# Grizzly Bear Carrying Capacity in the North Cascades Ecosystem

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## INTRODUCTION AND OBJECTIVE

Historical records indicate grizzly bears (*Ursus arctos*) once occurred throughout the North Cascades of Washington (Almack et al. 1993, Gaines et al. 2000) and into British Columbia, but the population has since declined due to intensive historical trapping, hunting, predator control, and habitat loss (USFWS 1997, 2011). 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 Grizzly Bear Ecosystem (NCE), officially designated in 1997, encompasses approximately 9,777 square miles 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 2013 the grizzly bear in the North Cascades was determined to be warranted for Endangered status but the up-listing has not yet occurred (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. in press).

Habitat for grizzly bears in the North Cascades Ecosystem was evaluated in the early 1990's to determine whether the recovery area contained adequate habitat for recovery and maintenance of a grizzly bear population (Almack et al. 1993, Gaines et al. 1994, USFWS 1997). The evaluation concluded that a small number of grizzly bears persisted in the North Cascades and, based on the qualitative assessment of a science review team (Servheen et al. 1991), that habitat was of sufficient quality and quantity to support a population of 200-400 bears. Since that time understanding of grizzly bear habitat use and population ecology, and methods to estimate the potential carrying capacity of wildlife populations within ecosystems have advanced tremendously. Our primary goal was to synthesize these advances and integrate spatial habitat data and hypothetical demographic parameters to address two specific questions: 1) what is the potential carrying capacity for grizzly bears in the North Cascades Ecosystem? and 2) how do roads influence carrying capacity?

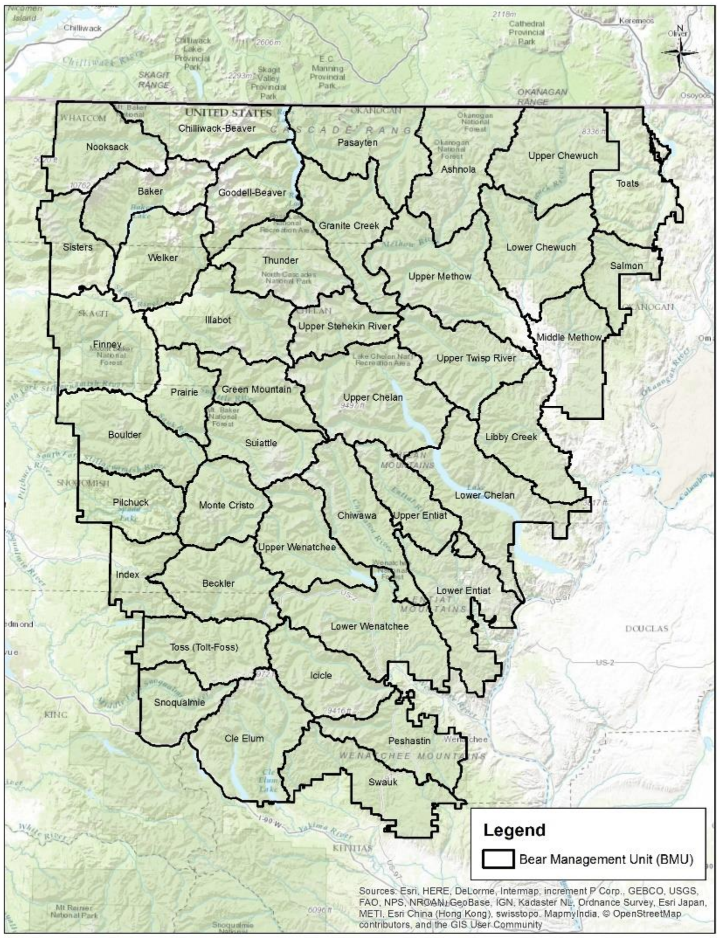
## ANALYSIS AREA

The US portion of the North Cascades Grizzly Bear Ecosystem is approximately 25,322 $km^2$ (9,777 $mi^2$) and consists of a range of land uses from designated wilderness to multiple use resource lands to heavily populated urban areas (Figure 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, then transitions rapidly to dry forests and dry, lowland valleys on the eastern portion of the ecosystem. Elevation ranges from 25 m in the western valleys, to peaks exceeding 3,200 m. Road densities vary across the landscape with a large expanse of predominantly roadless area in the central region of the ecosystem. The NCE is divided into Bear Management Units (BMUs) to identify assessment units for monitoring and evaluation of cumulative effects (IGBC 1998, Gaines et al. 2003). These analysis units approximate a female grizzly bear home range and are large enough to allow the assessment of seasonal habitats and the cumulative effects of human activities on these habitats. There are 42 BMUs in the NCE.

## METHODS

We used individual-based models to investigate potential population outcomes based on empirical information regarding habitat associations and demography (Heinrichs et al. 2010, Spencer et al. 2011, Huber at al. 2014). 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. We coordinated with the North Cascades Grizzly Bear Ecosystem Technical Team and Science Team (hereafter referred to collectively as "Science Team") to develop a modeling framework that provided the appropriate information and flexibility to address our two key questions: 1) what is the potential carrying capacity for grizzly bears in the North Cascades Ecosystem? and 2) how do roads influence carrying capacity? Because there are no data for grizzly bear habitat use or NCE specific population data, we used data from other grizzly bear populations in the western US and Canada and expert knowledge from biologists familiar with the NCE and grizzly bears to populate HexSim parameters. We obtained data from the literature on resource selection, home range size, dispersal, survival, fecundity and effects of roads that were verified with experts.

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




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 model scenarios. We used information obtained from the literature and feedback from the Science Team to develop multiple scenarios to assure key model variables were included to allow scenario evaluation specific to grizzly bears. We conducted a preliminary analysis to address the uncertainty associated with modeling a potential population based on information collected for other existing populations by conducting sensitivity analyses of key variables. The results of the sensitivity analysis will be presented elsewhere (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 model input is provided in Appendix S1. Because female survival influences population trend more than male survival (Hovey and McLellan 1996, Mace and Waller 1996, Harris et al. 2007), and to reduce the complexity of the model, we used a female-only, single-sex model structure.

**HexSim Input**

*Hexagons*

The landscape was represented as a grid of 16.2 ha (500m diameter) hexagons. We chose this hexagon size to capture effects of open roads because 500m has been identified as the distance that seems to have the most impact on bears (disturbance from roads and high-use trails). The IGBC Task Force (1998) summarized a selection of 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 can vary from <100m to 1000m and recommended a distance of 500m as a means for evaluating the effects of human activities, such as roads, on grizzly bear habitat.

*Spatial Data*

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 a resource selection function (RSF) approach developed by Proctor et al. (2015) for the Trans-Border study area that encompassed portions of eastern Washington, Idaho, Montana, eastern BC and Alberta (hereafter referred to as the *Trans-Border RSF Model*). Our resource map was developed by applying the Proctor et al. (2015) RSF parameters and coefficients with local spatial data layers.

The Trans-Border RSF Model is a relatively simple and repeatable RSF. However, there can be challenges with extrapolating information from one landscape to another, thus we felt it was necessary to evaluate the application of the Trans-Border RSF model to the NCE. A two-step evaluation was completed: 1) an analysis of mean annual and summer precipitation rates in the NCE compared to the Trans-Border ecosystem (as modeled by Hamann et al. 2013) and 2) a review of the extrapolated RSF map by local experts and the Science Team. Although the Trans-Border RSF Model was developed in an interior ecosystem that did not include coastal habitats, and may be a better representation of the eastern half of the North Cascades Ecosystem, based on our evaluation, the Science Team concurred that the extrapolated RSF map was a reasonable approximation of habitat conditions for grizzly bears in the NCE.

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)<br>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 & 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 | |

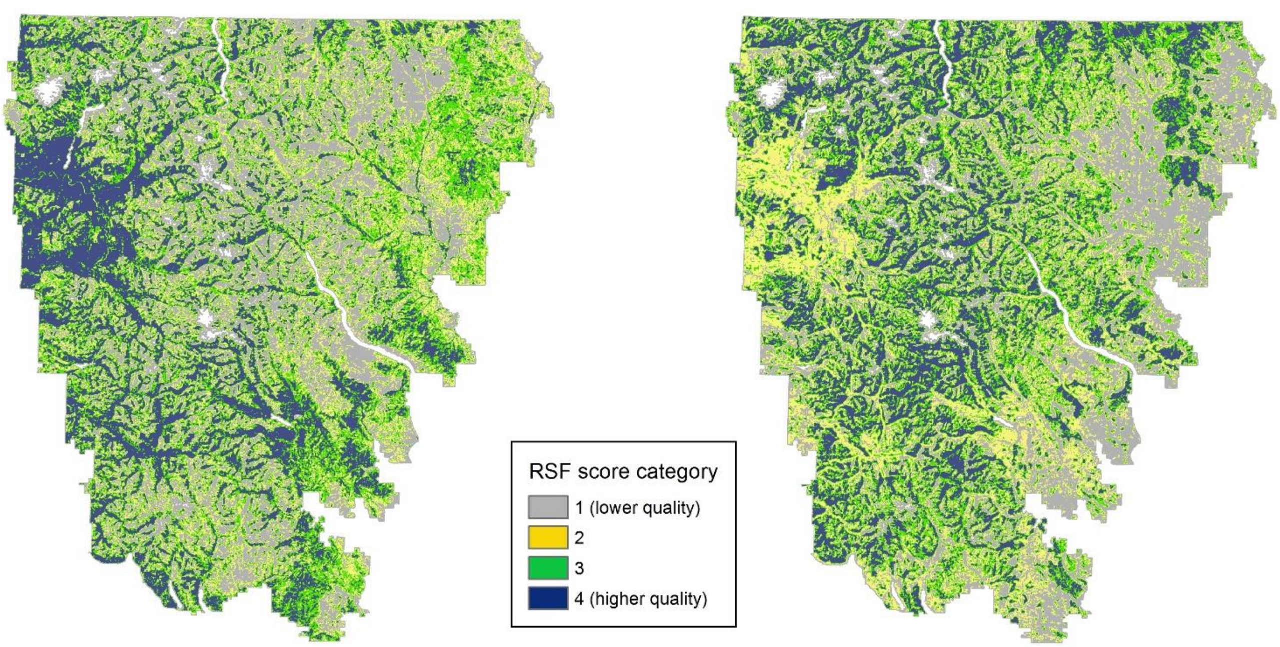
To develop the initial resource map and to classify habitat for HexSim we classified the RSF scores into four equal area categories (1 = low quality habitat to 4 = best quality habitat) and removed non-habitat (i.e. ice, rock, large water bodies). Hexagons were scored by calculating the focal sum of pixel values (at 250m radius). This initial resource map functioned as our baseline scenario (i.e. no adjustments to habitat effectiveness as a result of human influences/roads).

*Habitat Effectiveness*

Several studies have documented the influences that roads, highways, and human access have on grizzly bear populations and use of habitats (Boulanger and Stenhouse 2014, Archibald et al. 1987, Kasworm and Manley 1990, Mace and Waller 1996, 1998; Mace et al. 1996, 1999; Mattson et al. 1987, McLellan and Shackleton 1988, 1989). The effects of roads and human access on grizzly bears include 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 (see Gaines et al. 2003 for review). We structured the population model to examine how roads may influence habitat effectiveness for grizzly bears and carrying capacity of grizzly bears in the NCE. For this modeling framework we assumed grizzly bears may be displaced from habitats within 500m of an open road. We developed population simulation scenarios that incorporated adjustments to resource quality based on proximity to open roads. Within 250 meters of an open road, resource values were decreased by 60%. Within 250-500m of an open road, resource values were decreased by 40%. These values were determined based on an evaluation of data from other ecosystems (IGBC Task Force 1998) and habitat effectiveness changes displayed by black bears in the NCE (Gaines et al. 2005). We did not attempt to model road influences based on traffic volumes, as that level of data was not available for the entire ecosystem.

Figure 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 based on equal area quartiles to display relative habitat quality across the NCE (1/gray = lower quality habitat to 4/blue = best quality habitat) and to score the hexagons used by HexSim. Figure 2a. The habitat layer without considering the influence of roads. Figure 2b. The habitat layer adjusted for the influence of roads.

2a) 2b)




*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). Grizzly bear home range data for the NCE was not available. To account for uncertainty in the NCE population we selected female home-range parameter values based on data available from other grizzly bear populations as reviewed by the Science Team. As recommended by the Science Team, we discarded the largest and smallest values, as they were not likely representative of the NCE, and selected the minimum, median and maximum from the remaining home range sizes. Thus, the home-range sizes used in the carrying capacity models were 100km$^2$, 280km$^2$ and 440km$^2$. 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 establish a home range (or float), but they would not be allowed to reproduce, as generally occurs in wild bear populations.

*Survival*

Survival rates of females were incorporated into the model relative to age class and resource quality. Survival values for each age class were estimated based on data available from other grizzly bear populations as reviewed by the Science Team. Although there were extensive data available in the literature relative to survival estimates for the four age classes, (cub, yearling, subadult and adult), no quantifiable information on the relationship between survivorship and habitat quality was available. As such we estimated female survival for cubs, yearlings, subadults, and adults in low, moderate and high quality habitat based on general published values. 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.

*Reproduction*

Grizzly bears have one of the slowest 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) (Nowak 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 in grizzly bears is defined as the average number of young per adult female per year. Fecundity values were estimated based on data available from other grizzly bear populations as reviewed by the Science Team. In our model only adult females with home ranges that met the moderate or high habitat quality class 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 (0.386), in the moderate habitat quality class as the mean value from the literature (0.302), and zero in the low habitat quality class. The age of first reproduction was set at six years.

*Dispersal*

Movement parameters for dispersing individuals were based on data from other grizzly bear populations. Female grizzly bears do not generally disperse long distances, and tend to establish home ranges that are near or overlap their natal home range (Proctor et al. 2002). 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 value of 12.05 km. Only individuals that had failed to acquire adequate resources to establish a home range dispersed. Marcot et al. (2015) found that HexSim population estimates had relatively low sensitivity to dispersal movement parameters compared to other model parameters they investigated.

*Scenarios*

Our preliminary analysis resulted in a suite of six different model scenarios that we believed were the most plausible candidates and likely bound the actual carrying capacity of the NCE (Table 3). Each model was run for a total of 150 years, including a 50 year "burn-in" period followed by a 100 year simulation period. This modeling exercise assumed we were estimating carrying capacity for an existing population (rather than a small recovering population). The model simulations started with 1000 individuals randomly placed across the landscape. 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). Modeled individuals were assigned to four age classes: cub (<1 year), yearling (age 1 year), sub-adult (age 2-5 years) and adult (age >6 years). 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.

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 250m resource values were decreased by 60%. Within 250-500m, 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 250m resource values were decreased by 60%. Within 250-500m, 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 250m resource values were decreased by 60%. Within 250-500m, resource values were decreased by 40%. |

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 BMU. 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.).

To calibrate our model results we compared our population outcomes with density estimates for other ecosystems. 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. Although these other ecosystems may not be a carrying capacity, a comparison of density estimates provided a plausibility test of model outcomes.

## RESULTS and DISCUSSION

The range of model outcomes with road effects indicates the NCE is capable of supporting a grizzly bear population that ranges from a low of 83 females to a high of 402 females (Table 4). Results varied greatly depending on the home range size and, as expected, larger home ranges resulted in smaller carrying capacity estimates. The HexSim modeling framework also allowed us to demonstrate the negative impact that open roads can have on habitat effectiveness, and ultimately carrying capacity for grizzly bears. Accounting for road displacement and subsequent reductions in habitat effectiveness resulted in a reduction in total female population estimates ranging from 31-34% (Table 4) as compared to the baseline scenarios.

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% |

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

*Model Calibration: Is our model reflecting reality?*

HexSim provided a range of potential grizzly bear carrying capacity values for the NCE. To examine if these estimates were reasonable we compared our results to density estimates from other ecosystems (Appendix S1: Table S4). The density estimates in Table S4. came from a variety of ecosystems, some that may not be at carrying capacity. As such these population estimate comparisons may be conservative. Ignoring the highest and lowest values in Table S4, we used the next high/low values as the high estimate (30 bears/1000km$^2$) and low estimate (8 bears/1000km$^2$). The mid-range estimate for the NCE was equal to the median value (17 bears/1000km$^2$) (Table S4). Applying these density estimates to the area of the NCE provided population estimates. Based on this comparison, approximately 215 - 758 total bears (males and females) or 108 - 379 females reflect the range of values reported in the literature we reviewed. Additionally, the Recovery Review Team (Servheen et al 1991) estimated that the North Cascades Recovery area would likely support 200 - 400 bears. Our calculated estimates from all three home range sizes *with* roads, of 83 - 402 females, slightly exceeded the range estimated from other ecosystems.

Spatial patterns of grizzly bear occupancy within the NCE were generally consistent across the model variants (Figure 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. Beckler, Finney, and Prairie were the three BMUs that generally had the highest number of individuals across scenarios. This seemed reasonable given the 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 BMUs increasing in density. Suiattle, Thunder and Chilliwack-Beaver were the three BMUs that generally had the lowest density of bears until we considered roads and the pattern shifted to Toats, Middle Methow and Swauk BMUs. 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. When we examined the spatial pattern for the most plausible mid-range carrying capacity model, 280_BR, we found the distribution of grizzly bears to follow an expected pattern corresponding to areas with higher quality habitat and less influence from roads (Figure 4). 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. This was an artifact of our model framework that could be ameliorated in future iterations.

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, insects, and human garbage (Knight et al. 1988; Mattson et al. 1991a,b; Schwartz et al. 2003b). Anadromous fish are recognized as an important food source for grizzly bear that have access to such resources. We considered including a category of habitat for grizzly bears that would reflect this food resource. However, we did not carry it through at this time. A preliminary analysis revealed this to be a very complex topic. A substantial portion of fish bearing streams and rivers in the NCE were located within the 500m road buffer so improvements to resource quality would be discounted by road displacement in the model structure. This 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). This topic could be explored in future iterations of this model, though empirical data for grizzly bear use of anadromous fish is still missing for the NCE.

Recreational trails, particularly motorized and high use trails, can also displace grizzly bear and reduce habitat effectiveness. In the North Continental Divide Ecosystem, Mace and Waller (1996) found bears used habitats less than expected within 813-1,129 meters of non-motorized trails, while Kasworm and Manley (1990) found bears in the Cabinet-Yaak Ecosystem used areas within 122 meters of trails less than expected. In Yellowstone, grizzly bears avoided areas near occupied backcountry campsites and used areas that were near trails and more than 500 m from forest cover far less than expected (Gunther 1990). We did not include trails at this time but this is an area that deserves further attention in future iterations.

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 in order to replicate the TransBorder Model as closely as possible. However, we recognize that the landscape has changed since that time and spatial patterns would adjust to a degree. Additionally, ecological relationships are dynamic, particularly with regard to changes in habitat resulting from disturbances such as wildfire and climate change. 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 $km^2$ (1000ac). 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, however, following a fire, food resources generally become plentiful and these areas often become highly used habitats by bears (Zager et al. 1983, Hamer and Herrero 1987, Apps et al. 2004). We must recognize that disturbances will alter this landscape and adaptive management will be essential for effective wildlife conservation.

Through modeled simulations we have estimated the carrying capacity of grizzly bear in the NCE, which can inform efforts to restore grizzly bear to this ecosystem. Further modeling efforts could begin to explore strategies for grizzly bear restoration, including where to best locate grizzly bear in the ecosystem in the early stages of recovery and how long it will take the population to reach carrying capacity. Single sex models have limitations for representing small population processes (including Allee effects and demographic stochasticity) that can contribute to small population extinction and meta-population instability. As such creating a two-sex model would be a logical next step in order to use this model for simulating population recovery.

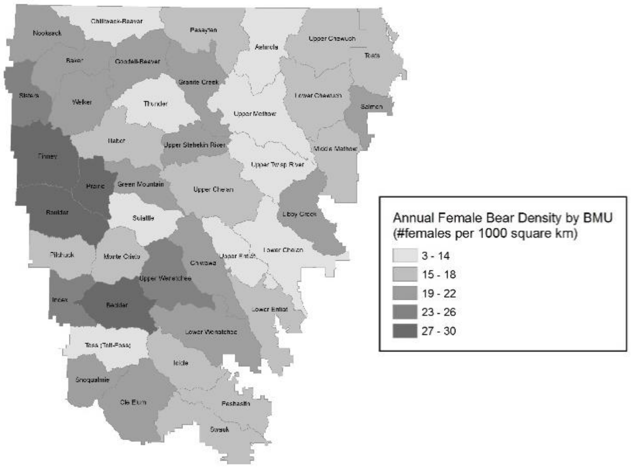
**CONCLUSION**

Our complete suite of models was designed to acknowledge the inherent variability and uncertainty in modeling a population with extrapolated parameters. We feel confident that we have presented a range of values that contains the true value. We suggest the mid-range home range (280_BR) results present the most plausible scenario for this ecosystem. 280_BR incorporates the influence of roads and presents a reasonable 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). Accordingly, values from 280_BR represent our best estimate of the likely carrying capacity of the NCE. When we compare 280_BR to other ecosystem population densities we find the estimated carrying capacity of 139 females falls well within the comparable range. This would translate into a total population (female and male) estimate of approximately 278 grizzly bears.

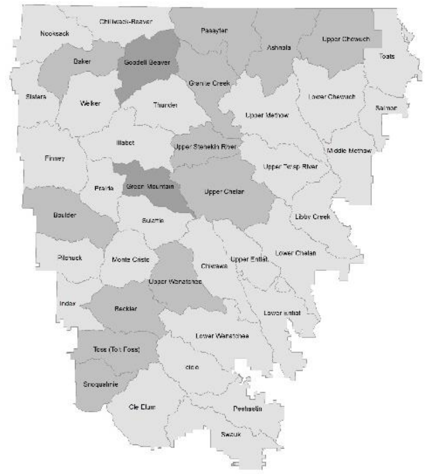
Figure 3. Change in spatial distribution of mean annual female grizzly bear density (# per 1000km2) by BMU in the North Cascades Ecosystem as a result of adding roads to the population model with three different home range sizes (100km$^2$, 280km$^2$, and 440 km$^2$). Color scheme and range of values was held constant within each home range to show the influence of roads on modeled density outcomes.

**Home Range: 100km$^2$**

Scenario: 100_Base

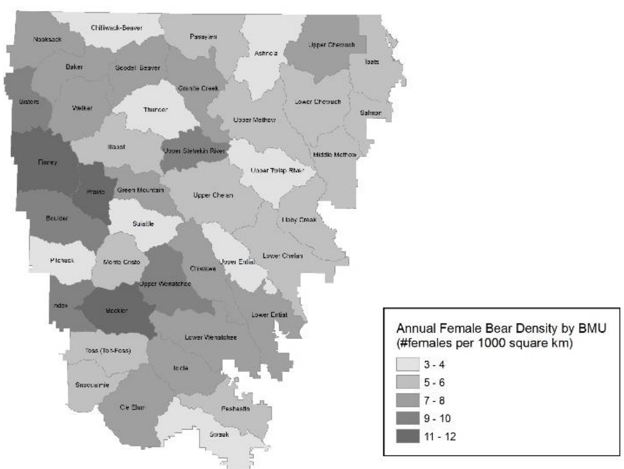



Scenario: 100_BR

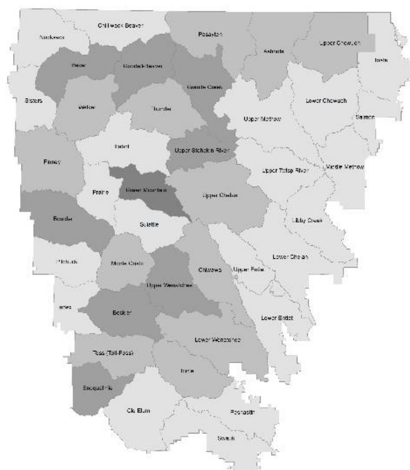


Home Range: 280km$^2$

Scenario: 280_Base

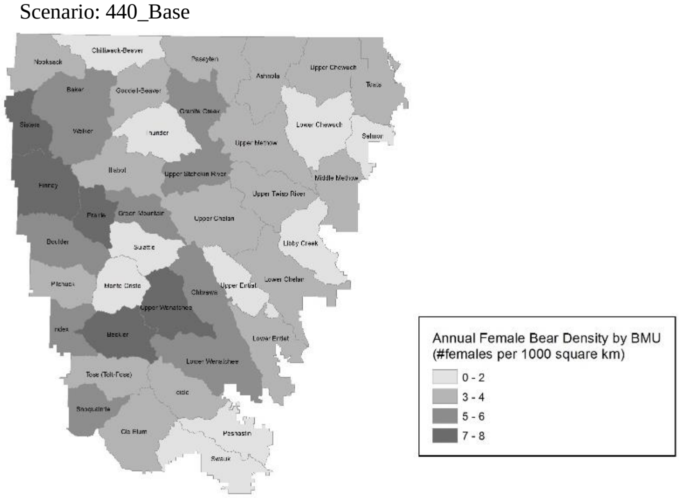



Scenario: 280_BR



Home Range: 440 km$^2$

Scenario: 440_Base




Scenario: 440_BR

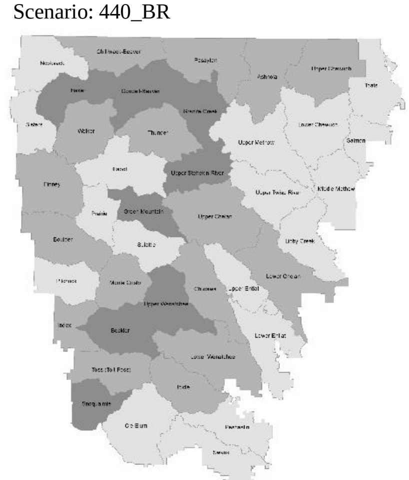
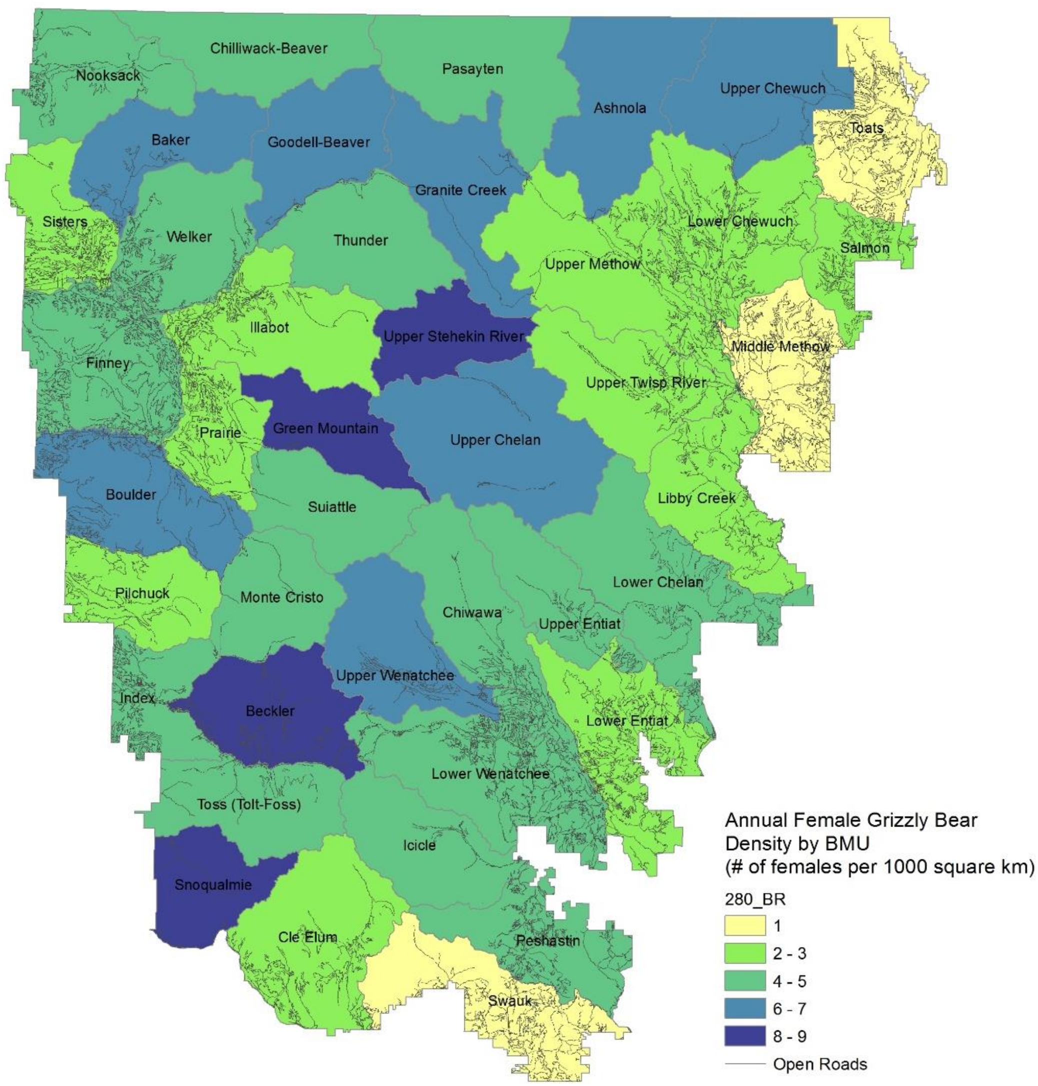


Figure 4. Spatial distribution of female grizzly bear for the most plausible carrying capacity scenario (280_BR) within the NCE. This scenario used a home range of 280km$^2$ and included the habitat layer adjusted for the influence of open roads.



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Appendix S1. Literature sources and associated data values for demographic parameters used in the development of the NCE grizzly bear carrying capacity models.

Table S1. Sources used to determine home range sizes for NCE grizzly bear carrying capacity models. Home range sizes presented in the literature have been calculated with a variety of methods and estimators. We used a range of values (reviewed by the Science Team) to capture some of the variability in published home range estimates.

| Location | Home Range Area ($km^2$) | Source |
|---|---|---|
| Revelstoke, BC | 89 | Woods et al. (1997)* |
| North Continental Divide Ecosystem | 108 | Mace and Roberts (2011) |
| Mission Mtns, MT | 133 | Servheen and Lee (1979)* |
| Parsnip, BC | 173 | Ciarnello et al. (2001) |
| North Continental Divide Ecosystem | 213 | Mace and Roberts (2011) |
| Central Canadian Rocky Mtns | 223 | Gibeau et al. (2001) |
| East Front MT | 226 | Schallenberger and Jonkel (1980)* |
| North Fork Flathead | 253 | McLellan and Hovey (2001) |
| Yellowstone | 281 | Blanchard and Knight (1991) |
| Jasper, AB | 331 | Russell et al. (1979)* |
| West Central Alberta | 364 | Nagy et al. (1988)* |
| Selkirk, ID | 402 | Almack (1985)* |
| Cabinet-Yaak Ecosystem | 412 | Kasworm et al. (2009) |
| Cabinet-Yaak Ecosystem | 433 | Kasworm pers. comm 16 March 2016 |
| Central Rockies Ecosystem, AB | 520 | Stevens, S. (2002) in Nielson et al. (2004) |
| East Front MT | 642 | Aune (1994) |
| * in McLoughlin et al. (1999) | | |

Table S2. Sources used to determine survival estimates for NCE grizzly bear carrying capacity models.

| Location | Cub | Yearlings | SubAdult | Adult | Source |
|---|---|---|---|---|---|
| Alberta | 0.55 | na | 0.88 | 0.96 | Boulanger and Stenhouse (2014) |
| Alberta | 0.78 | 0.78 | Na | 0.93 | Wielgus and Bunnell (1994) |
| Banff | 0.79 | 0.91 | 0.92 | 0.96 | Garshelis et al. (2005) |
| Cabinet-Yaak Ecosystem | 0.68 | 0.88 | 0.77 | 0.93 | Wakinnen and Kasworm (2004) |
| Cabinet-Yaak Ecosystem | 0.63 | 0.92 | 0.81 | 0.95 | Kasworm et al. (2015) |
| Flathead, BC | 0.87 | 0.94 | 0.93 | 0.95 | Hovey and McLellan (1996) |
| North Continental Divide Ecosystem | 0.61 | 0.68 | 0.85 | 0.95 | Mace et al. (2012) |
| SE BC | 0.82 | 0.88 | 0.93 | 0.93 | McLellan (1989) |
| Selkirk Ecosystem | 0.88 | 0.78 | 0.90 | 0.94 | Wakinnen and Kasworm (2004) |
| Summary of 12 other studies | na | na | 0.92 | 0.93 | McLellan et al. (2000) |
| Swan Mtns, MT | 0.79 | 0.90 | 0.83 | 0.90 | Mace and Waller 1998 |
| Yellowstone | 0.84 | 0.84 | 0.80 | 0.94 | Eberhardt 1995 |
| Yellowstone | na | na | 0.89 | 0.92 | Eberhardt et al. (1994) |
| Montana | 0.85 | 0.85 | 0.92 | 0.97 | Aune and Kasworm (1989) |

Table S3. Sources used to determine fecundity estimates for NCE grizzly bear carrying capacity models.

| Location | Fecundity rate | Source |
|---|---|---|
| SE BC | 0.246 | McLellan (1989) |
| Swan Mtns, MT | 0.261 | Mace and Waller (1998) |
| Alberta | 0.272 | Boulanger and Stenhouse (2014) |
| Cabinet-Yaak Ecosystem | 0.287 | Wakkinen and Kasworm (2004) |
| Selkirk Ecosystem | 0.288 | Wakkinen and Kasworm (2004) |
| Yellowstone | 0.312 | Schwartz and White (2008) |
| North Continental Divide Ecosystem | 0.367 | Mace et al. (2012) |
| Cabinet-Yaak Ecosystem | 0.386 | Kasworm et al. (2015) |

Table S4. Grizzly bear population density estimates from other ecosystems used in comparison with carrying capacity estimates for NCE.

| Location | Date of estimate | Density (bears/1000 $km^2$) | Density (bears/$km^2$) | Source |
|---|---|---|---|---|
| Jasper NP, Alberta | 1990 | 12 | 0.012 | Schwartz et al. (2003) |
| SW Alberta (Waterton) | 2000 | 15 | 0.015 | |
| N BC, Prophet River | 2001 | 21 | 0.021 | |
| SE BC (Selkirks) | 2000 | 27 | 0.027 | |
| Flathead River, MT | 1989 | 80 | 0.080 | |
| | | | | |
| Yellowstone NP | 2015 | 17 | 0.017 | IGBST (2015) and YNP (2015) |
| Greater Yellowstone Ecosystem | 2015 | 13 | 0.013 | |
| | | | | |
| North Continental Divide Ecosystem | 2013 | 9 | 0.009 | USFWS (2013) |
| | | | | |
| Alberta Yellowhead & South Jasper | 2015 | | 0.008 | Stenhouse et al. (2015) |
| | | | | |
| Glacier NP | 2000 | 30 | 0.030 | Kendall et al. (2008) |
| | | | | |
| Cabinet-Yaak Ecosystem | 2015 | 5 | 0.005 | Kendall et al. (2016) |
| | | | | |
| Yahk | 2007 | 8 | 0.008 | Proctor et al. (2007) |
| South Purcell | | 13 | 0.013 | |
| Central Purcell | | 19 | 0.019 | |
| South Selkirk | | 14 | 0.014 | |
| | | | | |
| *NCE (high estimate)* | | *30* | *0.030* | *NCE derived estimates* |
| *NCE (mid estimate)* | | *17* | *0.013* | |
| *NCE (low estimate)* | | *8* | *0.008* | |