

Effects of forest management, prey, and predators on the habitat selection of fishers in the South
Cascades of Washington.

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Abstract

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One of the most common reasons for failure of wildlife reintroductions is releasing animals into low quality habitat that does not meet resource needs. Food availability and the presence of potential predators or competitors in the reintroduction area are integral aspects of habitat quality that are rarely assessed prior to reintroductions. The fisher (*Pekania pennanti*) is a commonly reintroduced species that requires complex forest structure for reproduction, relies on a variety of prey, and interacts with a number of other carnivore species. In this thesis, I assessed prey availability for a reintroduced population of fishers and modeled their habitat selection based on forest structure, prey, and predators to better understand what factors could influence reintroduction success of fishers. In the first chapter, I evaluated the relationship between forest management and prey availability for fishers. I conducted habitat surveys, live trapping, and sign surveys for mammalian prey in forests that differed in management history. I then assessed how

forest management and habitat influenced prey diversity and community structure. I found equally diverse but distinct prey communities in forests with different management histories. The prey community in old stands consisted of abundant small rodent species, while younger stands had higher abundance of snowshoe hares (*Lepus americanus*) and mountain beavers (*Aplodontia rufa*). I identified a potential disconnect between preferred habitats of fishers and two common prey species, mountain beavers and snowshoe hares. In the second chapter, I examined the relative importance of landscape features and species interactions in determining habitat selection of fishers. I used species detections at 134 remote cameras stations, remotely sensed forest structure data, and telemetry locations of fishers to construct a resource selection function assessing the relative importance of prey, predators, and forest structure in habitat selection by fishers. I found that the probability of fisher use increased in older forests, in close proximity to recently disturbed stands, and in areas with moderate snowshoe hare abundance. Additionally, I documented a potential food-safety tradeoff for fishers between bobcats (*Lynx rufus*) and snowshoe hares, which fishers may mediate through temporal avoidance of bobcats. Selection for old forests close to recently disturbed stands and the preference of important prey for young stands suggests that habitat mosaics of these forests are valuable for fishers in the Pacific Northwest. Managers should seek to create heterogeneous forest habitats where young stands are intermixed in a matrix of old forest to provide for all habitat needs of recovering fishers. I documented complex relationships between forest structure, prey, predators, and fisher habitat selection, highlighting the importance of addressing species interactions prior to reintroductions.

TABLE OF CONTENTS

	Page
LIST OF FIGURES	ii
LIST OF TABLES	iv
CHAPTER 1 – General Introduction.....	1
CHAPTER 2 – Prey Availability for Fishers in the South Cascades of Washington	8
ABSTRACT	8
INTRODUCTION	8
STUDY AREA	12
METHODS	14
RESULTS	19
DISCUSSION	25
CHAPTER 3 – Habitat Use and Species Interactions of Reintroduced Fishers in Washington...	31
ABSTRACT	31
INTRODUCTION	32
STUDY AREA	36
METHODS	37
RESULTS	45
DISCUSSION	53
CHAPTER 4 – General Conclusion	62
LITERATURE CITED	65
APPENDIX.....	77

LIST OF FIGURES

Figure 1.1. Map of our study area in the South Cascade Mountains of Washington. Habitat and prey sampling locations shown as blue circles.	14
Figure 1.2. Site layout for habitat sampling and prey surveys. Black dots indicate locations of surveys for hare pellets, mountain beaver burrows, and squirrel middens. Red crosses indicate habitat-sampling locations. Blue dots indicate Sherman trap locations. Scale in meters.	16
Figure 1.3. Non-metric multidimensional scaling ordination (NMDS) of mammalian prey community plotted showing both site scores and prey group scores for 21 sites in the South Cascades of Washington. Plot “a” shows the first and second ordination axes, plot “b” shows the first and third, and plot “c” shows the second and third. Site points are squares for summer 2016 and circles for summer 2017. Arrows indicate correlation between the overstory and understory principal components and the ordination axes. Ellipses show the 95% confidence ellipse for the centroid of each age class. The final ordination achieved a stress level of 0.114 in 3-dimensions. The final solution was reached after 20 random starts out of a maximum allowed 200 starts.	25
Figure 1.4. Boxplots of (a) species richness and (b) small mammal diversity at 21 sites in the South Cascades of Washington.	25
Figure 2.1. Camera trap photo showing bait and lure set up. Scent lure was poured on moss and attached to the tree in a small piece of corrugated plastic to limit washout by rain.	39
Figure 2.2. Camera locations and species detected for 134 camera stations in the South Cascades of Washington. Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017.	47
Figure 2.3. Predicted response curves from top resource selection function (RSF) for fishers. Plots show relative probability of use across the measured range of stand age (a), snowshoe hare detections (b) and distance to recently disturbed stand (c). The snowshoe hare plot shows the interactions with sex with females in black and males in grey. Dashed lines represent 95% confidence intervals on the prediction. Telemetry data used in the RSF were collected from January 2016 through January 2018 in the South Cascades of Washington.	49
Figure 2.4. Scatter plot showing the expected number of snowshoe hare detections and the expected number of bobcat detections at used and available sites for the fisher resource selection function ($n = 10618$).	50
Figure 2.5. Diel activity overlap of fishers with bobcats (a), fishers with coyotes (b), and bobcats with coyotes (c) based on independent detection events at 134 camera locations in the South Cascades of Washington. Plots are kernel density estimates of activity and $\hat{\Delta}_1$ is a measure of activity overlap between species (Ridout and Linkie 2009). Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017.	53

Figure A1. Frequency of categories (bins) of RSF scores for withheld fisher locations for 5-fold cross validation. Mean (\pm SE) frequency values (a). Frequency values for each cross-validation test are shown in unique colors (b). A Spearman-rank correlation for mean frequency by bins ($r_s = 0.88$, $p < 0.001$) indicates the model predicted cross-validated use locations well.....80

LIST OF TABLES

Table 1.1. Variable loadings for the first two principle components from a principal component analysis of understory habitat variables.	20
Table 1.2. Variable loadings for the first two principle components from a principal component analysis of overstory habitat variables.	21
Table 1.3. The top five permutational multivariate analysis of variance models for mammalian prey community at 21 sites in the South Cascade Mountains of Washington. Models were ranked by Akaike Information Criterion corrected for small sample sizes.	22
Table 1.4. Parameter importance of variables included in mammalian prey community permutational multivariate analysis of variance. Importance values based on Akaike Information Criterion corrected for small sample sizes (Burnham and Anderson 2002).	23
Table 1.5. Response of small mammal species to overstory and understory habitat conditions based on interpretation of non-metric multidimensional scaling. “+” indicates an increase in abundance, “-“ indicates a decrease in abundance, and “0” indicates no clear response.	23
Table 2.1. Description and range of unscaled values for habitat and landscape covariates used in hare, coyote, and bobcat detection models and fisher resource selection functions, including randomly chosen available points ($n = 10618$).	41
Table 2.2. Parameter estimates, standard errors (SE), and p-values for the top negative binomial regression models for number of snowshoe hare, bobcat, and coyote detections from 134 camera locations in the South Cascades of Washington. Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017. All parameters on the log scale.	47
Table 2.3. The top five negative binomial regression models for coyote, bobcat, and hare detections from 134 camera locations in the South Cascades of Washington. Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017. Models were ranked using Akaike Information Criterion corrected for small sample sizes (AICc).	48
Table 2.4. Parameter estimates and bootstrapped confidence intervals of top fisher resource selection function based on telemetry data collected from January 2016 through January 2018 in the South Cascades of Washington. Parameter estimates are on the logit scale.	49
Table 2.5. The top five resource selection functions for fishers in the South Cascades of Washington based on telemetry data collected from January 2016 through January 2018. Models were ranked using Akaike Information Criterion corrected for small sample sizes (AICc).	50
Table A1. Correlations among covariates used in hare, bobcat, and coyote detection models and fisher resources selection functions ($n = 10618$).	77

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Effects of forest management, prey, and predators on the space use of fishers in the South
Cascades of Washington.

CHAPTER 1

General Introduction

Reintroductions are a common tool in wildlife management and conservation, and have multiple purposes. Wildlife managers may pursue reintroductions of common species to restore ecological function or game populations (Witmer 1990, Woodruff 2015). More commonly, however, reintroductions attempt to re-establish species of conservation concern within their historical range (Russell et al. 1994, Walters et al. 2010). Recovery plans for endangered and threatened species often incorporate reintroduction efforts (Cook et al. 2010a), yet many reintroductions fail to establish populations, and success rates have not increased through time (Griffith et al. 1989, Fischer and Lindenmayer 2000). Identifying what factors influence reintroduction success, and evaluating these factors prior to reintroduction is key to the success of reintroductions and conservation of threatened and endangered species.

One of the most effective predictors of reintroduction success is habitat quality (Wolf et al. 1998, IUCN SSC 2013). Therefore, understanding what constitutes quality habitat for a species, and assessing habitat prior to reintroductions is integral to the success of reintroductions. However, habitat quality is a complex concept that incorporates not only landscape features, such as vegetation and climate (Masse et al. 2014, Fattebert et al. 2015, Pedersen et al. 2017), but also species interactions (Creel and Creel 1996, Swanson et al. 2016). For example, habitat quality for black-footed ferrets (*Mustela nigripes*) is highly dependent on the presence and abundance of prairie dogs (*Cynomys* spp.), the ferrets primary prey (Jachowski et al. 2011).

Predators and competitors also influence habitat quality and can limit success of reintroduction attempts, such as with barred bandicoots (*Perameles gunnii*) in Australia (Cook et al. 2010a, Spurgeon et al. 2015). Therefore, understanding the habitat needs of a species, and evaluating the presence and configuration of resources on the landscape prior to reintroductions will likely increase reintroduction success rates. Some reintroductions are preceded by feasibility assessments that include some degree of habitat assessment, but species interactions are often only minimally incorporated into these assessments, and formal assessments of prey and predator populations are rare (Breitenmoser et al. 2001, Lewis and Hayes 2004, Callas and Figura 2008, Hiller 2015).

Assessing habitat quality prior to reintroductions can identify quality habitats and improve success, but habitat selection patterns of reintroduced populations may differ from other populations for numerous reasons. Animals select habitats based on previous experiences (Davis and Stamps 2004), and when natal habitat preferences are combined with potentially new habitat types in reintroduction areas, unique habitat selection patterns may emerge. Additionally, human influences in the reintroduction area since extirpation occurred may have changed the distribution of habitats and other species on the landscape. Climate induced habitat changes may also alter habitat selection patterns of a reintroduced species when compared to historical or source populations. Therefore, assessing habitat selection of reintroduced populations post-release is necessary for successful management and conservation of the species.

While a species responds to landscape features, food availability, competitors, and predators, none of these factors act independently. Species have evolved to prefer habitats that provide food and protection from predators, but human influences on landscapes have changed habitats and the associations between species and their habitats (MacDonald et al. 2005, Kays et

al. 2017). These complexities may result in tradeoffs that are common in ecology, such as food-safety tradeoffs, where locations with the most food may also be the riskiest (Emerson and Brown 2015, Pomeroy and Lindström 2018). Understanding the distributions and interactions of habitat, food availability, competitors, and predators will increase the immediate success of reintroductions and the long-term success of wildlife conservation.

While these factors influence reintroductions of all species, mesopredators often face such tradeoffs because of their relationships with prey and other carnivores (Grassel et al. 2015, Cremona et al. 2017). Mesopredators compete with dominant carnivores for food, and this may result in spatial association in areas with high prey availability (Bischof et al. 2014). However, this positive association leads to increased risk of competition and/or predation. Mesopredators may balance this risk by using alternate resources to avoid dominant carnivores (Sivy et al. 2018), using habitats that provide refuge and reduce riskiness (Steinmetz et al. 2013, Hernandez-Santin et al. 2016), or avoiding dominant carnivores temporally (Bischof et al. 2014).

Here, I examined the habitat selection of reintroduced fishers (*Pekania pennanti*) in relation to landscape features, prey, and other carnivores. I assessed how this information could be used to inform future reintroductions of carnivores and to manage lands for the recovery of fishers, a species of conservation concern on the Pacific Coast of the United States. Fishers prefer mature forests that provide structural diversity, which they rely on for den and rest sites (Weir et al. 2012, Zhao et al. 2012, Zielinski and Gray 2018). However, there is increasing evidence that fishers will also use unmanaged mid-seral stands and heterogeneous forest mosaics (Raley et al. 2012, Sauder and Rachlow 2015, Lewis et al. 2016). Fishers are dietary generalists that eat a variety of prey, and small and medium-sized mammals are the most important prey items throughout their range (Zielinski and Duncan 2004, Weir et al. 2005, McNeil et al. 2017,

Kirby et al. 2018). This diet results in competition with other carnivores, particularly bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), both of which are also known to kill fishers (Wengert et al. 2014, Sweitzer et al. 2015).

Fishers underwent a major range contraction in the 19th and 20th centuries due to large scale trapping and logging efforts (Lewis et al. 2012). Their range contracted to approximately 43% of its original size and they were extirpated from many areas, particularly at the southern extent of their range (Lewis et al. 2012). Changes in land management practices and trapping regulations resulted in fisher recovery across much of their historical range (McNeil et al. 2017, Kirby et al. 2018). Additionally, fishers are one of the most commonly reintroduced carnivore species in North America and translocations have had a moderate success rate (Lewis et al. 2012). However, fisher recovery in the eastern United States has been much more successful than in the western United States, where fishers are still listed as an endangered species in Washington and a sensitive species in Oregon (<https://wdfw.wa.gov>; <http://www.dfw.state.or.us/>). Remnant populations in California have not expanded substantially, and reintroduction efforts have been less successful in the West than in the East (Lewis et al. 2012).

While many reintroductions of fishers have been attempted, few have conducted feasibility assessments prior to implementation. Of those that have, assessment of prey resources and potential predators or competitors were rarely included (Serfass et al. 1994, Apps 1995, Hiller 2015). Predation and prey availability both affect fisher survival and population size (Bowman et al. 2006, Jensen et al. 2012, Wengert et al. 2014), and accounting for these factors during reintroductions could increase probability of success.

One hypothesis for the lower success of fishers in the West is increased pressure from other carnivores. Recent work in California highlighted the impact of intraguild predation on survival of fishers and found that bobcats, coyotes, and cougars (*Puma concolor*) all prey on fishers with bobcats being a major cause of female mortality (Wengert et al. 2014, Gabriel et al. 2015). Predator communities are more diverse on the West Coast than in the East, potentially leading to both increased competition and predation (Lapoint et al. 2015). Further human habitat alterations may have increased contact rates between fishers and other carnivores (Wengert et al. 2014, Sweitzer et al. 2015). Additionally, Lapoint et al (2015) found that modern fishers in the East are larger than historic specimens, which they suggest may be due to decreased competition from other carnivores for larger prey.

It is also possible that lack of success of fisher conservation in the West is related to prey availability. Fishers rely on small and medium-sized mammals as prey throughout their range (Weir et al. 2012, Lapoint et al. 2015, Kirby et al. 2018), and it is possible that habitat alterations since the extirpation of fishers have reduced prey availability (Carey and Johnson 1995, Carey 2000, Griffin and Mills 2007). Additionally, extensive road systems may have increased access of coyotes and bobcats into historical fisher habitat, increasing competition for prey resources (Spencer et al. 2015, Sweitzer et al. 2015). The use of younger forests and heterogeneous landscapes by fishers may be related to increased prey availability in these habitats, though this relationship has never been tested (Raley et al. 2012, Sauder and Rachlow 2015). Use of these habitats may further expose fishers to dominant generalist predators like bobcats and coyotes.

The Washington Department of Fish and Wildlife (WDFW) began a fisher recovery program in 2008. Fishers were initially reintroduced on the Olympic Peninsula and monitored to assess establishment success, survival, reproduction, and habitat selection. Female fishers

selected for mid-seral forests and males showed no strong selection patterns. Lewis et al. (2016) hypothesized this selection may have been related to prey availability, but no data on prey availability were collected. In 2015, WDFW began reintroducing fishers into the South Cascade Mountains of Washington. WDFW implanted all released fishers with very high frequency (VHF) radio-transmitters (Holohil AI-2HM) and tracked animals to monitor the reintroduction. I saw this as an opportunity to gain a better understanding of how forest structure, prey, and predators all influence habitat selection by fishers and inform future reintroductions of fishers.

The goal of this thesis is to assess how forest structure, prey availability, and carnivore distributions interact to shape habitat selection of a reintroduced population of fishers in the South Cascades of Washington. While previous research has assessed habitat selection, diet, and interactions with other carnivores independently, these three factors have never been assessed in concert. Simultaneously examining these three factors in unison may increase our understanding of how fishers respond to tradeoffs between these factors and what factors are most important to address prior to reintroductions.

I first assessed prey availability for fishers by examining how forest management and vegetation conditions influenced the diversity and composition of the small and medium-sized mammal community. Likely prey for fishers include snowshoe hares (*Lepus americanus*), mountain beavers (*Aplodontia rufa*), Douglas squirrels (*Tamiasciurus douglasii*), and a suite of small rodent species (*Peromyscus* spp., *Myodes gapperi*, *Microtus oregoni*, and *Neotamias townsendii*). I conducted live trapping and sign surveys to assess prey abundance in forests that differed in management history. I expected that prey diversity would be highest in older forests, but that larger prey items, snowshoe hares and mountain beavers, would be most abundant in young stands.

I also used camera trap surveys, along with the telemetry locations of fishers, to assess the influence of forest structure, prey availability, and other carnivores on habitat selection by fishers. I set camera traps throughout the study area in forests that varied in management history to document snowshoe hares, bobcats, and coyotes. I modeled the relationships between habitat and camera detections of snowshoe hares, coyotes, and bobcats to understand habitat use of these species and predict their presence across the landscape. I then used predicted snowshoe hare, bobcat, and coyote use, along with forest structure variables in a resource selection function (RSF) to assess habitat selection by fishers based on the telemetry locations. I expected fishers to use mature forests, forests with high snowshoe hare abundance, and low predicted use by bobcats and coyotes. I also examined temporal activity patterns of bobcats, coyotes, and fishers and expected fishers to show temporal avoidance of other carnivores, particularly if I did not find spatial avoidance.

This work will identify what habitat factors influence habitat selection by fishers. This knowledge will benefit future reintroduction efforts by allowing managers to focus on assessing those factors that are most important when resources for feasibility assessments are limited. Additionally, our findings can be used to successfully manage landscapes for recovery of fishers in Washington State.

CHAPTER 2

Prey Availability for Fishers in the South Cascades of Washington

ABSTRACT Understanding habitat associations of species is an integral step for conservation and management of wildlife. Small mammal species play a variety of important ecological roles, including as members of terrestrial food webs. Prey abundance is important to the conservation of carnivores, particularly during reintroduction efforts, where establishing self-sustaining populations relies on sufficient prey. We evaluated the effects of forest management on the small and medium-sized mammalian prey community in a region with a population of reintroduced fishers (*Pekania pennanti*) in the South Cascade Mountains of Washington. We estimated the abundance of prey species at 21 sites that differed in land ownership and management history, and we assessed the effects of management history and understory and overstory vegetation on the mammalian prey community using permutational multivariate analysis of variance and non-metric multidimensional scaling. We found distinct but equally diverse prey communities in heavily managed versus unmanaged forest stands. Additionally, we documented a discrepancy between the habitat selection of important fisher prey species and known habitat preferences of fishers. Our results add to growing evidence indicating that heterogeneous forest types provide valuable habitat for fishers in the Pacific Northwest, suggesting that land managers should seek to maintain a mosaic of mature and younger forest stands that provide complex structure for denning and resting as well as important prey resources.

INTRODUCTION

Understanding the relationships between habitat and wildlife communities is key to conservation and ecosystem management. Knowing preferred habitats of a species permits preservation of remaining habitats, restoration of degraded habitats, and land management to maintain habitats.

Examining relationships at a community level allows for a focus on ecosystem functions in addition to individual species (Roberge and Angelstam 2004). Small mammal communities play important ecological roles as seed dispersers, disease vectors, and prey for other species (McShea 2000, Lindemann et al. 2015). Therefore, understanding how habitat conditions influences the small mammal community is key to maintaining these ecological functions.

Many carnivores rely on small and medium-sized mammals as prey (Zielinski and Duncan 2004, Hodges and Mills 2008, Roberts et al. 2015, Witczuk et al. 2015), and conservation of carnivores thus depends on the presence of sufficient prey. Knowledge regarding prey base is increasingly important when conservation goals include expansion of remnant carnivore populations or establishing new populations (Jachowski et al. 2011, Bhattarai and Kindlmann 2012, Suryawanshi et al. 2017). Carnivore populations will not succeed in habitats without sufficient prey, and relocation or reintroduction efforts are doomed to fail if prey availability is low. Therefore, understanding prey-habitat relationships is needed for science-based carnivore reintroductions.

Reintroductions are a common tool in wildlife conservation, and prey resources influence the probability of success of these programs (Cook et al. 2010a, Fisher et al. 2014, Spurgeon et al. 2015). However, prey communities are not always assessed prior to reintroductions, resulting in reintroductions being conducted with incomplete information. Lack of information on habitat quality (including prey) is often cited as a reason for reintroduction failure (Lewis and Hayes 2004, Cook et al. 2010b). While evaluating prey abundance prior to reintroductions is ideal, evaluation after the reintroduction has occurred can inform management of the reintroduced population and improve future reintroduction and augmentation efforts.

Here, we evaluate the relationship between forest structure and prey availability in a region where fishers (*Pekania pennanti*) were reintroduced. Fishers are one of the most commonly reintroduced carnivores in North America (Lewis et al. 2012). Fishers are dietary generalists, and small and medium-sized mammals are a major diet component (Zielinski et al. 1999, Weir et al. 2005). After undergoing a major range contraction in the early 20th century (Powell 1993), fishers have recovered to substantial portions of their historical range, particularly in eastern North America (Lewis et al. 2012). Many reintroductions have been attempted to assist recovery of fishers, but these attempts have been more successful in the East than in the West (Lewis et al. 2012), and remnant populations have not expanded in the West as they have in the East (Powell 1993, Gabriel et al. 2015).

Lower success of reintroductions of fishers in the West, and the lack of range expansion of remnant populations could be related to prey availability. Habitat changes related to logging and forest management may have reduced small and medium-sized prey abundance (Carey and Johnson 1995, Carey 2000, Griffin and Mills 2007). Carey and Johnson (1995) and Carey (2011) found higher abundance of small mammals and squirrels in old growth forests compared to young and managed forests, suggesting that large scale logging may have reduced prey populations in the West. Also, prevalence of logging roads may have increased potential for competition between fishers and other carnivores (Spencer et al. 2015, Sweitzer et al. 2015). While relationships between small mammal abundance and forest conditions have been assessed (Carey and Johnson 1995, Carey 2000, Arjo et al. 2007, Griffin and Mills 2007), the majority of this work has focused on immediate impacts of logging treatments, and not general habitat use patterns of small mammals (Suzuki and Hayes 2003, Gitzen et al. 2007, Wilk et al. 2010).

Additionally, relationships between mammalian prey abundance and forest conditions have not been assessed in the context of fisher conservation.

In addition to abundance of important prey items, prey diversity may play a key role in success of carnivore reintroductions. Fisher populations are responsive to temporal variation in prey abundance (Bowman et al. 2006, Jensen et al. 2012), and a diverse prey community will be more stable through time (Doak et al. 1998, Tilman et al. 1998, Petchy 2000). Because reintroduced populations are small, stable prey communities can help reduce environmental stochasticity, reducing the probability of extinction and failure of reintroduction efforts (Alvarez 2001, Koprowski et al. 2005).

Fishers are an endangered species in Washington (<https://wdfw.wa.gov>), and a statewide reintroduction program began in 2008 with reintroductions on the Olympic Peninsula of Washington (Lewis et al. 2016). Fishers on the Olympic Peninsula selected for mosaic forests with a range of seral stages, predominantly unmanaged mid-seral forest (Lewis et al. 2016). Previous fisher habitat selection research has also found that fishers select for a diversity of forest types and edge habitats (Raley et al. 2012, Sauder and Rachlow 2015). Fishers may select for mid-seral forests and stand diversity because these areas have higher diversity and abundance of prey, but this hypothesis has not been tested. Understanding how mammalian prey communities respond to forest habitat and management conditions will improve recovery efforts of fishers on the West Coast, including reintroductions.

Because of a lack of information on prey availability for fishers in Washington, we assessed how forest habitat characteristics affected community structure and diversity of small and medium-sized mammals within the range of a reintroduced population of fishers. We expected that prey diversity would be highest in older forests, but that snowshoe hares (*Lepus*

americanus) and mountain beavers (*Aplodontia rufa*), two important large prey items, would be most abundant in young stands with high stem density (Arjo et al. 2007, Griffin and Mills 2007).

STUDY AREA

Our study area was a 5000 km² area of the South Cascades of Washington and included sites in Gifford Pinchot National Forest, Mount Rainier National Park, Elbe and Tahoma State Forests and surrounding private lands (Figure 1.1). This area is dominated by conifer forests ranging from young, intensively managed stands to old growth forests. Dominant tree species include Douglas fir (*Pseudotsuga menziesii*), silver fir (*Abies amabilis*), noble fir (*Abies procera*), and Western hemlock (*Tsuga heterophylla*). Dominant understory plants include Oregon grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), blueberry (*Vaccinium spp.*), salmonberry (*Rubus spectabilis*), and a number of fern species. The elevation of our study area ranges from 235 to 3314 m with a mean of 974 m. The elevation of our study sites ranged from 403 to 1494 m with a mean of 952 m. The mean July and January temperatures were 25.8° and -1.5° C respectively and average precipitation was 140 cm (67 cm snowfall) in the town of Packwood, Washington near the center of our study area (Western Regional Climate Center 2016; <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wa6262>).

Potential mammalian prey species in the Washington Cascades included snowshoe hares, mountain beavers, mice (*Peromyscus* spp.), voles (*Microtus* spp.; *Myodes* spp.), chipmunks (*Neotamias* spp.), and squirrels (*Tamiasciurus* spp.). Potential avian prey include ruffed grouse (*Bonasa umbellus*), sooty grouse (*Dendragapus fuliginosus*) and a variety of song bird species (Passeriformes). Porcupines (*Erethizon dorsatum*) were rare in our study area. Our work focused solely on mammalian prey due to the dominance of mammals in the diet of fishers (Weir et al. 2005, Kirby et al. 2018)

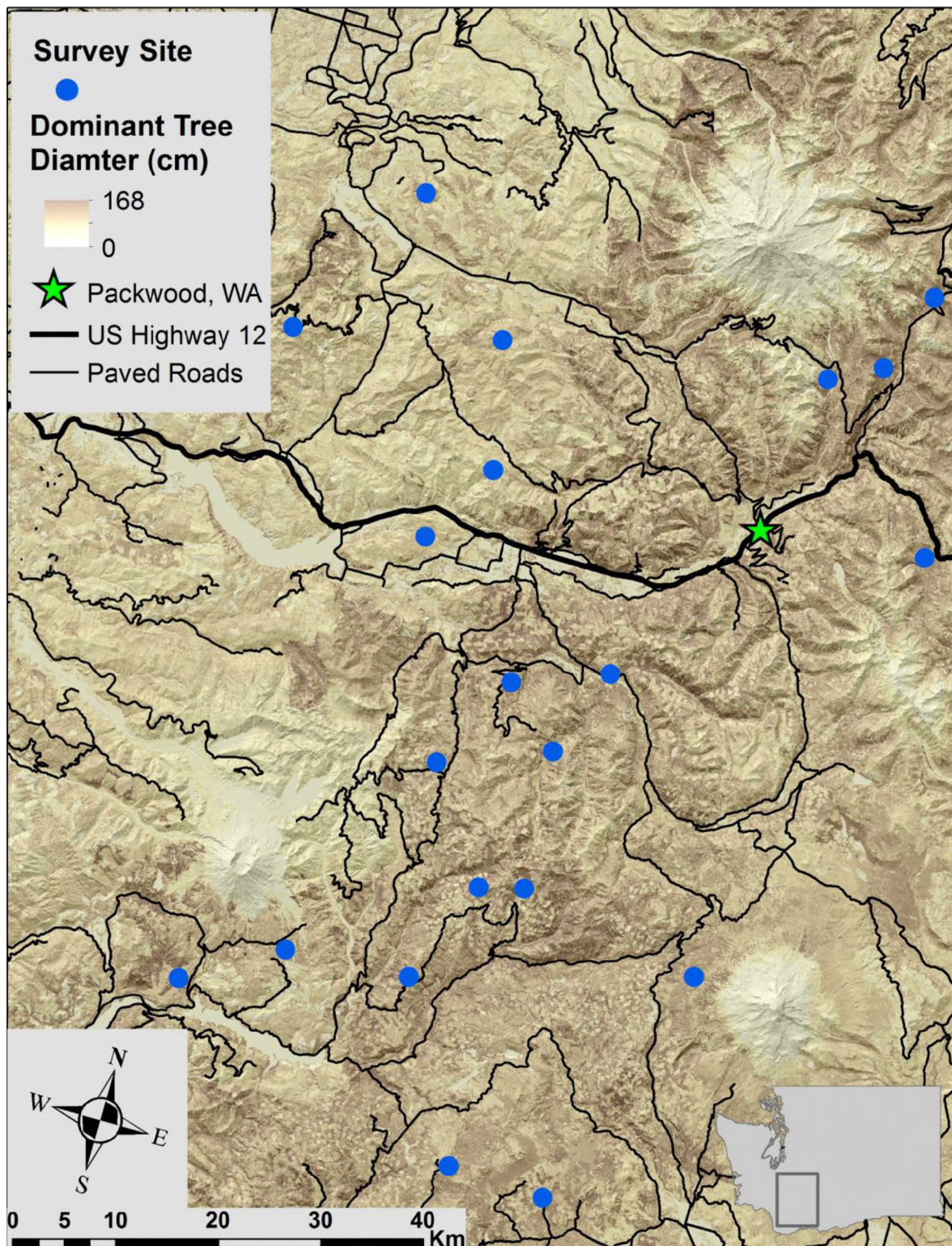


Figure 1.1. Map of our study area in the South Cascade Mountains of Washington. Habitat and prey sampling locations shown as blue circles. Major mountain peaks in the area include (top to bottom) Mt. Rainier, Mt. St. Helens, and Mt. Adams.

METHODS

Site Selection

We used the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA; <http://lemma.forestry.oregonstate.edu>) dataset for site selection and for large scale forest structure data. The LEMMA data was produced using a gradient nearest neighbor approach. Multivariate relationships between satellite imagery, environmental variables and field plot data were used to produce a 30-m resolution raster of forest structure. We used two forest structure variables (canopy cover and quadratic mean diameter of dominant trees) to quantify suitable fisher habitat. We placed a grid of 1 km² hexagons over the study area, and classified each hexagon as suitable fisher habitat if greater than 50% of the hexagon area contained forest with >60% canopy cover and > 29 cm average quadratic mean diameter of dominant trees (Halsey et al. 2015). We then calculated the average forest age of each hexagon as a proxy for forest management intensity. Based on data available from ground plots to validate of the LEMMA data, these variables had a mean correlation of 0.76 (range: 0.75 – 0.77) with true values (<http://lemma.forestry.oregonstate.edu>).

We conducted prey surveys at locations that spanned a gradient of management intensity in the South Cascades of Washington. We categorized hexagons into three age classes: young (<110 years), middle-aged (110 – 180 years) and old (>180 years) stands. Sample sites were placed in the center of randomly selected hexagons within each age category and we required that all surrounding hexagons were of the same age class and suitable fisher habitat (i.e. continuous 7km² area). This requirement was to ensure that each site was in the core of the

respective forest type and to minimize the effects of edge habitats on our sampling. For accessibility, we limited sites to be within 1 km of roads or within 3 km of a road if near a trail.

We sampled a total of 21 sites that varied in stand age and ownership, 10 in the summer (June to September) of 2016 and 11 in the summer of 2017. We sampled 14 sites in Gifford Pinchot National Forest (5 old, 6 mid, 3 young), three sites in Mount Rainier National Park (2 old, 1 mid), two sites in state forests (2 young), and two sites in private industrial forests (2 young).

Habitat Characteristics

Habitat characteristics were measured at 25 points in a 300-m x 300-m grid at each site (Figure 1.2). We estimated percent cover of two size classes of woody debris (5-25cm, >25 cm) and understory species using line intercept methods (Canfield 1941). For overstory conditions, we measured diameter at breast height (DBH) and documented species and status (alive/dead) of all trees >5cm DBH within a 5.64 m radius (0.1 ha) circular plot at each point (Klenner and Sullivan 2009). We calculated basal area by converting DBH into an area estimate assuming a cylinder and calculated stem density of trees >5 cm DBH by dividing the number of trees surveyed by total area surveyed. We visually estimated the percent coverage of shrub species within the 5.64 m radius overstory plot within six categories: <5%, 5-25%, 25-50%, 50-75%, 75-95%, and >95%.

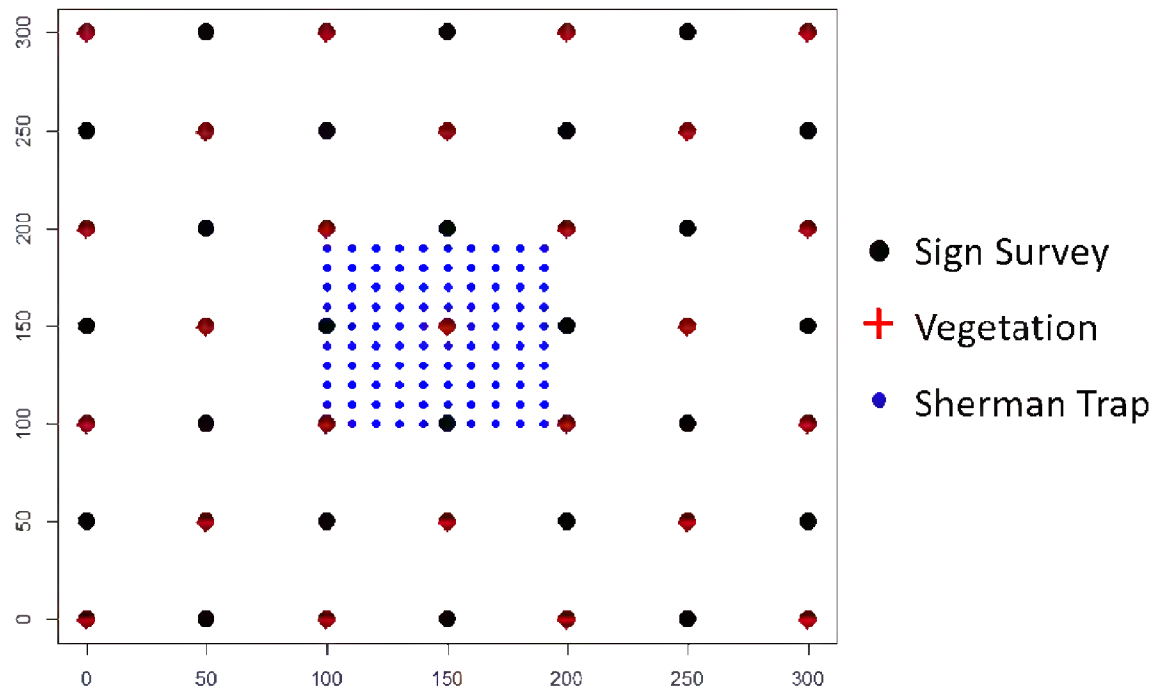


Figure 1.2. Site layout for habitat sampling and prey surveys. Black dots indicate locations of surveys for snowshoe hare pellets, mountain beaver burrows, and squirrel middens. Red crosses indicate habitat-sampling locations. Blue dots indicate Sherman trap locations. Scale in meters.

Mammalian Prey Abundance

At each site, mark-recapture surveys were used to estimate densities of small mammals. We established a 90-m x 90-m grid (0.81 ha) of 100 Sherman traps (LFA; 3 x 3.5 x 9.5”) with 10 m spacing for live captures of mice, voles and chipmunks (Figure 1.2). Traps were placed and pre-baited at each site for three days prior to trapping. Traps were baited with a combination of oats, seeds, dried mealworms (to reduce shrew (*Sorex* spp.) mortality; Do et al. 2013), and polyester batting. We trapped each site for 3-4 consecutive days after pre-baiting, with fewer trap nights on sites with high recapture rates. Traps were checked in the morning and evening and left open 24 hours per day. Captured individuals, except shrews and shrew moles (*Neurotrichus gibbsii*), were marked with numbered ear tags (1005-1 Monel ear tag; National Band Company), weighed, identified to species and sex, and released.

We surveyed snowshoe hare pellets, squirrel middens and mountain beaver burrows at 49 points spaced 50 m apart to obtain an index of abundance for these prey species (Figure 1.2). We counted snowshoe hare pellets in a 0.546 meter radius (1 m^2) plot at each survey point (Murray et al. 2002, Hodges and Mills 2008). We recorded midden presence within a 2 m radius plot in 2016 (Doumas and Koprowski 2013) and within the entire 5.64 m radius overstory plot in 2017. To standardize the two years of data, we scaled the number of points where middens were detected by the search area. Mountain beaver burrows were recorded within the 5.64 m radius overstory plots during both years.

Statistical Analysis

We used MARK 8.2 (Cooch and White 2018) to estimate abundance of each live trapped prey species at each site using the Huggins' conditional likelihood closed capture model. For each species we examined the effect of site, time (morning/evening trap session), and type (new/recapture) on capture probabilities. We ran all possible models including a null model (8 total) and selected the top model based on AIC (Burnham and Anderson 2002). The full model failed to converge for any prey group because of the high number of parameters. Sites where no individuals of a species were captured were assumed to have abundance of zero and excluded from MARK analysis. Juvenile *Peromyscus* spp. are not visually identifiable to species. For prey community analyses, we calculated abundance of Keen's mice and Deer mice separately and excluded juvenile *Peromyscus* spp. because of different habitat use patterns between the two species (Carey and Harrington 2001).

Because of the large number of measured habitat variables, we used summary measures and principle component analysis (PCA) to reduce the dimensionality of our habitat variables. We initially reduced understory variables to five summary variables from the individual species

data collected. These variables were percent groundcover (line intercept percent cover of all herbaceous species), percent cover of berry producing species (line intercept percent cover of all berry producing species), percent seedling cover (line intercept percent cover of all trees <1 m tall), percent cover of woody debris, and percent cover of all shrub species from visual estimates. We conducted a PCA on these five variables to further reduce dimensionality. We likewise conducted a PCA on eight overstory variables: DBH, basal area, stem density, percent of trees that were dead, basal area of deciduous species, basal area of Douglas fir, basal area of western hemlock, and basal area of true fir species (*Abies* spp.). We used parallel analysis to select the number of principal components to use for habitat use modeling (Horn 1965, Schmid-Holmes and Drickamer 2001, Dinno 2012). With this approach, we used two components from the understory PCA and two components from the overstory PCA. For interpretation of PCA results, we focused on the parameters that had PCA loadings $>|0.4|$ (Summerville et al. 2006, Delciellos et al. 2016)

We used permutational multivariate analysis of variance (PERMANOVA) to examine the effects of age class, study year, overstory vegetation, and understory vegetation on small mammal community composition at each of our 21 sites (Anderson et al. 2008). We constructed a Bray-Curtis dissimilarity matrix for our 21 sites based on the abundance of live trapped species and relative abundance of larger prey. The covariates used in the PERMANOVA analysis were year, the first two overstory principal components, the first two understory principal components, and the age class of the site (young, middle-aged, old). We ran 9999 permutations for each tested model. We tested all possible models ($n = 64$) and used AICc to conduct model selection and calculate parameter importance (Burnham and Anderson 2002).

To visualize and further interpret the effects of forest age and vegetation on the mammalian prey community, we used Non-metric Multidimensional Scaling ordination (NMDS). Our NMDS was based on the same dissimilarity matrix used for the PERMANOVA. We plotted site and species scores in ordination space and used the “envfit” function in the “vegan” package (Oksanen et al. 2018) to visualize correlations between the overstory and understory principal components and ordination axes to further understand how environmental variables influence the small mammal community. PERMANOVA and NMDS were conducted using the ‘vegan’ package (Oksanen et al. 2018) in R (R Core Team 2018).

We also examined the effects of forest structure on prey diversity. We calculated prey species richness at each site, and we calculated diversity of the live trapped small mammal community using the Shannon diversity index.

$$H = - \sum_{i=1}^S p_i * \ln(p_i)$$

Where p_i is the proportion of individuals belonging to species i , and S is the total number of species. To examine potential effects of forest management on prey diversity and richness, we used analysis of variance to assess whether species richness and diversity differed by forest age class.

RESULTS

Small Mammal Capture Summary

We captured 785 individuals of our five small mammal species of interest: 444 Keen’s mice at 20 sites, 70 deer mice at 18 sites, 28 Oregon voles at 6 sites, 74 red-backed voles at 15 sites, and 88 Townsend’s chipmunks at 15 sites. We excluded 81 unidentifiable *Peromyscus spp.* from analyses. We also captured a number of species that we did not use in our analyses because of low capture numbers or inability to individually mark animals. These captures were 208

shrews (*Sorex* spp.), 8 shrew moles (*Neurotrichus gibbsii*), 2 Pacific jumping mice (*Zapus trinotatus*), 1 long-tailed vole (*Microtus longicaudus*), 1 flying squirrel (*Glaucomys sabrinus*), and 1 dark-eyed junco (*Junco hyemalis*). Of our species of interest, we captured 162 individuals in 2016 and 543 individuals in 2017. This dramatic increase was predominantly driven by *Peromyscus* spp. (88 captures in 2016, 426 captures in 2017). A conifer mast event occurred in Mt. Rainier National Park in 2016 (J. Hille Ris Lambers, pers. comm.), which is a likely explanation for the boom in *Peromyscus* spp. the following summer.

Principal Components Analysis

The first understory principal component was associated with reduced herbaceous cover and increased woody debris. The second understory principal component was associated with increased shrub and seedling cover. Cumulatively, the first two understory principal components explained 64% of the variation in the data (Table 1.1). The first overstory principal component was associated with stands of small diameter, high density trees with low Douglas fir basal area. The second overstory principal component was associated with stands of low total basal area, low true fir basal area, and high deciduous species basal area. Cumulatively the first two overstory principal components explained 57% of the variation in the data (Table 1.2).

Table 1.1. Variable loadings for the first two principle components from a principal component analysis of understory habitat variables.

Habitat variable	Understory principal component 1 (UPC1)	Understory principal component 2 (UPC2)
% herbaceous cover	-0.598	-0.289
% berry cover	-0.467	-0.328
% seedling cover	-0.173	0.717
% woody debris cover	0.507	0.000
% shrub cover	-0.371	0.543
Eigenvalue	1.92	1.32
% Variance Explained	0.38	0.26

Table 1.2. Variable loadings for the first two principle components from a principal component analysis of overstory habitat variables.

Habitat variable	Overstory principal component 1 (OPC1)	Overstory principal component 2 (OPC2)
Tree diameter	-0.493	-0.213
Total basal area	-0.208	-0.541
Douglas fir basal area	-0.441	0.098
Stem density	0.431	-0.134
Percent dead	-0.343	-0.207
True fir basal area	0.184	-0.647
Hemlock basal area	0.347	0.091
Deciduous basal area	-0.247	0.406
Eigenvalue	2.75	1.75
% Variance Explained	0.34	0.22

Prey Habitat Selection

Model selection failed to identify a clear top model. All 64 models had a ΔAICc less than 10, and 35 models had a ΔAICc less than 2 (Table 1.3). Based on parameter importance (PI) calculations, year was the most important variable (PI = 0.61), followed by the first overstory principal component (PI = 0.50) and the second understory principal component (PI = 0.50; Table 1.4). All parameters had importance values greater than 0.3, suggesting that all parameters were important in determining prey community. Our final NMDS ordination had three dimensions, a stress value of 0.114, and a non-metric r-squared of 0.987 between the distance matrix and ordination distances, suggesting good fit (Clarke 1993). Visualization of the NMDS revealed that old and young stands had distinct mammalian prey communities, whereas middle-aged forests overlapped with both young and old stands (Figure 1.3). The prey community in old stands was characterized by high abundance of red-backed voles, Keen's mice, and Townsend's chipmunks and low abundance of Oregon voles, deer mice, mountain beavers, and snowshoe hares. Middle-aged stands had high squirrel abundance, moderate snowshoe hare abundance, and

low small mammal abundance. Young stands had high abundance of mountain beavers, Oregon voles, and deer mice, moderate abundance of snowshoe hares, and low abundance of squirrels, red-backed voles, Keen's mice, and Townsend's chipmunks.

All four habitat principal components related to the mammalian prey community. Sites with high density of small diameter trees had higher abundance of snowshoe hares and chipmunks, and lower abundance of Oregon voles. Sites with low total basal area and high basal area of deciduous trees had higher abundance of snowshoe hares, mountain beavers, and Oregon voles and lower abundance of red-backed voles. Sites with low herbaceous cover and high woody debris had higher abundance of snowshoe hares and lower abundance of Oregon voles, mountain beavers, and deer mice. Sites with high seedling and shrub cover had higher abundance of snowshoe hares and lower abundance of Oregon voles and deer mice (Table 1.5). Neither prey richness ($F_{2,18} = 0.328, p = 0.72$) nor diversity ($F_{2,18} = 1.34, p = 0.29$) were affected by forest age class (Figure 1.4).

Table 1.3. The top five permutational multivariate analysis of variance models for mammalian prey community at 21 sites in the South Cascade Mountains of Washington. Models were ranked by Akaike Information Criterion corrected for small sample sizes.

Model	AICc	Δ AICc	R^2
Overstory PC1 + age class + year	-36.45	0.00	0.48
Overstory PC1 + year	-36.38	0.07	0.30
Overstory PC1 + Overstory PC2 + year	-36.38	0.08	0.39
Overstory PC2 + Understory PC2 + year	-36.37	0.08	0.39
Understory PC2 + year	-36.26	0.19	0.29

PC = principal component axis

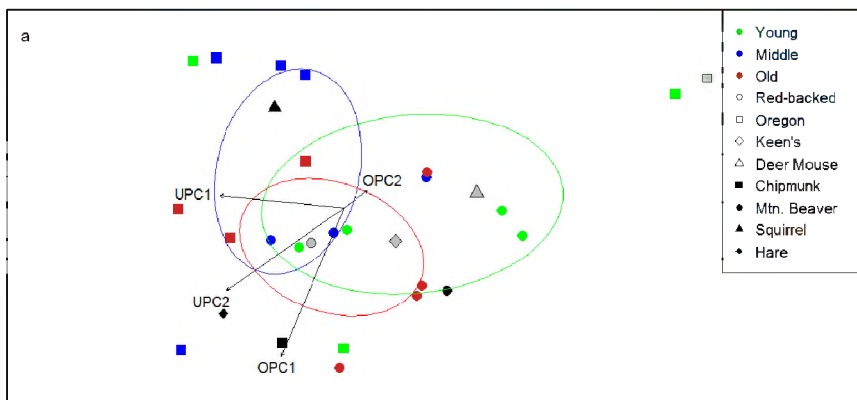
Table 1.4. Parameter importance of variables included in mammalian prey community permutational multivariate analysis of variance. Importance values based on Akaike Information Criterion corrected for small sample sizes (Burnham and Anderson 2002).

Parameter	Importance
Overstory PC1	0.5026
Overstory PC2	0.3903
Understory PC1	0.4138
Understory PC2	0.5049
Class	0.3334
Year	0.6143

Table 1.5. Response of small mammal species to overstory and understory habitat conditions based on interpretation of non-metric multidimensional scaling. “+” indicates an increase in abundance, “-“ indicates a decrease in abundance, and “0” indicates no clear response.

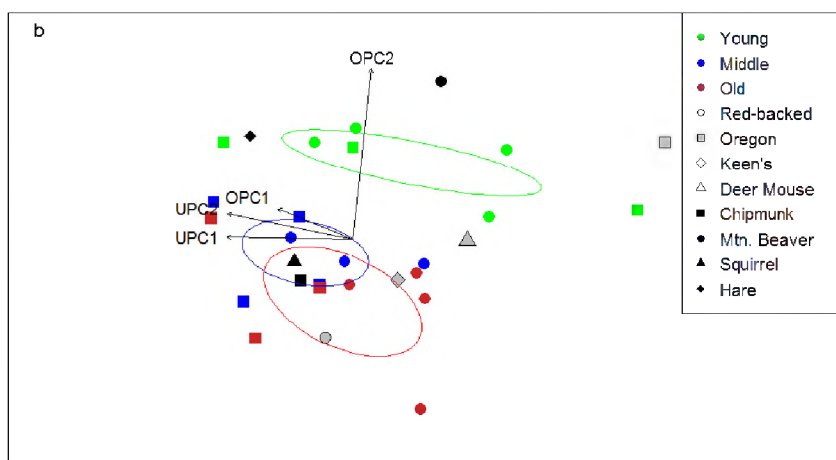
Species	OPC1: Small diameter, dense trees	OPC2: Low total basal area, high deciduous basal area	UPC1: Low herbaceous cover, high woody debris	UPC2: High shrub cover, high seedling cover
Snowshoe hares	+	+	+	+
Mountain beavers	+	+	-	0
Squirrels	-	0	+	0
Keen's mice	0	-	-	0
Deer mice	0	0	-	-
Oregon voles	-	+	-	-
Red-backed voles	0	-	0	0
Townsend's chipmunk	+	-	+	+

NMDS axis 2



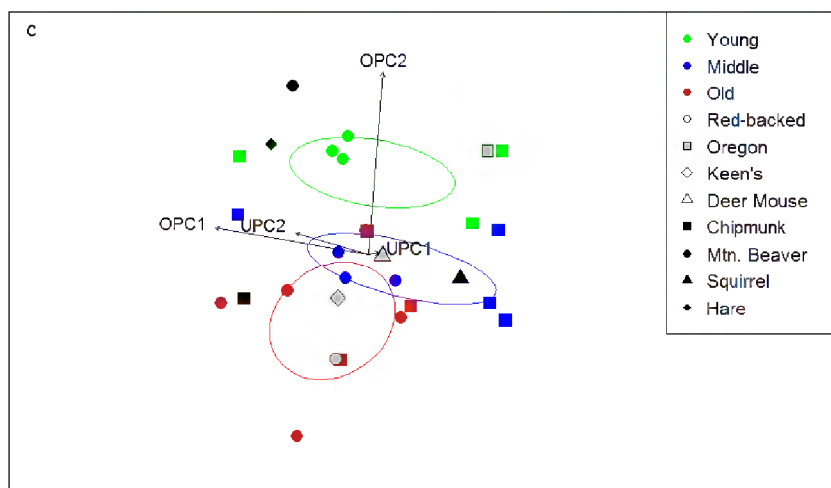
NMDS axis 1

NMDS axis 3



NMDS axis 1

NMDS axis 3



NMDS axis 2

Figure 1.3. Non-metric multidimensional scaling ordination (NMDS) of mammalian prey community plotted showing both site scores and prey group scores for 21 sites in the South Cascades of Washington. Plot “a” shows the first and second ordination axes, plot “b” shows the first and third, and plot “c” shows the second and third axes. Site points are squares for summer 2016 and circles for summer 2017. Arrows indicate correlation between the overstory and understory principal components and the ordination axes. Ellipses show the 95% confidence ellipse for the centroid of each age class.

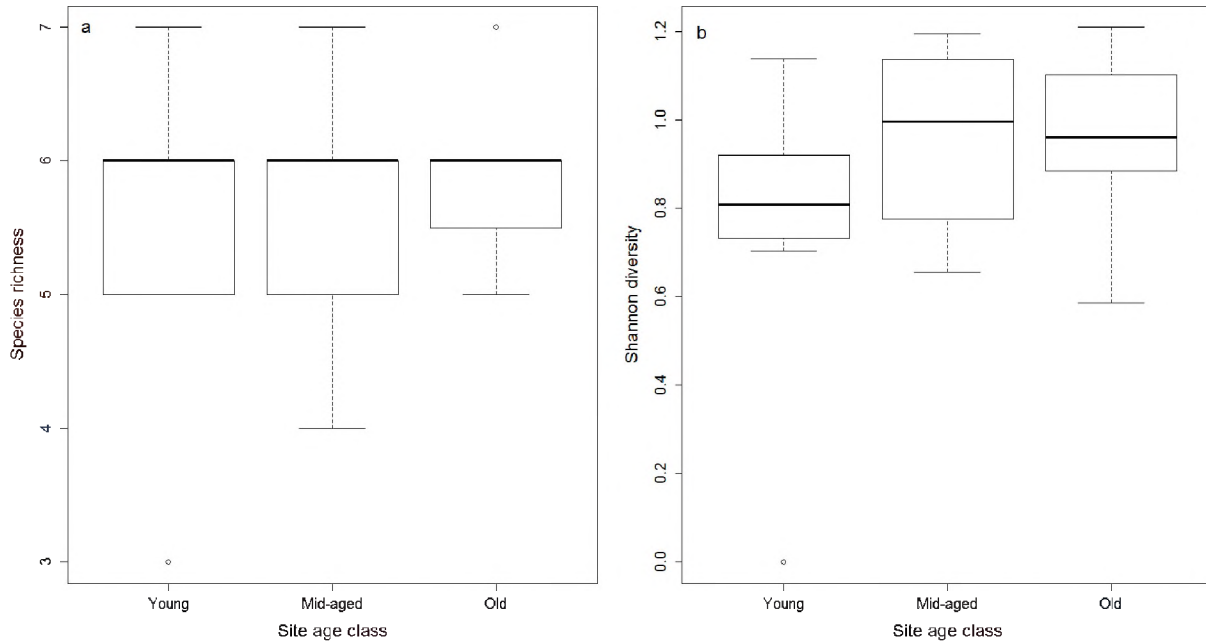


Figure 1.4. Boxplots of (a) species richness and (b) small mammal diversity at 21 sites in the South Cascades of Washington.

DISCUSSION

Our analyses reveal equally diverse, yet unique mammalian prey communities across a range of forest types in the South Cascades of Washington. While mature forests had high abundance of small mammal species, larger prey species such as squirrels, snowshoe hares, and mountain beavers tended to be more abundant in middle-aged to younger forests. Small and medium sized mammals also responded to understory vegetation conditions, with mice, voles, and mountain beavers being most common at sites with high herbaceous cover, while snowshoe hares, squirrels, and chipmunks preferred sites with high woody debris and shrub cover. Fishers

consume a wide variety of prey species (Martin 1994, Zielinski et al. 1999), and providing abundant and diverse prey will require maintaining forest mosaics that maximize habitat and prey diversity, while meeting the habitat needs of fishers.

The small rodent community in our study area was dominated by Keen's mice, with red-backed voles and chipmunks also common. These three species were all positively associated with older forests, and small rodent abundance was highest in older stands. All three of these species have been identified as important prey items for fishers (Zielinski et al. 1999, Weir et al. 2005). However, increased prevalence of small rodents in the diet of fishers appears to be related to an absence of larger prey items, and in areas where snowshoe hares or porcupines are abundant, small rodents play a smaller role in the diet of fishers (Martin 1994, Zielinski et al. 1999, Weir et al. 2005). Therefore, while small rodents are abundant in older stands, fishers in our study area may rely on younger stand to provide their preferred prey.

Previous diet research has identified snowshoe hares and mountain beavers as major prey items for fishers (Lewis and Hayes 2004, Weir et al. 2005, Bowman et al. 2006, Pace and Prugh, unpublished data). These results suggest that reintroduced fishers in the South Cascades of Washington may rely on middle-aged or young stands to provide sufficient prey. Along with knowledge that fishers also rely on complex forest structures for den and rest sites (Weir et al. 2005, Zielinski and Gray 2018), our results indicate that heterogeneous forest types provide necessary resources for fishers in the Pacific Northwest.

A feasibility assessment for the reintroduction of fishers to Washington identified snowshoe hares and mountain beavers as probable important prey items, but did not evaluate distributions of these prey items within the reintroduction areas (Lewis and Hayes 2004). Initial diet analysis of fishers released onto the Olympic peninsula confirmed that snowshoe hares and

mountain beavers were key prey items (Pace and Prugh, unpublished data). While conducting prey surveys prior to the reintroduction would have been ideal for selecting release locations, our post-release prey surveys will improve understanding of fisher habitat selection by providing a more complete understanding of prey availability across forest types.

Snowshoe hares are one of the most important prey items for fishers throughout their range (Powell 1993, Weir et al. 2005, Bowman et al. 2006), and while we documented snowshoe hares in forest of all age classes, they were most abundant in young and middle aged stands. Snowshoe hares also preferred stands with high stem density of small diameter trees, as well as shrubby understories. While these conditions may be more prominent in younger stands, they can occur in forests of any age, as many old stands have patches of dense understory cover. The range of snowshoe hares in the Pacific Northwest matches the historical range of old growth Douglas fir forests (Powell 1993), and we documented snowshoe hares in these habitats. But, in other regions, snowshoe hares are strongly associated with conifer stands with high stem density (Lewis et al. 2011, Cheng et al. 2015). Our data agree with past research in that snowshoe hares prefer stands of thick, small trees. This preference suggests that fishers preferred prey may use forests types distinct from preferred forests of fishers. Different preferences of fishers and their prey highlights the importance of assessing all aspects of habitat quality prior to reintroduction efforts.

Mountain beavers were strongly associated with young stands in our study system and we did not detect mountain beavers in a stand >120 years old. Mountain beavers prefer young, moist, regenerating forests where there is abundant herbaceous vegetation and saplings (Hacker and Coblentz 1993, Arjo et al. 2007). This pattern results in mountain beavers being most

abundant in heavily managed forests where clearcuts and open patches are common (Arjo et al. 2007).

The habitat selection patterns we documented for snowshoe hares and mountain beavers were distinct from known habitat selection patterns of fishers (Powell 1993, Raley et al. 2012, Sauder and Rachlow 2014). These opposed patterns of habitat selection between fishers and two important prey items indicate a possible tradeoff for fishers between habitats that provide den sites and protection from predators and habitats that provide prey. This tradeoff likely affects females more strongly because of their stronger need for denning sites and increased threat from predation (Zielinski et al. 2004, Wengert et al. 2014). Females are particularly important to the success of fisher populations, and managers should be aware of this tradeoff while planning reintroductions (Lewis 2013).

Our findings could help to inform forestry practices that facilitate the recovery and expansion of fishers in Washington and beyond. The maintenance of mosaic habitats, with remnant old forests interspersed with harvested and thinned stands, will likely meet the forest structure and prey needs of fishers. Thinning practices that maintain large trees and allow for the growth of dense understory may also create optimal habitat for fishers. Legacy trees can provide the structure necessary for den and rest sites for fishers, while thickets of regenerating young trees can provide the cover preferred by snowshoe hares. Canopy cover has been identified as a key component of fisher habitat throughout their range (Powell 1993, Sauder and Rachlow 2014), and creating hare habitat within closed canopy forests will likely require selective harvest approaches.

While snowshoe hares and mountain beavers may be important prey items in our study area, fishers have diverse diets and rely on a variety of mammalian prey (Martin 1994, Zielinski

and Duncan 2004, Weir et al. 2005). We also witnessed large temporal variation in prey availability, suggesting that maintaining a diverse prey community may be important for success of fishers in the West. Fisher populations fluctuate with prey populations (Bowman et al. 2006, Jensen et al. 2012), and these fluctuations could lead to the failure of a small, reintroduced population. Prey diversity increases the stability of total prey biomass through time (Doak et al. 1998, Tilman et al. 1998). We observed equal prey diversity across stands of different ages; however, prey communities were distinct between young and old stands. While snowshoe hares and mountain beavers were abundant in young stands, red-backed voles and Keen's mice, two other common prey items (Weir et al. 2005), were most abundant in older stands. Therefore, maintaining diverse habitats that provide diverse prey communities will be important for fishers in the Pacific Northwest.

Our prey surveys can be used in developing management strategies for fishers in the Pacific Northwest. They also highlight the importance of assessing prey prior to reintroductions. Reintroductions are a common tool in wildlife conservation (Fischer and Lindenmayer 2000), and are likely to be more common with increasing pressures of habitat loss, climate change, and invasive species (Carter et al. 2017). We documented a disconnect between known habitat selection patterns of fishers and habitat selection of two preferred prey species. Lack of information on habitat quality, or releasing animals into low quality habitat are two common causes of reintroduction failure (Griffith et al. 1989, Cook et al. 2010b). Knowing about disconnects between prey and preferred habitats prior to reintroductions could allow managers to account for these tradeoffs in selection of reintroduction locations. However, many reintroductions occur with only knowledge about landscape features. If fishers were released into an area based solely on their needs for old forests with complex structure, availability of

preferred prey may not be sufficient in those locations, potentially leading to the failure of reintroduction efforts. We encourage conservation practitioners to assess all aspects of habitat quality prior to reintroductions to maximize the probability of success. While this may be challenging with limited resources, the cost of failed reintroductions can be much higher than the cost of prey surveys.

CHAPTER 3

Habitat Use and Species Interactions of Reintroduced Fishers in Washington

ABSTRACT Effective management of reintroduced species requires knowledge of the mechanisms underlying habitat use. Fishers (*Pekania pennanti*) are one of the most commonly reintroduced carnivores in North America, and a species of conservation concern in their western range. While habitat use and diet have been assessed, the relative importance of resource requirements and species interactions is unknown. We examined the relative importance of landscape features and species interactions in determining habitat use of a reintroduced population of fishers in the South Cascades of Washington. We used detections of prey and predators at 134 remote cameras stations, remotely sensed forest structure data, and telemetry locations of fishers in a resource selection function to assess relative importance of prey, predators, and forest structure in fisher habitat selection. We found that fishers select habitats based on forest conditions and prey availability, whereas bobcat and coyote presence did not affect their habitat selection. The probability of fisher use was greatest in older stands, in close proximity to recently disturbed stands, and in areas with moderate numbers of snowshoe hare (*Lepus americanus*) detections. Bobcat and snowshoe hare detections were positively correlated, suggesting that fishers may experience a food-safety tradeoff in our study system. Temporal patterns in photo detections indicate that fishers may mediate this danger by avoiding bobcats temporally. Our findings suggest that fishers in Washington prefer mosaic habitats of old and recently disturbed stands where they have access to resting structures and snowshoe hares. Forest managers should seek to maintain and create these habitats to accelerate fisher recovery, and future reintroductions should target these areas to promote success. Our results also highlight the

importance of assessing prey availability and potential for competition and predation prior to reintroduction efforts, as fishers responded both these factors in either space or time.

INTRODUCTION

Wildlife translocations are becoming an increasingly common tool in wildlife conservation (Tear et al. 1993, Cook et al. 2010a, White et al. 2015). However, success of these programs is variable, and many reintroductions fail to establish viable populations (Griffith et al. 1989, Fischer and Lindenmayer 2000, White et al. 2015). One of the most important factors in determining reintroduction success is habitat quality of the reintroduction locations (Wolf et al. 1998, Cochran-Biederman et al. 2015). Habitat quality is determined by the resource requirements of a species, and is influenced by both landscape features and species interactions (Hutchinson 1957, Soberón 2007). Understanding the resource requirements of a species is integral during species reintroductions, where establishing viable populations from a small initial population requires proper site selection and future management (IUCN SSC 2013).

Selecting locations for reintroductions relies on understanding the habitat features that a species selects for, and the biological interactions that drive this selection (Case and Gilpin 1974, Creel and Creel 1996, Sergio and Hiraldo 2008, Périquet et al. 2015, Swanson et al. 2016). While evaluating some aspects of habitat quality is common in reintroductions, many factors interact to influence habitat quality. Landscape features such as vegetation, topography, and climate are most frequently considered when planning reintroductions (Seddon et al. 2007, Cochran-Biederman et al. 2015), likely because of the availability of these broad-scale data through remote sensing. However, species interactions are also integral to reintroduction success, and are less frequently assessed prior to reintroductions (Cook et al. 2010a, Fisher et al. 2014). Competition and predation influence all species, and can impact the success of reintroduction

programs (Griffin et al. 2000, Cook et al. 2010a, Spurgeon et al. 2015). For carnivores, prey availability is also integral to habitat quality, and therefore reintroduction success (Fisher et al. 2014, Spurgeon et al. 2015). Many reintroduction programs assume that competition and predation from other species will be low enough for the reintroduction to succeed, and that prey availability is sufficient in what is otherwise deemed high quality habitat. Both landscape features and species interactions influence success of reintroductions, but the relative importance of these factors is inconsistent between species and requires further investigation (Griffith et al. 1989, Short et al. 1992, Jachowski et al. 2011, Mundahl et al. 2012). Limited assessment of habitat quality is often related to limited time and funds to conduct assessments. Understanding what factors influence habitat quality for a reintroduced species will allow managers to focus on factors that matter most.

While assessing landscape features and species interactions prior to reintroductions is ideal, examining post-release habitat selection of reintroduced animals can provide insights into the relative importance of these factors and provide information for future reintroduction efforts (Sarrazin and Barbault 1996). Here, we examined how forest structure, prey availability, and carnivore distributions influenced habitat selection of a reintroduced population of fishers (*Pekania pennanti*) in the South Cascades of Washington. Fishers range across the northern forests of North America in habitats that provide complex structure (Powell 1993, Lewis et al. 2016). Particularly in the Pacific Northwest, fishers have been considered old growth specialists that rely on large diameter trees for den and rest sites. Trapping and logging in the early 20th century led to a major range contraction of fishers (Powell 1993, Lewis et al. 2012). Regulations and trapping bans resulted in recovery of fishers across much of their range, but populations in California, Oregon, and Washington are still of conservation concern (Powell 1993, Lewis et al.

2012, Lapoint et al. 2015). Many reintroductions have been attempted to assist fisher recovery, but these attempts have been more successful in the East than in the West (Lewis et al. 2012), and remnant populations in the West have not expanded following trapping prohibitions and regulations, as they have in the East (Powell 1993, Gabriel et al. 2015). Examining the importance of forest structure, prey, and predators in fisher habitat selection can guide future reintroductions on which features should be emphasized in reintroduction planning, and guide land managers on how to promote population growth and expansion of fishers.

Competition and predation from larger carnivores may contribute to the lower success of fisher conservation activities in their western range (Wengert et al. 2014, Lapoint et al. 2015). Common predators of fishers include bobcats (*Lynx rufus*), cougars (*Puma concolor*), and coyotes (*Canis latrans*), and the proportion of mortalities attributed to predation is higher in western populations than eastern populations (Koen et al. 2007, Wengert et al. 2014, Gabriel et al. 2015, Lapoint et al. 2015). Fishers in the West coexist with a larger carnivore community than those in the East (Lapoint et al. 2015). Fisher habitat-suitability models have incorporated the probability of bobcat presence prior to a reintroduction (Halsey et al. 2015), however, to our knowledge, no one has attempted to document the influence of predators on fisher habitat selection.

Additionally, human influences may have altered prey and predator communities, limiting expansion of fishers in the West into their historical range. Fishers have been absent from our study area for decades, and habitats and communities have changed in this time. Small and medium-size mammals are an important prey source for fishers throughout their range (Zielinski et al. 1999, Van Why and Giuliano 2001, Weir et al. 2005), and prey communities are influenced by logging and forest management practices (Carey and Johnson 1995, Carey 2000,

Griffin and Mills 2007). Logging and land conversion may have also increased the presence of bobcats and coyotes in historical fisher habitat, increasing competition for prey resources (Spencer et al. 2015, Sweitzer et al. 2015). Snowshoe hares (*Lepus americanus*) can be a particularly important prey item for fishers where they occur sympatrically (Weir et al. 2005, Bowman et al. 2006) and are influenced by forest disturbance (Griffin and Mills 2007, Cheng et al. 2015). Hares are also common prey of bobcats and coyotes, potentially leading to competition (Dibello et al. 1990, Witczuk 2009).

Preliminary analyses indicated that hares are a major component of the diet of fishers on the Olympic Peninsula of Washington (Pace and Prugh, unpublished data). It is often hypothesized that fisher habitat selection is related to prey availability (Buskirk and Powell 1994, Raley et al. 2012, Sauder and Rachlow 2015), but few studies have directly assessed this relationship (Arthur et al. 1989), and it has never been assessed in the fisher's western range. Fisher habitat use has predominantly been examined with respect to forest structure (Raley et al. 2012), particularly at den and rest sites (Zielinski et al. 2004, Weir et al. 2012, Zhao et al. 2012, Aubry et al. 2013). Lewis et al. (2016) found that female fishers on the Olympic Peninsula selected for unmanaged mid-seral forests and moderate elevations while males did not show strong selective patterns. However, it was not evaluated whether fishers were selecting for these habitat features alone or for associated prey and predator densities.

Fishers were reintroduced to the South Cascades of Washington from December 2015 to February 2017 as part of a larger fisher recovery program in Washington State (Lewis et al. 2017). We used remote cameras and aerial telemetry to quantify the distribution of species recognized as prey and predators of fishers on the landscape, and we then used fisher location data to develop a resource selection function (RSF) that incorporated both forest-cover and

species interaction covariates to understand how fishers responded to forest-cover characteristics, prey availability, and the carnivore community. We expected that fishers would select for older forests, areas with high abundance of snowshoe hares, and areas with low abundance of bobcats and coyotes. Further, due to potential competition with bobcats and coyotes for prey, we expected to observe distinct temporal activity patterns between fishers and bobcats and coyotes. We also examined differences in habitat selection patterns between the sexes, expecting males to be less sensitive to interactions with predators due to their larger size and relatively lower susceptibility to predation (Wengert et al. 2014).

STUDY AREA

Our study area was a 10000 km² region of the South Cascades of Washington comprised of Gifford Pinchot National Forest (6100 km²), Mt. Rainier National Park (1000 km²), Washington Department of Natural Resources land (1000 km²) and surrounding private lands (~1900 km²). This area is dominated by conifer forests ranging from young, intensively managed stands to unmanaged, old growth forests. Dominant tree species included Douglas fir (*Pseudotsuga menziesii*), silver fir (*Abies amabilis*), noble fir (*Abies procera*), and Western hemlock (*Tsuga heterophylla*). Dominant understory plants included Oregon grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), blueberry (*Vaccinium spp.*), salmonberry (*Rubus spectabilis*) and a number of fern species. The elevation ranges from 37 to 4392 m with a mean of 964 m. The elevation of our study sites ranged from 417 to 1491 m with a mean of 921 m. The mean July and January temperatures were 25.8° and -1.5° C and average precipitation was 140 cm (67 cm snowfall) in the town of Packwood, Washington near the center of our study area (Western Regional Climate Center 2016, <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?wa6262>).

METHODS

Fisher Reintroduction

From December 2015 to February 2017, the Washington Department of Fish and Wildlife (WDFW), National Park Service, and Conservation Northwest released 69 fishers into the study area from a source population in central British Columbia (Lewis et al. 2017). Each fisher was equipped with a very high frequency (VHF) radio-transmitter (Holohil AI-2HM; Carp Ontario K0A1L0, Canada) to allow biologists to monitor the locations, movements, and survival of released fishers. WDFW and partners tracked released fishers via aerial telemetry approximately once per week from December 2015 through January 2018, for a total of 73 telemetry flights. These flights and limited ground telemetry produced 793 locations. We removed all locations less than 1 month post-release to reduce the influence of initial exploratory behavior on our analyses. We also removed all locations determined to be low accuracy by the pilot and observers. This screening resulted in a total of 527 usable locations from 63 fishers (37 females, 26 males).

Camera Trapping Site Selection

We used the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA; <http://lemma.forestry.oregonstate.edu>) dataset for site selection and for large-scale forest structure data. The LEMMA data was produced using a gradient nearest neighbor approach. Multivariate relationships between satellite imagery, environmental variables and field plot data were used to produce a 30 m resolution raster of forest structure. We used five forest structure variables from these data: age, stand height, canopy cover, basal area, and quadratic mean diameter of dominant trees. Based on ground plot data, validation of the LEMMA data indicated

that these variables had a mean correlation of 0.75 (range: 0.72 – 0.77) with true values

(<http://lemma.forestry.oregonstate.edu>).

We placed remote cameras at locations within suitable fisher habitat that spanned a gradient of management intensity. Camera sites ranged from plantation style industrial forests to unmanaged old growth forest. Using the LEMMA data, we calculated the average age of 1 km² hexagons across our study area and categorized hexagons as young (<110 years), middle-aged (110-180 years), and old (>180 years) stands. We then categorized hexagons as suitable fisher habitat if the majority of the hexagon contained forests with >60% canopy cover and >29 cm average quadratic mean diameter of dominant trees (Halsey et al. 2015). We required that five of six surrounding hexagons be the same age class and suitable fisher habitat (i.e. continuous 6 km² area). We randomly selected hexagons in each age category that met these criteria for monitoring via remote cameras ($n = 134$ camera stations total, 45 in young, 50 in middle-aged, and 39 in old stands).

From August 2016 through September 2017, we placed remote cameras within 300 m of each hexagon's center, with exact locations selected to increase likelihood of detections. For example, we placed cameras along game trails if we found any within the 300 m search area. Each location was sampled for a six-week period, with some variation due to logistics of access and camera malfunction. Each station consisted of one Bushnell Aggressor trail camera (Model #119776C, Bushnell Outdoor Products, Overland Park, KS, USA), a chicken leg, and a scent lure (Caven's Gusto, Minnesota Trapline Products, Pennock, MN, USA). We placed cameras on trees at approximately 0.5 m from the ground. We attached bait and lure to a second tree between 2 and 4 m away from the camera at the same height. We placed bait north of cameras (with few exceptions) to minimize sun glare in photos (Figure 2.1). We set corrugated plastic hair snares at

99 camera stations (38 young, 36 middle-aged, and 25 old; Jenkins and Happe 2015). We tested the effect of hair snare presence on the number of detections of hares, bobcats, and coyotes using negative binomial regression. Hair snare presence did not affect detection of any species ($p > 0.4$ for all species). We set cameras to take a three-picture burst with each motion detection and a delay of five seconds between successive triggers. We visited cameras after approximately three weeks to check batteries, replace SD memory cards, and refresh bait and lure. We used cameras to document the number and time of detections of snowshoe hares, bobcats, and coyotes as a measure of relative activity. We selected to focus on these species because of the importance of snowshoe hares in the fisher diet (Weir et al. 2005), and because of documented predation of fishers by bobcats and coyotes (Wengert et al. 2014).

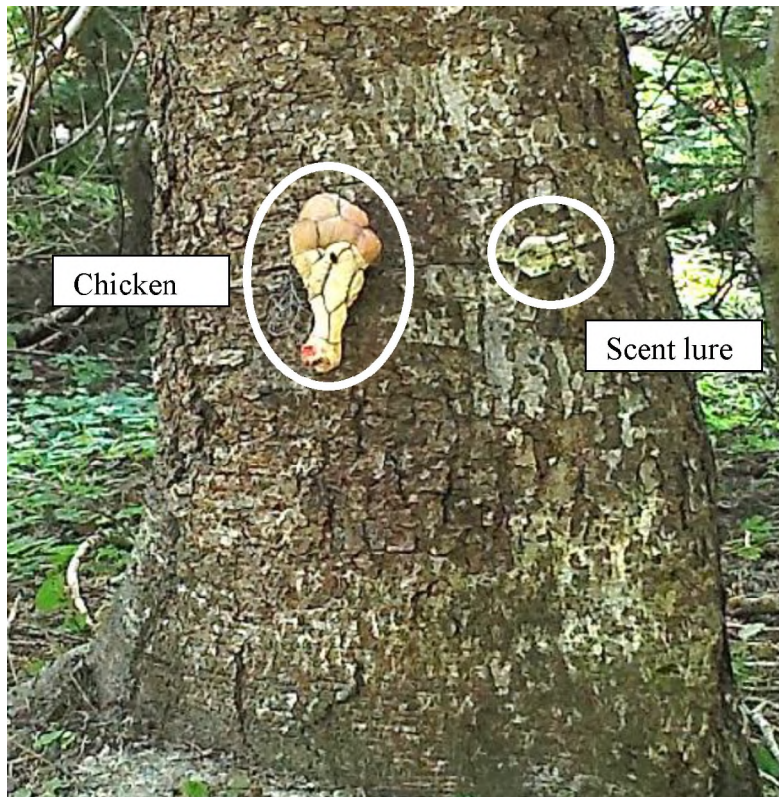


Figure 2.1. Camera trap photo showing bait and lure set up. Scent lure was poured on moss and attached to the tree in a small piece of corrugated plastic to limit washout by rain.

Statistical Analysis

Forest and Topography Covariates.— To evaluate habitat relationships of prey, predators, and fishers, we used forest structure and landscape data available from LEMMA and the United States Geological Survey (<https://nationalmap.gov/>), and conducted analyses using ArcGIS (Environmental Systems Research Institute, Inc., Redlands, CA, USA). We created a 250 m buffer around each camera location, fisher telemetry location, and randomly selected available location (see below for details) and used a custom zonal statistics tool for overlapping polygons in ArcMap 10.4 to extract the average age, basal area (BA), canopy cover (CC), stand height, and quadratic mean diameter of dominant and co-dominant trees (DBH) for each location. Because prey items known to be important to fishers are abundant in regenerating and young forests (Arjo et al. 2007, Cheng et al. 2015, Pace and Prugh, unpublished data), we also calculated the distance to the nearest recently disturbed stand for each point. We assigned points within recently disturbed stands a value of zero for distance to recently disturbed stand. We defined a recently disturbed stand as a stand <30 years old. We first used the “majority filter tool” in ArcMap to remove clusters of less than five pixels that were more likely to be relics of sampling error and not representative of actual recently disturbed stands. We also extracted the average elevation, slope, and aspect within the 250 m buffer of each location from a digital elevation model from the USGS National Elevation Database (National Elevation Dataset: <http://ned.usgs.gov/>). Finally, we calculated the distance from each location to the nearest linear feature (any road or trail), paved road, and unpaved road. Our full covariate set was: age, BA, CC, DBH, and height of overstory trees, elevation, slope, aspect, distance to linear feature, distance to unpaved road, distance to paved road, and distance to young stand. We scaled all variables by mean and standard deviation prior to analyses to be able to compare relative effect

sizes. We log transformed distance to paved and unpaved road prior to scaling due to highly skewed distributions. We included a quadratic term for slope and distance to recently disturbed stand to account for a possible non-linear responses to these variables (Table 2.1). We repeated analyses with a 1000 m buffer and results were consistent across scale.

Table 2.1. Description and range of unscaled values for habitat and landscape covariates used in hare, coyote, and bobcat detection models and fisher resource selection functions, including randomly chosen available points ($n = 10618$).

Source	Description	Units	Min	Max	Mean
LEMMA	Age of dominant trees	Years	0	404	104
LEMMA	Basal area of live trees >2.5cm dbh	m ² /ha	0	91	41
LEMMA	Canopy cover of all live trees	Percent	0	95	73
LEMMA	Quadratic mean diameter of dominant trees	cm	0	104	33
LEMMA	Average height of dominant trees	m	0	58	20
NED	Elevation	m	68	1719	861
NED	Slope	Degrees	0	44	15
NED	Aspect	Degrees from south	0	180	89
WDNR	Distance to nearest paved road	m	12	6264	1750
WDNR	Distance to nearest unpaved road	m	5	8853	483
WDNR	Distance to nearest road or trail	m	0	1636	206
LEMMA	Distance to nearest stand <30 years old	m	0	2271	261

LEMMA = Landscape Ecology, Modeling, Mapping, and Analysis data; NED = National Elevation Database; WDNR = Washington State Department of Natural Resources

Prey and Predator Modeling.— Due to the home range size of bobcats and coyotes (5 – 100 km²; Laundré and Keller 1984, Donovan et al. 2011, Melville et al. 2015) being large enough to encompass multiple camera stations (mean distance to nearest camera 2.7 km, range 0.8 to 12.7 km), the independence assumption was violated and therefore occupancy modeling was not appropriate. We used number of independent detections of hares, bobcats, and coyotes as a metric of relative use (Swanson et al. 2016, Rich et al. 2017). We defined independent detections as photos at least 60 minutes apart (Lucherini et al. 2009, de Satgé et al. 2017). We

used Timelapse2 (Greenberg and Godin 2015) to process photos and extract date, time, and species identification.

To create covariates for predators and prey to include in our fisher RSF (see below), we modeled the detections of hares, bobcats, and coyotes at cameras as a function of topographic and linear features using negative binomial regression in the R package “MASS” (Ripley et al. 2018). We used negative binomial regression due to overdispersion in the detection data. We did not include forest structure variables because 1) it would reduce problems with collinearity in the fisher model (see below); and 2) post-hoc evaluation revealed that top topography-only models were within two AICc of top models that included forest structure data, suggesting they were well supported. Therefore, the variables included in hare, bobcat, and coyote models were elevation, slope (including a quadratic effect), aspect, distance to paved road, distance to unpaved road, and distance to linear feature. Because of high correlation between distance to linear features and distance to unpaved roads, we initially tested single-variable models for each of these variables for each species and selected the best performing variable based on AICc to include in the full model set. Our response variable was the number of detections per 100 trap nights. We tested all possible combinations of these variables (64 models) and selected the top model for each species based on AICc. We did not conduct model averaging because of collinearity between variables, which can lead to biased parameter estimates through model averaging (Freckleton 2011). We assessed model fit using cross validation and tested for collinearity by calculating variance inflation factors (VIF) for all variables (Appendix 1). We used the top model for each species to map relative intensity of use by hares, bobcats, and coyotes across our study area.

Fisher Resource Selection Function.— We used the fisher telemetry data to model population level habitat selection of fishers with a used-available RSF (Johnson et al. 2006, McLoughlin et al. 2006, Duquette et al. 2017). We initially planned to use two-species occupancy models (Richmond et al. 2010), but insufficient fisher detections on cameras precluded this approach. The telemetry data also permitted us to examine sex differences in habitat selection. Used-available designs produce probabilities of use proportional to probability of habitat use from a used-unused design (Johnson et al. 2006). Because of limited data, we could not assess composition of established home ranges on the broader landscape. We instead assessed how the population utilized the landscape they were released into based on what was available. We compared habitat variables of fisher telemetry locations to available locations using mixed-effects logistic regression (Gillies et al. 2006). We included a random intercept for individual fishers to account for unbalanced samples of telemetry locations (Fattebert et al. 2015).

We used 10,000 randomly selected available locations to represent available habitats in our analysis. We selected the number of available locations by examining the mean and coefficient of variation (CV) of covariate values using 1000 iterations of different sample sizes and selecting the sample size above which means and CVs stabilized (Northrup et al. 2013). A sample of 10,000 locations is a commonly suggested threshold, as large samples of available points provide a better approximation of landscape availability (Lele and Keim 2006, Barbet-Massin et al. 2012, Northrup et al. 2013). As a measure of relative use by prey and predators, we estimated the predicted number of detections of snowshoe hares, bobcats, and coyotes at each used and available location based on top models described above for each species. Because we used predicted hare, bobcat, and coyote detections in the RSF, we limited telemetry and available

locations to those occurring within the range of habitat covariates that coincided with areas where we deployed camera stations. We also limited available points to be within the minimum convex polygon of fisher telemetry points (Aarts et al. 2008, Northrup et al. 2013). Out of 527 telemetry locations, we used 460 for the final analysis.

We used the forest structure variables (age, BA, CC, DBH, height), distance to recently disturbed stand, the quadratic effect of distance to recently disturbed stand, and prey and predator detections to evaluate fisher resource selection. Because of high correlations among forest structure variables (Appendix 1), we began with single variable models to identify the best forest structure covariate using AICc. Stand age was the best forest structure variable. We also included interactions between sex and all covariates to test for habitat selection differences between the sexes. Our final variable set was stand age, distance to recently disturbed stand, detections of snowshoe hares (linear and quadratic term), detections of bobcats, detections of coyotes, and an interaction between sex and each variable. We ran all possible models ($n = 486$) and tested for collinearity by calculating VIFs. We selected the top model with all parameter VIFs < 2 based on AICc. We tested model goodness-of-fit with k-fold cross validation (Boyce et al. 2002).

Temporal Overlap.— We assessed temporal overlap of activity of fishers, bobcats, and coyotes using the “overlap” package in R (Meredith and Ridout 2017). We first reduced the camera detection data to create independent detection events for each species as described above. We then extracted the time of day of each detection event and calculated a kernel density estimate of diel activity for each species. We then calculated $\hat{\Delta}_1$, a measure of activity overlap that ranges from 0-1, with a value of one indicating perfect overlap and a zero indicating no overlap (Ridout and Linkie 2009).

$$\hat{\Delta} = \int_0^1 \min\{\hat{f}(t), \hat{g}(t)\} dt \quad (\text{Eq 1})$$

where $\hat{f}(t)$ and $\hat{g}(t)$ are the estimated activity densities for two species. Ridout and Linkie (2009) found $\hat{\Delta}_1$ to perform better than other overlap measures with small sample sizes. High overlap suggests two species are active during the same times of day.

RESULTS

We deployed 134 camera stations for a total of 6016 trap nights. Cameras were deployed and functional for a mean duration of 45 days, with a range of 17 to 84 days due to malfunctions, displacement by wildlife, and limited winter access. We detected hares, bobcats, coyotes, and fishers at 62 (50% of cameras), 32 (24%), 30 (22%), and 12 (9%) cameras respectively. Forty-six cameras did not detect any of these species (Figure 2.2).

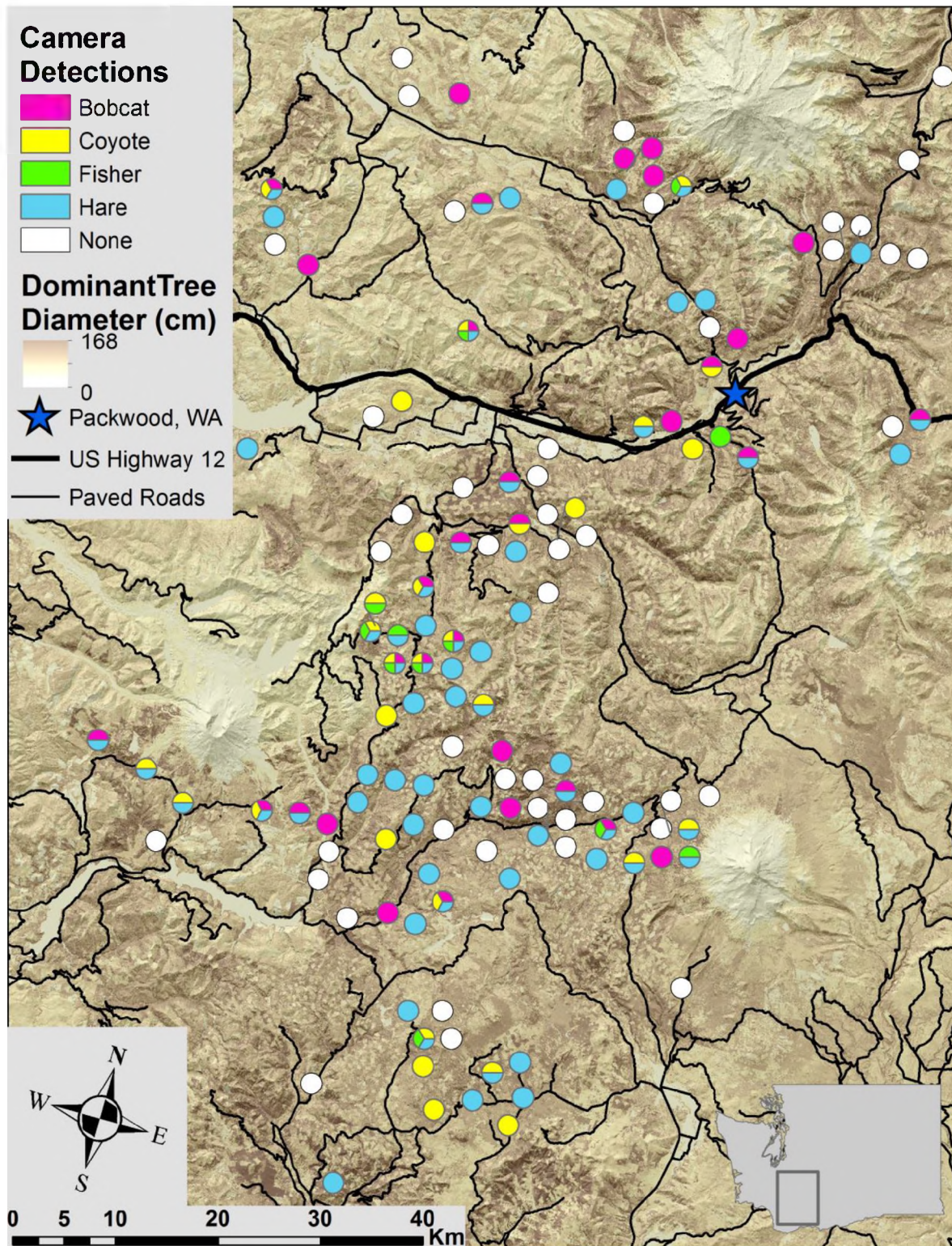


Figure 2.2. Camera locations and species detected for 134 camera stations in the South Cascades of Washington. Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017.

The top snowshoe hare detection model indicated hare detection rates increased at higher elevations, on northerly aspects, closer to unpaved roads, and closer to paved roads. Detection rates of bobcats increased on northerly aspects and closer to unpaved roads. Detection rates of coyotes increased on shallower slopes, closer to linear features, and closer to main roads (Table 2.2). All parameters in all top models had VIFs less than two suggesting collinearity was minimal.

Table 2.2. Parameter estimates, standard errors (SE), and p-values for the top negative binomial regression models for number of snowshoe hare, bobcat, and coyote detections from 134 camera locations in the South Cascades of Washington. Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017. All parameters on the log scale.

Species	Parameter	Estimate	SE	p
Hare detections	Intercept	1.43	0.2	<0.001
	Aspect	0.720	0.2	<0.001
	Elevation	0.827	0.26	0.001
	Dist. to unpaved road	-0.622	0.17	<0.001
	Dist. to paved road	0.349	0.21	0.098
Bobcat detections	Intercept	-0.227	0.23	0.321
	Aspect	0.655	0.24	0.007
	Dist. to unpaved road	-0.554	0.2	0.006
Coyote detections	Intercept	-0.988	0.29	<0.001
	Slope	-1.19	0.3	<0.001
	Dist. to linear feature	-0.878	0.39	0.024
	Dist. to paved road	-0.916	0.27	<0.001

Table 2.3. The top five negative binomial regression models for coyote, bobcat, and hare detections from 134 camera locations in the South Cascades of Washington. Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017. Models were ranked using Akaike Information Criterion corrected for small sample sizes (AICc).

Species	Model	AICc	Δ AICc	AICc Weight
Hare	Elevation + aspect + unpaved road + paved road	601.37	0	0.14
	Elevation + aspect + unpaved road	601.63	0.27	0.13
	Elevation + aspect + slope + unpaved road	602.14	0.78	0.1
	Elevation + aspect + slope + unpaved road + paved road	602.62	1.26	0.08
	Elevation + aspect + slope ² + unpaved road + paved road	603.17	1.81	0.06
Bobcat	Aspect + unpaved road	283.71	0	0.15
	Aspect + slope ² + unpaved Road	284.29	0.59	0.11
	Aspect + unpaved road + paved road	285.15	1.45	0.07
	Aspect + slope + unpaved road	285.39	1.69	0.06
	Elevation + aspect + unpaved road	285.43	1.73	0.06
Coyote	Slope + linear feature + paved road	280.97	0	0.33
	Elevation + slope + linear feature + paved road	281.77	0.8	0.22
	Slope + slope ² + linear feature + paved road	283.08	2.11	0.11
	Elevation + slope + slope ² + linear feature + paved road	283.73	2.76	0.08
	Slope + paved road	283.85	2.88	0.08

Stand age was the best forest structure variable for the fisher RSF. The top fisher RSF model included main effects of age and distance to recently disturbed stand, a quadratic effect of predicted snowshoe hare detections, and an interaction between sex and snowshoe hare detections. Both sexes selected for locations in older stands, locations closer to recently disturbed stands, and locations with moderate snowshoe hare detections. The interaction term suggested males showed weaker selection for snowshoe hares than females (Figure 2.3; Table 2.4). Hare detections and bobcat detections were positively correlated ($r = 0.58$, $p = <0.001$; Figure 2.4),

which resulted in variance inflation and precluded both variables being included in the same model. This correlation indicates a possible food-safety tradeoff. All other parameter combinations had VIFs less than two, suggesting collinearity was minimal. The model tested well in cross validation (Appendix 1; Spearman-rank correlation: $r_s = 0.88$, $p < 0.001$).

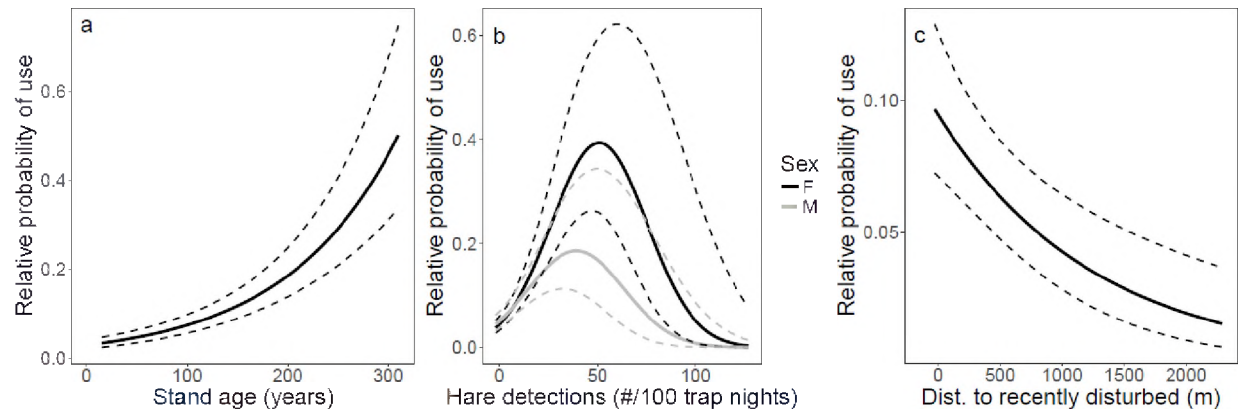


Figure 2.3. Predicted response curves from top resource selection function (RSF) for fishers. Plots show relative probability of use across the measured range of stand age (a), snowshoe hare detections (b) and distance to recently disturbed stand (c). The snowshoe hare plot shows the interactions with sex with females in black and males in grey. Dashed lines represent 95% confidence intervals on the prediction. Telemetry data used in the RSF were collected from January 2016 through January 2018 in the South Cascades of Washington.

Table 2.4. Parameter estimates and bootstrapped confidence intervals of top fisher resource selection function based on telemetry data collected from January 2016 through January 2018 in the South Cascades of Washington. Parameter estimates are on the logit scale.

Parameter	Estimate	SE	P
Intercept	-7.85	0.137	<0.001
Stand age	0.531	0.049	<0.001
Dist. to disturbed stand	-0.231	0.060	<0.001
Predicted hare detections (Females)	0.648	0.065	<0.001
Predicted hare detections (Males)	0.476	0.080	<0.001
Squared predicted hare detections	-0.064	0.012	<0.001

Table 2.5. The top five resource selection functions for fishers in the South Cascades of Washington based on telemetry data collected from January 2016 through January 2018. Models were ranked using Akaike Information Criterion corrected for small sample sizes (AICc).

Model	AICc	Δ AICc	AICc Weight
Age + dist. to disturbed + Sex:hare + hare ²	6982.69	0	0.26
Age + dist. to disturbed + Sex:hare + hare ² + coyote	6984.24	1.55	0.12
Sex:age + dist. to disturbed + Sex:hare + hare ²	6984.35	1.66	0.11
Age + Sex:dist. to disturbed + Sex:hare + hare ²	6984.54	1.85	0.10
Sex:age + dist. to disturbed + Sex:hare + hare ² + coyote	6985.90	3.21	0.05

Age = Stand age, dist. to disturbed = distance to recently disturbed stand, sex = sex of fisher, hare = snowshoe hare detections

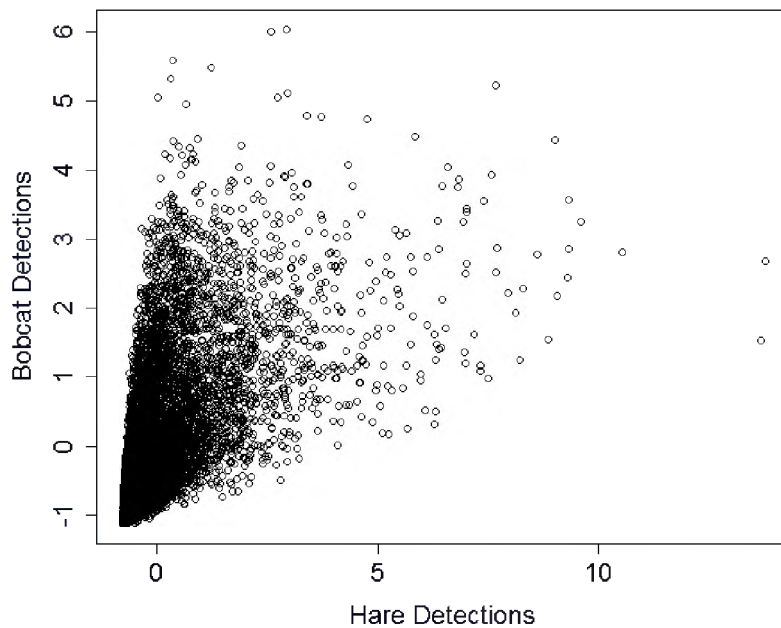


Figure 2.4. Scatter plot showing the expected number of snowshoe hare detections and the expected number of bobcat detections at used and available sites for the fisher resource selection function ($n = 10618$).

Fishers were predominantly diurnal with the highest activity from morning to midday.

Activity patterns of fishers contrasted both coyotes and bobcats which were predominantly nocturnal and crepuscular, respectively (Figure 2.5). Even with these activity peaks, all species showed low levels of activity throughout the day and night resulting in moderate to high overlap.

Fishers had lower overlap with both bobcats ($\hat{\Delta}_1=0.71$, 95%CI: 0.57 - 0.85) and coyotes ($\hat{\Delta}_1=0.74$, 95%CI: 0.61 - 0.86) than bobcats and coyotes had with each other ($\hat{\Delta}_1= 0.80$, 95%CI: 0.68 - 0.91), but not to a significant degree.

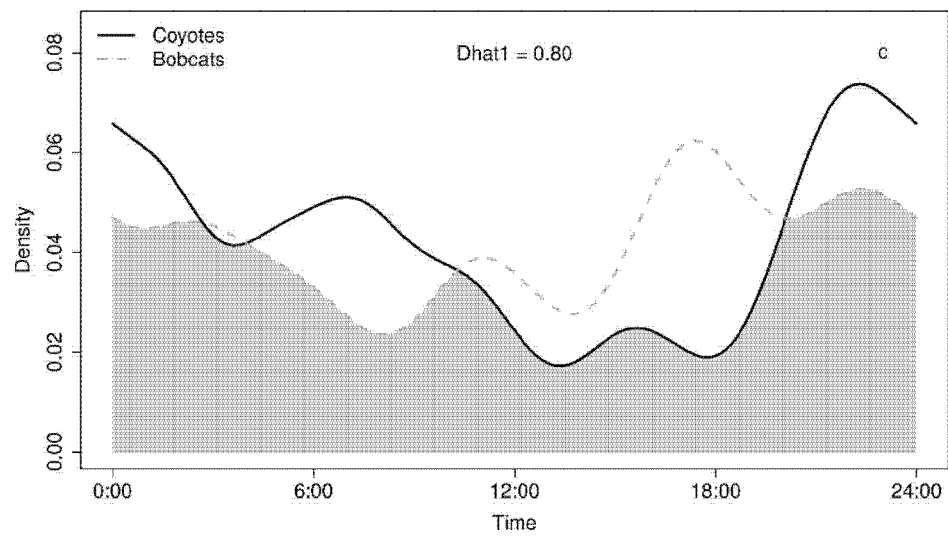
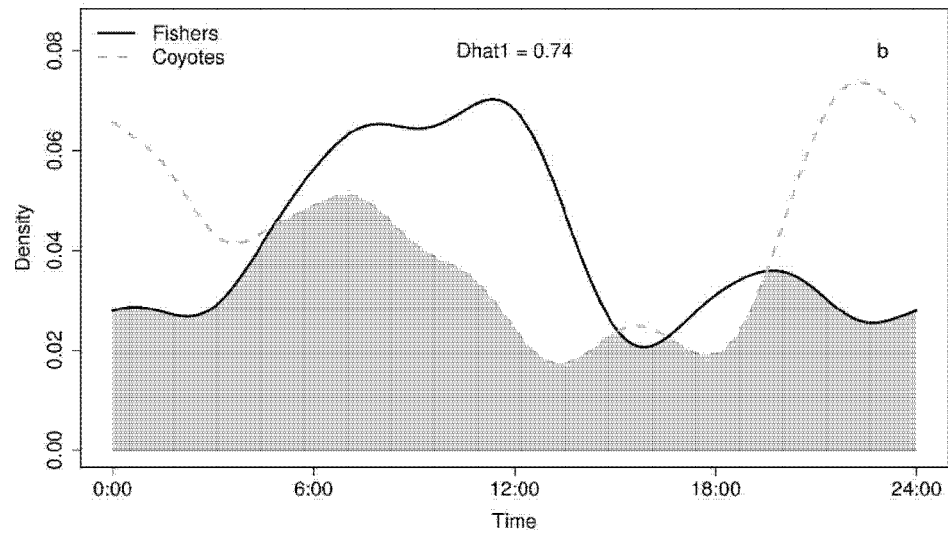
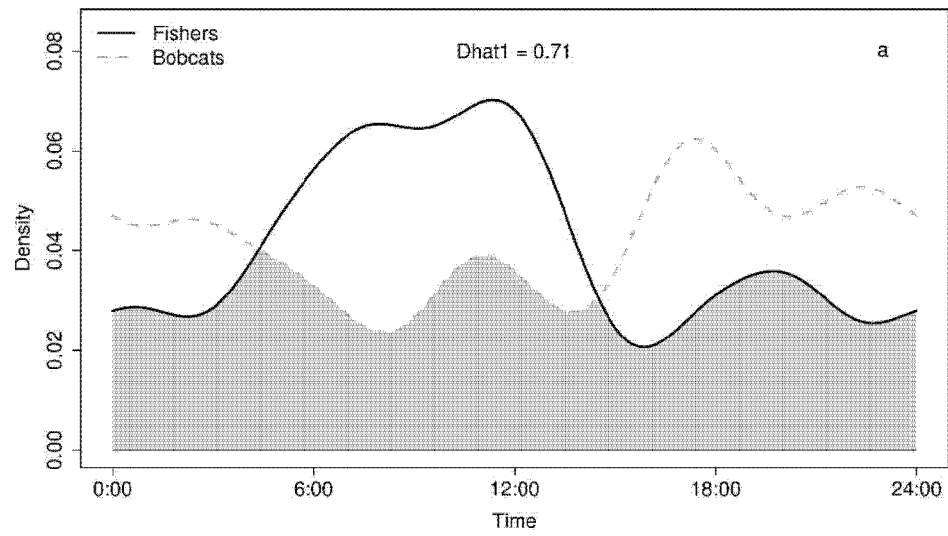


Figure 2.5. Diel activity overlap of fishers with bobcats (a), fishers with coyotes (b), and bobcats with coyotes (c) based on independent detection events at 134 camera locations in the South Cascades of Washington. Plots are kernel density estimates of activity and $\hat{\Delta}_1$ is a measure of activity overlap between species (Ridout and Linkie 2009). Each camera was deployed for approximately six weeks and camera trapping occurred between August 2016 and September 2017.

DISCUSSION

During reintroductions, evaluating habitat quality of the reintroduction area is vital to success, and interactions with other species are key determinants of habitat quality. However, many reintroductions fail to thoroughly evaluate species interactions when assessing feasibility of the project (Lewis and Hayes 2004, Callas and Figura 2008, Hiller 2015). We examined habitat selection of reintroduced fishers, which were released without assessment of prey availability or other competitors, and found that prey availability was a strong driver of habitat selection. We also document a possible food-safety tradeoff for fishers based on a positive correlation between camera detections of snowshoe hares and bobcats, and possible temporal avoidance of bobcats by fishers. Our findings highlight the importance of evaluating species interactions prior to reintroductions, even for a generalist predator such as fishers. Fishers responded to both prey and other carnivores, and evaluating these factors prior to release can inform selection of release locations and feasibility of reintroduction programs.

Additionally, our findings provide an understanding of habitat selection by reintroduced fishers that will be useful for future management. Our data reveal that fishers in our study area selected habitat based on both forest structure and prey availability but did not respond strongly to the presence of larger carnivores. Both females and males selected for older forests and moderate relative abundance of prey. While selecting for older stands, both sexes also preferred areas close to recently disturbed stands. These selection patterns are consistent with previous studies of fisher habitat selection in highlighting the importance of mature forests (Weir et al.

2012, Aubry et al. 2013, Sauder and Rachlow 2014), but also provide evidence for the importance of diverse, mosaic habitats for fishers in the South Cascade Mountains of Washington.

Selection by fishers for older stands is well documented and likely reflects a reliance on forest structure for den and rest sites (Lofroth et al. 2011, Raley et al. 2012, Aubry et al. 2013). Selection for proximity to edge and habitat diversity has been documented previously and has been hypothesized to relate to higher prey diversity in diverse habitats (Raley et al. 2012, Sauder and Rachlow 2015). We interpret this pattern as selection for proximity to prey, as snowshoe hare prefer young, dense stands (Lewis et al. 2011). A similar pattern has been observed in Idaho and on the Olympic peninsula, with fishers using forest habitat mosaics (Sauder and Rachlow 2015, Lewis et al. 2016). These selection patterns indicate that habitat diversity is important for fishers. Previous research identified fishers as specialists of mature forest that avoid habitats with low canopy cover, and particularly in the Pacific Northwest, fishers were considered old growth specialists (Aubry and Houston 1992, Powell 1993, Weir 2003). Our results add to growing evidence that fishers utilize forest habitat mosaics and unmanaged mid-seral forests more than previously thought (Raley et al. 2012, Sauder and Rachlow 2015, Lewis et al. 2016). Given current habitat conditions in the Pacific Northwest after the large scale loss of old growth forests in low and mid-elevation landscapes, mosaics of young and old forests appear to be important habitats for fishers in this system. Our results indicate that fishers prefer old forest, but that intermixing younger stands may increase habitat quality. Further assessment of the amount of old growth forest necessary for fisher persistence could improve habitat management and reintroduction planning in the future.

Selection for snowshoe hares, and the habitat selection differences between fishers and snowshoe hares, provides additional evidence that mosaic landscapes may be important for fisher conservation where snowshoe hares are an important prey item. Snowshoe hares prefer younger stands with high density, small trees (Lewis et al. 2011). This habitat is distinct from the habitats preferred by fishers, and selecting release sites based purely on known forest associations of fishers could have placed fishers in areas with insufficient prey. Stands of large diameter trees with complex structure adjacent to younger, denser stands may provide fishers protective cover and abundant prey. Fishers in our study area selected for national forest lands, which contain the highest diversity of forest types in our study area. While Gifford Pinchot National Forest (GPNF) accounted for 50% of our study area by area, 80% of fisher locations were within the national forest. Compared to private, state, and national park lands, GPNF is managed with an emphasis on mixed use, including recreation, conservation, and resource extraction. Clearcuts are nearly absent in the National Forest, but salvage logging, stewardship logging, and thinning projects create disturbances throughout the landscape (www.fs.usda.gov/detail/giffordpinchot/). These management practices follow the Northwest Forest Plan (NWFP; United States Department of Agriculture and United States Department of the Interior 1994), which was established to protect Spotted Owl (*Strix occidentalis*) habitat on federal lands. Adhering to the management strategies proposed in the NWFP likely maintains abundant, quality habitat for fishers within GPNF. Habitat mosaics in other ownerships may differ in composition and configuration compared to GPNF mosaics, resulting in lower quality fisher habitat. Compared to private and state timber land, where clearcut logging and tree plantations are common, and Mt. Rainier National Park, where disturbance is rare, Gifford Pinchot National Forest may provide the best landscape-scale habitat for fishers in the South Cascade Mountains of Washington.

Selection by fishers for moderate abundance of snowshoe hares supports the importance of assessing prey prior to reintroductions. While feasibility assessments often discuss prey availability, formal assessments are rare (Serfass et al. 1994, Apps 1995, Breitenmoser et al. 2001, Hiller 2015). Assessment of prey prior to reintroductions appears to be more common for specialist predators (Steury and Murray 2004, Jachowski et al. 2011, Licht et al. 2016), but response of fishers to a particular prey item indicates importance for generalist predators too. Evaluating prey prior to reintroductions is frequently recommended (Breitenmoser et al. 2001, IUCN SSC 2013), but in many cases, no or minimal assessment is done, basing habitat quality solely off of widely available remotely sensed and GIS data of landscape and vegetative features (Serfass et al. 1994, Apps 1995, Lewis and Hayes 2004).

Selection by fishers for moderate snowshoe hare abundance and avoidance of sites with the highest snowshoe hare abundance may be related to a food safety-tradeoff. While fishers did not show spatial avoidance of bobcats, bobcats were positively associated with snowshoe hares, meaning that sites with the most abundant food could also be the riskiest for fishers. Food-safety tradeoffs are common in ecology (Hammerschlag et al. 2010, Emerson and Brown 2015, Pomeroy and Lindström 2018), and this potential tradeoff highlights the challenges faced by mesopredators who compete for food with potential predators (Bischof et al. 2014). By selecting sites with moderate levels of prey availability, fishers may be responding to the risk of both competition and predation from bobcats. It may be that moderate abundances of snowshoe hares are sufficient to support fishers. Alternatively, it may be that fishers are selecting sites of moderate snowshoe hare abundance to minimize risk, and must supplement with increased consumption of other prey items.

Fishers may mediate the potential food-safety tradeoff through temporal avoidance of bobcats as well. While temporal overlap was moderate, our diel activity data showed predominantly diurnal activity patterns by fishers and predominantly nocturnal activity patterns by bobcats. Previous research on activity patterns by fishers has produced inconsistent results including nocturnal, crepuscular, and no clear activity patterns (Arthur and Krohn 1991, Powell 1993, Paragi et al. 1994, Weir and Corbould 2007). The diurnal activity peak of fishers in our study system may indicate temporal avoidance of bobcats, but a better understanding of typical fisher activity patterns, particularly in habitats without bobcats, would be needed to test this hypothesis. Food-safety tradeoffs could pose a significant risk to reintroduction efforts, particularly if reintroduced species are not familiar with local predators and do not have proper risk responses (Griffin et al. 2000). Evaluation of prey, predator and competitor distributions prior to reintroductions could identify the possibility of food-safety tradeoffs for reintroduced species, and identify specific locations where prey availability is high and predator or competitor abundance is not.

Assessing prey abundance prior to reintroductions can be complicated if a species relies on a variety of prey items. Many carnivores have diverse diets (Zielinski et al. 1999, Gómez-Ortiz et al. 2015, Witczuk et al. 2015), and assessing abundance of all prey species can be prohibitively expensive. Identifying important prey items based on studies of the source population or populations in similar ecosystems can allow managers to identify and focus on quantifying important prey species in the reintroduction area. We focused on assessing the response of fishers to snowshoe hares. Although fishers have diverse diets including a variety of small and medium-sized mammal species (Zielinski and Duncan 2004, Weir et al. 2005), snowshoe hares are likely an important prey item in our study system. Weir et al. (2005)

conducted diet analysis on 256 fisher stomachs in British Columbia, including the source area for the reintroduced population we studied, and found that snowshoe hare, red squirrel, red-backed vole, and porcupine were the most common prey items. Analysis of 94 scats from fishers on the Olympic Peninsula also identified snowshoe hares as a predominant prey item, accounting for 30% of recorded diet items (Pace and Prugh, unpublished data). The positive spatial association between fishers and snowshoe hares suggests that we identified an important prey item among the diversity of species that fishers consume. When assessing many prey items is not feasible, using relevant literature to identify important prey to assess prior to reintroductions can identify individual prey items that managers can focus on.

Assessing multiple prey species is more feasible when techniques are available to assess multiple prey simultaneously, such as with camera traps. In addition to snowshoe hares, our cameras documented squirrels, small rodents, and porcupines. We explored including squirrels and small rodents as a covariate in the fisher RSF, but topography did not explain detections effectively and thus any habitat-association predictions would be suspect. Adding forest structure variables did not improve fit for either squirrels or small rodents. We detected porcupines (*Erethizon dorsatum*) at only one camera station. This finding, along with expert knowledge, suggests porcupines are rare in our study area (J. Lewis pers. comm.). Mountain beavers have also been identified as an important prey item in Washington (Pace and Prugh, unpublished data), and selection by fishers for forest edge may reflect access to mountain beavers, which prefer moist habitats in regenerating forests (Arjo et al. 2007). However, we did not detect mountain beavers at any camera stations, so we were unable to include them in our analysis.

While interpreting our habitat selection results, it is important to consider that this is a reintroduced population on a foreign landscape. The low population density of founder

individuals may mean that animals are selecting the highest quality habitat and that our data may indicate fisher selection of the highest quality habitats available. However, these animals did not arrive with complete information about the new landscape they were released into, and it may take several generations for fishers to find and establish territories in areas reflecting optimal habitat. Additionally, even after excluding locations from the first month post release, the telemetry data includes a mix of locations pre- and post-establishment of home ranges, and selection patterns may differ depending on home-range establishment. The month-long period was likely long enough for fishers to sample the new landscape and begin using preferred habitats, and at a broad level our analysis does reveal habitat selection patterns of the population.

Our omission of topographical variables from the RSF of fishers was a conscious decision based on concerns with collinearity if we included both topographic variables used to model prey and predator detections and the predicted values of prey and predator detections in the RSF. It is possible that the response of fishers with snowshoe hares was actually selection for the habitat features preferred by snowshoe hares (i.e. high elevation, northerly aspects, and proximity to linear features). However, we argue that selection for topographic features themselves is unlikely and that any relationship fishers have with topographical variables is due to the resources available in these locations. By accounting for forest structure, proximity to edge, prey availability, and predator distributions in the RSF, we accounted for these resources without including topographical variables.

While fishers were once part of this landscape, they have been absent from our study area for 50 years or more. Habitat, species distributions, and species dynamics have undoubtedly changed in this time. Additionally, the reintroduced animals come from a different system and may select habitats differently from fishers that historically occurred in the South Cascades.

Reintroduced animals were captured from a managed, mosaic landscape in central British Columbia that has a history of disturbance including both logging and large-scale fires (Weir et al. 2009). The region is dominated by lodgepole pine (*Pinus contorta*), with thick stands of lodgepole pine common after fires (Weir 2003). Common prey in the area include snowshoe hare, red squirrels, and porcupines (Weir 2003, Weir et al. 2005). The parallels between the source area landscape and our habitat selection results may indicate that reintroduced fishers select habitat patterns that are familiar to them on the new landscape.

We were able to evaluate fisher habitat selection through this work. However, we did not assess if or how survival and reproduction of fishers was influenced by different habitat types. To gain a complete understanding of habitat quality for fishers, a fitness link is necessary to identify what habitats lead to population persistence and growth (Armstrong and Seddon 2008). Long term monitoring of reintroduced population that includes assessment of habitat selection, survival, and reproduction will allow for a thorough understanding of what constitutes quality habitat for a species.

Reintroductions are likely to become increasingly important in wildlife management and conservation as climate change, land use change, and other factors continue to threaten wildlife populations (Carter et al. 2017). Understanding species interactions is imperative for wildlife reintroductions. When selecting reintroduction sites, managers often account for historical range and suitable habitat for the target species, but do not quantify availability of food resources or abundance of predators and competitors. The assumption is made that what is determined to be quality habitat based on landscape features will provide sufficient food and protective cover. We documented that this may not be the case. Old growth forests that are considered quality habitat for fishers may not provide abundant snowshoe hares, a preferred prey item of fishers. And

fishers may also experience high levels of competition with bobcats for their prey.

Understanding these interspecific relationships prior to reintroductions can help managers increase the likelihood of reintroduction success. With increasing human impacts on wildlife habitats, we encourage managers to explicitly account for species interactions and evaluate food availability and potential for antagonistic interactions. This is particularly important in landscapes that have experienced invasion by non-native species, range expansion by resident species, and habitat alterations.

CHAPTER 4

General Conclusion

Reintroductions are a common tool in ecology, and both the number of reintroduction attempts and the number of species being reintroduced is continually increasing (Seddon et al. 2014). Assessing all aspects of habitat quality prior to release, and monitoring habitat selection of reintroduced animals post release is key to success of reintroduction programs (Armstrong and Seddon 2008). Here, we used an ongoing fisher reintroduction program to study how forest structure, prey, and predators influence fisher habitat quality and selection. We found a potential discrepancy between preferred habitats of fishers and their prey, selection by fishers for locations with moderate prey abundance, and a food-safety tradeoff for fishers in the South Cascades of Washington.

While there is increasing evidence of flexibility in habitat use (Raley et al. 2012, Sauder and Rachlow 2015), fishers are known to rely on mature forest structure for resting and breeding (Aubry et al. 2013, Zielinski and Gray 2018). In contrast, two preferred prey species, mountain beavers and snowshoe hares, were most abundant in younger forests. While fishers eat a diversity of prey, mountain beavers and snowshoe hares are two of their most common prey items (Weir et al. 2005, Pace and Prugh, unpublished data). This finding suggests that locations that may meet habitat needs of fishers in terms of vegetative structure, may not provide optimal prey communities, highlighting the importance of evaluating food availability prior to reintroduction efforts. This information can also be used to manage landscapes in the South Cascades for fishers. Creating landscapes of heterogeneous forest types, with patches of harvest dispersed in a matrix of mature forest, may meet the multiple resource needs of fishers.

Selection by fishers to be in locations close to recently disturbed stands and with moderate snowshoe hare abundance further supports these arguments. While selecting older forests, fishers also selected sites to be close to stands <30 years old. Based on our prey-habitat relationships, we hypothesize this trend is related to increased prey abundance in recently disturbed stands. This pattern, along with direct selection for sites with moderate snowshoe hare abundance suggests fishers selected areas based on prey availability, and that assessing prey availability prior to reintroductions could increase success through proper site selection. Selection for proximity to recently disturbed stands provides further evidence for the importance of forest mosaics for fishers.

We also documented a potential food-safety tradeoff for fishers in our study area. While spatial avoidance of predators was not included in the top resource selection function, we found a positive correlation between snowshoe hare and bobcat presence based on camera data. This correlation suggests that by selecting for areas with high snowshoe hare abundance, fishers may have increased their exposure to a known competitor and predator. Fishers may mediate this tradeoff by selecting for sites with moderate snowshoe hare abundance, where prey is available but risk is reduced compared to sites with the highest prey abundance. Further, examination of temporal activity patterns revealed distinct activity patterns between bobcats and fishers, suggesting fishers may have used temporal avoidance to mediate this tradeoff. Understanding the presence of such tradeoffs on the landscape prior to reintroductions could be key to success. While hares and bobcats were positively correlated, there were sites with high snowshoe hare abundance and low bobcat abundance. Exploring the nuance of these relationships could provide improved information for selection of reintroduction locations where prey abundance is high and predator abundance is low.

In combination, these findings revealed that both prey and predators influence fishers post-release. Evaluating relationships between vegetation, prey, and predators prior to reintroductions can identify discrepancies between prey abundance and preferred habitat of the reintroduced species and habitat selection tradeoffs that the reintroduced species may face. Knowing this information prior to the reintroduction allows managers to select release locations that will maximize the probability of success, and identify management strategies that may increase the probability of success. We encourage conservation practitioners to account for all aspects of habitat quality prior to reintroduction efforts.

Adaptive management is also key to the success of reintroductions, and studying habitat selection of released animals can identify what management strategies may be necessary (Armstrong et al. 2007). Our findings suggest that potential causes of decline in this reintroduced population of fishers could include competition with bobcats or lower prey availability in preferred forest types of fishers. Studying habitat selection post release allows identification of potential limiting factors for the reintroduced species, and this information can be used to manage the reintroduced population and plan future reintroductions. We therefore also encourage thorough monitoring of reintroduced populations not just to monitor survival, but also to gain better understanding of habitat selection and the factors that influence success.

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APPENDIX A

This appendix contains a correlation table of all variables used in predator and prey detection modeling and the fisher resources selection function in Chapter 2 (Table A1) and the cross validation scores for the final fisher resource selection function (Figure A1)

Table A1. Correlations among covariates used in hare, bobcat, and coyote detection models and fisher resources selection functions ($n = 10618$).

	Elevation	Basal area	Canopy cover	Stand age	Tree diameter	Stand height	Aspect	Slope	Dist. to linear feature
Elevation	1	0.35	0.17	0.6	0.23	0.02	-0.01	0.24	0.36
Basal area	0.35	1	0.8	0.82	0.87	0.85	0.05	0.23	0.31
Canopy cover	0.17	0.8	1	0.49	0.59	0.67	0.09	0.2	0.12
Stand age	0.6	0.82	0.49	1	0.86	0.69	0.01	0.21	0.41
Tree diameter	0.23	0.87	0.59	0.86	1	0.95	-0.03	0.21	0.3
Stand height	0.02	0.85	0.67	0.69	0.95	1	-0.01	0.2	0.21
Aspect	-0.01	0.05	0.09	0.01	-0.03	-0.01	1	0.01	0.03
Slope	0.24	0.23	0.2	0.21	0.21	0.2	0.01	1	0.24
Dist. to linear feature	0.36	0.31	0.12	0.41	0.3	0.21	0.03	0.24	1
Dist. to paved road	0.31	0.14	0.16	0.14	0.04	0	0.04	0.24	0.23
Dist. to unpaved road	0.48	0.4	0.13	0.55	0.4	0.28	0	0.24	0.7
Dist. to disturbed stand	0.4	0.56	0.41	0.57	0.51	0.45	0.01	0.09	0.39
Slope ²	0.12	0	-0.11	0.11	0.05	0	-0.01	0.25	0.21

Coyote det.	-0.22	-0.19	-0.24	-0.15	-0.13	-0.13	-0.02	-0.44	-0.21
Bobcat det.	-0.24	-0.16	0.01	-0.28	-0.23	-0.15	0.72	-0.08	-0.34
Hare det.	0.33	0.01	0.04	0.08	-0.07	-0.13	0.52	-0.02	-0.16
Dist. to disturbed stand ²	0.17	0.16	0.07	0.21	0.14	0.1	-0.02	-0.02	0.25

Table A1. Continued

	Dist. to paved road	Dist. to unpaved road	Dist. to disturbed stand	Slope ²	Coyote det.	Bobcat det.	Hare det.	Dist. to disturbed stand ²
Elevation	0.31	0.48	0.4	0.12	-0.22	-0.24	0.33	0.17
Basal area	0.14	0.4	0.56	0	-0.19	-0.16	0.01	0.16
Canopy cover	0.16	0.13	0.41	-0.11	-0.24	0.01	0.04	0.07
Stand age	0.14	0.55	0.57	0.11	-0.15	-0.28	0.08	0.21
Tree diameter	0.04	0.4	0.51	0.05	-0.13	-0.23	-0.07	0.14
Stand height	0	0.28	0.45	0	-0.13	-0.15	-0.13	0.1
Aspect	0.04	0	0.01	-0.01	-0.02	0.72	0.52	-0.02
Slope	0.24	0.24	0.09	0.25	-0.44	-0.08	-0.02	-0.02
Dist. to linear feature	0.23	0.7	0.39	0.21	-0.21	-0.34	-0.16	0.25
Dist. to paved road	1	0.1	0.19	0.01	-0.6	0	-0.13	0.11
Dist. to unpaved road	0.1	1	0.43	0.23	-0.12	-0.53	-0.21	0.27
Dist. to disturbed stand	0.19	0.43	1	-0.02	-0.18	-0.19	0	0.73

Slope ²	0.01	0.23	-0.02	1	0.16	-0.13	-0.05	-0.01
Coyote det.	-0.6	-0.12	-0.18	0.16	1	0.01	0.09	-0.06
Bobcat det.	0	-0.53	-0.19	-0.13	0.01	1	0.58	-0.13
Hare det.	-0.13	-0.21	0	-0.05	0.09	0.58	1	-0.05
Dist. to disturbed stand ²	0.11	0.27	0.73	-0.01	-0.06	-0.13	-0.05	1

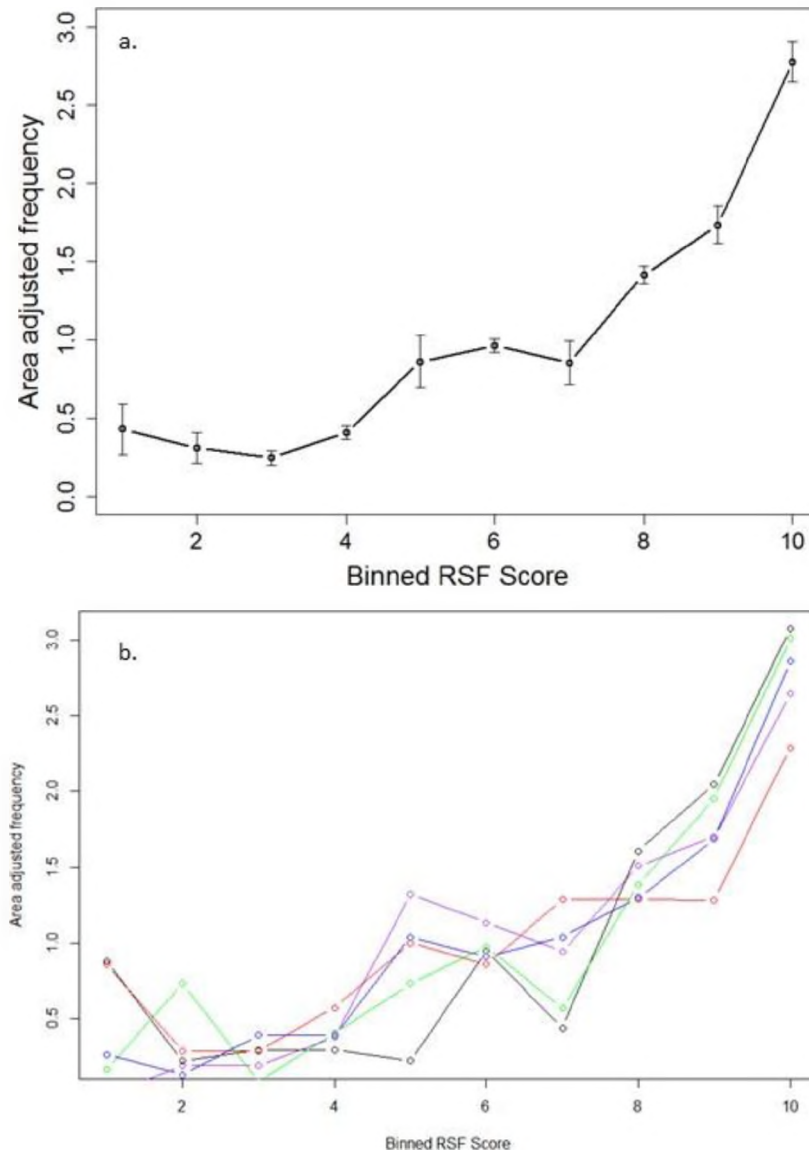


Figure A1. Frequency of categories (bins) of RSF scores for withheld fisher locations for 5-fold cross validation. Mean (\pm SE) frequency values (a). Frequency values for each cross-validation test are shown in unique colors (b). A Spearman-rank correlation for mean frequency by bins ($r_s = 0.88$, $p < 0.001$) indicates the model predicted cross-validated use locations well.