Using non-invasive techniques to examine patterns of black bear (*Ursus americanus*) abundance in the North Cascades Ecosystem, Washington State

Kristen A. Richardson

A thesis
submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington
2013

Committee:
Dr. Aaron Wirsing
Dr. William Gaines
Dr. Joshua Lawler

Program Authorized to Offer Degree:
School of Environmental and Forest Sciences

University of Washington

Abstract

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Chair of the Supervisory Committee:
Dr. Aaron Wirsing, Assistant Professor
School of Environmental and Forest Sciences

Recent advances in non-invasive research methods have facilitated less costly evaluations of bear populations across wide geographic ranges. Non-invasive hair-snagging and genetic tagging allow identification of species, sex, and individual bears without necessitating direct capture or observation. From 2008 to 2011 a large, multi-agency project deployed barbed wire hair-snag corrals to collect DNA samples from black bears (*Ursus americanus*) in the North Cascades Ecosystem (NCE) of Washington State. Using the genetic and detection data, I examined the influence of human activities and habitat characteristics on bear abundance across heterogenous landscapes of the NCE. Bear abundance was positively associated with the proportion of the landscape in shrubfields, open mesic forests, and dry forests with moderate overstory tree canopy closure. A positive northward trend in abundance existed, but was strongest for female bears. Male abundance was higher on national park lands and did not differ between roaded, frontcountry areas and designated wilderness after accounting for habitat variation. This finding

suggests that roadless wilderness areas are not acting as source areas or refugia for bears from human activities. No other research to date in Washington State has examined the influence of habitat and anthropogenic variables on black bears across such a large geographic expanse, and the results of my study should help guide management of black bear populations in the NCE. Effective and science-based management of black bears is especially important given the challenge of maintaining viable populations of long-lived species with relatively low fecundity.

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ACKNOWLEDGEMENTS

Many people have contributed towards the completion of this thesis. First, I would like to thank my major advisor and committee chair, Dr. Aaron Wirsing. I am very grateful for his continuous support throughout the development of this project and his commitment to my education and success. Secondly, I thank Dr. William Gaines for inviting me to join the bear project. Because of his willingness to take a chance with me, I was able to spend the past three field seasons in some of the most beautiful areas of this country, conducting research that furthered my understanding of, and passion for, carnivore research and conservation. Both Dr. Wirsing and Dr. Gaines have been valuable mentors, consistently challenging and enlightening me throughout this project. I would also like to thank my third committee member, Dr. Josh Lawler, for his valuable contribution to the development of the analytical methods used in this thesis.

I am very grateful to Robert Long, Paula MacKay, and James Begley for the tremendous amount of work and knowledge they poured into the project. I owe a special thanks to Peter Singleton for the many hours he spent helping me with habitat mapping and analyses. I thank Scott Fitkin and Roger Christophersen for their coordination and field efforts towards the project. I also thank Andrea Lyons for her continued support as I pursued a Master of Science. I am particularly grateful to Aja Woodrow, John Wagenknecht, Jesse McCarty, Ray Robertson, and Lindsay Welfelt for all the laughter, sweat, and support they shared with me through many days and nights in the backcountry. I also thank Janet Millard and Keri Heniff for their generosity of time and tools over the past couple years. I am grateful to the Takher family for their generous support while preparing this manuscript. I acknowledge my siblings—Scott Richardson and Anne and Gurpreet Takher—for their love and encouraging me to continue my education. I

thank my parents, Chet and Vivi Richardson, as well as Stephen Phillips, for encouraging me through stressful times with patience and love and consistently pointing me to the truth.

INTRODUCTION

Bears are often described as “umbrella” species because their broad habitat and space-use requirements encompass those of many other species (Noss et al. 1996). Moreover, their status is often used as an indicator of ecosystem health (Hummel and Pettigrew 1991, Minta et al. 1999). Still the most widespread bear species in North America, black bears (*Ursus americanus*) were once ubiquitous across the continent but remaining populations have become increasingly isolated (Schoen 1990, Hummel and Pettigrew 1991). Black bears have large home ranges and are highly sensitive to landscape fragmentation (Beier and Noss 1998), and the largest threats to this species are human-caused mortality (Koehler and Pierce 2005) and loss of habitat (Hummel and Pettigrew 1991, NRC 1997). Washington State has one of the largest black bear populations in the lower 48 states (WDFW 1997), and this carnivore currently occupies much of its historic range in the North Cascasdes Ecosystem (NCE)—a large, contiguous block of federal land in north-central Washington that is composed of diverse habitat types. Yet, black bear populations in the NCE are increasingly threatened by human population growth and disturbance. Understanding the black bear’s relationship with habitat characteristics and human activities in the NCE can help establish the mechanisms underlying threats to the species and aid in the development of effective conservation policy. As an indicator species, the black bear can be a valuable environmental monitor, reflecting landscape changes occurring across large regions.

To date, few black bear studies have examined individual behavior across large geographic areas and multiple ecosystems due to the challenges associated with studying wide-ranging carnivores. Black bears are difficult to study because of their wide-ranging movements, long life-spans, and solitary and cryptic behavior (Minta et al. 1999, Demarais and Krausman 2000). Direct techniques such as radio-telemetry and mark-recapture are limited by the high cost of applying consistent effort across large geographic ranges (Apps et al. 2004). In addition, they can subject populations to additional stress and mortality (Miller 1990), and financial costs can preclude rigorous sampling across large areas. Prior telemetry studies on black bear home ranges and resource selection were conducted in two regions of the NCE and provided valuable information on black bear habitat use (Koehler and Pierce 2003, Lyons et al. 2003, Gaines et al. 2005). However, while these studies revealed habitat relationships at fine resolutions, the logistical challenges and cost of direct capture prohibited investigations across the entire NCE. Therefore, the status of Washington's bear populations remain poorly understood and wildlife managers rely on harvest data to monitor NCE black bear populations. Harvest data, however, is inadequate to ascertain population status and fully evaluate the effects of human activities on local population viability (Bunnell and Tait 1985, Miller 1990, Garshelis and Hristienko 2006, Coster et al. 2011). Harvest statistics can be a poor indicator of population trends (Miller 1990, Garshelis and Hristienko 2006, Coster et al. 2011), and the necessary assumptions for estimating demographic parameters are rarely met by the small harvest sample sizes (Bunnell and Tait 1985).

Recent advances in non-invasive sampling methods now allow for less costly evaluations of bears and other large carnivores across wide geographic ranges, without necessitating capture or direct observation (Apps et al. 2004, Long et al. 2011). For example, non-invasive hair capture and genetic tagging is an inexpensive method of identifying individual animals, and the number of animals sampled far exceeds that of most telemetry studies (Woods et al. 1999, Apps et al. 2004). Hair-snagging enables the sampling of black bears over a large geographic range, and captured hair with sufficient DNA can reveal species, sex, and genotypes of individual bears. The data acquired through non-invasive methods can be used to assess bear resource use at broad scales, providing information about ecosystem health and instructing management over large landscapes.

From 2008 through 2011, the Cascasdes Carnivore Connectivity Project—a collaborative effort between the US Forest Service and the Western Transportation Institute—conducted non-invasive DNA sampling of black bears in the NCE. Genetic samples were initially obtained with the purpose of empirically testing large carnivore habitat connectivity models and assessing the impact of the state's highway system as a putative barrier to panmixia among black bear populations (Long et al. 2012). Male and female bears may exhibit different habitat use patterns, and females are particularly important for the productivity of a population. Therefore, using the project's detection and genetic data, my objectives were to identify the habitat characteristics and anthropogenic activities that influence sex-specific abundance (male, female, and female-with-offpsring) of black bears in the NCE. High densities of roads can reduce black bear habitat use and survival (Brody and Pelton 1989, Schwartz and Franzman 1992, Kasworm and Their 1994), and black bears may exhibit greater road avoidance where hunting levels are high (Young and Beecham 1986, Kasworm and Manely 1990, Gaines et al. 2005). Accordingly, I predicted that bear abundance would be negatively associated with high densities of human activity, with a more pronounced effect for females with offspring and in areas with high hunter access. Under the hypothesis that females (especially females accompanied by offspring) require tree cover for security, I predicted that female bears would exhibit a stronger association with closed canopy forest types than males (Young and Beecham 1986, Heyden and Meslow 1999, Cunningham et al. 2003, Malcom and Van Deelen 2010), and that the importance of tree cover would depend on the degree of disturbance by human activities (Demarais and Krausman 2000). In addition, I expected that vegetative types associated with high quality bear foods would be positively related to bear abundance because, in the absence of human influences, black bear habitat use is nutritionally driven (Bunnell and Tait 1981, Elowe and Dodge 1989, Schoen 1990). I also anticipated that streams and deciduous forests would exert greater influence on bear composition on the drier, east slopes of the Cascades where moisture can be limited. Furthermore, male black bears are more vulnerable to hunting than females (Bunnell and Tait 1981, Bunnell and Tait 1985, Koehler and Pierce 2005, Czetwertynski et al. 2007). Therefore, under the assumption that current levels of black bear harvest are sustainable, I predicted males would exhibit a negative association with areas of high hunter access and positive association with areas of low or no hunter access, whereas the reverse would be true for females.

METHODS

Study area

The NCE covers approximately 24,000 square-km of north-central Washington and is one the largest contiguous blocks of federal land in the continental United States (Gaines et al. 2000). It includes the North Cascades National Park Service Complex (NCNP) and most of the Mount-Baker Snoqualmie National Forest (MBSNF) and Okanogan-Wenatchee (OWNF) national forests. The area is bounded on the north by the United States-Canada border, on the west by the western edge of the MBSNF, on the east by OWNF and state lands west of the Columbia and Okanogan Rivers, and, for the purpose of this study, on the south by national forest lands within 30 km south of Interstate 90. Approximately 85% of the land is federally owned, 5% state owned, and 10% privately owned (Gaines et al. 2000). We deployed carnivore survey sites on federal lands only.

Elevations on the west slopes of the NCE range from approximately 150 m to 3,285 m, with most ridge systems near 1,525 m. The crest varies from 2,100 m to 3,213 m, and elevations on the east slopes range from 762 m to 2,712 m (Gaines et al. 1994). The western portion of the NCE has an annual precipitation of 170-300 cm, falling mostly as rain. With the Cascade crest blocking maritime flow and casting a rain shadow, the eastern portion of the NCE is much drier, with an annual precipitation of 25-50 cm that falls mostly as snow (Gaines et al. 1994).

Common coniferous forest types on the western slopes include stands dominated by Western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga mensiezii*), Pacific fir (*Abies amabilis*), and mountain hemlock (*Tsuga mertensiana*). The eastern slopes consist of coniferous forests dominated by subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmanii*), Douglas fir and ponderosa pine (*Pinus ponderosa*).

Field methods

We used hair collection methods to obtain black bear DNA samples from mid-May through mid-October, depending on weather conditions. A map of hexagonal sampling units was overlaid across the NCE to maximize sampling efficiency. Each hexagon had an area of 2500 ha, slightly smaller than an average female black bear home range (Lyons et al. 2003, Koehler and Pierce 2003). We deployed two barbed wire hair-snag corrals (Woods et al. 1999, Kendall and McKelvey 2008) within each hexagon, with a minimum distance of two km between each corral. Corrals were located > 100 m from any hiking trail, > 500 m from any backcountry campground or open road, and > 1 km from any established frontcountry campground. Project warning signs were posted at each site. We placed corrals non-randomly (i.e., researcher choice) within the hexagon to maximize the likelihood of visitation by bears. The corrals were comprised of an 25-30 m single strand of 4-prong barbed wire stretched in a circle around trees, at a height of 45-50 cm above the ground—optimal height for capturing adult bear hair. At the center of the circle we constructed a pile of debris about one meter in width and height, and on it poured 1.5 liters of liquid scent lure—emulsified fish heads and cattle blood. Attracted by the lure, bears approached the debris pile and usually left hair on ≥ 1 barb when crossing over or under the wire (Figure 1). At frontcountry sites (national forest lands with motorized vehicle access) we revisited each corral after 14 days, removing the corral if we found hair samples and re-luring if no samples were found. We burned the tweezers and barbs in between each sample collection to minimize cross-contamination (one barb with hair was considered one unique sample). In the backcountry (designated wilderness and national park lands), we automatically re-lured every site at the 2-week revisit due to challenging access. After a 28-day deployment, we removed all corral sites regardless of hair sampling success. We did not resample completed hexagons in subsequent years; each new year survey hexagons were chosen in such a way as to spread sampling throughout the study area, and across a variety of habitats and potential subpopulations. We deployed a total of 529 corrals (Figure 2), with the largest sampling efforts focused in 2010 and 2011.

Genetics

We subsampled hair samples based on quality (e.g., presence of root and/or number of hairs in a clump), proximity to other samples, and differences in color (e.g., if blonde hair was on a barb adjacent to one with black hair, we selected both samples). Subjective subsampling allowed us to minimize our costs while increasing the likelihood that samples had sufficient DNA for genetic analysis and were obtained from unique individuals (Kendall and McKelvey 2008). Selected hair samples were transported to the Wildlife Genetics International (WGI) lab in Nelson, British Columbia under a CITES clearance. If a unique sample (from one barb) was suspected to have captured > 1 bear, the lab separated the hair and analyzed it as different samples. Samples were analyzed using 6 microsatellite markers for individual identification, 1 for sex determination, and an additional 14 for higher resolution relatedness and genetic structuring (D. Paetkau, WGI, pers. comm. and R. Long, pers. comm.).

I identified mother-offspring pairs captured at the same corral using the parentage analysis software CERVUS 3.0 (Marshall et al. 1998). Because the study design precluded estimating the proportion of potential parents sampled, I conducted 2 maternity simulations under different assumptions: the first simulation assumed my sample captured 1% of the potential parents in the population, and the other simulation assumed 20% of potential parents were captured. Maternity assignments did not differ depending on the simulation used; therefore, 20% of candidate mothers sampled was a robust assumption and used for subsequent analyses. I used the more conservative delta estimate—the difference in likelihood of odds (LOD) scores between the first and second most likely candidate mothers—to determine confidence, rather than a positive LOD. I accounted for possible genotyping error while minimizing misclassification of full siblings as mother-offspring pairs by requiring that all identified pairs share an allele at all but one locus (Proctor et al. 2004). Because I had no prior mother-offspring information, I used a strict 95% confidence level for declaring mother-offspring pairs. Because the genetics do not reveal a bear's age, I cannot discern whether a matched offspring is a first-year cub or an offspring from prior reproductive years. It is possible that two females identified as a mother-offspring pair may have visited the corral independently of each other (Boulanger et al. 2004a) because sub-adult females often remain in their natal areas (Elowe and Dodge 1989, Costello et al. 2008, Costello 2010). An adult female and matched male offspring, however, are likely travelling together, given that sub-adult males usually disperse from their maternal range (Schwartz and Franzmann 1992, Costello et al. 2008, Costello 2010). Therefore, I considered mother-offspring pairs identified at the same corral as evidence of any reproduction at the corral site, rather than reproduction during the sampling year. I also removed all identified offspring from my abundance estimates in order to meet the assumption of independence of observations.

Habitat and human activity variables

I employed a scale-dependent design because animals often make habitat choices at multiple spatial scales. I quantifed the habitat and human activity variables within 2.3-km (Level 1) and 1.0-km (Level 2) radius buffers placed around each corral site. A 2.3-km radius yields the average size of black bear core-use areas as reported by Gaines (2002) and a 1.0-km radius minimizes overlap between adjacent buffers. Our sampling design prevented me from using a larger scale of analysis (e.g., average home range area); a scale larger than the average core-use size would have yielded extensive overlap between adjacent buffers, and, given that animals' home ranges are not actually circular, would likely have incorporated large amounts of habitat unused by bears. Both 2.3-km and 1.0-km distances are beyond the estimated attraction radius of corral sites (i.e., beyond the distance at which the capture probability is 15%, suggesting that the bear was already using the surrounding habitat and not simply drawn to the area by the scent lure; Boulanger et al. 2004b).

I included in my analyses only potentially important habitat and human activity (Appendix: Table S1) characteristics identified by prior ursid research. Vegetative cover classes were delineated using Lemma gradient nearest-neighbor (GNN) species-size maps (Ohmann and Gregory 2002), an Ecoshare plant association group map (PAG; Henderson et al. 2011), and the Pacific Northwest Regional Gap Analysis Project map (GAP; Grossmann et al. 2008). I divided coniferous forests into 3 overstory canopy cover classes (open = 10 to < 40%, moderate = ≥ 40% to < 70%, and closed = ≥ 70%; Young and Beecham 1986, Heyden and Meslow 1999, Bull et al. 2001, Malcom and Van Deelen 2010) and 4 moisture classes (dry, mesic, moist, and wet;

Appendix: Table S2) to account for understory production of bear foods. I classified deciduous forests (Lyons et al. 2003) as pixels with hardwoods comprising ≥ 7.5% of the total live tree basal area. Open vegetation classes—dry grassland/shrubland, mesic meadow/grassland/dwarf-shrubland (hereafter referred to as 'mesic meadow'), shrubfield, and wetland/wet meadow (Appendix: Table S3; Gaines 2002, Lyons et al. 2003, Koehler et al. 2003)—were mapped using a combination of the non-forest (< 10% tree canopy cover) mask in the Lemma GNN species-size data and GAP data. I quantified all vegetative cover classes as proportion of the Level 1 or Level 2 buffered area. I did not quantify metrics of habitat spatial configuration, nor habitat characteristics such as "greenness", so that my approach could be easily interpreted and repeated by wildlife managers. I also measured the stream density (km/km^2; Heyden and Meslow 1999, Fescke et al. 2002) of each buffered landscape using stream layers provided by the Washington Department of Natural Resources (WADNR). Because the resolution of measured streams in the WADNR layer varied depending on land ownership, I filtered the layer to include only major rivers and streams and thereby create a more consistent map across the NCE. I standardized easting and northing UTM coordinates by their respective ranges and included them as explanatory variables to detect potential directional trends in bear abundance. Non-vegetated cover types (e.g., bare rock, open water, permanent snow fields and glaciers) and human developments were considered unsuitable habitat and deducted from the total area within the buffers (Apps et al. 2004).

Human activity variables (Appendix: Table S1) measured within Level 1 and Level 2 buffers were road density (Brody and Pelton 1989, Fecske et al. 2002, Gaines et al. 2005, Reynolds-Hogland and Mitchell 2007), trail density (Kasworm and Manley 1990), and hunter access. Road density measurements included roads of maintenance levels 1 through 5 from the national forest data library, all open national park roads, and private roads. I included all trails identified by the USFS, NPS, and WADNR and defined hunter access by three levels: high (national forest lands with motorized vehicle access), moderate (designated wilderness areas), and none (national park lands). I conducted all habitat and human activity quantification in ArcMap 10 (ESRI 2011).

Analysis

Although field protocol required a minimum of 2 km between corral sites, at this distance multiple corrals may have sampled the same landscape (i.e., corrals may have been "clustered" within a landscape). Because unknown broad-scale geographic processes may be influencing the abundance of black bears in an area, I avoided pseudoreplication by including "cluster" as a random effect in all analyses (Bolker et al. 2008). I considered corrals part of the same cluster if their buffers overlapped by ≥ 20%, unless separated by a major highway or large body of water. A threshold of 20% overlap best matched cluster assignment based on bear behavior and potential ease of movement between corrals (e.g., within the same drainage or without large amounts of cover types between the corrals that are unlikely to be used by bears).

For each response variable (i.e., overall bear abundance, male abundance, female abundance, and female-with-offspring abundance at the Level 1 or Level 2 spatial scale), I fit generalized linear mixed effects models (GLMMs, poisson and log-link error structure) with the Laplace likelihood approximation to estimate model parameters using the lme4 package in R (Bates et al. 2011). Small cubs may be able to avoid the wire because the height is set for optimal capture of adult bears (Woods et al. 1999), so some females captured without offspring at a corral may have been reproductive. Thus, to be conservative, female bear abundance included all identified females, regardless of known reproductive status.

I constructed a candidate set of meaningful models for each response, where habitat and human activity variables were considered fixed effects and cluster was always included as a random effect. In building the candidate sets, I only considered fixed effects exhibiting at least marginal univariate associations ($P < 0.20$; Tables 1, 2, S4, and S5), unless a variable was part of an *a priori* hypothesized interaction effect. For example, because the need for security cover is dependent on the intensity of human disturbances (Demarais and Krausman 2000), I hypothesized that bears would be positively associated with closed canopy forests in areas of high human activity while negatively associated with canopy closure in low human activity areas. Therefore, I included an interaction between closed mesic forests and hunter access.

Due to lack of normality, I used Spearman's Rank Correlation Coefficient (ρ) to assess monotonic associations between explanatory variables. I considered collinearity between variables to be problematic when $\rho \geq 0.70$ (Apps et al. 2004), and thus did not include those variables in the same candidate model. I used Akaike's Information Criteria (AIC; Burnham and Anderson 2002) to identify which model(s) best described the structure of the data. I considered models with AIC values within 2 of the model with the smallest AIC (i.e., $\Delta_i < 2$) to have substantial empirical support. Models including covariates with 90% confidence intervals (*CI*s) overlapping 0 were dropped from the top model set because they contributed little improvement in model fit (Anderson 2008, Arnold 2010). If the remaining top model sets included > 1 model, I employed multimodel inference by calculating weighted averages of the parameter estimates (Burnham and Anderson 2002) using the MuMIn package (Bartoń 2012). I computed relative importance of individual predictor variables by summing the Akaike weights (w_i) of all candidate models including the variable (Burnham and Anderson 2002).

I quantified goodness of fit of top models with Nakagawa and Schielzeth's R^2_{GLMM} because traditional R^2 statistics cannot be appropriately generalized from linear models to GLMMs (Nakagawa and Schielzeth 2013). Marginal R^2_{GLMM} ($R^2_{\mathrm{GLMM}(m)}$) represents the variance explained by the fixed effects and conditional R^2_{GLMM} ($R^2_{\mathrm{GLMM}(c)}$) represents the variance explained by the entire model (the difference between the two R^2_{GLMM}s is attributed to the variance explained by the random effect alone). The R^2_{GLMM} metric is estimated from the data and does not perfectly describe model fit. However, it can provide a relative understanding of the predictive power of a model (Nakagawa and Schielzeth 2013).

Parameter estimates are partial regression coefficients whose values are conditional upon other variables in the model; therefore, while a categorical effect has the same explanatory classification across scales, its coefficient estimates may differ. Thus, I report differences in estimated bear abundance among hunter access levels based on coefficients from univariate predictor models. I conducted all statistical analyses in R (R Development Core Team 2012).

RESULTS

From 2008 through 2011, we deployed 529 barbed-wire hair-snag corrals in the NCE (Figure 2). We detected bears at 384 corral sites. From our collected hair samples, WGI genotyped 498 individuals from 306 corrals: 222 male bears, 239 females, 1 bear of unknown sex, and 36 offspring identified at corrals with mothers. Of the female bears, 29 were captured at a corral with offspring. An additional 39 individual bears were genotyped from tissue samples collected from 2005 to 2009 by Rich Beausoleil of the Washington Department of Fish and Wildlife (WDFW) and used only in maternity simulations. Forty-nine individual bears were captured at > 1 corral location (43 bears at 2 corrals and 6 bears at 3 corrals). Because we detected most of these individuals at neighboring sites (i.e., within the same or adjacent sampling hexagons, meaning that they were unlikely to be a dispersing bear), I randomly reassigned all individual bears to one detection location. No bears were detected at > 1 corral together. I removed from analyses sites where we detected bears but the hair lacked sufficient DNA for individual identification (n = 78), yielding a remaining sample size of 451 corral sites.

A combination of human activity and habitat variables best explained overall bear abundance in the NCE. At the larger, Level 1 scale, only one model had $\Delta_i < 2$ and no covariates with 90% *CI*s overlapping 0 (Tables 3 and S6). Therefore, I did not average multiple models but instead used this top model for inference. Hunter access, northing, and proportion of the buffered landscape in moderate dry forest, open mesic forest, and shrubfields were included in the top model (Tables 3 and 4). Bear abundance was lowest in areas of high hunter access (nearly half that of national park lands, $\beta_2 = 0.692$, $Z = 4.174$, $P < 0.001$; Table S4). Estimated bear abundance was also higher (by 34%) in areas with moderate hunter access than those with high hunter access ($\beta_2 = 0.294$, $Z = 2.704$ $P = 0.007$; Table S4). Bear abundance differed between wilderness areas (moderate hunter access) and National Park lands (releveled $\beta_2 = 0.397$, $Z = 2.369$, $P = 0.018$; Table S4), where no hunting areas showed an approximate 49% increase in overall bear numbers (Table S4). However, after accounting for habitat effects, there were only significant differences in estimated bear numbers between national park land and the other hunter access levels ($\beta_2 = 0.374$, SE = 0.185, 90% *CI* = 0.095, 0.653 and releveled $\beta_2 = 0.270$, SE = 0.160, 90% *CI* = 0.029, 0.511), but no difference between high hunter access areas and those with moderate access ($\beta_2 = 0.105$, SE = 0.123, 90% *CI* = -0.082, 0.290; Table 4). Bears were positively associated with moderate dry forests, open mesic forests, and shrubfields (Table 4). A significant north-south trend existed, with bear abundance rising as northing increased ($\beta_6 = 0.627$, SE = 0.200, 90% *CI* = 0.324, 0.929; Table 4). All variables exhibited high relative importance values, but open mesic forest, shrubfield, and northing had the highest ($\Sigma w_i = 1.00$) while moderate dry forest had the lowest ($\Sigma w_i = 0.92$; Table 4). The fixed effects of the top model explained approximately 16% of the variation in bear abundance while the spatial clustering of sites explained little or no variation after fixed effects were included ($R^2_{\mathrm{GLMM}(m)}$ and $R^2_{\mathrm{GLMM}(c)} = 0.157$; Tables 3 and S6) . At the smaller, Level 2 scale, only one model had empirical support from the data ($\Delta_i > 2$; Tables 3 and S7). The top-ranked model included the same variables as Level 1, and the habitat variables and northing also exerted a positive effect on bear abundance at this scale. However, the positive effects of moderate dry forest, open mesic forest, and shrubfields are weaker at the Level 2 scale (Table 4). The fixed effects of the final model describing bear abundance at Level 2 appear explained slightly less variation than Level 1 ($R^2_{\mathrm{GLMM}(m)} = 0.134$) while the random effect (clusters) explained about 1% of variation in bear numbers ($R^2_{\mathrm{GLMM}(c)} = 0.145$; Table 3 and S7).

At the Level 1 scale, 3 models of male bear abundance had substantial empirical support ($\Delta_i < 2$; Table S8). However, one model included a covariate with a 90% *CI* overlapping 0 and was not used for averaging parameter estimates. Hunter access, proportion of landscape in moderate dry forest, open mesic forest, moderate moist forest, shrubfield, and northing coordinates were included in the final averaged model (Tables 3 and 5). Male bear abundance increased significantly (by 138%) from high hunter access to no hunter access ($\beta_2 = 0.868$, $Z = 3.530$, $P < 0.001$; Table S4), and from high to moderate hunter access areas (by 53%, $\beta_1 = 0.425$ $Z = 2.542$, $P = 0.011$; Table S4). Male numbers were higher where no hunting is allowed than in wilderness areas (releveled $\beta_2 = 0.442$, $Z = 1{,}809$, $P = 0.071$; Table S4), but the effect was weaker than that between high and no hunter access. However, only the difference in male bear abundance between areas of high hunter access and those with no hunting appeared to be driven by hunting at the Level 1 scale; it was the only hunter access coefficient with a 90% *CI* that did not overlap 0 once habitat characteristics were included in the model ($\beta_2 = 0.619$, SE = 0.258, 90% *CI* = 0.195, 1.044; Table 5). At the larger scale, male bears were positively associated with moderate dry forests, open mesic forests, shrubfields, and northing, while negatively associated with moderate moist forests (Table 5). Northing had the lowest relative importance (0.59; Table 5) in relation to male abundance, followed by moderate moist forest (0.69; Table 5). Hunter access, moderate dry forest, open mesic forest, and shrubfield were included in both top models (relative importance = 0.88, 0.84, 1.00, and 0.99, respectively; Table 5), although proportion of landscape in open mesic forest appeared to exhibit the largest effect on male abundance and shrubfield the second largest effect (Table 3). Fixed effects in the top-ranked model explained about 18% of the variation in male abundance ($R^2_{\mathrm{GLMM}(m)} = 0.177$; Tables 3 and S8), with little additional explanation coming from the random effect ($R^2_{\mathrm{GLMM}(c)} = 0.179$; Tables 3 and S8).

At the Level 2 scale, only one model had $\Delta_i < 2$ and 90% *CI*s excluding 0 for all covariates (Tables 3 and S9). Accordingly, I used this model as the top model and did not model average. Hunter access was again the only human activity variable included in the top model and, at Level 2, had the highest relative importance (0.97) in explaining male abundance (Table 5). At the smaller scale, estimated male abundance was higher in the national park than in frontcountry areas ($\beta_2 = 0.575$, SE = 0.259, 90% *CI* = 0.184, 0.966) and wilderness areas (releveled $\beta_3 = 0.392$, SE = 0.240, 90% *CI* = 0.029, 0.755; Table 5). Male bears were negatively associated with closed moist forests and deciduous forests. Males were also positively associated with northing at this scale, although it had the least relative importance of the variables in the top model ($\Sigma w_i = 0.78$; Table 5). While the top Level 2 model explained more variation as a whole ($R^2_{\mathrm{GLMM}(c)} = 0.244$) than the highest ranked model at the Level 1 scale, less deviance was attributed to the fixed effects and more to the spatial clustering of the corral sites ($R^2_{\mathrm{GLMM}(m)}$ = 0.158; Table 5).

At the larger, Level 1 landscape scale, 4 models had support ($\Delta_i < 2$) in describing female abundance (Table S10), although 2 included non-significant covariates and were therefore dropped from subsequent model averaging. The 2 remaining models explained relatively little of the variation in female bear numbers ($R^2_{\mathrm{GLMM}(m)}$ and $R^2_{\mathrm{GLMM}(c)} < 0.06$ for both models; Tables 3 and S10). While a difference in female bear abundance existed between areas of high hunting and those with no hunting (an increase of 72% on national park lands, $\beta_2 = 0.542$, $Z = 2.467$, $P = 0.014$; Table S5), the difference does not appear to be attributed to hunting as hunter access was not included in the models with substantial empirical support (Tables 3 and S10). A north-south trend had the greatest relative importance ($\Sigma w_i = 0.89$), with higher female abundance at more northern site locations ($\beta_2 = 0.687$, SE = 1.360, 90% *CI* = 0.323, 1.052; Table 6). Shrubfields were also positively related to female abundance ($\beta_1 = 2.722$, SE = 1.360, 90% *CI* = 0.485, 4.960; Table 6). At the smaller spatial scale, only one model was considered to best describe female abundance (Tables 3 and S11). The top model explained even less variation in female abundance (marginal and conditional R^2_{GLMM} = 0.036; Tables 3 and S11) than the top model at the Level 1 scale. Northing was the only variable explaining female abundance at this scale (Σw_i = 0.91), exerting a positive effect ($\beta_1 = 0.665$, SE = 0.218, 90% *CI* = 0.336, 0.994; Table 6).

Female-with-offspring bear abundance at the Level 1 scale was best described by 2 models (Table 3). Four models had $\Delta_i < 2$, but 2 of those had covariates with 90% *CI*s overlapping 0 and were excluded from model averaging (Table S12). Only one of the top models included fixed effects: hunter access and proportion of landscape in moderate dry forest (Tables 3 and S12). Moderate dry forest held greater relative importance than hunter access ($\Sigma w_i = 0.71$

and 0.60, respectively) and was positively associated with female-with-offspring bear abundance (β_3 = 4.900, SE = 2.450, 90% *CI*s = 0.870, 8.931; Table 7). Abundance did not differ by hunter access alone ($P > 0.150$ for all covariates; Table S5), but after accounting for the effect of moderate dry forest, estimated abundance was higher in wilderness areas than those of high hunter access (β_1 = 1.027, SE = 0.542, 90% *CI* = 0.135, 1.918; Table 7). However, the null model (intercept and random effect only) had similar support in describing female-with-offspring abundance (Tables 3 and S12). Indeed, the spatial clustering of females-with-offspring on the landscape explained much more variance than the fixed effects in the top-ranking model, as demonstrated by the large difference between marginal and conditional R^2_{GLMM} values ($R^2_{\mathrm{GLMM}(m)} = 0.070$, $R^2_{\mathrm{GLMM}(c)} = 0.302$; Table 12).

At the smaller, Level 2 spatial scale, 5 models were supported ($\Delta_i < 2$; Table S13). Only 2 models were used for parameter estimation, however, because they had no covariates with 90% *CI*s overlapping 0. Closed dry forests and shrubfields were included as fixed effects in calculating weighted averages of model coefficients (Tables 3 and S13). Female-with-offspring abundance was positively associated with both closed, dry forests (β_1 = 2.701, SE = 1.474, 90% *CI* = 0.276, 5.126) and shrubfields (β_2 = 4.221, SE = 2.328, 90% *CI* = 0.392, 8.049), and the two habitat types were of similar relative importance (Σw_i = 0.61 and 0.58, respectively; Table 7). The null model was one of the top models, and the fixed effects explained even less variation in abundance than at the Level 1 scale, with most of the variance explained by the random effect alone (null model $R^2_{\mathrm{GLMM}} = 0.310$; Tables 3 and S13).

DISCUSSION

This study presents the first evaluation of habitat and human activity associations of black bears across such a large geographic expanse using non-invasive genetic techniques. My results confirm that even at a broad, landscape scale, male bears are positively associated with more open forests while negatively or not associated with closed canopies. Furthermore, the consistent, positive associations of males with cover types comprised of high potential for bear foods supports the hypothesis that foraging drives bear habitat selection (Bunnell and Tait 1981, Elowe and Dodge 1989, Schoen 1990)—even at coarse resolutions and over large geographic areas with varying habitat types. My results also confirm that relative bear abundance, particularly that of males, is negatively correlated with hunting at a broad, landscape scale. However, the similar estimates of male abundance in frontcountry and designated wilderness were contrary to my prediction that bear abundance would be higher in roadless, wilderness areas than on roaded, national forest lands. This suggests that designated wilderness are not acting as refugia for bears from anthropogenic pressures. Also, the lack of habitat and human activity variables in female abundance models was surprising and suggests a need for further research regarding sex-specific scales of analyses.

Open mesic and moderate dry forests appeared important for black bears in the NCE, with bear abundance rising as the proportion of landscape in these forest types increased. This finding supports my prediction of an increase in bear abundance alongside proportions of open mesic forests resulting from the open canopy allowing for higher understory growth (i.e., potential forage for bears) on the basis that, in the absence of humans, black bear habitat use is nutritionally driven (Bunnel and Tait 1981, Elowe and Dodge 1989, Schoen 1990). The dry and mesic forest types also included plant associations with potential for abundant bear foods (e.g., *Vaccinium* shrubs and *Calamagrostis rubescens*; Appendix: Table S2). The positive association with forests of moderate canopy closure is not surprising given that the canopy likely provides enough openings for bear food production while also providing cover. Past research has suggested that black bears may be attracted to areas where secure cover is adjacent to high quality food sources (Lindzey et al. 1986, Lyons et al. 2003). It may be that forests of moderate canopy closure provide a combination of security and food resources and thus have higher bear abundance.

Shrubfields appeared to be the most important vegetative cover type for black bears in this study. It was the only habitat class included in top models for all types of bears: males, females, and females-with-offspring. Their positive association with the proportion of shrubfields on the landscape is consistent with the findings of Koehler and Pierce (2003). This association may result from the tendency of shrubfields to produce high quantities of shrub fruits as forage for bears, which is further supported by Gaines' (2002) observations of bears using shrubfields in the north-eastern portion of the current study area.

Hunter access was highly correlated with and thus likely exerts a strong effect on male bear abundance. In this study, hunter access showed high relative importance at both scales of analysis. As hunting is not compensatory in bear populations (Beecham 1980), and 98% of known black bear mortalities during a past study in Washington state were human-caused (Koehler and Pierce 2005), I predicted that bear abundance would be higher in areas of no hunter access than those of moderate or high hunter access. However, the lack of significant difference between bear numbers in high and moderate hunting areas after accounting for habitat suggests that the high hunt—occurring in designated wilderness with no motorized vehicle access—exerts a similar amount of pressure on bear populations as do general season hunts. Indeed, Koehler and Pierce (2005) observed similar survival rates among black bears in their Snoqualmie study area (mainly private and national forest lands with high road density) and those from the Okanogan study area (primarily roadless, designated wilderness). My results corroborate their observations and suggest that, like the roaded landscapes, bear mortality may limit the ability of designated wilderness to serve as refugia from human pressures or as source areas (i.e., areas with growing bear populations that supply dispersing individuals).

While male abundance was associated with varying levels of hunting, hunter access did not appear to affect female abundance. This lack of effect for females may be due to the fact that females are less vulnerable to hunter-harvest mortality than males (Bunnell and Tait 1981, Bunnell and Tait 1985, Koehler and Pierce 2005, Czetwertynski et al. 2007). Male bears have larger home ranges and greater mobility, thereby increasing their chance of encountering a hunter (Bunnell and Tait 1980, Miller 1990, Koehler and Pierce 2003, Koehler and Pierce 2005). In fact, throughout Washington, male mortality rates were much higher than those for females on both roaded frontcountry lands and roadless wilderness areas (Koehler and Pierce 2005).

Both male and female bear abundance increased as survey sites moved further north within the NCE, which may be due to a variety of factors including variable road use, timber harvest, and the national park location. In fact, northing was the single most important variable describing female abundance across both analysis levels. My study did not measure volume of use on roads, but Gaines and colleagues (2005) found that probabilities of black bear habitat use was affected by traffic volumes. Vehicular traffic likely decreases as the study area moves north from Interstate 90 to State Route 20. In addition, other anthropogenic sources of disturbance, such as timber harvest, may be greater in southern parts of the NCE—the Interstate 90 corridor is a checkerboard of privately owned lands whereas federal lands become more prevalent and contiguous in the north. On the other hand, habitat components other than those measured in this study may vary from north to south. Yet, regardless of the mechanism underlying this northward trend, wildlife management policies in the NCE should reflect the varying levels of bear abundance.

The lack of variation in female abundance explained by my measured habitat and human activity variables suggests that perhaps my scale of analysis was not appropriate for this segment of the black bear population. Scale has two fundamental components: extent and grain. Extent refers to the spatial expanse of the landscape, whereas grain refers to the finest spatial resolution measured. Wildlife can exhibit different behaviors depending on the grain or extent examined by the observer. My study altered the extent of the measured landscape, but not grain. It is well documented that male and female bears can occupy landscapes differently (Young and Beecham 1986, Bull et al. 2001, Koehler and Pierce 2003). My identification of significant effects on males at a coarse habitat grain may be due to their wider-ranging movements and response to broader-scale features than females. Although the extent of my Level 1 landscape represented the average core-use area of a female black bear, female habitat evaluations may require measurements at a finer resolution. Females have smaller home ranges and more restricted movements than males, particularly those females travelling with offspring (Kohler and Pierce 2003, Lyons et al. 2003). In addition, the high degree of philopatry among females (Elowe and Dodge 1989, Costello et al. 2008, Costello 2010) may result in female offspring perceiving the landscape and its resources like their mother (Koehler and Pierce 2003). Therefore, female habitat use may be more a reflection of maternal behavior and natal area rather than optimal resource selection.

Washington State is facing an increasing human population with a potential for further loss of black bear habitat. While it is the smallest in size of the eleven Western states, it hosts the second largest human population (WDFW 2008) and anticipates the highest future growth rates in the Pacific Northwest (a projected population of > 8.8 million by 2040; WOFM 2013). Furthermore, black bears may face additional pressure from increasing international demand for illegally traded parts. However, the degree of threats to black bear populations vary geographically across the NCE. The broad spatial expanse of this study facilitated an evaluation of habitat and human activity effects occurring across entire landscapes and varying disturbance levels; bear numbers were found to be correlated with more open, dry and mesic forests, and similar between areas open to general season hunts and roadless areas designated only for the high hunt. In addition, this research parallels a study evaluating habitat connectivity for carnivores in the NCE. The Cascades Carnivore Connectivity Project (CCCP) is using black bear genetic data to assess whether Washington State's highway system is serving as a barrier to panmixia among black bear subpopulations, as well as to locate fracture zones and potential habitat linkages (Long et al. 2012). The CCCP's landscape genetics combined with the results of this study will yield valuable information for input into future black bear population viability analyses. For example, models should include a much higher projected population persistence for bears within the National Park. Black bears are a necessary part of Washington's conservation strategy for large carnivores, and this study provides critical information about habitat and anthropogenic influences across a large portion of their geographic range in the state.

MANAGEMENT IMPLICATIONS

Brody and Pelton (1989) asserted that hunting exhibits a stronger influence on the dynamics of local black bear populations than habitat quality. My research revealed that across a large geographic area, male bear abundance was consistently associated with varying levels of hunter access. Even though the WDFW currently establishes hunting seasons based on the percentage and age of females in the harvest rather than that of males (WDFW 2008), the removal of males alone can have significant impacts on bear populations. For example, the disproportionate removal of males can alter the genetic structure of a population by changing sex ratios, bear densities, and patterns of dispersal (Milner et al. 2007, Coster and Kovak 2012). Furthermore, the lack of apparent difference in bear abundance between high and moderate hunter access suggests that wilderness areas may not act as a source if frontcountry populations are overexploited. By implication, wildlife managers should not be complacent about intense hunting pressure in the frontcountry because of proximity to roadless areas, and reevaluation of management policies that rely on designated wilderness as replacement for harvested populations is warranted.

The results of this study suggest that, in order to promote the persistence of black bear populations, wildlife managers should preserve areas with abundant shrubfields and promote a mosaic of forests with open and moderate tree canopy closure. Maintaining gaps in the overstory tree canopy in order to encourage growth of understory forage for bears is particularly important in managed forests where closed canopies of even-aged stands suppress understory vegetation. In addition, fire suppression on the east slopes of the NCE has led to more homogenous forests. Restoration efforts aimed at restoring heterogeneity and gaps in the canopy would benefit black bear populations by stimulating bear food production.

The positive northward trend in bear abundance (with the strongest effect on female abundance) implies that populations should be managed more conservatively (e.g., conservation-orientated with stricter hunting regulations) in the southern regions of the NCE. In addition, the differences in the observed number of habitat effects on male vs. female abundance suggest that wildlife managers may need to adopt a multi-scale (both extent and grain), sex-specific approach when managing landscapes for sustainable bear populations. The consequences of error in management are high for such a long-lived species that exhibits low fecundity and occurs at low densities; populations reduced below the desired levels will require long recovery times (Kolenosky 1986, Miller 1990, Hummel and Pettigrew 1991, NRC 1997). Accordingly, wildlife managers should adopt a conservative management approach until funds are available for more thorough and accurate estimations of the NCE’s bear populations.

ACKNOWLEDGEMENTS

Funding was largely provided by the Okanogan-Wenatchee National Forest, the U.S. Fish and Wildlife Service, and the Western Transportation Institute. Additional funding was provided by Seattle City Light, the School of Environmental and Forest Sciences at the University of Washington, the Alice and Byron Lockwood Foundation, Conservation Northwest, Elinor Patterson Baker Trust, Gear for Good, Great Northern Conservation Cooperative, Klorfine Foundation, Oregon Zoo, Patagonia, the Mountaineers Foundation, TransWild Alliance, Wilburforce Foundation, and Wildlife Land Trust. I thank W. Gaines, A. Wirsing, and J. Lawler for their wisdom and guidance in the development of the project and their reviews of the manuscript. R. Long, P. MacKay, and J. Begley contributed greatly to sampling methodology and data collection and entry. I thank P. Singleton for his help with the mapping and analytical methods used in this study. J. Smith provided valuable comments on ealier versions of the manuscript. I also thank A. Lyons for her continued support of the project and S. Fitkin, R. Christophersen, A. Woodrow, J. Wagenknecht, and J. McCarty, R. Robertson, and L. Welfelt for their field efforts.

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Figure 1. Remote camera image of barbed wire hair-snag corral.

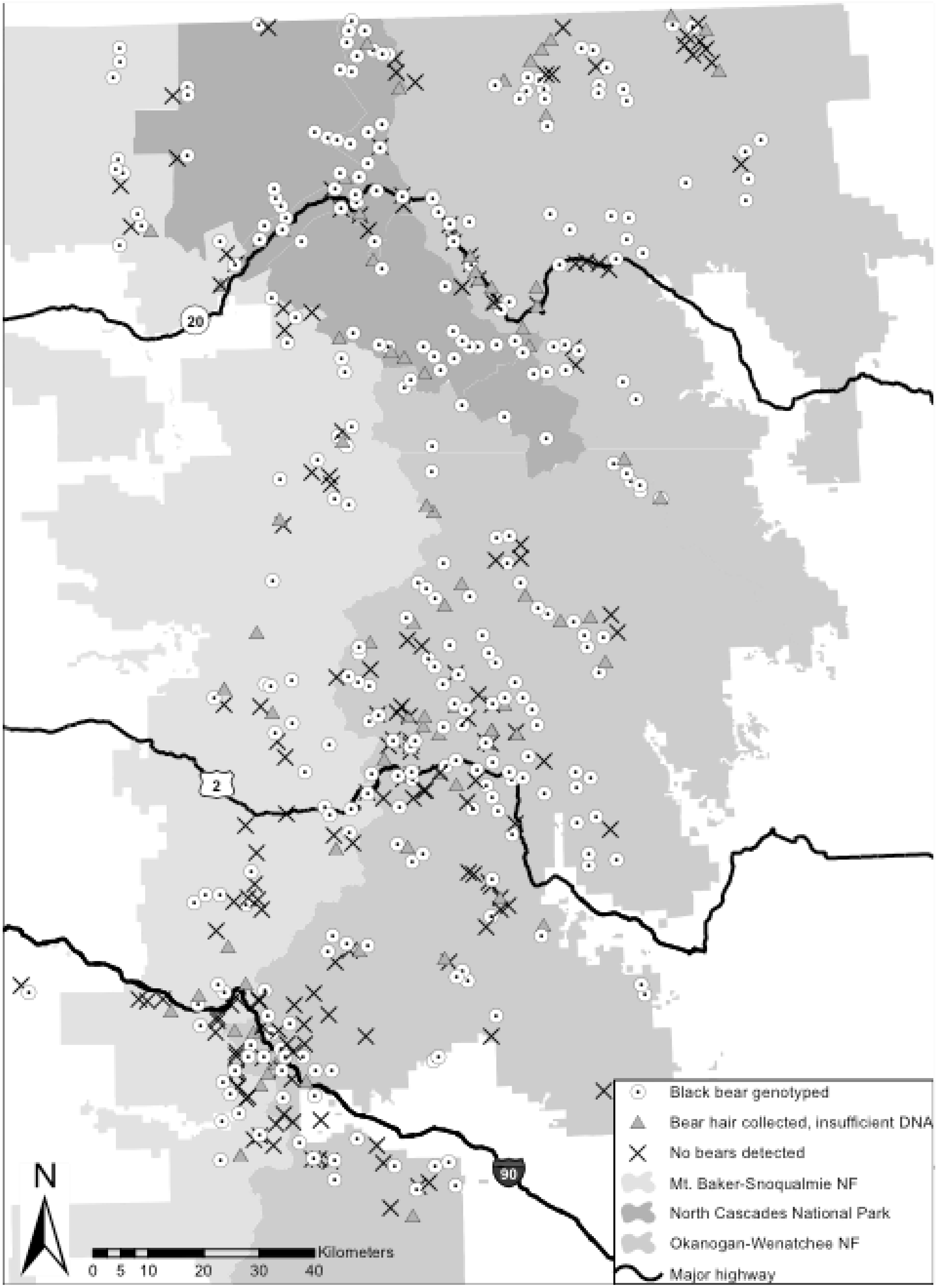

Figure 2. Map of barbed wire hair-snag corrals deployed in the North Cascades Ecosystem (NCE) from 2008-2011 and associated results.

Table 1. The variables considered in developing candidate generalized linear mixed effects models (GLMMs) describing overall and sex-specific bear abundance at the larger, Level 1 landscape scale (2.3k-radius buffers). Variables retained had univariate significance of $P < .20$, unless part of an *a priori* hypothesized interaction. Variables that share a letter are considered correlated (have a monotonic association of $\rho \geq .70$) and were not included in the same candidate model.

Overall abundance	Male abundance	Female abundance	Female with offspring
Easting	Easting	Northing	Hunter access
Northing	Northing	Hunter access-C	Moderate dry forest
Hunter access-C	Hunter access-C	Road density-C	
Road density-C	Road density-C	Stream density	
Open dry forest-A	Open dry forest-A	Open moist forest	
Open mesic forest	Open mesic forest	Closed moist forest	
Moderate dry forest-A	Moderate dry forest-A	Shrubfield	
Moderate mesic forest	Moderate mesic forest		
Moderate moist forest	Moderate moist forest		
Closed mesic forest	Closed mesic forest		
Closed moist forest	Closed moist forest		
Deciduous forest	Deciduous forest		
Shrubfield	Shrubfield		
Mesic meadow/grassland/ dwarf-shrubland	Mesic meadow/grassland/ dwarf-shrubland		
	Stream density		

Table 2. The variables considered in developing candidate generalized linear mixed effects models (GLMMs) describing overall and sex-specific bear abundance at the smaller, Level 2 landscape scale (1.0k-radius buffers). Variables retained had univariate significance of $P < .20$, unless part of an *a priori* hypothesized interaction. Variables that share a letter are considered correlated (have a monotonic association of $\rho \geq .70$) and were not included in the same candidate model.

Overall abundance	Male abundance	Female abundance	Female with offspring
Easting	Easting	Northing	Hunter access
Northing	Northing	Hunter access-C	Closed dry forest
Hunter access-C	Hunter access-C	Road density-C	Shrubfield
Road density-C	Road density-C	Open mesic forest	
Open dry forest-A	Open dry forest-A		
Open mesic forest	Open mesic forest		
Moderate dry forest-A	Moderate dry forest-A,B		
Moderate moist forest	Moderate mesic forest		
Closed moist forest	Moderate moist forest		
Deciduous forest	Closed dry forest-B		
Shrubfield	Closed moist forest		
Mesic meadow/grassland/dwarf-shrubland	Mesic meadow/grassland/dwarf-shrubland		
	Deciduous forest		
	Shrubfield		

Table 3. Top ranking generalized linear mixed effects models (GLMMs) describing bear abundance in the North Cascades Ecosystem. Top models had substantial empirical support in the data: $\Delta_i < 2$ and no covariates with 90% *CI*s overlapping 0.

Model #	Model variables	AIC	Δ_i	w_i	$R^2_{\mathrm{GLMM}(m)}$[a]	$R^2_{\mathrm{GLMM}(c)}$[b]
	Overall bear abundance: Level 1					
A33	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing	492.8	0	0.3623	0.1571	0.1571
	Overall bear abundance: Level 2					
a35	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing	502.6	0	0.4501	0.1340	0.1452
	Male abundance: Level 1					
M33	Hunter access + Moderate dry forest + Open mesic forest + Moderate moist forest+ Shrubfield	417.9	0.0	0.2949	0.1771	0.1789
M31	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing	419.1	1.2	0.1633	0.1744	0.1926
	Male abundance: Level 2					
m45	Hunter access + Closed moist forest + Deciduous forest + Northing	429.1	0.0	0.2827	0.1576	0.2436
	Female abundance: Level 1					
F44	Shrubfield + Northing	429.4	0.0	0.2482	0.0507	0.0507
F30	Northing	431.2	1.8	0.1034	0.0359	0.0359
	Female abundance: Level 2					
f4	Northing	431.2	0.0	0.2972	0.0359	0.0359

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table 3 continued.

Model #	Model variables	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
	Female-with-offspring abundance: Level 1					
FC3	Hunter access + Moderate dry forest	159.3	0.0	0.3015	0.0702	0.3017
FC7	Null model (Intercept + Random effect)	160.7	1.3	0.1558	NA	0.3097
	Female-with-offspring abundance: Level 2					
fc4	Closed dry forest + Shrubfield	159.1	0.0	0.2060	0.0405	0.2442
fc16	Null model (Intercept + Random effect)	160.7	1.5	0.0964	NA	0.3097

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table 4. Estimated parameters, lower and upper 90% confidence limits (*LCL* and *UCL*), and relative importance (Σw_i) from the top generalized linear mixed effects (GLMM) model(s) describing overall bear abundance at the 2 landscape scales.

Level 1

Coefficient	$\hat{\beta}$ ± SE	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-0.8104±0.1323	-1.0103	-0.6105		0.4447
Moderate hunter access	0.1045±0.1231	-0.0815	0.2904	0.97	1.1101
No hunter access	0.3741±0.1847	0.0952	0.6531		1.4537
Moderate dry forest	1.8431±0.5677	0.9856	2.7007	0.92	6.3163
Open mesic forest	2.7552±0.9023	1.3922	4.1182	1.00	15.7242
Shrubfield	3.1427±1.0113	1.6152	4.6702	1.00	23.1655
Northing	0.6268±0.2002	0.3244	0.9293	1.00	1.8717
Releveled intercept	-0.7060±0.1807	-0.9789	-0.4330		0.4936
High hunter access	-0.1045±0.1231	-0.2904	0.0815		0.9008
No hunter access	0.2697±0.1596	0.0286	0.5108		1.3095

Level 2

Coefficient	$\hat{\beta}$ ± SE	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-0.6567±0.1236	-0.8433	-0.4700		0.5186
Moderate hunter access	0.1192±0.1213	-0.0640	0.3024	0.99	1.1265
No hunter access	0.4302±0.1796	0.1589	0.7015		1.5375
Moderate dry forest	1.2809±0.4916	0.5383	2.0234	0.79	3.5998
Open mesic forest	1.5264±0.7182	0.4415	2.6113	0.75	4.6016
Shrubfield	1.4461±0.6204	0.5089	2.3832	0.84	4.6016
Northing	0.6686±0.1989	0.3682	0.9691	0.99	
Releveled intercept	-0.5375±0.1705	-0.7951	-0.2799		0.5842
High hunter access	-0.1192±0.1213	-0.3024	0.0640		0.8877
No hunter access	0.3110±0.1596	0.0700	0.5520		1.3648

Table 5. Estimated parameters, lower and upper 90% confidence limits (*LCL* and *UCL*), and relative importance (Σw_i) from the top generalized linear mixed effects (GLMM) model(s) describing male bear abundance at the 2 landscape scales. The intercept represents the reference estimate for high hunter access and the releveled intercept represents the reference estimate for moderate hunter access.

Level 1

Coefficient	$\hat{\beta}$ ± SE[a]	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-1.5935±0.3196	-2.1193	-1.0678		0.2032
Moderate hunter access	0.2626±0.1783	-0.0307	0.5560	0.88	1.3003
No hunter access	0.6193±0.2579	0.1951	1.0436		1.8577
Moderate dry forest	3.3318±0.7963	2.0221	4.6416	0.84	27.9900
Open mesic forest	4.9478±1.2301	2.9244	6.9711	1.00	140.8617
Moderate moist forest	-4.9065±1.9821	-8.1668	-1.6463	0.69	0.0074
Shrubfield	3.8240±1.4374	1.4597	6.1883	0.99	45.7855
Northing	0.6975±0.3049	0.1960	1.1990	0.59	2.0088
Releveled intercept	-1.3309±0.3664	-1.9335	-0.7282		0.2642
High hunter access	-0.2626±0.1783	-0.5560	0.0307		0.7690
No hunter access	0.3567±0.2220	-0.0085	0.7219		1.4286

Level 2

Coefficient	$\hat{\beta}$ ± SE	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-0.9967±0.2292	-1.3430	-0.6505		0.3691
Moderate hunter access	0.1829±0.1784	-0.0865	0.4524	0.97	1.2007
No hunter access	0.5748±0.2589	0.1838	0.9658		1.7768
Closed moist forest	-1.3577±0.5777	-2.2303	-0.4851	0.90	0.2573
Deciduous forest	-2.7331±1.2293	-4.5899	-0.8763	0.69	0.0650
Northing	0.7123±0.3345	0.2069	1.2176	0.78	2.0386
Releveled intercept	-0.8138±0.2885	-1.2496	-0.3780		0.4432
High hunter access	-0.1829±0.1784	-0.4524	0.0865		0.8328
No hunter access	0.3919±0.2404	0.0288	0.7550		1.4798

[a] Model-averaged parameter estimates.

Table 6. Estimated parameters, lower and upper 90% confidence limits (*LCL* and *UCL*), and relative importance (Σw_i) from the top generalized linear mixed effects (GLMM) model(s) describing female bear abundance at the 2 landscape scales.

Level 1

Coefficient	$\hat{\beta} \pm$ SE[a]	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-1.0884±0.1653	-1.3603	-0.8166		0.3367
Shrubfield	2.7224±1.3603	0.4849	4.9599	0.80	15.2164
Northing	0.6873±0.2217	0.3226	1.0520	0.89	1.9884

Level 2

Coefficient	$\hat{\beta} \pm$ SE	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-0.9945±0.1401	-1.2061	-0.7830		0.3699
Northing	0.6652±0.2179	0.3360	0.9944	0.91	1.9448

[a] Model-averaged parameter estimates.

Table 7. Estimated parameters, lower and upper 90% confidence limits (*LCL* and *UCL*), and relative importance (Σw_i) from the top generalized linear mixed effects (GLMM) model(s) describing female-with-offspring bear abundance at the 2 landscape scales. At Level 1, the intercept represents the reference estimate for high hunter access and the releveled intercept represents the reference estimate for moderate hunter access.

Level 1

Coefficient	$\hat{\beta} \pm \mathrm{SE}^{a}$	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-3.8199±0.5834	-4.7794	-2.8603		0.0219
Moderate hunter access	1.0265±0.5418	0.1354	1.9176	0.60	2.7913
No hunter access	0.7269±0.9939	-0.9079	2.3617		2.0687
Moderate dry forest	4.9000±2.4504	0.8695	8.9305	0.71	134.2904
Releveled intercept	-3.1432±0.3561	-3.7289	-2.5574		0.0431
High hunter access	-1.0265±0.5418	-1.9176	-0.1354		0.3583
No hunter access	-0.2996±0.9381	-1.8427	1.2435		0.7411

Level 2

Coefficient	$\hat{\beta} \pm \mathrm{SE}^{a}$	*LCL*	*UCL*	Σw_i	Exp($\hat{\beta}$)
Intercept	-3.5959±0.4134	-4.2759	-2.9159		0.0274
Closed dry forest	2.7011±1.4741	0.2763	5.1258	0.61	14.8959
Shrubfield	4.2207±2.3275	0.3923	8.0492	0.58	68.0842

[a] Model-averaged parameter estimates.

APPENDIX

Table S1. Habitat and human activity variables. *See table S2 or **table S4 for variable definitions and sources.

Variable	Units	Range	Definition	Source
Open dry coniferous forest	Proportion of buffer	0-0.41	Canopy closure 10-<40%; *	Lemma gnn, *
Open mesic coniferous forest	Proportion of buffer	0-0.49	Canopy closure 10-<40%; *	Lemma gnn, *
Open moist coniferous forest	Proportion of buffer	0-0.24	Canopy closure 10-<40%; *	Lemma gnn, *
Open wet coniferous forest	Proportion of buffer	0-0.06	Canopy closure 10-<40%; *	Lemma gnn, *
Moderate dry coniferous forest	Proportion of buffer	0-0.53	Canopy closure 40-<70%; *	Lemma gnn, *
Moderate mesic coniferous forest	Proportion of buffer	0-0.65	Canopy closure 40-<70%; *	Lemma gnn, *
Moderate moist coniferous forest	Proportion of buffer	0-0.39	Canopy closure 40-<70%; *	Lemma gnn, *
Moderate wet coniferous forest	Proportion of buffer	0-0.06	Canopy closure 40-<70%; *	Lemma gnn, *
Closed dry coniferous forest	Proportion of buffer	0-0.66	Canopy closure ≥70%; *	Lemma gnn, *
Closed mesic coniferous forest	Proportion of buffer	0-0.87	Canopy closure ≥70%; *	Lemma gnn, *
Closed moist coniferous forest	Proportion of buffer	0-0.75	Canopy closure ≥70%; *	Lemma gnn, *
Closed wet coniferous forest	Proportion of buffer	0-0.24	Canopy closure ≥70%; *	Lemma gnn, *
Deciduous forest	Proportion of buffer	0-0.65	Pixels >7.5% live tree basal area	Lemma gnn
Dry grassland/shrubland	Proportion of buffer	0-0.32	Canopy closure <10%; **	**
Mesic meadow/grassland/dwarf-shrubland	Proportion of buffer	0-0.45	Canopy closure <10%; **	**
Shrubfield	Proportion of buffer	0-0.52	Canopy closure <10%; **	**
Wetland/wet meadow	Proportion of buffer	0-0.14	Canopy closure <10%; **	**
Stream density	km/km2	0-6.07	Density of perennial streams within buffer	WADNR

Table S1 continued.

Variable	Units	Range	Definition	Source
Road density	km/km2	0-4.56	Density of road within buffer. Measured roads include: USFS roads maintenance level 1-5 on NF lands managed by the USFS, all open NPS roads within NOCA NP boundary, all open roads on non-USFS managed lands outside NOCA NP boundary.	USFS, NPS, WADNR
Trail density	km/km2	0-2.28	Density of trails within buffer.	USFS, NPS, WADNR
Hunter access	Categorical: High, Low, or None	None-High	High hunter acess=NF lands with motorized vehicle access; Low hunter access=designated wilderness areas; No hunter access=North Cascades National Park	USFS, NPS
Easting	NA	0-1	UTM X coordinates standardized by range	NA
Northing	NA	0-1	UTM Y coordinates standardized by range	NA

Table S2. Moisture gradient assignments to Ecoshare's Plant Association Group (PAG) layer by east or west of Cascade crest.

VALUE	*PAG Name (or Plant Association if source=2010 layer)*	*Moisture_West*	*Moisture_East*	*Source*
501	Northern Artemesia-Agropyron steppe	—	dry	WA Cascades PAG 2012: Table 3
1001	PP/AGSP-PUTR dry shrub-grass	—	dry	WA Cascades PAG 2012: Table 3
1071	Ponderosa pine/nonforest-dry	—	dry	W. Washington PAG 2010 layer Metadata
1401	DF-PP/AGSP-PUTR-FEID-ARUV	dry	dry	WA Cascades PAG 2012: Table 3
1403	DF/CARU-SPBE-PAMY-ARUV-SYOR	dry	dry	WA Cascades PAG 2012: Table 3
1404	DF/SYAL-PHMA	dry	mesic	WA Cascades PAG 2012: Table 3
1405	DF/VACA-VAME-VAMY	dry	mesic	WA Cascades PAG 2012: Table 3
1406	DF/GASH-HODI-ROGY	mesic	mesic	WA Cascades PAG 2012: Table 3
1409	DF-ES/riparian	—	wet	WA Cascades PAG 2012: Table 3
1471	Douglas-fir/nonforest-dry	dry	dry	W. Washington PAG 2010 layer Metadata
1601	GF/ARNE-HODI-SYOR	—	dry	WA Cascades PAG 2012: Table 3
1603	GF/CARU-SPBE-CAGE-PHMA	—	dry	WA Cascades PAG 2012: Table 3
1604	GF/ACCI-ACTR-BENE-BEAQ	—	moist	WA Cascades PAG 2012: Table 3
1671	Grand fir/nonforest-dry	—	dry	W. Washington PAG 2010 layer Metadata
1901	WH/GASH-XETE-VAME-HODI-ARNE	dry	dry	WA Cascades PAG 2012: Table 3
1902	Western hemlock/rhododendron	mesic	—	W. Washington PAG 2010 layer Metadata
1903	WH/GASH-BENE-RHMA-PAMY-CLUN	mesic	mesic	WA Cascades PAG 2012: Table 3
1904	WH/VAAL-XETE-COCA	dry	—	WA Cascades PAG 2012: Table 3
1906	WH/ACCI-GASH-BENE-ACTR-POMU	mesic	mesic	WA Cascades PAG 2012: Table 3
1907	WH/POMU-TIUN-OXOR-ARNU3	moist	moist	WA Cascades PAG 2012: Table 3
1909	WH/OXOR-POMU-VAAL	mesic	moist	WA Cascades PAG 2012: Table 3
1910	WH/OPHO-ATFI-LYAM	wet	wet	WA Cascades PAG 2012: Table 3
1971	Western hemlock/nonforest-dry	dry	mesic	W. Washington PAG 2010 layer Metadata
1991	Western hemlock/nonforest-wet	wet	—	W. Washington PAG 2010 layer Metadata
2202	PSF/GASH-BENE-ACTR-RHMA-dry VAAL	dry	moist	WA Cascades PAG 2012: Table 3
2203	Pacific silver fir/Alaska huckleberry, dry	dry	—	W. Washington PAG 2010 layer Metadata
2204	PSF/VAME-RHAL-XETE-VAAL	mesic	mesic	WA Cascades PAG 2012: Table 3

Table S2 continued.

VALUE	*PAG Name (or Plant Association if source=2010 layer)*	*Moisture_West*	*Moisture_East*	*Source*
2205	Pacific silver fir/big huckleberry-Cascades azalea	dry	—	W. Washington PAG 2010 layer Metadata
2206	Pacific silver fir/vine maple-vanillaleaf	mesic	—	W. Washington PAG 2010 layer Metadata
2207	PSF/VAAL-CLUN-MADI2-TIUN	moist	moist	WA Cascades PAG 2012: Table 3
2208	PSF/OXOR-ERMO-BLSP-VAAL	moist	—	WA Cascades PAG 2012: Table 3
2209	PSF/OPHO-LYAM	wet	wet	WA Cascades PAG 2012: Table 3
2271	Pacific silver fir/nonforest-dry	dry	mesic	W. Washington PAG 2010 layer Metadata
2291	Pacific silver fir/nonforest-wet	wet	wet	W. Washington PAG 2010 layer Metadata
2301	Mountain hemlock/rhododendron, warm	mesic	—	W. Washington PAG 2010 layer Metadata
2302	MH/VASC-VAMY-LUHI-XETE	dry	mesic	WA Cascades PAG 2012: Table 3
2303	Mountain hemlock/big huckleberry-fool's huckleberry	mesic	—	W. Washington PAG 2010 layer Metadata
2304	MH/VAME-RHAL-XETE	mesic	moist	WA Cascades PAG 2012: Table 3
2305	MH/VAAL-CLUN-RUPE	moist	moist	WA Cascades PAG 2012: Table 3
2306	TSME/OPHO-VAAL-CABI	wet	wet	WA Cascades PAG 2012: Table 3
2371	Mountain hemlock/nonforest-dry	dry	mesic	W. Washington PAG 2010 layer Metadata
2391	Mountain hemlock/nonforest-wet	wet	—	W. Washington PAG 2010 layer Metadata
2501	PIAL/VASC-LUHI-CARU	dry	mesic	WA Cascades PAG 2012: Table 3
2502	SAF/CARU-PAMY	dry	dry	WA Cascades PAG 2012: Table 3
2503	SAF/VASC-VACA-VAME-LIBOL	dry	mesic	WA Cascades PAG 2012: Table 3
2504	SAF/VAME-LULA	dry	mesic	WA Cascades PAG 2012: Table 3
2505	SAF/RHAL-XETE-ARLA-POPU	dry	moist	WA Cascades PAG 2012: Table 3
2507	SAF/TRCA3-ATFI-GYDR-STAM-riparian	wet	wet	WA Cascades PAG 2012: Table 3
2571	Subalpine fir/nonforest-dry	dry	dry	W. Washington PAG 2010 layer Metadata
3201	Dry Continental PKL	dry	mesic	WA Cascades PAG 2012: Table 3
3205	Moist, Maritime PKL	mesic	moist	WA Cascades PAG 2012: Table 3
3301	Alpine	mesic	mesic	WA Cascades PAG 2012: Table 3

Table S3. Definition and sources of non-forested vegetative cover classes.

Habitat Variable	*Lemma/GAP Name*	*Source*
Agriculture	Agriculture	Lemma Non-forest Mask
	Cultivated Cropland	NW GAP analysis
	Cultivated Crops	Lemma Non-forest Mask
Dry grassland/shrubland	Columbia Basin Foothill and Canyon Dry Grassland	Lemma Non-forest Mask, NW GAP analysis
	Columbia Basin Palouse Prairie	Lemma Non-forest Mask, NW GAP analysis
	Columbia Plateau Low Sagebrush Steppe	Lemma Non-forest Mask, NW GAP analysis
	Columbia Plateau Scabland Shrubland	Lemma Non-forest Mask, NW GAP analysis
	Columbia Plateau Steppe and Grassland	Lemma Non-forest Mask, NW GAP analysis
	Inter-Mountain Basins Big Sagebrush Shrubland	Lemma Non-forest Mask, NW GAP analysis
	Inter-Mountain Basins Big Sagebrush Steppe	Lemma Non-forest Mask, NW GAP analysis
	Inter-Mountain Basins Montane Sagebrush Steppe	Lemma Non-forest Mask, NW GAP analysis
	Inter-Mountain Basins Semi-Desert Grassland	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Dry Douglas-fir-(Madrone) Forest	NW GAP analysis
	Northern Rocky Mountain Ponderosa Pine Woodland and Savanna	NW GAP analysis
	Recently burned forest	NW GAP analysis
	Recently burned grassland	NW GAP analysis
Shrubfield	Columbia Basin Foothill Riparian Woodland and Shrubland	Lemma Non-forest Mask
	Columbia Basin Foothill Riparian Woodland and Shrubland	NW GAP analysis
	Great Basin Foothill and Lower Montane Riparian Woodland and Shrubland	Lemma Non-forest Mask
	Great Basin Foothill and Lower Montane Riparian Woodland and Shrubland	NW GAP analysis
	Harvested forest-shrub regeneration	NW GAP analysis
	Harvested forest-tree regeneration	NW GAP analysis
	Introduced Upland Vegetation - Shrub	NW GAP analysis
	North Pacific Avalanche Chute Shrubland	Lemma Non-forest Mask
	North Pacific Avalanche Chute Shrubland	NW GAP analysis
	North Pacific Broadleaf Landslide Forest and Shrubland	NW GAP analysis
	North Pacific Lowland Riparian Forest and Shrubland	Lemma Non-forest Mask

Table S3 continued.

Habitat Variable	*Lemma/GAP Name*	*Source*
Shrubfield *cont.*	North Pacific Lowland Riparian Forest and Shrubland	NW GAP analysis
	North Pacific Montane Riparian Woodland and Shrubland	Lemma Non-forest Mask
	North Pacific Montane Riparian Woodland and Shrubland	NW GAP analysis
	North Pacific Montane Shrubland	Lemma Non-forest Mask
	North Pacific Montane Shrubland	NW GAP analysis
	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland	Lemma Non-forest Mask
	Northern Rocky Mountain Lower Montane Riparian Woodland and Shrubland	NW GAP analysis
	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland	Lemma Non-forest Mask
	Northern Rocky Mountain Montane-Foothill Deciduous Shrubland	NW GAP analysis
	Northern Rocky Mountain Subalpine Deciduous Shrubland	Lemma Non-forest Mask
	Northern Rocky Mountain Subalpine Deciduous Shrubland	NW GAP analysis
	Rocky Mountain Lower Montane Riparian Woodland and Shrubland	Lemma Non-forest Mask
	Rocky Mountain Lower Montane Riparian Woodland and Shrubland	NW GAP analysis
	Rocky Mountain Subalpine-Montane Riparian Shrubland	Lemma Non-forest Mask
	Rocky Mountain Subalpine-Montane Riparian Shrubland	NW GAP analysis
	Rocky Mountain Subalpine-Montane Riparian Woodland	NW GAP analysis
Mesic meadow/grassland /dwarf-shrubland	East Cascades Mesic Montane Mixed-Conifer Forest and Woodland	NW GAP analysis
	Harvested forest-grass regeneration	NW GAP analysis
	Inter-Mountain Basins Aspen-Mixed Conifer Forest and Woodland	NW GAP analysis
	Introduced Upland Vegetation - Annual and Biennial Forbland	Lemma Non-forest Mask
	Introduced Upland Vegetation - Annual Grassland	Lemma Non-forest Mask, NW GAP analysis
	Introduced Upland Vegetation - Perennial Grassland	NW GAP analysis
	Invasive Annual / Perennial Grassland / Forbland	Lemma Non-forest Mask

Table S3 continued.

Habitat Variable	*Lemma/GAP Name*	*Source*
Mesic meadow/grassland /dwarfshrubland	North Pacific Alpine and Subalpine Dry Grassland	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Dry and Mesic Alpine Dwarf-Shrubland, Fell-field and Meadow	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Dry-Mesic Silver Fir-Western Hemlock-Douglas-fir Forest	NW GAP analysis
	North Pacific Herbaceous Bald and Bluff	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Maritime Dry-Mesic Douglas-fir-Western Hemlock Forest	NW GAP analysis
	North Pacific Maritime Mesic Subalpine Parkland	NW GAP analysis
	North Pacific Mesic Western Hemlock-Silver Fir Forest	NW GAP analysis
	North Pacific Mountain Hemlock Forest	NW GAP analysis
	Northern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest	NW GAP analysis
	Northern Rocky Mountain Lower Montane, Foothill and Valley Grassland	Lemma Non-forest Mask, NW GAP analysis
	Northern Rocky Mountain Subalpine Woodland and Parkland	NW GAP analysis
	Northern Rocky Mountain Subalpine-Upper Montane Grassland	Lemma Non-forest Mask, NW GAP analysis
	Northern Rocky Mountain Western Larch Savanna	NW GAP analysis
	Rocky Mountain Alpine Fell-Field	Lemma Non-forest Mask, NW GAP analysis
	Rocky Mountain Alpine Tundra/Fell-field/Dwarf-shrub Map Unit	NW GAP analysis
	Rocky Mountain Aspen Forest and Woodland	NW GAP analysis
	Rocky Mountain Lodgepole Pine Forest	NW GAP analysis
	Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland	NW GAP analysis
Wetland/wet meadow	Inter-Mountain Basins Alkaline Closed Depression	Lemma Non-forest Mask
	Inter-Mountain Basins Playa	NW GAP analysis
	North American Arid West Emergent Marsh	Lemma Non-forest Mask
	North American Arid West Emergent Marsh	NW GAP analysis
	North Pacific Bog and Fen	Lemma Non-forest Mask

Table S3 continued.

Habitat Variable	*Lemma/GAP Name*	*Source*
Wetland/wet meadow *cont.*	North Pacific Bog and Fen	NW GAP analysis
	North Pacific Hardwood-Conifer Swamp	NW GAP analysis
	North Pacific Maritime Mesic-Wet Douglas-fir-Western Hemlock Forest	NW GAP analysis
	North Pacific Shrub Swamp	Lemma Non-forest Mask
	North Pacific Shrub Swamp	NW GAP analysis
	Rocky Mountain Subalpine Mesic-Wet Spruce-Fir Forest and Woodland	NW GAP analysis
	Temperate Pacific Freshwater Aquatic Bed	Lemma Non-forest Mask
	Temperate Pacific Freshwater Emergent Marsh	Lemma Non-forest Mask
	Temperate Pacific Freshwater Emergent Marsh	NW GAP analysis
	Temperate Pacific Subalpine-Montane Wet Meadow	Lemma Non-forest Mask
	Temperate Pacific Subalpine-Montane Wet Meadow	NW GAP analysis
NA	Developed, High Intensity	Lemma Non-forest Mask, NW GAP analysis
	Developed, Low Intensity	Lemma Non-forest Mask, NW GAP analysis
	Developed, Medium Intensity	Lemma Non-forest Mask, NW GAP analysis
	Developed, Open Space	Lemma Non-forest Mask, NW GAP analysis
	Inter-Mountain Basins Cliff and Canyon	Lemma Non-forest Mask, NW GAP analysis
	Non-specific Disturbed	NW GAP analysis
	North American Alpine Ice Field	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Alpine and Subalpine Bedrock and Scree	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Montane Massive Bedrock, Cliff and Talus	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Serpentine Barren	Lemma Non-forest Mask, NW GAP analysis
	North Pacific Wooded Volcanic Flowage	NW GAP analysis
	Open Water	Lemma Non-forest Mask, NW GAP analysis
	Pasture/Hay	Lemma Non-forest Mask, NW GAP analysis
	Quarries, Mines and Gravel Pits	NW GAP analysis
	Quarries/Strip Mines/Gravel Pits	Lemma Non-forest Mask

Table S3 continued.

Habitat Variable	*Lemma/GAP Name*	*Source*
NA *cont.*	Rocky Mountain Alpine Bedrock and Scree	Lemma Non-forest Mask, NW GAP analysis
	Rocky Mountain Cliff, Canyon and Massive Bedrock	Lemma Non-forest Mask, NW GAP analysis
	Temperate Pacific Intertidal Mudflat	Lemma Non-forest Mask
	Unconsolidated Shore	Lemma Non-forest Mask, NW GAP analysis

Table S4. Parameter estimates for univariate generalized linear mixed effects models (GLMMs) describing overall and male bear abundance in the North Cascades Ecosystem. Variables with bolded values have univariate significance of $P < .20$ and were used in developing candidate sets of multivariate GLMMs.

	Level 1				Level 2			
	Overall abundance		Males		Overall abundance		Males	
Variable	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Easting	**0.6710**	**0.0222**	**1.2645**	**0.0047**	**0.6710**	**0.0222**	**1.2645**	**0.0047**
Northing	**0.8849**	**<0.0001**	**1.1778**	**<0.0001**	**0.8849**	**<0.0001**	**1.1778**	**<0.0001**
Hunter Access:								
High (Intercept)	-0.1571	0.0313	-1.0277	<0.0001	-0.1571	0.0313	-1.0277	<0.0001
Moderate	**0.2943**	**0.0069**	**0.4254**	**0.0110**	**0.2943**	**0.0069**	**0.4254**	**0.0110**
None	**0.6917**	**<0.0001**	**0.8679**	**0.0004**	**0.6917**	<0.0001	**0.8679**	**0.0004**
Hunter Access (releveled):								
Moderate (Intercept)	0.1372	<0.0001	-0.6023	<0.0001	0.1372	<0.0001	-0.6023	<0.0001
High	**-0.2943**	**0.0069**	**-0.4254**	**0.0110**	**-0.2943**	**0.0069**	**-0.4254**	**0.0110**
None	**0.3974**	**0.0179**	**0.4424**	**0.0705**	**0.3974**	**0.0179**	**0.4424**	**0.0705**
Road Density	**-0.1505**	**0.0105**	**-0.2635**	**0.0052**	**-0.1207**	**0.0099**	**-0.2002**	**0.0073**
Trail Density	0.1674	0.3530	0.2084	0.4360	**0.1425**	**0.1530**	**0.2041**	**0.1710**
Stream Density	0.0022	0.9770	**-0.1782**	**0.1394**	0.0252	0.5350	0.0095	0.8760
Open Dry Forest	**1.6982**	**0.0527**	**3.1793**	**0.0087**	**1.2953**	**0.1160**	**2.4754**	**0.0305**
Open Mesic Forest	**3.1333**	**0.0017**	**4.8760**	**0.0005**	**1.8254**	**0.0266**	**1.9633**	**0.1080**

Table S4 continued.

	Level 1				Level 2			
	Overall abundance		Males		Overall abundance		Males	
Variable	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Open Moist Forest	-1.0678	0.6000	1.3684	0.6320	-0.7326	0.7010	0.7480	0.7760
Open Wet Forest	14.7487	0.3200	16.6005	0.4640	-1.1492	0.8970	0.8080	0.9500
Moderate Dry Forest	**1.0579**	**0.0608**	**1.7968**	**0.0284**	**0.8558**	**0.0926**	**1.4180**	**0.0579**
Moderate Mesic Forest	**1.5128**	**0.0370**	**2.5790**	**0.0147**	0.6280	0.2930	**1.2605**	**0.1430**
Moderate Moist Forest	**-3.9007**	**0.0036**	**-6.6751**	**0.0021**	**-2.4140**	**0.0147**	**-4.5047**	**0.0076**
Moderate Wet Forest	-6.6597	0.4620	-13.5890	0.3540	-4.4209	0.4990	-4.8335	0.6350
Closed Dry Forest	0.4417	0.3510	0.4047	0.5770	0.4327	0.2530	**0.9004**	**0.1030**
Closed Mesic Forest	**-0.5328**	**0.1700**	**-1.3239**	**0.0262**	-0.1692	0.5570	-0.4963	0.2620
Closed Moist Forest	**-1.6404**	**0.0001**	**-2.6858**	**0.0001**	**-1.0767**	**0.0019**	**-2.1442**	**0.0001**
Closed Wet Forest	-0.7841	0.6530	-2.9903	0.2900	0.0012	0.9990	-1.1497	0.5410
Deciduous Forest	**-1.6769**	**0.0861**	**-4.6588**	**0.0129**	**-1.2600**	**0.0763**	**-2.8644**	**0.0247**
Dry grassland/shrubland	-1.7513	0.4420	-0.1149	0.9710	-2.0697	0.3550	-0.1665	0.9570
Shrubfield	**3.2635**	**0.0026**	**4.3460**	**0.0067**	**1.4025**	**0.0333**	**2.2572**	**0.0168**
Mesic meadow/ grassland/dwarf-shrubland	**1.6964**	**0.0215**	**3.8169**	**0.0002**	**1.6567**	**0.0201**	**3.3720**	**0.0004**
Wetland/wet meadow	-2.3855	0.6750	-6.5540	0.4670	-1.0670	0.8040	-2.8303	0.6810

Table S5. Parameter estimates for univariate generalized linear mixed effects models (GLMMs) describing female and female-with-offspring abundance in the North Cascades Ecosystem. Variables with bolded values have univariate significance of *P* < .20 and were used in developing candidate sets of multivariate GLMMs.

	Level 1				Level 2			
	Females		Females-with-offspring		Females		Females-with-offspring	
Variable	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Easting	0.2213	0.5200	-0.1035	0.9390	0.2213	0.5200	-0.1035	0.9390
Northing	**0.6652**	**0.0023**	0.8438	0.3410	**0.6652**	**0.0023**	0.8438	0.3410
Hunter Access:								
High (Intercept)	-0.7567	<0.0001	-3.5741	<0.0001	-0.7567	<0.0001	-3.5741	<2E-16
Moderate	0.2033	0.1410	**0.7164**	**0.1590**	0.2033	0.1410	**0.7164**	**0.1590**
None	**0.5416**	**0.0136**	0.3384	0.7310	**0.5416**	**0.0136**	0.3384	0.7310
Hunter Access (releveled):								
Moderate (Intercept)	-0.5534	<0.0001	-2.8577	<0.0001	-0.5534	<0.0001	-2.8577	<0.0001
High	-0.2032	0.1410	**-0.7164**	**0.1590**	-0.2032	0.1410	**-0.7164**	**0.1590**
None	0.3383	0.1340	-0.3780	0.6950	0.3383	0.1340	-0.3780	0.6950
Road Density	**-0.0881**	**0.2000**	-0.0778	0.7730	**-0.0766**	**0.1720**	-0.0738	0.7360
Trail Density	0.1572	0.4800	0.8815	0.2750	0.1220	0.3300	0.1480	0.7450
Stream Density	**0.1653**	**0.0953**	-0.0651	0.8690	0.0425	0.4140	-0.1045	0.5910
Open Dry Forest	0.3259	0.7830	-0.3818	0.9380	0.1862	0.8670	-2.2354	0.6640
Open Mesic Forest	0.9921	0.4510	-7.5329	0.3000	**1.2962**	**0.2030**	-9.3573	0.2720

Table S5 continued.

	Level 1				Level 2			
	Females		Females-with-offspring		Females		Females-with-offspring	
Variable	Estimate	*P*	Estimate	*P*	Estimate	*P*	Estimate	*P*
Open Moist Forest	**-4.1618**	**0.1380**	-2.0888	0.8290	-3.0666	0.2600	-3.1130	0.7660
Open Wet Forest	19.4492	0.2640	49.1439	0.3720	-1.6601	0.8840	-41.2443	0.5550
Moderate Dry Forest	0.5444	0.4430	**3.2970**	**0.1460**	0.5128	0.4200	2.6010	0.2150
Moderate Mesic Forest	0.2024	0.8170	-1.4934	0.6990	-0.1932	0.7950	-2.2155	0.5340
Moderate Moist Forest	-1.8733	0.2370	-5.7730	0.3990	-1.0281	0.3700	-0.4019	0.9230
Moderate Wet Forest	1.5778	0.8870	36.0118	0.2360	-1.9909	0.8010	24.6781	0.2190
Closed Dry Forest	0.6312	0.2630	2.0351	0.2880	0.1587	0.7410	**2.1478**	**0.1570**
Closed Mesic Forest	0.0322	0.9460	-1.1643	0.5300	0.0177	0.9600	-0.7280	0.5990
Closed Moist Forest	**-0.8814**	**0.0785**	-0.9513	0.6270	-0.3375	0.3990	-0.5349	0.7330
Closed Wet Forest	1.1855	0.5460	-2.6020	0.7830	1.0578	0.4240	-2.6138	0.6660
Deciduous Forest	0.3417	0.7290	0.5644	0.8760	0.0107	0.9890	-1.0406	0.7450
Dry grassland/shrubland	-3.3286	0.2840	-8.5483	0.6250	-4.0225	0.2110	-9.4857	0.6130
Shrubfield	**2.5191**	**0.0634**	4.2951	0.3510	0.6743	0.4410	**3.1496**	**0.1900**
Mesic meadow/ grassland/dwarf-shrubland	-0.5216	0.6070	-1.1009	0.7930	-0.3289	0.7540	-4.1930	0.4630
Wetland/wet meadow	2.2690	0.7340	-14.3014	0.7000	2.0500	0.6810	-8.1832	0.7540

Table S6. Top 10 generalized linear mixed effects models (GLMMs) describing overall bear abundance in the North Cascades Ecosystem at the larger, Level 1 landscape scale (2.3k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Model in bold had substantial support ($\Delta_i < 2$ and does not include any covariates with 90% *CI*s overlapping 0) and was used for inference.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\mathrm{GLMM}(m)}$ [a]	$R^2_{\mathrm{GLMM}(c)}$ [b]
A33	**Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing**	**-238.3957**	**492.7913**	**0.0000**	**0.3623**	**0.1571**	**0.1571**
A35c	Hunter access + Moderate dry forest + Open mesic forest + Moderate moist forest+ Shrubfield + Northing	-238.0186	494.0372	1.2459	0.1943	0.1575	0.1575
A34	Hunter access + Moderate dry forest + Open mesic forest + Closed moist forest+ Shrubfield + Northing	-238.3088	494.6176	1.8263	0.1454	0.1569	0.1569
A35	Hunter access + Moderate dry forest + Open mesic forest + Closed mesic forest + Shrubfield + Northing	-238.3372	494.6744	1.8831	0.1413	0.1573	0.1573
A37	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing + Easting*Deciduous forest	-237.7656	497.5311	4.7398	0.0339	0.1581	0.1581
A36	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing + Easting*Stream density	-237.8079	497.6158	4.8245	0.0325	0.1569	0.1569
A30	Hunter access + Open dry forest + Open mesic forest + Shrubfield + Northing	-241.0052	498.0105	5.2192	0.0267	0.1447	0.1447
A17	Open mesic forest + Closed moist forest + Shrubfield + Northing	-243.3872	498.7745	5.9832	0.0182	0.1387	0.1635

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S6 continued.

Model #	Model variables	log[l]	AIC	Δ_i	w_i	$R^2_{\mathrm{GLMM}(m)}$[a]	$R^2_{\mathrm{GLMM}(c)}$[b]
A32	Hunter access + Open dry forest + Open mesic forest + Closed mesic forest + Shrubfield + Northing	-240.8574	499.7148	6.9235	0.0114	0.1453	0.1453
A32c	Hunter access + Open dry forest + Open mesic forest + Moderate moist forest + Shrubfield + Northing	-240.8871	499.7742	6.9829	0.0110	0.1453	0.1453

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S7. Top 10 generalized linear mixed effects models (GLMMs) describing overall bear abundance in the North Cascades Ecosystem at the smaller, Level 2 landscape scale (1.0k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Model in bold had substantial support ($\Delta_i < 2$ and does not include any covariates with 90% *CI*s overlapping 0) and was used for inference.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
a35	**Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing**	**-243.2957**	**502.5913**	**0.0000**	**0.4501**	**0.1340**	**0.1452**
a60	Hunter access + Moderate dry forest + Shrubfield + Northing	-245.3418	504.6836	2.0923	0.1581	0.1274	0.1459
a31	Hunter access + Moderate dry forest + Open mesic forest + Northing	-245.7676	505.5351	2.9438	0.1033	0.1180	0.1416
a34	Hunter access + Open dry forest + Open mesic forest + Shrubfield + Northing	-245.0511	506.1021	3.5108	0.0778	0.1238	0.1396
a62	Hunter access + Open dry forest + Shrubfield + Northing	-246.3899	506.7797	4.1884	0.0554	0.1202	0.1407
a63	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing + Easting*Deciduous forest	-242.5558	507.1115	4.5202	0.0470	0.1381	0.1505
a36	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing + Easting*Stream density	-243.1413	508.2826	5.6912	0.0262	0.1338	0.1443
a42	Hunter access + Shrubfield + Mesic meadow + Northing	-247.3805	508.7609	6.1696	0.0206	0.1137	0.1484

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S7 continued.

Model #	Model variables	log[l]	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
a37	Hunter access + Closed moist forest + Open mesic forest + Northing	-247.6780	509.3559	6.7646	0.0153	0.1095	0.1467
a30	Hunter access + Open dry forest + Open mesic forest + Northing	-247.8243	509.6486	7.0572	0.0132	0.1055	0.1368

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S8. Top 10 generalized linear mixed effects models (GLMMs) describing male bear abundance in the North Cascades Ecosystem at the larger, Level 1 landscape scale (2.3k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Models in bold had substantial support ($\Delta_i < 2$ and do not include any covariates with 90% *CI*s overlapping 0) and were used in subsequent model averaging.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\mathrm{GLMM}(m)}$[a]	$R^2_{\mathrm{GLMM}(c)}$[b]
M33	**Hunter access + Moderate dry forest + Open mesic forest + Moderate moist forest+ Shrubfield**	**-200.9434**	**417.8869**	**0.0000**	**0.2949**	**0.1771**	**0.1789**
M35	Hunter access + Moderate dry forest + Open mesic forest + Moderate moist forest+ Shrubfield + Northing	-200.1463	418.2925	0.4056	0.2408	0.1812	0.1887
M31	**Hunter access + Moderate dry forest + Open mesic forest + Shrubfield + Northing**	**-201.5344**	**419.0688**	**1.1819**	**0.1633**	**0.1744**	**0.1926**
M34	Hunter access + Moderate dry forest + Open mesic forest + Closed moist forest+ Shrubfield + Northing	-201.5320	421.0639	3.1770	0.0602	0.1742	0.1920
M11	Open dry forest + Open mesic forest + Moderate mesic forest + Moderate moist forest + Closed mesic forest + Closed moist forest + Deciduous forest + Shrubfield + Mesic meadow + Easting + Northing	-197.8427	421.6853	3.7984	0.0441	0.2060	0.2451
M10	Open dry forest + Open mesic forest + Moderate mesic forest + Moderate moist forest + Closed mesic forest + Closed moist forest + Deciduous forest + Shrubfield + Mesic meadow	-199.9478	421.8956	4.0087	0.0397	0.1904	0.2331

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S8 continued.

Model #	Model variables	log[l]	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
M55	Hunter access + Moderate dry forest + Open mesic forest + Shrubfield	-204.2017	422.4035	4.5166	0.0308	0.1574	0.1789
M57	Full model (Road density + Moderate dry forest + Open mesic forest + Moderate mesic forest + Moderate moist forest + Closed mesic forest + Closed moist forest + Deciduous forest + Shrubfield + Mesic meadow + Easting + Northing + Stream density + Road density*Closed mesic forest + Easting*Stream density)	-194.6406	423.2813	5.3944	0.0199	0.2142	0.2221
M26	Hunter access + Open dry forest + Open mesic forest + Shrubfield + Northing	-203.7007	423.4014	5.5145	0.0187	0.1573	0.1876
M32	Hunter access + Moderate dry forest + Open mesic forest + Closed moist forest+ Shrubfield	-203.7910	423.5821	5.6952	0.0171	0.1628	0.1886

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S9. Top 10 generalized linear mixed effects models (GLMMs) describing male bear abundance in the North Cascades Ecosystem at the smaller, Level 2 landscape scale (1.0k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Model in bold had substantial support ($\Delta_i < 2$ and does not include any covariates with 90% *CI*s overlapping 0) and was used for inference.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
m45	**Hunter access + Closed moist forest + Deciduous forest + Northing**	**-207.5620**	**429.1240**	**0.0000**	**0.2827**	**0.1576**	**0.2436**
m48	Hunter access + Moderate moist forest + Closed moist forest + Deciduous forest + Northing	-207.1070	430.2140	1.0900	0.1639	0.1599	0.2415
m47	Hunter access + Moderate moist forest + Closed moist forest + Deciduous forest	-208.9191	431.8382	2.7142	0.0728	0.1452	0.2285
m44	Hunter access + Closed moist forest + Deciduous forest	-209.9252	431.8503	2.7263	0.0723	0.1379	0.2295
m46	Hunter access + Closed moist forest + Deciduous forest*Easting + Northing	-207.1518	432.3036	3.1796	0.0577	0.1563	0.2429
m43	Hunter access + Closed moist forest + Mesic meadow + Northing	-209.1583	432.3165	3.1925	0.0573	0.1366	0.2300
m54	Hunter access + Shrubfield + Mesic meadow + Northing	-209.4152	432.8305	3.7065	0.0443	0.1250	0.2134
m42	Hunter access + Closed moist forest + Mesic meadow	-210.5162	433.0323	3.9083	0.0401	0.1230	0.2208
m50	Hunter access + Closed moist forest + Open mesic forest + Shrubfield + Northing	-208.6679	433.3359	4.2119	0.0344	0.1442	0.2156
m51	Hunter access + Closed moist forest + Open mesic forest + Northing + Easting*Deciduous forest	-207.1204	434.2408	5.1168	0.0219	0.1557	0.2411

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S10. Top 10 generalized linear mixed effects models (GLMMs) describing female bear abundance in the North Cascades Ecosystem at the larger, Level 1 landscape scale (2.3k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Models in bold had substantial support ($\Delta_i < 2$ and do not include any covariates with 90% *CI*s overlapping 0) and were used in subsequent model averaging.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\mathrm{GLMM}(m)}$[a]	$R^2_{\mathrm{GLMM}(c)}$[b]
F44	**Shrubfield + Northing**	**-210.7167**	**429.4334**	**0.0000**	**0.2497**	**0.0507**	**0.0507**
F36	Stream density + Shrubfield + Northing	-209.8264	429.6527	0.2193	0.2238	0.0577	0.0577
F30	**Northing**	**-212.5920**	**431.1840**	**1.7506**	**0.1041**	**0.0359**	**0.0359**
F8	Shrubfield + Closed moist forest + Northing	-210.7083	431.4167	1.9832	0.0926	0.0507	0.0507
F35	Shrubfield + Open moist forest + Closed moist forest + Northing	-210.3727	432.7454	3.3119	0.0477	0.0531	0.0531
F14	Hunter access + Shrubfield + Northing	-210.4283	432.8567	3.4232	0.0451	0.0506	0.0506
F39	Hunter access + Shrubfield + Stream density + Northing	-209.4924	432.9848	3.5514	0.0423	0.0578	0.0578
F42	Hunter access + Northing	-211.7546	433.5093	4.0758	0.0325	0.0397	0.0397
F20	Hunter access + Shrubfield + Closed moist forest + Northing	-210.4196	434.8391	5.4057	0.0167	0.0507	0.0507
F37	Open moist forest + Closed moist forest + Northing	-212.4568	434.9136	5.4801	0.0161	0.0370	0.0370

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S11. Top 10 generalized linear mixed effects models (GLMMs) describing female bear abundance in the North Cascades Ecosystem at the smaller, Level 2 landscape scale (1.0k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Model in bold had substantial support ($\Delta_i < 2$ and does not include any covariates with 90% *CI*s overlapping 0) and was used for inference.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
f4	**Northing**	**-212.5920**	**431.1840**	**0.0000**	**0.2972**	**0.0359**	**0.0359**
f5	Open mesic forest + Northing	-212.1898	432.3796	1.1956	0.1634	0.0375	0.0375
f12	Road density + Northing	-212.5879	433.1757	1.9917	0.1098	0.0359	0.0359
f11	Hunter access + Northing	-211.7546	433.5093	2.3253	0.0929	0.0397	0.0397
f6	Open mesic forest*Northing	-212.0666	434.1331	2.9491	0.0680	0.0374	0.0374
f14	Road density + Open mesic forest + Northing	-212.1758	434.3516	3.1676	0.0610	0.0376	0.0376
f13	Hunter access + Open mesic forest + Northing	-211.3945	434.7889	3.6049	0.0490	0.0412	0.0412
f17	Hunter access*Closed mesic forest + Northing	-209.6610	435.3221	4.1381	0.0375	0.0479	0.0479
f1	Hunter access	-214.1246	436.2491	5.0651	0.0236	0.0211	0.0211
f19	Hunter access*Closed mesic forest + Open mesic forest + Northing	-209.1768	436.3535	5.1695	0.0224	0.0499	0.0499

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S12. Top 10 generalized linear mixed effects models (GLMMs) describing female-with-offspring bear abundance in the North Cascades Ecosystem at the larger, Level 1 landscape scale (2.3k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Models in bold had substantial support ($\Delta_i < 2$ and do not include any covariates with 90% *CI*s overlapping 0) and were used in subsequent model averaging.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\mathrm{GLMM}(m)}$[a]	$R^2_{\mathrm{GLMM}(c)}$[b]
FC3	**Hunter access + Moderate dry forest**	**-74.6699**	**159.3398**	**0.0000**	**0.3015**	**0.0702**	**0.3017**
FC2	Moderate dry forest	-77.0676	160.1353	0.7955	0.2026	0.0173	0.3052
FC7	**Null model (Intercept + Random effect)**	**-78.3298**	**160.6596**	**1.3198**	**0.1558**	**NA**	**0.3097**
FC4	Hunter access*Moderate dry forest	-73.5570	161.1140	1.7742	0.1242	0.1018	0.3091
FC1	Hunter access	-77.0222	162.0444	2.7046	0.0780	0.0236	0.3039
FC10	Hunter access*Closed mesic forest + Moderate dry forest	-73.3041	162.6082	3.2684	0.0588	0.0851	0.3068
FC8	Full model (Hunter access + Moderate dry forest + Closed mesic forest + Easting + Stream density + Hunter access*Closed mesic forest + Easting*Stream density)	-71.5635	165.1270	5.7872	0.0167	0.1078	0.2922
FC6	Road density*Closed mesic forest	-77.6358	165.2717	5.9319	0.0155	0.0125	0.3088
FC11	Stream density*Easting	-77.7147	165.4293	6.0895	0.0144	0.0112	0.3111
FC5	Hunter access*Closed mesic forest	-76.2274	166.4548	7.1150	0.0086	0.0327	0.2926

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)

Table S13. Top 10 generalized linear mixed effects models (GLMMs) describing female-with-offspring bear abundance in the North Cascades Ecosystem at the smaller, Level 2 landscape scale (1.0k-radius buffers). I used Akaike's Information Criteria (AIC) to determine the best models within the candidate set of models. Models are ranked according to Δ_i values. Table also reports corresponding maximized log-likelihood (log[*l*]), Akaike weights (w_i; relative likelihood of models in set), and estimated model fit (R^2_{GLMM}s). Models in bold had substantial support ($\Delta_i < 2$ and do not include any covariates with 90% *CI*s overlapping 0) and were used in subsequent model averaging.

Model #	Model variables	log[*l*]	AIC	Δ_i	w_i	$R^2_{\text{GLMM}(m)}$[a]	$R^2_{\text{GLMM}(c)}$[b]
fc4	**Closed dry forest + Shrubfield**	**-75.5710**	**159.1419**	**0.0000**	**0.2060**	**0.0405**	**0.2442**
fc2	Closed dry forest	-77.1278	160.2556	1.1137	0.1180	0.0172	0.3024
fc16	**Null model (Intercept + Random effect)**	**-78.3298**	**160.6596**	**1.5177**	**0.0964**	**NA**	**0.3097**
fc3	Shrubfield	-77.4411	160.8822	1.7403	0.0863	0.0105	0.2706
fc11	Hunter access + Closed dry forest + Shrubfield	-74.4877	160.9753	1.8334	0.0824	0.0641	0.2339
fc19	Hunter access*Shrubfield	-73.7595	161.5189	2.3770	0.0628	0.6676	0.7222
fc8	Hunter access + Closed dry forest	-75.7689	161.5378	2.3959	0.0622	0.0428	0.2998
fc1	Hunter access	-77.0222	162.0444	2.9025	0.0483	0.0236	0.3039
fc25	Closed dry forest + Shrubfield + Easting*Stream density	-74.0235	162.0471	2.9052	0.0482	0.0782	0.2646
fc10	Hunter access + Shrubfield	-76.3778	162.7557	3.6138	0.0338	0.0310	0.2649

[a] Marginal R^2 for GLMMs, representing variance explained by fixed effects (Nakagawa and Schielzeth 2013)

[b] Conditional R^2 for GLMMs, representing variance explained by entire model (Nakagawa and Schielzeth 2013)