FINDING FISHERS: DETERMINING THE DISTRIBUTION OF A RARE FOREST MESOCARNIVORE IN THE NORTHERN ROCKY MOUNTAINS

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FINDING FISHERS: DETERMINING THE DISTRIBUTION OF A RARE FOREST MESOCARNIVORE IN THE NORTHERN ROCKY MOUNTAINS

By

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B. S., McGill University, Montreal, Canada, 2011

Thesis

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Fisher Occupancy in the Northern Rocky Mountains: Establishing a Spatial Framework and Method for Monitoring and Examining Spatial and Temporal Overlap with Competitors

Co-Chairperson: Dr. Paul M. Lukacs
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ABSTRACT

The Northern Rocky Mountain fisher population (*Pekania pennanti*), is classified as a Species of Greatest Conservation Need and is of special concern to state, federal, and tribal entities. In this thesis, we present methods to effectively survey fishers across the northern Rockies of Idaho and Montana, and provide estimates of fisher distribution at a population range-wide scale through occupancy analyses. We also assess factors that influence fisher occurrence through covariate analyses and identify core fisher habitat in the northern Rockies through spatial occupancy modeling. By sampling broadly across the landscape, we provide baseline distributional data for comparison against future monitoring efforts. Additionally, we use data from camera traps to evaluate previously unexplored patterns of co-occurrence between fishers and four sympatric larger predators found throughout the northern Rockies. We examine spatiotemporal associations through two-step multi-species occupancy analyses and daily activity pattern overlap. Effective monitoring allows us to better understand the current status of a population of concern, assess changes in population trends, and determine the factors that influence these trends.
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Chapter 1

Finding fishers: Determining fisher distribution in the Northern Rocky Mountains

Abstract

Monitoring rare and elusive carnivores is inherently challenging as they often occur at low densities and require more resources to effectively assess status and trend. Fishers (Pekania pennanti) are elusive mesocarnivores in the mustelid family and are endemic to North America. The Northern Rocky Mountain fisher population is of special concern to conservation and management agencies and has been petitioned for listing as threatened many times under the Endangered Species Act. As part of a large-scale, multi-state monitoring effort, we estimated fisher occupancy in the northern Rockies and determined the extent of fisher presence in western Montana. During the winter of 2018-2019, we deployed over 320 remotely-trigged cameras and hair snares in randomly selected, spatially-balanced 7.5 km x 7.5 km grid cells across western Montana, Idaho and eastern Washington. We divided grid cells into two habitat strata based on the proportion of predicted fisher habitat contained within each cell. We used single-species, single-season occupancy modeling in a Bayesian framework to estimate fisher occupancy and detection probabilities across their Northern Rocky Mountain range. We assessed factors that influence fisher distribution through occupancy modeling that considered existing predicted fisher habitat, site-level environmental characteristics, and the influence of historic translocations and historic harvest. We used a spatial occupancy model to determine patterns in the spatial distribution of fishers across the northern Rockies. We detected fishers in 32 out of 318 (10%) of
our surveyed cells, and estimated that overall, 160 out of 1143 (14%) grid cells were occupied by fisher (95% CI = [23 cells (2%), 218 cells (19%)]) across our study area. We detected a strong effect of habitat stratum on fisher occupancy, demonstrated by a higher probability of occupancy in the stratum with the greater proportion of predicted habitat. Our covariate model demonstrated that fisher occupancy was positively associated with our stratum that contained a greater proportion of predicted fisher habitat and proximity to nearest historic (2000-2015) harvest location. Fisher occupancy was weakly and positively associated with increased canopy cover and greater distance from historic translocation sites. Our spatial model identified two core areas with higher predicted occupancy estimations: a larger area across the Idaho Nez Perce-Clearwater National Forest, and a smaller area in the Cabinet Mountain Range crossing the northern border of Idaho and Montana. Determining the current distribution of fishers across their northern Rocky Mountain range provides baseline occupancy estimates for repeated monitoring and allows biologists to monitor trends in fisher distribution over time. By incorporating our increasing understanding of fisher habitat with contemporary analytical techniques, we determined the current distribution of fishers in the northern Rockies, improved our definition of suitable fisher habitat, and identified core habitat for future conservation and management efforts.
Introduction

Monitoring rare and elusive carnivores is inherently challenging as these species typically occur at low densities and are often species of conservation concern (Thompson 2004, Long and Mackay 2012). Sampling rare species is costly, requiring increased sampling effort and sampling across large areas and in difficult terrain (Thompson 2004, Mackenzie et al. 2006). Despite this increased effort, surveying rare species often results in lower sample sizes, making it difficult to confidently determine population distribution, status and trends. These challenges make long-term monitoring programs difficult to successfully implement for rare carnivores.

We often prioritize rare species for conservation due to their heightened vulnerability to disturbance and resulting greater extinction risk (Thompson 2004, Raphael and Molina 2009). Rare species often have critical conservation needs, requiring rigorous regulatory compliances. However, for many populations of rare species, too little is known to adequately implement comprehensive conservation strategies. Effective monitoring allows us to better understand the current status of these populations, assess changes in population trends, and determine the factors that influence these trends (Yoccoz et al. 2001). Additionally, monitoring rare species can identify core areas with vital habitat which can be prioritized for management and conservation efforts.

While population metrics such as abundance, survival, and recruitment provide important demographic information, evaluating these variables for rare, elusive species can be difficult, time-consuming, and expensive. Occupancy modeling is an effective tool for assessing population metrics, such as the distribution of a population, and is especially useful in the study of rare and elusive species (MacKenzie et al. 2002, 2006, Slauson et al. 2012, Fuller et al. 2016). Occupancy, often expressed by presence/absence data, can be defined as the proportion of
sample units that are occupied by the target species, and is widely used in large-scale monitoring of rare species (MacKenzie et al. 2006, Fuller et al. 2016, Manlick et al. 2017, Lukacs et al. 2020). Occupancy can be used as a proxy for distribution of a population at multiple spatial scales (e.g. across a forest or across a population’s geographic range [Lofroth et al. 2011]), which can inform management decisions at forest-wide, state-wide, and range-wide levels. Occupancy modeling can also assess the relationship between species occurrence and site-specific covariates. Once baseline occupancy estimates are determined, biologists can monitor changes in occupancy over time and can examine the effects of disturbance or management events.

Fishers (*Pekania pennanti*) are elusive mesocarnivores in the mustelid family that occur across northern North America at low-densities. Fishers historically ranged across much of the forests areas of the continent (Roy 1991, Lewis et al. 2012, Krohn et al. 2012). In the mid-19th to 20th centuries, the distribution of fishers across North America significantly contracted due to unregulated harvest, predator eradication programs, and habitat loss and fragmentation (Roy et al. 1991, Powell et al. 1993, 2012, Krohn et al. 2012, Lewis et al. 2012). Currently, fisher populations in the eastern and midwestern United States are recolonizing their range, however distributions of western populations remain restricted (Olson et al. 2014, Krohn et al. 2012, Lewis et al. 2012). In response, State Wildlife Action Plans have identified western fisher populations, including the Northern Rocky Mountain fisher population, as Species of Greatest Conservation Need and have developed strategies to conserve fishers and their vital habitat for long-term persistence.

The Northern Rocky Mountain fisher population was designated as a distinct population segment in 2011 (USFWS 2011) and is believed to have historically ranged from western
Montana through north-central Idaho and into northeast Washington, USA (USFWS 2017). Although fishers were presumed extinct in Montana and Idaho by the 1930s (Weckwerth and Wright 1968, Powell 1993), unique haplotype identification has shown that a small native population persisted in the Selway–Bitterroot Mountains (Vinkey et al. 2006, Schwartz 2007). Despite translocation efforts in the mid- to late-20th century, it is uncertain if fishers in the northern Rockies presently exist to the extent of their presumed historic range (Roy 1991, Vinkey 2003, Lewis et al. 2012, USFWS 2017). This uncertainty has contributed to repeated petitions for listing the Northern Rocky Mountain fisher population as threatened under the Endangered Species Act, most recently in 2017 (USFWS 2017). In addition, the lack of historical fisher records, including range data, has made it difficult to determine the extent of historic fisher habitat in the northern Rockies. Thus, more comprehensive monitoring strategies are needed to help inform limited conservation resource allocation.

Recent advances in identifying key characteristics of fisher habitat at multiple spatial scales in the northern Rockies has enhanced our understanding fisher habitat selection and has facilitated the creation of fisher habitat models (Olson et al. 2014, Sauder and Rachlow 2014, 2015). At fine spatial scales, fishers select for habitat characteristics that fulfill resting and denning requirements, specifically dense canopy cover and large trees, snags, and logs (Raley et al. 2012, Aubry et al. 2013, Sauder and Rachlow 2015). Within core areas of home ranges, strong predictors for fisher occupancy in the northern Rockies are forest heterogeneity, high proportion of canopy cover, and landscape edge (Sauder and Rachlow 2015). At the landscape level, Olson et al. (2014) found that tall canopy height (25-50 m), montane riparian corridors and drainages, greater mean annual precipitation, and mid-level average temperatures in the coldest month were all important variables that contributed to fisher habitat characteristics in the
northern Rockies. Sauder and Rachlow (2014) found that Northern Rocky Mountain fishers selected for mature forest in large, highly contiguous patches, and avoided open areas.

Habitat models (Olson et al. 2014, Sauder 2014) indicate core fisher habit in the northern Rockies principally occurs in Idaho, but extends into western Montana, which generally has limited high-quality predicted habitat. Despite the lack of historic (pre-1959; Weckworth and Wright 1968) records and predicted habitat, verified fisher sightings and trapping records can be found in the drier areas of western Montana (USFWS 2017). Verified observations in these drier areas may indicate that the definition of suitable fisher habitat in the northern Rockies needs to be revised.

Our objective was to establish a comprehensive, repeatable framework for monitoring the Northern Rocky Mountain fisher population across their entire geographic range. As our study provides the first year of long-term collaborative fisher monitoring, we sought to determine the current distribution of the Northern Rocky Mountain fisher population to provide baseline data as a means of evaluating future conservation efforts. These data will allow us to quantify the effects of prospective management and conservation actions by assessing any changes in fisher distribution. To guide conservation priorities and continued monitoring efforts, we also aimed to determine patterns in the spatial distribution of fishers while identifying core fisher areas in the northern Rockies. Finally, we examined the influence of predicted habitat and site-specific environmental characteristics on fisher distribution, and addressed the influence of past translocations and historic harvest (2000-2015) locations on fisher occurrence. We predicted probability of fisher occupancy would be higher in sites that contained a greater proportion of predicted fisher habitat and that were characterized by a negative topographic position index (indicating valleys and drainages, Weiss 2001), tall and dense canopy structure, low to medium
elevation, and reduced snow severity. We predicted fisher occupancy would be lower in areas farther from historic release sites and farther from locations with consistent historic harvest records.

**Study Area**

Our study area spanned the Rocky Mountain Range in western Montana, Idaho and eastern Washington, USA, including the Selkirk and Cabinet Mountains in the north down through the Bitterroot Mountains and the Nez-Perce Clearwater National Forest in the south (Figure 1). We sampled across the purported historic geographic range of the Northern Rocky Mountain fisher population, in areas categorized by predicted fisher habitat (Olson et al. 2014, Sauder 2014) as well as those with records of historic harvest and verified fisher sightings.

We overlaid a standardized survey grid with 56.25 km² (7.5 km x 7.5 km) cell size across our study area, where grid cell size was determined based on fisher female home range size (Sauder 2014). Grid cells were devised to fit precisely within the framework of a previously established wolverine (*Gulo gulo*) survey (Lukacs et al. 2020) such that large-scale, collaborative monitoring for both species can be combined in the future. We divided our study area into two strata (Figure 1), and used the proportion of modeled fisher habitat within each cell (Olson et al. 2014) to determine inclusion in the sampling frame. Our wet forest stratum contained those cells typified by warm, moist, mesic habitat that had ≥ 40% predicted fisher habitat. Our dry forest stratum contained cells that did not fall within the warm, moist habitat type but contained ≥ 15% predicted fisher habitat or were within 10 km of a recent (2002-2018), verified fisher observation. We conducted a power analysis (Appendix I) to guide sample size, resulting in increased sampling effort in the dry forest stratum (wet forest stratum: 86/450 (19%) selected
cells vs. dry forest stratum: 242/693 (35%) selected cells). We used a Generalized Random Tessellation Stratified (GRTS) sampling procedure (Stevens and Olsen 2004) to select an appropriate spatially-balanced sample of cells in our study area (Figure 1).

An additional 20 survey stations were deployed in the Idaho Nez Perce-Clearwater National Forest, as part of an intensified sampling effort examining fisher occupancy at the Nez Perce-Clearwater forest-wide scale. These stations were sampled using the same survey grid and protocols as our study, but were deployed in cells that were not part of our original GRTS selection process (Figure 1).

**Field Methods**

We surveyed selected cells in the winter of 2018-2019, as the first year of a long-term fisher monitoring study. Winter trapping improved fisher detections while reducing the possibility of damage to cameras by bears (Jordan et al. 2011, Slauson et al. 2012, Krohner and Ausband 2018). Surveying in the winter also reduced survey biases associated with fisher movement across the landscape at other times of the year (Powell 1993, Slauson et al. 2012, Sauder and Rachlow 2015).

To reduce bias in cell and site selection dictated by accessibility, we classified selected cells as either accessible or inaccessible and surveyed sites regardless of their designation. We revisited accessible stations monthly throughout the study season to collect genetic samples and replenish meat bait and long-call scent lure. An inaccessible designation was given to sites that were too remote to access in the winter or were associated with safety issues such as avalanche hazards. We deployed inaccessible stations, baited with a remote scent-pump dispenser (Robert Long, Woodland Park Zoo, Seattle WA, USA), in late fall and retrieved them in late spring after
snowmelt allowed access. Inaccessible sites were not revisited during the study season. Differences in station design between accessible and inaccessible sites are described in Appendix II.

Within each randomly selected grid cell, we chose one survey site per cell based on field judgements (i.e., high-quality fine-scale habitat characteristics described by Sauder and Rachlow 2014, 2015), while considering predicted habitat (Olson et al. 2014, Sauder and Rachlow 2014) if present within the cell. We constrained survey site locations to be > 2 km from any adjacent station, > 200 m from a road or trail, and > 500 m from a campground. Each baited survey station consisted of a motion-triggered Reconyx™ camera (RECONYX® Inc. Holmen, WI, USA) and a noninvasive tree-mounted hair snare. We positioned cameras so that the detection frame included the bait and hair snare on the tree as well as the ground at the base of the tree. This allowed us to capture animals climbing the bait tree as well as those walking in front of the camera. We baited accessible sites with roadkill game meat and a long-call scent lure. We baited inaccessible sites with a scent pump dispenser that dripped a small amount of liquid lure onto a cow femur once per day. More detailed field methods are further described in Appendix II.

We stored and analyzed camera images using the Colorado Parks and Wildlife (CPW) Photo Warehouse software (Ivan and Newkirk 2016). We recorded species presence at each station, and considered multiple individuals detected in the same image as independent detections. The U.S.D.A. Forest Service Rocky Mountain Research Station (RMRS; Missoula, Montana, U.S.A) performed DNA analysis down to species and haplotype.
Statistical Analyses

We used a single-season, single-species occupancy model as described by MacKenzie et al. (2002, 2006) and assessed detection probability, $p$, to account for false absences (i.e., an individual is not detected but is still present in the cell). We defined the probability of occupancy ($\psi$) as the probability that a randomly selected cell in the study area contained at least one fisher (i.e., fisher(s) were present in the cell). We defined detection probability ($p$) as the probability that at least one fisher was detected given the cell was occupied (MacKenzie et al. 2002, 2006).

We restricted our sampling period to Dec 15, 2018 - March 14, 2019 to ensure all accessible cell deployments were complete, while also avoiding the start of the fisher breeding season in the spring (Powell 1993, Sauder and Rachlow 2015). We divided this sampling period into three, 30-day occasions and created an associated encounter history for each camera station.

We completed three separate occupancy analyses including regional occupancy estimation, occupancy covariate analysis and spatial occupancy analysis. Determining the probability of occupancy at a state-wide level (i.e. Idaho and Montana), as well as across the region, provided estimates beyond the naïve occupancy calculated from surveyed cells. These regional estimates yield baseline values for comparison with future monitoring efforts. Through occupancy covariate analysis, we assessed how factors relating to our $a$ priori predictions affected fisher occurrence. Spatial occupancy analysis generated occupancy estimates for each grid cell, which allows us to identify spatial patterns of fisher distribution within the northern Rockies.

As the additional Nez Perce-Clearwater cells were outside of our original sampling design, we did not include their detection data in our regional occupancy estimates. These cells were included in our covariate analyses to increase sample size and improve precision.
Additional Nez Perce-Clearwater cells with positive fisher detections were also included in our spatial occupancy models, and were used to replace predicted occupancy with known presence (ψ = 1) for the associated grid cells. To demonstrate the applicability of our sampling frame at a smaller, forest-wide scale, we modeled predicted occupancy across the Nez Perce-Clearwater National Forest as part of a case study presented in Appendix III. We included detection information from all non-wilderness cells within the forest, both those part of our original GRTS selection as well as the additional selected cells.

**Regional Distribution**

We modeled predicted occupancy across all possible cells in our study area, including both surveyed and unsurveyed cells, while considering detection probability and testing for an effect of state and stratum. While stratum aligned with previous predicted habitat models and *a priori* biological hypotheses, parsing out predicted occupancy in our study area by state allowed us to provide information at the state level to help inform future management decisions such as changes in harvest quotas. We fit predicted occupancy models in JAGS (Plummer 2003) for 20,000 iterations of 3 MCMC chains following a burn-in of 10,000. We assessed model fit by examining posterior density plots, and assessed MCMC chain convergence by examining model trace plots and covariate $\hat{R}$ values.

**Occupancy Covariate Analysis**

Based on *a priori* predictions, we modeled occupancy as a logit-linear function of site-level environmental characteristics and topographic features, and included forest stratum (dry forest versus wet forest) as a sampling design covariate (Table 1). We obtained 30 m resolution continuous canopy structure layers (Existing Vegetation Cover and Existing Vegetation Height)
and DEM layers (elevation, aspect, and slope) from the LandFire Remap dataset (2016). We calculated topographic position index (TPI) at a 1km and 2 km neighborhood scale for each survey station using this elevation layer and the ‘spatialEco’ package in R (Evans 2019, R Core Team 2019). We used 1 km x 1 km resolution daily snow depth and snow-water equivalent (SWE) models from the National Snow & Ice Data Center (NSIDC) SNODAS dataset (NOHRSC 2019) to derive the overall daily maximum snow depth and maximum SWE at each survey site. To test for an effect of historic harvest, both incidental and regulated, on fisher occupancy, we calculated the Haversine distance (Sinnott 1984) from each survey station to the nearest historic (2000-2015) harvest location, obtained from Idaho and Montana state agencies (Figure 2). To assess the influence of proximity to historic translocation sites, we calculated the Haversine distance from each survey station to the nearest of five historic release sites in the northern Rockies (Weckwerth and Wright 1968, Roy 1991, Heinemeyer 1993, Vinkey 2003.; Figure 2). We modeled detection probability as a logit-linear function of sampling design covariates, i.e., forest stratum (wet forest vs. dry forest) and differing bait types (accessible meat bait vs. inaccessible pump stations). We standardized all continuous covariates (mean = 0 and variance = 1). We considered several covariates related to survey effort and sampling design in our detection probability analyses. We modeled detection probability as a logit-linear function of forest stratum (wet forest vs. dry forest), bait type (roadkill meat vs. pump station), and state (Idaho vs. Montana).

We tested for multicollinearity between all proposed variables by calculating Pearson correlation coefficients. If variables were highly correlated ($r \geq 0.50$), we retained the variable that was best supported by previous work as a predictor of fisher occupancy. As vegetation height was highly correlated with canopy cover ($r = 0.79$) and maximum daily snow depth was
highly correlated with maximum daily SWE ($r = 0.99$), we included canopy cover and snow water equivalent in our analyses rather than vegetation height and snow depth. Similarly, we did not include an elevation covariate due to its collinearity with maximum daily SWE ($r = 0.57$).

We evaluated heterogeneity of occupancy and detection probability across sites by modeling these parameters in a Bayesian framework along with the aforementioned covariates using:

$$\text{logit}(\theta_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_k x_{ik}$$

at site $i$ and with $k$ number of covariates associated with the site (MacKenzie et al. 2002, 2006). To examine covariate effects, we used normally distributed priors for all parameters in the logit-linear model, with a mean of zero and a precision of 0.001. All models were performed in JAGS (Plummer 2003) and run for 15,000 iterations of 3 MCMC chains following a burn-in of 5,000 iterations.

**Spatial Occupancy**

We assessed patterns of fisher spatial distribution and tested for spatial autocorrelation through a spatial occupancy model described by Johnson et al. (2013). This model allowed us to estimate occupancy over a large extent, and accounted for variation in occupancy probabilities by examining the effect of proximity of cells. We used the stocc package (Johnson et al. 2013) in R (R Core Team 2019) to fit an ICAR (intrinsic conditionally autoregressive) spatial model restricted to a 25-km threshold. Results from non-spatial occupancy analyses demonstrated the need to include habitat stratum (wet vs. dry forest) as an occupancy covariate in our spatial
model, and indicated that detection probability should be held constant. We ran our spatial model for 25,000 iterations of 5 MCMC chains following a burn-in of 5,000 iterations.

Results

Of 324 baited remote camera and hair snare stations, we excluded six from analyses due to camera malfunctions or misdirection, resulting in 318 sampled cells (Table 2). We detected fishers on camera in 32 of the 318 cells (10%), of which 18 were in the wet forest stratum and 14 were in the dry stratum (Figure 3). We detected fishers in 23 cells in Idaho and 9 cells in Montana. Our 318 functional cameras yielded 322,595 total images, including 8,547 images of fisher. Additionally, we detected fishers on camera in 9 of the 20 Nez Perce-Clearwater Idaho cells, resulting in a total of 41 cells with fisher detections across the entire region (Figure 3). When examining detections by site and by visit, genetic detections did not perform as well as cameras (Appendix IV) and thus were excluded from occupancy analyses.

We considered several covariates related to survey effort and fisher habitat in our detection probability analyses. There were no differences in detection probabilities between states ($\beta = 0.032, 95\% \text{ CI} = (-1.044, 1.109)$), forest stratum ($\beta = -0.739, 95\% \text{ CI} = (-1.745, 0.288)$), or bait type ($\beta = -0.88, 95\% \text{ CI} = (-0.959, 0.789)$). Our results supported estimating a constant, not a variable, detection probability in our occupancy analyses.

Regional Distribution

Posterior density plots demonstrated good model fit and results indicated MCMC chain convergence for all parameters ($\hat{R} \leq 1.002$ for each parameter). Detection probability for these models was held constant and was estimated at 0.52 ($95\% \text{ CI} = 0.39, 0.64$). There was no effect of state on predicted occupancy ($\beta = -0.62, 95\% \text{ CI} = (-1.64, 0.41)$), however there was a strong
effect of habitat stratum on fisher occupancy ($\beta = -1.14$, 95% CI = (-2.14, -0.21)), demonstrated by a higher probability of occupancy in the wet forest stratum (Figure 4). Predicted occupancy was highest in the Idaho wet forest, and lowest in the Montana dry forest (Table 3), resulting in an overall regional occupancy estimate of $\hat{\psi} = 0.14$ (95% CI = (0.02, 0.19). We estimated fishers occupied 160 (14%) total grid cells, 111 (24.8%) wet forest cells, 49 (7.1%) dry forest cells, 30 (6.1%) Montana cells, and 130 (20.3%) Idaho cells.

**Occupancy Covariate Analysis**

Our most general covariate model included maximum daily SWE in both linear and quadratic terms; however, examining the residual plots of the SWE covariates indicated lack of fit and we ultimately excluded SWE from our global model. Thus, our global model contained a detection probability covariate for bait type (scent pump vs. meat bait) and contained occupancy covariates for the wet forest stratum (the intercept), dry forest stratum, additional Nez Perce-Clearwater cells, canopy cover, TPI at a 2-km neighborhood, distance from nearest historic harvest location, and distance from nearest historic translocation site. Results indicated adequate model fit for our global model (Bayesian p-value = 0.73).

Our final covariate model contained occupancy covariates for the wet forest stratum (the intercept), dry forest stratum, canopy cover, distance from nearest historic harvest and distance from nearest historic translocation site (Table 4). All other occupancy and detection probability covariates had no significant effect on fisher occupancy. Detection probability was constant across sites and we estimated an overall detection probability of $p = 0.54$ (95% CI = 0.43, 0.65). This aligns with our detection probability estimate for our predicted occupancy model. Results indicated good model fit (Bayesian p-value = 0.61), and MCMC chain convergence for all parameters ($\hat{R} < 1.002$ for each parameter). Habitat stratum was the dominant predictive variable,
and dry forest was negatively associated with fisher occupancy ($\beta = -1.17$, 95% CI = (-2.04, -0.88)) compared to wet forest (the intercept). Distance to nearest historic harvest (2000-2015; incidental and regulated), was also strongly negatively associated with fisher occupancy ($\beta = -1.11$, 95% CI = (-1.82, -0.50)) indicating that shorter minimum distances had a positive effect on occupancy. Both canopy cover ($\beta = 0.37$, 95% CI = (-0.03, 0.82)), and distance to nearest historic translocation release site ($\beta = 0.40$, 95% CI = (-0.01, 0.83)) were weakly positively associated with fisher occupancy.

**Spatial Occupancy**

Our spatial model estimated detection probability at $p = 0.53$ (95% CI = 0.46, 0.60) which aligns with estimates from our non-spatial occupancy models. Due to its strong effect in non-spatial models, habitat stratum was included as a covariate in our spatial model. The spatial model indicated two core areas with higher predicted occupancy in the Northern Rockies: a large area across the Idaho Clearwater and Nez-Perce National Forests and a smaller area in the Cabinet Mountain Range crossing the border between Idaho and Montana (Figure 5).

**Discussion**

We demonstrated an effective and successful way to monitor a rare and elusive mesocarnivore population across a large geographic area in difficult, montane terrain. We defined current fisher distribution and provided the first fisher detection probability (0.52) and occupancy (0.14; 160 cells) estimates in the northern Rockies at a population range-wide scale. By sampling broadly across both probable and possible fisher habitat, we can further refine a standardized sampling area for long-term fisher monitoring. Our framework is repeatable for future fisher monitoring in the northern Rockies and can be duplicated at multiple scales, for example to determine fisher
occupancy at a forest-wide or state region-wide spatial scale. In addition, our fisher sampling framework promotes effective multi-species monitoring, and will be incorporated into ongoing wolverine monitoring efforts (Lukacs et al. 2020) into the future.

Spatial occupancy analyses identified two core areas with higher predicted occupancy estimations: a large area across the Nez-Perce Clearwater National Forest, and a smaller area in the Cabinet Mountain Range crossing the northern end of the shared border of Idaho and Montana. Our results provide empirical evidence supporting previous inference that these areas serve as core habitat for fishers within the northern Rockies (Sauder, unpublished). The prevalence of native haplotype observations in the Nez Perce-Clearwater National Forest (Appendix IV) may indicate that this core area has been of conservation importance for some time. Genetic research by Vinkey et al. (2006) and Schwartz (2007) established that the Nez Perce-Clearwater is where fishers survived their minimum population numbers, while our results from both spatial and non-spatial analyses demonstrate that fishers currently occupy this area to a greater extent. However, our results also demonstrate an absence of fisher detections in large areas across the landscape, even within predicted fisher habitat, which suggests the need for continued monitoring to address drivers of fisher distribution and reassess currently defined suitable fisher habitat. Identifying core habitat allows us to make effective use of conservation dollars, and avoid futile attempts to maintain fisher presence in areas where they are not able to persist long-term. Future conservation actions should consider prioritizing areas identified as core habitat.

Our study design prioritized detecting fisher presence to maximize precision in our occupancy estimates, which limited our power to detect covariate relationships. By selecting station sites within grid cells that optimized fisher detections, we did not sample across a broad
range of covariate values but instead restricted the extent of observed site-level environmental covariates. Any covariate fit issues or lack of associations may be best explained by this limitation. However, our ability to detect a slight association between occupancy and canopy structure demonstrates the importance of considering fine-scale habitat characteristics when defining suitable fisher habitat in the northern Rockies.

We predicted that proximity to historic translocation release sites and proximity to historic (2000–2015) harvest locations would have positive effects on fisher occupancy. While this result proved true when examining the relationship between historic harvest and probability of occupancy, we found the opposite when examining the relationship between historic translocations and fisher occurrence. While fishers appear to be mostly absent from translocation areas, we would like to note that these translocations occurred 30–60 years ago (Weckwerth and Wright 1968, Roy 1991, Vinkey 2003). Determining relative translocation success and resulting cause of absence is challenging after this extent of time. However, our genetic data presents evidence of non-native haplotypes (Vinkey et al. 2006, Schwartz 2007) in the Nez Perce-Clearwater National Forest, which may indicate that fishers have departed original release sites and converged in the core areas identified in our spatial occupancy analysis. The relationship between fisher occurrence and historic harvest may indicate fishers have persisted in the same areas for the past decades, which lends additional support to the importance of these core areas.

We addressed numerous sampling biases in our monitoring framework, which allowed us to achieve high precision in our occupancy and detection probability estimates. Surveying in the winter reduced bias associated with fisher movement across the landscape at other times of the year. Late spring surveys that coincide with fisher breeding season can be biased towards detecting males in search of a mate, fall surveys can be biased towards detecting dispersing
young, and summer surveys can be biased against detecting breeding females as they constrain movement to den locations (Powell 1993, Slauson et al. 2012, Sauder and Rachlow 2015). While winter surveys minimize biological biases, site accessibility issues often undermine winter surveys, especially in montane environments. To account for potential bias associated with winter accessibility, we surveyed inaccessible sites using remote scent pump dispensers. Our analyses demonstrated no difference in detection probability between site bait types, validating the efficacy of the pump dispensers and promoting continued use of this tool in future fisher monitoring. Finally, while the use of bait attractants in research has been viewed with scrutiny, recent studies have shown that local environmental characteristics have a greater effect on fisher movement than the presence of bait (Stewart et al. 2019). We conclude that bait is an essential tool for monitoring fishers and other rare and elusive species, as bait maximizes detection rates and protects against underestimating species distributions (Thompson 2004, Fuller et al. 2016, Stewart et al. 2019).

Determining the current distribution of Northern Rocky Mountain fishers at a population range-wide, landscape level is necessary to make scientifically sound conservation and management decisions. Our results provide baseline data for comparison against future monitoring efforts, which allows biologists to assess changes in fisher distribution due to management or disturbance events, e.g., land-use changes, logging, climate change, wildfires, translocations, or changes in harvest quotas (Weir and Corbould 2008, Lawler et al. 2012, Olson et al. 2014, Sauder and Rachlow 2015, Fuller et al. 2016). The ability to assess trends in fisher distribution and quantify the effects of these events is imperative. Although the Northern Rocky Mountain fisher population is classified as a Species of Greatest Conservation Need (SGCN) across its range, its management status varies by state. In Washington, fishers are classified as a
state-endangered species, in Idaho they are a furbearer with a closed season, and in Montana, they are a furbearer with a limited quota. Variation in management status across the three states creates the potential for future management actions to be divergent across fisher management units (FMUs) and among states. Indeed, Montana Fish, Wildlife, and Parks closed fisher harvest in the Cabinet FMU the year following data collection for this project. Therefore, when considering SGCN State Wildlife Action Plans for Northern Rocky Mountain fishers, the need for continued multi-state collaboration is apparent.

The collaboration between agencies in the Northern Rocky Mountains has allowed for the implementation of a repeatable, long-term fisher monitoring program. Our research provided the necessary first step for this long-term action plan, and defined a suitable sampling framework for fisher monitoring into the future. Future monitoring could address habitat connectivity between core areas and could reassess habitat suitability in the dry forests where fishers have persisted. Additionally, future analyses could examine the importance of rest structure use (i.e., large diameter trees, snags, and logs) and assess how the presence of these structures influences fisher occurrence in drier forest types. Our monitoring framework will guide conservation efforts in the goal of maintaining fisher distribution across all suitable habitat in the northern Rockies. Our results facilitate this possibility by quantifying fisher occupancy throughout the northern Rocky Mountain region, thus creating a platform for future fisher conservation and management to be conducted collaboratively and adaptively across three states.
Literature Cited


U.S. Fish and Wildlife Service [USFWS]. 2011. Endangered and threatened wildlife and plants; 12-month finding on a petition to list a distinct population segment of the fisher in its United States Northern Rocky Mountain range as endangered or threatened with critical habitat; proposed rule. Federal Register 76:38503-38532. June 30.


Table 1. Description of covariates with hypothesized direction of effect, associated citation, resolution and source of covariate information. LF = LandFire Remap Dataset (2016). SNODAS = National Snow & Ice Data Center: Snow Data Assimilation System. SWE = Snow-Water Equivalent. Not all covariates were included in the final model.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Description</th>
<th>Direction</th>
<th>Citation</th>
<th>Resolution</th>
<th>Source (units)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wet Forest</td>
<td>Cell Proportion of Predicted Habitat</td>
<td>Positive ↑</td>
<td>Olson et al. 2014, Sauder and Rachlow 2014</td>
<td>Grid Cell (56.25 km²)</td>
<td>1) Existing habitat models and stratification procedures</td>
</tr>
<tr>
<td>Dry Forest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CanCov</td>
<td>Site-Level Canopy Structure</td>
<td>Positive ↑</td>
<td>Olson et al. 2014, Sauder and Rachlow 2014</td>
<td>30 m</td>
<td>1) LF Existing Canopy Cover (%)</td>
</tr>
<tr>
<td>CanHeight</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2) LF Existing Vegetation Height (m)</td>
</tr>
<tr>
<td>Elev</td>
<td>Elevation</td>
<td>Negative ↓, Quadratic</td>
<td>Garton and Jones 1994, Jordan et al. 2011, Raley et al. 2012, Lewis et al. 2014</td>
<td>30 m</td>
<td>1) LF DEM Elevation (m)</td>
</tr>
<tr>
<td>TPI@1km</td>
<td>Topographic Position Index</td>
<td>Negative</td>
<td>Weiss 2001, Swartz et al. 2013, Olson et al. 2014, Evans 2019</td>
<td>1 km, 2 km Neighborhood</td>
<td>1) Calculated from LF elevation (km)</td>
</tr>
<tr>
<td>TPI@2km</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Max_SWE</td>
<td>Snow Severity</td>
<td>Negative ↓</td>
<td>Raley et al. 2012, Olson et al. 2014, Manlick et al. 2017</td>
<td>1 km</td>
<td>1) SNODAS: SWE (m)</td>
</tr>
<tr>
<td>Max_SnowDepth</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>2) SNODAS: Snow Depth (m)</td>
</tr>
<tr>
<td>Dist_Harvest</td>
<td>Distance from Historic Harvest (2000-2015)</td>
<td>Negative ↓</td>
<td>Montana Fish, Wildlife &amp; Parks; Idaho Department of Fish and Game</td>
<td>Haversine km</td>
<td>1) Calculated from nearest historic harvest site (km)</td>
</tr>
<tr>
<td>Dist_Trans</td>
<td>Distance from Historic Translocation Site</td>
<td>Negative ↓</td>
<td>Williams 1963, Roy 1991, Heinemeyer 1993, Vinkey 2003</td>
<td>Haversine km</td>
<td>1) Calculated from nearest historic release site (km)</td>
</tr>
<tr>
<td>--</td>
<td>Proximity to Cells</td>
<td>Positive ↑</td>
<td>Johnson et al. 2013</td>
<td>25 km Threshold</td>
<td>1) Spatial occupancy model (km)</td>
</tr>
</tbody>
</table>
**Table 2.** Number of grid cells sampled in the winter of 2018-19, broken down by state and habitat stratum.

<table>
<thead>
<tr>
<th></th>
<th>Wet Forest Stratum</th>
<th>Dry Forest Stratum</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Montana</td>
<td>6</td>
<td>164</td>
<td>170</td>
</tr>
<tr>
<td>Idaho</td>
<td>77</td>
<td>70</td>
<td>147</td>
</tr>
<tr>
<td>Washington</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Nez-Clearwater</td>
<td>20</td>
<td>0</td>
<td>20</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>104</strong></td>
<td><strong>234</strong></td>
<td><strong>338</strong></td>
</tr>
</tbody>
</table>
Table 3. Estimated occupancy ($\hat{\psi}$) and associated 95% credible interval overall and by region in Idaho (ID) and Montana (MT), USA.

<table>
<thead>
<tr>
<th>Region</th>
<th>$\hat{\psi}$</th>
<th>95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>ID Wet Forest</td>
<td>0.25</td>
<td>(0.16, 0.39)</td>
</tr>
<tr>
<td>MT Wet Forest</td>
<td>0.17</td>
<td>(0.05, 0.36)</td>
</tr>
<tr>
<td>ID Dry Forest</td>
<td>0.10</td>
<td>(0.04, 0.19)</td>
</tr>
<tr>
<td>MT Dry Forest</td>
<td>0.06</td>
<td>(0.03, 0.10)</td>
</tr>
<tr>
<td>Overall</td>
<td>0.14</td>
<td>(0.02, 0.19)</td>
</tr>
</tbody>
</table>
Table 4. JAGS output for final fisher covariate model derived from encounter histories from remote camera detections. Data were collected in Montana, Idaho and Washington from December 15, 2018 to March 14, 2019.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>97.5%</th>
<th>Rhat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept (\psi)</td>
<td>-1.73</td>
<td>0.37</td>
<td>-2.47</td>
<td>-1.97</td>
<td>-1.72</td>
<td>-1.48</td>
<td>-1.04</td>
<td>1.001</td>
</tr>
<tr>
<td>DryForest</td>
<td>-1.17</td>
<td>0.44</td>
<td>-2.0</td>
<td>-1.45</td>
<td>-1.17</td>
<td>-0.88</td>
<td>-0.33</td>
<td>1.001</td>
</tr>
<tr>
<td>CanCov</td>
<td>0.37</td>
<td>0.22</td>
<td>-0.03</td>
<td>0.22</td>
<td>0.37</td>
<td>0.52</td>
<td>0.82</td>
<td>1.001</td>
</tr>
<tr>
<td>HarvestDist</td>
<td>-1.11</td>
<td>0.34</td>
<td>-1.82</td>
<td>-1.32</td>
<td>-1.08</td>
<td>-0.87</td>
<td>-0.50</td>
<td>1.002</td>
</tr>
<tr>
<td>TransDist</td>
<td>0.40</td>
<td>0.21</td>
<td>-0.01</td>
<td>0.26</td>
<td>0.40</td>
<td>0.54</td>
<td>0.83</td>
<td>1.001</td>
</tr>
<tr>
<td>Bayesian p-value</td>
<td>0.61</td>
<td>0.49</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.001</td>
</tr>
</tbody>
</table>

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Figures

Figure 1. Study area for the 2018-2019 Northern Rocky Mountain fisher population monitoring effort in Montana, Idaho and northeastern Washington, USA, including sampled 7.5 x 7.5 km survey cells, and additional Nez Perce National Forest survey cells. Grid cells were randomly selected using a GRTS sampling procedure (Stevens and Olsen 2004). Based on modeled fisher habitat (Olson et al. 2014), cells were divided into two strata. The Wet Forest Stratum contained cells that fell within a warm, moist, mesic habitat type and ≥ 40% of each cell was modeled fisher habitat. The Dry Forest Stratum contained cells that did not fall within the warm, moist habitat type and ≥ 15% of each cell was modeled fisher habitat OR cells were within 10 km of a recent (2002-2018), verified fisher observation.
Figure 2. Map of historic translocated fisher release sites and historic (2000-2015) harvest locations (regulated and incidental) in Montana and Idaho, USA.
Figure 3. Map of 7.5 km x 7.5 km grid cells with remote camera fisher detections from Dec 15 2018 - March 14 2019 in Idaho and Montana, USA. During this study season, fishers were detected in 32 grid cells across the study area.
Figure 4. Predicted fisher occupancy for wet and dry forest strata in both Montana and Idaho, USA, December 2018 – March 2019. There is a strong effect of habitat stratum on fisher occupancy, shown by a higher probability of occupancy in the wet compared with the dry forest stratum.
Figure 5. Results from a spatial fisher occupancy model across 7.5 x 7.5 km grid cells in Montana and Idaho, USA, winter of 2018-2019. Warmer colors indicate higher predicted occupancy, while cooler colors indicate lower predicted occupancy.
Chapter 2

Examining patterns of co-occurrence of fishers and four sympatric competitors in the Northern Rocky Mountains

Abstract

The Northern Rocky Mountain ecosystem contains one of the most diverse carnivore communities in North America. Understanding the dynamics of competition and coexistence within predator communities is essential for the effective conservation and management of species of conservation concern, such as the fisher (*Pekania pennanti*). As a small mesocarnivore in the weasel family, fishers are vulnerable to negative interspecific interactions with other mesocarnivores as well as larger, dominant predators. However, fishers may employ mechanisms that minimize ecological overlap to facilitate coexistence with sympatric carnivore species. We analyzed data from 338 camera traps across western Montana, Idaho, and northeastern Washington, USA, spanning the geographic range of the Northern Rocky Mountain fisher population, from December 2018-March 2019. To test the hypothesis that fishers might exhibit fine-scale spatial or temporal avoidance to limit competitive interactions with these dominant carnivores, we examined fine-scale spatiotemporal associations between fishers and four of their dominant competitors: cougars (*Puma concolor*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*). We detected weak negative spatial associations between fishers and cougars and between fishers and bobcats. Contrary to our hypothesis, fishers were positively associated with wolverines. There was no evidence that fishers exhibit avoidance across the diel period to limit competitive interactions, as there was relatively high overlap in activity between fishers and their dominant competitors. Our data demonstrate that the
competitive dynamics of a diverse carnivore community is complex. We show that fine-scale fisher occurrence in the northern Rockies may be restricted by the presence of cougars and bobcats, but fishers do not appear to be constrained by coyotes or wolverines. Fishers may employ landscape-level habitat partitioning to limit antagonistic interactions with dominant competitors in the Northern Rocky Mountain ecosystem.

**Introduction**

Understanding the dynamics of predator communities is an important component of wildlife conservation. Competition among predators can affect ecological communities, predator-prey dynamics and trophic systems, as well as reintroduction and translocation efforts (Roy 1991, Noss et al. 1996, Ives et al. 2005, Stoskopf 2012, Lapoint et al. 2015). When carnivore species co-occur across a landscape, a hierarchy of relative dominance can ensue, where the dominant competitors limit the subordinate competitors and their realized niche (Begon et al. 2006, Lapoint et al. 2015). This hierarchy can be assessed by examining the interspecific interactions between sympatric competitors. These interactions can be categorized as either interference competition, demonstrated by kleptoparasitism and in extreme cases intraguild predation, or exploitation competition, demonstrated by prey switching and spatiotemporal shifts by the subordinate competitors (Begon et al. 2006, Hunter and Caro 2008, LaPoint et al. 2015). Despite the pressures of interspecific competition, coexistence between sympatric predators frequently occurs. Co-occurrence can be facilitated by mechanisms that minimize ecological overlap, including niche partitioning and spatiotemporal separation (Ives et al. 2005, Begon et al. 2006, de Satgé et al. 2017, Green et al. 2018).
Small carnivore species are under the greatest competitive pressure, as they are vulnerable to negative interspecific interactions with carnivore species of a similar size, as well as antagonistic interactions with larger, dominant predators (Polis et al. 1989, Hunter and Caro 2008, Lapoint et al. 2015, de Satgé et al. 2017). Therefore, to effectively conserve and manage an at-risk mesocarnivore species, it is important to understand the competitive dynamics of the local carnivore community.

The fisher (*Pekania pennanti*), a mesocarnivore in the weasel family Mustelidae, is a species of conservation concern in many of its western populations. As the Northern Rocky Mountain ecosystem contains one of the most extensive and diverse carnivore communities in the United States, fishers in the northern Rockies must contend with increased predator complexity and associated deleterious interspecific interactions compared to other fisher populations in North America. Previous studies have shown that despite continued conservation efforts, fishers in the northern Rockies have exhibited limited range expansion and have instead experienced an increase in range overlap with their sympatric predators (Lapoint et al. 2015, Raley et al. 2012).

Though interspecific killing of fishers is uncommon, predation has been shown to be a significant source of mortality in many western populations. In Montana, Roy (1991) found a high level of fisher mortality attributed to interspecific killing (9 of 14 mortalities) within the first five months following the 1988-1990 fisher release in the Cabinet Mountains. Roy (1991) cautioned against future translocation efforts that do not take the current local carnivore community into consideration. Heinemeyer (1993) found similarly high mortality due to predation (7 of 14 mortalities) in the first two months following the 1990-1991 reintroductions in the Cabinet Mountains. These accounts of interspecific mortality are much higher than other
translocation and general studies on fisher populations outside of the Rocky Mountains, many of which considered mortality over a longer period of years (Koen et al. 2007, Lewis 2014, Gabriel et al. 2015). Acquiring a more thorough understanding of the dynamics of co-occurrence between fishers and other sympatric carnivore species in the northern Rockies could direct future fisher translocation efforts and inform conservation recommendations.

Recent studies have successfully used remote camera traps to examine spatiotemporal relationships between competing sympatric carnivore species (Robinson et al. 2014, Sweitzer and Furnas 2016, Cusack et al. 2017, de Satgé et al. 2017, Krohner and Ausband 2018). We examined the spatial and temporal associations between fishers and their sympatric dominant carnivore species in the northern Rockies through a large-scale, baited remote camera study. How co-occurrence with other carnivore species influences the distribution and temporal activity of fishers across the landscape is a previously unexplored area of research in the northern Rockies. We limited our focal species to fishers and four carnivore species found throughout the northern Rockies that have been documented as the most frequent fisher predators in the literature: cougars (*Puma concolor*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*; Roy 1991, Krohn et al. 1995, Raley et al. 2012, Wengert et al. 2014). We used data from baited remote camera traps in conjunction with current statistical techniques to assess how the presence of these four carnivore species correlates with the occupancy and daily temporal activity patterns of fishers.

We hypothesize fishers exhibit spatial avoidance to limit competitive interactions and predict that fisher occurrence will be negatively associated with the presence of all dominant competitors. However, as the large dietary overlap of mesocarnivores has been thought to intensify competition and interspecific killing events (Donadio and Buskirk 2006, Lapoint et al.
2015), dominant sympatric mesocarnivores may have a greater effect on fisher occurrence. As cougars are an apex carnivore documented to predate on wolverines, coyotes, and bobcats (Ackerman et al. 1984, Krebs et al. 2004, Knopff et al. 2010), the presence of cougars may exclude these mesocarnivore species. Thus, we alternatively predict that fishers will be negatively associated with the presence of wolverines, coyotes, and bobcats, but will be positively associated with the presence of cougars.

If fishers do not exhibit spatial avoidance of their dominant sympatric carnivores, we hypothesize that fishers exhibit temporal avoidance to limit competitive interactions. We predict fisher detections will be negatively associated with detections of dominant competitors in time, as exhibited by a separation in daily activity patterns.

**Field Methods**

We deployed baited camera traps in the winter of 2018-2019 as part of a broad-scale fisher monitoring study (Chapter 1; Figure 1). Our study area spanned the current estimated geographic range of Northern Rocky Mountain fishers, from western Montana through north-central Idaho and into northeastern Washington, USA (USFS 2017). We divided our study area into 56.25 km² (7.5 km x 7.5 km) grid cells, where cell size corresponded to female fisher home range size (Sauder 2014). Fisher cells were designed to align within the grid system of an established wolverine survey (Lukacs et al. 2020) to allow for simultaneous monitoring of both mustelid species in the future.

Based on modeled fisher habitat (Olson et al. 2014, Sauder and Rachlow 2014), we separated grid cells into two habitat strata (Figure 1). Cells within the wet forest stratum contained a higher proportion of modeled habitat (i.e. ≥ 40% of each cell encompassed predicted
fisher habitat). Cells within the dry forest stratum contained a lower proportion of modeled fisher habitat (< 40% but ≥ 15%) OR contained < 15% modeled habitat but were within 10 km of a recent (2002-2018), verified fisher observation. We used a Generalized Random Tessellation Stratified (GRTS) sampling procedure (Stevens and Olsen 2004) to randomly select spatially-balanced survey cells in each stratum. We deployed one baited motion-triggered Reconyx™ camera trap in each selected cell (RECONYX® Inc. Holmen, WI, USA). Site locations were based on our knowledge of fine-scale fisher habitat preferences (Sauder 2014), while accounting for distance from roads, trails, and campgrounds. Sites were required to be > 2 km from any adjacent station, > 200 m from a road or trail and > 500 m from the nearest campground.

In choosing camera trap locations we were not limited by accessibility, as both accessible and inaccessible sites were surveyed. We baited survey stations to improve detection probability and broaden the surveyed area beyond the visible detection zone immediately in front of the camera (Fuller et al. 2016). Bait consisted of either roadkill meat combined with a long-call scent lure (accessible sites), or a scent pump dispenser (inaccessible sites). The camera detection frame was positioned so that both the bait on the tree and the ground at the base of the tree was visible. This ensured all species present at the survey site had the potential to be detected, not just those able to climb the bait tree. More detailed field methods can be found in Appendix II.

We analyzed camera images using the Colorado Parks and Wildlife CPW Photo Warehouse software (Ivan and Newkirk 2016). We recorded and classified all species captured on camera, and consulted expert opinion when cataloging detections of cryptic species. Multiple individuals present in the same image were considered independently.
Statistical Analyses

Spatial analyses: Multi-species occupancy

A multispecies occupancy model is an effective tool for analyzing how competitive interactions affect occupancy dynamics such as detection probabilities and spatial associations between competing species (MacKenzie et al. 2006, Sweitzer and Furnas 2016, Cusack et al. 2017, Green et al. 2018). Multispecies occupancy models can be used to assess how fine-scale (camera trap site) spatial associations between sympatric competitors affects regional co-occurrence.

We used single-season, two-step, Bayesian multi-species occupancy models as described by Waddle et al. (2010) and Monterroso et al. (2020). We first created single-species, single-season occupancy models to estimate occupancy \((\psi)\) and detection probability \((p)\) of our five target species (MacKenzie et al. 2002, 2006). We divided our sampling period, December 15, 2018 - March 14, 2019, into three occasions, all 30 days in length. We then created encounter histories and modeled covariates as logit-linear functions of \(\psi\) and \(p\) for each focal species. We tested for an effect of habitat stratum on species occupancy, and bait type on species detection probability using:

\[
\text{logit}(\theta_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_k x_{ik}
\]

at site \(i\) and with \(k\) number of covariates associated with the site (MacKenzie et al. 2002, 2006). We used Normal-distributions as priors for all model parameters, with mean = 0 and precision = 0.001. All single-species models were performed in JAGS (Plummer 2003) and run for 15,000 iterations of 3 MCMC chains following a burn-in of 5,000 iterations. We determined best model fit for single species covariate models using Bayesian p-values, and evaluated MCMC chain convergence by examining posterior density plots and parameter \(R\) values. We
included significant covariates from single-species models in our multi-species pairwise occupancy modeling.

We modeled pairwise species combinations using conditional occupancy at each site where:

\[
\begin{align*}
\psi_i^s &= \text{probability of occurrence of the subordinate competitor species (fisher) at each site, } i \\
\psi_i^D &= \text{probability of occurrence of the dominant competitor species at each site, } i \\
\psi_i^{s|D} \text{ and } \psi_i^{s|\bar{D}} &= \text{conditional probability of occurrence of subordinate species given that the dominant species is present or absent respectively at each site, } i
\end{align*}
\]

To assess spatial relationships, we estimated a species interaction factor (\(\phi, \text{SIF}\)) for each pairwise species combination (Richmond et al. 2010) where:

\[
\phi = \frac{\psi^D \times \psi_i^{s|D}}{\left(\psi^D \times \psi_i^{s|D} + (1 - \psi^D) \times \psi_i^{s|\bar{D}}\right)}
\]

A resulting SIF of \(\phi < 1\) indicated spatial avoidance, and \(\phi > 1\) indicated spatial association or species co-occurrence (Richmond et al. 2010, Monterosso et al. In press). Multi-species model parameters were given priors with normally distributed distributions, mean = 0 and precision = 0.001. All multi-species models were performed in JAGS (Plummer 2003) and run for 20,000 iterations of 3 MCMC chains following a burn-in of 10,000 iterations. We assessed support for pairwise SIF and Multi-species model fit by examining the posterior distributions and MCMC chain convergence of each parameter.
**Temporal analyses: Daily activity pattern overlap**

To assess daily temporal overlap between fishers and their dominant competitors, we defined independent detection events for all fisher, cougar, wolverine, coyote and bobcat detections. We defined detection events as the remote camera capture of a new individual for the first time. To avoid violating assumptions of independence, we considered consecutive images within 30 minutes of the first capture as one detection event.

We assessed daily activity pattern overlap between fishers and their dominant competitors via univariate kernel-density estimation of temporal activity using the R package ‘overlap’ (Ridout and Linkie 2009, Meredith and Ridout 2018, R Core Team 2019). The ‘overlap’ package plots kernel density curves using the von Mises kernel method (Taylor 2008, Ridout and Linkie 2009) then calculates the area under both density curves and estimates the coefficient of overlapping (\(\Delta\); Ridout and Linkie 2009). \(\Delta = 0\) indicates no overlap in activity patterns and \(\Delta = 1\) indicates complete overlap. Confidence intervals are determined via bootstrapping. To satisfy detection event sample size requirements (Lashley et al. 2018), we did not separate daily activity patterns by habitat stratum, but instead conducted temporal analyses while considering detections across the entire study area.

**Results**

As part of a large-scale fisher-monitoring project, we deployed 344 baited remote camera stations over the winter of 2018-2019 across the states of Idaho and Montana. We excluded six cameras from analyses due to season-long malfunctions, which resulted in data from 338 cameras (335,118 total images).
When examining the number of images, detections events, and cells with detections, bobcats were the most common species observed, whereas wolverines were the least common (Table 1). Although fishers were detected in fewer cells than all other species besides wolverines, they had more images and detection events than all other species besides bobcats (Table 1).

**Spatial analyses: Single-species occupancy**

Single species model results indicated good model fit (Bayesian p-values ranged from \( p = 0.51 \) for the wolverine model to \( p = 0.60 \) for the fisher model), and MCMC chain convergence (\( R \leq 1.005 \)) for all parameters (Appendix V). Focal species occupancy estimates were highest for bobcats (\( \hat{\psi} = 0.41, 95\% \text{ CI} = (0.35, 0.50) \)), followed by coyotes (\( \hat{\psi} = 0.30, 95\% \text{ CI} = (0.24, 0.37) \)), wolverines (\( \hat{\psi} = 0.22, 95\% \text{ CI} = (0.13, 0.43) \)), cougars (\( \hat{\psi} = 0.19, 95\% \text{ CI} = (0.17, 0.25) \)), and finally fishers (\( \hat{\psi} = 0.14, 95\% \text{ CI} = (0.12, 0.16) \)). We retained the stratum covariate in our multi-species pairwise model, due to study design revisit differences between habitat strata. In addition, habitat stratum was found to have a significant effect on predicted occupancy in all single-species models except the bobcat model (Appendix V).

**Spatial analyses: Multi-species occupancy**

Fishers co-occurred less often than expected with cougars and bobcats (Table 2). Although fisher occurrence was weakly and negatively associated with bobcat and cougar occurrence, this association was not significant (i.e. the 95% credible interval overlapped 1). Fishers and wolverines co-occurred more often than expected, as indicated by a significant positive spatial association (Table 2). Fishers and coyotes appeared to have no spatial association or disassociation. JAGS output for multi-species models can be found in Appendix VI.
Temporal analyses: Daily activity curve overlap

Daily activity curve overlap between fishers and their dominant competitors was relatively high, indicated by coefficients of overlapping \( \Delta \geq 0.77 \) (Table 3; Figure 2). Diel activity curves demonstrated fishers were generally active through the 24-hour day but had a slight peak in activity from sunrise to midday (Figure 2). Cougars were generally active at crepuscular times, with a larger peak in activity around sunset hours. Wolverines were active throughout the day (sunrise to sunset) and had a peak in diel activity immediately following sunrise. Coyotes and bobcats had no discernable activity pattern and were active equally throughout the 24-hour day (Figure 2).

Discussion

Examining spatio-temporal associations between fishers and their dominant competitors has not been previously explored in the Northern Rocky Mountains. Our study design and ability to sample across a broad landscape provided the large sample sizes necessary to effectively determine patterns of co-occurrence. Understanding the competitive dynamics within the diverse Northern Rocky Mountain carnivore community can help identify how the presence of dominant competitors influences fisher distribution across the landscape.

We hypothesized fishers would exhibit spatial avoidance to limit negative interactions with their dominant competitors. Contrary to our hypothesis, our analyses indicated that the presence of coyotes did not influence fisher detections, but instead demonstrated that these species occur independently. Fishers are considered a semi-arboreal species (Powell 1993), and their ability to limit interactions with coyotes by seeking refuge in trees may preclude spatial avoidance behaviors at the scale we examined. Habitat partitioning may instead occur at a scale
within survey sites, i.e. at the level of access to escape cover. As previous studies show predation by cougars and bobcats are a significant source of fisher mortality (Roy 1991, Wengert et al. 2014, Gabriel et al. 2015), we expect spatial avoidance to be important. Our results demonstrated a weak negative association between detections of fishers and cougars, as well as between detections of fishers and bobcats. Additionally, few cameras had detections of both species (fishers and bobcats \( n = 7 \), fishers and cougars \( n = 2 \)). Our results may reflect differences in forest stratum and bait type preferences between species, rather than intraguild avoidance behavior. Contrary to fishers, the dry habitat stratum had a positive effect on probability of cougar occupancy (Appendix V). While bait type did not affect fisher occurrence, scent pump stations had a negative effect on bobcat occupancy (Appendix V).

Our results indicate fishers do not employ fine-scale spatial avoidance to limit negative interactions with wolverines. Contrary to our hypothesis, our results yielded strong support for fine-scale co-occurrence between fishers and wolverines. While there have been documented cases of wolverine predation on fisher (Roy 1991, Weir and Corbould 2008), examples are few. Therefore, fishers may not need to exhibit fine-scale avoidance behaviors. Our results may instead support landscape-level habitat partitioning between fishers and wolverines, as the dry habitat stratum had a negative effect on fisher occurrence but a positive effect on wolverine occurrence (Appendix V). In addition, previous research has demonstrated wolverines typically select high-elevation habitats, with deep snow (Inman et al. 2012), while fishers prefer low to mid elevation landscapes, and avoid areas with deep, soft snow due to their high foot-loading (Krohn et al. 1995, 2004, Raley et al. 2012).

We designed grid cells in our study to fit precisely within the larger (15 km x 15 km) cells of a previously established wolverine survey (Lukacs et al. 2020), such that monitoring for
both species can be combined in the future. Our single-species models estimated wolverine occupancy across the study area at $\hat{\psi} = 0.22$, 95% CI = (0.13 - 0.43), whereas Lukacs et al. (2020) reported a more precise wolverine occupancy rate across their larger study area at $\hat{\psi} = 0.33$, 95% CI = (0.27 - 0.39). Although our estimates only provide wolverine occupancy rates within the elevational bounds of fisher habitat, our 95% credible interval of occupancy values overlaps related values from the wolverine survey. Our evidence supporting fisher and wolverine co-occurrence and our similarities in wolverine occupancy estimates promote concurrent monitoring of fishers and wolverines in the northern Rockies and suggest that data from our study can be applied to optimize detections of both rare species.

Previous studies have not examined the potential effects of competitive interactions on fisher temporal activity in the northern Rockies. Contrary to our hypotheses, we found no evidence that fishers exhibit temporal avoidance to limit competitive interactions, as all coefficients of overlapping were relatively high. However, minimizing temporal overlap to facilitate coexistence may directly relate to prey abundance and is rare compared to mechanisms that allow for resource and habitat partitioning (Schoener 1974). By analyzing the times of detection events from camera traps, we were successful in defining species-specific diel activity patterns and detected a peak in fisher activity from sunrise to midday. This is a novel result, as previous studies concluded that fishers do not have a defined activity pattern but are instead active throughout the diel period (Powell 1993, Roy 1991, Weir and Corbould 2008). We attribute our ability to detect a peak in fisher activity by successfully optimizing fisher detections to increase the sample size of our fisher detection events.

Investigating the effects of competitive interactions can be difficult, as many factors can allow sympatric carnivores to successfully co-exist. For example, high quality habitat may
provide ample prey resources in addition to protection from predators. Thus, optimal habitat may support many carnivore species while limiting negative interspecific interactions. For example, canopy cover is an important component of fisher habitat (Raley et al. 2012, Aubry et al. 2013, Sauder and Rachlow 2015) and is thought to provide protection from predators (Powell 1993, Raley et al. 2012). However, areas with high proportion of canopy cover provide refuge from high snow accumulation, which benefits coyotes (Dowd et al. 2014) as well as fishers (Krohn et al. 1995, 2004, Sauder and Rachlow 2015). The presence of canopy cover is also an important factor in cougar den site selection (Elbroch et al. 2015). Therefore, lack of significant spatiotemporal disassociations between fishers and their dominant competitors may simply be reflective of optimum habitat, instead of illuminating mechanisms fishers employ to successfully co-occur with other carnivore species.

Our results indicate that continued monitoring of Northern Rocky Mountain fishers and their sympatric competitors can be achieved in a multi-species framework. Though our sampling design was intended to optimize detections of fishers, the presence of bait facilitated detections of other sympatric carnivore species, from weasels (Mustela spp.) to grizzly bears (Ursus arctos). Future monitoring could use multiple years of data to assess time-to-encounter across paired species (Karanth et al. 2017), which calculates the minimum time between detections of a dominant competitor and a subordinate competitor when they occur at the same camera location. Time-to-encounter enables analyzing the combined spatiotemporal relationships between sympatric competitors. With just one year of data, our sample sizes were too low to confidently perform this analysis with any precision (i.e., the number of cells with both fisher and dominant competitor detections ranged from $n = 2$ for cougars to $n = 10$ for coyotes).
The Northern Rockies Mountains contain a wide diversity of local carnivore species, and fisher conservation should be placed in the context of the resident carnivore community. The complexity of the resident carnivore community affects competition for prey and resources (i.e., resting and denning sites) and can also affect the connectivity and size of core habitat areas (Stoskopf 2012). The majority of fisher translocations to the Northern Rocky Mountains selected source populations from British Columbia, Canada (Weckwerth and Wright 1968, Vinkey 2003), which has a similar resident carnivore community. However, the most recent (1989-91) fisher translocations released individuals from midwestern states (i.e., Minnesota and Wisconsin, USA), which resulted in high initial mortality rates (Roy 1991, Heinemeyer 1993). While there is some overlap in carnivore community between these source populations and the northern Rockies, cougars and wolverines have been extirpated from midwestern and eastern North America (Aubry et al. 2007, LaRue et al. 2012). Genetic results from our broad-scale fisher monitoring study (Chapter 1, Appendix IV) demonstrate greater genetic detections of haplotypes originating from Montana and British Columbia, than from the Midwestern U.S. (Vinkey et al. 2006). Therefore, to optimize translocation success, our findings suggest future fisher augmentations should select a source population from a carnivore community similar to that in the northern Rockies, which may mitigate mortality of released individuals that lack learned methods to contend with local dominant competitors (Miller et al. 1990a, Miller et al. 1990b, Stoskopf 2012).

The effective conservation and management of a Species of Greatest Conservation Need, like Northern Rocky Mountain fishers, requires understanding the competitive dynamics of the local carnivore community. We demonstrated the utility of camera data to define previously unknown patterns of co-occurrence between fishers and their dominant competitors through the
identification of fine-scale spatial and temporal relationships. In addition to fine-scale spatial avoidance, landscape-level habitat partitioning may limit antagonistic interactions between fishers and their dominant competitors in the Northern Rocky Mountain ecosystem. Our results establish that patterns of co-occurrence are complex and do not simply follow the relative hierarchy between fishers and their dominant competitors.

**Literature Cited**


Tables

**Table 1.** Number of cells with detections (percent), number of images with detections, and total independent detection events of fishers, cougars, wolverines, coyotes and bobcats. Data were obtained from 344 baited remote camera traps deployed in the winter of 2018-2019 as part of a large-scale fisher monitoring study across Montana and Idaho, USA.

<table>
<thead>
<tr>
<th>Species</th>
<th>Total Images</th>
<th>Detection Events</th>
<th>Cells with Detections</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fisher</td>
<td>10,395</td>
<td>499</td>
<td>41 (11.9%)</td>
</tr>
<tr>
<td>Cougar</td>
<td>4,911</td>
<td>167</td>
<td>58 (16.8%)</td>
</tr>
<tr>
<td>Wolverine</td>
<td>2,041</td>
<td>95</td>
<td>31 (9.0%)</td>
</tr>
<tr>
<td>Coyote</td>
<td>2,522</td>
<td>246</td>
<td>68 (19.8%)</td>
</tr>
<tr>
<td>Bobcat</td>
<td>34,852</td>
<td>1194</td>
<td>89 (25.9%)</td>
</tr>
</tbody>
</table>
Table 2. Species Interaction Factors ($\phi$) and 95% credible intervals from pairwise multispecies models of fishers and four dominant competitors. A resulting SIF of $\phi < 1$ indicates spatial avoidance, and $\phi > 1$ indicates spatial association. A 95% credible interval that does not overlap 1 indicates a significant spatial relationship.

<table>
<thead>
<tr>
<th></th>
<th>Cougar</th>
<th>Wolverine</th>
<th>Coyote</th>
<th>Bobcat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fisher</td>
<td>0.66 (0.09, 1.63)</td>
<td>3.460 (1.78, 5.36)</td>
<td>0.92 (0.12, 2.28)</td>
<td>0.34 (0.01, 1.13)</td>
</tr>
</tbody>
</table>
Table 3. Coefficient of overlapping ($\Delta$) with 95% bootstrapped confidence intervals for all pairwise species daily activity pattern analyses, where $\Delta = 0$ indicates no overlap in activity patterns and $\Delta = 1$ indicates complete overlap.

<table>
<thead>
<tr>
<th>Species pair</th>
<th>$\Delta$ estimate</th>
<th>Bootstrapped 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fisher &amp; Cougar</td>
<td>0.77</td>
<td>(0.69, 0.84)</td>
</tr>
<tr>
<td>Fisher &amp; Wolverine</td>
<td>0.85</td>
<td>(0.76, 0.93)</td>
</tr>
<tr>
<td>Fisher &amp; Coyote</td>
<td>0.87</td>
<td>(0.82, 0.92)</td>
</tr>
<tr>
<td>Fisher &amp; Bobcat</td>
<td>0.86</td>
<td>(0.82, 0.90)</td>
</tr>
</tbody>
</table>
Figure 1. Study area and camera trap locations in Idaho, Montana and northeastern Washington, USA. Cameras were deployed over the winter of 2018–2019, with one remote camera station per randomly selected 7.5 km x 7.5 km grid cell.
Figure 2. Daily activity overlap plots of fishers (*Pekania pennanti*) and (a) cougars (*Puma concolor*) ($\Delta = 0.78$), (b) wolverines (*Gulo gulo*) ($\Delta = 0.85$), (c) coyotes (*Canis latrans*) ($\Delta = 0.88$), and (d) bobcats (*Lynx rufus*) ($\Delta = 0.87$) in the northern Rockies. Camera trap data were collected in Idaho and Montana, USA, 2018-2019.
APPENDIX I: Power Analysis

We performed a power analysis to determine the number of grid cells we needed to sample in each forest stratum (wet forest vs. dry forest). The example below is our dry forest power analysis. Previous literature for western fisher (*Pekania pennanti*) populations supported a simulated detection probability held constant at $p = 0.4$, and simulated probabilities of occupancy at low $\psi = 0.1$ and high $\psi = 0.3$ (Zielinski et al. 2013, Sweitzer et al. 2016). The coefficient of variation ($\text{CV} = \frac{sd(\hat{\psi})}{\text{mean}(\hat{\psi})}$) can be used as an indicator of precision, and a CV < 20% is typical when estimating abundance (Pollock et al. 1990, Kristensen and Kovach 2018). Our power analysis determined to achieve a goal of CV = 20%, we needed to survey 230 to 245 cells in the dry forest stratum (Figure A-1).

---

```r
# Krohner JAGS Occupancy Simulation Code
```

```r
library(mcmcplots)
library(R2jags)
library(ggplot2)
setwd("/Users/Jess/Desktop/UM/Research Design/Research Design Lab/FinalProject")
```

```r
# Simulation
```
truePsi = c(0.1,0.3) # creates vector of two values of psi
nSite = rep(c(200,225,250,275,300), 100) # creates vector of five values of n, replicates 100
                    times to get a sample size of 100 for each of the 10 psi/n combinations (1000 total
data simulations)

#### Function to simulate encounter history #####
sim <- function(nSite, truePsi){
  nOcc <- 15                        # number of occasions, k = 15 weeks
  nSite <- 200                     # number of sites sampled for example run
  truePsi <- 0.1                    # true value of occupancy for example run
  truep <- 0.4                      # true value of detection probability, p =0.4

  EH <- matrix( 0, nSite, nOcc )    # Encounter history matrix (initially all 0, unoccupied)

  for( i in 1:nSite){              # loop over sites for sample run
    if( runif(1) < truePsi){       # test for occupied, if the cell is truly unoccupied we don't need to
      continue                      # test for detection
    }
    for( j in 1:nOcc ){           # if the cell is truly occupied, first loop over occasions
      if( runif(1) < truep ){     # then test for detection
        EH[i,j] <- 1              # then update encounter history for truly occupied cells
      }
    }
  }

  occ.data <- list( y=EH, nSite=nSite, nOcc=nOcc )
  occ.inits <- function(){
    # default initial values
  }
}
list( z = rep( 1, nSite ), # z: site is truly occupied
    b0.psi = runif( 1, -3, 3 ), # initial value for flat psi prior
    b0.p = runif( 1, -3, 3 ) # initial value for flat p prior
)

# set parameters to track in JAGS
occ.parms <- c( "b0.psi", "b0.p","mean.psi", "mean.p" )

# set up for MCMC run
ni <- 10000 # number of iterations
nt <- 1 # no thinning, output is total number of iterations
nb <- 2000 # burn/don't count the first nb number of iterations
nc <- 3 # number of chains

# run the MCMC chain in JAGS
occ.result <- jags( occ.data,
    occ.inits,
    occ.parms,
    "occup.txt",
    n.chains=nc,
    n.iter=ni,
    n.burnin=nb,
    n.thin=nt
)

occ.result
mcmcplot( occ.result )

###################################################
# return results
###################################################
# given true Psi, either 0.1 or 0.3 = truePsi
# given true p , 0.4 = truep
# number of cameras = nSite
# average estimated psi = occ.result$BUGSoutput$mean$mean.psi
# average estimated p = occ.result$BUGSoutput$mean$mean.p
# estimated psi sd = occ.result$BUGSoutput$sd$mean.psi
# estimated p sd = occ.result$BUGSoutput$sd$mean.p
# estimated cv = occ.result$BUGSoutput$sd$mean.psi/occ.result$BUGSoutput$mean$mean.psi

return(list(true_psi = truePsi,
            true_p = truep,
            nsite = nSite,
            est_psi = occ.result$BUGSoutput$mean$mean.psi,
            est_p = occ.result$BUGSoutput$mean$mean.p,
est_psi_sd = occ.result$BUGSoutput$sd$mean.psi,
est_p_sd = occ.result$BUGSoutput$sd$mean.p,
est_cv =
occ.result$BUGSoutput$sd$mean.psi/occ.result$BUGSoutput$mean$mean.psi)
}

out <- lapply(nSite, sim, truePsi = truePsi[1])
out2 <- lapply(nSite, sim, truePsi = truePsi[2])

########################################################
# Output parameters
########################################################
t0 <- c(out, out2)
t1 <- lapply(t0, unlist) # creates vector of output
t2 <- lapply(t1, rbind) # transforms output vector into a matrix
t3 <- lapply(t2, as.data.frame) # transforms output matrix into a dataframe
t4 <- do.call( rbind, t3) # combines the data frames for both psis
t4
head(t4)

########################################################
# Save Data as CSV
########################################################
write.csv(t4, file = "fulloccupoutput.csv", row.names=TRUE)
occdataset <- read.csv("fulloccupoutput.csv")

########################################################
# Average CV for each psi
########################################################
psi1 <- read.csv("lowoccupoutput.csv") #dataset for psi = 0.1 only
avcv1 <- mean(psi1$est_cv) # average cv for psi 0.1 = 0.194483
psi2 <- read.csv("medoccupoutput.csv") #dataset for psi = 0.3 only
avcv2 <- mean(psi2$est_cv) # average cv for psi 0.3 = 0.09770959

########################################################
# Plot CV by sample size for both psi values
########################################################
require(ggplot2)
# Note: to duplicate results, change “data = t4” to “data = fulloccupoutput” in graphing code

###### Scatter Plot ######


Figure A-1. Estimated average coefficients of variation (CV) by number of camera traps for two simulated datasets with detection probability held constant ($p = 0.4$) and varying probabilities of occupancy ($\psi = 0.1$, $\psi = 0.3$). We assessed number of grid cells we needed to survey to meet our goals of a CV of 1) 10% or 2) 20%. Our results demonstrated a need to survey 230 to 245 stations in the dry forest stratum.
APPENDIX II: Survey Station Methods

Cameras

Each survey station consisted of a motion-triggered camera fit with a 32 GB memory card. There were several Reconyx™ infrared flash camera models deployed: Ultrafire™, Hyperfire HC600™, PC800™, and PC900™, and HP2X™ cameras (RECONYX® Inc. Holmen, WI, USA). We specified camera settings to three pictures per trigger, minimum available delay between photos within each trigger event, no delay between trigger events, highest available sensitivity, highest available resolution, and maximum flash. We deployed cameras so that they faced north, avoiding east-west directions where low sun angles at sunrise and sunset could cause image distortion. Cameras were attached to trees ~ 5-6 m from their paired bait tree, and the camera detection frame was positioned so that both the bait on the tree and the ground at the base of the tree was visible. Cameras at inaccessible stations were rotated horizontally to accommodate snow accumulation and resulting variable ground height throughout the winter. We standardized detection frame positioning by taking test photos at every station. Station deployment and revisit details beyond this appendix can be found in a document by the Northern Rockies Fisher Working Group (2018).
**Bait and Lure**

**Table 1.** Description of differences in baited camera and hair snare station protocol for three site types: 1) inaccessible, 2) accessible: wet stratum, and 3) accessible: dry stratum.

<table>
<thead>
<tr>
<th>Site type:</th>
<th>Field Methods:</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inaccessible</strong></td>
<td><strong>Deployment</strong>: Late Fall, <strong>Retrieval</strong>: Late Spring or Summer, <strong>Bait/Lure Type</strong>: Scent pump dispenser: drips small amount of liquid lure onto a cow femur once daily</td>
</tr>
<tr>
<td><strong>Accessible: Wet Forest Stratum</strong></td>
<td><strong>Deployment</strong>: December 1st – 15th, <strong>Rechecks</strong>: Three 30-day rechecks (sampling periods), <strong>Retrieval</strong>: March 1st – 15th, <strong>Bait/Lure Type</strong>: Meat bait: 15-20 lbs of roadkill game meat AND Long call scent lure: mix of skunk quill, marten lure, etc.</td>
</tr>
<tr>
<td><strong>Accessible: Dry Forest Stratum</strong></td>
<td><strong>Deployment</strong>: December 1st – 15th, <strong>Rechecks</strong>: Two 45-day rechecks (sampling periods), <strong>Retrieval</strong>: March 1st – 15th, <strong>Bait/Lure Type</strong>: Meat bait: 15-20 lbs of roadkill game meat AND Long call scent lure: mix of skunk quill, marten lure, etc.</td>
</tr>
</tbody>
</table>

We standardized roadkill meat bait size to 6.8-7.3 kg of game meat, and consisted of either a deer (*Odocoileus virginianus*) hindquarter, 2 deer front quarters, an elk (*Cervus canadensis*) quarter, or a skinned beaver carcass (*Castor canadensis*). We secured bait to a tree bole 2.5-3 m above the ground (Figure A-1). Bait trees were required to be > 30 cm DBH, 6 m from the camera tree, and > 1.5 m from the nearest surrounding tree to prevent animals from jumping to the bait from an adjacent tree.

Long-call scent lure consisted of a recipe developed for fisher surveys by Eric Lofroth (British Columbia, Canada) and modified by Robert Long and Joel Sauder to function with their scent pump dispensers. We baited accessible sites with a 7.6 cm³ sponge saturated in scent lure. The sponge was secured to the bait tree just above the meat bait (Figure A-1). We baited inaccessible sites with a scent pump dispenser (Robert Long, Woodland Park Zoo, Seattle, USA) that dripped a small amount of liquid scent lure onto a cow femur suspended under the pump...
once per day for the duration of the study season (Figure A-2). We secured scent pumps to a tree bole 2.5-3 m above the ground.

Lure Recipe (per gallon):

<table>
<thead>
<tr>
<th>Ingredient</th>
<th>Quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Propylene glycol; food grade</td>
<td>72 oz</td>
</tr>
<tr>
<td>Water</td>
<td>48 oz</td>
</tr>
<tr>
<td>Beaver castor oil (liquid)</td>
<td>2 oz</td>
</tr>
<tr>
<td>Hawbaker’s Marten Lure</td>
<td>4 oz</td>
</tr>
<tr>
<td>Skunk essence (100% pure skunk quill)</td>
<td>1 oz</td>
</tr>
<tr>
<td>Anise oil</td>
<td>1 oz</td>
</tr>
</tbody>
</table>

_Hair Snares_

We deployed a noninvasive tree-mounted hair snares at each station (Figures A-1, A-2). DNA samples were collected via five 0.30 caliber gun brushes attached to a 7.5 cm x 56 cm corrugated plastic “collar” modeled after Figura and Knox (Northern Rockies Fishers Working Group 2018). We attached each DNA collar to its associated bait tree measuring > 30 cm DBH. Collars were positioned 20-30 cm underneath the bait. Bait trees were separated from adjacent trees by at least 1.5 m to prevent animals from jumping from surrounding trees to the bait tree. Hair snare positioning allowed us to collect genetic material from focal species as they climbed up the tree to get at the bait. To limit human contamination, we wore gloves to install and change gun brushes, and we used a small, hand-held blowtorch to sterilize gun brushes at the end of each visit.

_Literature Cited_

Figure A-2. Accessible station deployment includes fisher scent lure sponge, fisher bait, and fisher gun brush collar. During revisits, components are moved up the tree to stay above accumulating snow (Northern Rockies Fisher Working Group 2018).
Inaccessible Station

Figure A-3. Inaccessible station deployment includes a scent dispenser and cow femur instead of meat bait and fisher lure sponge. All elements are deployed high up the tree to account for snow accumulation over the winter. Camera orientation is sideways (Northern Rockies Fisher Working Group 2018).
APPENDIX III: Case Study: Nez-Perce Clearwater National Forest (Chapter 1)

We collaborated with the US Forest Service to assess current fisher distribution in the non-wilderness portions of the Nez Perce-Clearwater National Forest (NPC). We provided baseline occupancy estimates to evaluate any changes in fisher distribution resulting from potential future adjustments to timber harvest in this area.

As part of this intensified sampling effort, 20 survey stations were deployed in addition to the original 34 selected grid cells within the bounds of the NPC. These stations were sampled using the same survey grid and protocols as our study, but were deployed in cells that were not part of our original selection process. Instead, an additional power analysis and Generalized Random Tessellation Stratified (GRTS) sampling procedure (Stevens and Olsen 2004) were performed to guide sample size and select an appropriate spatially-balanced sample from the total 154 non-wilderness grid cells within the NPC National Forest. As NPC forest objectives are to maintain fisher distribution in the wet forest stratum, stratum was not considered in the NPC GRTS cell selection. All additional selected cells fell with the wet forest.

Within our sampling period of December 15, 2018 to March 14, 2019, fishers were detected in 18 (33%) of the 54 surveyed grid cells. We used a single-season, single-species occupancy model as described by MacKenzie et al. (2002, 2006) to provide estimates beyond the naïve occupancy calculated from surveyed cells, and assessed detection probability to account for false absences. We modeled predicted occupancy across all possible non-wilderness cells in the NPC, including both surveyed and unsurveyed cells. Forest stratum was not considered as a covariate in our model.

Occupancy results (Table 1) demonstrated good model fit (Bayesian p-value = 0.59) and indicated MCMC chain convergence for all parameters (\( \hat{R} \leq 1.002 \) for each parameter).
Detection probability was held constant and was estimated at 0.50 (95% CI = 0.32, 0.67). We estimated that overall fisher occupancy was 0.40 (95% CI = 0.27, 0.57). Thus, we predict that overall, 62 cells (40%) of the 154 non-wilderness NPC grid cells are occupied.

Table 1. JAGS output for Nez-Perce model derived from encounter histories from remote camera detections. Data were collected in Montana, Idaho and Washington from December 15, 2018 to March 14, 2019.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>97.5%</th>
<th>Rhat</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept $p$</td>
<td>0.02</td>
<td>0.37</td>
<td>-0.75</td>
<td>0.22</td>
<td>0.03</td>
<td>0.27</td>
<td>0.71</td>
<td>1.001</td>
</tr>
<tr>
<td>Intercept $\psi$</td>
<td>-0.43</td>
<td>0.37</td>
<td>-1.10</td>
<td>-0.67</td>
<td>-0.245</td>
<td>-0.21</td>
<td>0.35</td>
<td>1.001</td>
</tr>
<tr>
<td>Mean $p$</td>
<td>0.50</td>
<td>0.09</td>
<td>0.32</td>
<td>0.45</td>
<td>0.51</td>
<td>0.57</td>
<td>0.67</td>
<td>1.002</td>
</tr>
<tr>
<td>Mean $\psi$</td>
<td>0.40</td>
<td>0.08</td>
<td>0.27</td>
<td>0.34</td>
<td>0.39</td>
<td>0.44</td>
<td>0.57</td>
<td>1.001</td>
</tr>
<tr>
<td>Bayesian $p$-value</td>
<td>0.60</td>
<td>0.49</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.001</td>
</tr>
</tbody>
</table>

Literature Cited


APPENDIX IV: Genetic Results

Montana

The U.S.D.A. Forest Service Rocky Mountain Research Station in Missoula, Montana performed DNA analysis down to the haplotype-level. We detected fisher genetics in eight of the surveyed cells in Montana, including multiple fishers in one cell, indicated by the presence of two different haplotypes (Table 1a). One cell in the Lolo National Forest detected fisher with a genetic haplotype unique to the northern Rockies (Vinkey et al. 2006, Schwartz 2007). Four cells had genetic detections of non-native haplotypes from the Midwest and British Columbia, Canada (Vinkey et al. 2006), possibly indicating the presence of decedents from previous translocation events. The remaining three cells did not have successful haplotype identification due to the presence of DNA from non-target-species or the poor quality of the samples. When examining detections by site and by visit, genetic detections did not perform as well as cameras (total cells by camera: \( n = 11 \), total cells by DNA: \( n = 8 \)) and thus were excluded from occupancy analyses.

Table 1a. Fisher haplotype genetic detection summary from Montana survey stations. *
Indicates unique haplotype native to the Northern Rocky Mountain fisher population.

<table>
<thead>
<tr>
<th>Haplotype</th>
<th>Number of Cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haplotype 4</td>
<td>1</td>
</tr>
<tr>
<td>Haplotype 5</td>
<td>1</td>
</tr>
<tr>
<td>Haplotype 4 and 5</td>
<td>1</td>
</tr>
<tr>
<td>Haplotype 6</td>
<td>1</td>
</tr>
<tr>
<td>Haplotype 12*</td>
<td>1</td>
</tr>
<tr>
<td>Unknown</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>8</strong></td>
</tr>
</tbody>
</table>
Idaho

We detected fisher genetics in 25 of the surveyed cells in Idaho, including multiple fishers in one cell, indicated by the presence of three differing haplotypes (Table 1b). Five cells in the Nez-Perce Clearwater National Forest and immediate surrounding area detected fisher with a genetic haplotype unique to the northern Rockies (Vinkey et al. 2006, Schwartz 2007). Sixteen cells had genetic detections of non-native haplotypes, including Haplotypes 5 and 10 that are common in the Midwest, and Haplotypes 4, 6, and 7 that are common in British Columbia, Canada (Vinkey et al. 2006). Detections of non-native haplotypes may indicate the presence of decedents from previous translocation events. The remaining three cells did not have successful haplotype identification due to the presence of DNA from non-target-species or the poor quality of the samples. When examining detections by site and by visit, genetic detections did not perform as well as cameras (total cells by camera: \( n = 38 \), total cells by DNA: \( n = 25 \)) and thus were excluded from occupancy analyses.

Table 1b. Fisher haplotype genetic detection summary from Idaho survey stations. * Indicates unique haplotype native to the Northern Rocky Mountain fisher population.

<table>
<thead>
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<th>Haplotype</th>
<th>Number of Cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haplotype 4</td>
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</tr>
<tr>
<td>Haplotype 4, 5 and 10</td>
<td>1</td>
</tr>
<tr>
<td>Haplotype 6</td>
<td>8</td>
</tr>
<tr>
<td>Haplotype 7</td>
<td>2</td>
</tr>
<tr>
<td>Haplotype 12*</td>
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<td>Unknown</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>25</strong></td>
</tr>
</tbody>
</table>
Literature Cited


APPENDIX V: Final single-species models (Chapter 2)

Final single-species models for fisher, cougar, wolverine, coyote, and bobcat models (Table 1). All single-species models were performed in JAGS (Plummer 2003) and run for 15,000 iterations of 3 MCMC chains following a burn-in of 5,000 iterations.
Table 1. JAGS output for final single-species covariate models. Remote camera data were collected in Montana, Idaho and northeastern Washington, USA, from December 15, 2018 to March 14, 2019.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>97.5%</th>
<th>Rhat</th>
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<td>Fisher</td>
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<td>-0.24</td>
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<td>0.65</td>
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<tr>
<td></td>
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<td>-0.45</td>
<td>1.001</td>
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<td>DryForest</td>
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<td>-1.74</td>
<td>-1.49</td>
<td>-1.03</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>Bayesian $p$-val</td>
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<td>Cougar</td>
<td>Intercept $p$</td>
<td>0.22</td>
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<td>-0.60</td>
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<td>0.48</td>
<td>0.89</td>
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<td></td>
<td>Removal $p$</td>
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<td>-2.84</td>
<td>-2.46</td>
<td>-1.72</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>Intercept $\psi$</td>
<td>-2.58</td>
<td>0.42</td>
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<td>-2.85</td>
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<td>-2.29</td>
<td>-1.81</td>
<td>1.002</td>
</tr>
<tr>
<td></td>
<td>DryForest</td>
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<td>0.44</td>
<td>0.63</td>
<td>1.13</td>
<td>1.42</td>
<td>1.72</td>
<td>2.36</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>Bayesian $p$-val</td>
<td>0.59</td>
<td>0.49</td>
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<td></td>
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</tr>
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<td>1.81</td>
<td>2.31</td>
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</tr>
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<td></td>
<td>1.001</td>
</tr>
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<td>Coyote</td>
<td>Intercept $p$</td>
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<td>-0.81</td>
<td>-0.66</td>
<td>-0.39</td>
<td>1.001</td>
</tr>
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<td>BaitType</td>
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<td>0.87</td>
<td>1.17</td>
<td>1.77</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>Intercept $\psi$</td>
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<td>0.32</td>
<td>-0.73</td>
<td>-0.37</td>
<td>-0.17</td>
<td>0.05</td>
<td>0.53</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>DryForest</td>
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<td>-1.82</td>
<td>-1.35</td>
<td>-1.12</td>
<td>-0.89</td>
<td>-0.47</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>Bayesian $p$-val</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1.001</td>
</tr>
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<td>Bobcat</td>
<td>Intercept $p$</td>
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<td>-0.47</td>
<td>-0.35</td>
<td>-0.14</td>
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<td>-0.54</td>
<td>-0.34</td>
<td>0.07</td>
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<td></td>
<td>DryForest</td>
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<td>0.02</td>
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<td>0.47</td>
<td>0.90</td>
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<tr>
<td></td>
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<td>1.001</td>
</tr>
</tbody>
</table>
Literature Cited

APPENDIX VI: Final multi-species models (Chapter 2)

Final multi-species models for fisher + cougar, fisher + wolverine, fisher + coyote, and fisher + bobcat models. All multi-species models were performed in JAGS (Plummer 2003) and run for 20,000 iterations of 3 MCMC chains following a burn-in of 10,000 iterations. We used single-season, two-step, Bayesian multi-species occupancy models as described by Waddle et al. (2010).

Table 1. JAGS output for final multi-species covariate models (F = Fisher, COU = Cougar, WLV = Wolverine, COY = Coyote, BCT = Bobcat). SIF is the species interaction factor (ϕ). ϕ < 1 indicates spatial avoidance, and ϕ > 1 indicates spatial association. A 95% credible interval that does not overlap 1 indicates a significant spatial relationship. Remote camera data were collected in Montana, Idaho and northeastern Washington, USA, from December 15, 2018 to March 14, 2019.

<table>
<thead>
<tr>
<th>Model</th>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>2.50%</th>
<th>25%</th>
<th>50%</th>
<th>75%</th>
<th>97.50%</th>
<th>Rhat</th>
</tr>
</thead>
<tbody>
<tr>
<td>F &amp; COU</td>
<td>F Intercept p</td>
<td>0.20</td>
<td>0.23</td>
<td>-0.25</td>
<td>0.05</td>
<td>0.21</td>
<td>0.36</td>
<td>0.64</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>F Intercept ψ</td>
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<td>-0.96</td>
<td>-0.80</td>
<td>-0.63</td>
<td>-0.31</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>F DryForest</td>
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<td>-2.56</td>
<td>-2.02</td>
<td>-1.74</td>
<td>-1.48</td>
<td>-0.99</td>
<td>1.001</td>
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<tr>
<td></td>
<td>COU Intercept p</td>
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<td>0.39</td>
<td>-0.65</td>
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<td>0.47</td>
<td>0.89</td>
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<td>COU Removal p</td>
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<td>0.59</td>
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<td>-2.81</td>
<td>-2.41</td>
<td>-1.67</td>
<td>1.001</td>
</tr>
<tr>
<td></td>
<td>COU Intercept ψ</td>
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<td>0.42</td>
<td>-3.43</td>
<td>-2.83</td>
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<td>-2.27</td>
<td>-1.77</td>
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</tr>
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<td>(F</td>
<td>COU) Intercept ψ</td>
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<td>2.41</td>
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<td>-4.03</td>
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<td>(F</td>
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<td>0.90</td>
<td>1.63</td>
<td>1.001</td>
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<td>F &amp; WLV</td>
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<td>0.23</td>
<td>-0.27</td>
<td>0.03</td>
<td>0.18</td>
<td>0.34</td>
<td>0.64</td>
<td>1.001</td>
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<td>-0.79</td>
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<td>WLV Intercept $\psi$</td>
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<td>(F</td>
<td>WLV) Intercept $\psi$</td>
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</tr>
<tr>
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<td>-5.73</td>
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<td>-7.78</td>
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<td>-3.69</td>
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<tr>
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<td>-1.24</td>
<td>-0.83</td>
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<td>WLV Intercept $\psi$</td>
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<td>-4.27</td>
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<td>-2.27</td>
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<td>0.53</td>
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<td>1.71</td>
<td>2.19</td>
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<tr>
<td>(F</td>
<td>WLV) Intercept $\psi$</td>
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<td>-0.42</td>
<td>0.85</td>
<td>7.23</td>
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<tr>
<td>(F</td>
<td>WLV) DryForest</td>
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<td>2.62</td>
<td>-8.45</td>
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<td>-0.84</td>
<td>0.36</td>
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<td>SIF</td>
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<td>1.78</td>
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<td>4.03</td>
<td>5.36</td>
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</tbody>
</table>

|                      |   F Intercept $p$ |   F Intercept $\psi$ |   F DryForest |   COY Intercept $p$ |   COY BaitType |   COY Intercept $\psi$ |   COY DryForest |   (F|COY) Intercept $\psi$ |   (F|COY) DryForest |   SIF      |
|----------------------|------------------|----------------------|--------------|---------------------|---------------|------------------------|-----------------|--------------------------|----------------------|-----------|
|                      | 0.20             | 0.23                 | -0.25        | 0.05                | 0.21          | 0.36                   | 0.64            | 1.001                    | 1.009                | 1.002     |
| F Intercept $p$      | -0.88            | 0.45                 | -1.79        | -1.14               | -0.86         | -0.61                  | -0.09           | 1.004                    | 1.003                | 1.003     |
| F Intercept $\psi$   | -1.77            | 0.57                 | -2.86        | -2.12               | -1.77         | -1.41                  | -0.65           | 1.002                    | 1.003                | 1.002     |
| F DryForest          | -0.84            | 0.23                 | -1.30        | -0.99               | -0.83         | -0.68                  | -0.39           | 1.004                    | 1.004                | 1.004     |
| COY Intercept $p$    | 0.87             | 0.46                 | -0.02        | 0.56                | 0.87          | 1.18                   | 1.78            | 1.002                    | 1.002                | 1.002     |
| COY BaitType         | -0.11            | 0.35                 | -0.72        | -0.35               | -0.14         | 0.10                   | 0.66            | 1.003                    | 1.003                | 1.003     |
| COY Intercept $\psi$ | -1.14            | 0.36                 | -1.88        | -1.37               | -1.13         | -0.90                  | -0.47           | 1.002                    | 1.002                | 1.002     |
| COY DryForest        | -1.00            | 0.44                 | -1.88        | -1.28               | -0.99         | -0.71                  | -0.16           | 1.001                    | 1.001                | 1.001     |
| (F|COY) Intercept $\psi$| -1.98           | 0.95                 | -4.04        | -2.56               | -1.91         | -1.33                  | -0.33           | 1.001                    | 1.001                | 1.001     |
| SIF                  | 0.92             | 0.57                 | 0.12         | 0.48                | 0.82          | 1.25                   | 2.28            | 1.001                    | 1.001                | 1.001     |

|                      |   F Intercept $p$ |   F Intercept $\psi$ |   F DryForest |   BCT Intercept $p$ |   BCT BaitType |   BCT Intercept $\psi$ |   BCT DryForest |   (F|BCT) Intercept $\psi$ |   (F|BCT) DryForest |   SIF      |
|----------------------|------------------|----------------------|--------------|---------------------|---------------|------------------------|-----------------|--------------------------|----------------------|-----------|
|                      | 0.20             | 0.23                 | -0.25        | 0.05                | 0.20          | 0.35                   | 0.63            | 1.001                    | 1.013                | 1.006     |
| F Intercept $p$      | -1.01            | 0.41                 | -1.88        | -1.24               | -0.99         | -0.75                  | -0.30           | 1.013                    | 1.013                | 1.013     |
| F Intercept $\psi$   | -1.22            | 0.54                 | -2.25        | -1.57               | -1.23         | -0.89                  | -0.14           | 1.006                    | 1.006                | 1.006     |
| F DryForest          | -0.48            | 0.18                 | -0.84        | -0.60               | -0.48         | -0.35                  | -0.14           | 1.001                    | 1.001                | 1.001     |
| BCT Intercept $p$    | -2.69            | 0.69                 | -4.19        | -3.11               | -2.65         | -2.21                  | -1.47           | 1.001                    | 1.001                | 1.001     |
| BCT BaitType         | -0.51            | 0.31                 | -1.10        | -0.72               | -0.52         | -0.31                  | 0.11            | 1.002                    | 1.002                | 1.002     |
| BCT Intercept $\psi$ | 0.21             | 0.34                 | -0.45        | -0.01               | 0.21          | 0.44                   | 0.88            | 1.001                    | 1.001                | 1.001     |
| BCT DryForest        | -0.83            | 0.50                 | -1.86        | -1.15               | -0.81         | -0.49                  | 0.12            | 1.004                    | 1.004                | 1.004     |
| (F|BCT) Intercept $\psi$| -3.48           | 1.35                 | -6.63        | -4.24               | -3.31         | -2.55                  | -1.30           | 1.001                    | 1.001                | 1.001     |
| SIF                  | 0.34             | 0.30                 | 0.01         | 0.11                | 0.25          | 0.48                   | 1.13            | 1.001                    | 1.001                | 1.001     |
Literature Cited
