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and Laura R. Prugh

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## Prey of reintroduced fishers and their habitat relationships in the Cascades Range, Washington



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### ABSTRACT

Conservation and recovery of forest carnivores requires an understanding of their habitat requirements, as well as requirements of their prey. In much of the western United States, trapping and habitat loss led to extirpations of fishers (*Pekania pennanti*) by the mid-20th century, and reintroductions are ongoing to restore fishers to portions of their former range. Fisher recovery in Washington State has been limited by isolation from other populations, but other potentially important factors, such as diet of fishers in this region and prey availability, have not been thoroughly investigated. We collected hair samples from potential prey and fishers for stable isotope analysis to identify important prey items for fishers within a reintroduction area in southern Washington. We then estimated the abundance of prey species at 21 sites across a gradient of forest structural classes within the fisher reintroduction area, and assessed the effects of forest age and vegetation on the prey community using permutational multivariate analysis of variance and non-metric multidimensional scaling. Stable isotopes revealed that larger prey items, including snowshoe hares (*Lepus americanus*) and/or mountain beavers (*Aplodontia rufa*), were the most important prey item(s) for fishers in the southern Cascades. We found distinct but equally diverse prey communities in old-growth (unmanaged) and young (heavily managed) forest stands, with snowshoe hares and mountain beavers most common in young forests, while chipmunks (*Neotamius* spp.) and small mammals were more common in older forests. Our results suggest a discrepancy between the habitats where important fisher prey are most abundant and habitat requirements of fishers. Snowshoe hares and mountain beavers were most abundant in young forests, whereas fishers are associated with landscapes dominated by older forest stands or those that provide large woody structures, which fishers use for denning and resting. Our results add to growing evidence that forest landscape mosaics provide valuable habitat for fishers in the Pacific Northwest, suggesting that both mature and younger forest stands are important for fishers and fisher recovery.

### 1. Introduction

Historical extirpations of carnivore populations have impacted ecosystems worldwide through cascading effects on smaller carnivores, herbivores, and vegetation (Prugh et al., 2009; Ripple et al., 2014). Recognition of the ecological importance of carnivores has prompted numerous programs to recover carnivores in recent decades, including reintroductions of species such as wolves (*Canis* spp.), lynx (*Lynx* spp.), and fishers (*Pekania pennanti*) forest ecosystems (Berger, 2007; Lewis et al., 2012; Phillips and Smith, 1997; Steury and Murray, 2004).

However, reintroduction programs have had mixed success establishing self-sustaining populations (Griffith et al., 1989; Lewis et al., 2012; Seddon et al., 2014; Stewart et al., 2017).

Recovery plans for forest carnivores often focus on known physical habitat requirements of a species (Acosta-Jamett and Simonetti, 2004; Aubry et al., 2013; Weir et al., 2012; Zielinski et al., 2005, 2004), but success of reintroductions may be limited if prey availability is insufficient (Steury and Murray, 2004; Robbins et al., 2004). Knowing which habitats support important prey species may therefore inform land management to facilitate recovery of carnivores, and this

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knowledge may be especially important when conservation goals include expansion of remnant carnivore populations or establishment of new ones (Bhattarai and Kindlmann, 2012; Hetherington and Gorman, 2007; Jachowski et al., 2011; Suryawanshi et al., 2017). Therefore, understanding prey-habitat relationships is needed for science-based carnivore reintroductions.

Quantitative information about the distribution and abundance of key prey species is often unavailable prior to carnivore reintroductions; indeed, lack of information on habitat quality, including prey abundance, is often cited as a reason for reintroduction failure (Cook et al., 2010; Lewis and Hayes, 2004). Carnivore populations respond to temporal variation in prey abundance (Bowman et al., 2006; Jensen et al., 2012), and a diverse prey community provides stability through time (Doak et al., 1998; Petchy, 2000; Tilman et al., 1998). Because reintroduced populations are often small, diverse prey communities can help reduce environmental stochasticity, reducing the probability of extinction and failure of reintroduction efforts (Alvarez, 2001; Koprowski et al., 2005). While evaluating prey communities prior to reintroductions is ideal, evaluation after the reintroduction can inform management of the reintroduced population and improve future reintroduction and augmentation efforts. Here, we examine prey availability and the diet of reintroduced fishers in the southern Cascade Mountains of Washington.

Fishers are medium-sized forest carnivores that historically occurred throughout boreal and temperate forests across North America. They were extirpated from most of their range by the early 20th century due to overharvest and habitat loss (Powell, 1993), but fisher populations have since been restored to substantial portions of their historical range, particularly in eastern and midwestern North America (Lewis et al., 2012). Fishers are one of the most successfully reintroduced carnivores in North America (Lewis et al., 2012; Stewart et al., 2017), and recovery has generally been more successful in eastern than in western North America (Lapoint et al., 2015; Lewis et al., 2012; Powell, 1993). Lower success of fisher reintroductions in the West, and the lack of range expansion of remnant western populations, could be related to low prey availability (Kirby et al., 2018; Lapoint et al., 2015). Relationships between fisher habitat selection and prey availability are frequently hypothesized, but rarely evaluated (Lewis et al., 2016; Raley et al., 2012; Sauder and Rachlow, 2015; Happe et al., 2019). Additionally, we are unaware of any published studies on the diet of fishers where they are sympatric with mountain beavers (*Aplodontia rufa*), a potentially important prey species.

Forest management in Washington is representative of much of the West coast of the United States. Federal forests in the Pacific Northwest include National Parks with no harvest activities, and National Forests managed under the Northwest Forest Plan (U.S. Department of Agriculture, 1994). Within the Northwest Forest Plan, portions of National Forests are managed as late successional reserves, whereas other areas (i.e., designated “matrix” areas) are managed to facilitate timber production and other forest products and values. Adjacent state-owned and private industrial forests are managed intensively for timber production on short harvest rotations. This results in forested landscapes with recent clear cuts, young and middle-aged managed forests, and stands of unharvested old-growth forest. The abundance of mammalian prey species varies across this gradient (Carey, 2011; Carey and Harrington, 2001; Gashwiler, 1970; Griffin and Mills, 2007; Lewis et al., 2011a), and gaining a greater understanding of prey communities across a forest structure and management gradient will aid recovery efforts for forest carnivores.

Fishers have been reintroduced to three areas in Washington State: the Olympic Peninsula (2008–2010), the southern Cascades (2015–2018), and the northern Cascades (2018–2020; Lewis et al., 2018). In the southern Cascades, 69 fishers were released over two winters from December 2015 to February 2017. Previous research in the reintroduction area documented fishers selecting for old forests, older forests close to young stands, and moderate abundance of

snowshoe hares (*Lepus americanus*; Parsons et al., 2019). Selection patterns related to young stands and snowshoe hare abundance suggested that prey availability strongly influenced fisher habitat use, but the distribution and abundance of prey in relation to habitat characteristics remains unknown.

We assessed forest habitat characteristics associated with the structure and diversity of small and medium-sized mammal communities within the range of a reintroduced population of fishers in the southern Cascade Mountains of Washington. We also collected hair samples from fishers and potential prey items and conducted isotopic analysis to identify important prey for fishers within the study area. We focused on mammalian prey due to their importance in the diet of fishers (Weir et al., 2005; Zielinski et al., 1999). We predicted that prey diversity would be highest in older forests, but that snowshoe hares and mountain beavers, two large and putatively important prey items, would be most abundant in young stands with high stem densities (Arjo et al., 2007; Griffin and Mills, 2007). By simultaneously evaluating dietary importance and prey abundance in different forest types, we seek to understand how the availability of important prey species for fishers is affected by forest management.

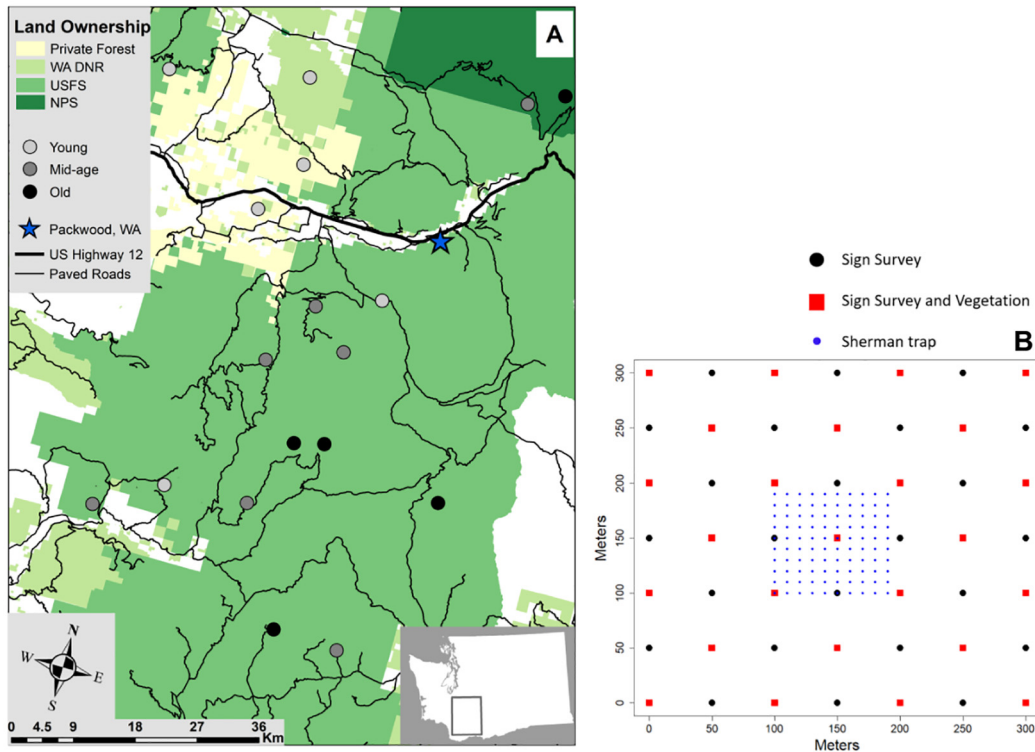
## 2. Methods

### 2.1. Study area

This study was conducted in a 5000 km<sup>2</sup> area of the southern Cascade Mountains of Washington and included sites in Gifford Pinchot National Forest, Mount Rainier National Park, Elbe and Tahoma State Forests, and surrounding private lands (Fig. 1a). 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*), huckleberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and a number of fern species. The elevation of the study area ranged from 235 to 3314 m, with a mean of 974 m. The elevation of 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 the study area (Western Regional Climate Center, Accessed March, 2019). Potential mammalian prey species in the Washington Cascades included snowshoe hares, mountain beavers, mice (*Peromyscus* spp.), southern red-backed voles (*Myodes gapperi*), microtine voles (*Microtus* spp.), shrews (*Sorex* spp.), Townsend’s chipmunks (*Neotamias townsendii*), and squirrels (*Tamiasciurus douglassii*; *Glaucomys sabrinus*) (Carey, 2011; Carey and Johnson, 1995; Gitzen et al., 2007; Lewis and Hayes, 2004). Porcupines (*Erethizon dorsatum*) were rare in the study area. Potential avian prey included ruffed grouse (*Bonasa umbellus*), sooty grouse (*Dendragapus fuliginosus*) and a variety of Passeriformes (Lewis and Hayes, 2004).

### 2.2. Site selection

We used the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA; <http://lemma.forestry.oregonstate.edu>) dataset, a 30-m resolution raster of forest structure variables, for site selection and for large-scale forest structure data. 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-km<sup>2</sup> hexagons over the study area, and we 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). This classification excluded areas with abundant clearcuts or areas of early regeneration, and we did not sample clearcut habitats because they are generally



**Fig. 1.** (A) Map of the study area in the southern Cascade Mountains of Washington. Habitat and prey sampling locations shown as light-grey (young stands), dark grey (middle-age) and black (old) circles. Background indicates forest ownership as private land, Washington Department of Natural Resources (WA DNR), US Forest Service (USFS), or National Park Service (NPS). (B) 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 squares indicate joint habitat-sampling and prey sign survey locations. Blue dots indicate Sherman trap locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

avoided by fishers (Powell, 1993, Sauder and Rachlow, 2014). We then used the LEMMA age of dominant trees data to calculate the average forest age of each hexagon to identify sites that ranged from young-stand characteristics to old-stand characteristics. Based on data available from ground plots to validate 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 used stand age to select sites because it is directly related to past management activities, as opposed to tree size which varies with silvicultural practices and biotic and abiotic factors.

We conducted prey surveys at locations that spanned a gradient of forest ages across land ownerships (Supplementary Table 1). We calculated the average stand age of all hexagons based on the LEMMA data, and categorized hexagons into three age-classes: young (< 110 years), middle-aged (110–180 years) and old (> 180 years) hexagons. Sample sites were placed in the center of randomly selected hexagons within each age category to ensure that each site was in the core of the respective forest type. To minimize the effects of edge habitats, we only sampled in hexagons that were surrounded by hexagons of the same age-class and suitable fisher habitat (i.e. continuous 7-km<sup>2</sup> area). Although most hexagons were composed of a mix of forest ages, this sampling approach provided us with the desired forest structure and management gradient. Young sites occurred predominantly on private, state, and sections of National Forest land where forests undergo intensive management. Middle-aged stands occurred predominantly in areas of National Forest that undergo moderate harvest activity. Old stands occurred in National Parks, wilderness areas, late successional reserves, and remote areas of National Forest that receive minimal active management. For efficiency, we limited our survey sites to those within 3 km of a road or trail. When collecting data at our survey sites, we visually confirmed that all sites occurred in stands of the appropriate age-class.

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).

### 2.3. Mammalian prey abundance

To estimate densities of small mammals (mice, voles, and chipmunks), we established a 90-m × 90-m grid (0.81 ha) of 100 Sherman traps (LFA; 3 × 3.5 × 9.5"; H.B. Sherman Traps, Inc., Tallahassee, FL, USA) with 10-m spacing (Fig. 1b). We placed traps and pre-baited at each site for three days prior to trapping. Traps were baited with a combination of oats, seeds, dried mealworms (to prevent mortality of shrews [*Sorex* spp.]; Do et al., 2013), and polyester batting. We trapped each site for 3–4 consecutive days, with fewer trap nights at sites with high recapture rates. We checked traps at 0700 and 1800 each day and left traps open 24 h per day. If we caught no new animals after the second morning, we stopped trapping after the third morning (3 sites). Captured individuals, except shrews and shrew moles (*Neurotrichus gibbsii*), were marked with numbered ear tags (1005–1 Monel ear tag; National Band Company, Newport, Kentucky, USA), weighed, identified to species and sex, and released. All animal handling procedures were approved by the University of Washington Institutional Animal Care and Use Committee (Protocol 4381-01) and followed the American Society of Mammalogists guidelines for use of wild animals (Sikes and The Animal Care, 2016). Trapping was conducted under Washington Department of Fish and Wildlife Scientific Collection Permits 16-276 (2016) and 17-048 (2017).

At each site, we conducted searches for 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 (Fig. 1b). We counted snowshoe hare pellets in a 0.564-m radius ( $1\text{-m}^2$ ) plot at each survey point (Hodges and Mills, 2008; Murray et al., 2002). We recorded midden presence within a 2-m radius plot in 2016 (sensu Doumas and Koprowski, 2013) and within a 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.

#### 2.4. Habitat characteristics

We measured habitat characteristics at 25 points in a 300-m  $\times$  300-m grid at each site (Fig. 1b). We estimated percent cover of two size classes of downed woody material (5–25 cm, > 25 cm) and understory species using line-intercept methods (Canfield, 1941). We used a 10-m transect and recorded the intercept distance for each species along the transect. Understory species cover data was later condensed to categories. For overstory conditions, we measured diameter at breast height (DBH) and documented species and status (alive/dead) of all trees > 5-cm DBH within a 5.64-m fixed radius plot (0.1 ha) 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%.

#### 2.5. Fisher diet estimation

To quantify the isotopic signatures of fisher prey items, we collected hair samples from a sample of individuals for all species of small mammals that we captured, and we opportunistically collected hair from road-killed individuals of larger prey species including snowshoe hares, mountain beavers, Douglas squirrels (*Tamiasciurus douglasii*), and grouse. We supplemented samples of snowshoe hares, mountain beavers and grouse with samples from specimens held by the Burke Museum at the University of Washington that were collected within the study area between 1975 and 1986 (Supplementary Table 2). We also obtained mountain beaver samples from animal control trappers working for Sierra Pacific Industries within the study area in the fall of 2017. In total, we collected samples from nine potential prey taxa: mice ( $n = 10$ ), red-backed voles ( $n = 5$ ), microtine voles ( $n = 4$ ), Townsend's chipmunks ( $n = 5$ ), Pacific jumping mice (*Zapus trinotatus*;  $n = 1$ ), shrews ( $n = 5$ ), Douglas squirrels ( $n = 5$ ), snowshoe hares ( $n = 5$ ), mountain beavers ( $n = 10$ ), and ruffed grouse ( $n = 3$ ).

Fishers were reintroduced to the study area between December 2015 and February 2017, and pre-release hair samples were collected from all individuals. From August 2016 – September 2017, we collected fisher hair samples from released individuals using non-invasive hair snares (Jenkins and Happe, 2015) placed at 99 stations and from recovered fisher mortalities. We placed hair snares at camera stations used on a project that evaluated carnivore habitat use in the study area, and site-selection followed procedures similar to those used for selecting small mammal trapping sites (Parsons et al., 2019). We baited hair-snare stations with a chicken leg and a scent lure (Caven's Gusto, Minnesota Trapline Products, Pennock, Minnesota, USA) and we left each station in place for six weeks. We obtained hair samples from fishers before they were released to determine whether the post-release hair samples had adequate time to integrate study area isotopic signatures. In total, we analyzed 29 fisher hair samples (8 from hair snares, 11 from mortalities, 10 pre-release).

All prey and 20 fisher hair samples were analyzed at the Cornell Stable Isotope Facility; 9 fisher hair samples were analyzed at the University of Wisconsin Stable Isotope Lab. Samples were rinsed with deionized water, dried for 24 h, and then washed in a 2:1 chloroform/

methanol solution to remove oils and debris. Samples were placed in tin capsules and analyzed for stable isotopes of carbon and nitrogen using a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyzer. We report isotope values as ratios in parts per thousand relative to international standards, Vienna-PeeDee Belemnite and atmospheric nitrogen (Kirby et al., 2018). We corrected for trophic discrimination with values developed for red foxes (*Vulpes vulpes*) and used in other carnivores, including fishers, 2.6‰ for  $^{13}\text{C}$  and 3.4‰ for  $^{15}\text{N}$  (Kirby et al., 2018; Roth and Hobson, 2000). Trophic discrimination accounts for the natural change in isotopic ratio that occurs when predators assimilate prey tissue.

#### 2.6. Statistical analysis

We used MARK 8.2 to estimate abundance of each live-trapped and marked prey species at each site using the Huggins' conditional likelihood closed capture model (Cooch and White, 2019). 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 Akaike's Information Criterion corrected for small sample sizes ( $\text{AIC}_c$ ; Burnham and Anderson, 2002). The full model failed to converge for any prey group because of the high number of parameters. We assumed abundance equaled zero at sites where no individuals of a species were captured. For prey community analyses, we calculated abundance of Keen's mice (*Peromyscus keeni*) and deer mice (*Peromyscus maniculatus*) separately and excluded juvenile *Peromyscus* spp. (which were not visually identifiable to species) 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 habitat variables used in evaluating prey habitat selection. 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 downed woody material, and percent cover of all shrub species from visual estimates. We conducted a PCA on the site mean values of these five variables to further reduce dimensionality. We also conducted a PCA on the site mean values of 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 selection modeling (Dinno, 2012; Horn, 1965; Schmid-Holmes and Drickamer, 2001). 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| (Delciellos et al., 2016; Summerville et al., 2006).

We used permutational multivariate analysis of variance (PERMANOVA) to examine the effects of site age-class, elevation, overstory vegetation, understory vegetation, and study year on small mammal community composition at each of the 21 sites (Anderson et al., 2008). We constructed a Bray-Curtis dissimilarity matrix for the 21 sites based on abundance of live-trapped and marked prey and relative abundance of larger prey. We standardized abundance estimates of each prey species by maximum value to ensure equal model weight. The covariates used in the PERMANOVA analysis were year, elevation, 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 ( $n = 128$ ) and used  $\text{AIC}_c$  to conduct model selection and calculate parameter importance (Burnham and Anderson, 2002). We calculated parameter importance (PI) as the cumulative weight of models

**Table 1**

Summary of abundance estimates for small mammals and sign surveys for medium-sized mammals at 21 sites in the southern Cascade Mountains of Washington. Estimates were obtained using a Huggins' mark-recapture model in program MARK for live-trapped species, and were based on counts of indices for others.

Species	Scientific name	Min	Max	Median	Mean	Number of sites
Live trapped abundance estimates (# of individuals/ha)						
Keen's mouse <sup>a</sup>	<i>Peromyscus keeni</i>	0.0	66.0	17.0	22.6	20
Deer mouse	<i>Peromyscus maniculatus</i>	0.0	15.6	2.4	4.0	18
Red-backed vole	<i>Myodes gapperi</i>	0.0	29.1	1.3	4.7	15
Oregon vole	<i>Microtus oregoni</i>	0.0	16.3	0.0	1.7	5
Chipmunk	<i>Neotamias townsendii</i>	0.0	25.4	4.8	6.7	15
Shrew (captures/100 trap nights)	<i>Sorex trowbridgii</i>	0.0	4.3	0.6	1.4	20
Sign survey abundance indices (# of sign/site)						
Mountain beaver burrows	<i>Aplodontia rufa</i>	0.0	18.0	0.0	3.0	7
Squirrel middens	<i>Tamiasciurus douglasii</i>	0.0	49.0	14.0	18.2	20
Hare pellets	<i>Lepus americanus</i>	0.0	608.0	54.0	100.0	18

containing each covariate.

To visualize the effects of stand 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 version 3.5.0 (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 (Shannon, 1948; Spellerberg and Fedor, 2003). To examine potential effects of forest age-class on prey diversity and richness, we used analysis of variance to assess whether species richness and diversity differed by stand age-class.

For isotope analysis, we used a cluster analysis (Legendre and Legendre, 2012) on carbon and nitrogen isotope ratios for fishers to distinguish samples from fishers that had integrated local isotopic signatures after release from those that had not. We calculated a Euclidean distance matrix based on carbon and nitrogen isotope values and conducted cluster analysis using the “vegan” package in R (Oksanen et al., 2018). We knew the individual fisher ID for 21 of the 29 samples that we collected either prior to release or from mortalities. We determined how long these animals had spent on the landscape based on release date and mortality date. For samples collected from hair snares, we identified probable individuals based on hair snare location, telemetry data, and sex of the fisher if it was identifiable from trail camera photos. Based on results of the cluster analysis and known fisher identities, we identified which samples displayed integration of local isotopic signatures and conducted diet analysis on those samples.

To reduce the number of prey groups, and because of high isotopic overlap between species, we combined all small mammals (shrews, mice, voles, and chipmunks) into one functional prey group and combined snowshoe hares and mountain beavers into another, resulting in four prey groups for analysis: small mammals, squirrels, hares/mountain beavers, and grouse (Kirby et al., 2018). To estimate the importance of each prey group for fishers, we used a Bayesian mixing model in the “MixSIAR” package in R (Stock and Semmens, 2016). We ran models based on uniform priors and incorporated trophic discrimination (Kirby et al., 2018). We ran three chains of 100,000 iterations, with a burn in of 50,000 iterations and thinned to every 50th sample. We present the results as Bayesian posterior probability distributions of the proportional contribution of each prey group to fisher diet.

### 3. Results

#### 3.1. Mammalian prey abundance

We captured 785 individuals of the five small mammal species of interest: 444 Keen's mice at 20 sites, 70 deer mice at 18 sites, 28 Oregon voles (*Microtus oregoni*) at 5 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 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, 8 shrew moles, 2 Pacific jumping mice, 1 long-tailed vole (*Microtus longicaudus*), 1 flying squirrel (*Glaucomys sabrinus*), and 1 dark-eyed junco (*Junco hyemalis*). Of the species of interest, we captured 162 individuals in 2016 and 543 individuals in 2017. This annual difference in capture success was predominantly driven by *Peromyscus* spp. (88 captures in 2016, 426 captures in 2017). MARK abundance estimates varied greatly between sites, with all species being absent from at least one site. For all species but red-backed voles, the model that included time of capture and whether or not an individual was a recapture was the best fitting model. The null model performed best for red-backed voles (Supplementary Table 3). Snowshoe hares and squirrels were the most frequently detected medium-sized mammals, while mountain beavers occurred at 7 of 21 sites (Table 1).

#### 3.2. Habitat characteristics

The first understory principal component was associated with reduced herbaceous cover and increased down woody material. 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 understory habitat data (Table 2). The first overstory principal component was associated with stands with small DBH trees, high tree density, and low Douglas-fir basal area. The second overstory principal component was

**Table 2**

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
% downed woody material	0.507	0.000
% shrub cover	-0.371	0.543
Eigenvalue	1.92	1.32
% Variance Explained	0.38	0.26

**Table 3**  
Variable loadings for the first two principle components from a principal component analysis of overstorey habitat variables.

Habitat variable	Overstorey principal component 1 (OPC1)	Overstorey 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

associated with stands of low total basal area, low true fir basal area, and high deciduous species basal area. Cumulatively the first two overstorey principal components explained 57% of the variation in the overstorey habitat data (Table 3).

### 3.3. Prey habitat selection

Model selection failed to identify a clear top PERMANOVA model of the effects of habitat on prey community composition. All 128 models had a  $\Delta AIC_c < 10$ , and 11 models had a  $\Delta AIC_c < 2$  (Table 4). Based on parameter importance (PI) calculations, year was the most important variable, followed by elevation, the first overstorey principal component, and the first understory principal component (Table 5). All 7 parameters had importance values  $> 0.3$ , suggesting that all parameters were important in determining prey community structure. Our final NMDS ordination had three dimensions, a stress value of 0.114, and a non-metric  $R^2$  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 (Fig. 2). 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 snowshoe hares, mountain beavers, Oregon voles, and deer mice, and low abundance of squirrels, red-backed voles, Keen's mice, and Townsend's chipmunks (Fig. 2, Supplementary Fig. 1).

All four habitat principal components related to the mammalian prey community. Snowshoe hares, mountain beavers, and chipmunks were more abundant at sites with a high density of smaller trees. Sites with low basal area and a higher proportion of deciduous trees had relatively high abundances of snowshoe hares, mountain beavers, and

**Table 4**  
The top five permutational multivariate analysis of variance models for mammalian prey community at 21 sites in the southern Cascade Mountains of Washington. Models were ranked by Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ). The full table is available in the supplementary material (Supplementary Table 4).

Model	$AIC_c$	$\Delta AIC_c$	Weight	$R^2$
Over PC1 + age-class + year + elevation	-41.78	0.00	0.04	0.44
Over PC1 + Under	-40.99	0.79	0.03	0.45
PC1 + age-class + year + elevation				
Under PC1 + age-class + year + elevation	-40.79	0.99	0.03	0.41
Age-class + year + elevation	-40.77	1.01	0.03	0.36
Over PC1 + year + elevation	-40.18	1.60	0.02	0.27

PC = principal component axis.

**Table 5**  
Parameter importance of variables included in mammalian prey community permutational multivariate analysis of variance. Importance values based on Akaike's Information Criterion corrected for small sample sizes ( $AIC_c$ ).

Parameter	Importance
Year	0.676
Elevation	0.612
Overstorey PC1	0.519
Understorey PC1	0.467
Stand age-class	0.449
Understorey PC2	0.411
Overstorey PC2	0.377

Oregon voles. Snowshoe hares, squirrels, and chipmunks were more abundant at sites with shrub-dominated understories, while mice, Oregon voles, and mountain beavers were more abundant in herbaceous understories (Table 6). 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. Mean (SE) species richness was 5.9 (0.26), 5.6 (0.37), and 5.4 (0.48) for old, middle-aged, and young stands respectively. Mean diversity was 0.96 (0.08), 0.95 (0.08), and 0.75 (0.14) for old, middle-aged, and young stands respectively.

### 3.4. Fisher diet estimation

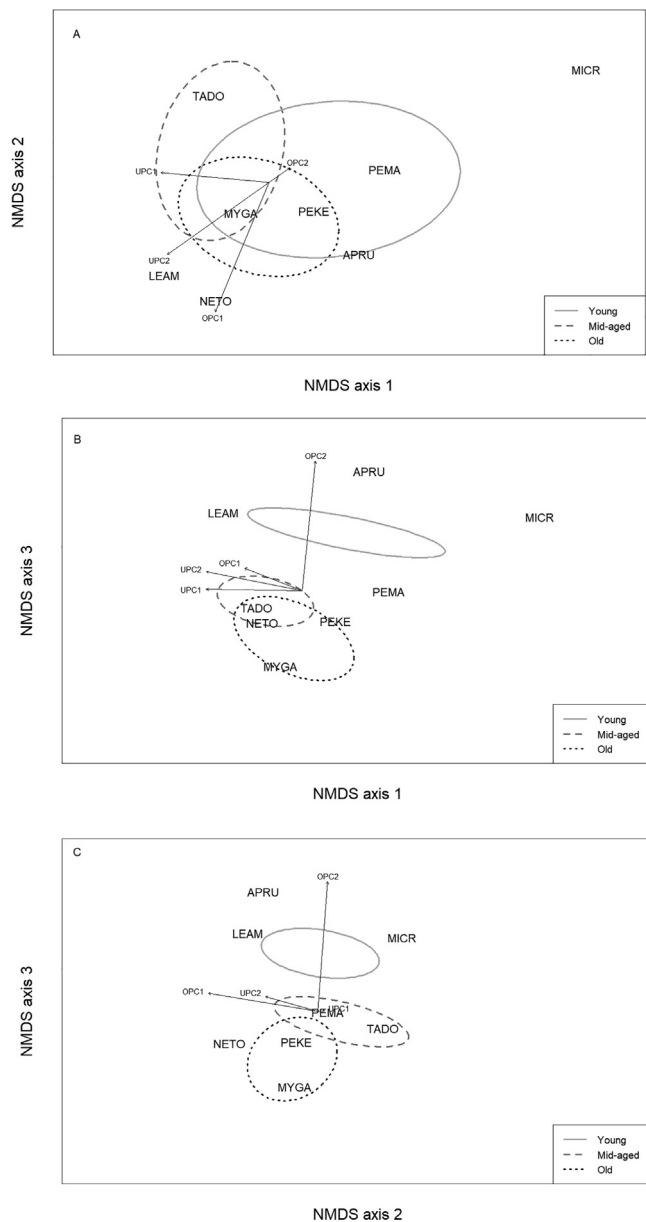
The cluster analysis identified two distinct groups of fisher hair samples; one group containing 12 samples and the other containing 17 (Fig. 3A). One group (Washington) had an average estimated duration on the landscape of 13.25 months (SE = 0.65) and the other group (British Columbia) had an average estimated duration on the landscape of 3.12 months (SE = 1.16). Other than two samples (one from a known individual and one from an unknown individual), every sample from an animal estimated to have spent at least 10 months in the study areas was classified as a Washington sample. Every sample from an animal known or estimated to have spent less than 10 months on the landscape grouped into British Columbia samples, including pre-release samples. Given that Washington samples had integrated isotopic signatures from the release site, (Fig. 3B), we limited the isotopic diet analysis to these samples ( $n = 12$ ).

The estimated diet contribution was 0.68 (95% credible interval 0.36–0.89) for hares/mountain beavers, 0.18 (0.01–0.53) for grouse, 0.08 (0.00–0.26) for small mammals, and 0.04 (0.00–0.11) for squirrels (Fig. 4). The wide 95% credible intervals of hares/mountain beavers and grouse is due to a high correlation ( $r = -0.86$ ) between posterior proportions of these groups. All Gelman-Rubin statistics of convergence were  $< 1.01$ . Due to geographic variation in isotopic signatures, we cannot comment on the diet of fishers from the source population without prey samples from the source population area.

## 4. Discussion

Our integrated analyses of prey habitat relationships and diet of fishers suggest that younger forests are likely to provide abundant prey for fishers reintroduced in the Pacific Northwest. Results from the isotope analysis indicated that snowshoe hares and/or mountain beavers were the most important prey items, and both these species were most abundant in young and middle-aged forests. While younger forests provide important prey habitat, mature forests and forests on federal land typically have a greater abundance of the large structures that fishers require for den and rest sites (Green et al., 2019; Weir et al., 2012; Zielinski et al., 2004). Thus, forest mosaics comprised of young, middle, and old-age stands may provide optimal habitat conditions that satisfy both prey and forest structure needs of fishers. Habitat diversity





**Fig. 2.** Non-metric multidimensional scaling ordination (NMDS) of the mammalian prey community at 21 sites in the southern Cascade Mountains of Washington. Ovals show the 95% confidence ellipse for the centroid of each age-classes' prey community. The four-letter abbreviations show each species location in ordination space. The arrows indicate correlation between the overstory and understory principal components and the ordination axes, with longer arrows indicated stronger correlation. Habitat variables associated with each principal component can be found in Tables 3 and 4. Species that occur within or near age-class ellipses were more common in those age-classes. Species that occur in the direction arrows point from the origin were positively related to those habitat covariates. 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. PEKE = Keen's mouse, PEMA = deer mouse, MYGA = red-backed vole, MICR = Oregon Vole, NETO = Chipmunk, TADO = Douglas squirrel, APRU = mountain beaver, LEAM = snowshoe hare, OPC = Overstory principal component, UPC = understory principal component. Ordination plots with site scores can be found in the Supplementary material.

will also maximize prey diversity, which could improve temporal stability of prey availability (Doak et al., 1998; Tilman et al., 1998). Stands of different ages hosted distinct prey communities, and while snowshoe hares and mountain beavers both preferred young stands, these species responded differently to understory conditions. Taken together, these

results provide evidence supporting the hypothesis that selection by fishers for diverse forest types is related to access to prey (Lewis et al., 2016; Raley et al., 2012; Sauder and Rachlow, 2015; Happe et al., 2019).

The small rodent community in the study area was dominated by Keen's mice, with red-backed voles and chipmunks also common. These three species were all associated with older forests. All three species have been identified as prey items for fishers (Weir et al., 2005; Zielinski et al., 1999). In areas where snowshoe hares or porcupines are abundant, small rodents are a less important component of fisher diet (Martin, 1994; Weir et al., 2005; Zielinski et al., 1999). Indeed, snowshoe hares and/or mountain beavers were preferred prey items in the study area and because of the significance of these species in the fishers diet, our findings suggest that fishers may use forest mosaics that include young and mid-age stands to increase their access to snowshoe hares and mountain beavers.

Snowshoe hares are one of the most important prey items for fishers throughout their range (Bowman et al., 2006; Powell, 1993; Weir et al., 2005), and while we documented snowshoe hares in forests 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 (OPC1 and 2), as well as shrubby understories (UPC1 and 2). 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. In other regions, however, snowshoe hares are strongly associated with conifer stands with high stem density (Cheng et al., 2015; Lewis et al., 2011a), and our data agree with past research in that snowshoe hares prefer stands with high densities of small trees. This preference suggests that important prey of fishers may use forests types that differ from the mature forests with complex structure used by fishers for denning (Raley et al., 2012). Differential habitat requirements of fishers and their prey highlights the importance of assessing multiple aspects of habitat quality prior to reintroduction efforts.

To our knowledge, consumption of mountain beavers by fishers has not been documented in the peer-reviewed literature. Unfortunately, due to isotopic similarity between snowshoe hares and mountain beavers, we were unable to distinguish consumption of these two species. However, the identification of mountain beavers in fisher scats from Washington's Olympic Peninsula (Lewis et al., 2011b; Pace, 2017) and the prevalence of mountain beavers in the southern Cascades reintroduction area suggest that mountain beavers are likely important prey for fishers in both areas. Mountain beavers prefer young, moist, regenerating forests where there is abundant herbaceous vegetation and saplings (Arjo et al., 2007; Hacker and Coblenz, 1993), and our results reflected this, as we did not detect mountain beavers at any sites located in hexagons with an average age > 120 years old. This pattern results in mountain beavers being most abundant in heavily managed forests where clearcuts and open patches are common (Arjo et al., 2007). Thus, the difference between preferred habitats of mountain beavers and habitat needs of fishers is even larger than the difference between snowshoe hares and fishers. The habitat needs of 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 abundant prey. Fishers may manage this tradeoff by using forest mosaics (Sauder and Rachlow, 2014) and older forests close to young stands (Parsons et al., 2019). Our results do not indicate what types of forest fishers are hunting in, and future research should assess whether fishers actively hunt in young forests, if young forests act as source habitats for prey that overflow into adjacent, older forests, and the role that forest retention and legacy structures play in habitat suitability and fisher hunting behavior.

While snowshoe hares and mountain beavers may be important prey items in the study area, fishers have diverse diets and rely on a variety of mammalian prey (Martin, 1994; Weir et al., 2005; Zielinski and Duncan, 2004). We also witnessed large temporal variation in prey

**Table 6**

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. OPC = Overstory principal component, UPC = understory principal component.

Species	OPC1: Small diameter, dense trees	OPC2: Low total basal area, high deciduous basal area	UPC1: Low herbaceous cover, high downed woody material	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 chipmunks	+	-	+	+

availability, suggesting that maintaining a diverse prey community may be important for success of fishers. A conifer mast event occurred in Mt. Rainier National Park in 2016 (J. Hille Ris Lambers, pers. comm.), which is a likely explanation for a dramatic increase in *Peromyscus* spp. the following summer. Fisher populations can fluctuate with prey populations and mast events, (Bowman et al., 2006; Jensen et al., 2012), and prey diversity has been shown to increase 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, diverse habitats may provide stability in the availability of small mammal prey. However, given the importance of larger prey items, such variation in small mammal populations may not have a strong effect on fisher population dynamics. Diversity of prey and cover types may also facilitate coexistence between fishers and other mesocarnivores on the landscape via for niche partitioning (Manlick et al., 2017).

Fishers, their prey, and forest management all operate at different spatial scales within this study area. This results in fisher home ranges encompassing large landscapes, with stands that vary by age and structure and likely support different prey communities. Although we did not evaluate prey availability at the scale of a fisher home range, these analyses provide insight into the forest types that particular prey species are found in, allowing managers to identify habitats and landscapes that are likely to provide abundant prey and security cover for fishers.

Our prey surveys and diet analysis can be used in developing management strategies for fishers in the Pacific Northwest. The maintenance of forest mosaics, with remnant old forests interspersed with burned, harvested, and thinned stands, could meet the forest structure needs of fishers while providing abundant and diverse prey. Limited thinning practices and burned areas that maintain large trees and allow for the growth of dense understory may also create quality habitat for fishers. Legacy trees, snags, and logs can provide the structure necessary for den and rest sites for fishers, while patches of regenerating young trees can provide the cover preferred by snowshoe hares. Fishers do require closed canopy forest, and Franklin et al. (2019) noted that the intensity of stand use by fishers increased greatly when retention harvest practices retained at least 50% forest cover. 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 retention harvest approaches. However, it should be noted that the south Cascades fisher population is in the early stages of the reintroduction, and it is not known whether the prey abundances we documented are high enough to sustain the population in the long term. In addition, this study was not designed to evaluate how different mosaic configurations or specific thinning practices affect fisher population viability. Future research

monitoring the success of fishers in relation to these factors would provide valuable additional information.

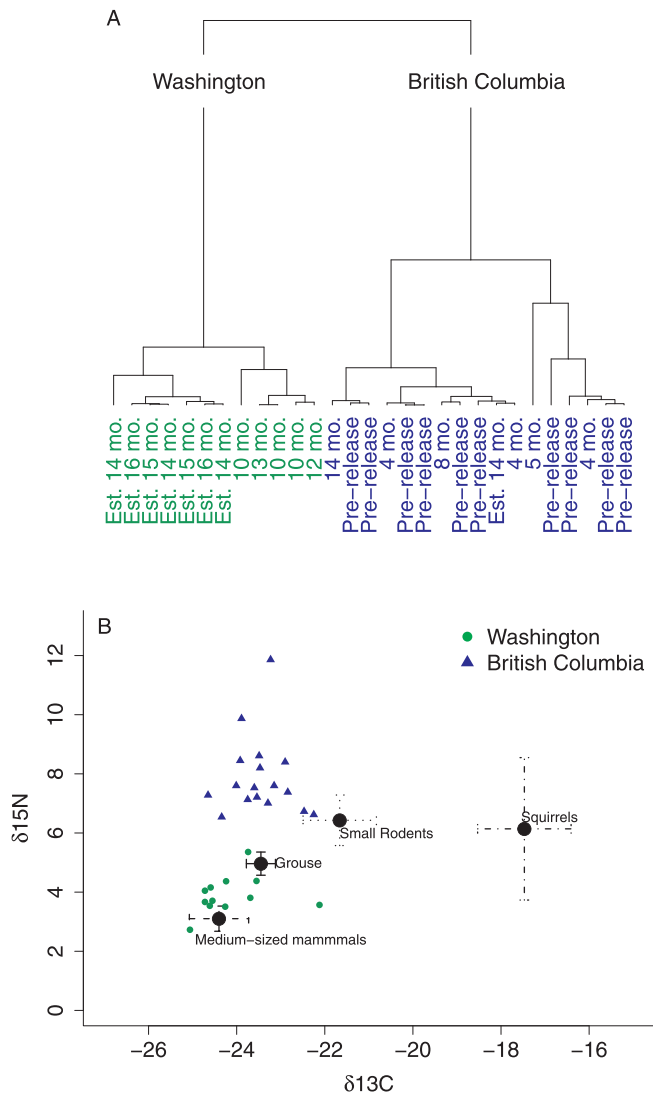
Our findings also highlight the importance of assessing prey population distribution and abundance prior to reintroductions. Reintroductions are a common tool in wildlife conservation (Fischer and Lindenmayer, 2000), and are likely to be more common with increasing pressures of habitat loss, climate change, and invasive species (Carter et al., 2017). We documented a distinction between known habitat requirements of fishers and habitat relationships of two important prey species. Lack of information on habitat quality, or releasing animals into low quality habitat are two common causes of reintroduction failure (Cook et al., 2010; Griffith et al., 1989). Understanding how structural habitat elements and vegetation independently influence prey distributions and carnivore habitat quality could allow managers to account for these complexities when selecting reintroduction locations. Forest structure is a key component of fisher habitat, but prey distributions are influenced by aspects of forest structure beyond those commonly considered important for fishers. 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 or slow recovery (Carlson et al., 2014). We encourage conservation practitioners to holistically assess habitat quality prior to carnivore 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.

#### CRediT authorship contribution statement

**Mitchell A. Parsons:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - review & editing, Visualization, Funding acquisition. **Jeffrey C. Lewis:** Conceptualization, Methodology, Investigation, Resources, Writing - review & editing, Supervision, Funding acquisition. **Jonathan N. Pauli:** Methodology, Resources, Writing - review & editing, Supervision. **Tara Chestnut:** Investigation, Resources, Writing - review & editing, Funding acquisition. **Jason I. Ransom:** Investigation, Resources, Writing - review & editing, Funding acquisition. **David O. Werntz:** Investigation, Resources, Writing - review & editing, Funding acquisition. **Laura R. Prugh:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

#### Declaration of Competing Interest

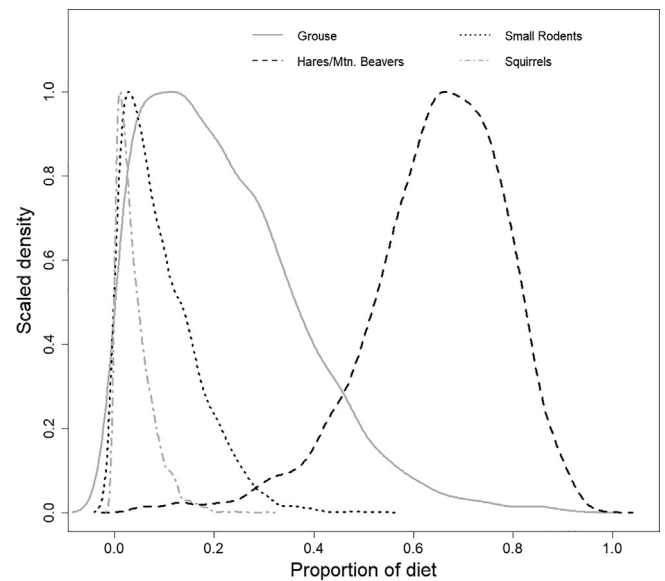
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.



**Fig. 3.** Cluster analysis of carbon and nitrogen isotopic ratios for fisher hair samples (A). Labels indicate how long a fisher spent in the study area post release. “Est.” indicates samples from unknown individuals where duration was estimated from camera trap photos and telemetry data. Biplot of isotopic signatures of fishers and potential prey items (B). Fisher samples that grouped with pre-release samples are shown as blue, fisher samples that separated from pre-release samples are shown as green. Black dots indicate the mean isotopic values of each prey group and error bars show plus/minus two standard errors on the mean. Medium-sized mammals include snowshoe hares and mountain beavers, and small rodents include mouse, vole, shrew, and chipmunk species. Post-release samples were collected from August 2016 – September 2017 in the southern Cascade Mountains in Washington. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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**Fig. 4.** Posterior distributions of the proportion of fisher diet composed of grouse, hares/mountain beavers, small rodents, and squirrels. Results based on MixSIAR output with three 100,000 iteration chains, a burn in of 50,000 iterations, thinned to every 50th iteration.

Park.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.117888>.

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## Supplementary Material

Table 1. The average age, ownership, elevation, species richness, and Shannon diversity index of 21 sites sampled for small mammal abundance and diversity in the southern Cascade Mountains in Washington, USA.

Site	Year Sampled	Age (yrs)	Ownership	Elevation (m)	Richness	Diversity
Young-A	2016	93	National Forest	530	5	0.80
Young-B	2016	103	National Forest	830	3	0.00
Young-C	2016	67	National Forest	1126	6	0.82
Young-D	2017	39	Private	403	7	1.14
Young-E	2017	88	State	1141	6	1.01
Young-F	2017	78	State	593	5	0.70
Young-G	2017	71	Private	1079	6	0.76
Mid-A	2016	125	National Forest	667	5	1.00
Mid-B	2016	139	National Forest	1098	4	0.69
Mid-C	2016	148	National Forest	496	5	1.09
Mid-D	2016	128	National Forest	988	6	1.20
Mid-E	2017	163	National Park	921	6	1.18
Mid-F	2017	106	National Forest	764	7	0.66
Mid-G	2017	129	National Forest	1113	6	0.86
Old-A	2016	250	National Forest	1058	7	1.10
Old-B	2016	213	Wilderness	1486	5	1.11
Old-C	2016	207	Wilderness	1039	6	1.21
Old-D	2017	243	National Park	1129	5	0.96
Old-E	2017	217	Wilderness	1296	6	0.96
Old-F	2017	219	National Forest	1290	6	0.81
Old-G	2017	217	National Park	1018	6	0.59

Table 2. Museum specimens used for isotopic analysis.

Species	Location	Year Collected	Accession Number	Museum Number
Snowshoe hare	Pierce County, WA	1987	199614	60071
Snowshoe hare	Pierce County, WA	1986	198910	35519
Snowshoe hare	Pierce County, WA	1976	197871	35952
Mountain beaver	Lewis County, WA	1974	197910	30788
Mountain beaver	Pierce County, WA	1975	197910	31867
Ruffed grouse	Pierce County, WA	1994	NA	51048

Table 3. AICc tables showing all 8 mark-recapture models for live-trapped small mammal abundance. Top models were chosen based on Akaike's Information Criterion corrected for small sample sizes (AICc). An "NA" in the AICc column indicates a model that did not converge due to over parameterization. Top models were used to estimate prey abundance at each site (Table 2).

Species	Model <sup>a</sup>	# Parameters	AICc	Delta AICc	AICc Weight
Keen's mouse	Time + recap	4	3013.35	0	1.00
	Site + time	40	3081.8	68.45	0.00
	Time	2	3146.12	132.77	0.00
	Site + recap	40	4132.94	1119.59	0.00
	Site	20	4161.72	1148.37	0.00
	Recap	2	4175.89	1162.54	0.00
	Null	1	4182.61	1169.26	0.00
	Site + time + recap	80	NA	Failed to converge	
Deer mouse	Time + recap	4	488.67	0	1.00
	Time	2	514.01	25.34	0.00
	Recap	2	630.4	141.73	0.00
	Null	1	634.33	145.66	0.00
	Site	18	NA	Failed to converge	
	Site + recap	36	NA	Failed to converge	
	Site + time	36	NA	Failed to converge	
	Site + time + recap	72	NA	Failed to converge	
Red-backed vole	Null	1	537.32	0	0.53
	Recap	2	539.07	1.75	0.22
	Time	2	539.33	2.01	0.20
	Time + recap	4	542.18	4.86	0.05
	Site	15	NA	Failed to converge	
	Site + recap	30	NA	Failed to converge	
	Site + time	30	NA	Failed to converge	
	Site + time + recap	60	NA	Failed to converge	
Oregon vole	Time + recap	4	213.57	0	0.30
	Recap	2	213.67	0.1	0.29
	Time	2	213.88	0.31	0.26

	Null	1	214.93	1.36	0.15
	Site	5	NA	Failed to converge	
	Site + recap	10	NA	Failed to converge	
	Site + time	10	NA	Failed to converge	
	Site + time + recap	20	NA	Failed to converge	
Chipmunk	Time + recap	4	715.96	0	1.00
	Recap	2	763.83	47.87	0.00
	Time	2	776.36	60.4	0.00
	Null	1	817.35	101.39	0.00
	Site	15	NA	Failed to converge	
	Site + recap	30	NA	Failed to converge	
	Site + time	30	NA	Failed to converge	
	Site + time + recap	60	NA	Failed to converge	

a: Model parameters – Time = time of capture session (morning/evening), recap = type of

capture (new/recapture), site = unique capture probability at each sampling site.

Table 4. Akaike Information Criteria scores (AICc), Delta AICc, and AICc weights for all 128 PERMANOVA models tested.

Formulas	AICcRSS	Delta	Weight
standresp ~ over1+class+year+Elevation	-41.78	0.00	0.04
standresp ~ over1+under1+class+year+Elevation	-40.99	0.79	0.03
standresp ~ under1+class+year+Elevation	-40.79	0.99	0.03
standresp ~ class+year+Elevation	-40.77	1.01	0.03
standresp ~ over1+year+Elevation	-40.18	1.60	0.02
standresp ~ over2+year+Elevation	-40.16	1.62	0.02
standresp ~ over2+under1+year+Elevation	-40.07	1.71	0.02
standresp ~ over1+over2+year+Elevation	-40.05	1.73	0.02
standresp ~ over1+under1+class+Elevation	-40.01	1.77	0.02
standresp ~ over1+class+year	-39.95	1.83	0.02
standresp ~ year+Elevation	-39.91	1.87	0.02
standresp ~ under2+year+Elevation	-39.73	2.05	0.02
standresp ~ over1+over2+under2+year	-39.62	2.16	0.01
standresp ~ over1+under2+year+Elevation	-39.61	2.17	0.01
standresp ~ over1+over2+year	-39.46	2.32	0.01
standresp ~ over2+under2+year	-39.46	2.32	0.01
standresp ~ over1+over2+under1+year+Elevation	-39.43	2.35	0.01
standresp ~ under1+class+Elevation	-39.43	2.35	0.01



standresp ~ over2+under2+year+Elevation	-39.26	2.52	0.01
standresp ~ over1+under2+class+year	-39.21	2.57	0.01
standresp ~ under1+year+Elevation	-39.17	2.61	0.01
standresp ~ under2+class+year	-39.13	2.65	0.01
standresp ~ over2+under1+under2+year	-39.13	2.65	0.01
standresp ~ over1+year	-39.12	2.66	0.01
standresp ~ over1+under2+class+year+Elevation	-39.10	2.68	0.01
standresp ~ under1+under2+year+Elevation	-39.07	2.71	0.01
standresp ~ over1+under2+year	-39.07	2.71	0.01
standresp ~ under2+year	-39.00	2.78	0.01
standresp ~ under2+class+year+Elevation	-38.97	2.81	0.01
standresp ~ over1+over2+under2+year+Elevation	-38.92	2.86	0.01
standresp ~ over2+under1+class+year+Elevation	-38.92	2.87	0.01
standresp ~ over2+under1+under2+year+Elevation	-38.91	2.87	0.01
standresp ~ over1+under1+year+Elevation	-38.87	2.91	0.01
standresp ~ class+Elevation	-38.86	2.92	0.01
standresp ~ over2+class+year+Elevation	-38.83	2.95	0.01
standresp ~ under1+under2+class+year	-38.83	2.95	0.01
standresp ~ over1+class+Elevation	-38.81	2.97	0.01
standresp ~ under1+under2+year	-38.75	3.03	0.01
standresp ~ over1+over2+under1+Elevation	-38.71	3.07	0.01
standresp ~ under1+under2+class+year+Elevation	-38.69	3.09	0.01
standresp ~ over1+under1+under2+year+Elevation	-38.65	3.13	0.01
standresp ~ over1+over2+under1+under2+year	-38.63	3.15	0.01
standresp ~ over1+under1+class+year	-38.48	3.30	0.01
standresp ~ over2+under1+Elevation	-38.48	3.30	0.01
standresp ~ over1+over2+under1+under2	-38.42	3.36	0.01
standresp ~ over1+under1+under2+Elevation	-38.35	3.44	0.01
standresp ~ over1+over2+under1+under2+year+Elevation	-38.32	3.46	0.01
standresp ~ over1+under1+Elevation	-38.28	3.50	0.01
standresp ~ over1+over2+class+year+Elevation	-38.23	3.56	0.01
standresp ~ over2+Elevation	-38.22	3.56	0.01
standresp ~ Elevation	-38.21	3.57	0.01
standresp ~ over1+under1+under2	-38.20	3.58	0.01
standresp ~ class+year	-38.18	3.60	0.01
standresp ~ over1+under1+under2+class+year+Elevation	-38.18	3.60	0.01
standresp ~ over1+under1+under2+year	-38.18	3.60	0.01
standresp ~ over1+under1+class	-38.12	3.66	0.01
standresp ~ under1+Elevation	-38.09	3.69	0.01
standresp ~ over1+under1+under2+class+year	-38.04	3.74	0.01
standresp ~ over1+over2+under1+year	-38.04	3.74	0.01
standresp ~ over2+year	-38.02	3.76	0.01
standresp ~ under1+class+year	-37.98	3.80	0.01
standresp ~ over1+Elevation	-37.94	3.84	0.01
standresp ~ over2+under1+year	-37.90	3.88	0.01

standresp ~ over1+over2+under1+under2+Elevation	-37.89	3.89	0.01
standresp ~ year	-37.85	3.93	0.01
standresp ~ over1+under1+under2+class	-37.84	3.94	0.01
standresp ~ over1+under1+year	-37.82	3.96	0.01
standresp ~ under1+under2+class	-37.79	3.99	0.01
standresp ~ over2+under1+class+Elevation	-37.78	4.00	0.01
standresp ~ under1+year	-37.78	4.00	0.01
standresp ~ over1+class	-37.74	4.04	0.01
standresp ~ under2+Elevation	-37.71	4.07	0.01
standresp ~ under1+under2+Elevation	-37.70	4.08	0.01
standresp ~ over1+under1+under2+class+Elevation	-37.57	4.21	0.01
standresp ~ over1+over2+class+year	-37.57	4.21	0.01
standresp ~ over1+over2+under1	-37.55	4.23	0.01
standresp ~ over1+under1	-37.52	4.26	0.01
standresp ~ over1+over2+under2	-37.51	4.28	0.01
standresp ~ over2+under2	-37.49	4.29	0.01
standresp ~ over1+over2+Elevation	-37.48	4.30	0.01
standresp ~ under1+under2	-37.46	4.32	0.01
standresp ~ under2+class	-37.44	4.34	0.00
standresp ~ over2+under1+under2	-37.44	4.34	0.00
standresp ~ over2+under2+Elevation	-37.38	4.40	0.00
standresp ~ over2+under1+under2+Elevation	-37.37	4.41	0.00
standresp ~ over1+under2+Elevation	-37.35	4.43	0.00
standresp ~ over1+over2	-37.35	4.43	0.00
standresp ~ under1+under2+class+Elevation	-37.33	4.45	0.00
standresp ~ under1+class	-37.32	4.46	0.00
standresp ~ under2	-37.32	4.46	0.00
standresp ~ over1+under2	-37.28	4.50	0.00
standresp ~ over1	-37.26	4.52	0.00
standresp ~ over2+class+Elevation	-37.24	4.54	0.00
standresp ~ over1+over2+under1+class+year+Elevation	-37.19	4.59	0.00
standresp ~ class	-37.02	4.76	0.00
standresp ~ under2+class+Elevation	-36.97	4.81	0.00
standresp ~ over1+under2+class	-36.92	4.86	0.00
standresp ~ under1	-36.91	4.87	0.00
standresp ~ over2+under2+class+year	-36.88	4.90	0.00
standresp ~ over2+under1	-36.77	5.01	0.00
standresp ~ over1+over2+under1+class+Elevation	-36.73	5.05	0.00
standresp ~ over2	-36.67	5.11	0.00
standresp~1	-36.65	5.13	0.00
standresp ~ over1+over2+under2+Elevation	-36.58	5.20	0.00
standresp ~ over1+over2+under2+class+year	-36.43	5.35	0.00
standresp ~ over2+under1+under2+class+year	-36.34	5.44	0.00
standresp ~ over1+under2+class+Elevation	-36.31	5.47	0.00
standresp ~ over2+class+year	-36.10	5.68	0.00

standresp ~ over2+under2+class+year+Elevation	-36.02	5.76	0.00
standresp ~ over2+under1+class+year	-35.74	6.04	0.00
standresp ~ over1+over2+class+Elevation	-35.72	6.06	0.00
standresp ~ over1+over2+class	-35.69	6.10	0.00
standresp ~ over2+under2+class	-35.62	6.16	0.00
standresp ~ over2+under1+under2+class	-35.62	6.16	0.00
standresp ~ over2+under1+under2+class+year+Elevation	-35.56	6.22	0.00
standresp ~ over1+over2+under1+class+year	-35.53	6.25	0.00
standresp ~ over1+over2+under1+class	-35.48	6.30	0.00
standresp ~ over2+under1+class	-35.39	6.39	0.00
standresp ~ over2+class	-35.31	6.47	0.00
standresp ~ over1+over2+under2+class+year+Elevation	-34.81	6.97	0.00
standresp ~ over2+under1+under2+class+Elevation	-34.73	7.05	0.00
standresp ~ over1+over2+under1+under2+class	-34.72	7.06	0.00
standresp ~ over2+under2+class+Elevation	-34.65	7.13	0.00
standresp ~ over1+over2+under1+under2+class+year	-34.52	7.26	0.00
standresp ~ over1+over2+under2+class	-34.50	7.28	0.00
standresp ~ over1+over2+under1+under2+class+Elevation	-33.43	8.36	0.00
standresp ~ over1+over2+under1+under2+class+year+Elevation	-33.34	8.44	0.00
standresp ~ over1+over2+under2+class+Elevation	-32.70	9.08	0.00

Figure 1. The full NMDS plots shown in figure 2 of the manuscript with site scores added.

Squares indicate sites sampled in 2016, circles indicate sites sampled in 2017.

