0.58	0.60
	6	0.55	0.54	0.56
	7	0.51	0.50	0.52
	8	0.47	0.45	0.48
1,210-1,280 m, 30-45% Openness	2	0.68	0.66	0.70

		3	0.64	0.63	0.66
		4	0.61	0.59	0.62
		5	0.57	0.55	0.58
		6	0.53	0.51	0.54
		7	0.49	0.47	0.50
		8	0.45	0.43	0.46
630-710 m, <15% Openness	2012	2	0.77	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.66	0.68
		6	0.63	0.62	0.64
		7	0.59	0.58	0.60
		8	0.55	0.54	0.57
680-740 m, 15-30% Openness		2	0.76	0.75	0.77
		3	0.73	0.72	0.74
		4	0.70	0.68	0.71
		5	0.66	0.65	0.67
		6	0.62	0.61	0.63
		7	0.58	0.57	0.60
		8	0.54	0.53	0.56
650-730 m, 30-45% Openness		2	0.76	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71

	5	0.67	0.65	0.68
	6	0.63	0.62	0.64
	7	0.59	0.58	0.60
	8	0.55	0.54	0.56
850-950 m, <15% Openness	2	0.73	0.72	0.75
	3	0.70	0.69	0.71
	4	0.67	0.66	0.67
	5	0.63	0.62	0.64
	6	0.59	0.58	0.60
	7	0.55	0.54	0.56
	8	0.51	0.50	0.52
890-920 m, 15-30% Openness	2	0.73	0.72	0.74
	3	0.70	0.69	0.71
	4	0.66	0.65	0.67
	5	0.63	0.62	0.63
	6	0.59	0.58	0.59
	7	0.55	0.54	0.56
	8	0.51	0.49	0.52
810-910 m, 30-45% Openness	2	0.74	0.73	0.75
	3	0.71	0.70	0.72
	4	0.67	0.67	0.68
	5	0.64	0.63	0.64
	6	0.60	0.59	0.61

	7	0.56	0.55	0.57
	8	0.52	0.51	0.53
1,060-1,080 m, <15% Openness	2	0.71	0.69	0.72
	3	0.67	0.66	0.68
	4	0.64	0.63	0.65
	5	0.60	0.59	0.61
	6	0.56	0.55	0.57
	7	0.52	0.51	0.53
	8	0.48	0.46	0.49
1,090-1,210 m, 15-30% Openness	2	0.70	0.68	0.71
	3	0.66	0.65	0.68
	4	0.63	0.62	0.64
	5	0.59	0.58	0.60
	6	0.55	0.54	0.56
	7	0.51	0.50	0.52
	8	0.47	0.45	0.48
1,210-1,280 m, 30-45% Openness	2	0.68	0.66	0.70
	3	0.64	0.63	0.66
	4	0.61	0.59	0.62
	5	0.57	0.55	0.58
	6	0.53	0.51	0.54
	7	0.49	0.47	0.50
	8	0.45	0.43	0.46

630-710 m, <15% Openness	2013	2	0.77	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.66	0.68
		6	0.63	0.62	0.64
		7	0.59	0.58	0.60
		8	0.55	0.54	0.57
680-740 m, 15-30% Openness		2	0.76	0.75	0.77
		3	0.73	0.72	0.74
		4	0.70	0.68	0.71
		5	0.66	0.65	0.67
		6	0.62	0.61	0.63
		7	0.58	0.57	0.60
		8	0.54	0.53	0.56
650-730 m, 30-45% Openness		2	0.76	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.65	0.68
		6	0.63	0.62	0.64
		7	0.59	0.58	0.60
		8	0.55	0.54	0.56
850-950 m, <15% Openness		2	0.73	0.72	0.75
		3	0.70	0.69	0.71

	4	0.67	0.66	0.67
	5	0.63	0.62	0.64
	6	0.59	0.58	0.60
	7	0.55	0.54	0.56
	8	0.51	0.50	0.52
890-920 m, 15-30% Openness	2	0.73	0.72	0.74
	3	0.70	0.69	0.71
	4	0.66	0.65	0.67
	5	0.63	0.62	0.63
	6	0.59	0.58	0.59
	7	0.55	0.54	0.56
	8	0.51	0.49	0.52
810-910 m, 30-45% Openness	2	0.74	0.73	0.75
	3	0.71	0.70	0.72
	4	0.67	0.67	0.68
	5	0.64	0.63	0.64
	6	0.60	0.59	0.61
	7	0.56	0.55	0.57
	8	0.52	0.51	0.53
1,060-1,080 m, <15% Openness	2	0.71	0.69	0.72
	3	0.67	0.66	0.68
	4	0.64	0.63	0.65
	5	0.60	0.59	0.61

		6	0.56	0.55	0.57
		7	0.52	0.51	0.53
		8	0.48	0.46	0.49
1,090-1,210 m, 15-30% Openness		2	0.70	0.68	0.71
		3	0.66	0.65	0.68
		4	0.63	0.62	0.64
		5	0.59	0.58	0.60
		6	0.55	0.54	0.56
		7	0.51	0.50	0.52
		8	0.47	0.45	0.48
1,210-1,280 m, 30-45% Openness		2	0.68	0.66	0.70
		3	0.64	0.63	0.66
		4	0.61	0.59	0.62
		5	0.57	0.55	0.58
		6	0.53	0.51	0.54
		7	0.49	0.47	0.50
		8	0.45	0.43	0.46
630-710 m, <15% Openness	2014	2	0.77	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.66	0.68
		6	0.63	0.62	0.64
		7	0.59	0.58	0.60

	8	0.55	0.54	0.57
680-740 m, 15-30% Openness	2	0.76	0.75	0.77
	3	0.73	0.72	0.74
	4	0.70	0.68	0.71
	5	0.66	0.65	0.67
	6	0.62	0.61	0.63
	7	0.58	0.57	0.60
	8	0.54	0.53	0.56
650-730 m, 30-45% Openness	2	0.76	0.75	0.78
	3	0.73	0.72	0.75
	4	0.70	0.69	0.71
	5	0.67	0.65	0.68
	6	0.63	0.62	0.64
	7	0.59	0.58	0.60
	8	0.55	0.54	0.56
850-950 m, <15% Openness	2	0.73	0.72	0.75
	3	0.70	0.69	0.71
	4	0.67	0.66	0.67
	5	0.63	0.62	0.64
	6	0.59	0.58	0.60
	7	0.55	0.54	0.56
	8	0.51	0.50	0.52
890-920 m, 15-30% Openness	2	0.73	0.72	0.74

	3	0.70	0.69	0.71
	4	0.66	0.65	0.67
	5	0.63	0.62	0.63
	6	0.59	0.58	0.59
	7	0.55	0.54	0.56
	8	0.51	0.49	0.52
810-910 m, 30-45% Openness	2	0.74	0.73	0.75
	3	0.71	0.70	0.72
	4	0.67	0.67	0.68
	5	0.64	0.63	0.64
	6	0.60	0.59	0.61
	7	0.56	0.55	0.57
	8	0.52	0.51	0.53
1,060-1,080 m, <15% Openness	2	0.71	0.69	0.72
	3	0.67	0.66	0.68
	4	0.64	0.63	0.65
	5	0.60	0.59	0.61
	6	0.56	0.55	0.57
	7	0.52	0.51	0.53
	8	0.48	0.46	0.49
1,090-1,210 m, 15-30% Openness	2	0.70	0.68	0.71
	3	0.66	0.65	0.68
	4	0.63	0.62	0.64

	5	0.59	0.58	0.60
	6	0.55	0.54	0.56
	7	0.51	0.50	0.52
	8	0.47	0.45	0.48
1,210-1,280 m, 30-45% Openness	2	0.68	0.66	0.70
	3	0.64	0.63	0.66
	4	0.61	0.59	0.62
	5	0.57	0.55	0.58
	6	0.53	0.51	0.54
	7	0.49	0.47	0.50
	8	0.45	0.43	0.46
630-710 m, <15% Openness 2015	2	0.77	0.75	0.78
	3	0.73	0.72	0.75
	4	0.70	0.69	0.71
	5	0.67	0.66	0.68
	6	0.63	0.62	0.64
	7	0.59	0.58	0.60
	8	0.55	0.54	0.57
680-740 m, 15-30% Openness	2	0.76	0.75	0.77
	3	0.73	0.72	0.74
	4	0.70	0.68	0.71
	5	0.66	0.65	0.67
	6	0.62	0.61	0.63

	7	0.58	0.57	0.60
	8	0.54	0.53	0.56
650-730 m, 30-45% Openness	2	0.76	0.75	0.78
	3	0.73	0.72	0.75
	4	0.70	0.69	0.71
	5	0.67	0.65	0.68
	6	0.63	0.62	0.64
	7	0.59	0.58	0.60
	8	0.55	0.54	0.56
850-950 m, <15% Openness	2	0.73	0.72	0.75
	3	0.70	0.69	0.71
	4	0.67	0.66	0.67
	5	0.63	0.62	0.64
	6	0.59	0.58	0.60
	7	0.55	0.54	0.56
	8	0.51	0.50	0.52
890-920 m, 15-30% Openness	2	0.73	0.72	0.74
	3	0.70	0.69	0.71
	4	0.66	0.65	0.67
	5	0.63	0.62	0.63
	6	0.59	0.58	0.59
	7	0.55	0.54	0.56
	8	0.51	0.49	0.52

810-910 m, 30-45% Openness	2	0.74	0.73	0.75
	3	0.71	0.70	0.72
	4	0.67	0.67	0.68
	5	0.64	0.63	0.64
	6	0.60	0.59	0.61
	7	0.56	0.55	0.57
	8	0.52	0.51	0.53
1,060-1,080 m, <15% Openness	2	0.71	0.69	0.72
	3	0.67	0.66	0.68
	4	0.64	0.63	0.65
	5	0.60	0.59	0.61
	6	0.56	0.55	0.57
	7	0.52	0.51	0.53
	8	0.48	0.46	0.49
1,090-1,210 m, 15-30% Openness	2	0.70	0.68	0.71
	3	0.66	0.65	0.68
	4	0.63	0.62	0.64
	5	0.59	0.58	0.60
	6	0.55	0.54	0.56
	7	0.51	0.50	0.52
	8	0.47	0.45	0.48
1,210-1,280 m, 30-45% Openness	2	0.68	0.66	0.70
	3	0.64	0.63	0.66

		4	0.61	0.59	0.62
		5	0.57	0.55	0.58
		6	0.53	0.51	0.54
		7	0.49	0.47	0.50
		8	0.45	0.43	0.46
630-710 m, <15% Openness	2016	2	0.77	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.66	0.68
		6	0.63	0.62	0.64
		7	0.59	0.58	0.60
		8	0.55	0.54	0.57
680-740 m, 15-30% Openness		2	0.76	0.75	0.77
		3	0.73	0.72	0.74
		4	0.70	0.68	0.71
		5	0.66	0.65	0.67
		6	0.62	0.61	0.63
		7	0.58	0.57	0.60
		8	0.54	0.53	0.56
650-730 m, 30-45% Openness		2	0.76	0.75	0.78
		3	0.73	0.72	0.75
		4	0.70	0.69	0.71
		5	0.67	0.65	0.68

	6	0.63	0.62	0.64
	7	0.59	0.58	0.60
	8	0.55	0.54	0.56
850-950 m, <15% Openness	2	0.73	0.72	0.75
	3	0.70	0.69	0.71
	4	0.67	0.66	0.67
	5	0.63	0.62	0.64
	6	0.59	0.58	0.60
	7	0.55	0.54	0.56
	8	0.51	0.50	0.52
890-920 m, 15-30% Openness	2	0.73	0.72	0.74
	3	0.70	0.69	0.71
	4	0.66	0.65	0.67
	5	0.63	0.62	0.63
	6	0.59	0.58	0.59
	7	0.55	0.54	0.56
	8	0.51	0.49	0.52
810-910 m, 30-45% Openness	2	0.74	0.73	0.75
	3	0.71	0.70	0.72
	4	0.67	0.67	0.68
	5	0.64	0.63	0.64
	6	0.60	0.59	0.61
	7	0.56	0.55	0.57

	8	0.52	0.51	0.53
1,060-1,080 m, <15% Openness	2	0.71	0.69	0.72
	3	0.67	0.66	0.68
	4	0.64	0.63	0.65
	5	0.60	0.59	0.61
	6	0.56	0.55	0.57
	7	0.52	0.51	0.53
	8	0.48	0.46	0.49
1,090-1,210 m, 15-30% Openness	2	0.70	0.68	0.71
	3	0.66	0.65	0.68
	4	0.63	0.62	0.64
	5	0.59	0.58	0.60
	6	0.55	0.54	0.56
	7	0.51	0.50	0.52
	8	0.47	0.45	0.48
1,210-1,280 m, 30-45% Openness	2	0.68	0.66	0.70
	3	0.64	0.63	0.66
	4	0.61	0.59	0.62
	5	0.57	0.55	0.58
	6	0.53	0.51	0.54
	7	0.49	0.47	0.50
	8	0.45	0.43	0.46

a- Humboldt's flying squirrel (*Glaucomys oregonensis*)b- Townsend's chipmunk (*Neotamias townsendii*)

Table 3.4. – Estimates of first capture probability (*p*) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present species, grid characteristics, year, trapping day (Day), the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Species	Grid	Year	Day	Estimate	LCI	UCI
HFS ^a	630-710 m, <15% Openness	2011	1	0.03	0.02	0.04
	680-740 m, 15-30% Openness		1	0.03	0.02	0.03
	650-730 m, 30-45% Openness		1	0.03	0.02	0.04
	850-950 m, <15% Openness		1	0.03	0.02	0.03
	890-920 m, 15-30% Openness		1	0.03	0.02	0.03
	810-910 m, 30-45% Openness		1	0.03	0.02	0.03
	1,060-1,080 m, <15% Opennes	S	1	0.02	0.02	0.03
	1,090-1,210 m, 15-30% Openn	ess	1	0.02	0.02	0.03
	1,210-1,280 m, 30-45% Openn	ess	1	0.02	0.02	0.03
	630-710 m, <15% Openness	2012	1	0.25	0.22	0.28
	680-740 m, 15-30% Openness		1	0.24	0.21	0.27
	650-730 m, 30-45% Openness		1	0.25	0.22	0.28
	850-950 m, <15% Openness		1	0.23	0.20	0.26
	890-920 m, 15-30% Openness		1	0.23	0.20	0.25
	810-910 m, 30-45% Openness		1	0.23	0.20	0.26
	1,060-1,080 m, <15% Opennes	S	1	0.21	0.18	0.24
	1,090-1,210 m, 15-30% Openn	ess	1	0.21	0.18	0.24
	1,210-1,280 m, 30-45% Openn	ess	1	0.20	0.17	0.23
	630-710 m, <15% Openness	2013	1	0.15	0.13	0.18

680-740 m, 15-30% Openness	1	0.15	0.13	0.17
650-730 m, 30-45% Openness	1	0.15	0.13	0.17
850-950 m, <15% Openness	1	0.14	0.12	0.16
890-920 m, 15-30% Openness	1	0.14	0.12	0.16
810-910 m, 30-45% Openness	1	0.14	0.12	0.16
1,060-1,080 m, <15% Openness	1	0.13	0.11	0.15
1,090-1,210 m, 15-30% Openness	1	0.12	0.10	0.15
1,210-1,280 m, 30-45% Openness	1	0.12	0.10	0.14
630-710 m, <15% Openness 2014	1	0.27	0.24	0.30
680-740 m, 15-30% Openness	1	0.27	0.24	0.30
650-730 m, 30-45% Openness	1	0.27	0.24	0.30
850-950 m, <15% Openness	1	0.25	0.22	0.28
890-920 m, 15-30% Openness	1	0.25	0.22	0.28
810-910 m, 30-45% Openness	1	0.25	0.23	0.28
1,060-1,080 m, <15% Openness	1	0.23	0.21	0.26
1,090-1,210 m, 15-30% Openness	1	0.23	0.20	0.26
1,210-1,280 m, 30-45% Openness	1	0.22	0.19	0.25
630-710 m, <15% Openness 2015	1	0.29	0.26	0.33
680-740 m, 15-30% Openness	1	0.29	0.26	0.33
650-730 m, 30-45% Openness	1	0.29	0.26	0.33
850-950 m, <15% Openness	1	0.27	0.24	0.31
890-920 m, 15-30% Openness	1	0.27	0.24	0.30
810-910 m, 30-45% Openness	1	0.28	0.25	0.31

1,090-1,210 m, 15-30% Openness 1 0.25 0.22 0.29 1,210-1,280 m, 30-45% Openness 1 0.24 0.20 0.28 630-710 m, <15% Openness 2016 1 0.26 0.22 0.31 680-740 m, 15-30% Openness 1 0.26 0.22 0.31 650-730 m, 30-45% Openness 1 0.26 0.22 0.31 850-950 m, <15% Openness 1 0.24 0.21 0.28 890-920 m, 15-30% Openness 1 0.24 0.21 0.28 810-910 m, 30-45% Openness 1 0.25 0.21 0.28 1,060-1,080 m, <15% Openness 1 0.22 0.19 0.26 1,090-1,210 m, 15-30% Openness 1 0.22 0.19 0.26 1,210-1,280 m, 30-45% Openness 1 0.24 0.22 0.27 2 0.20 0.18 0.23 3 0.17 0.15 0.19 4 0.14 0.12 0.17 5 0.12 0.10 0.14 6 0.10 0.88 0.12	1,060-1,080 m, <15% Openness		1	0.26	0.22	0.29
1,210-1,280 m, 30-45% Openness 1 0.24 0.20 0.28 630-710 m, <15% Openness	1,090-1,210 m, 15-30% Opennes	S	1	0.25	0.22	0.29
630-710 m, <15% Openness	1,210-1,280 m, 30-45% Opennes	S	1	0.24	0.20	0.28
680-740 m, 15-30% Openness 1 0.26 0.22 0.30 650-730 m, 30-45% Openness 1 0.26 0.22 0.31 850-950 m, <15% Openness	630-710 m, <15% Openness	2016	1	0.26	0.22	0.31
650-730 m, 30-45% Openness 1 0.26 0.22 0.31 850-950 m, <15% Openness	680-740 m, 15-30% Openness		1	0.26	0.22	0.30
850-950 m, <15% Openness	650-730 m, 30-45% Openness		1	0.26	0.22	0.31
890-920 m, 15-30% Openness 1 0.24 0.20 0.28 810-910 m, 30-45% Openness 1 0.25 0.21 0.28 1,060-1,080 m, <15% Openness	850-950 m, <15% Openness		1	0.24	0.21	0.28
810-910 m, 30-45% Openness 1 0.25 0.21 0.28 1,060-1,080 m, <15% Openness	890-920 m, 15-30% Openness		1	0.24	0.20	0.28
1,060-1,080 m, <15% Openness	810-910 m, 30-45% Openness		1	0.25	0.21	0.28
1,090-1,210 m, 15-30% Openness 1 0.22 0.19 0.26 1,210-1,280 m, 30-45% Openness 1 0.21 0.17 0.25 630-710 m, <15% Openness	1,060-1,080 m, <15% Openness		1	0.23	0.19	0.26
1,210-1,280 m, 30-45% Openness 1 0.21 0.17 0.25 630-710 m, <15% Openness	1,090-1,210 m, 15-30% Opennes	S	1	0.22	0.19	0.26
630-710 m, <15% Openness	1,210-1,280 m, 30-45% Opennes	8	1	0.21	0.17	0.25
2 0.20 0.18 0.23 3 0.17 0.15 0.19 4 0.14 0.12 0.17 5 0.12 0.10 0.14 6 0.10 0.08 0.12 7 0.08 0.06 0.10 8 0.06 0.05 0.08 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25	630-710 m, <15% Openness	2011	1	0.24	0.22	0.27
3 0.17 0.15 0.19 4 0.14 0.12 0.17 5 0.12 0.10 0.14 6 0.10 0.08 0.12 7 0.08 0.06 0.10 8 0.06 0.05 0.08 680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			2	0.20	0.18	0.23
4 0.14 0.12 0.17 5 0.12 0.10 0.14 6 0.10 0.08 0.12 7 0.08 0.06 0.10 8 0.06 0.05 0.08 680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			3	0.17	0.15	0.19
5 0.12 0.10 0.14 6 0.10 0.08 0.12 7 0.08 0.06 0.10 8 0.06 0.05 0.08 680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			4	0.14	0.12	0.17
6 0.10 0.08 0.12 7 0.08 0.06 0.10 8 0.06 0.05 0.08 680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			5	0.12	0.10	0.14
7 0.08 0.06 0.10 8 0.06 0.05 0.08 680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			6	0.10	0.08	0.12
8 0.06 0.05 0.08 680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			7	0.08	0.06	0.10
680-740 m, 15-30% Openness 1 0.30 0.27 0.33 2 0.26 0.23 0.28 3 0.22 0.19 0.25			8	0.06	0.05	0.08
2 0.26 0.23 0.28 3 0.22 0.19 0.25	680-740 m, 15-30% Openness		1	0.30	0.27	0.33
3 0.22 0.19 0.25			2	0.26	0.23	0.28
			3	0.22	0.19	0.25

TC^b

186

	4	0.18	0.16	0.21
	5	0.15	0.13	0.18
	6	0.13	0.10	0.15
	7	0.10	0.08	0.13
	8	0.08	0.07	0.11
650-730 m, 30-45% Openness	1	0.24	0.22	0.26
	2	0.20	0.18	0.23
	3	0.17	0.15	0.19
	4	0.14	0.12	0.16
	5	0.12	0.10	0.14
	6	0.10	0.08	0.12
	7	0.08	0.06	0.10
	8	0.06	0.05	0.08
850-950 m, <15% Openness	1	0.22	0.19	0.24
	2	0.18	0.16	0.21
	3	0.15	0.13	0.18
	4	0.13	0.11	0.15
	5	0.10	0.08	0.13
	6	0.09	0.07	0.11
	7	0.07	0.05	0.09
	8	0.06	0.04	0.07
890-920 m, 15-30% Openness	1	0.25	0.23	0.27
	2	0.21	0.19	0.24

	3	0.18	0.16	0.20
	4	0.15	0.13	0.17
	5	0.12	0.10	0.15
	6	0.10	0.08	0.12
	7	0.08	0.07	0.10
	8	0.07	0.05	0.09
810-910 m, 30-45% Openness	1	0.23	0.21	0.25
	2	0.19	0.17	0.22
	3	0.16	0.14	0.19
	4	0.13	0.11	0.16
	5	0.11	0.09	0.13
	6	0.09	0.07	0.11
	7	0.07	0.06	0.09
	8	0.06	0.05	0.08
1,060-1,080 m, <15% Openness	1	0.19	0.16	0.22
	2	0.15	0.13	0.19
	3	0.13	0.10	0.16
	4	0.11	0.08	0.13
	5	0.09	0.07	0.11
	6	0.07	0.05	0.09
	7	0.06	0.04	0.08
	8	0.05	0.03	0.06
1,090-1,210 m, 15-30% Openness	1	0.26	0.24	0.28

		2	0.22	0.20	0.24
		3	0.19	0.16	0.21
		4	0.15	0.13	0.18
		5	0.13	0.11	0.15
		6	0.11	0.09	0.13
		7	0.09	0.07	0.11
		8	0.07	0.05	0.09
1,210-1,280 m, 30-45% Opennes	S	1	0.33	0.30	0.37
		2	0.29	0.25	0.32
		3	0.24	0.21	0.28
		4	0.21	0.17	0.24
		5	0.17	0.14	0.21
		6	0.14	0.12	0.18
		7	0.12	0.09	0.15
		8	0.10	0.07	0.13
630-710 m, <15% Openness	2012	1	0.24	0.22	0.27
		2	0.20	0.18	0.23
		3	0.17	0.15	0.19
		4	0.14	0.12	0.17
		5	0.12	0.10	0.14
		6	0.10	0.08	0.12
		7	0.08	0.06	0.10
		8	0.06	0.05	0.08

680-740 m, 15-30% Openness	1	0.30	0.27	0.33
	2	0.26	0.23	0.28
	3	0.22	0.19	0.25
	4	0.18	0.16	0.21
	5	0.15	0.13	0.18
	6	0.13	0.10	0.15
	7	0.10	0.08	0.13
	8	0.08	0.07	0.11
650-730 m, 30-45% Openness	1	0.24	0.22	0.26
	2	0.20	0.18	0.23
	3	0.17	0.15	0.19
	4	0.14	0.12	0.16
	5	0.12	0.10	0.14
	6	0.10	0.08	0.12
	7	0.08	0.06	0.10
	8	0.06	0.05	0.08
850-950 m, <15% Openness	1	0.22	0.19	0.24
	2	0.18	0.16	0.21
	3	0.15	0.13	0.18
	4	0.13	0.11	0.15
	5	0.10	0.08	0.13
	6	0.09	0.07	0.11
	7	0.07	0.05	0.09

	8	0.06	0.04	0.07
890-920 m, 15-30% Openness	1	0.25	0.23	0.27
	2	0.21	0.19	0.24
	3	0.18	0.16	0.20
	4	0.15	0.13	0.17
	5	0.12	0.10	0.15
	6	0.10	0.08	0.12
	7	0.08	0.07	0.10
	8	0.07	0.05	0.09
810-910 m, 30-45% Openness	1	0.23	0.21	0.25
	2	0.19	0.17	0.22
	3	0.16	0.14	0.19
	4	0.13	0.11	0.16
	5	0.11	0.09	0.13
	6	0.09	0.07	0.11
	7	0.07	0.06	0.09
	8	0.06	0.05	0.08
1,060-1,080 m, <15% Openness	1	0.19	0.16	0.22
	2	0.15	0.13	0.19
	3	0.13	0.10	0.16
	4	0.11	0.08	0.13
	5	0.09	0.07	0.11
	6	0.07	0.05	0.09

			7	0.06	0.04	0.08
			8	0.05	0.03	0.06
1,09	00-1,210 m, 15-30% Openn	iess	1	0.26	0.24	0.28
			2	0.22	0.20	0.24
			3	0.19	0.16	0.21
			4	0.15	0.13	0.18
			5	0.13	0.11	0.15
			6	0.11	0.09	0.13
			7	0.09	0.07	0.11
			8	0.07	0.05	0.09
1,21	0-1,280 m, 30-45% Openn	iess	1	0.33	0.30	0.37
			2	0.29	0.25	0.32
			3	0.24	0.21	0.28
			4	0.21	0.17	0.24
			5	0.17	0.14	0.21
			6	0.14	0.12	0.18
			7	0.12	0.09	0.15
			8	0.10	0.07	0.13
630	-710 m, <15% Openness	2013	1	0.24	0.22	0.27
			2	0.20	0.18	0.23
			3	0.17	0.15	0.19
			4	0.14	0.12	0.17
			5	0.12	0.10	0.14

6	0.10	0.08	0.12
7	0.08	0.06	0.10
8	0.06	0.05	0.08
1	0.30	0.27	0.33
2	0.26	0.23	0.28
3	0.22	0.19	0.25
4	0.18	0.16	0.21
5	0.15	0.13	0.18
6	0.13	0.10	0.15
7	0.10	0.08	0.13
8	0.08	0.07	0.11
1	0.24	0.22	0.26
2	0.20	0.18	0.23
3	0.17	0.15	0.19
4	0.14	0.12	0.16
5	0.12	0.10	0.14
6	0.10	0.08	0.12
7	0.08	0.06	0.10
8	0.06	0.05	0.08
1	0.22	0.19	0.24
2	0.18	0.16	0.21
3	0.15	0.13	0.18
4	0.13	0.11	0.15
	6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 2 3 4 5 6 7 8 1 1 2 3 4 5 6 7 8 1 1 2 3 4 5 6 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 7 8 1 2 3 4 7 8 1 2 3 4 5 7 8 1 7 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 8 1 1 2 3 4 5 7 8 1 2 3 4 5 7 7 8 1 2 3 4 5 7 7 8 1 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 7 8 1 1 2 3 4 5 5 7 8 1 1 2 3 1 4 5 5 7 8 1 1 2 3 1 1 1 2 1 1 1 1 1 2 1 1 1 1 1 1	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	60.100.0870.080.0680.060.0510.300.2720.260.2330.220.1940.180.1650.150.1360.130.1070.100.0880.080.0710.240.2220.200.1830.170.1540.140.1250.120.1060.100.0870.080.0680.060.0510.220.1920.180.1630.150.1340.130.11

	5	0.10	0.08	0.13
	6	0.09	0.07	0.11
	7	0.07	0.05	0.09
	8	0.06	0.04	0.07
890-920 m, 15-30% Openness	1	0.25	0.23	0.27
	2	0.21	0.19	0.24
	3	0.18	0.16	0.20
	4	0.15	0.13	0.17
	5	0.12	0.10	0.15
	6	0.10	0.08	0.12
	7	0.08	0.07	0.10
	8	0.07	0.05	0.09
810-910 m, 30-45% Openness	1	0.23	0.21	0.25
	2	0.19	0.17	0.22
	3	0.16	0.14	0.19
	4	0.13	0.11	0.16
	5	0.11	0.09	0.13
	6	0.09	0.07	0.11
	7	0.07	0.06	0.09
	8	0.06	0.05	0.08
1,060-1,080 m, <15% Openness	1	0.19	0.16	0.22
	2	0.15	0.13	0.19
	3	0.13	0.10	0.16
		17		
------	------	------		
0.11	0.08	0.13		
0.09	0.07	0.11		
0.07	0.05	0.09		

		5	0.09	0.07	0.11
		6	0.07	0.05	0.09
		7	0.06	0.04	0.08
		8	0.05	0.03	0.06
1,090-1,210 m, 15-30% Opennes	s	1	0.26	0.24	0.28
		2	0.22	0.20	0.24
		3	0.19	0.16	0.21
		4	0.15	0.13	0.18
		5	0.13	0.11	0.15
		6	0.11	0.09	0.13
		7	0.09	0.07	0.11
		8	0.07	0.05	0.09
1,210-1,280 m, 30-45% Opennes	S	1	0.33	0.30	0.37
		2	0.29	0.25	0.32
		3	0.24	0.21	0.28
		4	0.21	0.17	0.24
		5	0.17	0.14	0.21
		6	0.14	0.12	0.18
		7	0.12	0.09	0.15
		8	0.10	0.07	0.13
630-710 m, <15% Openness	2014	1	0.24	0.22	0.27
		2	0.20	0.18	0.23

	3	0.17	0.15	0.19
	4	0.14	0.12	0.17
	5	0.12	0.10	0.14
	6	0.10	0.08	0.12
	7	0.08	0.06	0.10
	8	0.06	0.05	0.08
680-740 m, 15-30% Openness	1	0.30	0.27	0.33
	2	0.26	0.23	0.28
	3	0.22	0.19	0.25
	4	0.18	0.16	0.21
	5	0.15	0.13	0.18
	6	0.13	0.10	0.15
	7	0.10	0.08	0.13
	8	0.08	0.07	0.11
650-730 m, 30-45% Openness	1	0.24	0.22	0.26
	2	0.20	0.18	0.23
	3	0.17	0.15	0.19
	4	0.14	0.12	0.16
	5	0.12	0.10	0.14
	6	0.10	0.08	0.12
	7	0.08	0.06	0.10
	8	0.06	0.05	0.08
850-950 m, <15% Openness	1	0.22	0.19	0.24

	2	0.18	0.16	0.21
	3	0.15	0.13	0.18
	4	0.13	0.11	0.15
	5	0.10	0.08	0.13
	6	0.09	0.07	0.11
	7	0.07	0.05	0.09
	8	0.06	0.04	0.07
890-920 m, 15-30% Openness	1	0.25	0.23	0.27
	2	0.21	0.19	0.24
	3	0.18	0.16	0.20
	4	0.15	0.13	0.17
	5	0.12	0.10	0.15
	6	0.10	0.08	0.12
	7	0.08	0.07	0.10
	8	0.07	0.05	0.09
810-910 m, 30-45% Openness	1	0.23	0.21	0.25
	2	0.19	0.17	0.22
	3	0.16	0.14	0.19
	4	0.13	0.11	0.16
	5	0.11	0.09	0.13
	6	0.09	0.07	0.11
	7	0.07	0.06	0.09
	8	0.06	0.05	0.08

1,060-1,080 m, <15% Openness	1	0.19	0.16	0.22
	2	0.15	0.13	0.19
	3	0.13	0.10	0.16
	4	0.11	0.08	0.13
	5	0.09	0.07	0.11
	6	0.07	0.05	0.09
	7	0.06	0.04	0.08
	8	0.05	0.03	0.06
1,090-1,210 m, 15-30% Openness	1	0.26	0.24	0.28
	2	0.22	0.20	0.24
	3	0.19	0.16	0.21
	4	0.15	0.13	0.18
	5	0.13	0.11	0.15
	6	0.11	0.09	0.13
	7	0.09	0.07	0.11
	8	0.07	0.05	0.09
1,210-1,280 m, 30-45% Openness	1	0.33	0.30	0.37
	2	0.29	0.25	0.32
	3	0.24	0.21	0.28
	4	0.21	0.17	0.24
	5	0.17	0.14	0.21
	6	0.14	0.12	0.18
	7	0.12	0.09	0.15

		8	0.10	0.07	0.13
630-710 m, <15% Openness	2015	1	0.24	0.22	0.27
		2	0.20	0.18	0.23
		3	0.17	0.15	0.19
		4	0.14	0.12	0.17
		5	0.12	0.10	0.14
		6	0.10	0.08	0.12
		7	0.08	0.06	0.10
		8	0.06	0.05	0.08
680-740 m, 15-30% Openness		1	0.30	0.27	0.33
		2	0.26	0.23	0.28
		3	0.22	0.19	0.25
		4	0.18	0.16	0.21
		5	0.15	0.13	0.18
		6	0.13	0.10	0.15
		7	0.10	0.08	0.13
		8	0.08	0.07	0.11
650-730 m, 30-45% Openness		1	0.24	0.22	0.26
		2	0.20	0.18	0.23
		3	0.17	0.15	0.19
		4	0.14	0.12	0.16
		5	0.12	0.10	0.14
		6	0.10	0.08	0.12

	7	0.08	0.06	0.10
	8	0.06	0.05	0.08
850-950 m, <15% Openness	1	0.22	0.19	0.24
	2	0.18	0.16	0.21
	3	0.15	0.13	0.18
	4	0.13	0.11	0.15
	5	0.10	0.08	0.13
	6	0.09	0.07	0.11
	7	0.07	0.05	0.09
	8	0.06	0.04	0.07
890-920 m, 15-30% Openness	1	0.25	0.23	0.27
	2	0.21	0.19	0.24
	3	0.18	0.16	0.20
	4	0.15	0.13	0.17
	5	0.12	0.10	0.15
	6	0.10	0.08	0.12
	7	0.08	0.07	0.10
	8	0.07	0.05	0.09
810-910 m, 30-45% Openness	1	0.23	0.21	0.25
	2	0.19	0.17	0.22
	3	0.16	0.14	0.19
	4	0.13	0.11	0.16
	5	0.11	0.09	0.13

	6	0.09	0.07	0.11
	7	0.07	0.06	0.09
	8	0.06	0.05	0.08
1,060-1,080 m, <15% Openness	1	0.19	0.16	0.22
	2	0.15	0.13	0.19
	3	0.13	0.10	0.16
	4	0.11	0.08	0.13
	5	0.09	0.07	0.11
	6	0.07	0.05	0.09
	7	0.06	0.04	0.08
	8	0.05	0.03	0.06
1,090-1,210 m, 15-30% Openness	1	0.26	0.24	0.28
	2	0.22	0.20	0.24
	3	0.19	0.16	0.21
	4	0.15	0.13	0.18
	5	0.13	0.11	0.15
	6	0.11	0.09	0.13
	7	0.09	0.07	0.11
	8	0.07	0.05	0.09
1,210-1,280 m, 30-45% Openness	1	0.33	0.30	0.37
	2	0.29	0.25	0.32
	3	0.24	0.21	0.28
	4	0.21	0.17	0.24

		5	0.17	0.14	0.21
		6	0.14	0.12	0.18
		7	0.12	0.09	0.15
		8	0.10	0.07	0.13
630-710 m, <15% Openness	2016	1	0.24	0.22	0.27
		2	0.20	0.18	0.23
		3	0.17	0.15	0.19
		4	0.14	0.12	0.17
		5	0.12	0.10	0.14
		6	0.10	0.08	0.12
		7	0.08	0.06	0.10
		8	0.06	0.05	0.08
680-740 m, 15-30% Openness		1	0.30	0.27	0.33
		2	0.26	0.23	0.28
		3	0.22	0.19	0.25
		4	0.18	0.16	0.21
		5	0.15	0.13	0.18
		6	0.13	0.10	0.15
		7	0.10	0.08	0.13
		8	0.08	0.07	0.11
650-730 m, 30-45% Openness		1	0.24	0.22	0.26
		2	0.20	0.18	0.23
		3	0.17	0.15	0.19

	4	0.14	0.12	0.16
	5	0.12	0.10	0.14
	6	0.10	0.08	0.12
	7	0.08	0.06	0.10
	8	0.06	0.05	0.08
850-950 m, <15% Openness	1	0.22	0.19	0.24
	2	0.18	0.16	0.21
	3	0.15	0.13	0.18
	4	0.13	0.11	0.15
	5	0.10	0.08	0.13
	6	0.09	0.07	0.11
	7	0.07	0.05	0.09
	8	0.06	0.04	0.07
890-920 m, 15-30% Openness	1	0.25	0.23	0.27
	2	0.21	0.19	0.24
	3	0.18	0.16	0.20
	4	0.15	0.13	0.17
	5	0.12	0.10	0.15
	6	0.10	0.08	0.12
	7	0.08	0.07	0.10
	8	0.07	0.05	0.09
810-910 m, 30-45% Openness	1	0.23	0.21	0.25
	2	0.19	0.17	0.22

	3	0.16	0.14	0.19
	4	0.13	0.11	0.16
	5	0.11	0.09	0.13
	6	0.09	0.07	0.11
	7	0.07	0.06	0.09
	8	0.06	0.05	0.08
1,060-1,080 m, <15% Openness	1	0.19	0.16	0.22
	2	0.15	0.13	0.19
	3	0.13	0.10	0.16
	4	0.11	0.08	0.13
	5	0.09	0.07	0.11
	6	0.07	0.05	0.09
	7	0.06	0.04	0.08
	8	0.05	0.03	0.06
1,090-1,210 m, 15-30% Openness	1	0.26	0.24	0.28
	2	0.22	0.20	0.24
	3	0.19	0.16	0.21
	4	0.15	0.13	0.18
	5	0.13	0.11	0.15
	6	0.11	0.09	0.13
	7	0.09	0.07	0.11
	8	0.07	0.05	0.09
1,210-1,280 m, 30-45% Openness	1	0.33	0.30	0.37

2	0.29	0.25	0.32
3	0.24	0.21	0.28
4	0.21	0.17	0.24
5	0.17	0.14	0.21
6	0.14	0.12	0.18
7	0.12	0.09	0.15
8	0.10	0.07	0.13

a- Humboldt's flying squirrel (Glaucomys oregonensis)

b- Townsend's chipmunk (Neotamias townsendii)

204

Table 3.5. – Estimates of apparent annual survival (φ) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present species, grid characteristics, the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Species	Label	Interval	Estimate	LCI	UCI
HFS ^a	630-710 m, <15% Openness	2011-2012	0.47	0.43	0.51
		2012-2013	0.48	0.43	0.52
		2013-2014	0.47	0.43	0.51
		2014-2015	0.47	0.43	0.51
		2015-2016	0.47	0.43	0.51
	680-740 m, 15-30% Openness	2011-2012	0.48	0.44	0.52
		2012-2013	0.48	0.44	0.52
		2013-2014	0.48	0.43	0.53
		2014-2015	0.48	0.44	0.51
		2015-2016	0.47	0.44	0.51
	650-730 m, 30-45% Openness	2011-2012	0.48	0.44	0.52
		2012-2013	0.48	0.44	0.52
		2013-2014	0.48	0.44	0.52
		2014-2015	0.48	0.44	0.52
		2015-2016	0.48	0.44	0.52
	850-950 m, <15% Openness	2011-2012	0.49	0.45	0.52
		2012-2013	0.49	0.45	0.52
		2013-2014	0.48	0.45	0.52
		2014-2015	0.48	0.45	0.52

	2015-2016	0.48	0.45	0.52
890-920 m, 15-30% Openness	2011-2012	0.49	0.46	0.53
	2012-2013	0.49	0.46	0.53
	2013-2014	0.49	0.45	0.54
	2014-2015	0.49	0.46	0.52
	2015-2016	0.49	0.46	0.52
810-910 m, 30-45% Openness	2011-2012	0.48	0.45	0.52
	2012-2013	0.49	0.45	0.52
	2013-2014	0.48	0.45	0.52
	2014-2015	0.48	0.46	0.51
	2015-2016	0.48	0.46	0.51
1,060-1,080 m, <15% Openness	2011-2012	0.50	0.46	0.54
	2012-2013	0.49	0.45	0.54
	2013-2014	0.50	0.46	0.54
	2014-2015	0.50	0.46	0.53
	2015-2016	0.49	0.45	0.53
1,090-1,210 m, 15-30% Openness	2011-2012	0.50	0.46	0.54
	2012-2013	0.50	0.46	0.55
	2013-2014	0.50	0.44	0.57
	2014-2015	0.50	0.46	0.55
	2015-2016	0.50	0.46	0.54
1,210-1,280 m, 30-45% Openness	2011-2012	0.51	0.45	0.56
	2012-2013	0.51	0.45	0.57

		2013-2014	0.51	0.45	0.57
		2014-2015	0.51	0.46	0.56
		2015-2016	0.51	0.45	0.56
TC ^b	630-710 m, <15% Openness	2011-2012	0.15	0.13	0.17
		2012-2013	0.13	0.11	0.16
		2013-2014	0.29	0.25	0.34
		2014-2015	0.22	0.19	0.24
		2015-2016	0.18	0.16	0.21
	680-740 m, 15-30% Openness	2011-2012	0.15	0.13	0.17
		2012-2013	0.13	0.11	0.16
		2013-2014	0.30	0.26	0.34
		2014-2015	0.22	0.19	0.24
		2015-2016	0.18	0.16	0.21
	650-730 m, 30-45% Openness	2011-2012	0.15	0.13	0.18
		2012-2013	0.14	0.11	0.16
		2013-2014	0.30	0.26	0.34
		2014-2015	0.22	0.20	0.25
		2015-2016	0.19	0.17	0.21
	850-950 m, <15% Openness	2011-2012	0.15	0.13	0.18
		2012-2013	0.13	0.11	0.16
		2013-2014	0.29	0.25	0.34
		2014-2015	0.22	0.19	0.25
		2015-2016	0.18	0.16	0.21

0	n	0
4	υ	0

890-920 m, 15-30% Openness	2011-2012	0.15	0.13	0.17
	2012-2013	0.14	0.11	0.16
	2013-2014	0.30	0.27	0.34
	2014-2015	0.22	0.20	0.24
	2015-2016	0.19	0.17	0.21
810-910 m, 30-45% Openness	2011-2012	0.15	0.13	0.18
	2012-2013	0.14	0.12	0.16
	2013-2014	0.30	0.27	0.34
	2014-2015	0.22	0.20	0.25
	2015-2016	0.19	0.17	0.21
1,060-1,080 m, <15% Openness	2011-2012	0.15	0.13	0.18
	2012-2013	0.13	0.11	0.16
	2013-2014	0.30	0.26	0.34
	2014-2015	0.22	0.19	0.25
	2015-2016	0.19	0.16	0.21
1,090-1,210 m, 15-30% Openness	2011-2012	0.16	0.14	0.18
	2012-2013	0.14	0.12	0.16
	2013-2014	0.31	0.27	0.34
	2014-2015	0.23	0.21	0.25
	2015-2016	0.19	0.17	0.21
1,210-1,280 m, 30-45% Openness	2011-2012	0.16	0.14	0.19
	2012-2013	0.14	0.12	0.17
	2013-2014	0.31	0.27	0.36

2014-2015	0.23	0.21	0.26
2015-2016	0.20	0.17	0.23

a- Humboldt's flying squirrel (*Glaucomys oregonensis*)b- Townsend's chipmunk (*Neotamias townsendii*)

Table 3.6. – Estimates of recruitment (*f*) for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present species, grid characteristics, the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Species	Label	Interval	Estimate	LCI	UCI
HFS ^a	630-710 m, <15% Openness	2012-2013	0.68	0.54	0.79
		2013-2014	0.23	0.18	0.30
		2014-2015	0.36	0.32	0.41
	680-740 m, 15-30% Openness	2012-2013	0.67	0.52	0.78
		2013-2014	0.23	0.18	0.29
		2014-2015	0.36	0.30	0.41
	650-730 m, 30-45% Openness	2012-2013	0.73	0.54	0.86
		2013-2014	0.25	0.19	0.32
		2014-2015	0.39	0.33	0.46
	850-950 m, <15% Openness	2012-2013	0.74	0.60	0.85
		2013-2014	0.26	0.21	0.32
		2014-2015	0.40	0.36	0.44
	890-920 m, 15-30% Openness	2012-2013	0.77	0.60	0.88
		2013-2014	0.27	0.21	0.33
		2014-2015	0.41	0.36	0.46
	810-910 m, 30-45% Openness	2012-2013	0.71	0.57	0.82
		2013-2014	0.25	0.19	0.31
		2014-2015	0.38	0.34	0.42
	1,060-1,080 m, <15% Openness	2012-2013	0.79	0.61	0.90

		2013-2014	0.28	0.22	0.34
		2014-2015	0.42	0.37	0.47
	1,090-1,210 m, 15-30% Openness	2012-2013	0.78	0.58	0.90
		2013-2014	0.27	0.21	0.34
		2014-2015	0.41	0.35	0.48
	1,210-1,280 m, 30-45% Openness	2012-2013	0.86	0.54	0.97
		2013-2014	0.30	0.23	0.38
		2014-2015	0.46	0.38	0.54
TC ^b	630-710 m, <15% Openness	2012-2013	1.21	1.12	1.31
		2013-2014	0.45	0.40	0.50
		2014-2015	0.67	0.63	0.71
	680-740 m, 15-30% Openness	2012-2013	1.22	1.13	1.31
		2013-2014	0.45	0.41	0.50
		2014-2015	0.68	0.64	0.71
	650-730 m, 30-45% Openness	2012-2013	1.23	1.15	1.32
		2013-2014	0.46	0.41	0.50
		2014-2015	0.68	0.65	0.72
	850-950 m, <15% Openness	2012-2013	1.21	1.11	1.30
		2013-2014	0.45	0.40	0.50
		2014-2015	0.67	0.63	0.71
	890-920 m, 15-30% Openness	2012-2013	1.22	1.14	1.31
		2013-2014	0.45	0.41	0.50
		2014-2015	0.68	0.65	0.71

810-910 m, 30-45% Openness	2012-2013	1.24	1.15	1.33
	2013-2014	0.46	0.41	0.50
	2014-2015	0.69	0.65	0.72
1,060-1,080 m, <15% Openness	2012-2013	1.21	1.11	1.30
	2013-2014	0.45	0.40	0.50
	2014-2015	0.67	0.63	0.71
1,090-1,210 m, 15-30% Openness	2012-2013	1.23	1.14	1.31
	2013-2014	0.46	0.41	0.50
	2014-2015	0.68	0.65	0.71
1,210-1,280 m, 30-45% Openness	2012-2013	1.25	1.14	1.35
	2013-2014	0.46	0.41	0.51
	2014-2015	0.69	0.64	0.74

a- Humboldt's flying squirrel (Glaucomys oregonensis)

b- Townsend's chipmunk (Neotamias townsendii)

Table 3.7. – Model averaged estimates of population growth for Humboldt's flying squirrels (*Glaucomys oregonensis*) and Townsend's chipmunks (*Neotamias townsendii*) captured in natural successional forest in the H. J. Andrews Experimental Forest from 2011–2016. We present species, grid characteristics, the estimated interval and 95% confidence interval (LCL: Lower Confidence Limit and UCL: Upper Confidence Limit).

Species	Grid Characteristics	Interval	Estimate	LCI	UCI
HFS ^a	630-710 m, <15% Openness	2012-2013	1.45	1.27	1.62
		2013-2014	0.82	0.72	0.90
		2014-2015	0.82	0.73	0.88
	680-740 m, 15-30% Openness	2012-2013	1.45	1.28	1.62
		2013-2014	0.83	0.72	0.91
		2014-2015	0.82	0.74	0.88
	650-730 m, 30-45% Openness	2012-2013	1.45	1.28	1.63
		2013-2014	0.83	0.72	0.90
		2014-2015	0.82	0.74	0.89
	850-950 m, <15% Openness	2012-2013	1.46	1.29	1.63
		2013-2014	0.84	0.74	0.90
		2014-2015	0.83	0.74	0.89
	890-920 m, 15-30% Openness	2012-2013	1.46	1.29	1.63
		2013-2014	0.85	0.74	0.92
		2014-2015	0.83	0.75	0.89
	810-910 m, 30-45% Openness	2012-2013	1.46	1.29	1.63
		2013-2014	0.84	0.73	0.91
		2014-2015	0.83	0.75	0.89
	1,060-1,080 m, <15% Openness	2012-2013	1.47	1.29	1.64

		2013-2014	0.85	0.74	0.92
		2014-2015	0.84	0.75	0.90
	1,090-1,210 m, 15-30%				
	Openness	2012-2013	1.47	1.30	1.65
		2013-2014	0.86	0.73	0.93
		2014-2015	0.85	0.75	0.91
	1,210-1,280 m, 30-45%				
	Openness	2012-2013	1.48	1.30	1.66
		2013-2014	0.86	0.74	0.93
		2014-2015	0.85	0.75	0.92
TC ^a	630-710 m, <15% Openness	2012-2013	1.22	1.12	1.31
		2013-2014	0.68	0.64	0.73
		2014-2015	0.95	0.87	0.98
	680-740 m, 15-30% Openness	2012-2013	1.22	1.14	1.31
		2013-2014	0.69	0.64	0.73
		2014-2015	0.95	0.88	0.98
	650-730 m, 30-45% Openness	2012-2013	1.24	1.15	1.32
		2013-2014	0.69	0.64	0.73
		2014-2015	0.96	0.88	0.99
	850-950 m, <15% Openness	2012-2013	1.21	1.11	1.31
		2013-2014	0.68	0.63	0.73
		2014-2015	0.94	0.87	0.98
	890-920 m, 15-30% Openness	2012-2013	1.23	1.14	1.31

	2013-2014	0.69	0.64	0.73
	2014-2015	0.95	0.89	0.98
810-910 m, 30-45% Openness	2012-2013	1.24	1.15	1.33
	2013-2014	0.69	0.65	0.74
	2014-2015	0.96	0.88	0.99
1,060-1,080 m, <15% Openness	2012-2013	1.21	1.12	1.31
	2013-2014	0.68	0.63	0.73
	2014-2015	0.94	0.87	0.98
1,090-1,210 m, 15-30%				
Openness	2012-2013	1.23	1.15	1.32
	2013-2014	0.69	0.64	0.73
	2014-2015	0.96	0.89	0.98
1,210-1,280 m, 30-45%				
Openness	2012-2013	1.25	1.14	1.35
	2013-2014	0.70	0.64	0.74
	2014-2015	0.97	0.85	0.99

a- Humboldt's flying squirrel (Glaucomys oregonensis)

b- Townsend's chipmunk (Neotamias townsendii)