2021

A REINTRODUCTION RETROSPECTIVE: COMPARATIVE FISHER (PEKANIA PENNANTI) SURVIVAL AND PREY HABITAT USE IN THE CASCADE MOUNTAINS OF WASHINGTON STATE

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Recommended Citation

Humphries, Tanner S.T., "A REINTRODUCTION RETROSPECTIVE: COMPARATIVE FISHER (PEKANIA PENNANTI) SURVIVAL AND PREY HABITAT USE IN THE CASCADE MOUNTAINS OF WASHINGTON STATE" (2021). *Graduate Student Theses, Dissertations, & Professional Papers*. 11849.
https://scholarworks.umt.edu/etd/11849

A REINTRODUCTION RETROSPECTIVE: COMPARATIVE FISHER (PEKANIA PENNANTI) SURVIVAL AND PREY HABITAT USE IN THE CASCADE MOUNTAINS OF WASHINGTON STATE

By

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B. S., Western Washington University, Bellingham, Washington, 2013

Thesis

Presented in partial fulfillment of the requirements for the degree of

Master of Science
in Wildlife Biology

The University of Montana
Missoula, MT

December 2021

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ABSTRACT

Increasing human impacts on biodiversity highlight the global need for ecological restoration. For many wildlife species, reintroduction is necessary to re-establish populations in parts of their historic range where they have been extirpated. Reintroduction efforts are commonly used to help restore ecosystem integrity, but are often expensive, time consuming, and unsuccessful at generating self-sustaining populations. Thus, a more complete understanding of the factors affecting restoration success is important for ensuring successful outcomes and responsible stewardship. Fishers (*Pekania pennanti*) are one of the most commonly reintroduced carnivores in North America, but the success of such efforts is highly variable, potentially due to differences among sites in predator and prey assemblages. We examined factors associated with differences in survival rates between reintroduced fisher populations in the southern and northern Cascade Mountains, Washington, USA. Fisher survival rates, based on radio telemetry data, were significantly lower in the North Cascades than in the South Cascades. The relative abundance of important fisher prey species was significantly lower in the North than in the South. Our findings are consistent with the survival of reintroduced fishers being affected by differences in prey assemblages between release sites, though there are many other factors that also differ between the study areas, so we cannot necessarily infer that prey differences are the causative factor. We produced prey habitat maps across the North Cascades study area based on habitat use of three important fisher prey species: snowshoe hare (*Lepus americanus*), Douglas squirrel (*Tamiasciurus douglasii*), and mountain beaver (*Aplodontia rufa*). Future reintroduction efforts may benefit from preliminary assessment of prey assemblages, abundance, and habitat use prior to release site selection.

ACKNOWLEDGEMENTS

There are many people and entities that deserve my heart-felt thanks for assisting me in completing this thesis. Funding and support for this project was provided by the National Science Foundation Graduation Research Fellowship Program, Seattle City Light Wildlife Research Program, and North Coast and Cascades Research Learning Center. A sincere thanks to these entities for their generosity and support.

I also want to thank Mt. Baker-Snoqualmie National Forest, North Cascades National Park Service Complex, Washington Department of Natural Resources, and Sierra Pacific Industries for allowing me to access the land that sustained my research and the furry critters that inhabit it. Furthermore, I’d like to acknowledge that all fisher reintroductions took place on the lands of the Cowlitz Indian Tribe, Nisqually Indian Tribe, Confederated Tribes and Bands of the Yakama Nation, Puyallup Tribe of Indians, Muckleshoot Indian Tribe, Squaxin Island Tribe, Sauk-Suiattle Indian Tribe, and Upper Skagit Indian Tribe. Thank you all.

None of this would have been possible without the many field hands that assisted me in my field work. Thanks to Taylor Bruntil, Roger Christophersen, Jacob Irwin, and Kristin Rine for all your field assistance and Mitch Parsons for methodological and analytical guidance. I couldn’t have asked for a better crew to assist me through the mountains and along this journey.

To my advisor, Dr. Jedediah Brodie, and my committee members Dr. Scott Mills, Dr. Jason Ransom, and Dr. Michael Schwartz, thanks for your patience, guidance, and endless flow of knowledge. I feel incredibly blessed to have found an advisor whose depth of intellect is only eclipsed by his depth of character and a committee whose diverse skillset made this thesis a reality. You all have challenged and encouraged me to grow from a budding scientist to a

blossoming wildlife biologist and I look forward to continuing to learn from each of you well beyond the closing of this graduate school chapter.

Words cannot express the gravity of gratitude I have for the folks who have been by my side throughout this wild ride. To the Brodie Lab (both past and present): Daniel Bird, Daiane Carreira, Diandra Lewis, Mingyu Liu, Shu Woan Teoh, Jennifer Wall, Scott Waller, Peter Williams, and Sara Williams; I reflected every day on how lucky I was to be surrounded by such intelligent and driven individuals. Thanks for your endless advice and lifelong friendships. To the Wildlife Biology community and my fellow graduate students, what a blessing to be surrounded by such a compassionate and passionate group of individuals. A massive hug (despite pandemic concerns) to the love and support of my friends and family. I truly wouldn't be where I am today without each and every one of you guiding me along the way. Thanks for the reminders to step-away from my computer and into the mountains whenever my mental health was slipping. I am immensely indebted to the good fortune that brought all of you into my life.

Finally, I owe the deepest thanks to all the wild animals that share this Earth with us. I apologize for the harm we've caused and strive to spend my life working to undo some of the wrong we've done.

CHAPTER ONE

Comparative Survival of Reintroduced Fishers in the Northern and Southern Cascade Mountains of Washington State

ABSTRACT

Increasing human impacts on biodiversity highlight the global need for ecological restoration. For many wildlife species, reintroduction is necessary to re-establish populations in parts of their historic range where they have been extirpated. Reintroduction efforts are commonly used to help restore ecosystem integrity, but are often expensive, time consuming, and unsuccessful at generating self-sustaining populations. Thus, a more complete understanding of the factors affecting restoration success is important for ensuring successful outcomes and responsible stewardship. Fishers (*Pekania pennanti*) are one of the most commonly reintroduced carnivores in North America, but the success of such efforts is highly variable, potentially due to differences among sites in predator and prey assemblages. We examined factors associated with differences in survival rates between reintroduced fisher populations in the southern and northern Cascade Mountains, Washington, USA. We compared fisher survival rates between the two areas and used independent detections of prey and predators at 190 remote camera stations to assess how predator and prey relative abundance related to post-release fisher survival. Fisher survival rates, based on radio telemetry data, were significantly lower in the North Cascades than in the South Cascades. The relative abundance of important fisher prey species was significantly lower in the North than in the South, but predator relative abundance was not significantly different between study areas. Our findings are consistent with the survival of reintroduced fishers being affected by differences in prey assemblages across release sites, though there are many other differences

between the sites that we did not account for and so we cannot confirm that prey are the main driver of fisher survival. Future reintroduction efforts may benefit from preliminary assessment of prey abundance prior to release site selection.

INTRODUCTION

Increasing human impacts on biodiversity highlight the global need for ecological restoration (Gann et al. 2019). In recognition of this, the United Nations declared 2021-2030 the Decade on Ecosystem Restoration (Aronson et al. 2020) to galvanize action on global recovery of degraded ecosystems, ameliorate climate change, and protect biodiversity (Waltham et al. 2020). Restoration generally focuses on accelerating the succession of vegetation communities (Göthe et al. 2015, Liu et al. 2019). However, many animals have been lost from ecosystems around the world as well: for these wildlife species, “restoration” often takes the form of reintroduction. Indeed, reintroduction projects are widely used for re-establishing species in parts of their historic range where they have been extirpated (Seddon et al. 2007) and are a common strategy to help restore ecosystem integrity (Devineau et al. 2011, Seddon et al. 2014).

Wildlife reintroduction, however, is often expensive, time consuming, and unsuccessful at generating self-sustaining populations (Miller et al. 1999, Fischer and Lindenmayer 2000). The success of reintroduction projects varies for several reasons. Habitat quality, presence of predators and competitors, and prey availability can all affect the survival of released individuals. For example, translocation success of birds and mammals in Australia, Canada, Hawaii, New Zealand, and the United States was associated with habitat quality, release location, and the presence of competitors (Griffith et al. 1989). Furthermore, Canada lynx (*Lynx canadensis*) reintroduction success was associated with timing of release relative to the phase of the snowshoe hare population cycle, their dominant prey source (Steury and Murray 2004). Consideration of these predator-prey interactions is often overlooked in determining release site suitability and can be a critical aspect of improving the probability of reintroduction success (Seddon et al. 2007). Reintroduction projects can also fail due to poor planning, inappropriate or too few founder animals, and lack of management resources (Seddon et al. 2007). Reintroductions that fail, even when well-planned and executed, can reduce public support for continued conservation efforts of threatened species (Yalden 1993). Thus, a more complete understanding of the factors affecting restoration success is important for ensuring successful outcomes and responsible stewardship.

Fishers (*Pekania pennanti*; Mustelidae) are a useful species for assessing variation in restoration success. The species is one of the most commonly reintroduced carnivores in North America, but the success of such efforts is highly variable (Lewis et al. 2012). Fisher reintroduction in the eastern United States is, on average, twice as likely to succeed as in the western United States, potentially due to differences in predator and prey assemblages (Lewis et al. 2012). Bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and pumas (*Puma concolor*) all prey on fishers (Wengert et al. 2014, Gabriel et al. 2015) and may compete with them for prey as well (LaPoint et al. 2015). But while differences in prey availability and predator assemblages are hypothesized to explain some of the differences in fisher reintroduction success (Lewis et al. 2012, LaPoint et al. 2015, Parsons et al. 2019), this has not been explicitly tested.

Here we assess whether differences in fisher post-release survival across two reintroduction areas were associated with differences in predator and prey assemblages. Specifically, our objectives were to (1) compare fisher survival between the southern and northern regions of the Cascade Mountains of Washington State, USA, and (2) compare the relative abundance of fisher prey and predator species between the southern and northern Cascades study areas.

METHODS

Study System

Fishers historically occurred throughout late-successional coniferous forests of Washington State before they were extirpated in the early to mid 1900s due to over-trapping, habitat loss, and predator eradication programs (Powell 1993, Lewis and Stinson 1998, Lewis et al. 2020). With little known on the status of fishers, the Washington Department of Fish and Wildlife (WDFW) conducted a status review in 1997-1998 and concluded that fishers were extremely rare or extirpated in the state and, as a result, the fisher was listed as an endangered species in the State of Washington in 1998 (Lewis 2013). In 2008, the WDFW, the National Park Service (NPS), U.S. Geological Survey, and Conservation Northwest (a non-governmental organization) initiated a fisher recovery program on the Olympic Peninsula (Lewis 2014, Happe et al. 2017, 2019). In 2015, the NPS approved a proposal from North Cascades National Park Service Complex and Mount Rainier National Park to reintroduce fishers to the Cascade Mountains (Lewis et al. 2017). The overall goal of the project was to re-establish self-sustaining fisher populations in the southern and northern Cascades (Hayes and Lewis 2006).

Our study area was divided into two regions: the South Cascades (SOCA) and the North Cascades (NOCA; Figure 1.1). The southern region of the Cascades is a 10,000+ km^2 region comprised of Gifford Pinchot National Forest (~6,100 km^2), Mount Rainier National Park (~1,000 km^2), Washington Department of Natural Resources land (~1,000 km^2), and surrounding private lands (~1,900 km^2). This region has elevation ranges from 37 to 4,392 m with a mean of

964 m. The mean July and January temperatures were 25.8°C and -1.5°C, respectively, and average precipitation was 140 cm (67 cm snowfall) in the town of Packwood, Washington near the center of the southern study area (Parsons et al. 2019). The northern region of the Cascades is a 10,000+ km^2 region comprised of Mt. Baker-Snoqualmie National Forest (6,978 km^2), North Cascades National Park Service Complex (2,768 km^2), Washington Department of Natural Resources land (~600 km^2), and surrounding private lands (~1,000 km^2). This region has elevation ranges from 84 to 3,286 m with a mean of 2,134 m. The mean July and January temperatures were 25.3°C and -2.4°C, respectively, and average precipitation was 201.5 cm (98.8 cm snowfall) in the town of Darrington, Washington near the center of the northern study area (Western Regional Climate Center 2016).

Both regions are dominated by conifer forests, ranging from young, managed forests to old-growth, unmanaged forests. Dominant tree species include Douglas fir (*Pseudotsuga menziesii*), Pacific silver fir (*Abies amabilis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). Dominant understory plants include Oregon grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), huckleberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and several fern species. Potential fisher prey throughout the study areas include Douglas squirrel (*Tamiasciurus douglasii*), Townsend's chipmunk (*Neotamias townsendii*), northern flying squirrel (*Glaucomys sabrinus*), snowshoe hare (*Lepus americanus*), mountain beaver (*Aplodontia rufa*), porcupine (*Erethizon dorsatum*), and a suite of small mammals including mice and voles. Prevalence of small mammals in the diet of fishers appears to be related to an absence of larger prey, such as mountain beavers, squirrels, snowshoe hares, and porcupines, and in areas where larger prey are abundant, small mammals play a lesser role in the diet of fishers (Martin 1994, Zielinski et al. 1999, Weir et al. 2005). In the South Cascades, for example, snowshoe hares and mountain beavers together made up 68% of fisher diet compared to 8% for small mammals (Parsons et al. 2020). Fisher-preferred prey items in our study areas overlap extensively with larger carnivores that have been to known to prey on fishers (Sweitzer et al. 2016). This diet overlap can result in increased potential competition and predation events (Newsome et al. 2017). Possible fisher predators and competitors in our study system include American martens (*Martes americana*), bobcats, coyotes, pumas, Canada lynx (*Lynx canadensis*), and wolverine (*Gulo gulo*) in both regions, and gray wolf (*Canis lupus*) in the North and Cascade red fox (*Vulpes vulpes cascadensis*) in the South. Canada lynx, wolverines, gray wolves, and Cascade red foxes are rare species occurring at low densities in our study system.

Fisher Survival

From December 2015 to January 2020, 81 fishers were released into the South Cascades (69 from a source population in central British Columbia, Canada, and 12 from a source population in central and north-central Alberta, Canada; Lewis et al. 2020). Each of the fishers from British Columbia was equipped with a very high frequency (VHF) radio-transmitter (Holohil AI-2HM; Carp, Ontario Canada) surgically implanted into their abdomens to allow biologists to monitor movements and survival of the released fishers. Handling procedures for fishers met or exceeded guidelines of the American Society of Mammalogists and were performed in accordance with British Columbia Ministry of Forests, Lands, and Natural Resource Operations Wildlife Act (Permit WL 15-17879; Lewis et al. 2020). Fishers were tracked via aerial telemetry from December 2015 through September 2018 during 94 telemetry flights. These flights and additional limited ground telemetry produced 1,028 locations in the South Cascades.

From December 2018 to February 2020, 89 fishers were released into the North Cascades from a source population in central and north-central Alberta (Lewis et al. 2020). Eighty of the 89 fishers were equipped with VHF radio-transmitters using the same methods as employed in the South Cascades, the other nine were too small to be equipped with transmitters. Handling procedures for fishers were approved by the Calgary Zoo's Committee for Welfare, Ethics, and Research (CZWERC 2018-15) and Alberta Environment and Parks (Permits 18-721, 19-014, and 20-014; Lewis et al. 2020). From January 2019 to September 2021, 43 aerial telemetry flights were conducted; these flights and additional limited ground telemetry produced 485 locations in the North Cascades.

To address objective 1, we compared fisher survival rates in the southern and northern Cascades using Kaplan-Meier analysis (Kaplan and Meier 1958, Hosmer et al. 2008) with the *survival* package (Therneau 2019) in R (R Core Team 2021). We only included known mortalities from aerial telemetry (i.e., mortality signal) or on-ground telemetry efforts (i.e., mortality recovery) and excluded fishers with unknown fates. Seven fishers in the North (4.7% of the 149 animals collared across both study areas) were not detected on any flights between their release and the date of their mortality detection. Since the true number of days alive could not be determined for these fishers, two separate survival analyses were ran, one where these fishers were given an alive days value of 1 and another where these fishers were given an alive days value that was one day less than the total days between their release and the date of their mortality detection. We know that all seven fishers were alive for one day but had those fishers survived for longer than one day, we wanted to ensure that our final results and inference weren't affected by only assigning them an alive day value of 1; our two survival analyses therefore bracket the true but unknown number of alive days for these individuals. The lack of data for missing fishers reduced the precision of our survival estimates. It is important to note that these missing fishers with unknown fates could still have been contributing to the establishment of a self-sustaining population within the recovery area (Lewis et al. 2020).

The survival function (S(t)) in our models was the probability of an individual animal in a population surviving t units of time from the date of release. The survival probability at time t_i was calculated as:

$$S(t_i) = S(t_i - 1)\ (1 - \frac{d_i}{n_i})$$

Where $S(t_i - 1)$ was the probability of an individual animal being alive at time $(t_i - 1)$; n_i was the number of individual animals alive before time t_i; and d_i was the number of events (i.e., mortalities) at time t_i.

To explore additional factors that might have influenced fisher survival, we used Cox proportional-hazards models (Cox 1972) to investigate the association between survival (i.e., number of days alive) and five predictor variables: (1) sex, (2) animal weight (kg) at the time of release, (3) age class (juvenile, subadult, or adult) as determined by tooth age, (4) days in captivity (the total number of days between capture and release), and (5) release area (North or South). To test for collinearity, we calculated variance inflation factors (VIFs) for all covariate combinations and excluded models with two variables with VIFs > 2. Sex and weight were the only variable pair with VIFs > 2. We tested all possible combinations of our predictor variables (for 17 total models) and used model selection and model averaging to generate multi-model inference of all models within two Akaike's Information Criterion (AIC_c; corrected for small sample size) units of the top model (Burnham and Anderson 2002).

The Cox proportional-hazards model was expressed by the hazard function (h(t)) which represents the risk of dying at time t.

$$h(t) = h_0(t) \exp(b_1x_1 + b_2x_2 + \ldots + b_px_p)$$

Where t was survival time (i.e. number of days alive); h(t) was the hazard function determined by a set of p covariates ($x_1, x_2, \ldots, x_p$); $b_1, b_2, \ldots, b_p$ were coefficients that measure the impact (i.e. effect size) of p covariates; and h_0 was the baseline hazard corresponding to the value of the hazard if all x_p were equal to zero. The t in h(t) represents the fact that the hazard varies over time. We also assessed whether the age structure of the released individuals differed between the study areas by employing a chi-squared test of the proportion of individuals in each age class.

Relative abundance of potential predators and prey

To address objective 2, we used motion-triggered remote camera traps to document the number and time of detections of all target species in the study areas: fisher, American marten, bobcat, puma, coyote, gray wolf, Townsend's chipmunk, Douglas squirrel, northern flying squirrel, snowshoe hare, mountain beaver, and porcupine. From August 2016 through September 2017, 134 camera stations were deployed throughout the South Cascades using randomly selected 1 km^2 hexagons (Parsons et al. 2019). Camera stations were established within 300 m of each hexagon's center, with each location being selected to increase the likelihood of detection (e.g., along game trails). Each location was sampled for about six weeks with some variation in duration due to the logistics of access and camera malfunction. Each camera station consisted of a single Bushnell Aggressor trail camera (model 119776C; Bushnell Outdoor Products, Overland Park, KS, USA), a chicken leg, and a scent lure (Caven's Gusto; Minnesota Trapline Products, Pennock, MN, USA). Cameras were placed on trees at a height of ~0.5 m above the ground. Bait and lure were attached on a second tree 2 - 4 m away from, and to the north of, the camera tree at a height of ~0.5 - 1 m above the ground (Wait et al. 2018, Parsons et al. 2019). Cameras were set to take a burst of three photos with each motion detection followed by a delay of five seconds.

From June 2018 through July 2020, we deployed 56 camera stations throughout the North Cascades study area. The 2018 season served as a pre-release period and survey sites were selected using 1 km^2 hexagons overlaid across the intended release areas. Survey hexagons were chosen randomly within accessible areas. Hexagons were deemed “accessible” if they were within 1 km of roads or within 3 km of a road if near a trail, had less than 35° slope, and did not have major rivers or roads running through the hexagon. Camera stations were deployed within 150 m of each hexagon’s center, with each location being selected to increase the likelihood of detection. The 2019 season served as a post-release period and survey site locations were chosen based on general fisher use areas from aerial telemetry data. Four camera stations were established at each study site with one camera deployed within 150 m of the center point and the other three deployed at a random cardinal direction (NW, NE, SW, SE) and within 500 m of the center point. Again, camera locations were selected to increase the likelihood of detection. Each location was sampled for approximately one year with some variation in duration due to camera malfunction and logistics of access. Each camera station consisted of a single Browning Strike Force HD Pro trail camera (model BTC-5HDPX; Browning Trail Cameras, Birmingham, AL, USA) and a scent lure tube (Caven’s Gusto applied to cotton balls inside a camouflaged PVC tube that was covered on one end and screwed into an adjacent tree for weather protection and scent persistence). Camera stations and camera settings used the same methodologies as employed by Parsons et al. (2019).

We used the number of independent detections per 100 camera station trap nights of our 12 target species as a measure of relative abundance for each species (Swanson et al. 2016, Rich et al. 2017). Independent detections were defined as photos of the same species taken ≥ 60 minutes apart (Lucherini et al. 2009, de Satgé et al. 2017). A study of fishers in central Alberta, Canada found that there were only slightly fewer detection events with a 60-minute threshold than with a 30-minute threshold, and no difference from 120- or 180-minute thresholds (Burgar et al. 2018).

The relative abundance for each species was calculated for each camera station within each region and the mean across all camera stations was reported as:

$$Relative\ Abundance\ (per\ camera\ station){:}\ \frac{Total\ \#\ of\ Independent\ Detections}{Total\ \#\ of\ Trap\ Nights}\ x\ 100$$

The packages *Timelapse2* (Greenberg and Godin 2015), *digiKam* (Thomson et al. 2018), and *camtrapR* (Niedballa et al. 2016) were used for image processing and date and time extraction. We compared relative abundance, the number of independent photographic detections per 100 camera-days, for each species between NOCA and SOCA using t-tests, with Bonferroni-corrections to achieve a family-wise α = 0.05.

RESULTS

Fisher Survival

Using aerial and on-ground telemetry we obtained data on and evaluated post-release survival of 69 radio-transmitted fishers in SOCA and 80 radio-transmitted fishers in NOCA. We were unable to detect or lost the signal from some of the released fishers, resulting in fishers with unknown fates. These fishers were excluded from our analyses, resulting in totals of 57 and 48 fishers with known fates in the South and North, respectively. Seven fishers in the North were not detected on any flights between their release and the date of their mortality detection. Two separate survival analyses were ran, one where these fishers were given an alive days value of 1 and another where these fishers were given an alive days value that was one day less than the total days between their release and the date of their mortality detection. We observed a total of 27 fisher mortalities in the South and a total of 34 fisher mortalities in the North (Table 1.1).

We were able to recover the remains or the radio-transmitter (or both) for 21 of the fisher mortalities in SOCA and 17 in NOCA. The cause of death in SOCA could be determined for 13 individuals and included predation (8), human-caused (4), and intraspecific aggression (1); of the remaining eight fishers, the cause of death was considered unknown. The suspected cause of death could be determined for 10 of the NOCA fishers and included predation (5), human-caused (4), and natural accident (1); of the remaining seven fishers, the cause of death was considered unknown. DNA swabs were sequenced for nine of the depredated carcasses with four non-conclusive and five felid positive (2 in the South – confirmed puma and bobcat, 3 in the North – confirmed puma (2) and bobcat). The ability to determine cause of death was hindered due to difficulty in locating/recovering fishers shortly after they died and before they were scavenged or decomposed (Lewis et al. 2020). All other mortalities could not be recovered due to their remote and inaccessible locations.

Based on the survival analysis where the seven North Cascades fishers (not detected between release and mortality) were assigned an alive day value of 1, fisher survival was significantly lower in the North Cascades than in the South Cascades (Kaplan-Meier models; P = 0.0007; Figure 1.2). At 720 days post-release, fishers in the North Cascades had a survival estimate of 0.25 while fishers in the South Cascades had a survival estimate of 0.53. Based on the survival analysis where those seven fishers were assigned an alive day value that was one day less than the total days between release and mortality detection, fisher survival was still significantly lower in the North than the South (P = 0.0012). The top Cox proportional-hazards model indicated that fisher survival was associated with release area (Table 1.2). The top models also included days in captivity and exam weight, but neither were significantly associated with fisher survival time (Table 1.3). The age structure of released fishers did not differ significantly between the study areas ($\chi^2 = 99.69$, $P = 0.6012$).

Relative abundance of potential predators and prey

Parsons et al. (2019) deployed 134 camera stations for 6,016 trap nights in the South Cascades. Each camera station was functional for a mean duration of 45 days, with a range of 17 - 84 days (variation due to malfunctions, displacement by wildlife, and limited winter access). These camera stations recorded 3,004 independent detections of our target species (Table 1.4). We deployed 56 camera stations for 14,817 trap nights in the North Cascades. Each camera station was functional for a mean duration of 265 days, with a range of 45-382 days due to malfunctions and logistics of access. These camera stations recorded 1,487 independent detections of our target species (Table 1.4).

Nine of the mammal species were recorded in both release areas. The relative abundance (number of independent detections per 100 camera station trap nights) of our 12 target species varied between the North and South Cascades (Figures 1.3, 1.4, 1.5). The average number of independent detections was lower in the North than the South for four prey species (Townsend's chipmunk: NOCA = 0.04, SOCA = 17.26, $P < 0.001$; Douglas squirrel: NOCA = 4.00, SOCA = 17.17, $P < 0.001$; northern flying squirrel: NOCA = 0.37, SOCA = 5.05, $P < 0.001$; and snowshoe hare: NOCA = 1.13, SOCA = 5.11, $P < 0.001$; Figure 1.3). Relative abundance of fisher predators did not differ significantly between the study areas (Figure 1.4). The relative abundance of American marten, a potential fisher competitor, differed significantly between the study areas (NOCA = 0.09, SOCA = 0.62, P = 0.015; Figure 1.5). The relative abundance of fishers did not differ significantly between the two regions (Figure 1.5).

DISCUSSION

We found significant variation in fisher survival (an important component of reintroduction success) between two regions of the Cascade Mountains in Washington, with lower fisher survival in the North (0.25) than in the South (0.53). Reliable survival estimates are few for fisher studies due to characteristically low sample sizes (e.g., usually <10 fishers monitored each year; Weir and Corbould 2008). Annual survival estimates for fishers ≥ 1 year old range from 0.45 to 0.90 (Krohn et al. 1994, York 1996, Koen et al. 2007, Weir and Corbould 2008). The annual survival estimate of a translocated fisher population in the northern Sierra Nevada, California from 2009-2015 was 0.64 (Facka 2017). The average annual survival estimate for the first three cohorts of fishers released on the Olympic Peninsula in Washington from 2008-2011 was 0.67 (Lewis 2014).

There are numerous factors that differ between our study areas that could drive the differences in fisher survival. But it is possible that the lower fisher survival we detected in the North could be due to the significantly lower relative abundance of fisher prey species there than in the South. This would be consistent with studies showing that prey assemblages at release sites can strongly affect reintroduction success (Steury and Murray 2004, Halsey et al. 2015). Indeed, post-release survival to reproductive age is essential to the establishment and persistence of reintroduced populations (Parlato and Armstrong 2013) and prey availability is a primary factor affecting fisher survival (Bowman et al. 2006, Jensen et al. 2012, Wengert et al. 2014).

Fishers that survive through a breeding season may contribute to reproduction, genetic exchange, and population persistence.

In addition to differences in predator and prey assemblages, reintroduction success can potentially be influenced by differences in habitat characteristics. A study of fisher habitat selection in the South Cascades found that the highest quality habitat in terms of forest structure may not have been the highest quality in terms of food and safety (Parsons et al. 2019); fishers selected for mature forests with large diameter trees and snags used for den and rest sites, consistent with other studies (Zielinski et al. 2004, Weir et al. 2012, Aubry et al. 2013). However, fishers in the South Cascades selected those forests near recently disturbed stands (<30 years old), and for areas that had intermediate activity levels of snowshoe hares (Parsons et al. 2019), which prefer young, regenerating stands (Lewis et al. 2011). This suggests that fishers may balance their needs for forest structure and prey, highlighting the importance of habitat quality and heterogeneous land cover for fisher reintroduction success (Parsons et al. 2019). The North Cascades has similar habitat characteristics as the South Cascades, suggesting that fishers should show similar habitat selection in the two areas. Thus, the differences in survival between the North and the South that we estimated are more likely driven by differences in the relative abundance of fisher prey than differences in habitat.

Several caveats and assumptions affect the inferences of this study. All fishers translocated to the North Cascades came from a source population in Alberta, Canada, whereas the majority of the fishers translocated to the South Cascades came from a source population in British Columbia, Canada. We acknowledge that differences between the two source populations could be a contributing factor to differences in survival rates. While we note that all fishers were evaluated by a veterinary team to ensure that they passed health inspections before they were released, so as to ensure healthy founder populations in each area, there could have been genetic or learned behavioral differences between source populations that affected post-release survival. Differences in topography and weather patterns between the two regions may have also affected fisher survival. A mean elevation of 2,134 m and harsher winter conditions in the North Cascades (mean January temperature of -2.4°C and average snowfall accumulations of 98.8 cm) could have created more challenging conditions for recently released fishers adapting to their new environment in the North than in the South (mean elevation of 964 m, mean January temperature of -1.5°C, and average snowfall accumulations of 67 cm). However, fishers were released at similar elevations in both regions in mostly snow-free areas so should have faced similar challenges during their initial movements post-release in both regions. Two different remote camera types were used for species detections in the two study areas, which could have biased our detection rate comparisons. However, while prey detection rates were significantly higher in the South, predator detection rates tended to be (non-significantly) higher in the North, suggesting that neither the northern or southern cameras were consistently under or over-detecting species. Lastly, the differences in survival we observed may not matter as much if fisher reproduction is compensatory to survival, meaning that if fishers in the North Cascades reproduce more successfully than fishers in the South Cascades, there may not be population-level differences between the two reintroduction areas in the long run. At the time of our study, we lacked sufficient data to complete a post-release reproductive comparison between the North and the South.

Decreasing global biodiversity is a human-caused problem that highlights the necessity of human-driven responses in the form of ecosystem restoration. One strategy to slow global declines in biodiversity is to try to restore deteriorated ecosystems and extirpated species.

However, such projects need to be well-planned and executed to increase the probability of successful outcomes. Our findings provide evidence that variations in prey assemblages and abundance may influence the success of predator reintroduction. Identifying important prey (and, in some cases, predator) species and assessing their relative abundance could help improve a priori predictions of reintroduction success for a variety of species across the globe.

ACKNOWLEDGEMENTS

We thank T. R. Bruntil, R. G. Christophersen, J. B. Irwin, and K. M. Rine for field assistance and M. A. Parsons for methodological and analytical guidance. We thank Mt. Baker-Snoqualmie National Forest, North Cascades National Park Service Complex, Washington Department of Natural Resources, and Sierra Pacific Industries for land access. Funding was provided by a National Science Foundation Graduation Research Fellowship Program Grant, Seattle City Light Wildlife Research Grants Program, and North Coast and Cascades Research Learning Center. Fishers were reintroduced on the traditional lands of the Cowlitz Indian Tribe, Nisqually Indian Tribe, Confederated Tribes and Bands of the Yakama Nation, Puyallup Tribe of Indians, Muckleshoot Indian Tribe, Squaxin Island Tribe, Sauk-Suiattle Indian Tribe, and Upper Skagit Indian Tribe.

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FIGURES

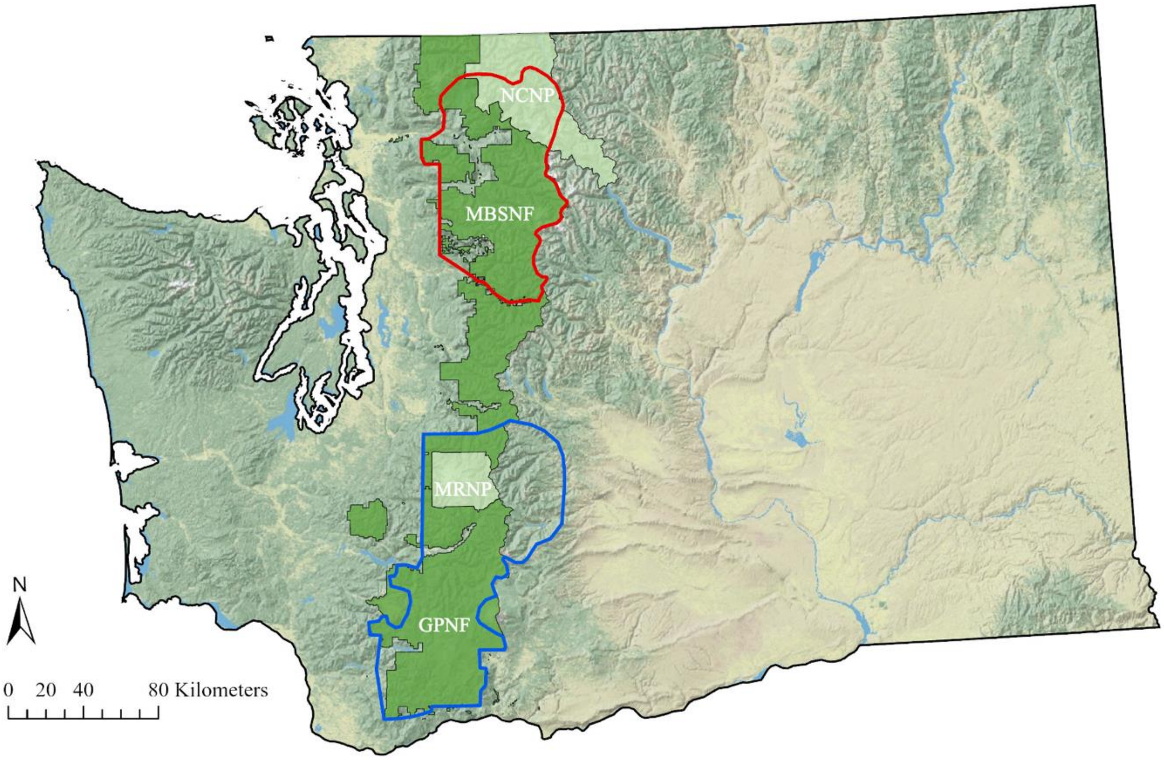
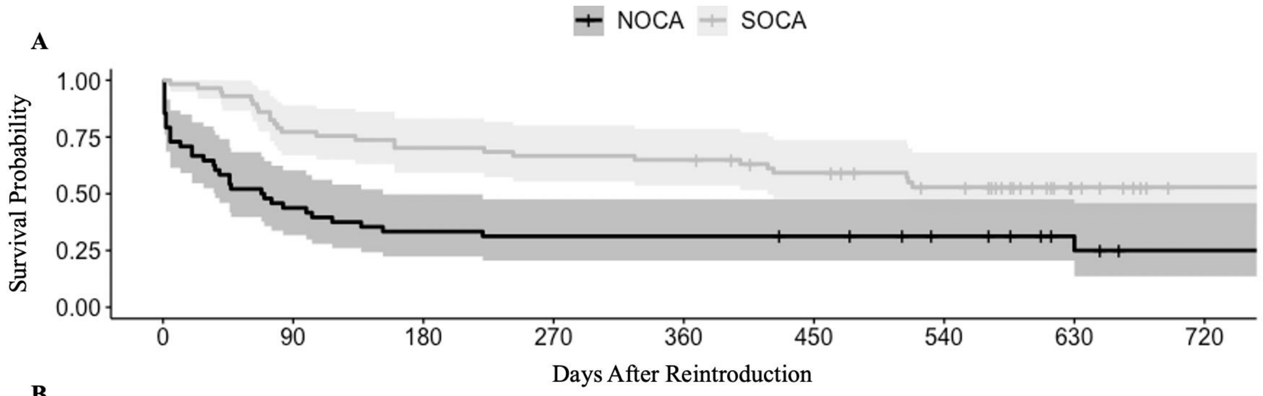


Figure 1.1. The southern and northern Cascade Mountains, Washington, USA. The southern region includes Mount Rainier National Park (MRNP) and Gifford Pinchot National Forest (GPNF) and the northern region includes North Cascades National Park Service Complex (NCNP) and Mt. Baker-Snoqualmie National Forest (MBSNF). The South Cascades study area is outlined in blue and the North Cascades study area is outlined in red.



B

Number at Risk: n (%)

	0	90	180	270	360	450	540	630	720
NOCA	48 (100)	21 (44)	16 (33)	15 (31)	15 (31)	14 (29)	10 (21)	5 (10)	2 (4)
SOCA	57 (100)	44 (77)	40 (70)	38 (67)	37 (65)	31 (54)	24 (42)	8 (14)	1 (2)

C

Cumulative Number of Mortalities

	0	90	180	270	360	450	540	630	720
NOCA	0	27	32	33	33	33	33	34	34
SOCA	0	13	17	19	20	23	26	26	26

Figure 1.2. (A) Kaplan-Meier survival curves for fishers reintroduced to the North Cascades (NOCA) and the South Cascades (SOCA) of Washington State, USA. Survival in the North was significantly lower than survival in the South (P = 0.0007). Shaded areas represent 95% confidence intervals. (B) Risk table showing the number (and %) of the fisher population at risk of death in each region. (C) Events table showing the cumulative number of confirmed mortalities.

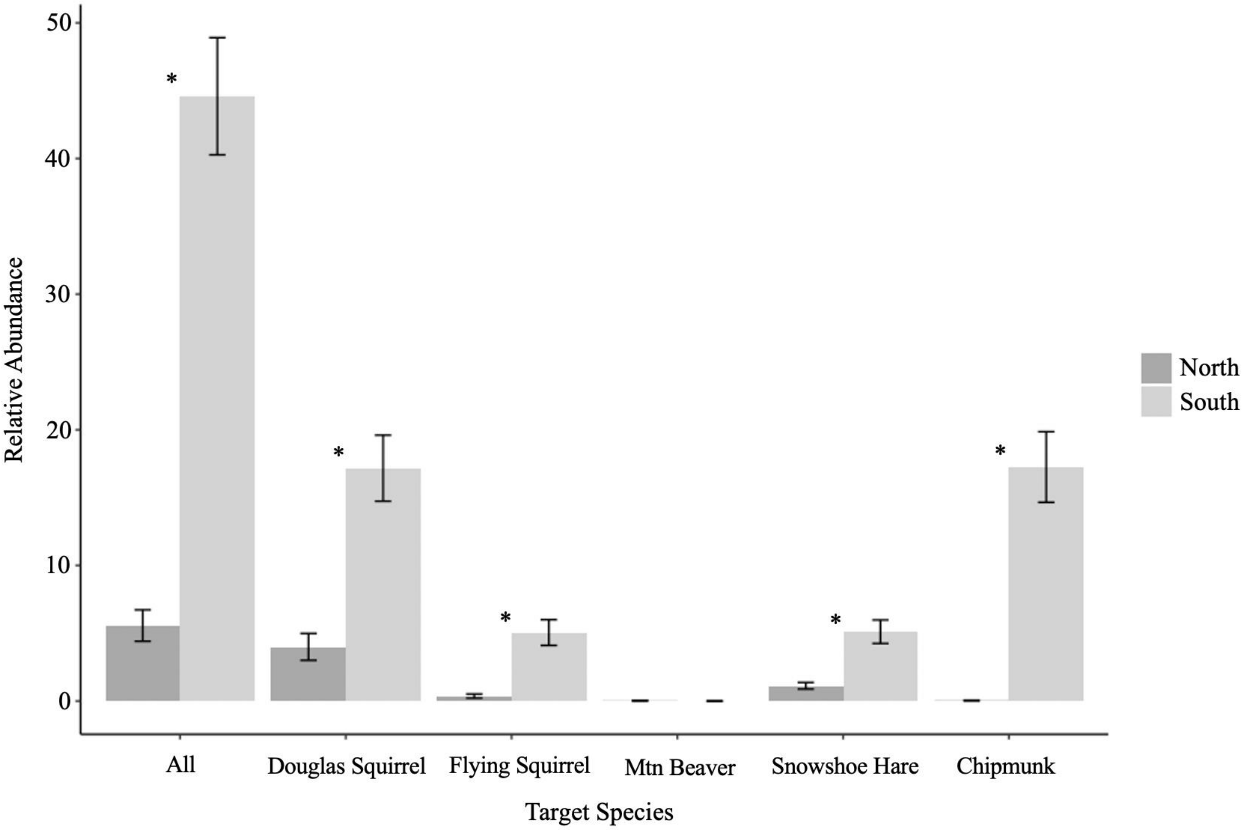


Figure 1.3. Average (±SE) number of independent detections (photos ≥ 60 mins apart) per 100 camera station trap nights for five potential fisher prey species in the North Cascades (NOCA) and South Cascades (SOCA) of Washington State, USA. Asterisks indicate species with relative abundance that differs significantly (at a Bonferroni-corrected, per-species $\alpha = 0.008$) between study areas based on Welch's two sample t-tests. The mean relative abundance for each species across all camera stations was reported.

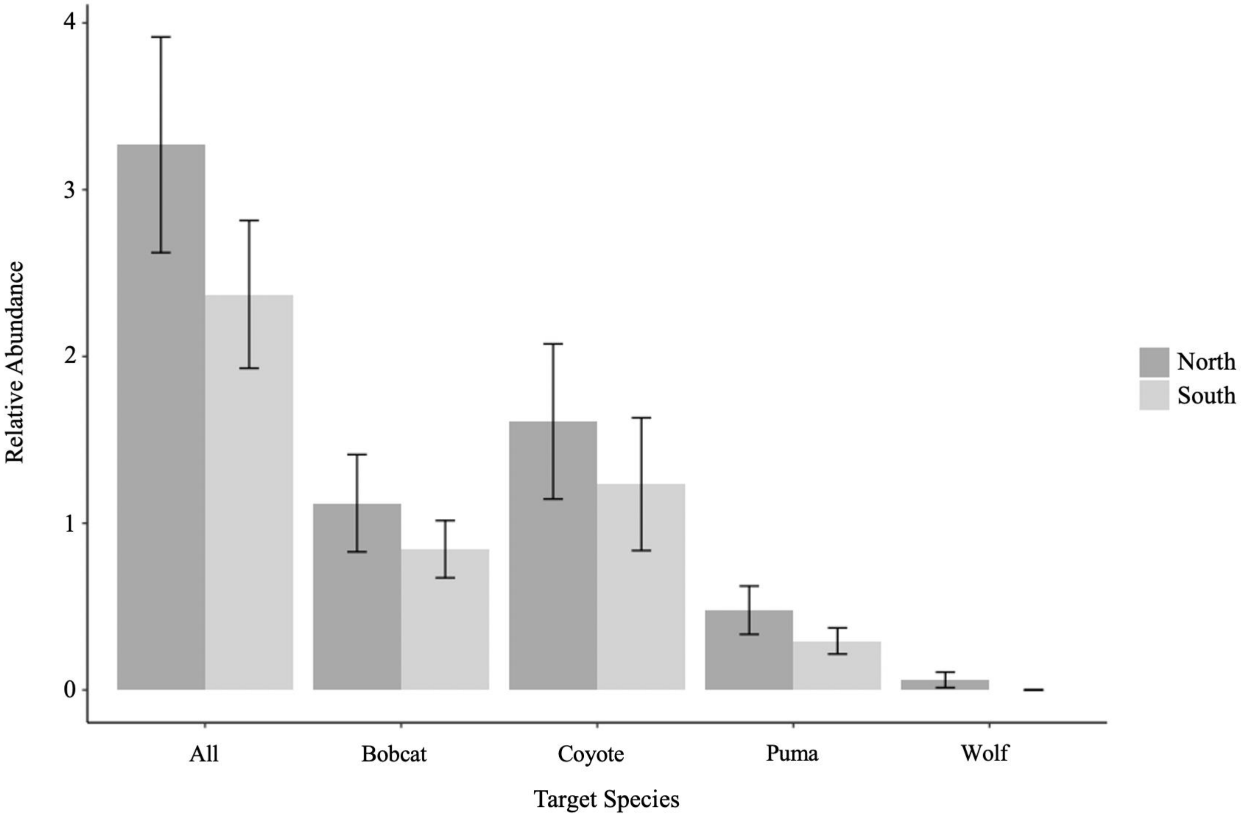


Figure 1.4. Average (±SE) number of independent detections (photos ≥60 mins apart) per 100 camera station trap nights for four potential fisher predator species in the North Cascades (NOCA) and South Cascades (SOCA) of Washington State, USA. Asterisks indicate species with relative abundance that differs significantly (at a Bonferroni-corrected, per-species $\alpha = 0.01$) between study areas based on Welch's two sample t-tests. The mean relative abundance for each species across all camera stations was reported.

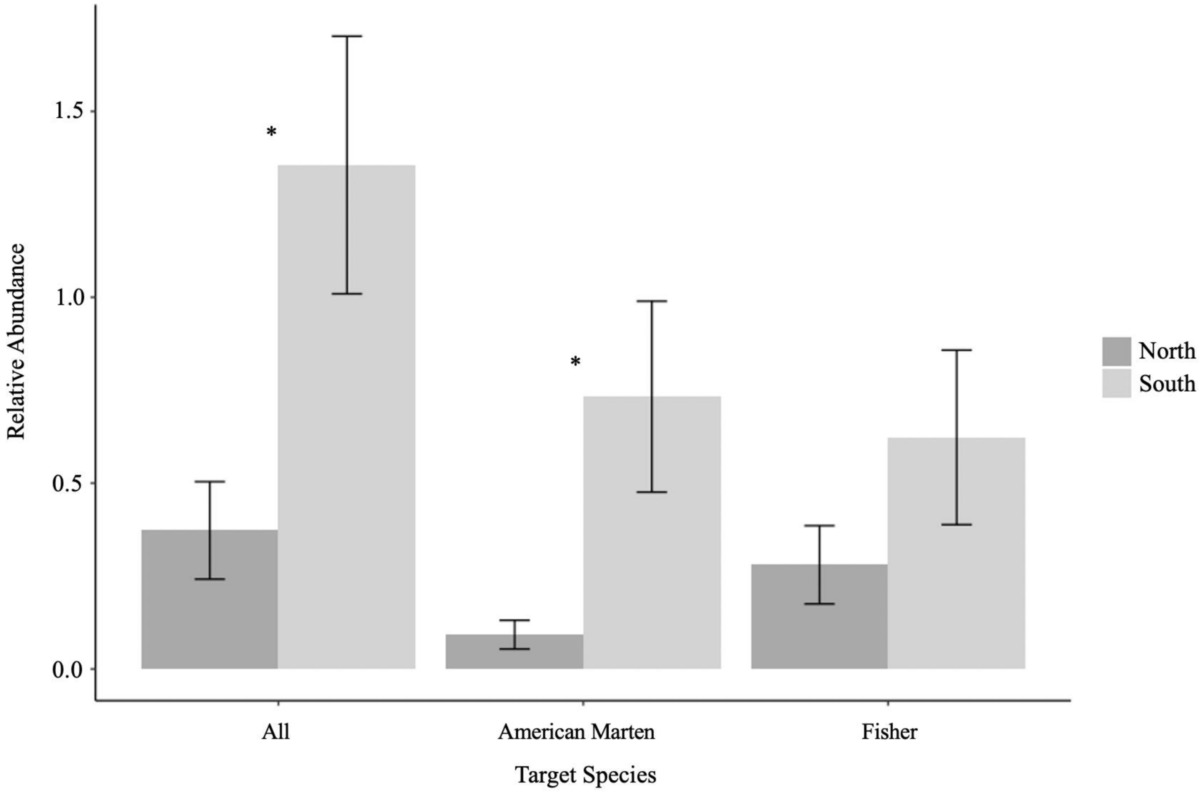


Figure 1.5. Average (±SE) number of independent detections (photos ≥ 60 mins apart) per 100 camera station trap nights for 2 weasel species in the North Cascades (NOCA) and South Cascades (SOCA) of Washington State, USA. Asterisks indicate species with relative abundance that differs significantly (at a Bonferroni-corrected, per-species α = 0.02) between study areas based on Welch’s two sample t-tests. The mean relative abundance for each species across all camera stations was reported.

TABLES

Table 1.1. Number of fishers released and tracked via aerial telemetry and on-ground telemetry efforts in the southern and northern regions of the Cascade Mountains in Washington State, USA, from December 2015 to September 2021 and the number of confirmed mortalities by sex and release area.

Release Area	Population Segment	Observation Period	Number of Fishers Released	Number of Fishers with Transmitters	Number of Fishers with Known Fates	Number of Mortalities
South	Females	December 2015-September 2018	45	38	31	17
South	Males	December 2015-September 2018	36	31	26	10
South	All Fishers	December 2015-September 2018	81	69	57	27
North	Females	January 2019 – September 2021	48	42	28	19
North	Males	January 2019 – September 2021	41	38	20	15
North	All Fishers	January 2019 – September 2021	89	80	48	34

Table 1.2. The top Cox proportional-hazards models (i.e., those within two AIC_c units of the top model) for fisher survival throughout the southern and northern Cascade Mountains of Washington State, USA.

Model	**AICc**	**Δ AICc**	**AICc Wt**
Survival ~ Release Area	444.11	0.00	0.41
Survival ~ Release Area + Days Captive	444.15	0.04	0.40
Survival ~ Release Area + Exam Weight	445.64	1.53	0.19

Table 1.3. Model-averaged coefficient estimates, standard errors (SE) and p-values for the top Cox proportional-hazards models (i.e., those within two AIC_c units of the top model) for fisher survival throughout the southern and northern Cascade Mountains of Washington State, USA.

Coefficient	**Estimate**	**SE**	**P-value**
Release Area	0.645	0.278	0.020
Days Captive	0.028	0.018	0.121
Exam Weight	0.126	0.157	0.423

Table 1.4. Camera stations record table for independent detections (photos taken ≥60 minutes apart) of 12 target species in the South Cascades (SOCA) and North Cascades (NOCA) of Washington State, USA.

Release Area	Target Species	Total Number of Independent Detections	Independent Detections Per Camera Station ($\bar{x}$ / cameras)	Range of Independent Detections Per Station
SOCA	Fisher	53	0.40	0-15
NOCA	Fisher	42	0.75	0-9
SOCA	American Marten	44	0.33	0-11
NOCA	American Marten	14	0.25	0-5
SOCA	Puma	16	0.12	0-2
NOCA	Puma	79	1.41	0-20
SOCA	Bobcat	54	0.40	0-6
NOCA	Bobcat	177	3.16	0-31
SOCA	Coyote	81	0.60	0-25
NOCA	Coyote	263	4.70	0-49
SOCA	Gray Wolf	0	0	0
NOCA	Gray Wolf	8	0.14	0-5
SOCA	Townsend’s Chipmunk	1,028	7.45	0-106
NOCA	Townsend’s Chipmunk	7	0.13	0-3
SOCA	Douglas Squirrel	1,107	8.26	0-111
NOCA	Douglas Squirrel	662	11.82	0-118
SOCA	Northern Flying Squirrel	304	2.27	0-42
NOCA	Northern Flying Squirrel	52	0.93	0-12
SOCA	Snowshoe Hare	317	2.37	0-48
NOCA	Snowshoe Hare	178	3.18	0-21
SOCA	Mountain Beaver	0	0	0
NOCA	Mountain Beaver	5	0.09	0-3
SOCA	Porcupine	0	0	0
NOCA	Porcupine	0	0	0

CHAPTER TWO

Fisher Prey Habitat Use in the Northern Cascade Mountains of Washington State

ABSTRACT

As climate change and loss of biodiversity grow in intensity, the global need for ecological restoration has become more acute. For threatened and endangered wildlife species, restoration often comes in the form of reintroduction – re-establishing populations in parts of their historic range from which they had been extirpated. However, reintroduction efforts can be costly, time-intensive, and often fail at generating self-sustaining populations. Thus, a more complete understanding of the factors affecting reintroduction success is important for ensuring successful outcomes. Fishers (*Pekania pennanti*) are one of the most commonly reintroduced carnivores in North America but the success of such efforts is highly variable, potentially due to differences among sites in prey availability. We examined and mapped habitat use of three important fisher prey species - snowshoe hare (*Lepus americanus*), Douglas squirrel (*Tamiasciurus douglasii*), and mountain beaver (*Aplodontia rufa*) – in the northern Cascade Mountains, Washington, USA. We compared model performance between field-measured and remotely sensed habitat variables in determining habitat use of our target species. We found that detections of snowshoe hare were negatively associated with deciduous tree basal area and deciduous tree canopy cover, detections of Douglas squirrel were positively associated with coniferous tree basal area and negatively with deciduous tree basal area, and detections of mountain beaver were negatively associated with coniferous tree basal area and positively with deciduous tree canopy cover. All of our top models with remotely sensed habitat variables performed better than our top models with field-measured habitat variables. Knowledge gained from our habitat use analyses and predictive prey

distribution maps may be useful in guiding site selection for future fisher reintroduction efforts. In general, wildlife reintroduction projects may benefit from joining field-based prey surveys with remotely sensed habitat variables to help determine optimal release site locations.

INTRODUCTION

Human-caused climate change and loss of biodiversity are degrading ecosystems around the world, highlighting the need for global ecological restoration to help ameliorate or reverse the ecological damage (Gann et al. 2019). Declines in the abundance of many species can reduce the stability of ecological communities (Cardinale et al. 2012, Giacomini and Galetti 2013, Dirzo et al. 2014). In recognition of this, the United Nations declared 2021-2030 the Decade on Ecosystem Restoration (Aronson et al. 2020) to galvanize action on the global recovery of degraded ecosystems. For threatened and endangered animals, reintroductions can serve as a means of ecological restoration. Reintroduction projects are widely employed to re-establish species in parts of their range where they have been extirpated, which can potentially help restore ecosystem stability (Seddon et al. 2007, Devineau et al. 2011, Seddon et al. 2014).

However, wildlife reintroduction projects are often expensive, time consuming, and unsuccessful at generating self-sustaining populations (Miller et al. 1999, Fischer and Lindenmayer 2000). Two main factors commonly affect the survival of released individuals and therefore the success of reintroduction projects: habitat quality and prey availability. For example, translocation success of water voles (*Arvicola terrestris*) in the UK was associated with variations in habitat quality (Moorhouse et al. 2009) while black-footed ferret (*Mustela nigripes*) reintroduction success in the US and northern Mexico was associated with the density of their prey (Jachowski et al. 2011). A lack of information on habitat quality and prey abundance before reintroduction is often cited as an explanation for a lack of successful project outcomes (Rantanen et al. 2010, Moseby et al. 2020). The abundance and habitat requirements of important prey species can determine habitat quality for the species being reintroduced (Miller et al. 1999, Seddon et al. 2007). But consideration of which habitats support important prey species is often overlooked in determining release site suitability (Seddon et al. 2007, Parsons et al. 2020).

Fishers (*Pekania pennanti*; Mustelidae) are one of the most commonly reintroduced carnivores in North America. However, reintroduction success across the continent has been highly variable (Lewis et al. 2012), potentially due to differences in prey availability (Kirby et al. 2018). Post-release survival to reproductive age is essential to the establishment and persistence of reintroduced populations (Parlato and Armstrong 2013) and prey availability is a primary factor affecting fisher survival (Bowman et al. 2006, Jensen et al. 2012, Wengert et al. 2014). A feasibility assessment for fisher reintroduction in Washington State identified snowshoe hare (*Lepus americanus*), Douglas squirrel (*Tamiasciurus douglasii*), and mountain beaver (*Aplodontia rufa*) as important prey species in the release areas but did not assess the distributions of these species prior to release (Lewis and Hayes 2004).

Preliminary assessments of prey abundance and presence across release areas are seldom conducted prior to species reintroductions. This is often a result of these assessments being too costly and time-demanding, requiring extensive field work to measure the desired variables. However, these preliminary assessments have been shown to be advantageous in increasing the probability of reintroduction success (Breitenmoser et al. 2001, Steury and Murray 2004, Rantanen et al. 2010, Halsey et al. 2015, Moseby et al. 2020). Exploring alternatives to strictly using field-measured variables could cut costs, save time, and increase the feasibility of employing preliminary prey assessments prior to initiation of reintroductions. For example, many parts of the world now have extensive remote sensing data available that can be used in habitat quality and species distribution assessments. But there are relatively few direct comparisons of habitat selection based on field-measured variables (expensive to collect but potentially conferring greater realism) versus remote sensing-derived variables (cheaper to collect and more spatially widespread but potentially ecologically coarse).

Here we measure the habitat use of three important fisher prey species in the northern Cascade Mountains of Washington State, USA. Specifically, our objective was to examine how the occurrence of each prey species was related to forest overstory and understory conditions.

METHODS

Study Area

Historically, fishers ranged throughout conifer forests of Washington State until over-trapping, habitat loss, and predator eradication programs led to their extirpation in the early to mid 1900s (Powell 1993, Lewis and Stinson 1998, Lewis et al. 2020). From the mid 1900s to the mid 1990s, the status of fishers in Washington State was unknown. In 1997-1998, the Washington Department of Fish and Wildlife (WDFW) conducted a status review and concluded that fishers were extremely rare or extirpated in the state. As a result, in 1998 the fisher was listed as an endangered species in the State of Washington (Lewis 2013). Fisher recovery efforts in the state were spearheaded by the WDFW, the National Park Service (NPS), U.S. Geological Survey, and Conservation Northwest (a non-governmental organization), through the initiation of a fisher reintroduction program on the Olympic Peninsula in 2008 (Lewis 2014, Happe et al. 2017, 2019). To restore fishers to the majority of their historic range, recovery efforts were extended to the Cascade Mountains following NPS approval of reintroduction proposals from North

Cascades National Park Service Complex and Mount Rainier National Park (Lewis et al. 2017). The overall goal was to re-establish self-sustaining fisher populations in the southern and northern Cascades, contributing to fisher recovery and potential down-listing of the species from endangered to threatened in the state (Hayes and Lewis 2006, Lewis 2017).

To assess fisher prey, we conducted field sampling in the northern Cascades from June 2018 through August 2019 (Figure 2.1). Our study area was a 10,000+ km^2 region comprised of Mt. Baker-Snoqualmie National Forest (6,978 km^2), North Cascades National Park Service Complex (2,768 km^2), Washington Department of Natural Resources land (~600 km^2), and surrounding private lands (~1,000 km^2). This region has elevation ranges from 84 to 3,286 m with a mean of 2,134 m. The mean July and January temperatures were 25.3°C and -2.4°C, respectively, and average precipitation was 201.5 cm (98.8 cm snowfall) in the town of Darrington, Washington, near the center of the northern study area (Western Regional Climate Center 2016). This region is dominated by conifer forests ranging from young, managed forests to old-growth, unmanaged forests. Dominant tree species include Douglas fir (*Pseudotsuga menziesii*), Pacific silver fir (*Abies amabilis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*). Dominant understory plants include Oregon grape (*Mahonia nervosa*), salal (*Gaultheria shallon*), huckleberry (*Vaccinium* spp.), salmonberry (*Rubus spectabilis*), and several fern species.

Fishers are generalist carnivores that consume a wide variety of prey species, with medium-sized mammals being their dominant food (Arthur et al. 1989, Powell 1993, Zielinski and Duncan 2004, Weir et al. 2005). Potential fisher prey in our study area included Douglas squirrel, Townsend's chipmunk (*Neotamias townsendii*), northern flying squirrel (*Glaucomys sabrinus*), snowshoe hare, mountain beaver, porcupine (*Erethizon dorsatum*), and a suite of small mammals such as mice and voles. Prevalence of small mammals in the diet of fishers mainly occurs when larger prey are absent; in areas where mountain beavers, squirrels, snowshoe hares, or porcupines are abundant, small mammals play only a small role in fisher diets (Martin 1994, Zielinski et al. 1999, Weir et al. 2005). In the South Cascades, for example, snowshoe hares and mountain beavers together made up 68% of fisher diet compared to 8% for small mammals (Parsons et al. 2020).

Field sampling

From June 2018 through August 2019, we sampled a total of 19 sites; 10 in the summer (June to August) of 2018, and nine in the summer of 2019 (Figure 2.1). The 2018 season served as a pre-release period and survey sites were selected using 1 km^2 hexagons overlaid across the intended release areas. Survey hexagons were chosen randomly within accessible areas. Hexagons were deemed “accessible” if they were within 1 km of roads or within 3 km of a road if near a trail, had less than 35° slope, and did not have major rivers or roads running through the hexagon. A 300 × 300 m grid of 49 points spaced 50 m apart was established in the center of each survey hexagon for the 2018 season (Figure 2.2). The 2019 season served as a post-release period and survey site locations were chosen based on general fisher use areas from aerial telemetry data. A 600 × 600 m grid of 49 points spaced 100 m apart was established in the center of each survey site for the 2019 season (Figure 2.2). The size of the sampling grid was doubled for the 2019 season to account for error associated with fisher aerial telemetry points (error ranging from 200 m to 1.6 km).

At each of the 49 points per site, we recorded the presence or absence of snowshoe hare pellets in a 0.564 m radius (1 m^2) circular plot at the center of each survey point and the presence or absence of Douglas squirrel middens and mountain beaver burrows in a 5.64 m radius (0.1 ha) circular plot (Murray et al. 2002, Hodges and Mills 2008). Field-measured habitat characteristics were collected at 25 of the 49 points at each site in a 300 × 300 m (2018) or 600 × 600 m (2019) sampling grid (Figure 2.2) using the same circular plot as the midden and burrow sign surveys. To record data on forest overstory conditions, we measured diameter at breast height (DBH) and documented species and health status (alive/dead) of all trees >10 cm DBH (Klenner and Sullivan 2009). We then calculated the cumulative basal area (m^2) for each tree species based on DBH measurements. To characterize the forest understory conditions, we measured coarse woody debris (CWD) and understory species at each point. For CWD, we recorded the total number of logs and stumps >10 cm DBH at the widest point. We estimated understory species percent cover using a 10 m line intercept (Canfield 1941) and visually estimated shrub species percent cover within six categories: < 5%, 5-25%, 25-50%, 50-75%, 75-95%, and >95%. We used four field-measured habitat variables in our analyses, with habitat points ($N = 413$) as sampling units: cumulative basal area (m^2) of coniferous and deciduous trees, shrub percent cover, and cumulative CWD. We collected data for 413 of 475 total habitat points, the 62 remaining points were unable to be surveyed due to inaccessibility.

Remote sensing data

Remotely sensed habitat variables were downloaded from the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA; LEMMA Team 2020) dataset from the United States Forest Service Pacific Northwest Research Station and Oregon State University. This dataset contains 30 m resolution raster of forest structure using a gradient nearest neighbor approach produced using multivariate relationships between satellite imagery, environmental variables, and field plot data (Ohmann et al. 2012). We used eight forest structure variables from these data: basal area (m^2), canopy cover (%), and quadratic mean diameter (cm; QMD) of deciduous and coniferous trees, and stand age (years) and height (m). Ohmann et al. (2012) validated the LEMMA data via ground truthing and estimated these eight variables had an average correlation of R = 0.75 with on-ground values from field plots.

Data analysis

We used the field-measured habitat characteristics and the remotely sensed forest structure variables from LEMMA to model habitat use of snowshoe hare, Douglas squirrel, and mountain beaver with a used-unused resource selection function (RSF; Manly et al. 2002, Boyce et al. 2002). For our RSFs, we employed mixed-effects logistic regression (Gillies et al. 2006) in R (R Core Team 2021). We scaled all variables to mean = 0 and standard deviation = 1 before analyses. To test for collinearity, we calculated variance inflation factors (VIFs) for all covariate combinations and did not run any models containing two variables with VIFs > 2. We tested all possible combinations of conifer and deciduous models separately to determine a “top conifer” and a “top deciduous” model for both field and remotely sensed variables. We ran a total of 16 models per species using field-measured habitat variables and a total of seven models per species using remotely sensed forest structure data. We used model selection and model averaging to generate multi-model inference of all models within ten Akaike’s Information Criterion (AIC_c; corrected for small sample size) units of the top model (Burnham and Anderson 2002). We compared the top field-measured and remotely sensed models for each species using AIC_c. We then used the top remotely sensed model for each prey species to predict and map the occurrence of each across the study area.

RESULTS

Prey Habitat Use

We collected fisher prey data at 870 of the 931 sign survey points; the 61 remaining points were unable to be surveyed due to inaccessibility. Of the surveyed points, 65 had snowshoe hare pellets, 359 had Douglas squirrel middens, and 11 had mountain beaver burrows. The top remotely sensed models for three fisher prey species included four remotely sensed habitat variables: deciduous canopy cover, deciduous basal area, stand age, and stand height (Figure 2.3).

Model selection with field-measured habitat variables identified seven top models ($\Delta AIC_c < 10$) for snowshoe hare (Table 2.1). The top snowshoe hare model with field-measured variables indicated that hare use was related negatively to deciduous tree basal area and positively to cumulative CWD (ΔAIC_c to next-best model: 1.85, McFadden's pseudo-r^2: 0.048; Tables 2.1 & 2.2). Values of McFadden's pseudo-r^2 between 0.2 and 0.4 are indicative of extremely good model fits, equivalent to a range of 0.7 to 0.9 for a linear function (Domenich and McFadden 1975). Some of the models also included shrub percent cover and conifer tree basal area but the model-averaged coefficients for these variables were not significantly associated with snowshoe hare occurrence (Table 2.2). Model selection with remotely sensed forest structure characteristics identified one top model for snowshoe hare (Table 2.3), where hare use was negatively related to deciduous tree canopy cover and stand age (McFadden's pseudo-r^2: 0.109; Tables 2.4). Our predictions showed a decrease in probability of use with an increase in deciduous canopy cover and an increase in stand age (Figure 2.4). The predictive prey map for snowshoe hare incorporated both variables and had probabilities of use ranging from 0.00 to 0.50 across our study area (Figure 2.5). Our top remotely sensed snowshoe hare model performed better than our top field-measured snowshoe hare model (ΔAIC_c = 27.82).

Model selection with field-measured habitat characteristics identified six top models (ΔAIC_c <10) for Douglas squirrel (Table 2.5). The top Douglas squirrel model with field-measured variables indicated that squirrel use was positively related to conifer tree basal area and negatively to deciduous tree basal area (ΔAIC_c to next-best model: 1.27; McFadden's pseudo-r^2: 0.054; Tables 2.5 & 2.6). Some of the models also included CWD and percent shrub cover, but the model-averaged coefficients for these variables were not significantly associated with Douglas squirrel use (Table 2.6). Model selection with remotely sensed forest structure characteristics identified two top models for Douglas squirrel (Table 2.7). The top Douglas squirrel model with remotely sensed variables indicated that squirrel use was negatively related to deciduous tree basal area and positively to stand height (ΔAIC_c to next-best model: 0.66; McFadden's pseudo-r^2: 0.152; Tables 2.7 & 2.8). The other model included stand age but the model-averaged coefficient for this variable was not significantly associated with Douglas squirrel use (Table 2.8). Our predictions showed a decrease in probability of use with an increase in deciduous basal area and an increase in probability of use with an increase in stand height (Figure 2.6). The predictive prey map for Douglas squirrel incorporated both variables and had probabilities of use ranging from 0.00 to 0.70 across our study area (Figure 2.7). Our top remotely sensed Douglas squirrel model performed better than our top field-measured Douglas squirrel model (ΔAIC_c: 115.49).

For mountain beaver, all 16 models with field-measured habitat characteristics were within 10 AIC_c units of the top model (Table 2.9). The top mountain beaver model with field-measured variables indicated that mountain beaver use was negatively related to conifer tree basal area (ΔAIC_c to next-best model: 0.48; McFadden's pseudo-r^2: 0.026; Tables 2.9 & 2.10) and positively to percent shrub cover, CWD, and deciduous tree basal area, but the model-averaged coefficients for these variables were not significantly associated with mountain beaver use (Table 2.10). Model selection with remotely sensed forest structure characteristics identified six top models ($\Delta AIC_c < 10$) for mountain beaver (Table 2.11). The top mountain beaver model with remotely sensed variables indicated that mountain beaver use was positively related to deciduous tree canopy cover (ΔAIC_c to next-best model: 1.80; McFadden's pseudo-r^2: 0.093; Tables 2.11 & 2.12). Some of the models also included coniferous tree basal area, coniferous tree QMD, stand age, and stand height, but the model-averaged coefficients for these variables were not significantly associated with mountain beaver use (Table 2.12). Our predictions showed an increase in probability of use with an increase in deciduous canopy cover (Figure 2.8). The predictive prey map for mountain beaver incorporated one variable and had probabilities of use ranging from 0.00 to 0.03 across our study area (Figure 2.9). Our top remotely sensed mountain beaver model performed better than our top field-measured mountain beaver model (ΔAIC_c: 7.97).

DISCUSSION

Snowshoe hares, Douglas squirrels, and mountain beavers have all been identified as important prey items for fishers in the Cascade Mountains (Lewis and Hayes 2004, Parsons et al. 2020). We found that snowshoe hares were negatively associated with both deciduous tree basal area and deciduous tree canopy cover. This is consistent with prior work showing that forests dominated by dense coniferous vegetation are preferred by snowshoe hares (Wolff 1980, Griffin and Mills 2007); Orr and Dodds (1982) found that snowshoe hare pellet counts were twice as high in habitats dominated by coniferous vegetation than in habitats dominated by deciduous plants. We found that Douglas squirrels in our study system were positively associated with coniferous tree basal area and negatively associated with deciduous tree basal area. These findings are consistent with prior research showing that Douglas squirrels use conifer trees for both shelter and food (Sullivan et al. 2017). Finally, for mountain beavers we found that habitat use was negatively associated with coniferous tree basal area and positively associated with deciduous tree canopy cover. Again, these results are consistent with prior research showing that mountain beavers generally prefer young, deciduous forests in moist environments (Arjo et al. 2007).

We found that remote sensing-based models fit the occurrence data for our study species much more parsimoniously than did the field-measured data. Assessing habitat conditions based on remote sensing is often easier and cheaper than conducting detailed field surveys and allows the extrapolation of model predictions over the entire study area (rather than just to areas where field measurements of habitat conditions were taken). But the use of remote sensing data runs the risk of not being as precise as field-collected data, for example by missing elements of the forest structure that are key determinants of species' habitat selection. For example, one of the most important field variables for snowshoe hare is horizontal cover (Holbrook et al. 2016, Kumar et al. 2017) which cannot be measured with remote sensing data and must be measured in the field. Our study did not take field-measurements of horizontal cover, thus our comparisons of remotely sensed versus field collected data were not necessarily fair for snowshoe hare. Measuring habitat with remotely sensed data, which span the study area, also allowed us to extrapolate our results across the entire study area, rather than restricting our prey habitat maps to the relatively tiny fraction of it that we were able to visit on foot to collect field measurements. Our findings suggest that wildlife reintroduction projects may benefit from joining field-based prey surveys with remotely sensed habitat variables to help determine optimal release site locations.

Mitigating human-caused degradation of the natural world and declines in global biodiversity require protecting intact ecosystems when possible as well as focused efforts to restore degraded ecosystems and reintroduce extirpated wildlife populations. However, we need to ensure that our efforts are successful, especially given how expensive reintroduction projects can be and how often they fail. Reintroduction success is influenced by the habitat quality of the release areas (Griffith et al. 1989, Miller et al. 1999, Fischer and Lindenmayer 2000). When assessing habitat quality, it is vital to consider not only vegetation and landscape characteristics, but also potential species interactions. For example, the success of carnivore reintroductions may depend on the availability of their prey (Miller et al. 1999, Seddon et al. 2007), suggesting that understanding the habitat requirements of these prey species could enhance carnivore reintroduction success.

In conclusion, we provide detailed habitat use estimates for three important prey species of the endangered fisher in Washington State. In our system, the analysis suggests that prey are available throughout the study area, with mountain beavers in riparian areas and hares and squirrels in upland conifer forests. This could be taken to mean that fishers could be reintroduced anywhere in the study area and that they would find prey there. But it is also notable that snowshoe hares and mountain beavers make up a larger proportion of fisher diet (68% in the South Cascades; Parsons et al. 2020), suggesting that release sites should be concentrated in transition areas between riparian and upland conifer forests where the dominant prey are more frequent. But in other systems, cumulative prey biomass may be distributed much more heterogeneously than in ours suggesting that, in general, carnivore reintroductions may benefit immensely from pre-release prey surveys.

ACKNOWLEDGEMENTS

We thank T. R. Bruntil, R. G. Christophersen, J. B. Irwin, and K. M. Rine for field assistance. We thank Mt. Baker-Snoqualmie National Forest, North Cascades National Park Service Complex, Washington Department of Natural Resources, and Sierra Pacific Industries for land access. Funding and other support was provided by a National Science Foundation Graduation Research Fellowship Program Grant, Seattle City Light Wildlife Research Grants Program, North Coast and Cascades Research Learning Center, North Cascades National Park, and the University of Montana. Fishers were reintroduced on the traditional lands of the Cowlitz Indian Tribe, Nisqually Indian Tribe, Confederated Tribes and Bands of the Yakama Nation, Puyallup Tribe of Indians, Muckleshoot Indian Tribe, Squaxin Island Tribe, Sauk-Suiattle Indian Tribe, and Upper Skagit Indian Tribe.

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FIGURES

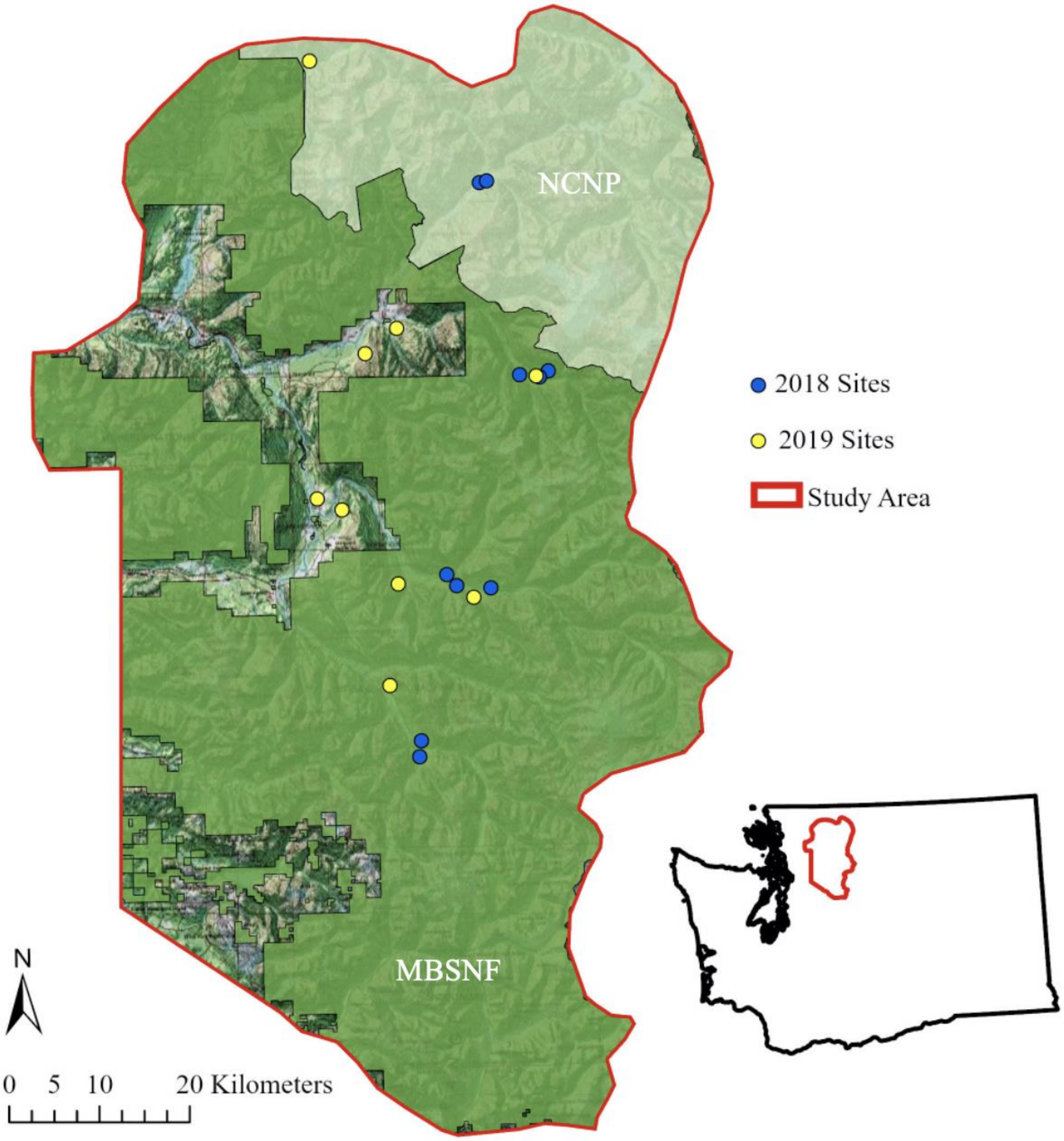

Figure 2.1. 2018 and 2019 study sites within the northern Cascade Mountains, Washington, USA. The northern Cascades include North Cascades National Park Service Complex (NCNP) and Mt. Baker-Snoqualmie National Forest (MBSNF).

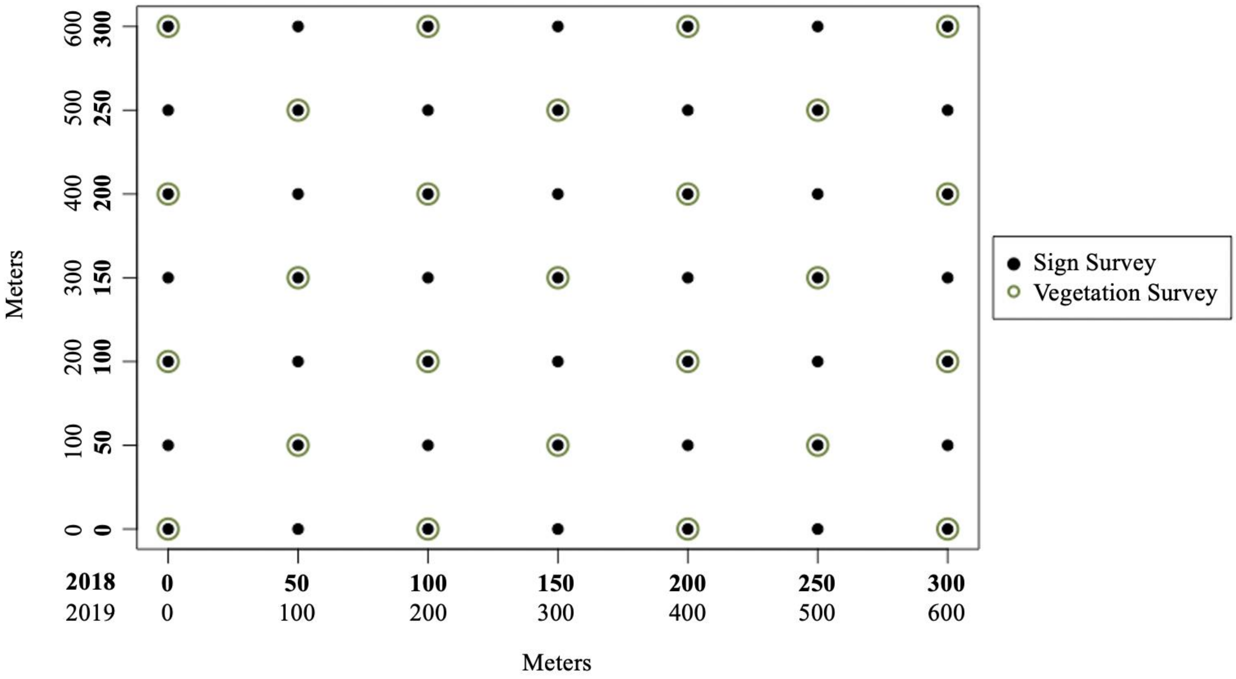

Figure 2.2. Sampling grid for habitat and prey surveys in the northern Cascade Mountains, Washington, USA. Black dots show locations of 49 sign surveys for snowshoe hare pellets, Douglas squirrel middens, and mountain beaver burrows. Green circles show locations of 25 vegetation surveys for habitat characteristics. Grid dimensions for the 2018 season are shown in bold.

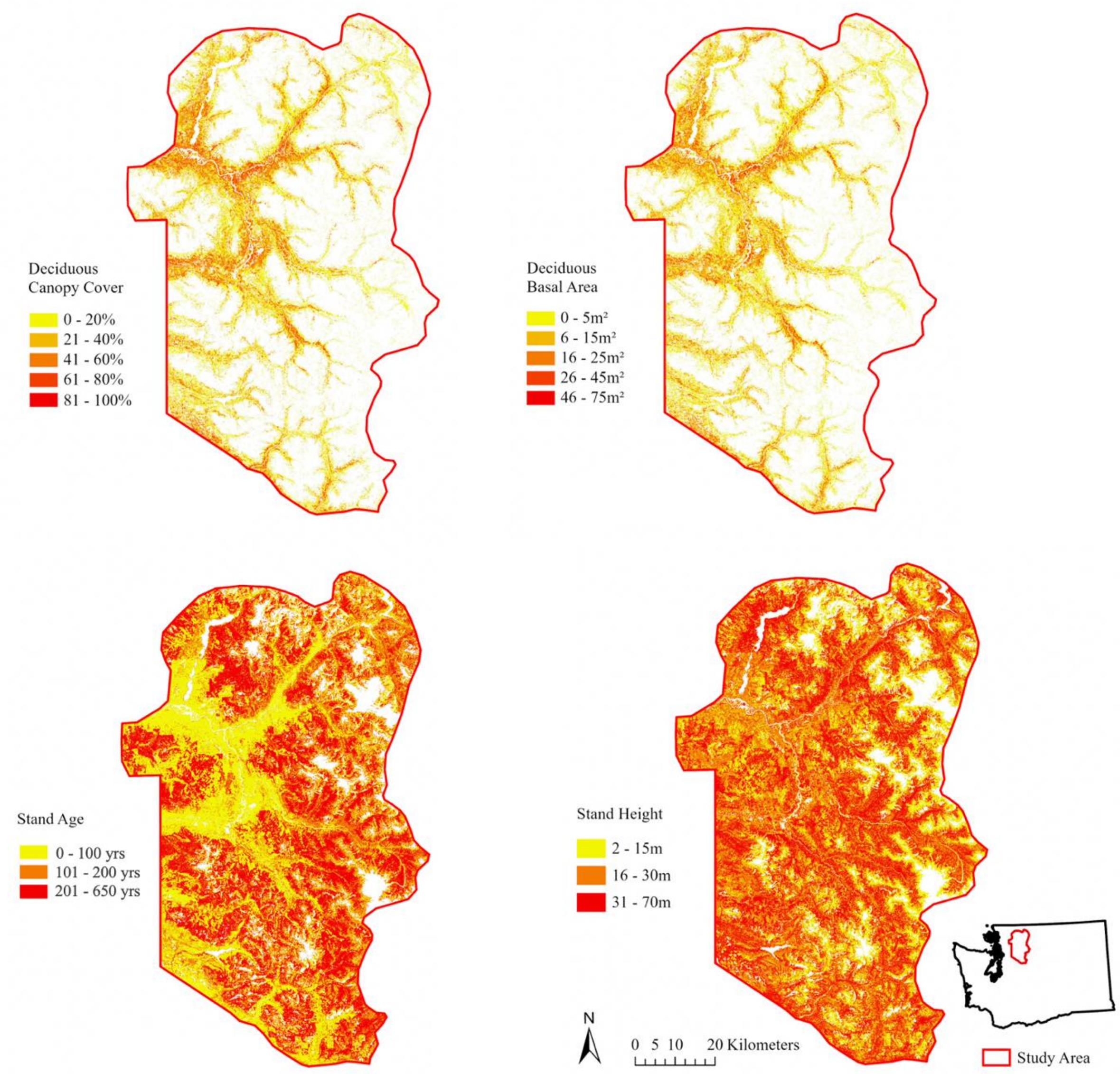

Figure 2.3. Four remotely sensed habitat variables from top models for snowshoe hare, Douglas squirrel, and mountain beavers in the northern Cascade Mountains, Washington, USA.

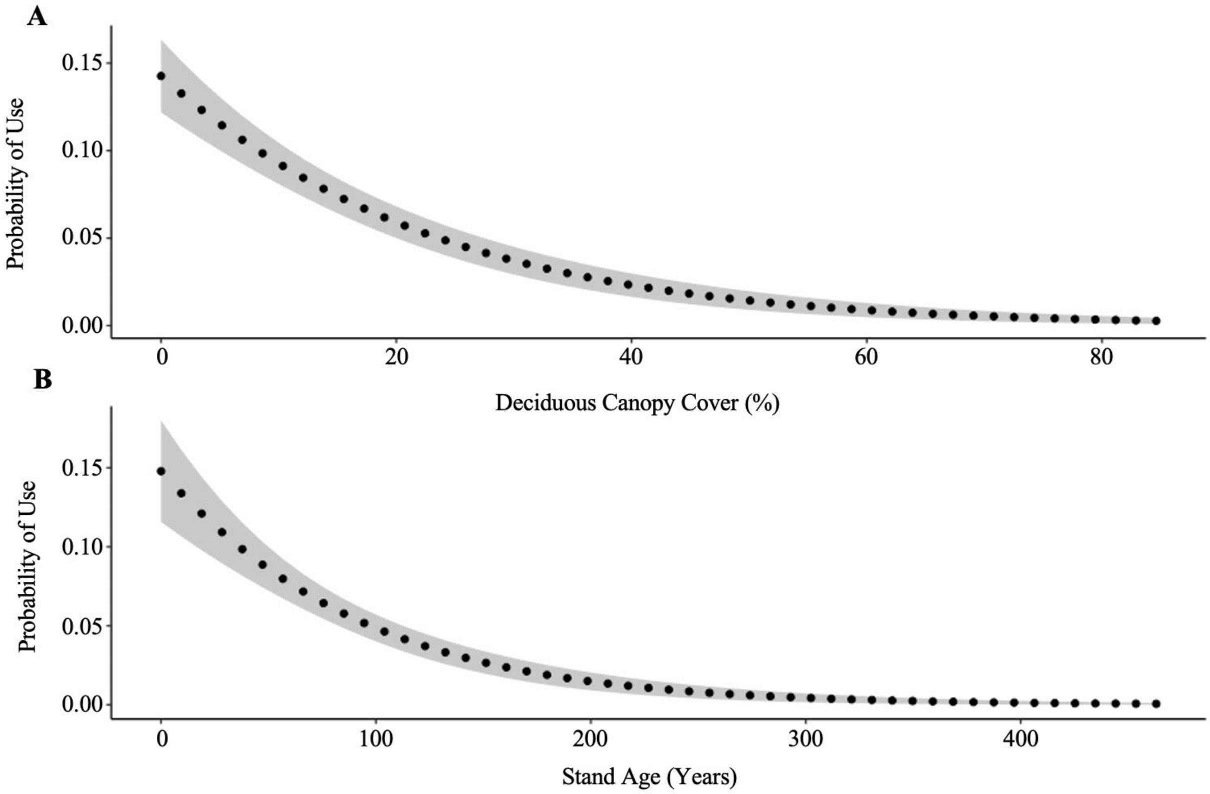

Figure 2.4. Snowshoe hare habitat use as a function of deciduous canopy cover (A) and forest stand age (B) based on remotely sensed data in the northern Cascade Mountains, Washington, USA. The dotted lines represent predicted values and the shaded areas represent 95% confidence intervals.

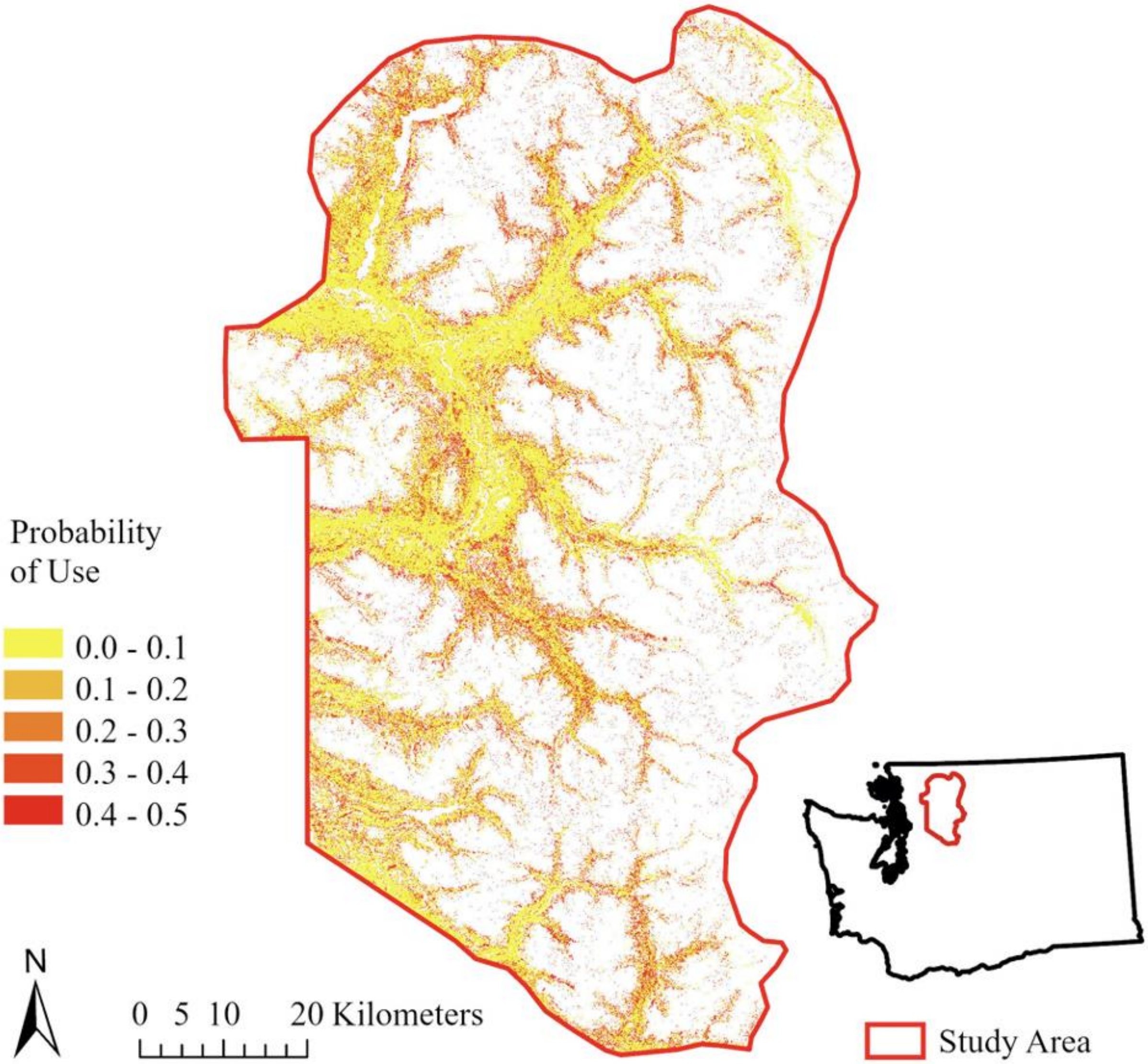

Figure 2.5. Predictive map showing the probability of snowshoe hare use based on remotely sensed deciduous canopy cover and stand age in the northern Cascade Mountains, Washington, USA.

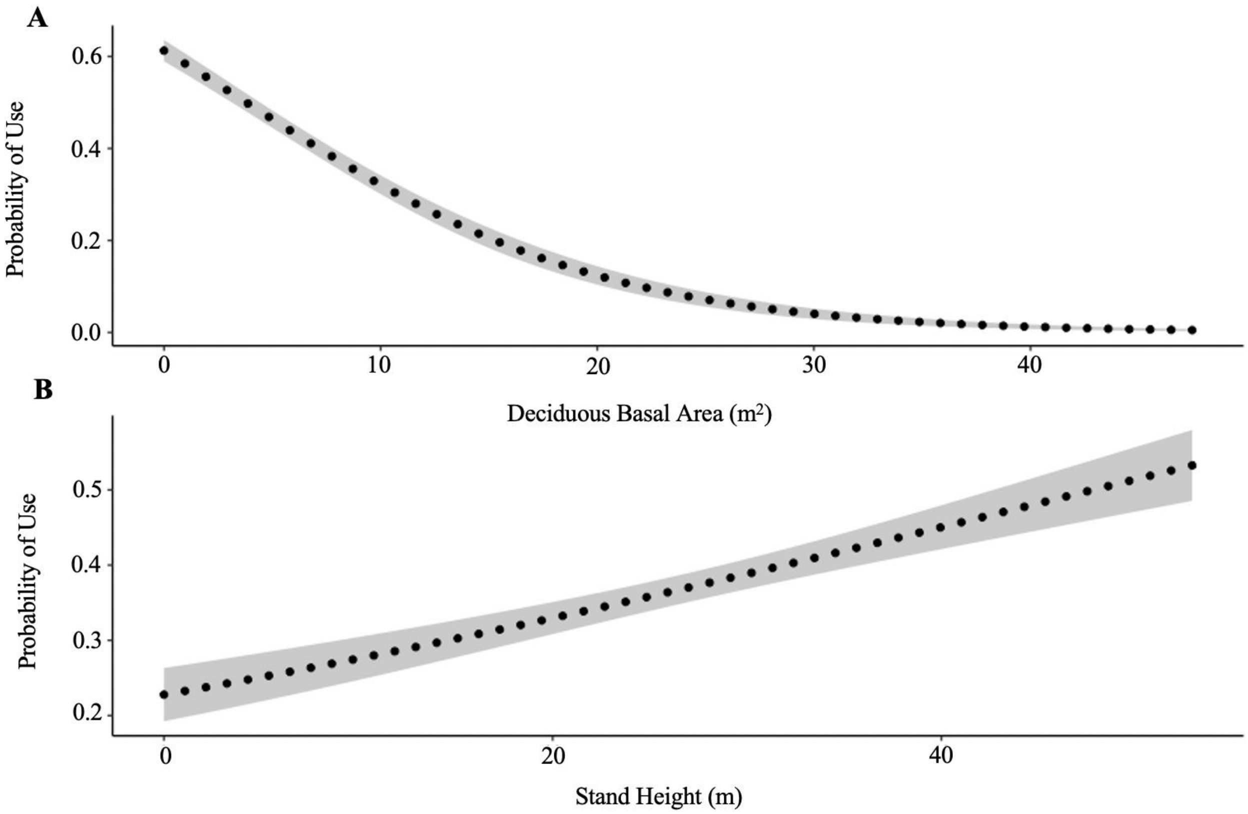

Figure 2.6. Douglas squirrel habitat use as a function of deciduous basal area (A) and forest stand height (B) based on remotely sensed data in the northern Cascade Mountains, Washington, USA. The dotted lines represent predicted values and the shaded areas represent 95% confidence intervals.

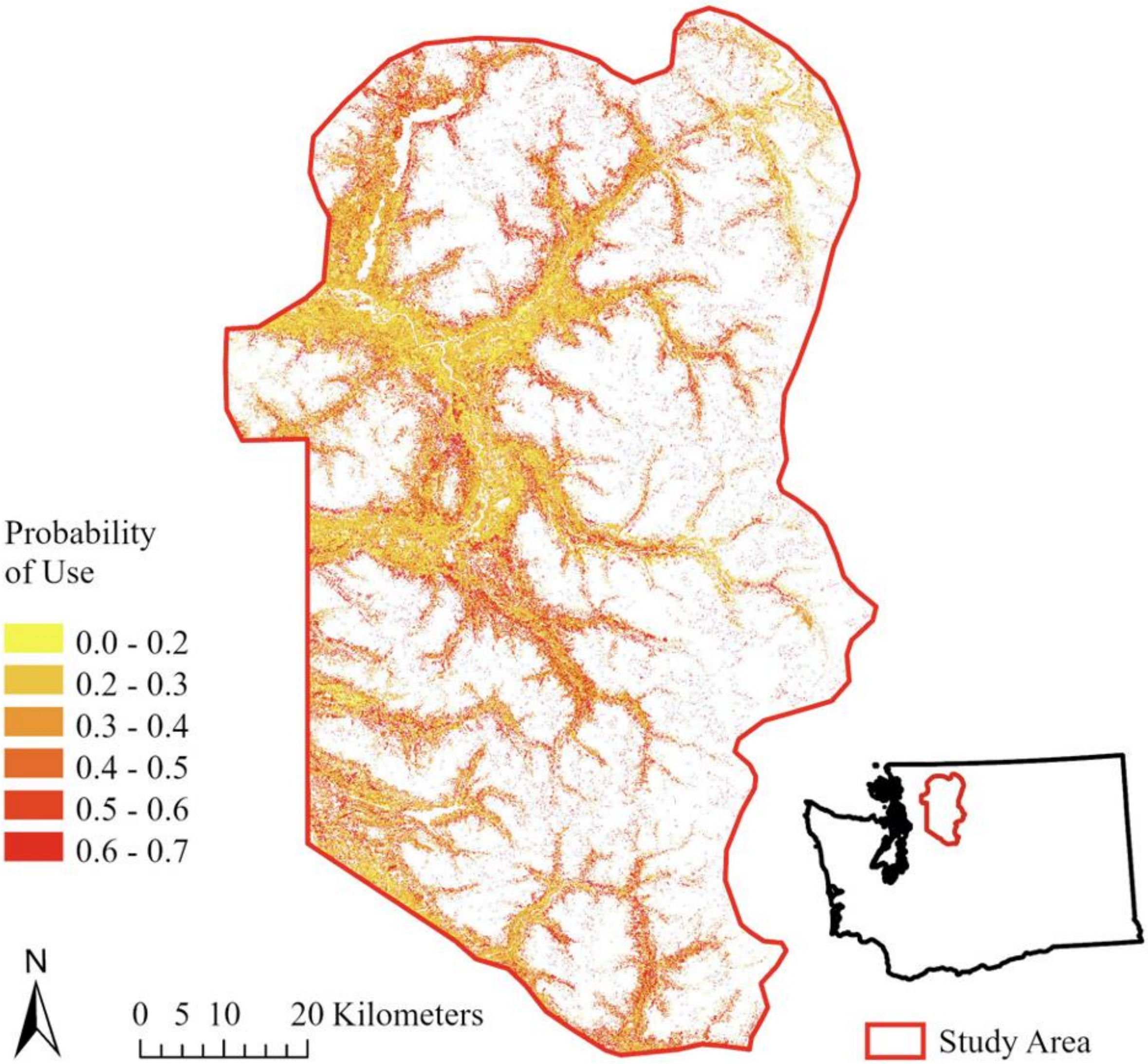

Figure 2.7. Predictive map showing the probability of Douglas squirrel use based on remotely sensed deciduous basal area and stand height in the northern Cascade Mountains, Washington, USA.

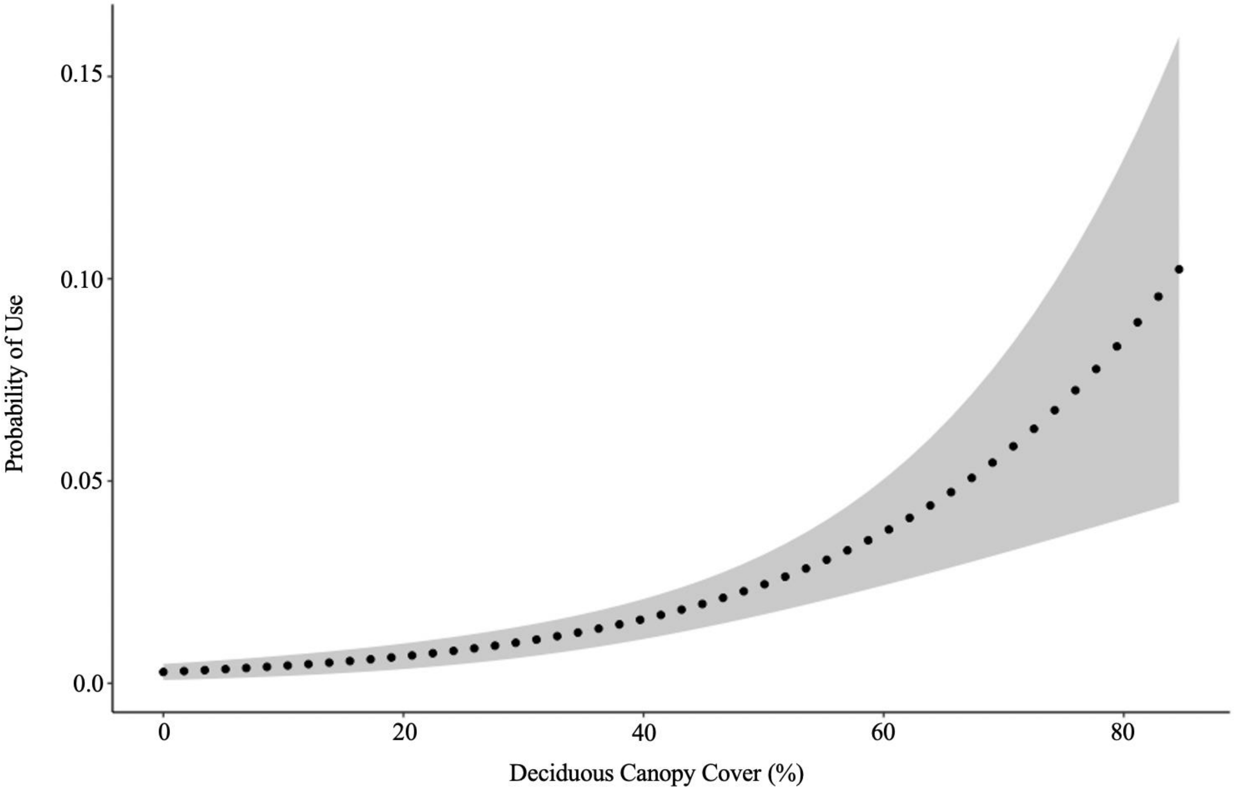

Figure 2.8. Mountain beaver habitat use as a function of deciduous canopy cover based on remotely sensed data in the northern Cascade Mountains, Washington, USA. The dotted line represents predicted values and the shaded area represents 95% confidence intervals.

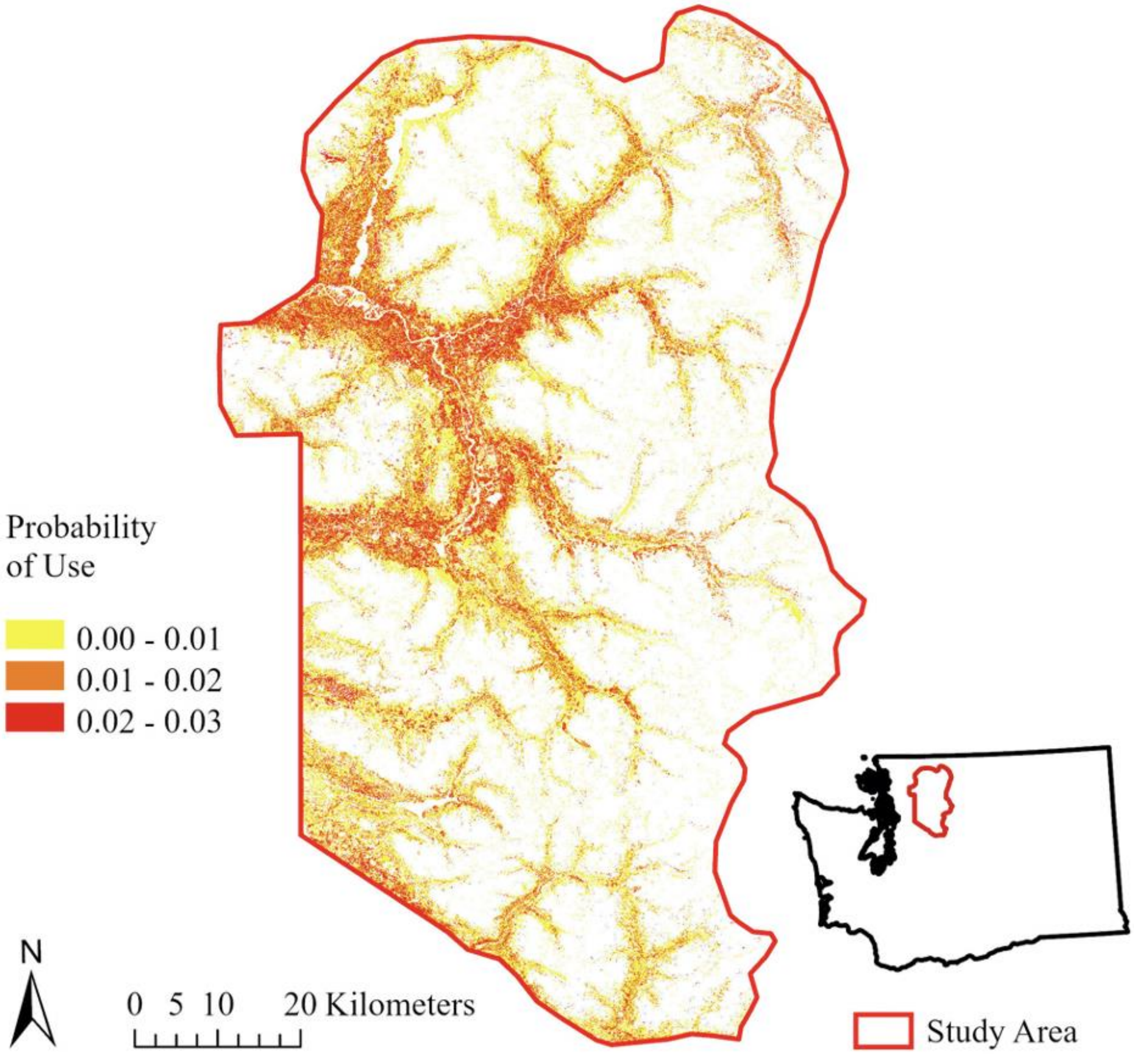

Figure 2.9. Predictive map showing the probability of mountain beaver use based on remotely sensed deciduous canopy cover in the northern Cascade Mountains, Washington, USA.

TABLES

Table 2.1. The top snowshoe hare models (i.e., those within 10 AIC_c units of the top model) based on field-measured habitat variables in the northern Cascade Mountains of Washington State, USA.

Model	**AICc**	**∆ AICc**	**AICc Wt**
Deciduous BA + CWD	445.92	0.00	0.51
Deciduous BA + Shrub Cover + CWD	447.77	1.85	0.20
Coniferous BA + Deciduous BA + CWD	447.90	1.97	0.19
Coniferous BA + Deciduous BA + Shrub Cover + CWD	449.76	3.84	0.08
CWD	455.22	9.30	0.00
Coniferous BA + Deciduous BA	455.27	9.35	0.00
Coniferous BA + Deciduous BA + Shrub	455.30	9.37	0.00

Table 2.2. Model-averaged coefficient estimates, standard errors (SE), and p-values for the top snowshoe hare models (i.e., those within 10 AIC_c units of the top model) based on field-measured habitat variables in the northern Cascade Mountains of Washington State, USA.

Coefficient	**Estimate**	**SE**	**P-value**
Deciduous BA	-1.633	0.892	0.068
CWD	0.383	0.098	< 0.001
Shrub Cover	0.057	0.135	0.674
Coniferous BA	0.031	0.123	0.805

Table 2.3. The top snowshoe hare model (i.e., within 10 AIC$_c$ units of the top model) based on remotely sensed habitat variables in the northern Cascade Mountains of Washington State, USA.

Model	**AICc**	**Δ AICc**	**AICc Wt**
Deciduous CC + Stand Age	418.10	0.00	0.99

Table 2.4. Model-averaged coefficient estimates, standard errors (SE), and p-values for the top snowshoe hare model (i.e., within 10 AIC_c units of the top model) based on remotely sensed habitat variables in the northern Cascade Mountains of Washington State, USA.

Coefficient	**Estimate**	**SE**	**P-value**
Deciduous CC	-1.087	0.201	< 0.001
Stand Age	-0.772	0.172	< 0.001

Table 2.5. The top Douglas squirrel models (i.e., those within 10 AIC_c units of the top model) based on field-measured habitat variables in the northern Cascade Mountains of Washington State, USA. BA = Basal Area, CWD = Coarse Woody Debris.

Model	**AICc**	**∆ AICc**	**AICc Wt**
Coniferous BA + Deciduous BA	1121.67	0.00	0.43
Coniferous BA + Deciduous BA + CWD	1122.94	1.27	0.23
Coniferous BA +Deciduous BA + Shrub Cover	1123.50	1.82	0.17
Coniferous BA + Deciduous BA + CWD + Shrub Cover	1124.28	2.61	0.12
Deciduous BA + CWD	1127.12	5.45	0.03
Deciduous BA + CWD + Shrub Cover	1128.61	6.94	0.01

Table 2.6. Model-averaged coefficient estimates, standard errors (SE), and p-values for the top Douglas squirrel models (i.e., those within 10 AIC_c units of the top model) based on field-measured habitat variables in the northern Cascade Mountains of Washington State, USA. BA = Basal Area, CWD = Coarse Woody Debris.

Coefficient	**Estimate**	**SE**	**P-value**
Coniferous BA	0.273	0.079	< 0.001
Deciduous BA	-1.207	0.287	< 0.001
CWD	0.100	0.099	0.311
Shrub Cover	-0.048	0.080	0.553

Table 2.7. The top Douglas squirrel models (i.e., those within 10 AIC$_c$ units of the top model) based on remotely sensed habitat variables in the northern Cascade Mountains of Washington State, USA. BA = Basal Area.

Model	**AICc**	**∆ AICc**	**AICc Wt**
Deciduous BA + Stand Height	1006.18	0.00	0.58
Deciduous BA + Stand Age	1006.84	0.66	0.42

Table 2.8. Model-averaged coefficient estimates, standard errors (SE), and p-values for the top Douglas squirrel models (i.e., those within 10 AIC_c units of the top model) based on remotely sensed habitat variables in the northern Cascade Mountains of Washington State, USA. BA = Basal Area.

Coefficient	**Estimate**	**SE**	**P-value**
Deciduous BA	-1.063	0.117	< 0.001
Stand Height	0.161	0.147	0.275
Stand Age	0.121	0.152	0.425

Table 2.9. The top mountain beaver models (i.e., those within 10 AIC_c units of the top model) based on field-measured habitat variables in the northern Cascade Mountains of Washington State, USA. BA = Basal Area, CWD = Coarse Woody Debris.

Model	**AICc**	**∆ AICc**	**AICc Wt**
Conifer BA	118.96	0.00	0.19
Conifer BA + Shrub Cover	119.44	0.48	0.15
Intercept	120.02	1.06	0.11
Conifer BA + CWD	120.40	1.45	0.09
Conifer BA + Deciduous BA	120.66	1.70	0.08
Conifer BA + Deciduous BA + Shrub Cover	121.38	2.42	0.06
Conifer BA + CWD + Shrub Cover	121.42	2.47	0.05
Deciduous BA	121.57	2.61	0.05
Shrub Cover	121.77	2.81	0.05
CWD	121.84	2.88	0.04
Conifer BA + Deciduous BA + CWD	122.32	3.36	0.04
CWD + Shrub Cover	123.16	4.20	0.02
Deciduous BA + CWD	123.27	4.32	0.02
Conifer BA + Deciduous BA + CWD + Shrub Cover	123.39	4.43	0.02
Deciduous BA + Shrub Cover	123.41	4.45	0.02
Deciduous BA + CWD + Shrub Cover	124.68	5.72	0.01

Table 2.10. Model-averaged coefficient estimates, standard errors (SE), and p-values for the top mountain beaver models (i.e., those within 10 AIC_c units of the top model) based on field-measured habitat variables in the northern Cascade Mountains of Washington State, USA. BA = Basal Area, CWD = Coarse Woody Debris.

Coefficient	**Estimate**	**SE**	**P-value**
Intercept	-4.637	0.516	< 0.001
Coniferous BA	-1.568	1.268	0.217
Shrub Cover	0.317	0.314	0.312
CWD	0.067	0.467	0.885
Deciduous BA	0.106	0.194	0.583

Table 2.11. The top mountain beaver models (i.e., those within 10 AIC$_c$ units of the top model) based on remotely sensed habitat variables in the northern Cascade Mountains of Washington State, USA. CC = Canopy Cover, BA = Basal Area, QMD = Quadratic Mean Diameter.

Model	**AICc**	**∆ AICc**	**AICc Wt**
Deciduous CC	110.99	0.00	0.46
Conifer BA + Coniferous QMD	112.79	1.80	0.19
Deciduous CC + Stand Age	112.95	1.96	0.17
Deciduous CC + Stand Height	112.96	1.97	0.17
Intercept	120.02	9.03	0.01
Stand Age	120.21	9.21	0.00

Table 2.12. Model-averaged coefficient estimates, standard errors (SE), and p-values for the top mountain beaver models (i.e., those within 10 AIC_c units of the top model) based on remotely sensed habitat variables in the northern Cascade Mountains of Washington State, USA. CC = Canopy Cover, BA = Basal Area, QMD = Quadratic Mean Diameter.

Coefficient	**Estimate**	**SE**	**P-value**
Deciduous CC	0.795	0.495	0.108
Conifer BA	-0.270	0.610	0.658
Conifer QMD	0.114	0.269	0.672
Stand Age	0.017	0.213	0.936
Stand Height	0.015	0.178	0.933
Intercept	-4.878	0.457	< 0.001