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Spatially explicit carrying capacity estimates to inform species specific recovery objectives: Grizzly bear (*Ursus arctos*) recovery in the North Cascades

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ABSTRACT

The worldwide decline of large carnivores is concerning, particularly given the important roles they play in shaping ecosystems and conserving biodiversity. Estimating the capacity of an ecosystem to support a large carnivore population is essential for establishing reasonable and quantifiable recovery goals, determining how population recovery may rely on connectivity, and determining the feasibility of investing limited public resources toward recovery. We present a case study that synthesized advances in habitat selection and spatially-explicit individual-based population modeling, while integrating habitat data, human activities, demographic parameters and complex life histories to estimate grizzly bear carrying capacity in the North Cascades Ecosystem in Washington. Because access management plays such a critical role in wildlife conservation, we also quantified road influence on carrying capacity. Carrying capacity estimatesranged from 83 to 402 female grizzly bears. As expected, larger home ranges resulted in smaller populations and roads decreased habitat effectiveness by over 30%. Because carrying capacity was estimated with a static habitat map, the output is best interpreted as an index of habitat carrying capacity under current conditions. The mid-range scenario results of 139 females, or a total population of 278 bears, represented the most plausible scenario for this ecosystem. Grizzly bear distribution generally corresponded to areas with higher quality habitat and less road influence near the central region of the ecosystem. Our results reaffirm the North Cascades Ecosystem's capacity to support a robust grizzly bear population. Our approach, however, can assist managers anywhere ecosystem-specific information is limited. This approach may be useful to land and wildlife managers as they consider grizzly bear population recovery objectives and make important decisions relative to the conservation of wildlife populations worldwide.

1. Introduction

The worldwide decline of large carnivores is a great concern, particularly given the important roles carnivore species play in shaping ecosystems and conserving biodiversity (Hummel et al., 1991; Clark et al., 1999; Clark et al., 2005; Ray et al., 2005; Redford, 2005; Estes et al., 2011). A rare opportunity exists in the North Cascades of Washington and southern British Columbia to recover and conserve a full complement of native mammaliancarnivore species, from American martens to grizzly bears, and is made possible in large part by the presence of a sizeable, contiguous block of public lands (Gaines et al., 2000).The conservation and recovery of carnivores in the Pacific Northwest has received considerable attention in recent years. While the process has been slow for several species, progress has been made. For example, research and monitoring has documented the reappearance of wolverines (*Gulogulo*) and gray wolves (*Canis lupus*) in the North Cascades (Aubry et al., 2007; Lofroth and Krebs, 2007; WDFW, 2011). In addition, there has been considerable advancement in our understanding of Canada lynx (*Lynx canadensis*) habitat use and prey relationships (Maletzke et al., 2008; Koehler et al., 2008; Vanbianchi et al., 2017a, 2017b). However, there are important information gaps that need to be addressed for the recovery of grizzly

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bears (*Ursus arctos*) in the North Cascades(Gaines et al., 2001).

Information gaps relative to specific population dynamics and habitats are common to large carnivore recovery efforts and this missing information, such assite specific population size, habitat use, demography and the ability of an ecosystem to support wildlife populations, can hamper successful recovery efforts (McKelvey et al., 2000). It is challenging but crucial to understand the relationship between a carnivore population and the habitat necessary to sustain the population into the future (Wilcove et al., 1998; Bartz et al., 2006). The advantages of the carrying capacity metric, which measures the maximum number of individuals the landscape can sustain (Armstrong and Seddon, 2008), relative to conservation have been well documented (Bartz et al., 2006; Ayllón et al., 2012). Carrying capacity providesa quantifiable means of addressing this information gap that goes beyond basic habitat selection (Hobbs and Hanley, 1990; Heinrichs et al., 2017) and can create a foundation for recovery objectives.

The increased availability of remotely sensed data has allowed for an increase in the use of predictive habitat and connectivity models to inform wildlife species conservation (Proctor et al., 2012; Squires et al., 2013; Heinrichs et al., 2017). Methods to estimate the potential carrying capacity of wildlife populations within ecosystems have also advanced tremendously, allowing us to incorporate complex life histories. Here we present an approach to develop ecosystem-specific population information for a large carnivore to inform ecosystem-specific conservation and recovery targets in conservation planning. Our approach maybe more broadly applicable to situations where a target species has been functionally extirpated (limited ecosystem specific-information is available) and managers have a desire to determine if recovery is feasible (in other words, can the area support a self-sustaining population) and if so, what is a reasonable conservation target. Our primary goal was to present a case study where we synthesize these advances and integrate spatial habitat data, current human uses, and demographic parameters to address a question specific to conservation and recovery of grizzly bears: what is the potential carrying capacity for grizzly bears in the North Cascades Ecosystem?

Several studies have documented the influences that roads, highways, and human access have on grizzly bear populations and use of habitats. The effects of roads and human access on grizzly bears include misidentification and increased potential for poaching, collisions with vehicles, food conditioning as a result of bears gaining access to human foods, and displacement of bears from important habitats due to disturbance from vehicle traffic or habitat removal (Archibald et al., 1987; Mattson et al., 1987; McLellan and Shackleton, 1988; Kasworm and Manley, 1990; Mace and Waller, 1996, 1998; Mace et al., 1996, 1999; Gaines et al., 2003; Boulanger and Stenhouse, 2014). Because human access can have such detrimental effects on grizzly bear populations, access management is a critical consideration relative to conserving grizzly bear habitat and populations. An important additional objective of this assessment was to quantify the influence of roads on carrying capacity.

2. Methods

2.1. Case study area

Historical records indicate grizzly bears once occurred throughout the North Cascades of Washington (Almack et al., 1993; Gaines et al., 2000) and into British Columbia. The population has since declined due to intensive historical trapping, hunting, predator control, and habitat loss (USFWS, 1997, 2011) such that the grizzly bear was federally listed as a threatened species by the US Fish and Wildlife Service in 1975 (USFWS, 1993). Six recovery areas (ecosystems) have been officially designated within the lower 48 states encompassing approximately 2% of the historical range of the grizzly bear (USFWS, 1993, 1997). The North Cascades Ecosystem (NCE), officially designated in 1997 as a grizzly bear recovery area, encompasses approximately 25,000 km^2 of land under multiple jurisdictions, including North Cascades National Park, Okanogan-Wenatchee National Forest, Mt. Baker-Snoqualmie National Forest, Washington Department of Fish and Wildlife and Washington Department of Natural Resources (USFWS, 1997). In 1991 the grizzly bear in the North Cascades was determined to be warranted for Endangered status but the up-listing has not yet occurred due to other listing priorities (USFWS, 2011). Although a very small number of grizzly bears may still inhabit the NCE, the NCE does not meet the accepted definition of a population (two adult females or one adult female tracked through two litters) and has been functionally extirpated (USFWS, 2000; Gaines et al., press).

The North Cascades Ecosystem was evaluated in the early 1990's to determine whether the recovery area contained adequate habitat for recovery and viability of a grizzly bear population (Almack et al., 1993; Gaines et al., 1994; USFWS, 1997). The evaluation concluded that habitat was of sufficient quality and quantity to support a population of 200–400 bears based on the professional judgment of a science review team (Servheen et al., 1991).This potential population estimate was useful to managers in determining whether or not to pursue recovery in the North Cascades. However, since that time our understanding of grizzly bear habitat use and population ecology, as well as the influences of human developments such as roads and highways (Archibald et al., 1987; Mattson et al., 1987; McLellan and Shackleton, 1988; Kasworm and Manley, 1990; Mace and Waller, 1996, 1998; Mace et al., 1996, 1999; Boulanger and Stenhouse, 2014) has greatly improved. These improvements in combination with advancements in carrying capacity estimate methodology allow us to provide a more rigorous and spatially-explicit population estimate to inform recovery efforts.

The NCE is comprised of 42 Grizzly Bear Management Units (GBMUs) that are used to subdivide the area for monitoring and evaluation of cumulative effects (IGBC, 1998; Gaines et al., 2003). These analysis units were delineated to approximate an average female grizzly bear home range and include seasonal habitats. The GBMUs are used to track the effects of human activities, such as roads and motorized trails, on grizzly bear habitat by monitoring the amount of core area (areas > 500 m from and open road), open road density (open to motorized access), and total road density (open and restricted roads) (IGBC, 1998).

The North Cascades Ecosystem includes one of the largest contiguous blocks of federal land remaining in the lower 48 United States (US). The US portion of the NCE is approximately 25,000 km^2 and consists of a range of land uses from designated wilderness to multiple use resource lands to heavily populated urban areas (Fig. 1). The landscape varies from marine temperate lowland forests in the western valleys, to extensive lush subalpine forests and alpine meadows along the central spine of the North Cascades Mountains. The landscape then transitions rapidly from dry forests to dry shrub-steppe in lowland valleys on the eastern portion of the ecosystem. Elevation ranges from 25 m in the western valleys to peaks exceeding 3200 m. The central portion of the ecosystem is largely un-roaded (about 60%), comprised of national forest wilderness areas and the North Cascades National Park. Human development and high road densities occur mainly on the periphery of the ecosystem. Three highways bisect the NCE: North Cascades Highway (US 20) in the northern portion, Stevens Pass highway (US 2) in the central portion, and Interstate 90 along the southern boundary of the ecosystem.

The situation in British Columbia is parallel. The existing grizzly bear population is imperiled with fewer than 10 animals (MFLNRO, 2012), in an area that has high habitat capability but faces the complex question of how to simultaneously manage for conservation and human activities (Gaines et al., 2000; MFLNRO, 2004; MFLNRO, 2012). Although the landscape used by grizzly bears is transboundary, our modeling effort focused on the recovery area within the United States to address US Endangered Species Act requirements.

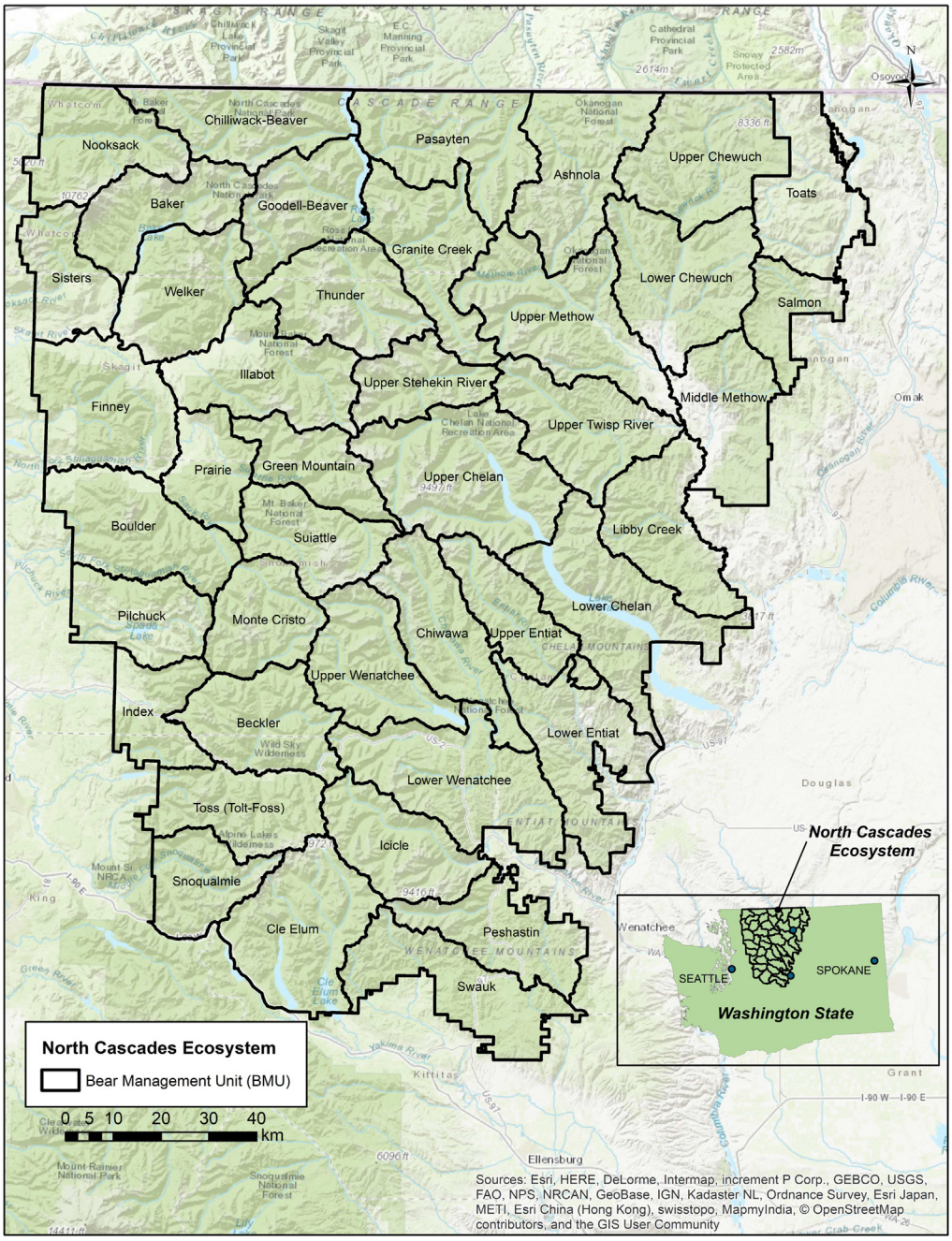

Fig. 1. The North Cascades Ecosystem and Grizzly Bear Management Units (GBMU) within Washington State, US.

2.2. Carrying capacity model

To estimate carrying capacity we developed a suite of spatially-explicit, individual-based population models using HexSim software (version 3.0.14, Schumaker, 2015) that integrated information on habitat selection, human activities and population dynamics. HexSim software provides a framework for implementing population simulation models that has been used to investigate potential population outcomes based on empirical information regarding habitat associations and demographic rates (Heinrichs et al., 2010; Spencer et al., 2011; Huber et al., 2014; Heinrichs et al., 2017).We used data from grizzly bear populations in the western US and Canada and expert knowledge from biologists on the North Cascades Grizzly Bear Science Team to populate HexSim parameters (resource selection, home range size, dispersal, survival, fecundity and effects of roads).

A large volume of information on grizzly bear population demographics and resource selection is available from other ecosystems. Because available data on grizzly bear demographics and habitat use can vary considerably, we created several different carrying capacity model scenarios. We developed multiple scenarios to assure key model variables were included and to address the uncertainty associated with modeling a potential population based on information collected for other existing populations. Additionally, we addressed uncertainty by conducting sensitivity analyses of key variables of survival and home range estimates (Lyons et al. in prep). Based on this preliminary analysis we determined a likely set of scenarios to examine carrying capacity of the NCE and the influence of roads. A complete description of all final model input is provided in Supplementary Material. Acknowledging that all models of populations and ecosystems are simplifications of complex, dynamic processes, we strived to develop

modeled simulations that included enough complexity to capture the important drivers of population dynamics while not overestimating our ability to detect the different biological processes (Lawler et al., 2011).

We used a female-only(single-sex) model structure because: 1) female grizzly bear demography, particularly survival, influences population trends more than males (Hovey and McLellan, 1996; Mace and Waller, 1996; Harris et al., 2007), 2) grizzly bear populations in the lower 48 and southern Canada, where they are not hunted, exhibit an average sex ratio of approximately 1:1 (see Table 9 in LeFranc et al., 1987), and 3) to reduce the complexity of the model. Modeled individuals were assigned to one of four age classes: cub (< 1 year), yearling (age 1 year), sub-adult (age 2–5 years) and adult (age ≥ 6 years).

2.3. HexSim input

2.3.1. HexSim

HexSim provides a flexible, spatially explicit population-modeling software package that simulates wildlife population dynamics and interactions (Schumaker, 2015). Simulations can range from simple and parsimonious to complex and biologically realistic (Huber et al., 2014). A sophisticated graphical user interface allows users to provide specific details about landscapes and habitat, life histories, disturbances, stressors and other information relative to the species of interest. Users create scenarios that include resource needs, life cycle definitions and a variety of life-history events, such as survival, reproduction, movement, and resource acquisition. Populations are composed of individuals with traits that describe age, resource availability, disturbance, and competition, among others, that can change probabilistically, or based on space and time. Combinations of trait values can also be used to stratify events such as survival, reproduction and movement (Schumaker, 2015). These combinations allow for greater flexibility in modeling the influence of resource quality on survival and reproduction and ultimately population outcomes.

2.3.2. Resource map and habitat effectiveness

HexSim represents spatial-data input as hexagonal grids. Each hexagon was assigned a habitat resource value based on the quality of habitat within the hexagon. Resource values and habitat quality classifications were calculated using the resource selection functions (RSF) developed by Proctor et al. (2015) for the Trans-Border study area that encompassed portions of eastern Washington, Idaho, Montana, and southeastern BC (hereafter referred to as the *Trans-Border RSF Model*). Although there can be challenges with extrapolating information from one landscape to another, the Trans-Border RSF Model provided a relatively straightforward and repeatable RSF. Our resource map was developed by applying the Proctor et al. (2015) RSF parameters of greenness, canopy openness, alpine vegetation, elevation and riparian vegetation and the associated coefficients to our ecosystem-specific spatial data layers (Table 1). This set of parameters included variables that provided a representation of the complex relationship between grizzly bear habitat selection motivated by food availability and quality while not addressing bear foods directly. This model did not include data on salmonids as distribution in the NCE is limited and bears rely primarily on vegetation. Greenness is an index of leafy green productivity (Mace et al., 1996; Nielsen et al., 2002), which in combination with canopy openness (Zager et al., 1983; Nielsen et al., 2004b) can be used to predict grizzly bear habitat use and is correlated with a diverse set of bear food resources (). Alpine and riparian habitats, including avalanche chutes, also provide diverse food resources for grizzly bears (McLellan and Hovey, 1995; Mace et al., 1996; McLellan and Hovey, 2001).

To develop the initial resource map and to classify habitat for HexSim we classified the RSF scores into four categories where hexagon resource values were a function of the area of good, moderate, and poor habitat within the hexagon, and good habitat areas provided four times the resource value of poor habitat areas (Class 1 = low quality habitat to Class 4 = best quality habitat). We removed non-habitat (i.e. ice, rock, large water bodies). A resource value was calculated for each hexagon by summing the habitat class values for all pixels within the hexagon (Fig. 2). This resource map functioned as our baseline scenario and did not include any adjustments to habitat effectiveness resulting from human influences or roads.

The Interagency Grizzly Bear Committee (IGBC) Access Task Force (1998) summarized studies that looked at the effects of roads on grizzly bear habitat use and found that the zone of influence that roads can have on grizzly bear habitat use may vary from < 100 m to 1000 m. As such, the IGBC Task Force recommended a distance of 500 m as a means for evaluating the effects of human activities, such as roads, on grizzly bear habitat. Thus, our study area was represented as a grid of 16.2 ha (500 m diameter) hexagons to account for the effects of roads.

We simulated populations with and without roads (Fig. 2) to quantify effects of roads on carrying capacity. One of the advantages of using a spatially explicit population model is the potential for integration of the resource selection and individual based population models that account for connectivity and population dynamics to present a more biologically realistic representation of grizzly bear distribution across the landscape (Heinrichs et al., 2017). We developed population simulation scenarios that incorporated adjustments to resource quality based on proximity to open roads. Within 250 m of an open road, resource values were decreased by 60%. Within 250-500 m of an open road, resource values were decreased by 40%. These adjustment values were determined based on an evaluation of data from other ecosystems (IGBC, 1998) and input from the North Cascades Science Team. We also considered how roads influence black bear resource selection in the NCE (Gaines et al., 2005), recognizing differences in how the bear species react to human activities (Kasworm and Manley, 1990). We did not attempt to model road influences based on traffic volumes, as that level of data was not available for the entire ecosystem.

Table 1
Parameters and associated coefficients in the Trans-Border RSF Model (Proctor et al., 2015) and data sources used to replicate parameters.

Parameter	Coefficient	Data sources for NCE
Greenness	14.597	2005 Landsat 5 Imagery (USGS) Greenness is a vegetation index derived from transformation of Landsat imagery that is associated with the reflectance characteristics of green vegetation. Correlates with a diverse set of bear food resources and found to be a good predictor of grizzly bear habitat use (as described in Proctor et al., 2015)
Canopy openness	0.014	Calculation = 1 - canopy cover of all live trees. Canopy cover was derived from Gradient Nearest Neighbor method (Ohmann and Gregory, 2002) which characterizes vegetation across landscapes.
Alpine vegetation	0.801	Ohmann et al. (2011) and Richardson (2013)
Elevation	0.00108	Digital Elevation Model
Riparian Vegetation	1.091	Krosby et al., 2014
Constant	−11.524	

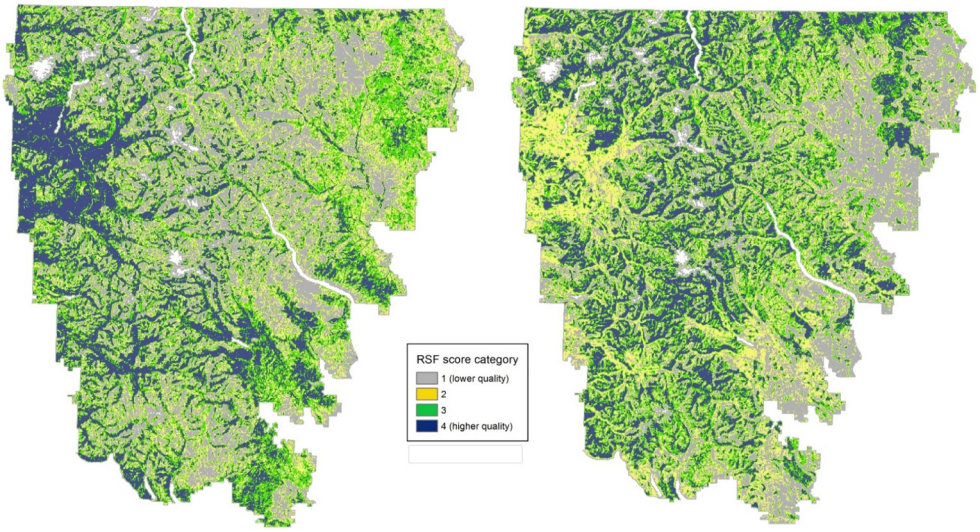

Fig. 2. Grizzly bear habitat in the NCE as derived by application of the Trans-Border RSF Model. Resultant RSF scores were divided into four classes to display relative habitat quality across the NCE where the best quality habitat was four times better than the lowest quality habitat (1/Gy = lower quality habitat to 4/blue = best quality habitat). The classes were used to score the hexagons used by HexSim. The map on the left depicts the habitat layer without considering the influence of roads while the map on the right depicts the habitat layer adjusted for the influence of roads. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3.3. Home range

Grizzly bears are long-lived mammals, generally living to be around 25 years old with relatively large space-use requirements (LeFranc et al., 1987). We selected annual female home-range parameter values based on a range of data available from studies of grizzly bear populations that would allow us to acknowledge the uncertainty of home range size in a recovering population and to examine the effects of changing home range sizes on carrying capacity estimates. A full description of the data is provided in Table S1 in Supplementary Material. We discarded the smallest and the two largest values to avoid giving too much influence to potential outliers. Additionally, members of the Science Team with experience in the other Grizzly Bear Recovery Areas indicated these values were not likely representative of the NCE. We selected the minimum, median and maximum from the remaining home range sizes. Thus, the home-range sizes used in the carrying capacity models were rounded to 100 km^2, 280 km^2 and 440 km^2. In our model, individual bears were classified as group members (female grizzly bears with established home ranges), or floaters (dispersing female grizzly bears without home ranges). In our model framework sub-adults could either establish a home range or float, but they would not be allowed to reproduce, as generally occurs in wild bear populations. Female bears were assigned to a resource quality class based on the sum of hexagon resource quality values within their home range. A home range in the high resource quality class had 40% of the home range in the high category. A home range in the Moderate resource quality class had 20% of the home range in the high category. Home ranges that did not meet the high or moderate classes defaulted to the low resource quality class.

2.3.4. Survival

Survival rates of females were incorporated into the model relative to age class (cubs, yearlings, sub adults, and adults) and resource quality (Table 2).Survival values for each age class were estimated based on data available from other grizzly bear populations. The HexSim framework is structured to evaluate the assumption that survival and reproduction may be higher in areas with better habitat. Providing for different rates of survival depending on habitat quality also allowed us to indirectly consider variations in availability of hyperphagia food items (McLellan, 2015), such as a variety of fruit bearing shrub species (i.e. *Vaccinium* spp., *Sambucus* spp., *Ribes* spp. *and Rubus* spp.). Although there were extensive data available in the literature relative to survival estimates for the four age classes used in our model simulations, no quantifiable information on the relationship between survivorship and habitat quality was available. As such we estimated female survival for cubs, yearlings, sub adults, and adults in low, moderate and high-quality habitat based on general published values (Supplemental Table S2.), and adjusted based on input from our Science Team. We determined the values for each life stage in the high habitat quality class as the highest value from our literature review, in the moderate habitat quality class as the mean value from the literature, and in the low habitat quality class as 25% less than the lowest value in the literature (Table 2).

Table 2
Annual female grizzly bear survival values for all combinations of age classes and resource quality classes used in population model. Values were determined for each life stage in the high habitat quality class as the highest value from our literature review, in the moderate habitat quality class as the mean value from the literature, and in the low habitat quality class as 25% less than the lowest value in the literature.

	Resource quality class*		
Age class	Low	Moderate	High
Cub	0.57	0.76	0.88
Yearlings	0.63	0.84	0.94
Sub-adult	0.65	0.86	0.93
Adult	0.71	0.94	0.98

* The resource quality class refers to bears whose home range meets the home range requirements as defined in HexSim. A home range in the high resource quality class had 40% of the home range in the high category. A home range in the Moderate resource quality class had 20% of the home range in the high category. Home ranges that did not meet the high or moderate classes defaulted to the low resource quality class.

2.3.5. Reproduction

Grizzly bears have one of the lowest reproductive rates among terrestrial mammals, resulting primarily from the late age of first reproduction (range 3–8 years old), small average litter size (range 1–4 cubs), and long interval between litters (generally 2–3 years)(Nowack and Paradiso, 1983; Schwartz et al., 2003a; Schwartz et al., 2003b). Given the above factors and considering natural mortality, it may take a single female grizzly bear 10 years to replace herself in a population (USFWS, 1993). Fecundity (m_x) in grizzly bears is defined as the average number of female young per adult female per year. In our model only adult females with home ranges that met the moderate or high habitat quality classification as defined in HexSim were allowed to reproduce. Similar to the survival estimates, we determined fecundity rates in the high habitat quality class as the highest value from our literature review (m_x = 0.386), in the moderate habitat quality class as the mean value from the literature (m_x = 0.302), and zero in the low habitat quality class (see Supplemental Table S3)·The age of first

reproduction was set at six years, the median of the reproductive range reported above.

As with the survival estimates, HexSim provides an opportunity to address the influence of habitat quality on reproduction. Although there were extensive data available in the literature relative to fecundity estimates for the four age classes used in our model simulations, there was limited quantifiable information on the relationship between reproduction and habitat quality. McLellan (2015) observed a density dependent relationship between huckleberry abundance, fecundity rates and subsequent population growth despite human disturbance. As such, the fecundity estimates used in our models were intended to portray that relationship where fecundity rates increase with better quality habitat.

2.3.6. Dispersal

Female grizzly bears do not generally disperse long distances, if at all, and tend to establish home ranges that are near or overlap their natal home range (McLellan and Hovey, 2001; Proctor et al., 2004; Støen et al., 2006). Although published information on female grizzly bear dispersal is limited, we found mean distances that ranged from 9.8 km (McLellan and Hovey, 2001) to 14.3 km (Proctor et al., 2004). We used the resulting mean dispersal value of 12.1 km. Only individuals that had failed to acquire adequate resources to establish a home range dispersed. Although limited data was available to inform the dispersal parameter, Marcot et al. (2015) found that HexSim population estimates had relatively low sensitivity to dispersal movement parameters compared to other model parameters they investigated. HexSim also includes an option to estimate the influence of resource availability on dispersal and movement. We considered areas on the landscape that were comprised of large bodies of water, ice or rock as impermeable to movement while areas of lower quality habitat were less permeable than higher quality habitat.

2.3.7. Scenarios

We evaluated the implications of different assumptions about home range size and road impacts using six model scenarios (Table 3). We evaluated all combinations of three different home range estimates (100 km^2, 280 km^2 and 440 km^2) and two habitat effectiveness estimates (with and without roads). These scenarios were identified by our Science Team as the most likely to bound the actual carrying capacity of the NCE (Table 3). The model simulations started with an initial population of 1000 individuals randomly placed across the landscape. Each model was run for a total of 150 years, including a 50 year "burn-in" period followed by a 100 year simulation period. The "burn-in" period allowed populations to approach equilibrium in the landscape and develop a representative distribution of age classes prior to the simulation period (Singleton, 2013). Because population simulations were based on a static habitat map these models do not represent population changes through time. The model outputs are best interpreted as indices of habitat carrying capacity under current conditions, given model assumptions.

We ran five population simulation replicates per scenario. Preliminary analysis indicated that five replicates were adequate to capture the variability in annual population size and distribution estimates produced by repeated simulations. We used simulation-duration mean number of individuals to represent the NCE carrying capacity metric. We summarized patterns of spatial distribution of the modeled populations across the NCE by calculating the annual mean number of female grizzly bears by GBMU. These simulated spatial distribution maps depicted areas where simulated grizzly bear would be expected to occupy the landscape (Fig. 3). All model output compilation, statistical analysis and mapping were conducted using R software (version 3.2.2, R Development Core Team, Vienna, Austria) and ArcGIS (version 10.3, ESRI, Inc.).

We validated the model by qualitatively comparing our population outcomes with published density estimates of grizzly bears from other ecosystems (See Supplemental Table S4). After removing the highest and lowest values, we used the high, median and low density estimates (number of bears per 1000 km^2) from other ecosystems and applied those to the NCE area to estimate the potential number of individuals in the grizzly bear population given different possible densities. Although these other ecosystems may not be at carrying capacity and comparisons may be conservative, density estimates provided a plausibility test of model outcomes.

3. Results

3.1. Carrying capacity estimates

The range of carrying capacity estimates varied widely depending on home range size and habitat effectiveness. Larger home range space requirements resulted in smaller overall populations regardless of the presence of roads. The baseline models without the impact of roads indicated the NCE would be capable of supporting a grizzly bear population that ranges from 126 to 586 female bears (Table 4). The range of model outcomes with road effects was comparatively lower and indicated the NCE is capable of supporting a grizzly bear population that ranges from a low of 83 females to a high of 402females (Table 4). Accounting for road displacement and subsequent reductions in habitat effectiveness resulted in a reduction in total female population estimates ranging from 31 to 34% (Table 4) as compared to the baseline scenarios.

3.2. Model calibration: comparing our carrying capacity population estimates to other ecosystems

Ignoring the highest and lowest density estimates from other ecosystems, the high density estimate for the North Cascades Ecosystem was 30 bears/1000 km^2, the mid-range density estimate was 17 bears/1000 km^2, and the low density estimate was 8 bears/1000 km^2 (Supplemental Table S4). Using those densities resulted in NCE population estimates of approximately 108–379 females, or 215–758 total

Table 3
Description of model scenarios developed to estimate carrying capacity for grizzly bears in the NCE. The number in the Scenario name refers to the home range size used in the model. All models used the same initial resource layer.

Scenario	Description	Parameters changed
100_Base	Baseline population settings. 100 km^2 home range size.	None
100_BR	Baseline model adjusted for potential displacement due to roads and subsequent reduction in resource value.	Resource values adjusted based on proximity to roads. Within 250 m resource values were decreased by 60%. Within 250-500 m, resource values were decreased by 40%.
280_Base	Baseline population settings. 280 km^2 home range size.	None
280_BR	Baseline model adjusted for potential displacement due to roads and subsequent reduction in resource value.	Resource values adjusted based on proximity to roads. Within 250 m resource values were decreased by 60%. Within 250-500 m, resource values were decreased by 40%.
440_Base	Baseline population settings. 440 km^2 home range size.	None
440_BR	Baseline model adjusted for potential displacement due to roads and subsequent reduction in resource value.	Resource values adjusted based on proximity to roads. Within 250 m resource values were decreased by 60%. Within 250–500 m, resource values were decreased by 40%.

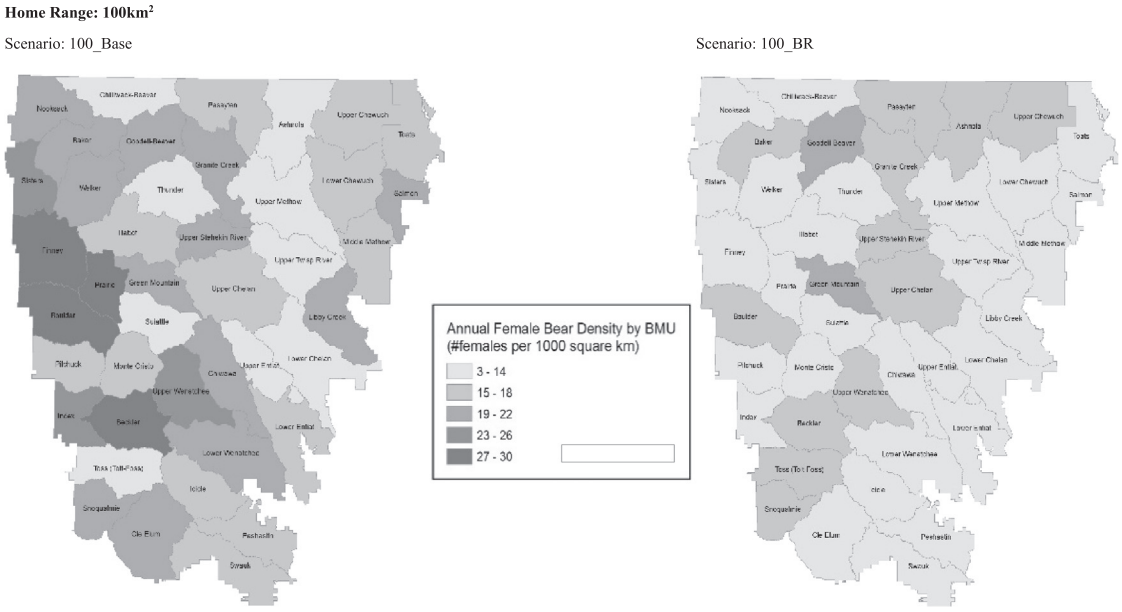

Fig. 3. Change in spatial distribution of mean annual female grizzly bear density (# per 1000 km^2) by GBMU in the North Cascades Ecosystem as a result of adding roads to the population model with three different home range sizes (100 km^2, 280 km^2, and 440 km^2). Color scheme and range of values was held constant within each home range to show the influence of roads on modeled density outcomes.

Fig. 3. (*continued*)

bears (males and females). These population estimates reflected the range of values reported in the literature we reviewed. Additionally, over 25 years ago, the Recovery Review Team (Servheen et al., 1991) estimated that the North Cascades Recovery area would likely support 200–400 bears. Our modeled carrying capacity estimates from all three home range sizes *with* roads, of 83–402 females, slightly exceeded the range estimated with data from other ecosystems.

3.3. Spatial patterns across the landscape

Spatial patterns of grizzly bear occupancy within the NCE were generally consistent across the model variants (Fig. 3). Predicted grizzly bear abundance followed the pattern of the RSF map for the baseline scenarios (i.e. more bears in areas of higher quality habitat) and then shifted considerably when the roads and resource score reductions were added to the model (Figs. 3 and 4). Beckler, Finney, and Prairie were the three GBMUs that generally had the highest number of individuals across scenarios and all had large amounts of high quality habitat mapped by the RSF model. However, including the influence of roads shifted the pattern to Goodell-Beaver, and Green Mountain with a variety of other GBMUs increasing in density. Suiattle, Thunder and Chilliwack-Beaver were the three GBMUs that generally had the lowest density of bears until we considered roads and the pattern shifted to Toats, Middle Methow and SwaukGBMUs. Suiattle, Thunder and Chilliwack-Beaver have a good deal of non-habitat in the form of steep rocky ridges and glaciers, potentially resulting in the relatively lower initial density estimates. The road related reduction in habitat quality was substantial in many of the BMUs.

Fig. 3. (*continued*)

Table 4
Simulation-duration mean number of female individuals for the total, group and floater populations in the NCE for six scenarios. The change in habitat effectiveness as a result of open roads was calculated as the percent change in total population size between scenarios (Base – BR). Group members were female grizzly bears in the total population with established home ranges and floaters were dispersing female grizzly bears in the total population without home ranges.

Scenario[a]	Total female population (# of female bears)	(SE)	Group member (# of female bears)	(SE)	Floater (# of female bears)	(SE)	Percent change in habitat effectiveness
100_Base	586	0.9	465	0.6	122	0.7	
100_BR	402	0.8	318	0.5	84	0.5	−31%
280_Base	208	0.6	165	0.4	44	0.4	
280_BR	139	0.5	110	0.3	29	0.3	−33%
440_Base	126	0.5	100	0.3	26	0.3	
440_BR	83	0.4	66	0.3	17	0.2	−34%

Base – baseline scenario with resource map not adjusted for road effects.
BR – baseline scenario with resource map adjusted for road effects.
[a] Scenarios are defined as follows. Additional information is located in Table 3.

4. Discussion

We have presented an approach that uses spatially-explicit population modeling tools, species-specific science expertise, and ecosystem habitat and human use data to inform the development of recovery objectives when the species of interest has been functionally extirpated from the recovery area and ecosystem-specific demography data are not available. This is a situation faced by many biologists as wide-ranging carnivores become increasingly isolated or are extirpated from the remaining wildlands (Clark et al., 2005; Estes et al., 2011). Establishing estimates of the capacity of an ecosystem to support a large carnivore population is important for 1) determining the feasibility of investing limited public resources to achieve population recovery and viability, 2) establishing reasonable and quantifiable recovery goals, 3) identifying areas within ecosystems that provide the highest quality habitats, and 4) determining the degree to which population recovery and long-term viability may rely on connectivity to other large-carnivore populations (e.g., metapopulations)(Proctor et al., 2012, 2015).Our complete suite of models was designed to acknowledge the inherent variability and uncertainty in modeling a population with extrapolated parameters and evaluated the effects of assumptions regarding home range size, resource quality associations, road effects, and human access.

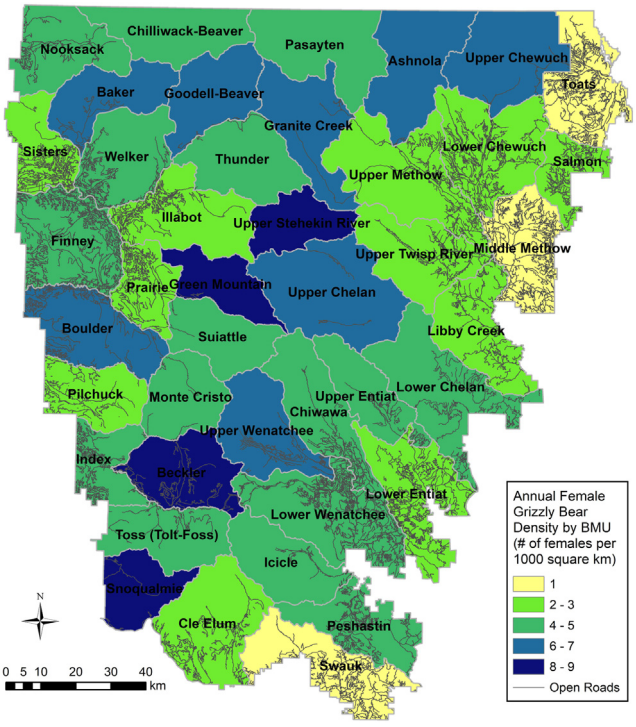

Fig. 4. Spatial distribution of mean female grizzly bear density (# per 1000 km^2) by GBMU for the most plausible carrying capacity scenario (280_BR) within the North Cascades Ecosystem. This scenario used a home range of 280 km^2 and included the habitat layer adjusted for the influence of open roads.

Our results varied greatly depending on the home range size and, as

expected, larger home ranges resulted in smaller carrying capacity estimates. Our modeled carrying capacity estimates from all three home range sizes with roads, of 83–402 females, slightly exceeded the range estimated from other ecosystems. We suggest the mid-range scenario (280_BR) results of 139 females, or a total population of 278 bears, represented the most plausible scenario and carrying capacity estimate for the NCE. When we compared Scenario 280_BR to other ecosystem population densities we found the estimated carrying capacity of 139 females fell well within the comparable range. Density estimates across the range of the grizzly bear varied widely. Although the density estimates from other study areas used different methods, thus affecting the value of direct comparison (Kendall et al., 2016), the range provided by the other estimates allowed us to validate our results.

Because the grizzly bear is a wide-ranging carnivore with substantial space needs, the ecosystems they inhabit can be quite diverse. A number of different factors can influence home range size, including population densities and habitat quality and food resources. In BC, coastal populations of grizzly bear that rely heavily on high-nutrient fisheries resources (MacHutchon et al., 1993) have home ranges that can be half the size of home ranges further inland (Ciarniello et al., 2003) and up to five times smaller than grizzly bears that are found in drier, interior landscapes (Ciarniello et al., 2003). In the Northern Continental Divide Ecosystem, Mace and Roberts (2011) found home ranges outside of Glacier National Park were twice the size of home ranges within the park. Similarly, Kendall et al. (2016) observed grizzly bears used the diverse habitats within their study area, centered on Glacier Park, disproportionately, and exhibited higher densities inside Glacier Park where habitat quality was greater and more secure (USFWS, 1993; Schwartz et al., 2006). Uncertainty and variability in resource quality and food availability was incorporated into our model of carrying capacity, in part by varying home range size. Scenario 280_BR incorporated the influence of roads and presented an average across the ecosystem, recognizing that we would expect grizzly bear home ranges on the east side of the ecosystem to be larger, while grizzly bear home ranges on the west side of the ecosystem would be relatively smaller, as observed in black bears in the NCE (Gaines et al., 2005) and grizzly bears in British Columbia (Gyug et al., 2004). The difference in home ranges across the NCE are not likely extreme because the NCE does not have typical coastal habitats due to human development along the Interstate 5 corridor along the western border of the ecosystem.

Individual based models provide an effective tool to evaluate effects of anthropogenic factors (Ayllón et al., 2012). The ecological reality of our model (Heinrichs et al., 2017) was improved through incorporation of road influences, habitat connectivity and demographic complexities. Simulation results corroborated the negative impacts of open roads on habitat effectiveness and ultimately carrying capacity for grizzly bears. Predicted grizzly bear abundance in the NCE followed the pattern of the RSF map for the baseline scenarios and then shifted considerably when the roads and resource score reductions were added to the model. We found the distribution of grizzly bears to follow an expected pattern corresponding to areas with higher quality habitat near the central region of the ecosystem where there was less influence from roads (Fig. 4). The North Continental Divide Ecosystem exhibited a similar pattern with substantially higher bear densities within Glacier National Parkas compared to outside the park. This pattern highlights the value of large protected core areas with secure habitat (Kendall et al., 2008). Reduced habitat effectiveness decreased carrying capacity estimates substantially, by over 30% in all cases. This value is obviously an artifact of model design but regardless, is a strong reflection of impacts of open roads. Habitat security, as related to open roads, has been shown to have substantial impacts on habitat selection and subsequently grizzly bear survival (Schwartz et al., 2010; Boulanger and Stenhouse, 2014) and population densities (Ciarniello et al., 2007). The modeling results also depict spatial distribution patterns and arrangements that not only highlight the highest quality GBMUs on the landscape, they may also be used to determine logical locations for prioritizing management actions when considered with other relevant information such as land ownership, jurisdiction, connectivity and other population dynamics. These tools provide transparent and scientifically based methods upon which to determine priorities.

The spatial distribution estimates along the international border may be somewhat inaccurate because our analysis area created a false barrier along the northern edge of our analysis area where bears could not disperse, and habitat values diminished. Although density has been shown to decline near edges of occupied habitat (Kendall et al., 2008), and was generally observed along the west, south and eastern borders of the NCE, the lower densities along the northern border with BC was likely an artifact of our model framework that could be ameliorated in future iterations.

Future model development and simulations maybe improved with additional information on fish distribution, specific hyperphagic food models, recreation trails and dynamic habitat changes, including effects of climate change. Although grizzly bears are considered carnivores, their diet is omnivorous, and in some areas are almost entirely herbivorous (Jacoby et al., 1999; Schwartz et al., 2003b). Grizzly bears will consume almost any food available including a variety of vegetation, living or dead mammals or fish and insects (Knight et al., 1988; Mattson et al., 1991a, 1991b; Schwartz et al., 2003b).However, there are a limited number of streams and rivers with productive salmon runs and the majority that do are located within the 500 m road buffer. The model structure did not currently account for spatial or temporal responses by bears, such as responding to roads by using fish runs on the side of rivers opposite roads or shifting activities to avoid daytime traffic. Also, any bias that may result from excluding this resource (with unknown use) in the models resulted in a more conservative estimate of bear density (i.e. more toward a minimum number of bears rather than an overestimation). Developments around hyperphagic food resource modeling have received increased attention as of late and observations in the Alberta, Cabinet-Yaak and Selkirk ecosystems suggest these resources, such as huckleberry patches, may have greater influence than initially understood (McLellan, 2015,Proctor et al., 2017).Of course, this RSF model does not model foods directly (Nielsen et al., 2010,) and actual population densities will depend on the association of the model predictor variables and spatial distribution of hyperphagia food supplies across the NCE (Schwartz et al., 2010; McLellan, 2015).Although our model accounted for variation in habitat quality, more explicit data on the quality and quantity of food resources would reduce some of the uncertainty in carrying capacity estimates.

Recreational trails, particularly motorized and high use trails, can also displace grizzly bear and reduce habitat effectiveness(Gunther, 1990; Kasworm and Manley, 1990; Mace and Waller, 1996). We did not include trails in our model because data on human use levels on trails was not available.

It is also important to note that these models are based on fixed assumptions regarding grizzly bear habitat selection and availability and population dynamics. We used a Landsat image from 2005 to replicate the TransBorder Model as closely as possible. However, the landscape has changed since then. For example, in the NCE wildfire has had a substantial impact on the landscape and continues to increase in severity. We examined data from the Monitoring Trends in Burn Severity Project (MTBS, 2014), which utilizes existing wildfire data from state and federal agencies in the western US to inventory and map fires $> 4\,km^2$ (1000 ac). The mean number of km^2 per year increased over the past three decades (1984–2014) from $148\,km^2$ per year (1985–1994), to $205\,km^2$ per year (1995–2004) to $250\,km^2$ per year (2005–2015). Depending on fire severity, recently burned areas are generally avoided by bears for the first few years after a fire while vegetation recovers. Once vegetation does recover, food resources, particularly huckleberry fields and other berry producing shrubs, generally become plentiful and these areas often become highly used by bears (Zager et al., 1983; Hamer and Herrero, 1987; Apps et al., 2004).Climate change is predicted to have significant impacts on the

landscape and result in higher fire intensity and frequency in the Pacific Northwest(McKenzie et al., 2004; Littell et al., 2010). Grizzly bears have been identified as having a low sensitivity to climate change because they are opportunistic, eat a diverse array of food resources, and are highly adaptable (Servheen and Cross, 2010; CCSD, 2013). Impacts to bears resolve more around potential for increased human-bear conflict, making adaptive management, education, proper food and garbage storage and human access management that much more important.

Further modeling efforts could explore small population growth or more complicated two-sex models. Continuing to explore strategies for grizzly bear recovery in the NCE might includean analysis of how the location of individual grizzly bears in the ecosystem influences the time it takes to reach carrying capacity. In the early stages of recovery this information could be useful in applying limited management resources. Additionally, single sex models have limitations for representing small population processes (including Allee effects and demographic stochasticity) that can contribute to small population extinction and metapopulation instability. As such creating a two-sex model would be a logical next step in order to use this model for simulating population recovery.

5. Conclusion

Recovering functionally extinct or very small wildlife populations presents a unique set of challenges. Using the proper set of tools to make the best use of limited resources is critical toward meeting those challenges. Our carrying capacity model provides one of those tools. We have provided a strategic assessment of the capability of the NCE to support a grizzly bear population. Our models rely heavily on a quality habitat layer and reliable estimates of grizzly bear survival, reproduction and home range. Through modeled simulations we estimated a range of carrying capacities of grizzly bear in the NCE that are substantially diminished by road influences. The information here may be useful to land and wildlife managers as they consider grizzly bear population recovery objectives, including number of bears, spatial distribution and the potential impacts of motorized routes in grizzly bear habitat. Our results reaffirm that the North Cascades Ecosystem has sufficient resources capable of supporting a robust grizzly bear population. These models and resultswill be valuable to managers as they make important decisions relative to the future of grizzly bears in the North Cascades and diminishing wildlife populations world-wide.

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Appendix A. Supplementary data

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