Research Article

Habitat Selection and Spatiotemporal Interactions of a Reintroduced Mesocarnivore

MITCHELL A. PARSONS,[1,2] *University of Washington, Box 352100, Seattle, WA 98195-2100, USA*

JEFFREY C. LEWIS, *Washington Department of Fish and Wildlife, PO Box 43200, Olympia, WA 98504-3200, USA*

BETH GARDNER, *University of Washington, Box 352100, Seattle, WA 98195-2100, USA*

TARA CHESTNUT, *National Park Service, Mount Rainier National Park, 55210 238th Avenue E, Ashford, WA 98304, USA*

JASON I. RANSOM, *National Park Service, North Cascades National Park Service Complex, 810 State Route 20, Sedro-Woolley, WA 98284, USA*

DAVID O. WERNTZ, *Conservation Northwest, 1829 10th Avenue W, Suite B, Seattle, WA 98119, USA*

LAURA R. PRUGH, *University of Washington, Box 352100, Seattle, WA 98195-2100, USA*

ABSTRACT Habitat quality and quantity are key factors in evaluating the potential for success of a wildlife translocation. However, because of the difficulty or cost of evaluating these factors, habitat assessments may not include valuable information on important habitat attributes including the abundance and distribution of prey, predators, and competitors. Fishers (*Pekania pennanti*) are one of the most commonly reintroduced carnivores in North America, and they are a species of conservation concern in their western range. We examined the relative importance of landscape features and species interactions in determining habitat use of a reintroduced population of fishers in the southern Cascade Mountains, Washington, USA. We used detections of prey and predators at 134 remote camera stations, remotely sensed forest structure data, and telemetry locations of fishers in a resource selection function to assess the relative importance of prey, predators, and forest structure in fisher habitat selection. Fishers selected habitats based on forest conditions and activity levels of snowshoe hares (*Lepus americanus*), whereas bobcat (*Lynx rufus*) and coyote (*Canis latrans*) activity levels did not directly affect habitat selection. The probability of fisher use increased in older stands, close to recently disturbed stands, and in areas with intermediate levels of hare activity. Bobcat and hare activity levels were positively correlated, and fishers avoided areas with the greatest hare activity, suggesting that fishers may experience a food-safety tradeoff in the study area. Temporal activity patterns in photo detections indicate that fishers may mediate this danger by avoiding bobcats temporally. Our findings suggest that fishers in Washington prefer habitat mosaics of old and recently disturbed stands where they have greater access to resting structures and hares. Management that maintains mosaics of young and old forest across large landscapes is likely to support fisher recovery. Future reintroduction efforts would benefit from an assessment of prey and predator abundance in proposed reintroduction areas before project initiation. © 2019 The Wildlife Society.

KEY WORDS bobcat, fisher, food-safety tradeoff, *Lepus americanus*, *lynx rufus*, *Pekania pennanti*, snowshoe hare, species interactions, temporal activity, Washington.

Translocations have become an increasingly common tool for wildlife conservation (Cook et al. 2010, Seddon et al. 2014, White et al. 2015). Although they are instrumental for effective conservation of many imperiled species, many reintroductions fail to establish viable populations (Fischer and Lindenmayer 2000, Seddon et al. 2014, White et al. 2015). One of the most important factors in determining reintroduction success is habitat quality (i.e., the ability of the environment to promote the survival, reproduction, and persistence of a population; Hutchinson 1957, Hall et al. 1997, Soberón 2007) in a reintroduction area

(Griffith et al. 1989, Wolf et al. 1998, Cochran-Biederman et al. 2015).

Reintroduction success can hinge on the quality of habitats across a reintroduction or recovery area, but often managers are unable to fully assess the suite of habitat factors that could influence this success because of cost, lack of data, or time (Seddon et al. 2014, Stewart et al. 2017). Managers often evaluate some aspects of habitat quality before reintroductions (Seddon et al. 2007, Cochran-Biederman et al. 2015), but reintroduction success is also influenced by more nuanced features, such as species interactions (Griffin et al. 2000, Cook et al. 2010, Fisher et al. 2014, Spurgeon et al. 2015). Consideration of species interactions is particularly important for carnivores because both prey availability and interactions with other carnivores are integral to habitat quality (Fisher et al. 2014, Spurgeon

et al. 2015). Landscape features and species interactions influence success of reintroductions, but how the relative importance of these factors varies among species requires further investigation (Griffith et al. 1989, Short et al. 1992, Jachowski et al. 2011, Mundahl et al. 2012).

Although assessing landscape features and species inter-actions before reintroductions is ideal, reintroductions themselves offer research opportunities. Examining post-release habitat selection can provide insights into the relative importance of different habitat characteristics and information for future reintroduction efforts (Sarrazin and Barbault 1996, Facka 2017). The fisher (*Pekania pennanti*) is a frequently reintroduced forest carnivore in North America, and improving the understanding of fisher habitat selection patterns could increase the success of future reintroductions.

Fishers occur in the boreal and temperate forest ecosystems of North America in forests that provide complex vertical and horizontal structure, including large diameter trees, snags, and downed trees (Powell 1993, Lewis et al. 2016). Particularly in the Pacific Northwest, fishers have been considered specialists of old-growth forests that rely on large diameter trees for den and rest sites (Zielinski et al. 2004, Raley et al. 2012, Weir et al. 2012). Trapping and logging in the early twentieth 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 eastern and central range in the northern United States and southern Canada, but fishers remain a species of conservation concern in California, Oregon, and Washington, USA (Powell 1993, Lewis et al. 2012, Lapoint et al. 2015, Stewart et al. 2017).

Many reintroductions have been attempted to assist fisher recovery, but these attempts have been more successful in eastern North America than in western North America (Lewis et al. 2012, but see Stewart et al. 2017). 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, Lapoint et al. 2015). Examining the importance of forest structure, prey, and predators in fisher habitat selection can guide feasibility assessments and implementation of future reintroductions. This information can also guide land managers tasked with providing forested landscapes that support self-sustaining populations of fishers (Facka 2017).

Research on fisher habitat selection has focused on their selection of forest structure at several spatial scales (Raley et al. 2012, Lapoint 2013, Sauder and Rachlow 2015), and especially at the scale of den and rest sites (Zielinski et al. 2004, Weir et al. 2012, Happe et al. 2014). Previous research has also identified important influences of prey and predators on fisher survival (Wengert et al. 2014, Gabriel et al. 2015) and body condition (Kirby et al. 2018). The influence of prey and predators on habitat selection is frequently hypothesized (Raley et al. 2012, Sauder and Rachlow 2015, Lewis et al. 2016) but has rarely been tested for fishers (Arthur et al. 1989). Logging activities

can alter the availability of preferred prey, including snowshoe hares (*Lepus americanus*; Griffin and Mills 2007), possibly limiting the success of reintroductions and the growth of remnant populations (Kirby et al. 2018). Logging and land conversion may have also increased the presence of bobcats (*Lynx rufus*) and coyotes (*Canis latrans*) in historical fisher habitat, thereby increasing predation risk (Wengert et al. 2014, Gabriel et al. 2015) and competition for snowshoe hares (Spencer et al. 2015, Sweitzer et al. 2016).

Fishers in western North America coexist with a more diverse carnivore community than fishers in the east (Lapoint et al. 2015), and intraguild predation is a major mortality source in California, particularly from bobcats and cougars (*Puma concolor*; Wengert et al. 2014, Gabriel et al. 2015). Bobcats and coyotes act as competitors and predators for fishers (Wengert et al. 2014), leading to a possible food-safety tradeoff for fishers (Bischof et al. 2014), where areas with abundant prey for fishers may also have a high abundance of bobcats and coyotes.

We studied a reintroduced fisher population in the southern Cascade Mountains in Washington to evaluate the influence of forest structure and the spatiotemporal activity patterns of hares, bobcats, and coyotes on fisher habitat selection. To balance needs for habitat structure, prey, and safety, we predicted that fishers would select for 1) older forests, 2) areas with greater activity levels of hares, and 3) areas with lower activity levels of bobcats and coyotes. If a food-safety trade-off exists for fishers, we expected that fishers would select for intermediate levels of hare activity to balance the trade-off between foraging efficiency and predation risk. Further, we expected fishers to temporally avoid bobcats and coyotes to reduce competition and predation risk. Coyotes and bobcats are predominantly crepuscular or nocturnal (Arjo and Pletscher 1999, Neale and Sacks 2001, Elizalde-Arellano et al. 2012, Lesmeister et al. 2015), so we expected fishers to display diurnal activity patterns. We also examined sex-specific patterns of fisher habitat selection, and we expected males to be less sensitive to interactions with bobcats and coyotes because of their larger body size and relatively lower susceptibility to predation (Wengert et al. 2014).

STUDY AREA

We worked in the southern Cascade Mountains, Washington, USA, from December 2015 through September 2017. Our study area was a 10,000-km^2 region comprised of Gifford Pinchot National Forest (6,100 km^2), Mt. Rainier National Park (1,000 km^2), Washington Department of Natural Resources land (1,000 km^2), and surrounding private lands (~1,900 km^2). Conifer forests dominated this landscape, 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 several fern species. Possible prey for fishers in the study area include snowshoe hare, Douglas squirrel (*Tamiasciurus douglasii*), mountain beaver (*Aplodontia rufa*), porcupine (*Erethizon dorsatum*), and a suite of small rodents. Possible predators of fishers include coyote, bobcats, and cougars. Other conspicuous species that may compete with or provide scavenging opportunities for fishers include black bears (*Ursus americanus*), elk (*Cervus canadensis*), and black-tailed deer (*Odocoileus hemionus*). Most of the study area consists of steep and rugged ridges and river valleys, and the southern portion contains a large, moderately high-elevation (1,400 m) plateau. The elevation ranges from 37 m to 4,392 m with a mean of 964 m. The elevation of our camera stations ranged from 417 m to 1,491 m with a mean of 921 m. The study period experienced a Mediterranean climate, with warm, dry summers from June through September, cool, wet winters from November through March, and cool and wet spring and fall. The mean July and January temperatures were 25.8°C 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).

METHODS

Fisher Telemetry

From December 2015 to February 2017, we released 69 fishers into the study area from a source population in central British Columbia (Lewis et al. 2018). We first equipped each fisher with a very high frequency radio-transmitter (Holohil AI-2HM; Carp, Ontario, Canada) to allow biologists to monitor the locations, movements, and survival of released fishers. We tracked released fishers via aerial telemetry approximately once per week from December 2015 through January 2018, during 73 telemetry flights. These flights and limited ground telemetry produced 793 locations. We removed all locations <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 (error >1 km) by the pilot and observers. Handling procedures for fishers met or exceeded the guidelines of the American Society of Mammalogists and were performed in accordance with British Columbia Ministry of Forests, Lands and Natural Resource Operations Wildlife Act Permit WL 15-17879, as amended.

Camera Stations

We used the Landscape Ecology, Modeling, Mapping and Analysis (LEMMA; Ohmann et al. 2012) data set for site selection and for large-scale forest structure data. Ohmann et al. (2012) used multivariate relationships between satellite imagery, environmental variables, and field plot data to produce a 30-m resolution raster of forest structure using a gradient nearest neighbor approach. We used 5 forest structure variables from these data: age, stand height, canopy cover, basal area, and quadratic mean diameter of dominant trees. Ohmann (2012) validated the LEMMA data via ground truthing, and estimated these 5 variables had an average correlation of 0.75 (range = 0.72–0.77) with true values from field plots.

Remote cameras provide the opportunity to non-invasively survey multiple species simultaneously and address ecological questions (Burton et al. 2015, Steenweg et al. 2016). We placed remote camera stations at locations within fisher habitat that spanned a gradient of management intensity, from areas within industrial forest landscapes to those in unmanaged old-growth forest landscapes. Using the LEMMA data, we calculated the average age of 1-km^2 hexagons across the study area and categorized hexagons as young (<110 yrs), middle-aged (110–180 yrs), and old (>180 yrs) stands. We then categorized hexagons as 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 5 of 6 surrounding hexagons be the same age class and suitable for fishers (i.e., continuous 6-km^2 area). We randomly selected hexagons in each age category that met these criteria for monitoring via remote camera stations ($n = 134$ camera stations; 45 in young, 50 in middle-aged, and 39 in old stands). The mean distance between camera stations was 2.7 km (range = 0.8–12.7 km). Typical home range sizes of bobcats, coyotes, and fishers (5–100 km^2; Laundré and Keller 1984, Donovan et al. 2011, Melville et al. 2015, Sauder and Rachlow 2015) are large enough to encompass multiple camera stations. Timber management in our study area, however, occurs at a smaller scale than these species home ranges (Average Land Resources Management Plan [LRMP] unit = 9 km^2, U.S. Forest Service 2018). Because one of our goals was to assess how forest structure affected habitat selection, we designed our sampling scheme at the spatial scale of forest management actions (i.e., stand scale or timber sale scale).

From August 2016 through September 2017, we placed camera stations within 300 m of each hexagon's center, with exact locations selected to increase the likelihood of detections. For example, we placed cameras along game trails found within the 300-m search area. We sampled each location for 6 weeks, with some variation in duration due to logistics of access and camera malfunction. Each station consisted of a single 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 above the ground. We attached bait and lure at approximately 0.5–1 m above the ground on a second tree 2–4 m away from the camera (Wait et al. 2018). We placed bait at this height to keep the bait in the frame while having a substantial portion of foreground visible. Moriarty et al. (2018) found no difference in detection of Pacific martens (*Martes caurina*) with bait placed at <0.5 m or 1.4 m. We placed bait north of cameras (with few exceptions) to minimize sun glare in photos (Fig. 1). We set cameras to take a 3-photo burst with each motion detection and a delay of 5 seconds between successive triggers. We set camera sensitivity to auto. We visited camera stations after approximately 3 weeks to check batteries, replace secure digital memory cards, and refresh bait and lure. We used cameras to document the number and

Figure 1. Bait and lure set-up at a camera station. We wrapped a chicken leg in galvanized poultry wire, and poured the scent lure on moss and placed the moss in a small piece of corrugated plastic to limit washout by rain. We attached both bait and lure to the tree using bailing wire.

time of detections of fishers, hares, bobcats, and coyotes as a measure of activity level and for temporal activity modeling.

Spatial Modeling of Prey and Predator Activity

We used detections of hares, bobcats, and coyotes at camera stations to develop spatially explicit models of activity level for each species to include in the fisher resource selection function (RSF). Because home ranges of bobcats and coyotes are large enough to encompass multiple camera stations, the assumption of independence among camera stations was violated and occupancy modeling was not appropriate (MacKenzie et al. 2002, Burton et al. 2015). We used the number of independent detections per 100 camera-station nights of hares, bobcats, and coyotes as a metric of activity level for each species (Swanson et al. 2016, Rich et al. 2017). We defined independent detections as photos taken ≥60 minutes apart (Lucherini et al. 2009, de Satgé et al. 2017). We used Program Timelapse2 (Greenberg and Godin 2015) to process photos, extract date and time, and identify species.

To model spatial activity patterns of hares, bobcats, and coyotes, we used landscape data available from the United States Geological Survey (USGS; 2017) and the Washington Department of Natural Resources (2017) and conducted analyses using ArcMap10.4 (Environmental Systems Research Institute, Redlands, CA, USA). We created a 250-m buffer around each camera station location and used a custom zonal statistics tool for overlapping polygons in ArcMap 10.4 to extract elevation, slope, and aspect of each location from a digital elevation model from the USGS National Elevation Database. We then calculated the distance from each location to the nearest linear feature (any road or trail), paved road, and unpaved road. We included the season of camera deployment as a covariate as summer (Jun–Oct) or winter (Nov–May) based on the time permanent snow becomes common throughout the study area.

We modeled spatial activity levels, measured as the number of independent detections, as a function of topographic and linear features using negative binomial regression in the R package MASS (Ripley et al. 2018; R version 3.4.4, https://www.R-project.org/, accessed 15 Sep 2017). We used negative binomial regression because of overdispersion in the detection data. We did not include forest structure variables because inclusion would lead to circularity in the fisher RSF and *post hoc* evaluation revealed that topography-only models were within 2 Akaike's Information Criterion corrected for small sample sizes (AIC$_c$; Burnham and Anderson 2002) of models that included forest structure data, and R^2 values for topography-only models were better or within 0.03 of models that included forest structure data, suggesting they were well supported. We included a quadratic effect of slope to test selection for intermediate values of slope. Therefore, the predictor variables included in hare, bobcat, and coyote models were elevation, slope (including quadratic effect), aspect, distance to paved road, distance to unpaved road, distance to linear feature, and season (Table 1). We log-transformed distance to paved and unpaved roads because of highly skewed distributions. We scaled all other variables by mean and standard deviation before analyses. To test for

Table 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, in the southern Cascade Mountains, Washington, USA, between August 2016 and September 2017 ($n = 10{,}618$).

Source[a]	Description	Units	Min.	Max.	$\bar{x}$
LEMMA	Age of dominant trees	yr	0	404	104
LEMMA	Basal area of live trees >2.5 cm dbh	m²/ha	0	91	41
LEMMA	Canopy cover of all live trees	%	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	1,719	861
NED	Slope	Degrees	0	44	15
NED	Aspect	Degrees from south	0	180	89
WDNR	Distance to nearest paved road	m	12	6,264	1,750
WDNR	Distance to nearest unpaved road	m	5	8,853	483
WDNR	Distance to nearest road or trail	m	0	1,636	206
LEMMA	Distance to nearest stand <30 years old	m	0	2,271	261

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

collinearity, we calculated variance inflation factors (VIFs) for all covariate combinations and excluded combinations with VIFs > 2 from the final model set (Table S1, available online in Supporting Information). Distance to linear feature and distance to unpaved road were the only variable pair that resulted in VIFs > 2. We initially tested single-variable models for each of these variables for each species and selected the best performing variable based on AIC_c to include in the full model set.

We tested all possible combinations of these predictor variables (128 models) and selected the model with the lowest AIC_c as the top negative binomial model of detections for each species (Burnham and Anderson 2002). We assessed model fit using cross-validation. We used the top model for each species to predict the activity level of hares, bobcats, and coyotes across our study area.

Fisher RSF

We used the fisher telemetry data, forest structure variables available from LEMMA, and predicted hare, bobcat, and coyote activity levels 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). The telemetry data provided broader spatial coverage than cameras in assessing fisher habitat selection and permitted us to examine sex-specific habitat selection. Because of limited data for each individual fisher, we could not assess the composition of established home ranges in the study area. We instead assessed how the population used the entire study area based on available habitat. We compared the habitat characteristics associated with fisher telemetry locations to characteristics of 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 did not include camera detections of fishers as used points in our RSF because few cameras detected fishers, there was high overlap between camera detections and telemetry locations, and we could not consistently identify individual fishers on camera.

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 1,000 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 because large samples of available points provide a better representation of landscape availability (Manly et al. 2004, Lele and Keim 2006, Barbet-Massin et al. 2012, Northrup et al. 2013). The large ratio of available to used points results in the model predicting a low probability of use for any location. These predictions, however, are the relative probability of use, and model coefficients still estimate the response of fishers to habitat covariates and reveal habitat selection patterns (Johnson et al. 2006, Barbet-Massin et al. 2012). Because we used hare, bobcat, and coyote activity levels predicted from camera 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). After all screening, we used 460 of the original 793 telemetry locations.

We created a 250-m buffer around each fisher telemetry location and randomly selected available location and used a custom zonal statistics tool for overlapping polygons in ArcMap 10.4 to extract the average age, basal area, canopy cover, stand height, and quadratic mean diameter of dominant and codominant trees for each location. Because hares are abundant in regenerating and young forests (Arjo et al. 2007, Cheng et al. 2015), we also calculated the distance to the nearest recently disturbed stand for each point. We defined a recently disturbed stand as <30 years old. We first used the majority filter tool in ArcMap to remove clusters of <5 pixels that were more likely to be relics of sampling error and not representative of actual recently disturbed stands. We assigned points within recently disturbed stands a value of zero for distance to a recently disturbed stand. We used a 250-m buffer (0.39 km^2) to reflect the size of the average stand in Gifford Pinchot National Forest (0.2 km^2, forest stands vary at a smaller scale than LRMP units; U.S. Forest Service 2018). We repeated analyses with a 1,000-m buffer and results were consistent between 250-m and 1,000-m buffers.

To predict hare, bobcat, and coyote activity levels for the fisher RSF, we then extracted the elevation, slope, aspect, distance to linear features, distance to paved roads, and distance to unpaved roads. We used these variables and the top hare, bobcat, and coyote activity level models to predict activity level of hares, bobcats, and coyotes at each fisher telemetry and randomly selected available location. Our full covariate set was age, basal area, canopy cover, quadratic mean diameter of dominant and codominant trees, height of overstory trees, distance to recently disturbed stand, hare activity level, bobcat activity level, and coyote activity level. We included a quadratic term for hare activity level to test for selection for intermediate levels of hare activity, reflecting a possible food-safety tradeoff. We also included interactions between sex and all covariates to test for habitat selection differences between the sexes. We scaled all variables by mean and standard deviation before analyses.

Because of high correlations among forest structure variables (Table S1), we began with single-variable models to identify the best forest structure covariate using AIC_c. This test identified stand age as the best forest structure variable. To test for collinearity among all variables, we calculated VIFs for all covariate combinations and excluded combinations with VIFs > 2 from the final model set. Hare and bobcat activity levels were the only variable pair that resulted in VIFs > 2 and we excluded models with both terms from the final model set. We ran all possible models ($n = 216$) and we selected the model with the lowest AIC_c as the top model (Burnham and Anderson 2002). We tested model goodness of fit with k-fold cross-validation (Boyce et al. 2002).

Temporal Activity

We assessed temporal activity patterns 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. 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 ranged from 0 to 1, with a value of 1 indicating perfect overlap and a zero indicating no overlap as

$$\hat{\Delta}_1 = \int_0^1 \min\{\hat{f}(t), \hat{g}(t)\}dt \qquad (1)$$

where $\hat{f}(t)$ and $\hat{g}(t)$ are the estimated activity densities for 2 species (Ridout and Linkie 2009). Ridout and Linkie (2009) reported $\hat{\Delta}_1$ to perform better than other overlap measures with small sample sizes. High overlap suggests 2 species are active during the same times of day. We used Watson's test for homogeneity of circular data to test differences in activity patterns between fishers, bobcats, and coyotes (Frey et al. 2017).

RESULTS

After screening locations, we used locations from 63 fishers, 37 females and 26 males. On average, we monitored fishers for 346 days (range = 62–695) before mortality or signal loss. We collected 460 usable locations from these fishers, averaging 7.3 locations/animal (range = 1–44). The average distance between successive locations was 8.0 ± 0.78 (SE) km, with little variation between males (7.3 ± 1.1 km) and females (8.3 ± 0.99 km).

We deployed 134 camera stations for 6,016 camera-station nights. We deployed the majority (110) of these camera stations during the snow-free months. Each camera station was deployed and functional for a mean duration of 45 days, with a range of 17–84 days due to malfunctions, displacement by wildlife, and limited winter access. We documented 53 independent detections of fishers ($\bar{x}$ = 0.40/camera, range = 0–15), 54 of bobcats (0.40, 0–6), 83 of coyotes (0.62, 0–25), and 317 of hares (2.37, 0–48). Naive occupancy of hares, bobcats, coyotes, and fishers was 0.46 (62 of 134 stations), 0.24 (32 stations), 0.22 (30 stations), and 0.09 (12 stations), respectively. Forty-six camera stations did not detect any of these species (Fig. 2).

The top hare spatial activity model indicated that hare activity levels increased at higher elevations, on northerly aspects, and closer to both paved and unpaved roads. Activity levels of bobcats increased on northerly aspects and closer to unpaved roads. Activity levels of coyotes increased on shallower slopes, closer to linear features, and closer to paved roads (Tables 2 and 3). Season was not included in the top spatial activity model for any species, suggesting little effect of season on our detection rates.

Among the forest structure covariates evaluated in the fisher RSF, stand age explained the most variation (Table 4). The top fisher RSF model included main effects of stand age and distance to recently disturbed stand, a quadratic effect of predicted hare activity level, and an interaction between sex and hare activity level (Table 5). Both sexes selected for locations in older stands and locations closer to recently disturbed stands. The quadratic response to hare activity level suggested that fishers avoided areas with the lowest and highest predicted levels of hare activity and selected areas with intermediate predicted levels of hare activity. The interaction term indicated males had a weaker selection for hares than females (Fig. 3; Table 6). Predicted snowshoe hare activity level and bobcat activity level were positively correlated (r = 0.58, $P \le 0.001$), which resulted in variance inflation and precluded both variables being included in the same model. The top RSF model tested well in cross-validation, indicating good model fit (Fig. S1; Spearman rank correlation: r_s = 0.88, $P < 0.001$, available online in supporting information).

Fishers displayed a predominantly diurnal activity pattern with the highest activity from morning to midday. Temporal activity patterns of fishers contrasted with coyotes and bobcats, which were predominantly nocturnal and crepuscular, respectively (Fig. 4). Even with these temporal activity peaks, all species were active during the day and night, resulting in moderate to high overlap in temporal activity. Fishers showed different temporal activity patterns than bobcats ($\hat{\Delta}_1$ = 0.71, 95% CI = 0.57–0.85; Watson's test for homogeneity, $P < 0.05$) and coyotes ($\hat{\Delta}_1$ = 0.74, 95% CI = 0.61–0.86, $P < 0.01$). Bobcats and coyotes did not have different activity patterns ($\hat{\Delta}_1$ = 0.80, 95% CI = 0.68–0.91, $P > 0.1$).

DISCUSSION

We examined habitat selection of reintroduced fishers, which were recently released in the southern Cascade Mountains of Washington without prior assessment of the abundance and distribution of prey or predators within the reintroduction area. Our findings revealed complex relationships between multiple aspects of habitat for fishers, and that the highest quality habitats in terms of forest structure may not be the highest quality in terms of food and safety. We found that fishers selected for old forests, which provide large diameter trees and snags necessary for den and rest sites (Zielinski et al. 2004, Weir et al. 2012, Aubry et al. 2013). However, fishers in our study area also selected these forests near recently disturbed stands, and they selected areas that had intermediate activity levels of snowshoe hares, which prefer young, regenerating stands (Lewis et al. 2011). These results suggest that fishers balance their needs for forest structure and prey, and that homogeneous land cover will not provide for all the needs of fishers. The strong positive correlation between predicted activity levels of snowshoe hares and bobcats suggests that areas that provide the most prey are also potentially the most dangerous for fishers, indicating a food-safety tradeoff. Our results suggest fishers mediate this tradeoff by avoiding areas of the highest hare activity levels or having distinct temporal activity patterns from bobcats. Our findings highlight that species interactions are important factors in habitat selection and incorporating these considerations may be valuable for

reintroduction planning, even for a generalist predator such as the fisher. Evaluating these factors before release can increase understanding of habitat requirements, informing the feasibility of a reintroduction program and the selection of release locations.

Selection by fishers for older stands likely reflects a reliance on complex forest structure for den and rest sites (Lofroth et al. 2011, Raley et al. 2012, Aubry et al. 2013). We found that fishers selected old stands and old stands near recently disturbed stands. Sauder and Rachlow (2015) similarly reported that home ranges of fishers in Idaho contained forest stand edges and closed canopy forest, and Facka (2017) reported that fishers could persist and reproduce on a managed forest landscape. Recent research on fishers in eastern North America has also reported that home ranges of some fishers incorporate edges, including semiurban areas, where prey may be particularly abundant (Lapoint 2013, Scharf et al. 2016, Ellington et al. 2017).

The growing evidence that fishers use edges, both forest and semiurban, suggests that they are more flexible in their habitat needs than previously thought. Although the extensive old-growth temperate rainforest of the Pacific Northwest is a unique land cover type for fishers (Powell 1982), current forest cover in this region is representative of much of western North America, with mosaics of young and old forests occurring broadly in this ecosystem (Weir et al. 2009, Sauder and Rachlow 2014, Facka 2017). Additionally, federal lands in Washington, Oregon, and California are all managed under the Northwest Forest Plan (NWFP; U.S. Department of Agriculture, and U.S. Department of the Interior 1994), which requires preservation of late-successional reserves within a matrix of limited harvest activities. These strategies likely create habitat for fishers, and lands managed under the NWFP currently support fisher populations. Future research that explicitly addresses the extent of mature forest needed within forest mosaics to
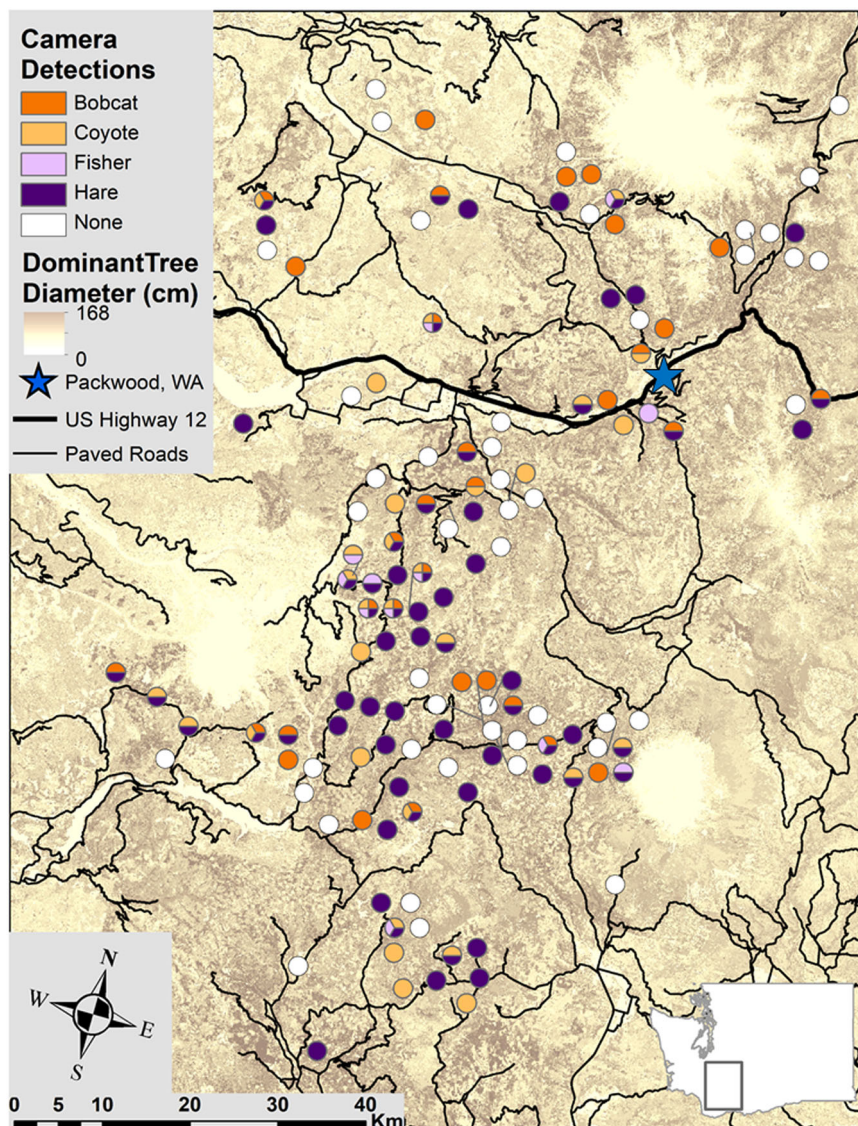

Figure 2. Locations and species detected for 134 camera stations in the southern Cascade Mountains, Washington, USA, August 2016–September 2017. We deployed each camera station for approximately 6 weeks.

Table 2. The top 5 negative binomial regression models for coyote, bobcat, and hare detections from 134 camera stations in the southern Cascade Mountains, Washington, USA. We deployed each camera for approximately 6 weeks and camera surveys occurred between August 2016 and September 2017. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC_c).

Species	Model[a]	AIC_c	ΔAIC_c	AIC_c weight
Hare	Elev + aspect + unpaved + paved	601.37	0.00	0.09
	Elev + aspect + unpaved	601.63	0.27	0.08
	Elev + aspect + unpaved + slope	602.14	0.78	0.07
	Elev + aspect + unpaved + slope + paved	602.62	1.26	0.05
	Elev + aspect + unpaved + paved + sea	602.89	1.53	0.05
Bobcat	Aspect + unpaved	283.71	0.00	0.08
	Aspect + unpaved + season	284.74	0.03	0.08
	Aspect + unpaved + slope^2	284.29	0.59	0.06
	Aspect + unpaved + season + slope^2	284.90	1.19	0.05
	Aspect + unpaved + paved	285.15	1.45	0.04
Coyote	Slope + linear + paved	280.97	0.00	0.19
	Slope + linear + paved + elev	281.77	0.80	0.13
	Slope + linear + paved + season	282.36	1.40	0.10
	Slope + linear + paved + elev + season	282.76	1.79	0.08
	Slope + linear + paved + slope^2	283.08	2.11	0.07

[a] Elev = elevation; linear = distance to linear feature (road or trail); paved = distance to paved road; unpaved = distance to unpaved road.

support fishers would be particularly valuable, and could focus on measures of patch size, patch configuration, and harvest intervals within these mosaics (Facka 2017).

Our study is unique in its explicit inclusion of prey in habitat selection modeling for fishers. Selection by fishers for intermediate activity levels of hares, as indicated by the inclusion of the quadratic effect in the top model, indicates that an assessment of prey populations before a reintroduction could provide valuable information for reintroduction planning. Male and female fishers selected for areas with intermediate activity levels of hares, but females showed stronger selection than males. This stronger selection by females could be explained by the energetic costs of reproduction and kit rearing, and their smaller home ranges (Sauder and Rachlow 2014, Lewis et al. 2016), which would make females more dependent on proximity and consistent access to prey. Although feasibility assessments often discuss

prey availability, an investigation of prey populations is uncommon before a reintroduction (Serfass et al. 1994, Apps 1995, Breitenmoser et al. 2001, Hiller 2015). Assessment of prey populations before reintroductions appears to be more common for specialist predators (Steury and Murray 2004, Jachowski et al. 2011, Licht et al. 2016), but the response of fishers to hare activity levels may indicate the importance of these assessments for generalist predators as well. For example, Kirby et al. (2018) hypothesized reduced body fat in Wisconsin fishers could be due to reduced abundance of snowshoe hares. It may be particularly important to evaluate the presence of large-bodied prey, such as hares, because consumption of large-bodied prey has been linked to expanding fisher populations (Lapoint et al. 2015).

Selection by fishers for sites with intermediate activity levels of hares and avoidance of sites with the highest activity levels of hares may indicate a food-safety tradeoff. Although fishers did not show spatial avoidance of bobcats, bobcats were positively associated with hares, meaning that sites where hares were most prevalent could also be the riskiest for fishers. Food-safety tradeoffs are not uncommon (Pomeroy and Lindström 2006, Hammerschlag et al. 2010, Emerson and Brown 2015), and highlight the challenges faced by mesopredators seeking prey (Bischof et al. 2014) and the challenges for reintroducing species in areas with numerous sympatric carnivores. By selecting sites with intermediate levels of prey activity, fishers may be responding to the risk of competition and predation

Table 3. Parameter estimates, standard errors (SE), and P values for the top negative binomial regression models for the number of snowshoe hare, bobcat, and coyote detections at 134 camera stations in the southern Cascade Mountains, Washington, USA, August 2016 through September 2017. We deployed each camera for approximately 6 weeks. All parameters estimates are on the log scale.

Species	Parameter	Estimate	SE	P
Hare detections	Intercept	6.16	1.54	<0.001
	Aspect	0.72	0.20	<0.001
	Elevation	0.83	0.26	0.001
	Distance to unpaved road	−0.49	0.14	<0.001
	Distance to paved road	−0.31	0.19	0.098
Bobcat detections	Intercept	2.05	0.91	0.023
	Aspect	0.66	0.24	0.007
	Distance to unpaved road	−0.44	0.16	0.006
Coyote detections	Intercept	4.70	1.63	0.004
	Slope	−1.19	0.30	<0.001
	Distance to linear feature	−0.88	0.39	0.024
	Distance to paved road	−0.81	0.24	<0.001

Table 4. Model rankings of the 5 single-variable resource selection function (RSF) models to select the top forest structure covariate to include in our final RSF model for fishers in the southern Cascade Mountains, Washington, USA. Models are based on telemetry data collected from January 2016 through January 2018 and we ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC_c).

Model	AIC_c	ΔAIC_c	AIC_c weight
Age	7,119.55	0.00	1
Basal area	7,170.50	50.95	0
Tree diameter	7,188.11	68.55	0
Canopy cover	7,211.18	91.62	0
Height	7,214.99	95.44	0

Table 5. The top 5 resource selection function models for fishers in the southern Cascade Mountains, Washington, USA, based on telemetry data collected from January 2016 through January 2018. We ranked models using Akaike's Information Criterion corrected for small sample sizes (AIC_c).

Model[a]	AIC_c	ΔAIC_c	AIC_c weight
Age + disturbed + sex × hare + hare^2	6,982.69	0.00	0.26
Age + disturbed + sex × hare + hare^2 + coyote	6,984.24	1.55	0.12
Sex × age + disturbed + sex × hare + hare^2	6,984.35	1.66	0.11
Age + sex × disturbed + sex × hare + hare^2	6,984.54	1.85	0.10
Sex × age + disturbed + sex × hare + hare^2 + coyote	6,985.90	3.21	0.05

[a] Age = stand age; coyote = coyote activity level; disturbed = distance to recently disturbed stand; hare = snowshoe hare activity level; sex = sex of fisher.
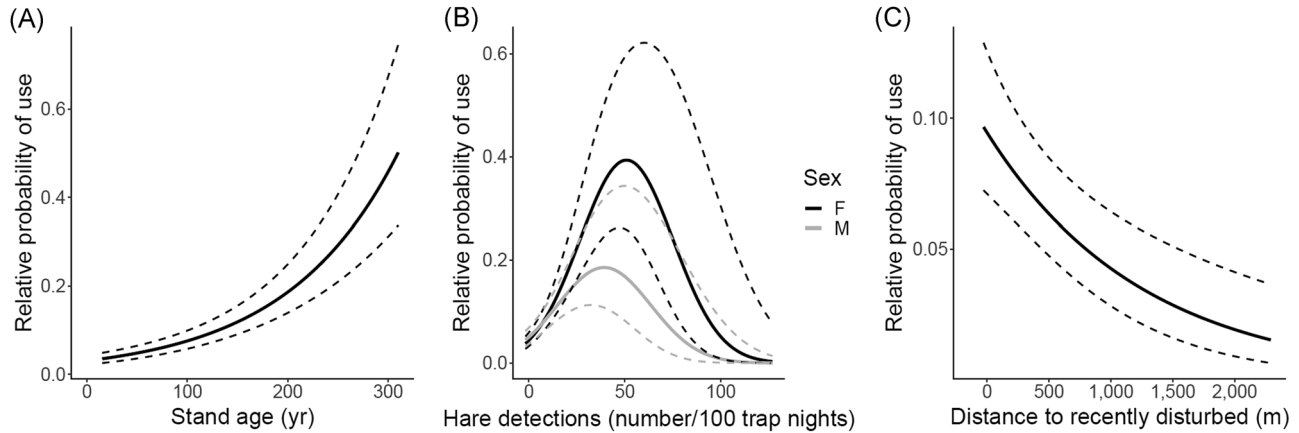
Figure 3. Predicted response curves from top resource selection function (RSF) for fishers. Plots show relative probability of use across the measured range of stand age (A), snowshoe hare activity level (B), and distance to recently disturbed stand (C). The hare plot shows the interactions with sex with females (F) in black and males (M) in gray. Dashed lines represent 95% confidence intervals on the prediction. We collected the telemetry data used in the RSF from January 2016 through January 2018 in the southern Cascade Mountains, Washington, USA.

from bobcats. It may be that intermediate abundances of hares are enough to support fishers because they exploit other prey species in these areas while also minimizing their risk to bobcat predation.

Fishers may also mediate the potential food-safety tradeoff through temporal avoidance of bobcats; bobcats and fishers had significantly different temporal activity patterns. The diurnal activity peak of fishers may indicate temporal avoidance of bobcats, but testing this hypothesis would require a better understanding of typical fisher activity patterns in areas with and without bobcats, which are unclear (Arthur and Krohn 1991, Powell 1993, Paragi et al. 1994, Weir and Corbould 2007). Our interpretation of a food-safety tradeoff relies on the assumption that bobcats pose a threat to fishers. Although McLellan et al. (2018) identified fishers as a

predator of lynx (*L. canadensis*) in Maine, we think our assumption is sound because of the prevalence of bobcats as predators of fishers in California, but future work should assess fisher–bobcat relationships throughout their range (Wengert et al. 2014, Gabriel et al. 2015). Food-safety tradeoffs could pose a significant risk to reintro-duction efforts, particularly if a reintroduced species lacked familiarity with local predators and thus lacked effective antipredator responses (Griffin et al. 2000).

When 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 selected the highest quality habitat and that our data may indicate fisher selection of the highest quality habitats available. These animals, however, did not arrive with complete information about the new landscape, 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 after 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 selected habitats, and at a broad level our analysis does reveal habitat selection patterns of the population. Our work also provides a baseline to assess how habitat selection can change over generations and as

Table 6. Parameter estimates and bootstrapped confidence intervals of the top fisher resource selection function model based on telemetry data collected from January 2016 through January 2018 in the southern Cascade Mountains, Washington, USA. Parameter estimates are on the logit scale.

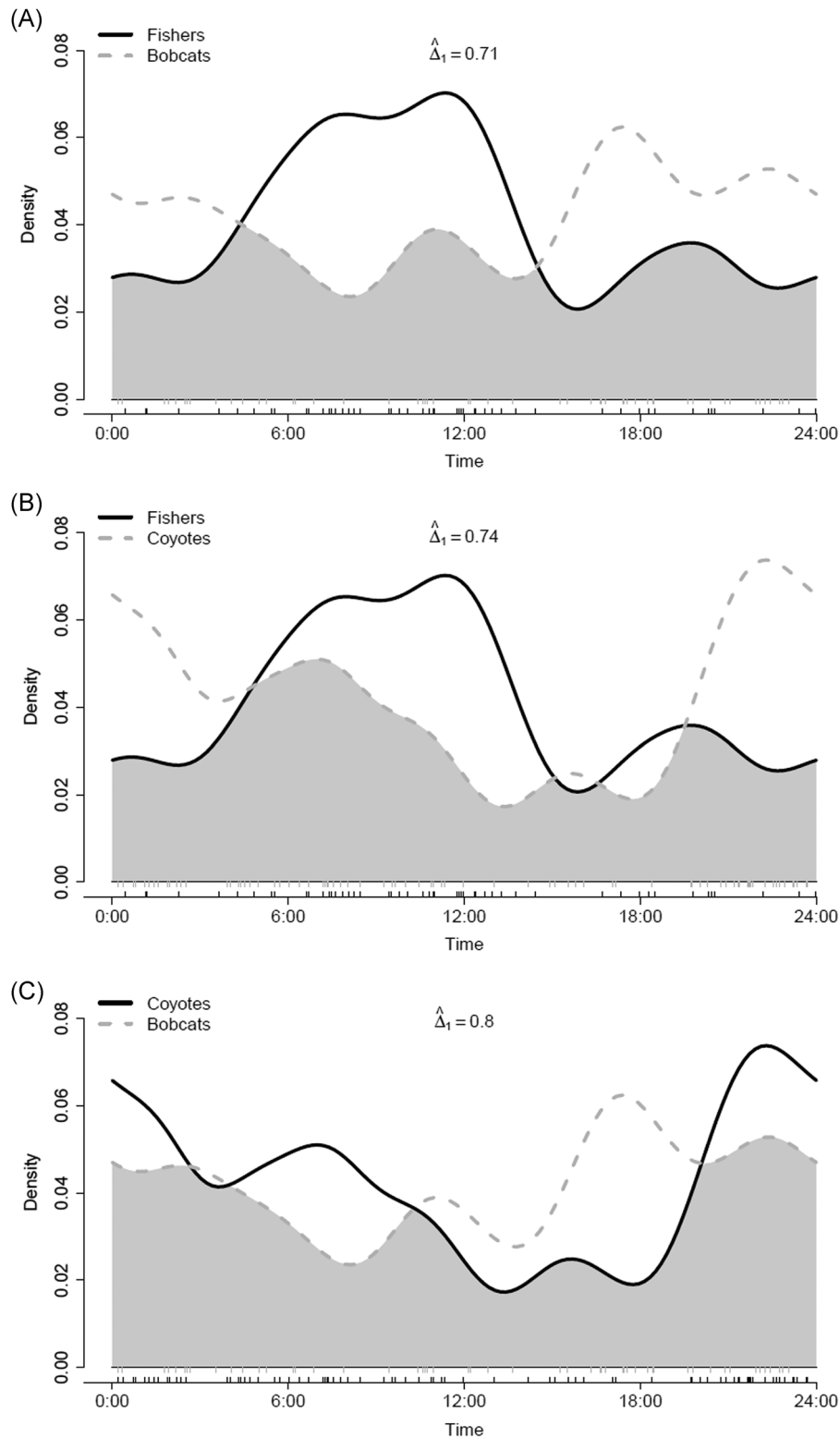| Parameter	Estimate	95% CI Lower	95% CI Upper
Intercept	−7.85	−7.88	−7.57
Stand age	0.53	0.52	0.63
Distance to disturbed stand	−0.23	−0.24	−0.11
Predicted hare activity level (females)	0.65	0.63	0.79
Predicted hare activity level (males)	0.48	0.46	0.63
Squared predicted hare detections	−0.06	−0.07	−0.04

Figure 4. 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 stations in the southern Cascade Mountains, Washington, August 2016 through September 2017. Plots are kernel density estimates of activity and $\hat{\Delta}_1$ is a measure of activity overlap between species (Ridout and Linkie 2009). We deployed each camera for approximately 6 weeks.

populations grow. Long-term assessment of habitat selection of reintroduced species could assess if released animals change habitat selection patterns with experience, or if there are differences in habitat selection between reintroduced and locally born individuals.

Although fishers were once part of this landscape, they have been absent from our study area for ≥ 50 years. Habitat characteristics, species distributions, and species dynamics have changed in this time. Additionally, the reintroduced animals came from a different system and may have selected

habitats differently from fishers that historically occurred in the southern Cascade Mountains of Washington. Reintroduced animals were captured from a managed, mosaic landscape in central British Columbia that has a history of disturbance including 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 included hares, red squirrels (*Tamiasciurus hudsonicus*), 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 selected habitat patterns that were familiar to them in the new landscape. Assessing habitat selection patterns of different source populations translocated to the same area could reveal effects of the founder population on habitat selection patterns.

MANGEMENT IMPLICATIONS

Selection for forest edges by fishers suggests fishers may be able to exist in areas previously considered unsuitable. As managers seek to recover this species, understanding the value of forest edges could increase prospective areas for reintroductions and recovery efforts. Differences in forest structure needs of fishers and snowshoe hares indicate that forest mosaics of young and old stands will provide habitat for fishers where snowshoe hares are an important prey source. Further, because of the positive correlation between bobcat and hare activity levels, and selection by fishers for areas with intermediate hare activity, successful reintroductions of fishers throughout their West Coast range will require coexistence with bobcats. Therefore, selecting reintroduction areas where forestry practices maintain individual large trees, snags, and logs that fishers use as protective cover from predators will be important (Zielinski and Gray 2018). With increasing human effects on wildlife habitats, we encourage managers to explicitly evaluate species interactions and prey availability, and the relationships between these factors.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.