Using Anthropogenic Parameters at Multiple Scales to Inform Conservation and Management of a Large Carnivore

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ABSTRACT

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Human influence on the environment is becoming increasingly pervasive across the globe, and can drastically impact ecological patterns and processes. For many terrestrial wildlife species, human influence can fragment critical habitat, increase mortality, and threaten habitat connectivity and ultimately the persistence of wildlife populations. This dissertation aims to use multiple conservation ecology methods and tools to test the impact of human influence on the population dynamics of a large carnivore in a human-dominated landscape.

To assess the impact of human activity on carnivore ecology, a series of empirical studies were conducted on a small population of American black bear (*Ursus americanus)* in the Western Great Basin, USA. A long-term dataset including geographic locations of animal habitat choices as well as mortality locations were used in multiple statistical models that tested the response of black bears to human activity. These analyses were conducted at multiple spatial and temporal resolutions to reveal nuances potentially overlooked if analyses were limited to a single resolution.

Individual studies, presented as dissertation chapters, examine the relationships between human activity and carnivore ecology. Collectively, the results of these studies find black bear ecology to be highly sensitive to the magnitude and spatial composition of human activity in the Lake Tahoe Basin, observable at both coarse and fine spatial resolutions. The results presented in this study on the influence of human activity on large carnivore population dynamics allow for a more thorough understanding of the various ways common conservation ecology methods and tools can be used to evaluate human-wildlife relationships.

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DEDICATION

I dedicate this work to my grandfathers E. Milton Wynn and Rev. George Grant Jr. who passed away during my years in graduate school. Their unconditional support of my passions has and continues to drive me personally and professionally.

CHAPTER ONE

Introduction

Carnivore populations experience numerous threats, including pressure from anthropogenic activity operating at multiple scales (Beever, Swihart et al. 2006, Mayor, Schneider et al. 2009, Cristescu, Stenhouse et al. 2013, Suryawanshi, Bhatia et al. 2014). There is significant literature on how human activity impacts large carnivore ecology and the role that management of both humans, and carnivores, can play in improving coexistence (Hostetler, McCown et al. 2009, Yackulic, Sanderson et al. 2011, Bateman and Fleming 2012, Bourbonnais, Nelson et al. 2013). Studies have shown that both major elements of human activity, like urban development, and apparently more minor elements, like recreation in forested areas, creates shifts in use of a landscape by carnivores (Markovchick-Nicholls, Regan et al. 2008, Ordenana, Crooks et al. 2010, De Angelo, Paviolo et al. 2011, Bateman and Fleming 2012).

Habitat selection, defined as the ways in which individual animals select resources across landscapes that differ in their biotic and abiotic conditions (Johnson 1980, Cushman 2006), is a critical part of an understanding of carnivore ecology. Animals make selection decisions using direct and indirect environmental cues that distinguish the quality of habitat and, ultimately, its potential to maximize fitness (Fretwell 1970, Murphy, Felzien et al. 1998, Jonzen 2008, Morris, Clark et al. 2008, Spear, Balkenhol et al. 2010).

Understanding how human modification of a landscape can affect habitat select is of particular importance for wide-ranging carnivores. Habitat can consist of a matrix combining different landcover types, including variations in anthropogenic land use (Tigas, Van Vuren et al. 2002, Whittington, St Clair et al. 2005, Christ, Ver Hoef et al. 2008). When animals select environments that significantly overlap with human activity, unfavorable human-wildlife interactions may result (Graham, Beckerman et al. 2005, de Azevedo and Murray 2007, Basille, Herfindal et al. 2009, Silva-Rodriguez, Soto-Gamboa et al. 2009). The consequences of such interactions can have a major impact on individual fitness of carnivores and wellbeing of humans with whom they interact (Delibes, Ferreras et al. 2001, Schlaepfer, Runge et al. 2002, Battin 2004). These situations, known generally as "human-wildlife conflict," take on many forms and encompass damage to or destruction of human property by wildlife, and human-caused disturbance to animals ((IUCN) 2003, Maehr, Layne et al. 2004). Extreme cases include wildlife attacks on humans (Packer, Ikanda et al. 2005) and human-induced mortality to wildlife (Bradley, Eric et al. 2003, Woodroffe and Frank 2005, Roger, Laffan et al. 2011).

A possible driver of habitat selection decisions leading to human-wildlife conflict is an animal's perception of false signals of habitat quality that can be caused by human modification to the environment (Howe, Obbard et al. 2007, Kanda, Fuller et al. 2009). Thus, understanding the relationships between habitat selection and human activity on the landscape is critical to an understanding of the root causes of human-wildlife conflict.

This dissertation focuses on the American black bear (*Ursus americanus*), a species of large carnivore that is recovering historical range across the United States (REF). Black bears have diverse diets, and have proven extremely adaptable to living across a range of habitats with a wide variety of human influence and activities. Population recovery and range expansion, however, have also led to an increasing incidence of unfavorable interactions with people (Hilty, Brooks et al. 2006, Beckmann and Lackey 2008, Spehar and Cooper 2008, Hostetler, McCown et al. 2009, Morzillo, Mertig et al. 2010, Peterson, Birckhead et al. 2010, Treves 2010, Treves, Martin et al. 2011, Lackey, Beckmann et al. 2013). The goal of the dissertation is to 1) identify how anthropogenic landscape patterns impact habitat selection, and mortality, of large carnivores; 2) Evaluate how analyses at multiple spatial resolutions change our understanding of human influence on patterns of carnivore behavior and ecology; and 3) Distinguish how tools and analytical approaches that have been developed at a global scale can be adapted and modified to be useful at a local scale and/or when examining species-specific issues.

Inclusion of anthropogenic variables is becoming more frequent in habitat selection analyses and helps demonstrate general patterns of attraction or avoidance of certain anthropogenic landscape features (Singleton, Gaines et al. 2002, Tucker, Clark et al. 2008, Sovada, Woodward et al. 2009, Vieira, Olifiers et al. 2009). However, many of these analyses are done at a relatively coarse scale (1km^2) and examine relatively few anthropogenic variables. Using a variety of local and species-specific anthropogenic variables can advance a nuanced understanding of habitat selection dynamics and provide well-informed wildlife management recommendations (Crooks and Soule 1999, Ordenana, Crooks et al. 2010, Burton, Sam et al. 2011, De Angelo, Paviolo et al. 2011). Modeling anthropogenic variables at multiple spatial resolutions may add nuance to our understanding of the way humans impact carnivore ecology, particularly when looking at analyses of habitat selection. -Chapter 2 of the dissertation uses multiple anthropogenic and biophysical landscape variables at two spatial and temporal resolutions to predict probability of black bear habitat selection in a human-dominated landscape.

For carnivores prone to conflict with humans, environments with high levels of human activity and/or attractive anthropogenic resources, might increase birth rates, but also can lead to increased mortality ; in the extreme, this can create spatially defined population sinks(Beckmann and Lackey 2008, Falcucci, Ciucci et al. 2009, Gehrt, Anchor et al. 2009). Areas with high wildlife mortality threats can potentially disrupt connectivity between populations (Mcrae, Dickson et al. 2008, Chetkiewicz and Boyce 2009, Carter, Brown et al. 2010) and may further compromise population persistence of carnivores.

Spatial patterns of the use of a landscape by humans and carnivores may operate at different scales, a phenomenon that may influence estimates of carnivore mortality risk in human-dominated landscapes. Hence, attempts to model the risk of mortality for carnivores at a single scale may fail to properly identify potential population sinks or may identify mortality risks that obscure the real drivers of carnivore deaths. In Chapter 3 of the dissertation, we use anthropogenic and biophysical variables at two spatial resolutions to evaluate the nuances of carnivore mortality risk in a heterogeneous landscape with increasing human activity.

Conservation biologists have developed a variety of tools that spatially display human influence on the environment and can be used to aid in understanding the impacts of humans on carnivore ecology (Hannah, Lohse et al. 1994). One such tool, The Human Footprint (HF) (Sanderson, Jaiteh et al. 2002), is a spatial index summarizing gradients of human influence on the environment at a global scale. The HF has been used to look at the persistence of wildlife, and in particular carnivores, at a continental scale (Laliberte 2004) or the scale of a species range (Yackulic, Sanderson et al. 2011), yet no rescaled and recalculated HF indices appear in the literature for evaluating the influence of human activity on carnivore ecology and conservation strategies at the local scale. By adapting the HF for use in regional and species-specific analyses of carnivore response to human influence we should be able to gain a better understanding of the factors that influence carnivore population persistence. Chapter 4 uses this approach to distinguish whether models using adaptations of the HF can enhance predictions of carnivore habitat selection and mortality risk.

Connectivity of suitable habitat for wide-ranging wildlife, and in particular carnivores, is also influenced by habitat heterogeneity from anthropogenic land use, and has received attention in the literature (Atwood, Young et al. 2011, Kininmonth, Beger et al. 2011, Munshi-South 2012, Walpole, Bowman et al. 2012, LaPoint, Gallery et al. 2013). It is standard for connectivity analyses to be based on habitat selection or species occurrence patterns, or even locations of protected areas. We contend that potential carnivore habitat connectivity in a human-dominated system should be based on complex analyses of habitat quality that include proxies for fitness potential, such as mortality and fecundity (Nielsen, Stenhouse et al. 2006). Combining information on selection probability with mortality risk yields accurate characterization of the landscape, which can inform our understanding of carnivore ecology and conservation (Falcucci, Ciucci et al. 2009, Roever, van Aarde et al. 2013, Sanchez-Mercado, Ferrer-Paris et al. 2014). In Chapter 5, we use results from Chapters 2 and 3 to construct habitat suitability models evaluating the impact of human activity on habitat quality for a large carnivore.

Analyses at multiple spatial resolutions, both of the structure of human landscapes, and the movements of animals within them, allow us to better understand how landscape composition can drive conflict and to design mitigation measures (Waller, Belant et al. 2013, Yan, Zeng et al. 2013, Gilroy, Medina Uribe et al. 2014). Moreover, management for protection of both humans and wildlife is extremely complex, and an understanding of how human behavior influences the behavior of wildlife species has considerable applications to mitigating human-wildlife conflict. Chapter 6 of the dissertation summarizes the general findings and discusses how the research contributes to the understanding of human impacts on wildlife ecology. We also discuss thoughts about the implications of these findings for further studies.

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CHAPTER TWO

Applying resource selection functions at multiple scales to evaluate the role of human activity in habitat selection of a large carnivore

Abstract

Large carnivores range widely, hence researchers often assume that habitat selection studies in this guild should reflect the scale of movement and be conducted at a coarse spatial resolution. We test this assumption by investigating how anthropogenic and environmental variables, examined at a nested set of scales, influence our understanding of large carnivore habitat selection and population persistence in landscapes with rapidly changing land use and increasing human influence. We use location data from a population of American black bear (*Ursus americanus*) in the Western Great Basin (WGB) of Western Nevada, USA to generate Resource Selection Probability Function (RSPF) models with nine environmental and anthropogenic variables as predictors of habitat selection. We use a GIS to create multiple landscape layers at coarse ($1km^2$) and fine ($30m^2$) spatial resolutions. Sex-specific buffers were used to generate "available" resource patches. The most parsimonious model was selected using AICc values and results were mapped for ease of use in management decisions. The most parsimonious models showed preferential habitat selection, but did not gain statistical power at finer spatial resolutions. Sub-alpine elevations and heavily forested areas had highest probabilities of selection, while areas within close distance to roads and areas of moderate to high human population density had lowest selection probability. Our analysis

shows the strong influence that human activity has on carnivore behavioral patterns in landscapes like the WGB with rapidly increasing human modification. Analyses of habitat selection at fine resolutions did not significantly vary from analyses at coarse resolutions, confirming the earlier assumption that large carnivores like black bears select habitat in a way that can be properly evaluated at coarse spatial resolutions. However, analyses conducted at a fine spatial resolution provided a more nuanced understanding of potential sex-based competition for habitat at the lowest levels of human population density. These methods provide a framework for conservation scientists to evaluate other measures of human impacts on large carnivore ecology.

Introduction

Understanding how animals select habitat is a primary goal of ecology (Manly 2002). The areas used for foraging, reproduction, and shelter signal characteristics of the landscape that are important to individual fitness and, across individuals, to population persistence (Schlaepfer, Runge et al. 2002, Battin 2004). As different habitats offer different quality cues, an individual is not expected to select habitat randomly, or in proportion to availability, but to show preference for habitat types that provide greater fitness potential (Remes 2000, Gilroy and Sutherland 2007, Part, Arlt et al. 2007).

Globally, human influence on the environment is pervasive (Sanderson, Jaiteh et al. 2002, Ellis and Ramankutty 2008, Manley, Parks et al. 2009), and the magnitude and spatial composition of these altered landscapes is known to impact wildlife (Cardille and Lambois 2010, Martin, Basille et al. 2010, Harju, Dzialak et al. 2011, Lesmerises, Dussault et al. 2012). Yackulic et al. (2011) demonstrated that across a wide range of large mammals, increasing human influence has a strong impact on population persistence. Their results also showed that although the presence of protected areas supports population persistence, the persistence of wide-ranging carnivores can still be in jeopardy, as individual animals face human-induced mortality when dispersing outside the boundaries of protected areas (Woodroffe and Ginsberg 1998). Urbanization and sprawling human development are increasingly defining the wildland-urban interface (Brown, Johnson et al. 2005, Hansen and Brown 2005). As a result, humans and wildlife frequently come into contact with one another both at this interface, and in the extensive low-density sprawling suburbs and exurbs that define modern cities (Bateman and Fleming 2012, Odden, Athreya et al. 2014). Even in areas devoid of significant human development, increased levels of recreation can have an impact on certain aspects of animal ecology (Goodrich and Berger 1994, Burt and Rice 2009, Hostetler and Reed 2014).

In many regions, variation in the type and extent of human activity results in significant and novel patterns of habitat heterogeneity (Crooks 2002, Kauffman, Varley et al. 2007, Manley, Parks et al. 2009). Hence, understanding habitat selection by large terrestrial carnivores requires an examination of how these animals respond to complex configurations of anthropogenic landscape variables. Although many studies have suggested that various types of human activity can influence large carnivore behavior (De Angelo, Paviolo et al. 2011, Bateman and Fleming 2012, Lesmerises, Dussault et al. 2012, Northrup, Stenhouse et al. 2012), few, if any, analyses of large carnivore habitat selection use a variety of location-specific anthropogenic variables to investigate habitat selection choices by large carnivores. This oversight may hinder the ability to accurately identify drivers of habitat selection choices by carnivores in regions with pervasive and increasing human influence.

Scale of analysis is an important and often crucial consideration in ecological and biodiversity studies (Wiens 1989, Beever, Swihart et al. 2006). Defining the scale used in a study, and addressing why a particular scale of analysis is most appropriate are both important elements of study design (Levin 1992). Spatial scale can refer to the spatial extent of the study, the spatial resolution at which the study is carried out, and the components under investigation (i.e. an individual, population, or community), all of which can impact the outcomes of the investigation (Beever, Swihart et al. 2006, Sawyer and Brashares 2013). Scales of habitat selection exhibit hierarchical relationships, thus it is important to examine habitat preference across a range of scales to better understand ecological patterns and processes (Johnson 1980, Mayor, Schneider et al. 2009). The failure to view habitat selection as a hierarchical process can lead to misconceptions concerning the value of particular habitats to animals (McLoughlin, Walton et al. 2004). Unfortunately, many studies of human impact on carnivore ecology model the variables at a single spatial and temporal scale (Martin, Basille et al. 2010, Lesmerises, Dussault et al. 2012, Dudus, Zalewski et al. 2014). This over-simplification of the system leads to the development of misinformation that can translate to mismanagement of critical natural resources and landscapes (Bowyer et al. 2006).

Boyce (2006) concluded that habitat selection is most likely to vary among scales when trade-offs exist between selection of different resources, a common issue in shared human-wildlife landscapes. Both Boyce (2006) and Bowyer and Kie (2006) suggest that foraging considerations are more likely to involve habitat selection at finer scales, whereas dispersal and other processes operate across larger scales, necessitating a multi-scale approach to habitat selection analyses. Temporal scale is also important to consider in analyzing habitat selection in systems with rapidly increasing human modification to the environment, as patterns of wildlife and human land use may vary periodically (Levin 1992). For example, a carnivore population may use the landscape in a certain way seasonally, or annually, but may exhibit a selection or avoidance response in the years following a climate event or natural disaster (Boyce 2006, Johnson, Breck et al. 2015).

In this study, we model habitat selection of the American black bear (*Ursus americanus*) in the WGB as a function of multiple anthropogenic, biological, and physical landscape variables. This information is important to help ecologists better understand drivers of human-carnivore conflict and human-induced mortality to bears, both of which are especially prevalent in the WGB. Black bears are an exceptionally good model to study the impact of human activity on large carnivore movement and behavior. The American black bear, like many large carnivores, has low reproductive rates and large spatial requirements. Black bears are habitat generalists and are found throughout North America in many different types of landscapes, allowing for comparisons across a range of ecological diversity, levels of human influence, and a diversity of human activity (Moyer, McCown et al. 2007, Baruch-Mordo, Breck et al. 2008, Beckmann, Karasin et al. 2008, Beston 2011). Habitat selection analyses can inform what characteristics of a landscape are especially important and most frequently selected for by black bears. Areas with these characteristics are thus considered "core" habitat for bears and may be used to inform management decisions (Atwood, Young et al. 2011).

The spatial resolution at which we analyze ecological patterns in a landscapes can largely influence how we characterize habitat, with a coarse resolution essentially averaging out spatial heterogeneity occurring at fine resolutions (Bowyer, Kie et al. 1996). In light of this, we assessed the impact of scale, in terms of spatial and temporal resolution of the data on model results. Using variables calculated at a coarse ($1km^2$) and fine ($30m^2$) spatial resolution, and including year of data collection as a covariate, we evaluated what scales of study produce the most nuanced understanding of human-carnivore dynamics in the WGB. We hypothesize that developing models using variables at multiple spatial resolutions will distinguish anthropogenic drivers of habitat selection decisions that would be obscured if evaluated at a single, coarse resolution. We also hypothesize that including the year of data collection will change model results, providing more information on how carnivore ecological patterns may shift than when models are carried out without distinguishing the year.

Methods

Study site and data collection

Surveys to assess male and female black bear habitat use were conducted in the eastern region of the Lake Tahoe Basin. This region is part of the Humboldt-Toiyabe forest system located between the Carson Range of the Sierra Nevada and the Sweetwater and Pinenut mountain ranges in Western Nevada and represents some of the most heavily forested areas in the State of Nevada (Raumann and Cablk 2008) (Fig. 1). Historically, frequent rainfall, thick woody vegetation, and pine forests characterize the western Sierra Nevada, while the rain shadow effect provides for a more arid, shrubland ecosystem in the more eastern regions (Manley, Murphy et al. 2004, Raumann and Cablk 2008). Although federally owned forest areas have remained protected, the WGB has undergone rapid residential and commercial development in the last half century with 2391 ha of forested land converted to developed land since 1940, driven by demand for recreational areas, resort hotels, and private vacation residences (Raumann and Cablk 2008). This development has caused a decline in forested areas and other native vegetation (Fig 2) (Beckmann and Lackey 2008, Raumann and Cablk 2008, Lackey, Beckmann et al. 2013). Previously forested areas were widely transformed to accommodate human-dominated land uses, while areas with currently intact forest are popular for outdoor recreation, with numerous ski slopes and camp sites established throughout the landscape (Goodrich and

Berger 1994, Burt and Rice 2009).

The WGB is home to over 60 mammal species (Schlesinger, Ramsos 2000), including a population of black bears estimated to be around 400 individuals (Lackey 2004, Lackey, Beckmann et al. 2013) with subpopulations inhabiting adjacent areas of the Western Great Basin, geographically separated by mountain ranges (Beckmann 2002, Lackey 2004). Very little analysis of potential black bear locations within the region had been investigated prior to this study, and aside from information regarding hotspots of black bear-human conflict (Beckmann and Lackey 2008), little was known about how black bears use this portion of the landscape.

For this study, we used GPS location data that were collected by the Nevada Department of Wildlife (NDOW) and Wildlife Conservation Society's (WCS) North America Program in an on-going long-term (19+ year) study (Beckmann and Berger 2003, Lackey, Beckmann et al. 2013) (Fig. 4). From May-November of 2005-2010, GPS collars were attached to 7 male and 17 female black bears via barrel traps in back country regions of the Carson and Pinenut Mountain Ranges or at the urban-wildland interface. Only adult animals were collared. GPS collars were set up to transmit location signals every 4 hours and emit a mortality signal when an animal did not move for 48 hours. Location data were collected in a database shared by NDOW and WCS project investigators and updated at the end of each field season (Jon Beckmann and Carl Lackey, pers. comm.). From May-November of 2011-2013, we set baited barrel and snare traps for black bears in remote forested regions of the Carson, Pinenut, and Sweetwater Mountain Ranges to capture and attach GPS collars to bears in backcountry areas with nominal human development but low to moderate human recreational activity.

Animals were captured and tranquilized according to the standards recognized by the State of Nevada.

Geographic Information Systems and Development of Landscape Parameters

We generated nine spatial data layers in a GIS (ESRI ArcMap 10.2.2) representing environmental features and the anthropogenic landscape in the WGB (Table 1). Although certain anthropogenic variables are often found in similar studies of wide-ranging large carnivores, such as distance to road and urban centers, we also used parameters that are specific to the WGB landscape with biological support for their impact to large carnivore behavioral ecology, such as distance to recreation site, distance to trail, distance to railway, and human population density (Goodrich and Berger 1994, Markovchick-Nicholls, Regan et al. 2008, Merenlender 2008, Burt and Rice 2009, Musiani, Anwar et al. 2010). The landcover layer was generated by specialists at NDOW specifically for biodiversity assessments in the WGB and projected at 1-meter resolution (Table 2). We used nearest neighbor tools in ArcMap to reclassify the layer to $30m^2$ (fine) and $1km^2$ (coarse) spatial resolutions for analyses. Feature layers representing major water bodies, railways, recreation sites, stream and road systems, and trails were acquired from NDOW and the Douglas County, Nevada open access GIS resources. We used the Euclidean distance tool in ArcMap to create layers representing the straight-line distance from any map cell to the nearest feature. These layers were also reclassified for projection at both $30m^2$ and $1km^2$ spatial resolutions. Feature layers representing urban polygons and human population density were available from the USDA's Lake Tahoe Basin Management Unit. These were also manipulated in ArcMap with nearest neighbor tools to classify and project them at $30m^2$ and $1km^2$ spatial resolution for analyses.

Due to the large quantity of data points and to avoid bias from autocorrelation of locations, we took a random sample of one-third of the total male and female GPS location points (male n= 2186 location points; female n= 5000 location points) and created shapefiles of male and female locations using ArcMap. We then used the Buffer tool to create circular buffers around each location point in accordance with the home range sizes of male and female black bears. This distance was conservatively set at 80km^2 for male home range and 20km^2 for female home range based on home range kernel estimates from a previous study of the backcountry black bear population in the WGB (Beckmann and Berger 2003). 4372 random locations were generated in ArcMap inside of the buffered male black bear "used" points to represent "available" resource units. This process was repeated for the buffered female black bear points to generate 10,000 randomly selected "available" locations. Each "available" location was within a buffer distance deemed to be the average distance a black bear can travel within a day (Cooper & Millspaugh, 1999; Compton et al., 2002; Boyce, 2006; Buskirk & Millspaugh, 2006; Ciarniello et al., 2007).

In order to better understand habitat selection probability, we identified habitat characteristics at GPS point locations in the study. We used Extraction Tools in ArcGIS to calculate values or characteristics (e.g. landcover type) for the nine variables at both coarse and fine spatial resolutions measured on the "used" points and "available" resource units (Ciarniello, Boyce et al. 2005, Ciarniello, Boyce et al. 2007). These location points and associated values were then exported into a spreadsheet and used by statistical software program JMP (SAS Program, 2014) for analyses.

Model construction and data analysis

We developed resource selection probability function (RSPF) models for two levels of spatial analysis using the coarse and fine scale landscape parameters and male and female black bear location data collected over the course of the study period. Resource selection analysis employed a logistic regression, using the logit command to compare characteristics of black bear "used" sites with "available" sites in the study region (Manly 2002, Sawyer and Brashares 2013). To test resource selection variability by year, we made additional models that partitioned the male and female black bear locations into separate datasets by year of GPS location fix (2005-2011).

For our logistic regression-based RSPF model, a black bear "used" GPS location was considered a "success" and given a value of 1, where an "available" resource unit was given a value of 0, and the nine landscape parameters (Table 1) used as predictor variables. The RSPF is assumed to take the form:

$$w^*(x) = \exp(\beta o + \beta_1 x_1 + \ldots \_ \beta_p x_p)/1 + \exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p)$$

where $x = (x_1, x_2, \ldots, x_p)$ holds the values for the X variables that are measured on a unit. Maximum likelihood estimates of the β parameters in the equation were calculated. We used chi-squared tests on deviances to assess whether there is any evidence that the probability of use of a location is related to a combination of the variables being considered. The RSPF model resulted in expected frequencies that are "accurate" to the landscape from which they are derived (Lele 2009).

For both spatial resolutions, we tested for collinearity of candidate variables using Pearson correlation coefficients, and variables with a correlation coefficient (r) > 0.7

were not included together in the models (Ciarniello, Boyce et al. 2007, Sawyer and Brashares 2013). We practiced backwards stepwise regression to identify the best fitting model. Our first RSPF model included all nine of our biophysical landscape variables, and we iteratively eliminated variables with a p-value above our threshold ($p=0.05$). We recorded AICc values for each model iteration (Burnham & Anderson, 1998; Zielinski et al., 2004; Harris et al., 2008; Horne et al., 2008; Kirk & Zielinski, 2009), and we considered models comparable if the delta AIC was < 2.0 (Ciarniello et al., 2007). The model with the lowest AICc value was considered most parsimonious and best fit for the data. For models with similar AICc values, we chose the model with fewer terms (Quinn & Keough, 2002).

We assessed the predictive capability of each model using a Spearman's rank correlation based on 5-fold cross validation (Boyce et al. 2002). In this procedure, we estimated an RSPF model using a random draw of 80% of the data. We then used this model to predict the frequency of occurrence in the withheld 20% of the data using 10 RSPF bins, and repeated the process 5 times, replacing the withheld 20% and removing the next 20% (Boyce et al. 2002). For our study, a model that had strong predictive capabilities would have a higher number of locations in bins with the highest RSPF scores. Once the final RSPF was derived, we used ArcMap 10.2 (ESRI, 2013) to map the probability of habitat selection over the entire study area.

Results

We used Spearman correlation to test relationships between input variables since many of the anthropogenic parameters (e.g. transportation routes, different regions of human development) have the potential to be highly correlated (Boyce, Pitt et al. 2010). The distance to rail variable was removed from subsequent analyses as it was highly correlated with distance to trail (ρ =0.95, p=<.0001). No other strong correlations were discovered in the data (Fig. 3).

When data layers were projected at the coarse spatial resolution, the landscape exhibited 29 different land cover categories, with 33.9% of the study site classified as Inter-Mountain Basin Mixed Salt Desert Scrub and 17.9% classified as Great Basin Pinyon-Juniper Woodland. When habitat selection analyses were conducted at a fine spatial resolution, the landscape was classified with 46 different landcover categories, with 33.7% of the study site classified as Inter-Mountain Basin Mixed Salt Desert Scrub and 16.5% classified as Great Basin Pinyon-Juniper Woodland.

Measured at the coarse spatial resolution, the majority (70.5%) of the landscape is within 5 kilometers of a road, and 28% of the landscape within 1 kilometer of a road. Also at the coarse resolution, 71.8% of the study landscape was 20 kilometers or more from a recreation site. At the coarse resolution, the majority (27%) of the study site was 10 or more kilometers from a permanent water body, with 21% of the study area within 3 kilometers of a water body. At the coarse resolution, 52% of the WGB landscape is less than 10 kilometers from a trail. Calculated at the coarse spatial resolution, 89.4% of the WGB landscape is within 1 kilometer of a permanent or seasonal stream.

For both male and female segments of the black bear population, there is no improvement in statistical power of the RSPF models when using fine resolution data to generate predictions of habitat selection choices.

Black bear location data used in model construction reflected the areas of the landscape inhabited by male and female individuals at the time of data collection, which was primarily the region from Lake Tahoe stretching East to the Pine Nut Mountain Range. However, the RSPF analysis allows us to estimate and map probability of habitat selection for a much larger region of the Lake Tahoe Basin based on the variables of interest, allowing for predictions of black bear hotspots as the population expands and colonizes new areas (Figs. 4,5 & 6).

Male RSPF Results – Coarse Spatial Resolution

Our habitat selection models at coarse spatial resolutions for male black bears in the WGB yielded seven of the nine variables measured at a coarse spatial resolution with confidence intervals that did not include zero, suggesting that those parameters were significant predictors of bear use of the landscape (Table 3). We assessed the most parsimonious model via 5-fold cross validation by fitting the model to the complete data set and using the cross validated predicted probabilities to provide a Receiver Operating Characteristic (ROC) analysis. The Area Under the Curve (AUC) from applying the fitted model to the validation data set is 0.9559 ($p<0.0001$), indicating a very good fit for the model when applied to the validation data.

Selection coefficients from the model indicate that black bears selected sites with higher forest cover and with increasingly longer distance to roads (Fig. 6). Selection for landcover varied, but generally male black bears selected heavily forested landcover over arid and semi-arid areas. They also selected alpine and subalpine subregions over montane subregions (Figs. 5&6). Human population density also had a significant nonlinear effect on male black bear locations, with selection most prevalent at the lowest human population densities (Fig. 6), whereas, black bears were more likely to select habitat away from urban polygons and closer to seasonal streams (Fig. 6). Closer distances to recreation sites were negatively associated with habitat selection probability, and the year of data collection proved to also influence habitat selection choices. Predictive accuracy for the coarse-resolution model using withheld model-testing data for validation was good ($r^2 = 0.6156$, $p < 0.0001$).

Male RSPF Results – Coarse Spatial Resolution and Fine Temporal Resolution

Breaking down the male black bear dataset into individual years, we used 721 GPS locations from the year 2005, 672 from 2006, 481 from 2007, and 312 from 2008 for 7 male animals to develop habitat selection models at coarse spatial resolutions and fine temporal resolution for male black bears in the WGB. All of the most parsimonious habitat selection models identified 6-8 variables that were significant predictors of habitat selection probability (Table 5). We assessed the most parsimonious model for each year via cross validation by fitting the model to the complete data set for that particular year and using the cross validated predicted probabilities to provide an Receiver Operating Characteristic (ROC) analysis. The Area Under the Curve (AUC) from applying the fitted model to the validation data set was very high for all models, indicating a very good fit for the model when applied to the validation data.

Five variables remained significant predictors of habitat selection across all 4 years: distance to trail, distance to stream, distance to recreation site, human population density, and landcover type (Table1). Distance to road was included in all of the models except from 2005, while urban polygon was only included in the 2005 and 2007 model. Although distance to major water body was only included in the 2006 and 2008 models, distance to stream was represented in the models for each year (Table 5). We found that although slight differences in coarse-resolution model variables were predicted from each of the four years of data collection for male bears, the distance to trail variable was unique to the fine-temporal resolution model. When the male bear data were measured at a coarse spatial and temporal resolution, distance to trail was not identified as a significant predictor of habitat selection.

Male RSPF Results – Fine Spatial Resolution and Coarse Temporal Resolution

Our habitat selection models at fine spatial resolutions for male black bears in the WGB yielded seven of the nine variables measured had confidence intervals that did not include zero, suggesting that those parameters were significant predictors of bear use of the landscape (Table 3). We assessed the most parsimonious model via cross validation by fitting the model to the complete data set and using the cross validated predicted probabilities to provide a Receiver Operating Characteristic (ROC) analysis. The Area Under the Curve (AUC) from applying the fitted model to the validation data set is 0.9569 ($p<0.0001$), indicating a very good fit for the model when applied to the validation data.

Habitat selection probability was similar for models using fine-resolution landscape variables and models using coarse-resolution data described above. In general, male black bears selected sites with higher forest cover and with increasingly longer distance to roads (Fig. 6). Selection for landcover varied, but generally male black bears selected heavily forested landcover over arid and semi-arid areas. They also selected alpine and subalpine subregions over montane subregions. Human population density also had a significant nonlinear effect on male black bear locations, with selection most prevalent at the lowest human population densities, whereas, black bears were more likely to select sites away from urban polygons and closer to seasonal streams (Fig. 6). Different from coarse-resolution models, sites within closer distances to permanent water bodies were preferred, and habitat selection probability increased as distance to trail increased. Fine-resolution models showed that year of data collection did not influence habitat selection choices (Table 2). Predictive accuracy for the coarse-resolution model using withheld model-testing data for validation was good ($r^2 = 0.5885$, $p < 0.0001$).

Male RSPF Results – Fine Spatial Resolution and Fine Temporal Resolution

Breaking down the male black bear dataset with variables at fine spatial resolutions into individual years, we used 721 GPS locations from the year 2005, 672 from 2006, 481 from 2007, and 312 from 2008 for 7 male animals to develop habitat selection models at fine spatial resolutions and fine temporal resolution for male black bears in the WGB (Table 5). All of the most parsimonious habitat selection models identified 6-8 variables that were significant predictors of habitat selection probability (Table 5). We assessed the most parsimonious model for each year via cross validation by fitting the model to the complete data set for that particular year and using the cross validated predicted probabilities to provide an Receiver Operating Characteristic (ROC) analysis. The Area Under the Curve (AUC) from applying the fitted model to the validation data set was very high for all models, indicating a very good fit for the model when applied to the validation data.

Five variables remained significant predictors of habitat selection across all four years: landcover type, distance to stream, distance to water, distance to road, and human population density (Table 5). Three of these (distance to stream, human population density, and landcover type) are similar to those that were included in the models with coarse spatial resolution and temporal resolution (Table 3). Urban polygon was included in all of the models except from 2006, while distance to trail was only included in the 2005 and 2006 models. Distance to recreation site was only included in the models from 2005 and 2007 (Table 5). Similar to the model constructed with coarse-resolution spatial variables, we found that although slight differences in fine-resolution model variables were predicted from each of the four years of data collection for male bears, only the distance to trail variable stood out as unique in the fine-temporal and only included in two of the coarse-temporal resolution models (years 2005 and 2006).

Female RSPF Results - Coarse Spatial Resolution

We used 5000 randomly selected GPS locations (201-415 per bear) out of a total of 14,540 locations for 17 female animals collected over the course of the study to develop habitat selection models for black bears in the WGB. 8 of the 9 variables measured at a coarse spatial resolution had confidence intervals that did not include zero, suggesting that those parameters were significant predictors of female bear habitat selection (Table 4). We assessed the most parsimonious model via cross validation by fitting the model to the complete data set and using the cross validated predicted probabilities to provide an ROC analysis. The Area Under the Curve (AUC) from applying the fitted model to the validation data set is 0.8362 ($p<0.0001$), indicating a very good fit for the model when applied to the validation data.

Similar to males, female black bears selected sites with higher forest cover and with increasingly longer distance to roads (Fig. 7). Selection for landcover varied, but generally female black bears selected heavily forested landcover over arid and semi-arid areas. They also selected alpine and subalpine subregions over montane subregions (Figs. 4&7). Human population density also had a significant nonlinear effect on female black bear locations, with selection most prevalent at the lowest human population densities (Fig. 7). Similarly, female black bears were more likely to select habitat away from urban polygons and closer to seasonal streams (Fig. 7). Also in keeping with male bears, closer distances to recreation sites were negatively associated with habitat selection probability, and the year of data collection proved to also influence habitat selection choices. Predictive accuracy for the coarse-resolution model using withheld model-testing data for validation was good ($r^2 = 0.6156$, $p < 0.0001$).

Female RSPF Results – Coarse Spatial Resolution and Fine Temporal Resolution

Breaking down the female black bear dataset into individual years, we used 1478 GPS locations from the year 2005, 940 from 2006, 350 from 2007, and 208 from 2008, 182 from 2009, 1140 from 2012, and 700 from 2011 for 17 female animals to develop habitat selection models at coarse spatial resolutions and fine temporal resolution for female black bears in the WGB. All of the most parsimonious habitat selection models identified 6-8 variables that were significant predictors of habitat selection probability

(Table 6). We assessed the most parsimonious model for each year via cross validation by fitting the model to the complete data set for that particular year and using the cross validated predicted probabilities to provide an ROC analysis. The AUC from applying the fitted model to the validation data set was very high for all models, indicating a very good fit for the model when applied to the validation data.

Four variables remained significant predictors of habitat selection across all 7 years: distance to trail, distance to road, distance to recreation site, and landcover type. Population density was included in all of the models except from 2005, while urban polygon was only included in the 2009 and 2010 models (Table 6). While population density was included in all but the 2005 model, distance to trail was represented in the models for each year (Table 6). We found that although slight differences in model variables were predicted from each of the four years of data collection for female bears, only the distance to trail variable stood out as unique in the fine-temporal versus coarse-temporal resolution models. Despite neither of the two water-related variables being consistent in all of the single-year models, every model includes at least one. In general, breaking down the habitat selection model into individual years did not yield much difference in terms of the significant variables used to predict probability of selection.

Female RSPF Results – Fine Spatial Resolution

We used 5000 randomly selected GPS locations (189-512 per bear) out of a total of 14,540 locations for 17 female animals collected over the course of the study to develop habitat selection models for black bears in the WGB. 8 of the 9 variables measured at a fine spatial resolution had confidence intervals that did not include zero, suggesting these parameters were significant predictors of bear use of the landscape (Table 4). We assessed the most parsimonious model via cross validation by fitting the model to the complete data set and using the cross validated predicted probabilities to provide an ROC analysis. The AUC from applying the fitted model to the validation data set is 0.8629 ($p<0.0001$), indicating a very good fit for the model when applied to the validation data.

The variables used in the most parsimonious models to predict habitat selection probability were identical for models using fine-resolution landscape variables and models using coarse-resolution data described above (Table 4). In general, female black bears selected sites with higher forest cover and with increasingly longer distance to roads (Fig. 7). Selection for landcover varied, but generally female black bears selected heavily forested landcover over arid and semi-arid areas. They also selected alpine and subalpine subregions over montane subregions. Human population density also had a significant nonlinear effect on female black bear locations, with selection most prevalent at the lowest human population densities, whereas, black bears were more likely to select sites away from urban polygons and closer to seasonal streams (Fig. 7). Predictive accuracy for the coarse-resolution model using withheld model-testing data for validation was not strong ($r^2 = 0.3320$, $p < 0.0001$).

Female RSPF Results – Fine Spatial Resolution and Fine Temporal Resolution

Breaking down the female black bear dataset into individual years, we used 1478 GPS locations from the year 2005, 940 from 2006, 350 from 2007, and 208 from 2008, 182 from 2009, 1140 from 2012, and 700 from 2011 for 17 female animals to develop habitat selection models at coarse spatial resolutions and fine temporal resolution for female black bears in the WGB. All of the most parsimonious habitat selection models identified 5-7 variables that were significant predictors of habitat selection probability (Table 6). We assessed the most parsimonious model for each year via cross validation by fitting the model to the complete data set for that particular year and using the cross validated predicted probabilities to provide an Receiver Operating Characteristic (ROC) analysis. The Area Under the Curve (AUC) from applying the fitted model to the validation data set was very high for all models, indicating a very good fit for the model when applied to the validation data.

Three variables remained significant predictors of habitat selection across all 7 years: landcover type, urban polygon, and human population density (Table 6). Two of these, human population density and landcover type, were also included in all 7 of the models measured at a coarse spatial and fine temporal resolution. A variable representing water availability was included in each year except 2008, and at least one variable representing a road or trail was included in each year except 2005 (Table 6). Similar to the model constructed with coarse-resolution spatial variables, we found that although slight differences in fine-resolution model variables were predicted from each of the four years of data collection for female bears

Discussion

Scale and estimations of habitat selection

Although the models using data at a fine spatial resolution out-performed the coarse-resolution models, the difference was nominal, suggesting that resolution of analysis is at best marginally relevant to habitat selection for black bears in the WGB. While human activity can be mapped at a fine resolution, the wide-ranging habits of bears may explain why they select habitat using coarse filters and are relatively insensitive to fine-resolution variations in human influence (Boyce 2006, Gehrt, Anchor et al. 2009). It is also possible that other ecological processes that operate at relatively coarse resolutions – e.g. the distribution of important food resources, or bear density - may drive the habitat selection patterns in this region (Beckmann and Berger 2003, Bowyer and Kie 2006).

Habitat selection analyses show that backcountry-dwelling black bears have a clear intolerance for regions of the landscape with human activity, and in particular, moderate to high human population density. Although both male and female bears occasionally pass through areas of high human population density and human development as they disperse to preferred habitat, overwhelmingly the bears collared during this study avoid these regions. While this avoidance behavior is supported by numerous other studies, it also suggests that human-bear conflicts may often be the result of mismanaged human resources becoming an attractant, rather than a preference of human landscapes on behalf of black bears (Beckmann and Berger 2003, Johnson, Breck et al. 2015).

Single-variable analyses using metrics at fine spatial resolutions demonstrated that currently male bears monopolize the most remote areas of the WGB, and female bears select habitat with slightly more human influence. It is possible that females are avoiding the regions of male dominance in order to find safe refuge during hibernation and to protect their cubs from infanticide (Freedman, Portier et al. 2003, Garrison, McCown et al. 2007, Reynolds-Hogland, Mitchell et al. 2007). This concept is supported by results indicating male black bears have a very high probability of selecting the regions with the absolute lowest human population density, while female bears have only a 2% probability of selecting the same regions of the landscape. Female bears instead have a high probability of selecting the next-lowest human population densities.

Although generally, fine resolution analyses did not strengthen model predictions, a failure to examine finer spatial resolutions for single-variable analyses would have led to the conclusion that the heterogeneity of human population density across the landscape had little effect on habitat preferences and sex-based competition of a wide-ranging carnivore like the black bear. Sampling at a coarse (1km^2) spatial resolution obscured small patches of the lowest human population densities, which were identified in fine-resolution models as important habitat for male black bears, and masked the importance of small changes in landscape that allowed female bears to avoid potentially aggressive males. Apart from competition with males as an explanation for female bear habitat use, it is also possible that areas of the landscape used by female bears had attractive shelter resources for hibernating with cubs, or more simply, that females are better able to tolerate low levels of human activity than male animals.

Black bear response to human activity

Incorporating anthropogenic variables into habitat selection analyses allows us to distinguish the elements of human activity that are tolerated or generally avoided by black bears in the WGB (Breck, Lance et al. 2009, Hostetler, McCown et al. 2009). In general, large patches of human development were avoided by black bears in favor of remote forested regions (Figs. 4&5). For both male and female black bears, sub-alpine densely-forested habitat overwhelmingly had the highest probability of selection, followed by areas with permanent water resources, results that are much in line with studies conducted in other regions of North America and supporting what is known about black bear biology (Carter, Brown et al. 2010, Obbard, Coady et al. 2010, Beston 2011). Areas of low, moderate, and high human development had negative associations with habitat selection and low probability of use, suggesting an overall intolerance of human activity, even when such human activity extended into primarily forested areas. This is likely a conservative estimate of black bear urban habitat use, as the animals targeted for this study were trapped in backcountry regions and likely had little experience in areas with elevated levels of human activity. Similarly, agricultural areas and mining sites also had negative relationships with habitat selection, which contrasts with bear studies in other parts of North America that indicate an attraction to the human food resources in these areas (Tietje and Ruff 1983, Wilson, Madel et al. 2005).

Using fine-resolution habitat selection models, and projecting the results of these models across the WGB, allows us to determine which areas are, or will be, critical core bear habitat. Our results suggest that current and future core areas for bear habitat are the regions directly East of Lake Tahoe, and the slopes of the Sierra Nevada southeast and northeast of the lake, the least arid regions of the study area (Figs. 4&5). Especially for male bears, the maps clearly indicate the importance of large water bodies as a part of critical habitat, and the importance of heavily forested regions for both sexes. It is clear that water availability is an important limiting factor for the individuals living in the WGB. With increasingly dry climate conditions in recent years (Coats, Perez-Losada et al. 2006, Dolanc, Safford et al. 2014), water availability will likely continue to drive many aspects of black bear dispersal and habitat use in the region. Evidence for this trend is also apparent in our findings that arid and semi-arid regions of the landscape are represented as “cold spots” for black bear habitat selection probability at both spatial resolutions. Although populations of black bears are present in many different North American ecosystems, the black bear selection choices we observed are similar to patterns observed even in areas with less pervasive human influence (Moyer, McCown et al. 2008, Carter, Brown et al. 2010, Obbard, Coady et al. 2010, Frary, Duchamp et al. 2011)

Similarly, both male and female black bears demonstrated an extremely low probability of selecting landcover types classified as “recently burned” at both spatial resolutions, a phenomenon that may become problematic as climate change in the region has led to changes in the fire regime, which may increase in frequency or extent (Hurteau, Bradford et al. 2014, Hurteau, Robards et al. 2014, Lydersen, Collins et al. 2014).

The observation that, in an area with extreme heterogeneity in the anthropogenic landscape, bears select areas of lower human influence suggests that changes in patterns of human development will have a direct impact on both habitat selection, and potentially spatial occupancy of habitat by bears. Fragmentation of black bear core habitat is, and will continue to be, of management concern in the WGB. Currently, numerous human recreation sites, roads, and residential development make up close to 7% of the landscape and populate the core areas of black bear habitat nearest Lake Tahoe, with the prospect of continued development in the near future (Raumann and Cablk 2008, Burt and Rice

2009). With potential hotspots of black bear habitat use throughout the eastern part of the WGB (Figs. 4&5), connectivity of this habitat, including safe dispersal areas, may be imperative for persistence of this black bear population.

Neither male nor female bears avoided areas close to roads at both spatial resolutions, suggesting that black bears in this region do not perceive roads as obstacles or deterrents to dispersal, but rather a marginally relevant feature in a landscape of largely contiguous forests. However, roads impose high mortality risk to many predators (Cramer and Portier 2001, Grilo, Bissonette et al. 2009, Schwartz, Haroldson et al. 2010), including black bears in the WGB (see Chapter 2) and therefore may become ecological traps or sinks where much of the landscape signals high quality habitat, but vehicle collisions elevate mortality rates to unsustainable levels (Kristan 2003, Battin 2004, Part, Arlt et al. 2007). This high-risk relationship between bears and roads, as well as other risk factors associated with the anthropogenic landscape in the WGB, warrant further study, as mortality risk factors may ultimately limit population growth of black bears in the region (see Chapter 2).

Recreation sites are areas of seasonal human activity, and our analyses show that they were not avoided by male or female black bears. Both male and female bears disproportionally selected areas close to these areas, with a 95% probability of selecting habitat within 1km from a recreation site. This pattern is likely due to the location of camp sites, hiking trails, and ski resorts in the high-quality heavily forested areas in the WGB that are preferred by black bears. Selection of these areas may also be due to food subsidies in the form of trash and supplies that are generated at such sites. Especially in periods of hyperphagia, bears may frequent recreation sites in order to easily access human food to prepare for hibernation, a factor that may drive human-bear conflict in the region and warrants future study (Goodrich and Berger 1994, Burt and Rice 2009, Goldstein, Poe et al. 2010).

Conclusions

Overwhelmingly, similar studies of habitat selection by large carnivores rely on indirect sampling methods of animal presence in a landscape, including hair snags, nest sites, feeding sign, etc. (Bourbonnais, Nelson et al. 2013, Fisher, Bradbury et al. 2013, Sollmann, Gardner et al. 2013). This study is unique in that it analyzes information from a long-term black bear study that includes precise location and movement data for a wide-ranging species. Access to these data allows us to make more concrete conclusions about actual habitat use, rather than estimate patterns based on information that may be biased from sampling efforts.

Analyzing habitat selection of wide-ranging terrestrial carnivores can be difficult, especially in shared human-wildlife landscapes like the WGB. An analysis of use and availability might undervalue the high-quality habitat where there was a high cost to dispersing through surrounding, low-quality areas (Bowyer and Kie 2006). In landscapes with substantial human influence, habitat selection analyses may instead over-predict the probability of selecting low-quality habitat because animals may traverse them frequently while seeking areas of higher quality. In light of this, further study needs to analyze the landscape in terms of the impacts of landscape heterogeneity on mortality risk of black bears to gain a conclusive understanding of mortality risk dynamics in the region (see Chapter 2).

This study highlights the utility of integrating anthropogenic landscape characteristics in habitat selection to inform management strategies. A nuanced representation of critical black bear habitat and general tolerance for varying levels of human activity is presented with models built with variables representing human influence in the WGB. Our study suggests that conservation planning to ensure persistence of the black bear population in the WGB requires a close look at changes in human activity patterns throughout the landscape to determine how human activity may influence mortality risk for black bears as well as overall habitat suitability throughout the region, ultimately informing protection of critical habitat (Nielsen, Stenhouse et al. 2006, Sawyer and Brashares 2013).

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FIGURES

FIGURE 1. The Western Great Basin (WGB) study system shown as part of the US Great Basin.

FIGURE 2. Gross change in area (ha) by landcover class from 1940-2002 in the southern WGB (Adapted from Raumann *et al*. 2008)

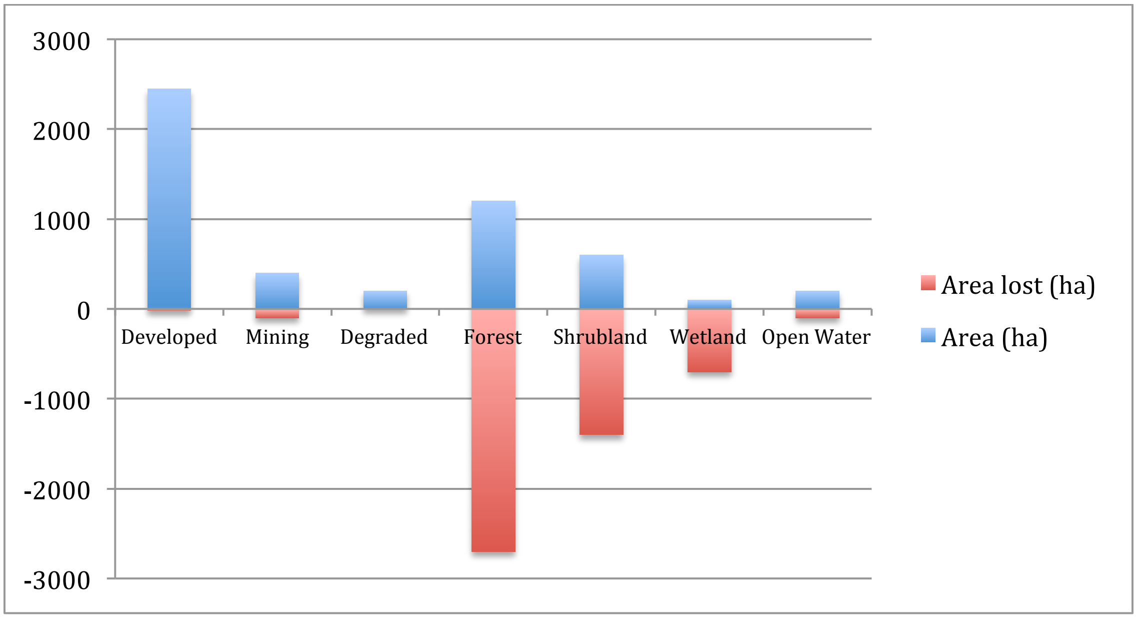
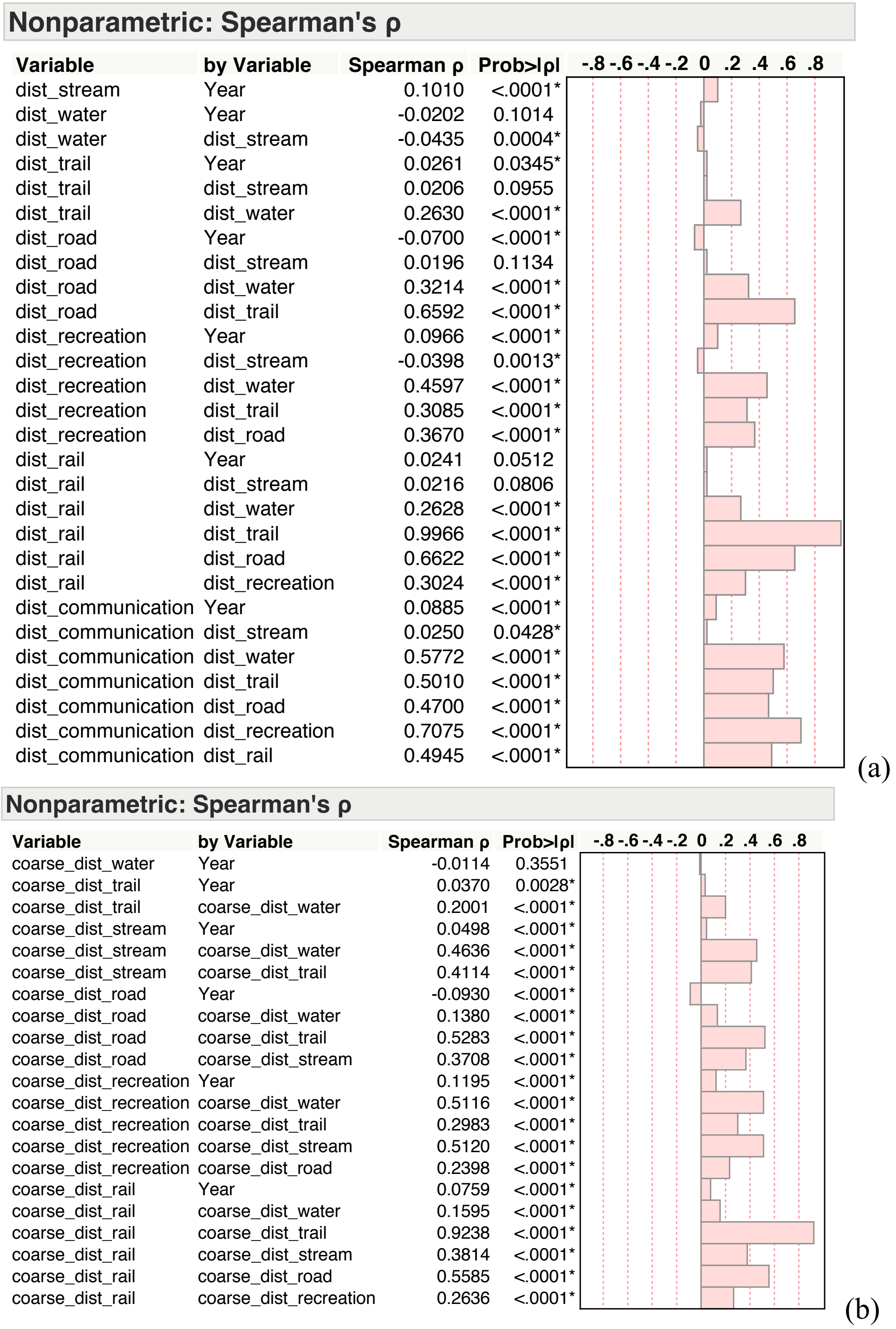


FIGURE 3. Spearman's ρ correlation test of RSPF model coarse (a) and fine (b) resolution variables. Distance to trail and distance to rail were highly correlated and thus distance to rail was eliminated from RSPF models.



Nonparametric: Spearman's ρ

Variable	by Variable	Spearman ρ	Prob>|ρ|
dist_stream	Year	0.1010	<.0001*
dist_water	Year	-0.0202	0.1014
dist_water	dist_stream	-0.0435	0.0004*
dist_trail	Year	0.0261	0.0345*
dist_trail	dist_stream	0.0206	0.0955
dist_trail	dist_water	0.2630	<.0001*
dist_road	Year	-0.0700	<.0001*
dist_road	dist_stream	0.0196	0.1134
dist_road	dist_water	0.3214	<.0001*
dist_road	dist_trail	0.6592	<.0001*
dist_recreation	Year	0.0966	<.0001*
dist_recreation	dist_stream	-0.0398	0.0013*
dist_recreation	dist_water	0.4597	<.0001*
dist_recreation	dist_trail	0.3085	<.0001*
dist_recreation	dist_road	0.3670	<.0001*
dist_rail	Year	0.0241	0.0512
dist_rail	dist_stream	0.0216	0.0806
dist_rail	dist_water	0.2628	<.0001*
dist_rail	dist_trail	0.9966	<.0001*
dist_rail	dist_road	0.6622	<.0001*
dist_rail	dist_recreation	0.3024	<.0001*
dist_communication	Year	0.0885	<.0001*
dist_communication	dist_stream	0.0250	0.0428*
dist_communication	dist_water	0.5772	<.0001*
dist_communication	dist_trail	0.5010	<.0001*
dist_communication	dist_road	0.4700	<.0001*
dist_communication	dist_recreation	0.7075	<.0001*
dist_communication	dist_rail	0.4945	<.0001*

Nonparametric: Spearman's ρ

Variable	by Variable	Spearman ρ	Prob>|ρ|
coarse_dist_water	Year	-0.0114	0.3551
coarse_dist_trail	Year	0.0370	0.0028*
coarse_dist_trail	coarse_dist_water	0.2001	<.0001*
coarse_dist_stream	Year	0.0498	<.0001*
coarse_dist_stream	coarse_dist_water	0.4636	<.0001*
coarse_dist_stream	coarse_dist_trail	0.4114	<.0001*
coarse_dist_road	Year	-0.0930	<.0001*
coarse_dist_road	coarse_dist_water	0.1380	<.0001*
coarse_dist_road	coarse_dist_trail	0.5283	<.0001*
coarse_dist_road	coarse_dist_stream	0.3708	<.0001*
coarse_dist_recreation	Year	0.1195	<.0001*
coarse_dist_recreation	coarse_dist_water	0.5116	<.0001*
coarse_dist_recreation	coarse_dist_trail	0.2983	<.0001*
coarse_dist_recreation	coarse_dist_stream	0.5120	<.0001*
coarse_dist_recreation	coarse_dist_road	0.2398	<.0001*
coarse_dist_rail	Year	0.0759	<.0001*
coarse_dist_rail	coarse_dist_water	0.1595	<.0001*
coarse_dist_rail	coarse_dist_trail	0.9238	<.0001*
coarse_dist_rail	coarse_dist_stream	0.3814	<.0001*
coarse_dist_rail	coarse_dist_road	0.5585	<.0001*
coarse_dist_rail	coarse_dist_recreation	0.2636	<.0001*

FIGURE 4. Map displaying black bear locations in the WGB and Western Great Basin.

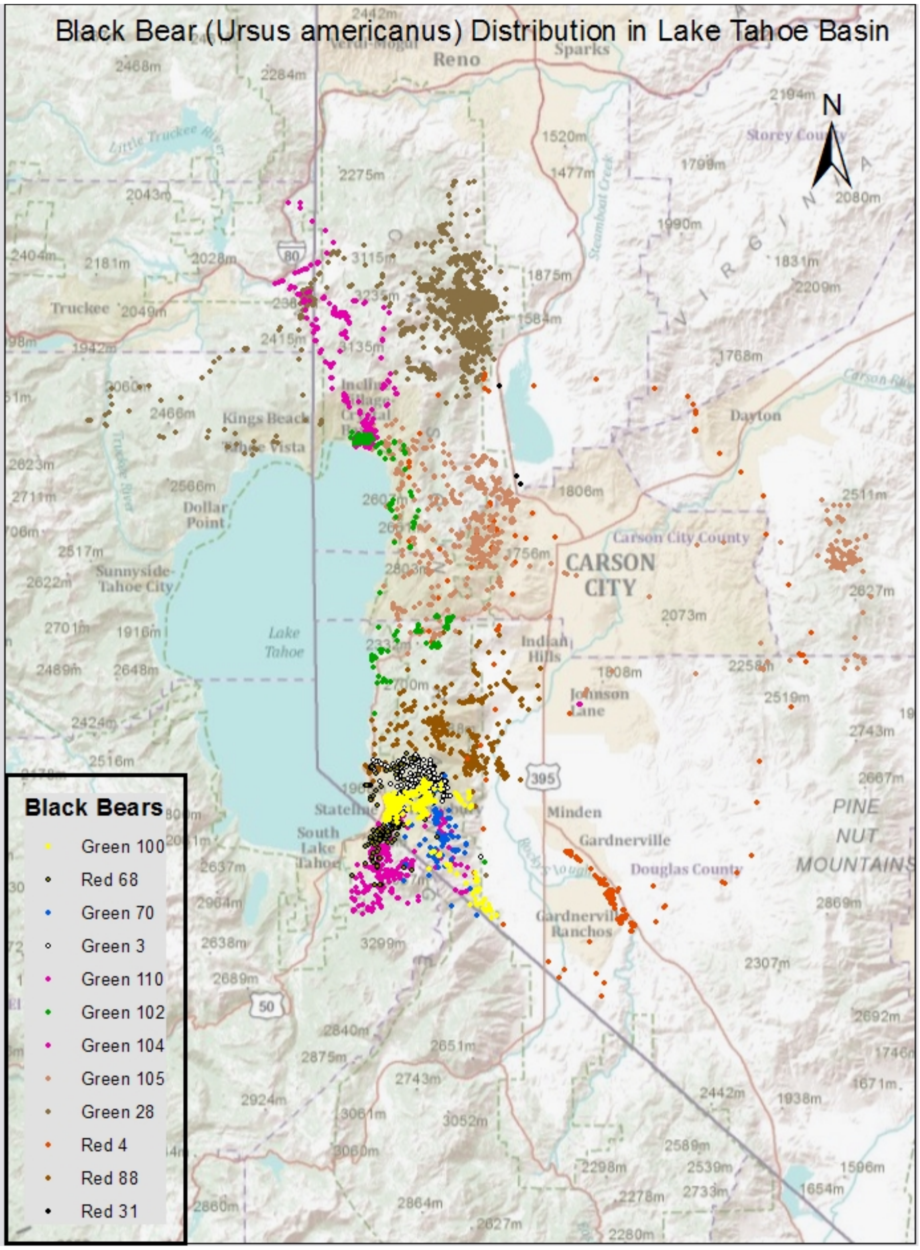


FIGURE 5. Map displaying female black bear habitat selection in the WGB based on average habitat selection probability for all significant landscape variables.

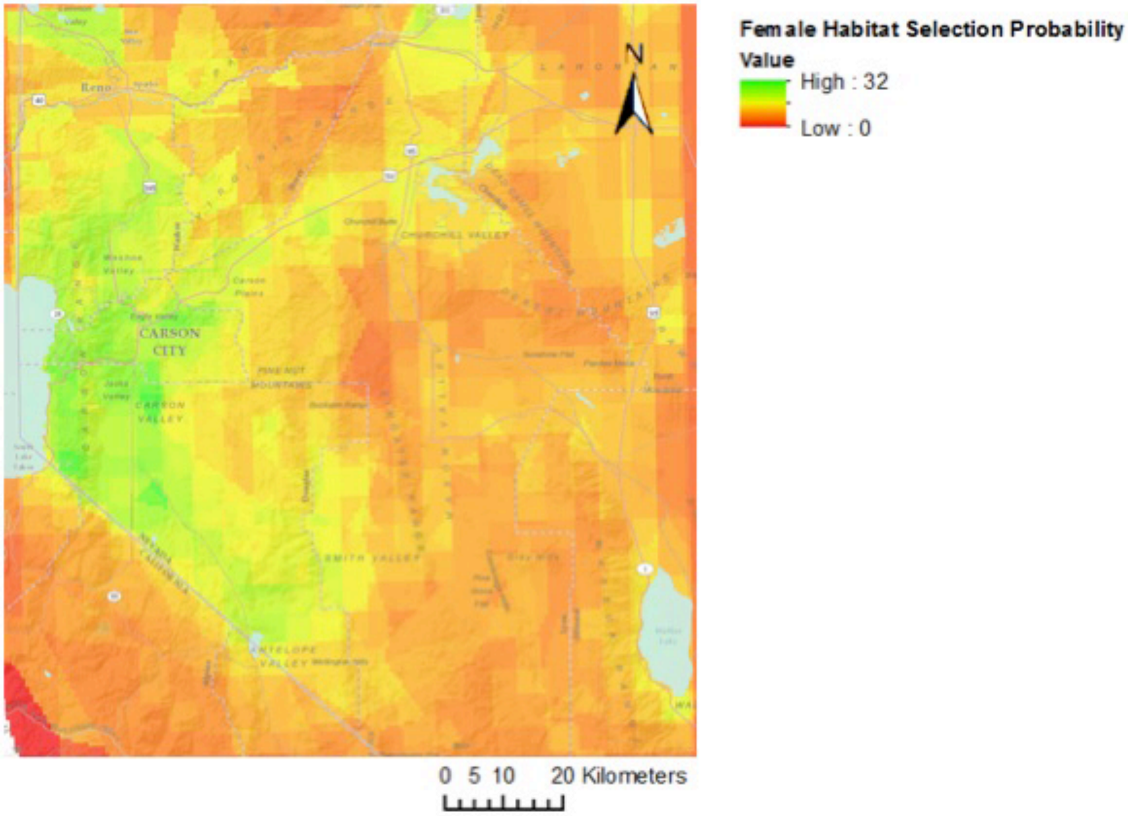


FIGURE 6. Map displaying male black bear habitat selection in the WGB based on average habitat selection probability for all significant landscape variables.

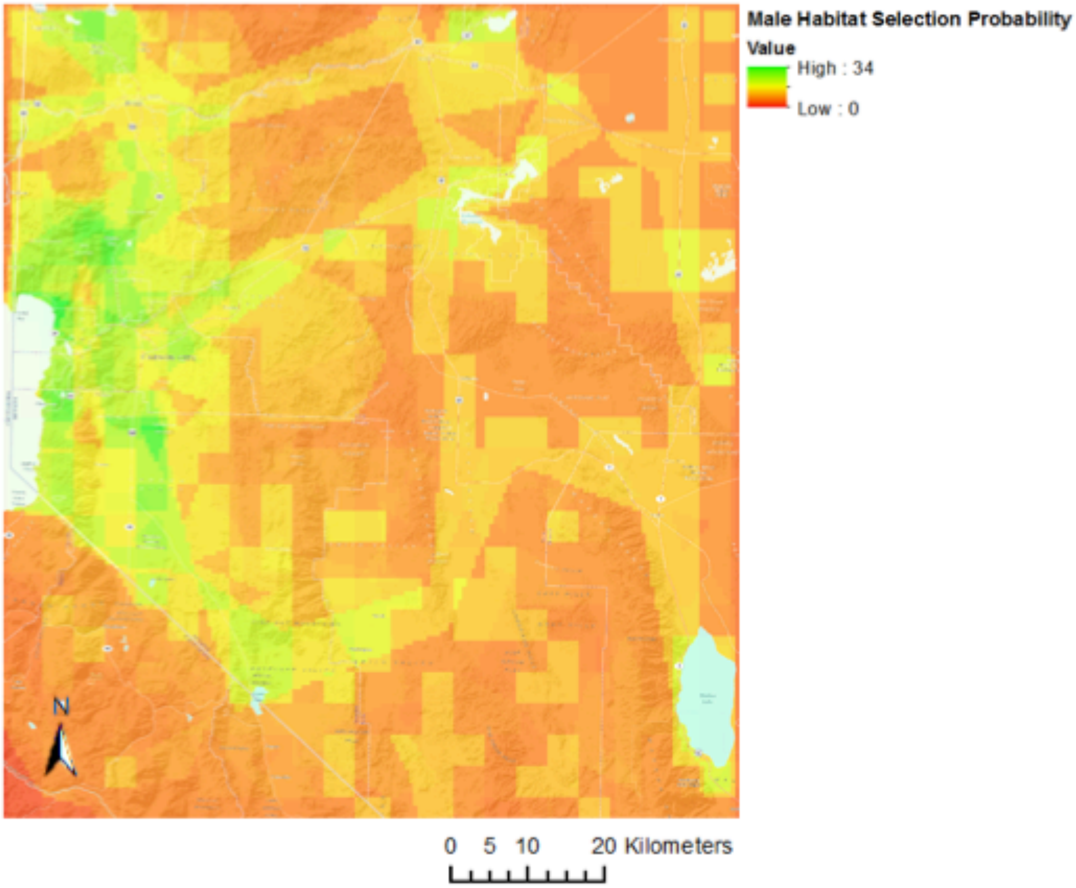


FIGURE 7. Habitat selection coefficients (β) for male black bears at coarse and fine spatial resolutions

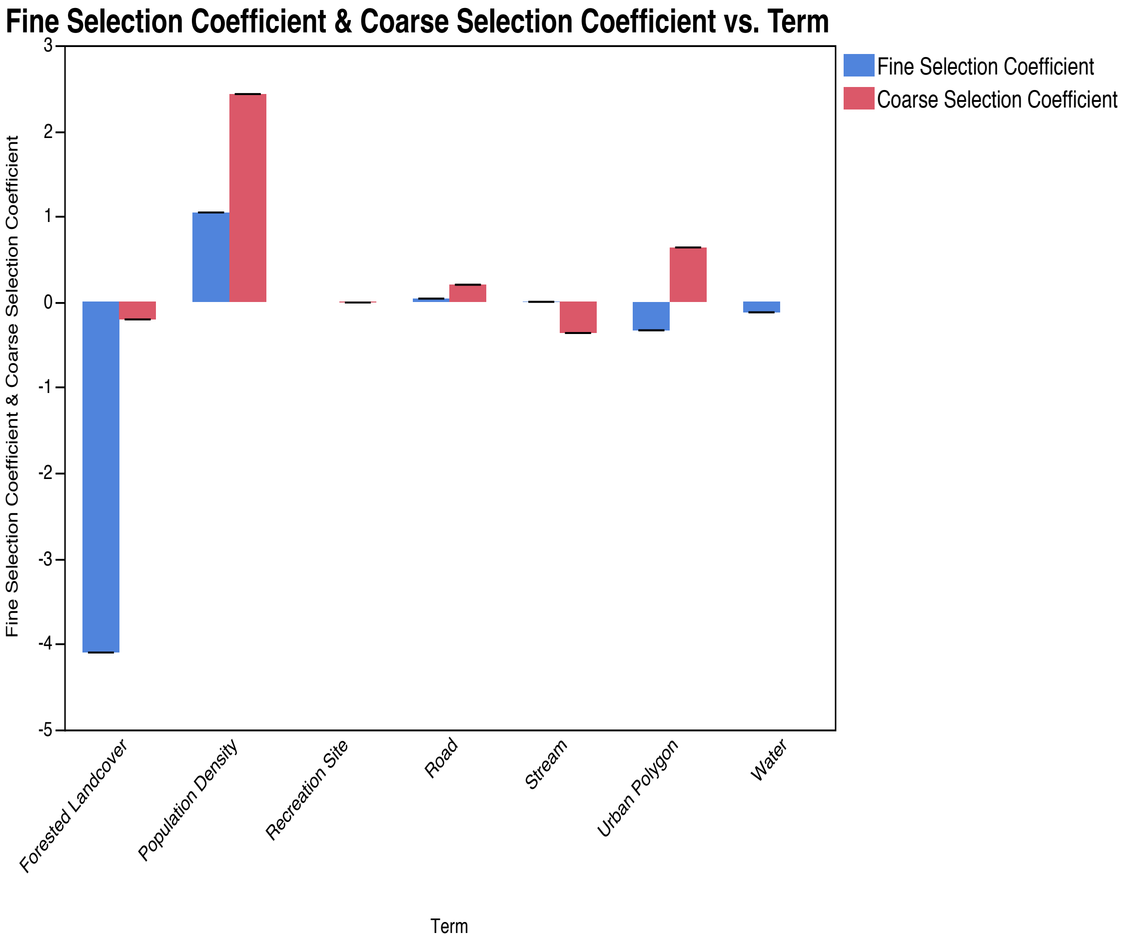
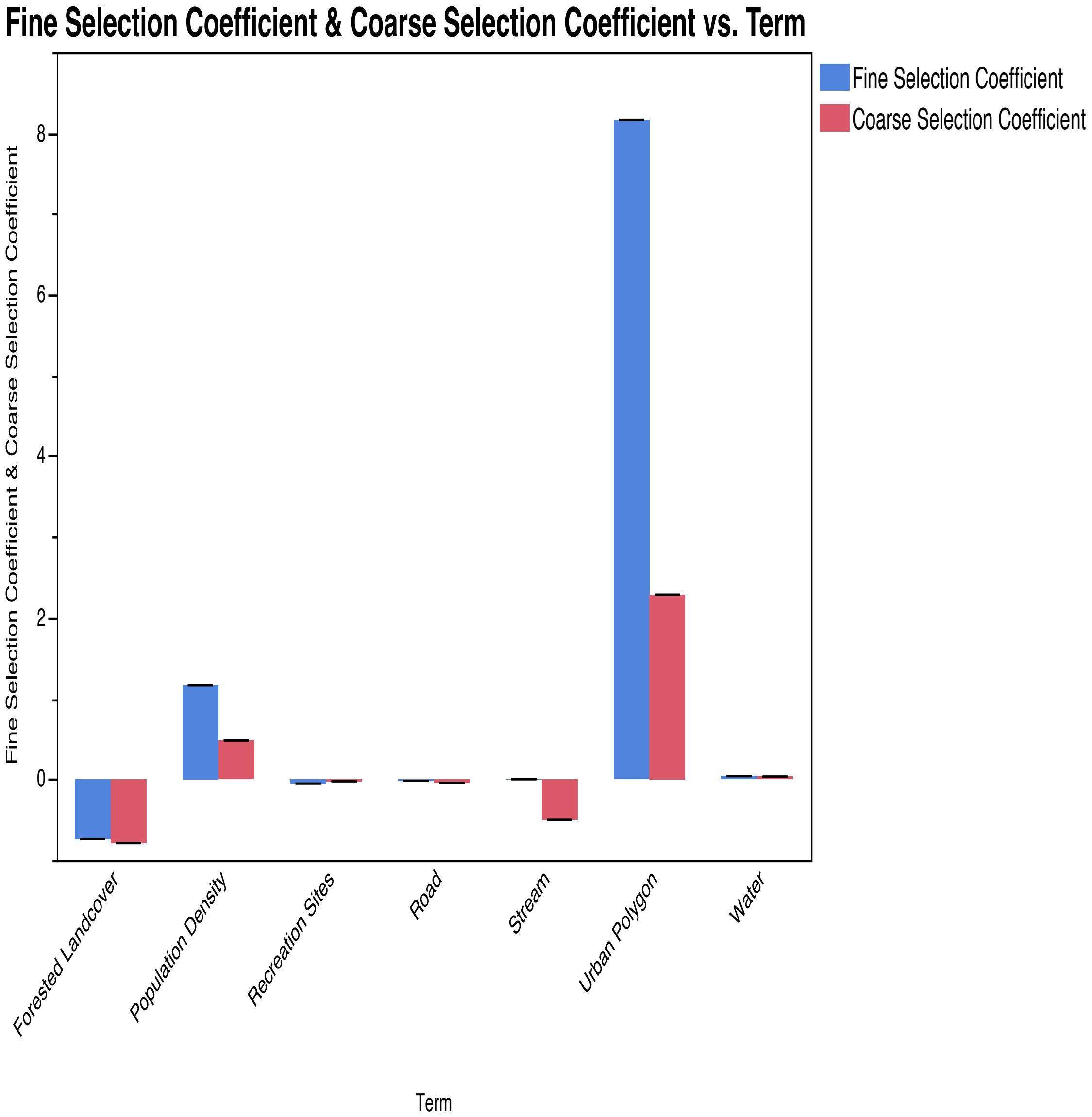


FIGURE 8. Habitat selection coefficients (β) for female black bears at coarse and fine spatial resolutions



TABLES

Table 1. Description of variables used to select candidate models for black bear habitat selection in the Lake Tahoe Basin study area

Landcover	Categorical	29 vegetative and anthropogenic landcover categories
Distance to Road	Continuous	Straight-line distance to nearest road in kilometers
Distance to Water Body	Continuous	Straight-line distance to nearest large water body in kilometers
Distance to Stream	Continuous	Straight-line distance to nearest permanent or seasonal stream in kilometers
Distance to Trail	Continuous	Straight-line distance to nearest hiking trail in kilometers
Distance to Rail	Continuous	Straight-line distance to nearest Amtrak or regional railroad line in kilometers
Urban Polygon	Categorical	Census-defined urban areas measured in sq kilometers
Human Population Density	Categorical	2010 census-defined human population density by zip code in persons/km^2
Distance to Recreation Site	Continuous	Straight-line distance to nearest recreation site, trail head, camp site, or ski lodge in kilometers

Table 2. Description of percentage of landscape for landcover categories measured at a coarse ($1km^2$) spatial resolution in the Lake Tahoe Basin

3	Mediterranean California Alpine Bedrock and Scree	0.188679245
6	Sierra Nevada Cliff and Canyon	0.188679245
8	Inter-Mountain Basins Cliff and Canyon	0.566037736
11	Inter-Mountain Basins Active and Stabilized Dune	0.566037736
14	Inter-Mountain Basins Playa	1.132075472
27	Northern Pacific Mesic Subalpine Woodland	0.377358491
37	Great Basin Pinyon-Juniper Woodland	17.9245283
47	Great Basin Semi-Desert Chaparral	0.566037736
48	Inter-Mountain Basins Big Sagebrush Shrubland	13.01886792
49	Great Basin Xeric Mixed Sagebrush Shrubland	6.981132075
58	Inter-Mountain Basins Mixed Salt Desert Scrub	33.96226415
62	Inter-Mountain Basins Montane Sagebrush Steppe	3.018867925
67	Inter-Mountain Basins Semi-Desert Shrub Steppe	0.754716981
76	Inter-Mountain Basins Semi-Desert Grassland	0.754716981
78	Rocky Mountain Subalpine-Montane Riparian Woodland	0.566037736
82	Inter-Mountain Basins Greasewood Flat	5.094339623
85	North American Arid West Emergent Marsh	0.188679245
98	Great Basin Foothill and Lower Montane Riparian Woodland and Shrubland	1.132075472
100	Mediterranean California Red Fir Forest and Woodland	0.754716981
102	Mediterranean California Ponderosa-Jeffrey Pine Forest and Woodland	1.132075472
107	North Pacific Montane Grassland	0.188679245
110	Open Water	3.962264151
111	Developed, Open Space - Low Intensity	1.509433962
112	Developed, Medium - High Intensity	0.566037736
114	Agriculture	3.773584906
116	Recently Burned	0.188679245
117	Recently Mined or Quarried	0.188679245
121	Invasive Annual Grassland	0.566037736
122	Invasive Annual and Biennial Forbland	0.188679245

TABLE 3. Construction of candidate RSPF models for male black bear habitat selection at coarse and fine spatial resolutions. The most parsimonious model is shown in italics.

Coarse resolution candidate models	**AICc**	**p-value**
Distance to water + urban polygon + distance to trail + distance to stream + distance to road + distance to recreation site + human population density + landcover	3419.93	<.0001
Distance to water + urban polygon + distance to stream + distance to road + distance to recreation site + human population density + landcover	3417.91	<.0001
Urban polygon + distance to stream + distance to road + distance to recreation site + human population density + landcover	3410.55	<.0001
Fine resolution candidate models	**AICc**	**p-value**
Distance to water + urban polygon + distance to trail + distance to stream + distance to road + distance to recreation site + human population density + landcover	3611.66	<.0001
Distance to water + urban polygon + distance to trail + distance to stream + distance to road + human population density + landcover	3612.56	<0.001
Distance to water + urban polygon + distance to trail + distance to stream + human population density + landcover	3614.18	<.0001

TABLE 4. Construction of candidate RSPF models for female black bear habitat selection at coarse and fine spatial resolutions. The most parsimonious model is shown in italics.

Coarse resolution candidate models	**AICc**	**p-value**
Distance to water + urban polygon + distance to trail + distance to stream + distance to road + distance to recreation site + human population density + landcover	14255	<.0001
Distance to water + urban polygon + distance to stream + distance to road + distance to recreation site + human population density + landcover	14147.1	<.0001
Fine resolution candidate models	**AICc**	**p-value**
Distance to water + urban polygon + distance to trail + distance to stream + distance to road + distance to recreation site + human population density + landcover	14994.6	<.0001

TABLE 5. Male black bear habitat selection model variables at fine temporal scale.

Year	**Coarse resolution habitat selection model variables**	**AICc**	**p-value**
2005	Urban polygon + **distance to trail** + **distance to stream** + **distance to recreation + human population density + landcover**	1015.5	<0.0001
2006	Distance to water + **distance to trail** + **distance to stream** + distance to road + **distance to recreation + human population density + landcover**	627.391	<0.0001
2007	Urban polygon + **distance to trail** + **distance to stream** + distance to road + **distance to recreation + human population density + landcover**	387.926	<0.0001
2008	Distance to water + urban polygon + **distance to trail** + **distance to stream** + distance to road + **distance to recreation + human population density + landcover**	314.824	<0.0001
Year	**Fine resolution habitat selection model variables**	**AICc**	**p-value**
2005	**Landcover** + urban polygon + **distance to stream** + **distance to water** + distance to trail + **distance to road** + **human population density** + distance to recreation site	1031.4	<0.0001
2006	**Landcover** + **distance to stream + distance to water** + distance to trail + **distance to road + human population density**	586.86	<0.0001
2007	**Landcover** + urban polygon + **distance to stream + distance to water** + **distance to road + human population density** + distance to recreation site	551.24	<0.0001
2008	**Landcover** + urban polygon + **distance to stream + distance to water + distance to road + human population density**	318.71	<0.0001

TABLE 6. Female black bear habitat selection RSPF models at fine temporal scale. Bold font shows common variables.

Year	Habitat Selection Model Variables	AICc	p-value
2005	Distance to water + **distance to trail** + distance to stream + **distance to road** + **distance to recreation site** + **landcover**	2619.35	<0.0001
2006	**Distance to trail** + distance to stream + **distance to road** + **distance to recreation site** + **landcover** + population density	1626.3	<0.0001
2007	Urban polygon + **distance to trail** + distance to stream + **distance to road** + **distance to recreation site** + population density + **landcover**	569.865	<0.0001
2008	Distance to water + urban polygon + **distance to trail** + distance to stream + **distance to road** + **distance to recreation site** + population density + **landcover**	159.013	<0.0001
2009	Distance to water + urban polygon + **distance to trail** + **distance to road** + **distance to recreation site** + population density + landcover	268.056	<0.0001
2010	Distance to water + urban polygon + **distance to trail** + **distance to road** + **distance to recreation site** + population density + **landcover**	2594.77	<0.0001
2011	Distance to water + urban polygon + **distance to trail** + distance to stream + **distance to road** + **distance to recreation site** + population density + **landcover**	1261.28	<0.0001
Year	**Habitat Selection Model Variables**	**AICc**	**p-value**
2005	Distance to stream + **urban polygon** + distance to recreation site + **landcover + population density**	2551.07	<0.0001
2006	**Urban polygon +** distance to trail + distance to stream + distance to water + distance to recreation site + **landcover** + **population density**	1816.6	<0.0001
2007	**Urban polygon** + distance to trail + distance to stream + distance to recreation site + **population density** + **landcover**	557.147	<0.0001
2008	**Urban polygon** + distance to road + distance to	159.013	<0.0001

	recreation site + **population density** + **landcover**		
2009	Distance to water **+ urban polygon** + distance to trail + distance to road + **distance to recreation site** + **population density** + landcover	190.095	<0.0001
2010	Distance to water + **urban polygon** + distance to road + **distance to recreation site** + population density + **landcover**	2043.84	<0.0001
2011	Distance to water + **urban polygon** + distance to trail + **population density** + **landcover**	898.005	<0.0001

CHAPTER THREE

Conflict carnivores: Assessing the impact of scale on estimates of carnivore mortality risk

Abstract

We examined the spatial distribution of 366 human-induced black bear mortalities in the Lake Tahoe Basin (WGB) of western Nevada. Data were collected over the period spanning 1996-2013. Our analyses investigated 1) the anthropogenic and landscape variables associated with mortality risk and 2) the impact of spatial and temporal resolution on analyses. We used logistic regression to model and map probability of mortality in the WGB based on anthropogenic land use variables and landscape features, while accounting for different causes of mortality. We tested the impact of refining spatial resolution and temporal resolution of our analyses on estimates of mortality risk for black bears. Human-induced mortalities of black bears were overwhelmingly concentrated near major roads, in the town of Incline Village in the northern WGB, and along the eastern foothills of the Carson Range of the Sierra Nevada mountains. Models analyzing the spatial distribution of bear mortalities caused by vehicle collisions yielded significantly different mortality risk results when assessed at coarse and fine spatial resolutions. Modeling at coarse ($1km^2$) spatial resolution suggests that mortality risk is associated with landcover type and distance to nearest stream; in contrast, models that use finer spatial resolution ($30m^2$) found that mortality risk can be better predicted as a function of distance to water, distance to major road, and landcover type. Overall, the majority of the WGB landscape poses low mortality risk to black bears, with noticeable moderate and high-risk areas characterized at fine spatial resolutions by a variety of

anthropogenic parameters. These results show that although large carnivores, such as black bears, view their landscapes at the coarse resolution when assessing home-range requirements and habitat selection, analyses show that mortality risk phenomena operate at a finer spatial resolution.

1. Introduction

Certain characteristics of large carnivore ecology, such as large spatial requirements, low reproductive rates, and low population densities, make them vulnerable to environmental disturbances (Treves and Naughton-Treves 1999, Woodroffe 2000). Many studies have documented the role of human land use in fragmenting carnivore habitat and driving population decline (Randa and Yunger 2006, Ordenana, Crooks et al. 2010, Burton, Sam et al. 2011, Linke, McDermid et al. 2013). Habitat loss and fragmentation have been, and continue to be, the primary cause of extinction at all spatial scales, from local populations to the scale of entire biomes (Millennium Ecosystem Assessment, 2005). The wide-ranging nature of large carnivores often causes them to spend time in unfavorable habitat when dispersing through a landscape matrix impacted by habitat fragmentation (Crooks 2002, Hanski, Zurita et al. 2013).

Exacerbating habitat fragmentation from human land use, globally increasing human development has forced humans and carnivores to share landscapes. When carnivores occupy environments overlapping with human activity, unfavorable human-carnivore interactions may result (Graham, Beckerman et al. 2005, de Azevedo and Murray 2007, Basille, Herfindal et al. 2009, Silva-Rodriguez, Soto-Gamboa et al. 2009), sometimes with major consequences for fitness (Delibes, Ferreras et al. 2001, Schlaepfer, Runge et al. 2002, Battin 2004). These situations, known generally as "human-carnivore conflict," take on many forms and encompass damage to or destruction of human property by carnivores, and human-caused disturbance to animals (Treves and Karanth

2003, Silva-Rodriguez, Soto-Gamboa et al. 2009). Extreme cases include carnivore attacks on humans (Packer, Ikanda et al. 2005) and more commonly, human-induced mortality to carnivores (Bradley, Eric et al. 2003, Woodroffe and Frank 2005, Roger, Laffan et al. 2011).

In certain systems with increasing human influence on the environment, high rates of human-induced mortality of carnivores can threaten carnivore population persistence. In light of this, conservation scientists and managers seek to understand the drivers of mortality risk, including the attraction of carnivores to high-risk areas. In general, the availability of resources that are attractive to both people and carnivores drives these interactions (Knight 2000, Conover 2001). Both the resources, and mortality resulting from conflict, can occur across a variety of habitat types and land uses from wilderness to urban areas (Graber 1986, Woodroffe and Ginsberg 1998, Treves and Karanth 2003). Many mortality events occur when wide-ranging carnivores disperse through parts of a landscape that are human dominated, particularly areas that require crossing high-speed road systems (Mech 1989, Woodroffe and Ginsberg 1998, Grilo, Bissonette et al. 2009, Roger, Laffan et al. 2011).

Ecologists use risk models to analyze and map the spatial patterns of mortality risk across a landscape. Although carnivore studies often use models constructed with both bio-physio environmental variables and parameters representing human land use, rarely are multiple anthropogenic variables used. In many systems, different types of human influence on the landscape may drive human-carnivore interactions and associated mortality events, including human recreational activities in backcountry areas (Goodrich and Berger 1994, Ruth, Smith et al. 2003, Markovchick-Nicholls, Regan et al. 2008, Goad, Pejchar et al. 2014, Pejchar, Reed et al. 2015). It is therefore important for mortality risk analyses to include anthropogenic variables that specifically reflect the diversity of human influence types and magnitudes across the landscape.

Mortality risk analyses are commonly constructed at a single coarse spatial resolution, justified by the assumption that this reflects the resolution at which carnivores use a landscape (i.e. home range, territory, etc.). Recent improvements in the resolution at which habitat and movement data are collected have allowed us to test this assumption. Although large carnivores have large home range areas, and appear to use coarse-resolution cues to navigate landscapes (Chapter 1), there is evidence that fine-resolution variables, especially variables representing anthropogenic land use (Chapter 3), may influence habitat selection or mortality risk (Mayor, Schneider et al. 2009, Basille, Van Moorter et al. 2013, Waller, Belant et al. 2013). Bowyer et al., (2006) asserts that there is a strong need in wildlife ecology studies to understand how patterns and dynamics of selection choices vary with scale, as well as to identify how patterns at one scale relate to processes operating at other scales. Many studies show that landscape heterogeneity can be observed at multiple scales, and identifying the response of wildlife to such heterogeneity is therefore best studied at coarse and fine scales (Beever, Swihart et al. 2006, Boyce 2006). Such studies will both provide a better understanding of the way in which carnivores view and use their environment and facilitate better management aimed at reducing threats from human activity.

To better understand how mortality risk for black bears is characterized across the landscape, and to evaluate the impact of analytical resolution on model predictions, we developed mortality risk models by analyzing the specific landscape characteristics at locations of human-induced mortality of black bears in the Lake Tahoe Basin (WGB) in Western Nevada. We created models using data at multiple spatial resolutions to evaluate the anthropogenic and environmental landscape features driving mortality risk for these black bears and translated these models into spatial representations (maps).

2. Study Area

The study area encompasses the eastern region of the Lake Tahoe Basin (WGB), a part of the Humboldt-Toiyabe forest system located between the Carson Range of the Sierra Nevada and the Sweetwater and Pinenut mountain ranges in Western Nevada. This region represents some of the most heavily forested areas in the State of Nevada (Raumann and Cablk 2008) (Fig. 1). Frequent rainfall, thick woody vegetation, and pine forests characterize the western Sierra Nevada, while the rain shadow effect provides for a more arid, shrubland ecosystem in the more eastern regions (Manley, Murphy et al. 2004, Raumann and Cablk 2008). Although federally owned forest areas have remained protected, the WGB has undergone rapid residential and commercial development in the last half century with 2391 ha of forested land converted to developed land since 1940, driven by demand for recreational areas, resort hotels, and private vacation residences (Raumann and Cablk 2008). This development has caused a decline in forested areas and other native vegetation (Fig 2) (Beckmann and Lackey 2008, Raumann and Cablk 2008, Lackey, Beckmann et al. 2013). Previously forested areas were widely transformed to accommodate human-dominated land uses, while areas with currently intact forest are popular for outdoor recreation, with numerous ski slopes and camp sites established throughout the landscape (Goodrich and Berger 1994, Burt and Rice 2009, Lackey, Beckmann et al. 2013).

The WGB is home to over 60 mammal species (Schlesinger, Ramsos 2000), including a population of black bears estimated to be around 400 individuals (Lackey 2004, Lackey, Beckmann et al. 2013) with genetically-linked subpopulations inhabiting distant areas of the US Great Basin, geographically separated by mountain ranges (Beckmann 2002, Beckmann and Berger 2003, Lackey 2004). Although mortality data collection for black bears is ongoing in the WGB, very little data on risk of black bear mortality within the region had been analyzed prior to this study, and aside from general information regarding hotspots of black bear-human conflict (Beckmann and Lackey 2008), little was known about how multiple anthropogenic landscape variables influence black bear mortality risk in this region.

3. Methods

3.1 Black bear mortality data collection

For this study, we used black bear mortality reports collected by the Nevada Department of Wildlife (NDOW) and Wildlife Conservation Society's (WCS) North America Program. From 1997-2013, authorities from NDOW responded to incidents of vehicle collisions with bears along local roadways as well as calls from residents about bear-related public safety concerns. Detailed reports for both of these issues were recorded upon response to the incident, and included a full description of the location and often an associated address. We also included reports of "sport hunt" mortalities beginning in 2011when the state of Nevada implemented a legal black bear hunting season. Hunters with a tag for bear harvest are required by law to record the precise location of where they took down the animal and report this information when delivering the animal carcass to NDOW authorities before they can process the animal. Tag information was also entered into the mortality database. Information on illegal black bear mortalities were gathered opportunistically from anonymous phone calls or tips from local residents. Last, accidental mortalities were recorded in detail by NDOW authorities and were a result of accidents incurred during various research processes. We visited the location of each mortality report and recorded a precise GPS location

"Illegal" mortalities have only been documented in 3 of the 16 years of data (2001, 2007, and 2011) and are likely from local residents who have faced severe property damage in the past from bears. "Public safety" mortalities occur when NDOW deploys agents to euthanize bears that appear to not be afraid of human presence, present a direct threat to humans, or are found using public areas with humans present. In the vast majority of cases, 'nuisance' calls result in these bears simply being caught and being subjected to deterrent techniques (i.e. rubber bullets and Karelian bear dogs) to discourage their use of an area. However, if their behavior is deemed unsafe for the general public, they can be considered for removal. Similarly, the "3-strikes" policy provides for NDOW to euthanize bears that have demonstrated behavior unsafe for the public on more than 3 or more occasions. In the vast majority of cases, bears are not lethally removed.

3.2 Geographic Information Systems and Development of Landscape Parameters

In order to predict mortality risk across the landscape, we used nine spatial data layers that were biologically relevant to large carnivores based on published literature in a GIS (ESRI ArcMap 10.2.2) representing environmental features and the anthropogenic landscape in the WGB (Table 2) (Van Why and Chamberlain 2003, Whittington, St Clair et al. 2005, Nellemann, Stoen et al. 2007, Goldstein, Poe et al. 2010, Obbard, Coady et al. 2010, Morzillo, Ferrari et al. 2011). Although certain anthropogenic variables are often found in similar studies of wide-ranging large carnivores, such as distance to road and human population density, we also used parameters that are specific to the WGB landscape with biological support for their impact to large carnivore behavioral ecology, such as distance to recreation site, distance to trail, and distance to railway (Goodrich and Berger 1994, Markovchick-Nicholls, Regan et al. 2008, Merenlender 2008, Burt and Rice 2009, Musiani, Anwar et al. 2010, Wynn-Grant 2015). The landcover layer was generated by specialists at NDOW specifically for biodiversity assessments in the WGB and projected at 1m^2 resolution. Feature layers representing major water bodies, railways, recreation sites, stream and road systems, and trails were acquired from NDOW and the Douglas County open access GIS resources. We used the Euclidean distance tool in ArcMap to create layers representing the straight-line distance from any map cell to the nearest feature. Feature layers representing urban polygons and human population density were available from the USDA's Lake Tahoe Basin Management Unit. All feature layers were reclassified in ArcMap with nearest neighbor tools to classify and project them at 30m^2 (fine) and 1km^2 (coarse) spatial resolution for analyses.

We took the GPS location points of mortality incidents (n= 366 location points) and created shapefiles using ArcMap. We then used the Buffer tool to create 5km^2

circular buffers around each location point (Treves, Martin et al. 2011). We generated random locations (n=732) using ArcMap outside of the buffered "used" mortality points to represent "available" resource units.

In order to better understand mortality risk, we identified habitat characteristics at mortality point locations in the study. We used Extraction Tools in ArcGIS to calculate values or characteristics (e.g. landcover type) for the nine variables at both coarse and fine spatial resolutions measured on the "used" points representing mortality and "available" resource units (Ciarniello, Boyce et al. 2005, Ciarniello, Boyce et al. 2007). These location points and associated values were then exported into a spreadsheet and used by statistical software program JMP (SAS Program, 2014) for analyses.

3.3 Model construction and data analysis

We developed resource selection probability function (RSPF) models for two levels of spatial analysis using the coarse and fine resolution landscape parameters and black bear mortality location data collected over the course of the study period. Resource selection analysis employed a logistic regression approach, using the logit command to compare characteristics of black bear mortality "used" sites with "available" sites in the study region (Manly 2002, Sawyer and Brashares 2013). To reflect resource selection variability on a temporal resolution, we partitioned the black bear mortality locations into separate datasets by season.

For our logistic regression-based RSPF model, a "used" GPS location was considered a "success" and given a value of 1, where an "available" resource unit was given a value of 0, and the nine variables (Table 2) used as predictor variables. The RSPF is assumed to take the form:

$$w^*(x) = exp(\beta o + \beta_1 x_1 + ... \_ \beta_p x_p)/1 + exp(\beta_0 + \beta_1 x_1 + ... + \beta_p x_p)$$

where $x = (x_1, x_2, ..., x_p)$ holds the values for the X variables that are measured on a unit. Maximum likelihood estimates of the β parameters in the equation was calculated. We used chi-squared tests on deviances to assess whether there is any evidence that the probability of use of a location is related to a combination of the variables being considered.

For both spatial resolutions, we tested for collinearity of candidate variables using Pearson correlation coefficients, and variables with a correlation coefficient $(r) > 0.7$ were not included together in the models (Ciarniello, Boyce et al. 2007, Sawyer and Brashares 2013). We practiced backwards stepwise regression to identify the best fitting model. Our first RSPF model included all nine of our biophysical landscape variables, and we iteratively eliminated variables with a p-value above our threshold ($p=0.05$). We recorded AICc values for each model iteration (Burnham & Anderson, 1998; Zielinski et al., 2004; Harris et al., 2008; Horne et al., 2008; Kirk & Zielinski, 2009), and we considered models comparable if the delta AIC was < 2.0 (Ciarniello et al., 2007). The model with the lowest AICc value was considered most parsimonious and best fit for the data. For models with similar AICc values, we chose the model with fewer terms (Quinn & Keough, 2002).

We assessed the predictive capability of each model using a Spearman's rank correlation based on 5-fold cross validation (Boyce et al. 2002). In this procedure, we estimated an RSPF model using a random draw of 80% of the data. We then used this model to predict the frequency of occurrence in the withheld 20% of the data using 10 RSPF bins, and repeated the process 5 times, replacing the withheld 20% and removing the next 20% (Boyce et al. 2002). For our study, a model that had strong predictive capabilities would have a higher number of locations in bins with the highest RSPF scores. Once the final RSPF was derived, we used ArcMap 10.2 (ESRI, 2013) to map the probability of habitat selection over the entire study area.

4. Results

4.1 Field sampling

Black bear mortality reports collected during the research period totaled 366 (vehicle collisions n=160; public safety n= 106; other n=40) with a general increase in number of incidents over the years (Table 1). We used ArcGIS to create a map of mortality incidents that shows what appear to be clusters of points in areas considered "hotpots" across the landscape.

4.2 Mortality trends

Data from human-induced mortality reports collected by NDOW since 1997 indicate that as both the black bear population and human population in the study area have increased, incidents of human-induced mortality to black bears has also increased (Beckmann and Berger 2003, Lackey 2004, Lackey, Beckmann et al. 2013). The year

2007 had a particularly high number of mortality reports (Fig. 3). These non-natural sources of black bear mortality are driven by bear-human interactions, ranging from conflict over shared resources to hunter off take. Vehicle collisions make up 44% (n=160) of total mortalities reported, and account for the majority of mortalities for most years up to 2008 (Fig. 3). In contrast, public safety-related mortalities accounted for 36% (n=106) of total mortalities reported and were the leading source of black bear mortality in the years 2008 and 2010. Sport hunt mortalities account for 39% (n=12) and 35% (n=11) of mortality reports for the years 2011 and 2012. Mortalities stemming from illegal activity were extremely rare (n=6) and only occurred in three years of the total study period (1997-2013). Black bear mortality reports from accidental and miscellaneous causes were also infrequent, contributing to 5% (n=18) and 7% (n=25) of total mortalities, respectively (Fig. 3).

Vehicle collision and public safety-related mortalities, the two most common types of human-induced mortality to black bears in the WGB, display temporal trends. Figure 4 shows the number of mortality incidents reported by month and suggests that public safety-related mortalities peak in the summer between June and August, with 57% (n=75) of all public safety mortalities occurring during these three months over the course of the study period. Contrastingly, incidents of vehicle collisions peak in the fall between September and November, with 61% (n=98) of all vehicle collision mortalities occurring during these three months over the course of the study period. A 2 sample t-test suggests that during the summer and fall months, these rates of public safety and vehicle collision mortalities are significantly different from each other (p=0.009). Unsurprisingly, these mortality types, and all mortality types, become extremely infrequent between January-March (n=9) when black bears in the WGB are typically in hibernation (Fig. 4).

We also investigated mortality trends by sex of bear (Fig. 5), finding that for most mortality types, incidents were as frequently reported for male as for female animals. However, 70% (n=93) of public safety-related mortalities involved male bears, and due to state hunting laws and possibly hunter selection, 76% of sport hunt mortalities were males.

Age of bear at time of mortality also varied considerably (Fig. 6). Overwhelmingly, cubs in their first year experienced the highest rate of mortality with 30% (n=109) of all reported mortality incidents. 63% (n=69) of mortalities for cubs in their first year were vehicle collisions, while 26% were public safety. We calculated that 43% (n=69) of all vehicle and 21% (n=28) of all public safety-related mortalities involved cubs in their first year, a trend supported by evidence from previous study in the region (Beckmann and Lackey 2008).

4.3 Landscape variables at multiple resolutions

Pearson's correlation tests between continuous variables indicated a strong correlation between distance to trail and distance to rail variables measured at both coarse and fine spatial resolutions (p=0.93 & p=0.95, respectively) (Fig. 9). We thus omitted distance to rail as a predictor in all model construction, since trails are more abundant across the landscape and have greater biological significance to black bear behavior (Baldwin and Bender 2008, Costello, Cain et al. 2013).

When modeled at the fine spatial resolution, we found that the majority (68%) of the WGB study area has a probability of mortality risk at or under 25%, which we are considering low risk. We found that 17% of study area has moderate (25-50%) probability of mortality risk, and 14% of the study area has high (50-75%) probability of mortality risk. The areas of highest (75-100%) probability of mortality risk compromise 6% of the WGB study area.

We uncovered more patterns by exploring the relationships between single landscape variables and mortality risk trends. First, we found that for the two most frequent causes of mortality for black bears (vehicle collisions and public safety), the majority of these incidents occurred within 2 kilometers from a water body (Fig. 7). Further, we found that regardless of whether types of mortality incidents were separated individually or analyzed as a group, the majority of all mortality incidents occurred in landcover types classified as "forested" (Fig. 8). Shrubland landcover types were the second-most frequently associated with mortality incidents for all mortality types except public safety mortalities, where the "low development" landcover classifications was the second-most frequent (Fig. 8).

4.1 Mortality risk with coarse-resolution variables

Out of the mortality risk models built with variables measured at coarse spatial resolutions, the most parsimonious model (based on AICc value) identified distance to stream, type of landcover, and human population density as significant predictors of mortality risk for black bears in the WGB (Table 3) (χ^2=71.3, p<0.0001). Mortality risk was negatively associated with distance to stream, forested landcover categories, and positively associated with population density and a number of vegetation types. We used ArcGIS to then project mortality risk and map it across the study system (Fig. 10). We also constructed models withholding locations of vehicle collisions from the dataset. Here, we found that models built with coarse-resolution variables identified only landcover type and human population density as significant predictors of mortality risk (χ^2=11.39, p=0.034) (Table 4). We then attempted to predict probability of mortality risk based solely on locations of vehicle collisions, and found that coarse-resolution models identified distance to road and human population density as the only significant predictors (χ^2=33.45, p=0.0002) (Table 5).

4.2 Mortality risk with fine-resolution variables

For all of the RSPF models constructed with fine-resolution variables, the most parsimonious identified more anthropogenic significant predictors of mortality risk than the most parsimonious models constructed with coarse-resolution variables. Out of the mortality risk models built with variables measured at fine spatial resolutions, the most parsimonious model (based on AICc value) identified urban polygon, distance to water, landcover type, human population density, and distance to recreation site as significant predictors of mortality risk for black bears in the WGB (Table 3) (χ^2=268.85, p<0.0001). Mortality was positively associated with close distances to water, forested and human-modified landcover categories, high human population densities, and close distances to recreation sites, and negatively associated low human population densities. Mortality risk was then mapped in the study system (Fig. 10). As with the coarse-resolution analyses, we also constructed models withholding locations of vehicle collisions from the dataset. Here, we found that models built with fine-resolution variables identified distance to stream, landcover type, and human population density as significant predictors of mortality risk for non-vehicle collision mortality types (χ^2=52.07, p=0.001) (Table 4). We then attempted to predict probability of mortality risk based solely on locations of vehicle collisions, and found that fine-resolution models identified multiple variables as significant predictors of mortality risk, including urban polygon, distance to trail, landcover type, human population density, and distance to recreation site (χ^2=216.08, p=0.0001) (Table 4). Surprisingly, distance to road and distance to water were not significant predictors of vehicle-collision mortality risk.

Variables at fine temporal resolution

We constructed RSPF models at fine (seasonal) temporal resolutions using landscape variables measured at both coarse and fine spatial resolution. We found that for each season, the most parsimonious model built with variables at a fine spatial resolution identified more anthropogenic variables as significant predictors of mortality risk than the most parsimonious models constructed with coarse-resolution variables. For the model representing mortality risk in the summer season and built with variables measured at fine spatial resolutions, the most parsimonious model identified distance to stream, landcover type, human population density, and distance to trail as significant predictors of mortality risk for black bears in the WGB (χ^2=63.64, $p<0.0001$). When mortality risk in the summer season was modeled with coarse resolution variables, we found that only two significant predictors emerged: landcover type and human population density (χ^2=10.12, $p<0.0064$). We repeated this process using fine-resolution temporal data representing mortality risk probability for each season and continually found that models constructed with variables at fine spatial resolution estimated more significant predictors of mortality risk than models using coarse variables.

5. Discussion

5.1 Scale impacts of modeling mortality risk

There have been numerous studies of black bear ecology and space use, and almost all of these studies have been at relatively coarse resolutions of analysis (Carter, Brown et al. 2010, Obbard, Coady et al. 2010, Merkle, Krausman et al. 2011). This is both because, until recently, few studies had the capacity to collect finer-grained data (Brody and Pelton 1989, Clark, Dunn et al. 1993, Van Why and Chamberlain 2003, Merkle, Krausman et al. 2011), and because of the assumption that since black bears are relatively wide ranging, and omnivorous in their diet, their behavior would not reflect finer resolution variation in landscape structure (Mitchell and Powell 2007, Moyer, McCown et al. 2007). Our results stand in contrast to this assumption. We found that RSPF models using a suite of parameters measured at fine ($30m^2$) spatial resolutions identified more anthropogenic variables that are significant predictors of mortality risk than models built using the same parameters measured at a more coarse ($1km^2$) spatial resolution. Clearly, while black bears may select habitat at coarse spatial resolutions (Clark, Hayes et al. 1998, Hersey, Edwards et al. 2005, Garneau, Boudreau et al. 2008, Moyer, McCown et al. 2008, Obbard, Coady et al. 2010, Wynn-Grant 2015), the human activities that drive the majority of mortality in this system operate at finer spatial resolutions and are not detected in analyses with coarse-resolution variables.

The importance of several landscape features is common across spatial and temporal resolutions: landcover type, distance to permanent or seasonal water source, and human population density were significant predictors of mortality risk in both models. However, the fine-resolution analyses also identified proximity to urban areas as a factor that increases risk of mortality. As conflict appears to be the root of black bear mortality (Bunnell and Tait 1985, Elowe, Fuller et al. 1991, Pace, Anderson et al. 2000, Hebblewhite, Percy et al. 2003, Koehler and Pierce 2005, Howe, Obbard et al. 2007, Beckmann and Lackey 2008, Beston 2011), and urban areas are densely populated, such a correlation is hardly surprising but was not observed in the coarse-resolution analysis.

The model at the finer spatial resolution also shows that distance to human recreation sites is a driver of mortality risk for black bears in the WGB, suggesting that management of certain human activities, regardless of human population density, may be critical to bear population persistence. Recreation sites are located in heavily forested regions, near water sources: prime black bear habitat. The mortality risk associated with these sites serve as an example of how the pervasiveness of human activity in the WGB, apart from regions with urban development can fragment the landscape for wide-ranging animals like bears and generate habitat heterogeneity that can lead to negative interactions between humans and wildlife. Black bears are likely already present near these recreation sites, and may become attracted to these sites due to the anthropogenic foods available in these areas. Further analysis will distinguish whether public safety-related mortalities are higher in these regions than others.

RSPF models constructed at fine spatial resolutions also did a better job of identifying drivers of mortality risk than coarse-resolution models when vehicle collision locations were segmented into separate analyses. When models were constructed excluding vehicle collision data, coarse and fine resolution models identified landcover type and human population density as significant predictors of black bear mortality. Fine-resolution spatial models also identified distance to stream as significant. Identification of streams highlights the importance of water sources in this xeric system; this critical variable is likely to become increasingly important in an area threatened with persistent declines in water availability (Coats 2010, Sahoo, Schladow et al. 2013), particularly in the face of climate change and higher demands for water by humans in the region.

Analysis of road mortality data, segregated from other causes of mortality, also benefitted from an analysis at a finer spatial resolution. Here, the model identified numerous environmental and anthropogenic landscape characteristics in the areas directly adjacent to major roads that strongly influence the probability of a bear being killed. These variables include distance to water, a strong driver of bear movement and habitat selection in a water-limited ecosystem (Carter, Brown et al. 2010, Bourbonnais, Nelson et al. 2013), and distance to recreation site, which may reflect a bear's willingness to cross dangerous roadways in search of anthropogenic food sources that can be found near camp sites, ski resorts, and other outdoor recreation facilities (Beckmann and Lackey 2008, Merkle, Krausman et al. 2011).

5.2 Black bear mortality trends

Our investigations of mortality risk for black bears in the WGB demonstrated that vehicle collisions are the leading source of human-induced mortality to these animals. Wide-ranging large mammals in systems fragmented by human development are often required to cross roads during daily, and seasonal movements in search of resources or during dispersal searching for relatively high quality habitat. Even in areas with low human influence, crossing roads is often fatal and can have devastating consequences for population growth, especially when paired with other population pressures (Grilo, Bissonette et al. 2009, Roger, Laffan et al. 2011, Forman, Beckmann et al. 2012).

Our results also indicate that not all bears share a similar risk for vehicle mortality; young cubs are much more likely to be struck by a vehicle than any other age group. Black bear cubs remain with their mothers until their second hibernation period, close to their second year of age (Farley and Robbins 1995). Our analyses suggest that the cubs killed in vehicle collisions are likely following their mothers across roads and being killed in the process. Further study is warranted to identify whether there is more movement across roads by bears in the fall (possibly during hyperphagia), or if there are changes in human road use during these times, as analyses indicated a spike in vehicle collisions between September-November. Also, since the majority of vehicle collisions involve cubs, future research should investigate whether female bears are reluctant to take their newborn cubs across roads during spring and summer, but are more likely to disperse farther distances with them in the fall when they are older and preparing for hibernation.

Further research is needed to investigate additional landscape patterns related to locations of black bear-vehicle collisions in the WGB, as our fine-resolution RSPF model suggested that a series of biophysical and anthropogenic variables, not including distance to road, are the strongest predictors of vehicle collision risk for black bears in the WGB. This may indicate, for example that certain landscape attractants are influencing sows to cross a particular stretch of road in search of resources, or that major roads are fragmenting areas of high-quality habitat for black bears, which may have long term implications for habitat connectivity necessary for population maintenance. Fig. 17 highlights the spatial clustering of vehicle collision mortalities and public safety mortalities, demonstrating that not all major roadways in the region have a history of mortality incidents, despite them having high probability of mortality risk.

Among adults, data show that males are more vulnerable to human induced mortality than females and are more likely to be killed both in sport hunting and in directed mortality by authorities to secure public safety. In years 2011, 2012, and 2013, the portion of the study period with sport hunting, the maximum legal hunter off-take was never realized (n=20 total bear harvest objective). Males are selectively killed because the state law limits the number of female bears that can be harvested each year to protect the population growth potential of bears in the WGB. Although the 2011 and 2012 state hunting laws protected females from being harvested beyond certain limits (n=6), continued research is necessary to determine whether the additional magnitudes and spatial arrangements of female mortalities may ultimately hinder population stability.

5.3 Mapping mortality risk

Mortality risk maps using data at fine spatial resolutions display the WGB landscape as largely at low mortality risk levels, with 68% of the study area displaying lowest risk scores (<25%) (Fig. 10). Patches of high-risk areas occur along stretches of highways south of the greater Reno area, in livestock-rich lands along the foothills of the southern WGB, and for public safety mortalities, in residential neighborhoods directly north and east of Lake Tahoe (Fig. 12). Although this spatial composition is typical of heavily forested landscapes, such mortality "hotspots" may be barriers to the successful movement and potentially dispersal of black bears, ultimately limiting their persistence. An understanding of the spatial patterns of mortality risk for bears allows scientists to identify the human behaviors that may contribute to heightened mortality rates for this small population of carnivores.

Management Implications

Increased prevalence of human-wildlife conflict in the WGB, often leading to black bear mortality, may be a limiting factor in the ultimate persistence of the population (Beckmann and Lackey 2008, Schwartz, Haroldson et al. 2010, Rich, Mitchell et al. 2012). This trend is of elevated concern as human population in the region is expected to continually increase, thus influencing frequency of black bear mortality incidents and possibly enhancing the magnitude in certain hotspots. Depending on natural death rates, human-induced mortality beyond sustainable levels may impact carnivore persistence in the WGB and throughout the region (Nielsen, McDermid et al. 2010, Bateman and Fleming 2012). Despite the high rates of human-induced mortality, this population of black bears continues to grow (λ=1.16) (Lackey, Beckmann et al. 2013) likely in part due to the conservation and management policies that resulted from conclusions of long term research on this population (Beckmann and Berger 2003). While highly variable in its form and level, human influence across the WGB is pervasive, and the response of black bears to this heterogeneous landscape is also highly variable spatially and temporally. In response to these patterns, research at multiple resolutions yields comprehensive ecological understanding of the system and properly guided wildlife management. This work sets the stage for answering questions of suitable habitat connectivity in the WGB and the possible implications for tolerance thresholds to human activity and population persistence.

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FIGURES

FIGURE 1. The Lake Tahoe Basin (WGB) study system shown as part of the US Great Basin.

FIGURE 2. Gross change in area (ha) by landcover class from 1940-2002 in the southern WGB (Adapted from Raumann *et al*. 2008).

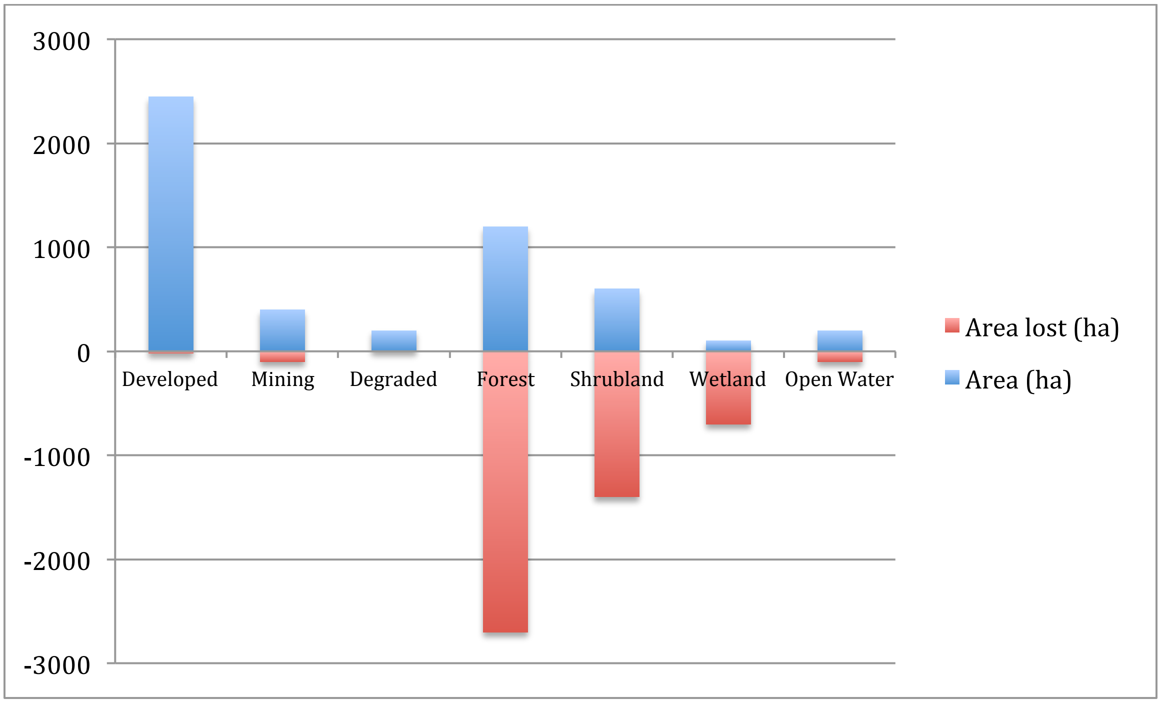


FIGURE 3. Categories and number of incidents of human-induced mortality to black bears in the WGB study system 1997-2013.

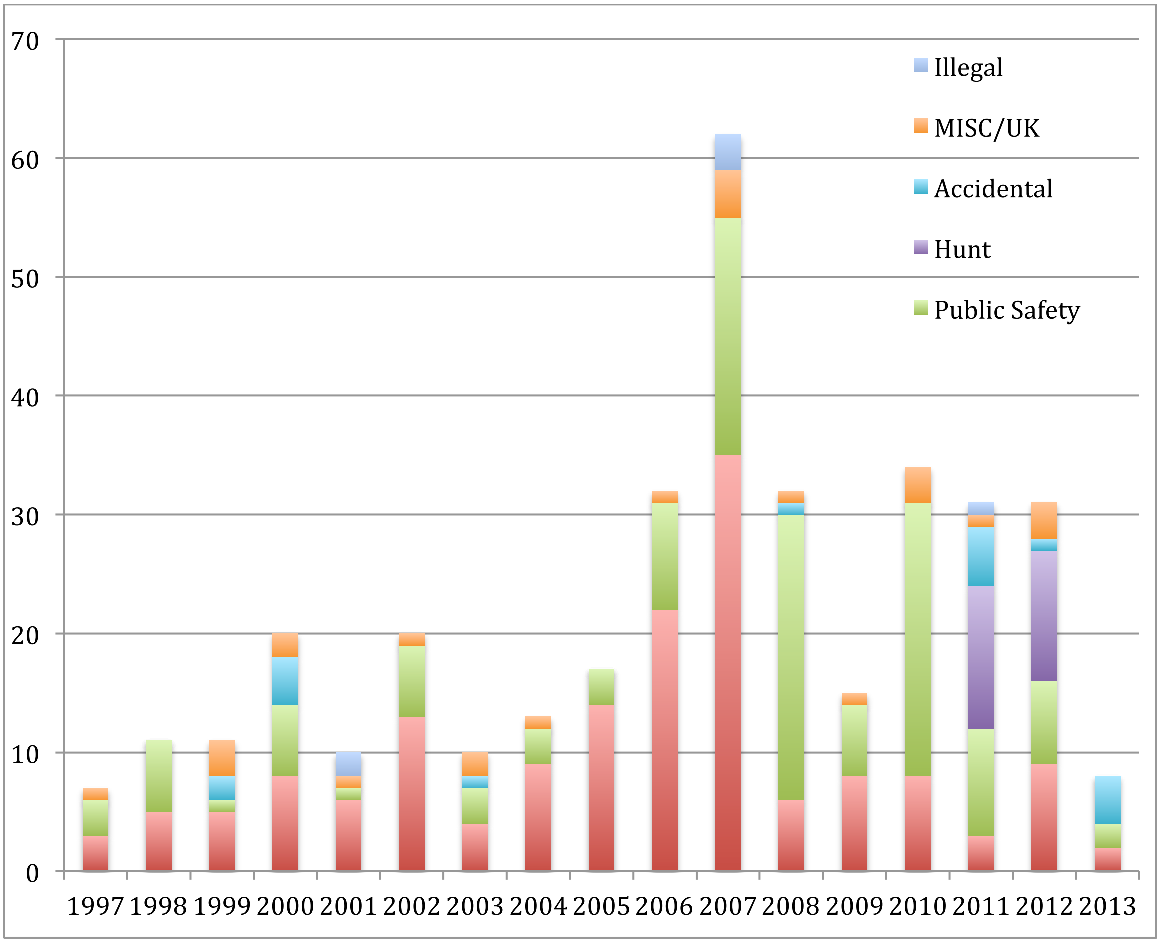


FIGURE 4. Temporal trends in frequency of the incidents of vehicle collision and all other mortality types for black bears in the WGB study system 1997-2013.

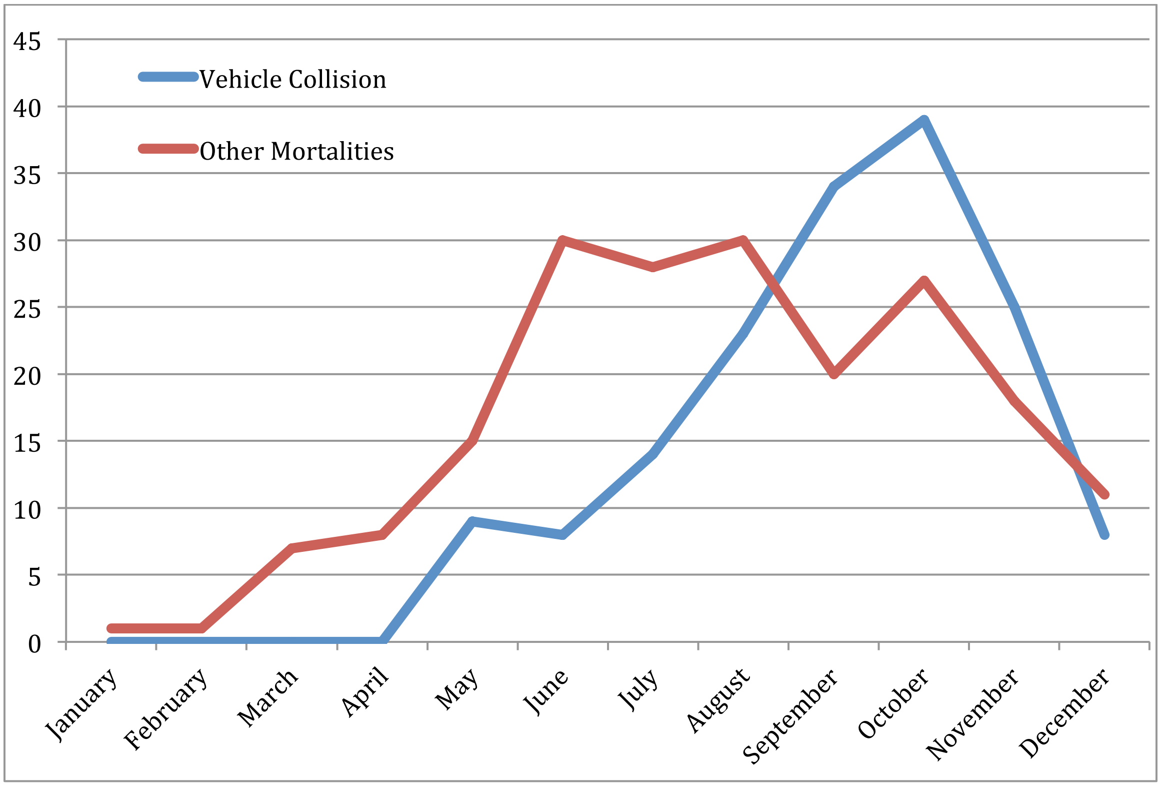


FIGURE 5. Incidents of mortality type by sex of bear in the WGB study system 1997-2013.

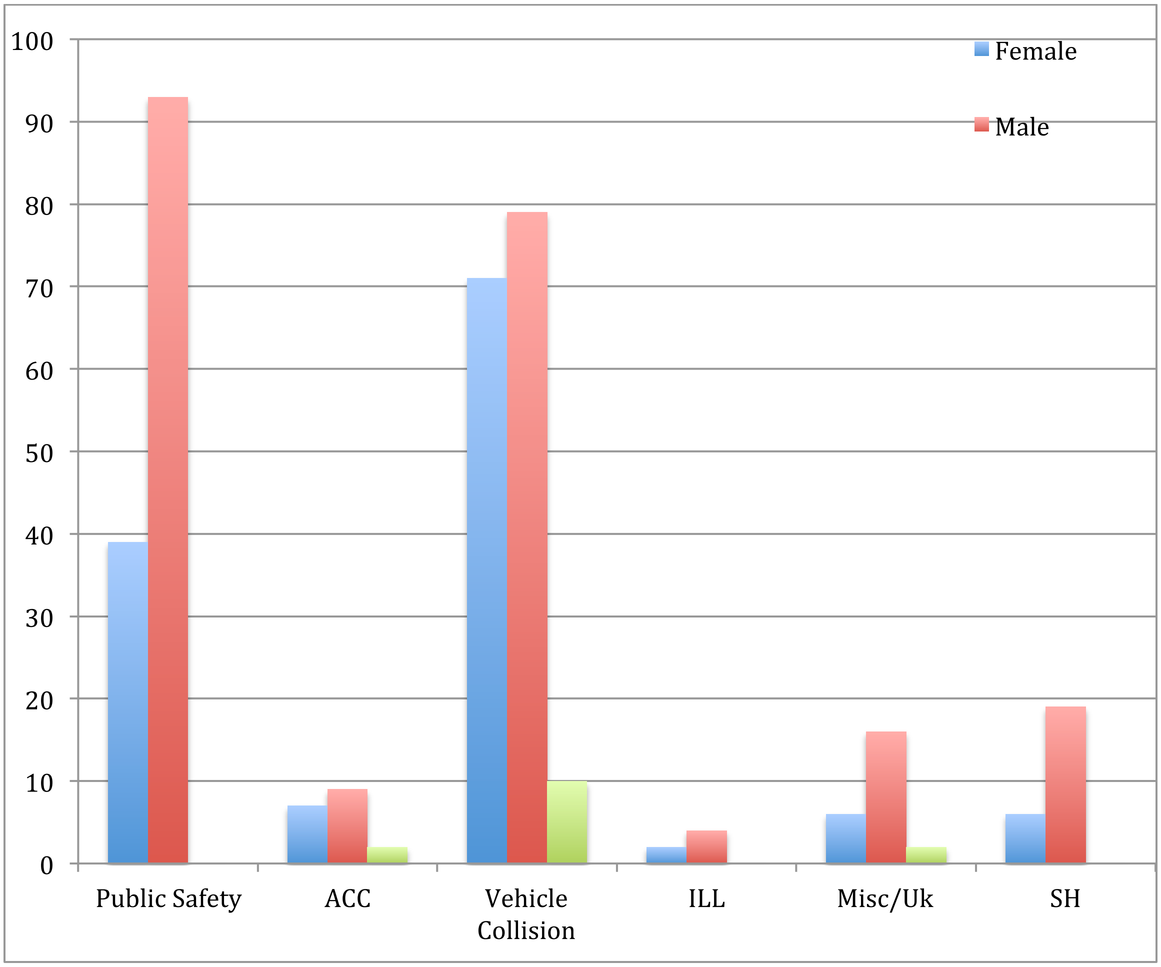


FIGURE 6. Incidents of mortality type by age of bear in the WGB study system 1997-2013.

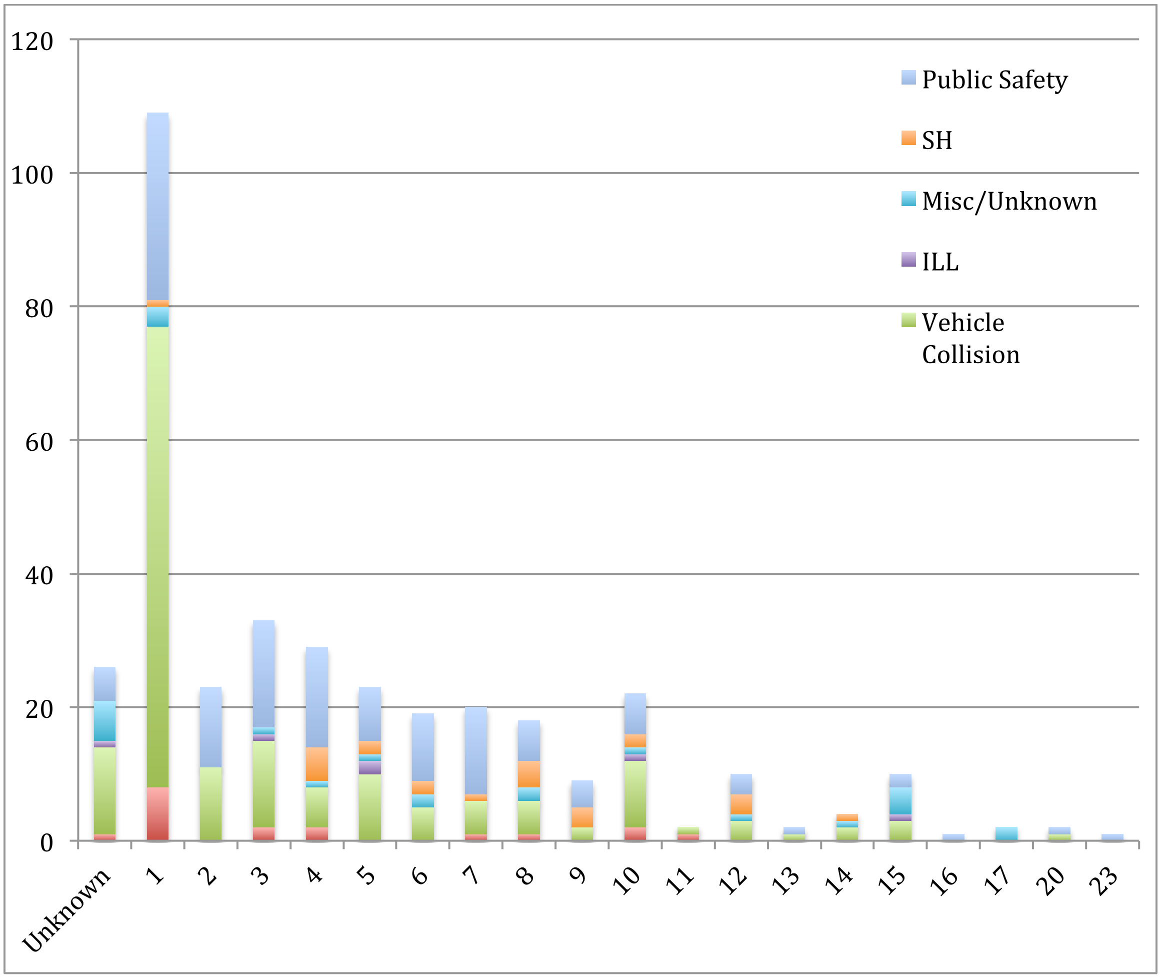


FIGURE 7. Vehicle collision and public safety mortality incidents in relation to distance to water body in the WGB study system 1997-2013.

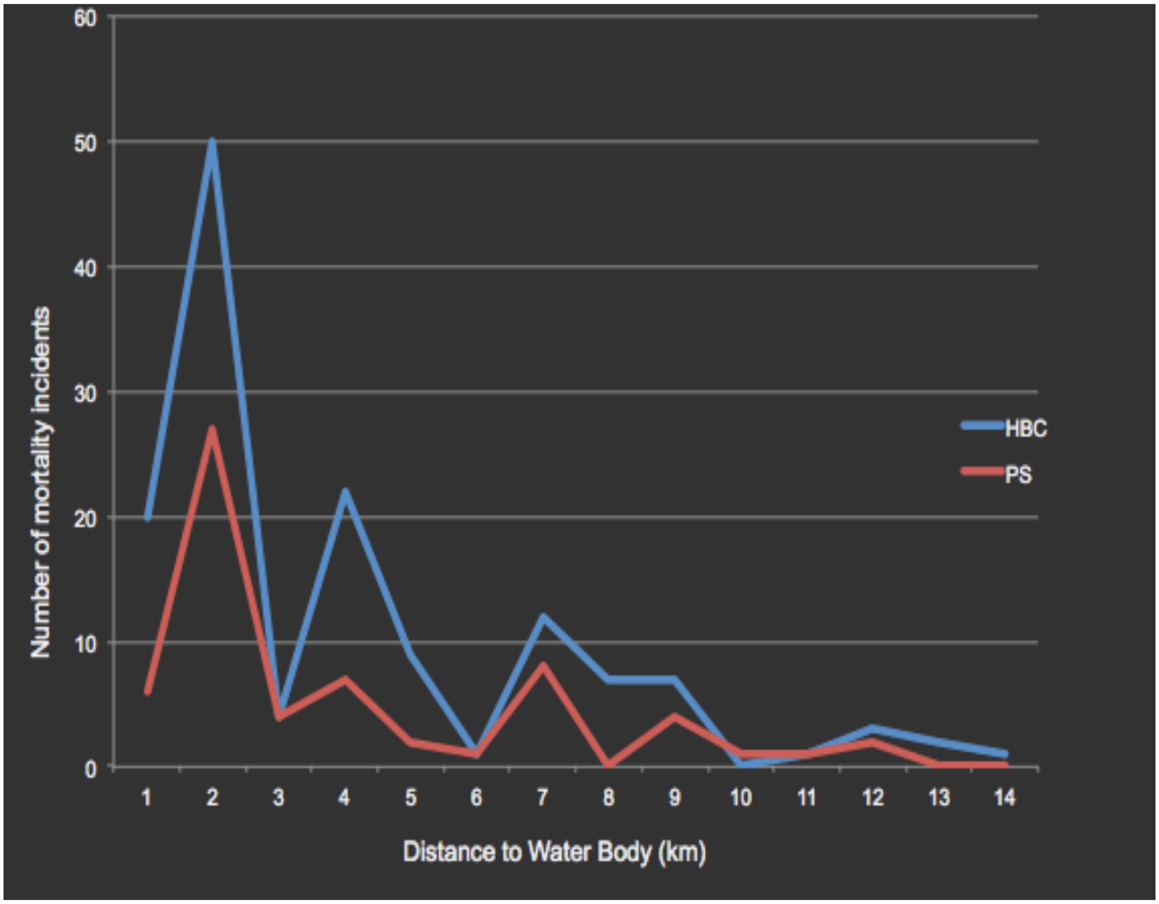


FIGURE 8. Incidents of mortality type landcover category in the WGB study system 1997-2013.

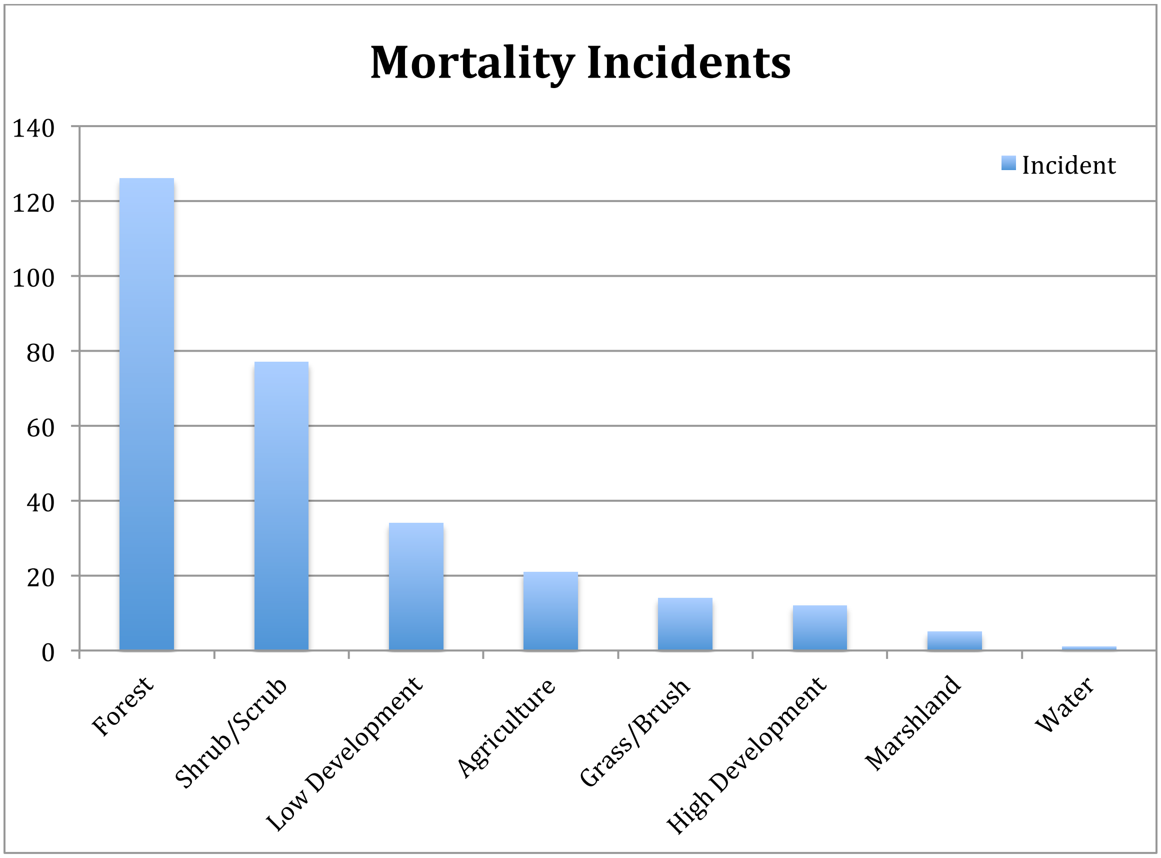
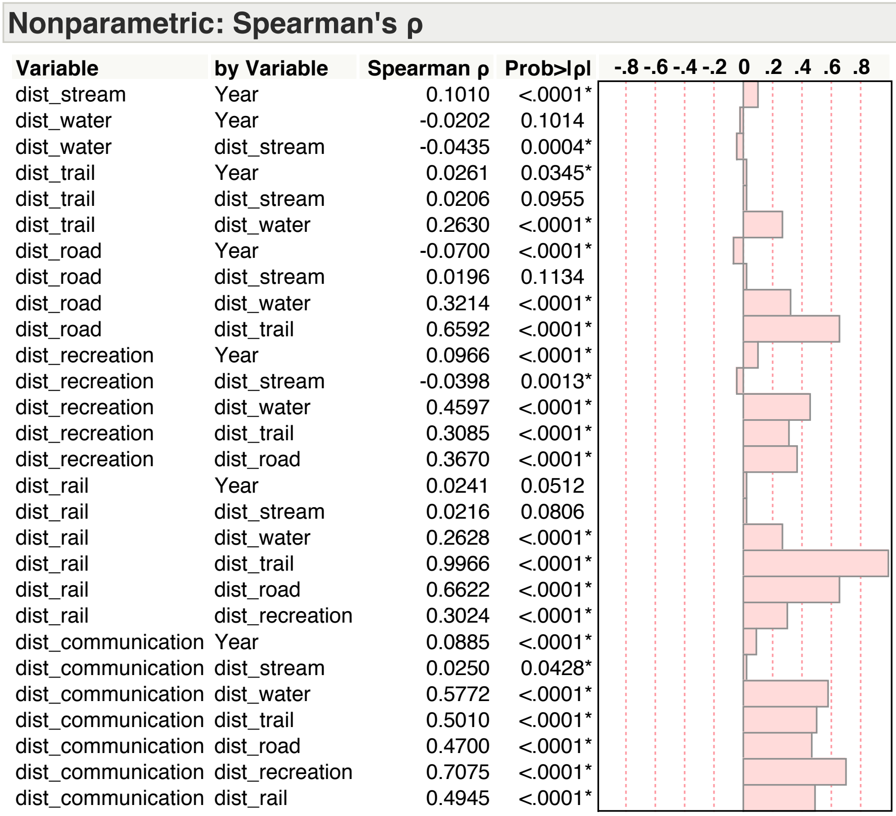


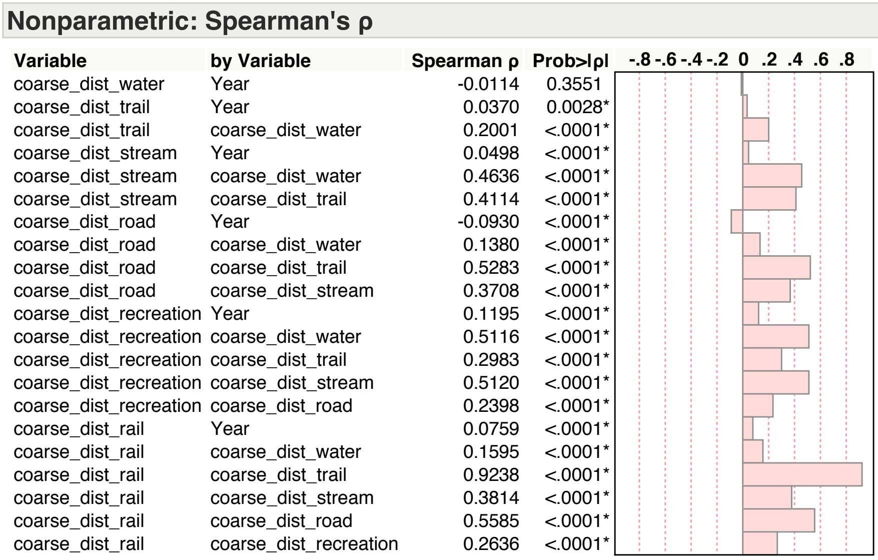
FIGURE 9. Spearman's ρ correlation test of RSPF model coarse (a) and fine (b) resolution variables. Distance to trail and distance to rail were highly correlated and thus distance to rail was eliminated from RSPF models.



Nonparametric: Spearman's ρ

Variable	by Variable	Spearman ρ	Prob>|ρ|
dist_stream	Year	0.1010	<.0001*
dist_water	Year	-0.0202	0.1014
dist_water	dist_stream	-0.0435	0.0004*
dist_trail	Year	0.0261	0.0345*
dist_trail	dist_stream	0.0206	0.0955
dist_trail	dist_water	0.2630	<.0001*
dist_road	Year	-0.0700	<.0001*
dist_road	dist_stream	0.0196	0.1134
dist_road	dist_water	0.3214	<.0001*
dist_road	dist_trail	0.6592	<.0001*
dist_recreation	Year	0.0966	<.0001*
dist_recreation	dist_stream	-0.0398	0.0013*
dist_recreation	dist_water	0.4597	<.0001*
dist_recreation	dist_trail	0.3085	<.0001*
dist_recreation	dist_road	0.3670	<.0001*
dist_rail	Year	0.0241	0.0512
dist_rail	dist_stream	0.0216	0.0806
dist_rail	dist_water	0.2628	<.0001*
dist_rail	dist_trail	0.9966	<.0001*
dist_rail	dist_road	0.6622	<.0001*
dist_rail	dist_recreation	0.3024	<.0001*
dist_communication	Year	0.0885	<.0001*
dist_communication	dist_stream	0.0250	0.0428*
dist_communication	dist_water	0.5772	<.0001*
dist_communication	dist_trail	0.5010	<.0001*
dist_communication	dist_road	0.4700	<.0001*
dist_communication	dist_recreation	0.7075	<.0001*
dist_communication	dist_rail	0.4945	<.0001*

(a)



Nonparametric: Spearman's ρ

Variable	by Variable	Spearman ρ	Prob>|ρ|
coarse_dist_water	Year	-0.0114	0.3551
coarse_dist_trail	Year	0.0370	0.0028*
coarse_dist_trail	coarse_dist_water	0.2001	<.0001*
coarse_dist_stream	Year	0.0498	<.0001*
coarse_dist_stream	coarse_dist_water	0.4636	<.0001*
coarse_dist_stream	coarse_dist_trail	0.4114	<.0001*
coarse_dist_road	Year	-0.0930	<.0001*
coarse_dist_road	coarse_dist_water	0.1380	<.0001*
coarse_dist_road	coarse_dist_trail	0.5283	<.0001*
coarse_dist_road	coarse_dist_stream	0.3708	<.0001*
coarse_dist_recreation	Year	0.1195	<.0001*
coarse_dist_recreation	coarse_dist_water	0.5116	<.0001*
coarse_dist_recreation	coarse_dist_trail	0.2983	<.0001*
coarse_dist_recreation	coarse_dist_stream	0.5120	<.0001*
coarse_dist_recreation	coarse_dist_road	0.2398	<.0001*
coarse_dist_rail	Year	0.0759	<.0001*
coarse_dist_rail	coarse_dist_water	0.1595	<.0001*
coarse_dist_rail	coarse_dist_trail	0.9238	<.0001*
coarse_dist_rail	coarse_dist_stream	0.3814	<.0001*
coarse_dist_rail	coarse_dist_road	0.5585	<.0001*
coarse_dist_rail	coarse_dist_recreation	0.2636	<.0001*

(b)

FIGURE 10. Map displaying coarse-resolution black bear mortality risk in the WGB based on average habitat selection probability for all significant landscape variables.

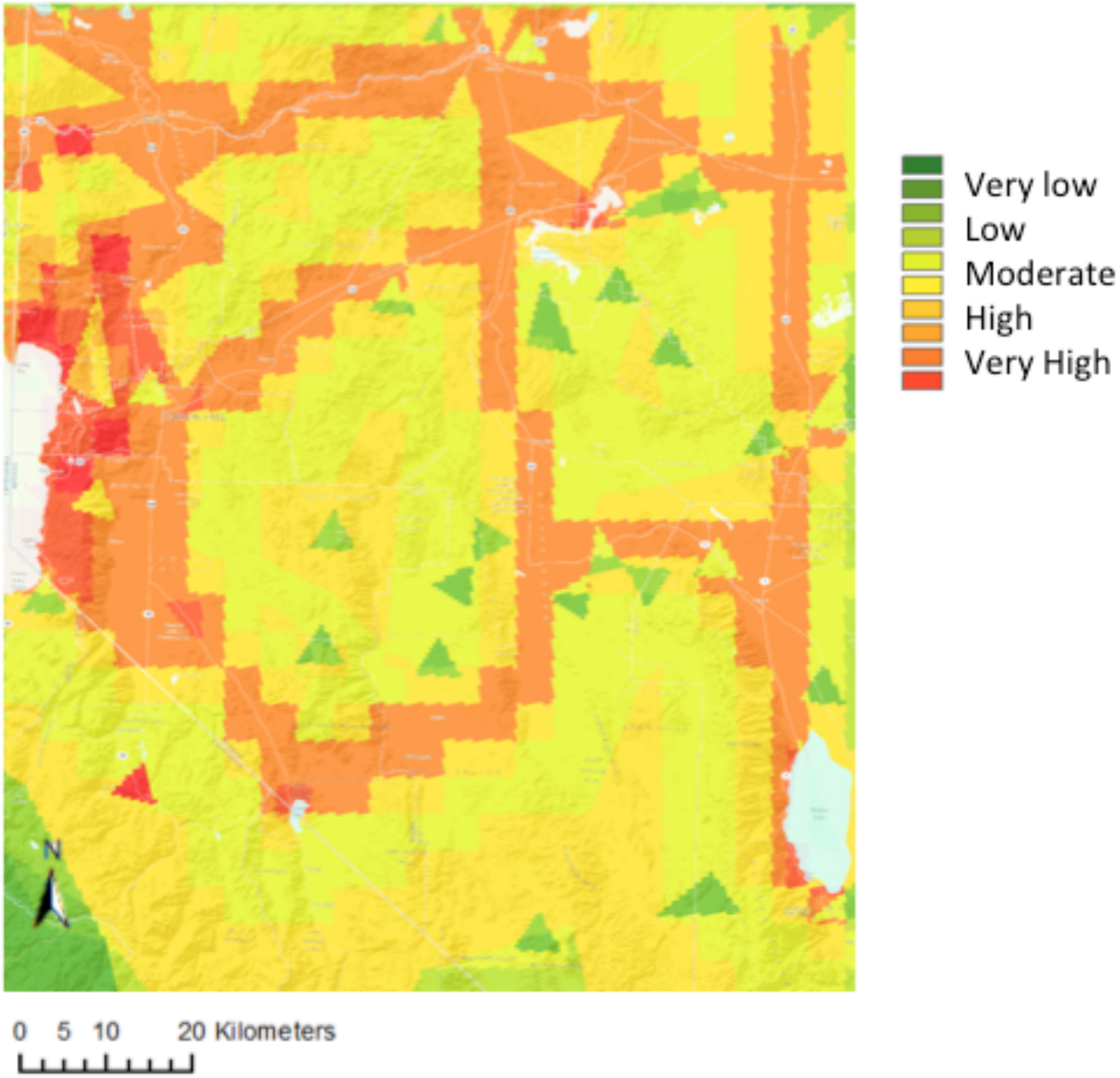


FIGURE 11. Map displaying fine-resolution black bear mortality risk in the WGB based on average habitat selection probability for all significant landscape variables.

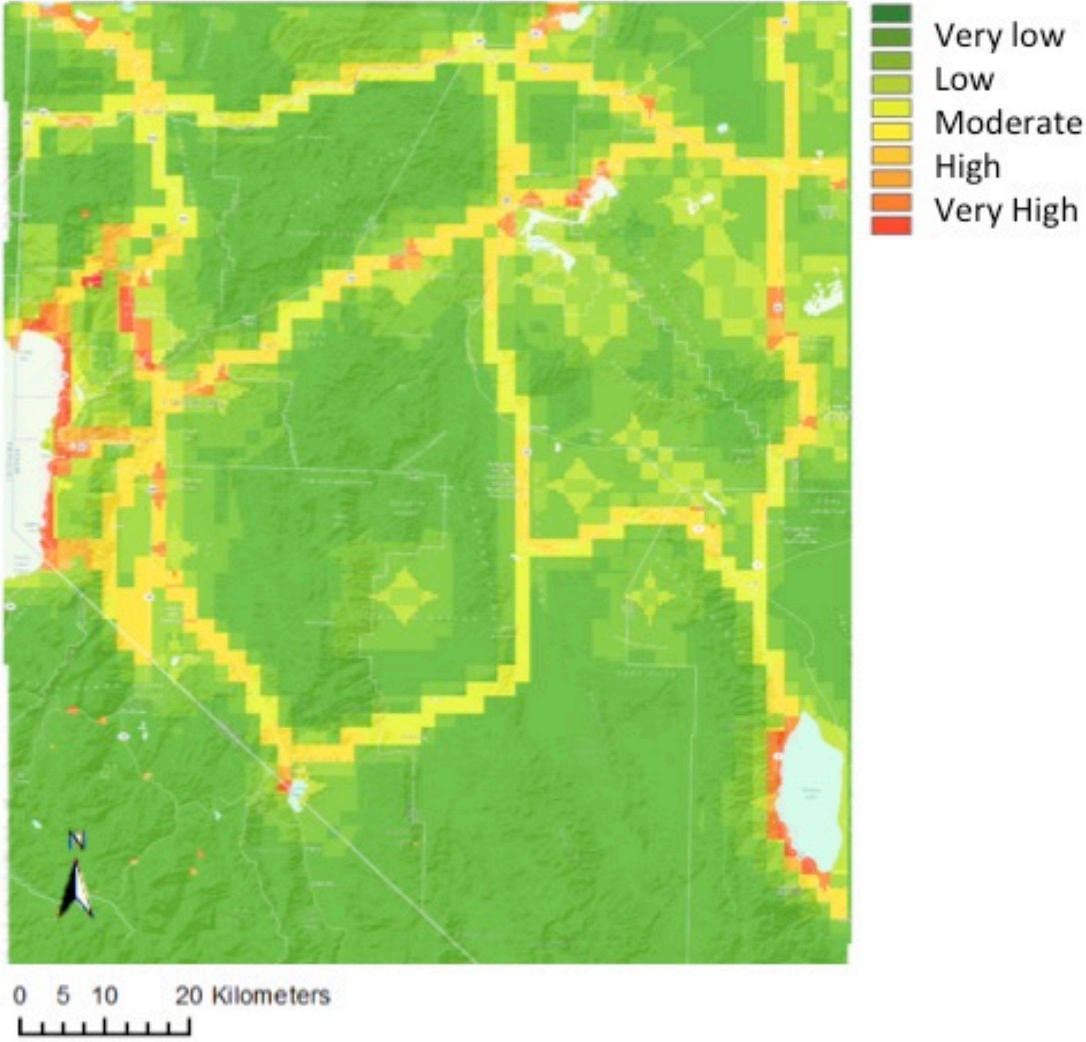


FIGURE 12. Map displaying locations of vehicle collisions against fine-resolution black bear mortality risk in the WGB.

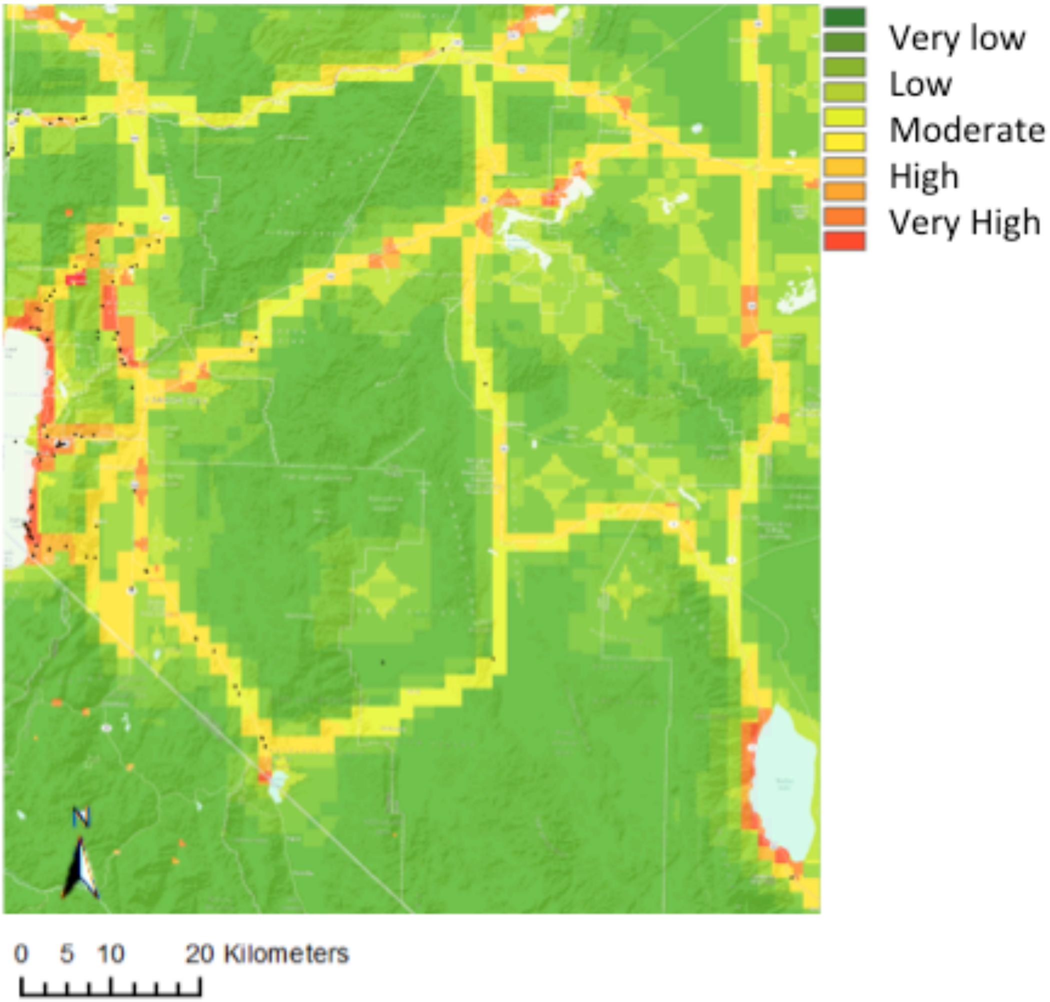
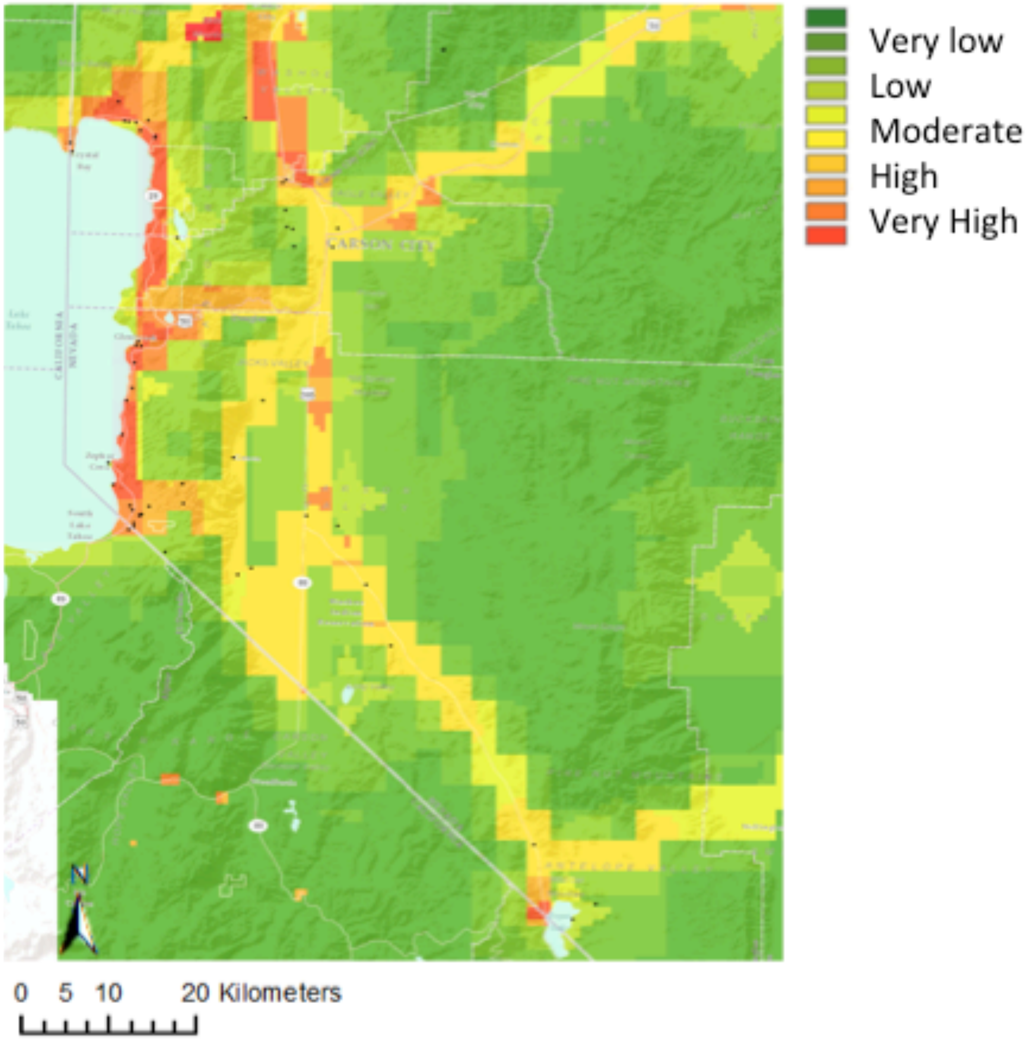


FIGURE 13. Map displaying locations of public safety mortalities against fine-resolution black bear mortality risk in the WGB.



TABLES

Table 1. Human-induced mortality to black bears reported to NDOW, 1997-2013. Illegal mortality types include poaching, unofficial hunting, trapping, and “other.” (NDOW, personal correspondence 2012).

1997	3	3	0	0	1	0	7
1998	5	6	0	0	0	0	11
1999	5	1	0	2	3	0	11
2000	8	6	0	4	2	0	20
2001	6	1	0	0	1	2	10
2002	13	6	0	0	1	0	20
2003	4	3	0	1	2	0	10
2004	9	3	0	0	1	0	13
2005	14	3	0	0	0	0	17
2006	22	9	0	0	1	0	32
2007	35	20	0	0	4	3	62
2008	6	24	0	1	1	0	32
2009	8	6	0	0	1	0	15
2010	8	23	0	0	3	0	34
2011	3	9	12	5	1	1	31
2012	9	7	11	1	3	0	31
2013	2	2	0	4	0	0	8
Cum. Total	**160**	**132**	**23**	**18**	**25**	**6**	**364**

Table 2. Description of variables used to select candidate models for black bear mortality risk in the Lake Tahoe Basin study area.

Landcover	Categorical	29 vegetative and anthropogenic landcover categories
Distance to Road	Continuous	Straight-line distance to nearest road in kilometers
Distance to Water Body	Continuous	Straight-line distance to nearest large water body in kilometers
Distance to Stream	Continuous	Straight-line distance to nearest permanent or seasonal stream in kilometers
Distance to Trail	Continuous	Straight-line distance to nearest hiking trail in kilometers
Distance to Rail	Continuous	Straight-line distance to nearest Amtrak or regional railroad line in kilometers
Urban Polygon	Categorical	Census-defined urban areas measured in sq kilometers
Human Population Density	Categorical	2010 census-defined human population density by zip code in persons/km^2
Distance to Recreation Site	Continuous	Straight-line distance to nearest recreation site, trail head, camp site, or ski lodge in kilometers

Table 3. The most parsimonious RSPF mortality risk models for coarse and fine scale variables

Coarse-resolution model	**AICc**	**p-value**
Landcover + distance to stream + distance to road + distance to trail + distance to water + urban polygon + human population density + distance to recreation site	570.245	<0.0001
Landcover + distance to stream + distance to trail + distance to water + urban polygon + human population density + distance to recreation site	567.882	<0.0001
Landcover + distance to stream + distance to trail + urban polygon + human population density + distance to recreation site	565.533	<0.0001
Landcover + distance to stream + distance to trail + urban polygon + human population density	563.259	<0.0001
Landcover + distance to stream + urban polygon + human population density	568.98	<0.0001
Landcover + distance to stream + human population density	561.679	<0.0001
Fine-resolution model	**AICc**	**p-value**
Landcover + distance to stream + distance to road + distance to trail + distance to water + urban polygon + human population density + distance to recreation site	564.24	<0.0001
Landcover + distance to road + distance to trail + distance to water + urban polygon + human population density + distance to recreation site	561.82	<0.0001
Distance to water + distance to road + landcover + urban polygon + human population density + distance to recreation site	556.032	<0.0001

Table 4. The most parsimonious RSPF mortality risk models for coarse and fine scale variables with and without vehicle collision incidents isolated. Both coarse and fine spatial resolutions are represented.

Coarse-resolution model without vehicle collisions	**AICc**	**p**
landcover + human population density	571.342	0.0034
Fine-resolution model without vehicle collisions	**AICc**	**p**
Distance to stream + landcover + human population density	534.31	0.0001

Coarse-resolution model with only vehicle collisions	**AICc**	**p**
Distance to road + human population density	523.873	0.0002

Fine-resolution model with only vehicle collisions	**AICc**	**p**
Landcover + human population density + distance to recreation site + distance to trail + urban polygon	353.03	0.0001

CHAPTER FOUR

The Human Footprint: a regional approach to evaluating carnivore persistence

Abstract

The Human Footprint (HF) was developed as a spatially explicit composite index of human influence at a global scale using a variety of surrogate datasets to evaluate human impact (e.g. human population density, access, energy use). Further development of the HF can include analyses at a regional or continental scale, and use as a deterministic variable to investigate how different levels of human influence impact the persistence of wildlife populations. We argue that for applied carnivore conservation initiatives, the HF requires appropriate adaptation to the particular system in question to ensure accuracy. We evaluated habitat selection and mortality risk of the American black bear *(Ursus americanus*) in the Western Great Basin (WGB) as a function of the HF by creating a new Human Footprint analysis using recalculated variables at the original 1km^2 spatial resolution and a finer 30m^2 spatial resolution. In addition to examining the HF at a finer scale of analysis, we again recalculated the HF using a modified set of variables that, while similar to the original global datasets, were collected at a regional scale and are species-relevant. The recalculation of the HF with regional and species-relevant variables improved the power of the HF to accurately predict drivers of black bear habitat selection and mortality risk, while rescaling the HF to a finer spatial resolution did not impact results of our analyses. This points to a strong correlation between variables used in the development of the HF and suggests that the careful selection of individual

variables, rather than composite indices, may be more useful in applied conservation contexts at local or regional scales. Further, the results provide a framework with which to model spatial dimensions of carnivore ecology with regard to human activity.

Introduction

Human modification of the environment is nearly ubiquitous across the globe, with implications for ecological patterns and processes, as well as for the conservation of wildlife and landscapes (Vitousek, Mooney et al. 1997, Ellis and Ramankutty 2008). With rapidly increasing human population, land use change, and human access to remote areas, the concept of what is “natural” now implicitly includes human presence or influence (Vitousek, Mooney et al. 1997). Quantitative mapping endeavors in the last few decades have allowed us to visualize the spatial arrangement and magnitude of human modification on terrestrial landscapes, as well as to use such maps to inform land use planning, both for conservation and development purposes (Hannah, Lohse et al. 1994).

The Human Footprint (HF) (Sanderson, Jaiteh et al. 2002) is a spatial index summarizing gradients of human influence on the environment at a global scale. The HF is a summary statistic that describes spatial variation of the impact that humanity has on different parts of the terrestrial surface of the Earth. In their analyses, Sanderson et al. also apply these data to the development of a metric that identifies the least affected areas of each biome on the globe, “The Last of the Wild.” Sanderson et al. acknowledge that individual species, and even ecosystems, respond differently to human impact, but suggest that the *Last of the Wild* identifies areas that have the potential to conserve the greatest biodiversity with the fewest conflicts over current human use.

Although the HF map has served as a powerful tool, its designers recognize that it may need to be altered for use at local or regional scales (Sanderson, Jaiteh et al. 2002).

Recent studies have supported this, showing that adapting the HF methodology to an ecoregional scale improves understanding of the magnitude and spatial pattern of human influence on the environment (Woolmer, Trombulak et al. 2008). Here, both a reduction in spatial resolution and an inclusion of regionally relevant data is necessary to properly apply the HF methodology to local and regional ecological studies. While the HF has been used to look at the persistence of wildlife, and in particular carnivores, at a continental scale (Laliberte 2004) or the scale of a species range (Yackulic, Sanderson et al. 2011), no rescaled and recalculated HF indices appear in the literature for evaluating the influence of human activity on carnivore ecology and conservation strategies at the local scale.

The wide-ranging nature of carnivores often leads them to share space and resources with humans, which exacerbates human-carnivore conflict (Knight 2000, Treves and Karanth 2003). Such negative interactions between humans and carnivores have been known to drastically increase mortality rates of carnivores, whether they live inside or outside protected areas (Woodroffe and Ginsberg 1998, (IUCN) 2003, Johnson, Vongkhamheng et al. 2006), with the level of conflict being driven by both ecological and human social variables (Linnell, Swenson et al. 2001, Treves and Karanth 2003, Hemson, Maclennan et al. 2009). Because the relationships between humans and carnivores are important to the persistence of these animals, indices like the HF can aid ecologists and conservation scientists in understanding how the human landscape influences variations in carnivore behavior and mortality risk. Traditional landscape classifications are based on ecological biomes and habitat types. Using the HF demonstrates the scale of human influence, allowing us to identify ecosystems that may be considered novel, and possibly risky, to populations of carnivores and other wildlife (Hobbs, Higgs et al. 2009, Morse, Pellissier et al. 2014). Uncovering these spatial patterns of potential conflict requires appropriate spatial resolution and proper selection of human landscape variables to accurately characterize the study system (Bourbonnais, Nelson et al. 2013, Linke, McDermid et al. 2013).

Rescaling and recalculating the HF is useful for applied conservation and also advances our understanding of the importance of scale in ecological studies. Landscape heterogeneity is of interest to ecologists, and measuring such heterogeneity at multiple scales has led to the conclusion that certain patterns or phenomena would be incompletely understood if only investigated at a single scale (Levin 1992, Beever, Swihart et al. 2006). Although the 1km^2 spatial resolution of the original HF may be appropriate to identify global trends in human influence on the environment, such a coarse resolution can mask regionally-specific landscape heterogeneity occurring at fine spatial resolutions (Boyce 2006).

The Western Great Basin (WGB) is experiencing rapid residential and commercial development driven by demand for recreational areas, resort hotels, and private vacation residences (Raumann and Cablk 2008). The WGB is home to over 60 mammal species (Zielinski, Truex et al. 2005), including a population of black bears with genetically-linked subpopulations inhabiting different areas of the basin, often geographically separated by mountain ranges (Beckmann 2002, Lackey 2004).

In this study, we focus our work on the impact of altering the spatial extent and resolution of the HF on evaluating the ecology and persistence black bears (*Ursus americanus*) in the rapidly developing WGB. We use regional and species-relevant variables to generate HF analyses at two different spatial resolutions: $30m^2$ and $1km^2$. This allows us to compare the impact of scale using regional and species-specific variables, and to understand how local variables influence results regardless of scale by comparing our rescaled and recalculated HF (here forth referred to as HF-WGB_{30m}) to the original HF analysis of Sanderson et al. 2002. We hypothesized that rescaling and recalculating the HF will yield a significantly different interpretation of the human landscape in the WGB than the original HF, with greater total area and higher magnitude of human impacts to the environment than originally calculated. We also hypothesized that black bear habitat selection and mortality risk analyses will both yield significantly different results with all types of HF inputs used, with HF-WGB_{30m} as the most nuanced and accurate base layer for analyses.

Materials and Methods

Study area

Our study area was the eastern region of the Western Great Basin (WGB), and portions of the Great Basin in s west-central Nevada, is a 130,794 ha area of land encompassing Lake Tahoe and the near surrounding landscape, bordered by the Sierra Nevada mountain range to the West and the Pinenut Range to the East (Fig. 1) (Manley, Parks et al. 2009). Historically frequent rainfall, thick woody vegetation, and pine forests characterize the western Sierra Nevada, while the rain shadow effect provides for a more arid, shrubland ecosystem in the more eastern regions (Manley, Murphy et al. 2004, Raumann and Cablk 2008).

Although federally owned forest areas (which constitute 60,702 ha) have remained protected, many parts of the WGB have undergone tremendous development in the last half century with some areas experiencing up to 45% conversion of vegetative landcover since 1940 (Raumann and Cablk 2008). This development has caused a decline in forested areas and other native vegetation (Fig 2) (Beckmann, Lackey et al. 2004, Raumann and Cablk 2008). Previously forested areas have been widely transformed to accommodate human-dominated land uses, while areas with currently intact forest are popular for outdoor recreation, with numerous ski slopes and camp sites established throughout the landscape (Goodrich and Berger 1994, Burt and Rice 2009)

In this shared human-bear landscape, complaints of human-bear conflict, as well as incidents of human-induced mortality of bears are on the rise (Lackey 2004, Beckmann and Lackey 2008). Even in regions of the WGB with low human population density, mining sites, recreational areas, livestock and horse corrals, and hiking and skiing trails can attract bears (Manley, Parks et al. 2009).

The Nevada Department of Wildlife (NDOW) and the Wildlife Conservation Society (WCS) collaborate on a long-term (1997-present, Jon Beckmann and Carl Lackey, pers. comm.) black bear monitoring and research project in the WGB. This project provided much of data for the current study.

Mapping protocol

We used the open-access Global Human Footprint dataset (WCS, CIESEN 2005) for our preliminary habitat selection and mortality risk analyses. To construct our location-specific datasets, we used the methods from Sanderson *et al.* (2002) to create spatial data layers similar to their Global Human Footprint, including: a) assigning spatial resolutions of 1km^2 and 30m^2 based on the scale of most accurate and available local data; b) development of 9 data layers representing human land use (Table 1) and assignment of related human influence scores between 0 and 10; c) calculating a human influence index via summation of human influence scores from all 9 datasets; and d) normalizing the human influence index by subregion.

Selection of spatial resolution

Fine-scale data from NDOW and other local government agencies were readily available for construction of the HF map of the WGB. We developed local HF data layers at 30m^2 spatial resolution. In order to compare the impact of spatial resolution with the 1km^2 resolution of the original HF (Sanderson, Jaiteh et al. 2002), we also created a HF layer by scaling these 30m^2 data to a coarser spatial resolution using nearest-neighbor techniques in ArcGIS 10.2 (ESRI, 2013)

Selection of datasets and assignment of influence scores

To construct the modified HF for the WGB study area, we used methods similar to WCS CIESEN (2005) for identifying appropriate local anthropogenic variables and assigning scores of human influence. Although certain anthropogenic variables were found in the original HF dataset, such as distance to road and human population density, we also used parameters that are specific to the WGB landscape with biological support for their impact to large carnivore behavioral ecology, such as distance to recreation site and distance to trail (Table 1) (Goodrich and Berger 1994, Markovchick-Nicholls, Regan et al. 2008, Merenlender 2008, Burt and Rice 2009, Musiani, Anwar et al. 2010). Feature layers representing railways, recreation sites, stream and road systems, and trails were acquired from NDOW and the Douglas County open access GIS resources. We used the Euclidean distance tool in ArcMap to create layers representing the straight-line distance from any map cell to the nearest feature. Feature layers representing urban polygons and human population density were available from the USDA's Lake Tahoe Basin Management Unit. We used nearest neighbor tools in ArcMap to reclassify all layers to $30m^2$ (fine) and $1km^2$ (coarse) resolutions for multi-scale analyses. We used 8 datasets (Table 1) and calculated "wild/not wild" scores for each, summing them for a comprehensive human influence index. Unlike the original HF, the HF-WGB_{30m} did not require normalization because all of the input variables were created to the spatial extent of a single biome.

Modeling habitat selection and mortality risk

For this study, we used GPS location data that were collected by the Nevada Department of Wildlife (NDOW) and Wildlife Conservation Society's (WCS) North America Program for 7 male and 17 female black bears (Jon Beckmann and Carl Lackey, pers. comm.; see Chapter 1 for detailed methods). Due to the large quantity of data points and to avoid bias from autocorrelation of locations, we took a random sample of one-third of the total male and female GPS location points (male n= 2186 location points; female n= 5000 location points) and created shapefiles of male and female locations using ArcMap. We then used the Buffer tool to create circular buffers around each location point in accordance with the home range sizes of male and female black bears.

This distance was conservatively set at 80km^2 for male home range and 20km^2 for female home range based on home range kernel estimates from a previous study of the black bear population in the WGB (Beckmann and Berger 2003). We generated 4372 random locations in ArcMap inside of the buffered male black bear location points to represent "available" resource units. This process was repeated for the buffered female black bear points to generate 10,000 randomly selected "available" locations. Each "available" location was within a buffer distance deemed to be the average distance a black bear can travel within a day (Cooper & Millspaugh, 1999; Compton et al., 2002; Boyce, 2006; Buskirk & Millspaugh, 2006; Ciarniello et al., 2007).

For mortality risk analyses, we took the GPS location points of mortality incidents (n= 366 location points) and created shapefiles using ArcMap. We then used the Buffer tool to create 5km^2 circular buffers around each location point (Treves, Martin et al. 2011). We generated 732 random locations in ArcMap outside of the buffered mortality location points to represent "available" resource units (see Chapter 2 for detailed methods).

In order to better understand habitat selection and mortality risk probability, we identified HF values at GPS point locations in the study. We used Extraction Tools in ArcGIS to calculate values for the HF at both coarse and fine spatial resolutions measured on the habitat selection and mortality location points and "available" resource units (Ciarniello, Boyce et al. 2005, Ciarniello, Boyce et al. 2007). These location points and associated values were then exported into a spreadsheet and used by statistical software program JMP (SAS Program, 2014) for analyses.

We developed resource selection probability function (RSPF) models for two levels of spatial analysis using the coarse and fine scale representations of the original and recalculated HF index and black bear location and mortality location data. Resource selection analysis employed a logistic regression, using the logit command to compare characteristics of black bear habitat selection and morality sites with “available” sites in the study region (Manly 2002, Sawyer and Brashares 2013). For our logistic regression-based RSPF model, a black bear “used” GPS location was considered a “success” and given a value of 1, where an “available” resource unit was given a value of 0, and the HF indices used as predictor variables. The RSPF is assumed to take the form:

$$w^*(x) = \exp(\beta o + \beta_1 x_1 + \ldots \_ \beta_p x_p)/1 + \exp(\beta_0 + \beta_1 x_1 + \ldots + \beta_p x_p)$$

where $x = (x_1, x_2, \ldots, x_p)$ holds the values for the X variables that are measured on a unit. Maximum likelihood estimates of the β parameters in the equation was calculated. We used chi-squared tests on deviances to assess whether there is any evidence that the probability of use of a location is related to a variable.

We assessed the predictive capability of each model using a Spearman’s rank correlation based on 5-fold cross validation (Boyce et al. 2002). In this procedure, we estimated an RSPF model using a random draw of 80% of the data. We then used this model to predict the frequency of occurrence in the withheld 20% of the data using 10 RSPF bins, and repeated the process 5 times, replacing the withheld 20% and removing the next 20% (Boyce et al. 2002). For our study, a model that had strong predictive capabilities would have a higher number of locations in bins with the highest RSPF scores. Once the final RSPF was derived, we used ArcMap 10.2 (ESRI, 2013) to map the probability of habitat selection over the entire study area.

Assessing the importance of mapping scale

Upon completing habitat selection and mortality risk models, we calculated two-way contingency tables showing the number of pixels in the habitat selection and mortality risk probability maps falling in each category of human footprint score. Here, we compared how the proportion of the landscape in each human footprint score category changed as habitat selection and mortality risk analysis results were compared at coarse and fine spatial scales. Kolmogorov-Smirnov tests were applied to test significance.

Assessing the importance of HF variables

Similar to the assessment of scale, our two-way contingency tables also included the number of units in the habitat selection and mortality risk probability maps falling in each category of human footprint score. This allows us to identify differences between the proportion of the landscape in each human footprint score with habitat selection and mortality risk results using the original and regional and species-specific parameters. Kolmogorov-Smirnov tests were applied to test significance.

Results

Recalculating and rescaling the HF

We reduced the spatial resolution of the original HF from $1km^2$ to $30m^2$ to create the HF_{30m}. This new data layer was not significantly different from the original HF in terms of its characterization of human influence in the WGB, nor its use in predicting black bear habitat selection and mortality risk. We also recalculated the original HF with regional and species-specific variables with a spatial resolution of 1km^2 (HF-WGB$_{1km}$) and 30m^2 (HF-WGB$_{30m}$). Again, we found that the HF-WGB$_{1km}$ and HF-WGB$_{30m}$ did not display significant differences in characterizing human influence in the WGB or in modeling black bear dynamics. Significant differences were found between the original HF and the HF-WGB$_{30m}$ in characterizing the spatial arrangement and magnitude of human influence across the WGB landscape. Significant differences were also found between the original HF and the HF-WGB$_{30m}$ when used in black bear habitat selection and mortality risk models. For clarity, we here forth describe the differences between the original HF and the HF-WGB$_{30m}$.

Both the original HF and the HF-WGB$_{30m}$ display a range of human footprint scores. We binned the scores into categories ranging from very low (HF score <20) to very high (HF score 80-100) (Fig. 3 & Table 2). There are distinct "hotspots" of very high and high human influence in areas with recent residential and commercial development: along US highways I-80, I-580, and US-50; in the greater Reno, NV metropolitan area; and in areas of urban development such as Incline Village, South Lake Tahoe, Carson City, and Gardnerville. These high HF areas fragment parts of the landscape with moderate HF scores (Fig 4). The majority of the landscape exhibits low HF scores (Table 2), found in the high-elevation Pine Nut and Sweetwater mountain ranges, as well as highly arid desert towards the eastern part of our study area, and includes many of the Federally mamaged forests.

We found that the original HF over-predicts the amount of landscape in the lowest categories of human influence (55.3% of the landscape has HF <20), compared with the HF-WGB$_{30m}$ (9.5% of the landscape at <20 HF score) (Table 2 & Fig. 3). We found that the original HF also under-predicts the amount of landscape at low and moderate levels of human influence showing 27% of the landscape at low, and 12.8 % of the landscape at moderate (20-40) scores of human influence, rather than 59.6 and 25.7% of the landscape, respectively, in the HF-WGB$_{30m}$. Finally, the original HF and the HF-WGB$_{30m}$ both estimate similar amounts of landscape at high and very high levels of human influence (Table 2 & Fig. 3).

Habitat selection

Black bear habitat selection analyzed using the original HF over-predicted the probability of habitat selection at very low and low HF scores (5.9% habitat selection probability for very low HF scores <20; 26.4% probability of habitat selection for low HF scores between 20-40). The same analysis under-predicts the probability of habitat selection at moderate levels of human influence (53% habitat selection probability for moderate HF scores between 40 and 60) compared with analyses carried out using the HF-WGB$_{30m}$ (3.9% and 24.8% habitat selection probability for very low and low HF scores; 66.2% habitat selection probability for moderate scores between 40 and 60) (Fig. 5).

Analyses using the original HF and the HF-WGB$_{30m}$ both suggested high probability of habitat selection for areas of the landscape at high HF values (48.65% and 52.06% habitat selection probability for HF scores >50, respectively). Habitat selection analyses using the HF-WGB$_{30m}$ map show higher probability of black bear habitat selection at low HF values and similar selection probabilities at low, moderate, and high HF scores on the landscape (Fig. 5).

Mortality Risk

When we plotted mortality locations against the original HF and HF-WGB$_{30m,}$ we found that the original HF misrepresented the human influence score at many mortality locations. When plotted against the original HF, 12% of mortalities occurred in areas of very low HF scores (<20) and 29% of mortalities occurred in low HF scores (between 20-40). The majority of mortalities (35%) occurred in areas with moderate HF scores (between 40-60), while 23% of mortalities occurred at high HF scores (between 60-80). Areas of very high (over 80) HF scores had less than 1% of mortalities.

The results from plotting mortality locations against the HF-WGB$_{30m}$ showed that less than 3% of mortalities occurred in areas with a very low HF-WGB$_{30m}$ score, while 45% of mortalities and 45% of mortalities occurred in areas of low and moderate HF-WGB$_{30m}$ scores, respectively. Only 5.5% of mortalities occurred in high HF-WGB$_{30m}$ scores and 0% of mortalities took place in very high HF-WGB$_{30m}$ scores.

Black bear mortality risk analyzed using the original HF over-predicted the probability of mortality at high and very high HF scores (65.8% mortality risk probability for high HF scores between 60 and 80; 1.5% mortality risk probability for high HF scores between 80 and 100) compared with analyses using the HF-WGB$_{30m}$ (25.5% mortality risk probability for high HF scores between 60 and 80; 0% mortality risk probability for high HF scores between 80 and 100). Mortality risk models constructed with the original

HF parameter also significantly under-predicted the probability of black bear mortality at moderate human footprint scores (20.4% probability mortality risk for moderate scores between 40-60), compared to the models constructed using the HF-WGB$_{30m}$ (63.7% probability of mortality risk for moderate scores between 40-60)(Fig 6).

Discussion

The recalculation of the HF using regional and species-relevant anthropogenic variables (HF-WGB$_{30m)}$ resulted in significantly different patterns of human influence across the landscape with variation in both the distribution and the scale of human influence. As noted by Woolmer *et al.* (2008) in their ecoregional recalculation of the HF, we found the original HF over-predicts the amount of landscape in the lowest and highest categories of human influence when compared with the HF-WGB$_{30m}$. Most importantly, as a result, the original HF then under-predicts the amount of landscape at moderate levels of human influence as compared with the HF-WGB$_{30m}$, regardless of the spatial resolution of analysis (Fig. 3).

Using the original HF versus the HF-WGB$_{30m}$ to model habitat selection leads us to under-predict the probability of bears selecting areas with moderate levels of human influence, while over-predicting the probability that bears will select areas with high levels of human influence. While one hypothesis suggests areas with high human influence may also have attractive food resources for bears, thus driving an apparent selection for this type of habitat in the WGB, this assumption does not reflect trends in the literature suggesting the avoidance of areas with high human influence (Frary, Duchamp et al. 2011, Merkle, Krausman et al. 2011, Noyce and Garshelis 2011, Pelletier, Obbard et al. 2011, Johnson, Breck et al. 2015), and may lead scientists and managers to recommend conservation policies using misleading information. Using the HF-WGB$_{30m}$ variables gives a much more accurate estimation that the probability of bears selecting areas with the highest levels of human influence, often in or near urban areas, is extremely unlikely, while bears are most likely to use habitat with moderate human influence (between scores of 40-60) that encompass a variety of land use and landcover types (see Johnson et al. 2015).

The original HF also over-predicted the probability of bears using habitat at the lowest levels of human influence, which is problematic, as the results of models using the HF-WGB$_{30m}$ signal that these areas of low human influence are unpopular for both humans and wildlife. They are generally at extremely high elevations or with limited water resources (Beckmann and Lackey 2004, Raumann and Cablk 2008). Conservation and management plans based on analyses using the original HF could potentially designate these areas of extremely low human influence as important conservation zones for large carnivores, when they are in fact unlikely to be used by these animals.

Since analyses using the original HF and the recalculated HF-WGB$_{30m}$ both suggest generally higher probability of black bear habitat selection for areas of the landscape at low and moderate HF values, and lower probability of habitat selection at high HF values, it is clear that the spatial arrangement and magnitude of human influence in the WGB have the potential to directly influence the behavioral ecology of black bears. Tolerance for human activity varies among wildlife species and relates to an animal's life history characteristics. Black bears in the region may use areas of moderate human influence because of competition for space, or as previous studies in this region have shown, anthropogenic food resources can attract bears to wildlife-urban interface areas of the landscape (Lackey 2004, Beckmann, Karasin et al. 2008, Beckmann and Lackey 2008), especially in the period of hyperphagia when bears aim to increase their weight and fat storage in preparation for months in hibernation (Johnson et al. 2015). Further, we may find that bears select these areas due to the trend that many types of human activity occur in forested, backcountry areas that are considered prime bear habitat, and thus elevate the human influence score of these areas (Merrill 1978, Ruth, Smith et al. 2003).

For mortality risk analyses, we found that using the original HF as a parameter under-predicts the probability of mortality at moderate HF levels, and over-predicts probability of mortality at high levels of HF compared with analyses using the HF-WGB_{30m}. These outputs mischaracterize the influence of human activity on carnivore ecology, appearing as though areas of moderate human influence are less risky to black bear population persistence than areas with high human influence. The HF-WGB_{30m} suggests that areas of the WGB landscape with moderate levels of human influence pose a high mortality risk for black bears, a phenomenon that has important implications for large carnivore conservation efforts that are often aimed at reducing mortality in areas with high human influence (Merkle, Krausman et al. 2011, Treves, Martin et al. 2011, Northrup, Stenhouse et al. 2012). In other studies, carnivores have been shown to experience highest rates of mortality in highly urbanized areas (Brashares, Arcese et al. 2001, De Angelo, Paviolo et al. 2011), whereas in the WGB, the pervasiveness of human influence has created a patchy landscape of various habitat qualities that may directly impact population persistence (see Chapter 4).

Our work has shown that using the HF in ecological modeling at different spatial extents and resolutions helps us more effectively evaluate how bears respond to human influence on the environment. These analyses can be further improved by accounting for the temporal differences in the patterns and processes within and between types of human activity, which can be tremendously important when interpreting results of habitat selection studies (Boyce 2006), as detailed in Chapters 1 and 2. In systems like the WGB, there are important temporal shifts in magnitude, type, and spatial arrangement of human activity in the WGB system that may greatly alter measurements of the human footprint on carnivore ecology (Goodrich and Berger 1994).

Management Implications

The results of this exercise are especially pertinent in the WGB and western Great Basin study area, where the popularity of backcountry recreation elevates the human footprint score of densely forested areas, and has potential implications for wildlife disturbance (Burt and Rice 2009). Using the original HF for habitat selection analyses could lead managers to misclassify areas of high human influence as better tolerated by bears than they actually are._Failing to recalculate the local HF using regional and species-relevant variables can thus misinform managers about how much and which areas of the landscape are in need of the most protection.

As the black bear population in the WGB continues to increase in size and expand its space use (Lackey 2004, Lackey, Beckmann et al. 2013), the reinterpretation of the HF is a key step for managers to have an improved understanding of the areas that may drive human-bear conflict. The incorrect assumption that bears avoid areas of moderate to high human influence, given by the analyses using the original HF, poses potential complications for the future of human-bear coexistence in shared landscapes (Beckmann and Berger 2003, Hostetler, McCown et al. 2009, Merkle, Krausman et al. 2011). Moreover, these data regarding habitat use suggest reasons for the prevalence of human-bear conflict in the WGB. Mortality resulting from this conflict may be a limiting factor in the ultimate persistence of the population (Beckmann and Lackey 2008, Schwartz, Haroldson et al. 2010, Rich, Mitchell et al. 2012). Depending on natural death rates, human-induced mortality beyond a certain limit may contribute to a tolerance threshold for carnivore persistence in the WGB and throughout the region (Nielsen, McDermid et al. 2010, Bateman and Fleming 2012). Development of multi-scale HF indices using regional and species-relevant data provides a framework from which conservation scientists can evaluate habitat suitability for black bears and estimate connectivity of high-quality habitat in the region.

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FIGURES

FIGURE 1. The Lake Tahoe Basin (WGB) study system including extreme western part of the Great Basin.

FIGURE 2. Gross change in area (ha) by landcover class from 1940-2002 in the southern WGB (Adapted from Raumann *et al*. 2008).

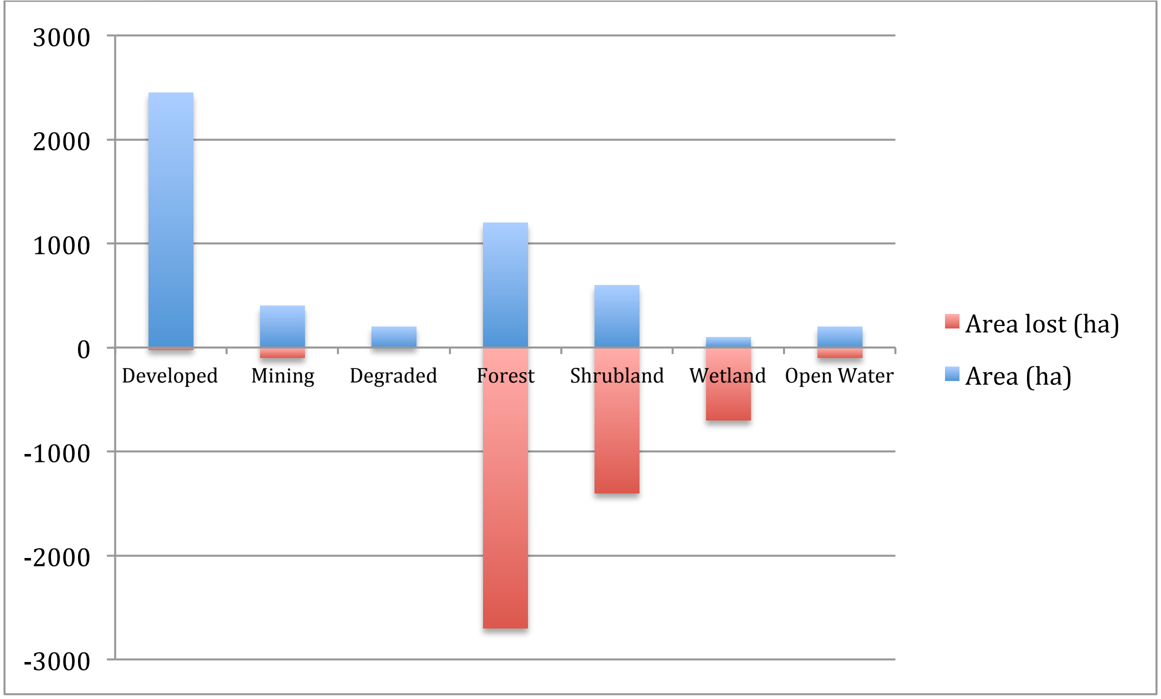


FIGURE 3. Proportion of the WGB landscape in each HF category for the original HF and the HF-WGB$_{30m}$. Higher values of HF reflect more human activity and access.

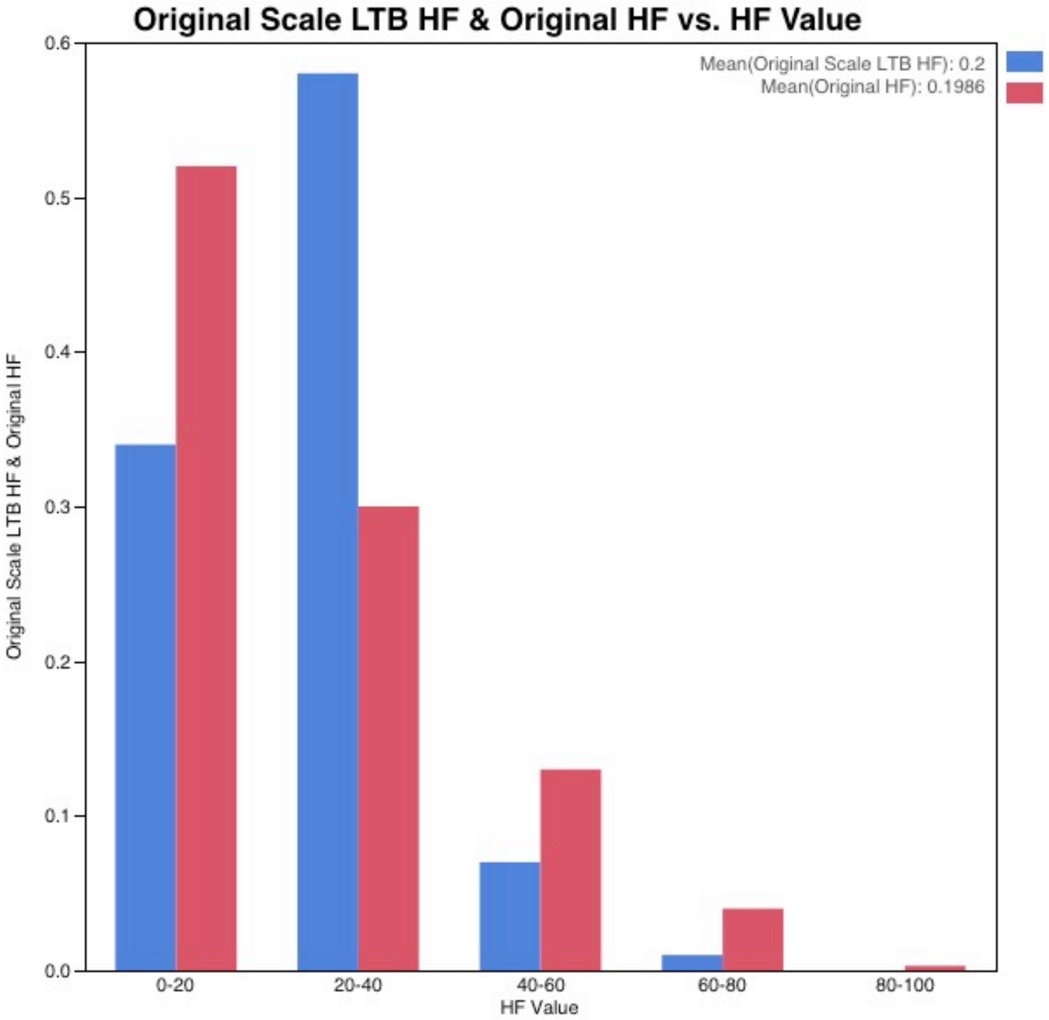
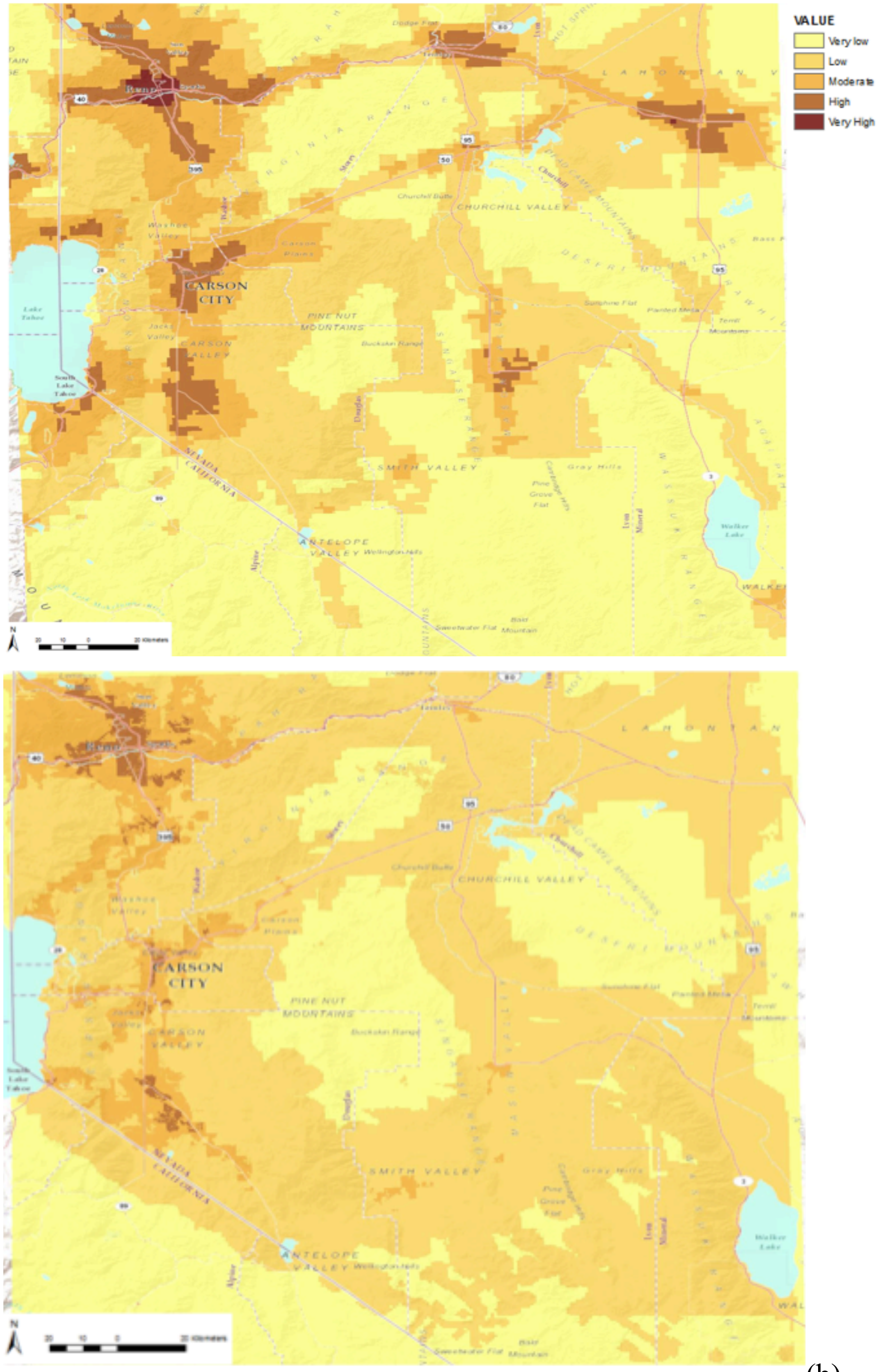


FIGURE 4. Map of human influence values in the WGB and western Great Basin from the Original HF (a) and the HF-WGB$_{30m}$ (b).



(a)

(b)

FIGURE 5. Contingency table showing the four different HF model predictions of black bear habitat selection in the WGB.

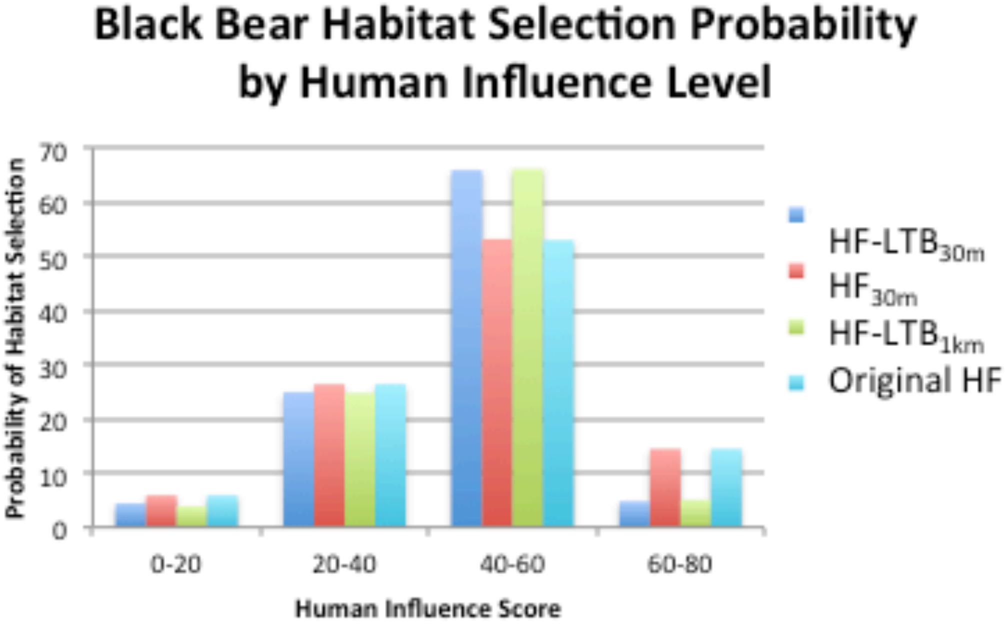


FIGURE 6. Contingency table showing the four different HF model predictions of black bear mortality risk in the WGB.

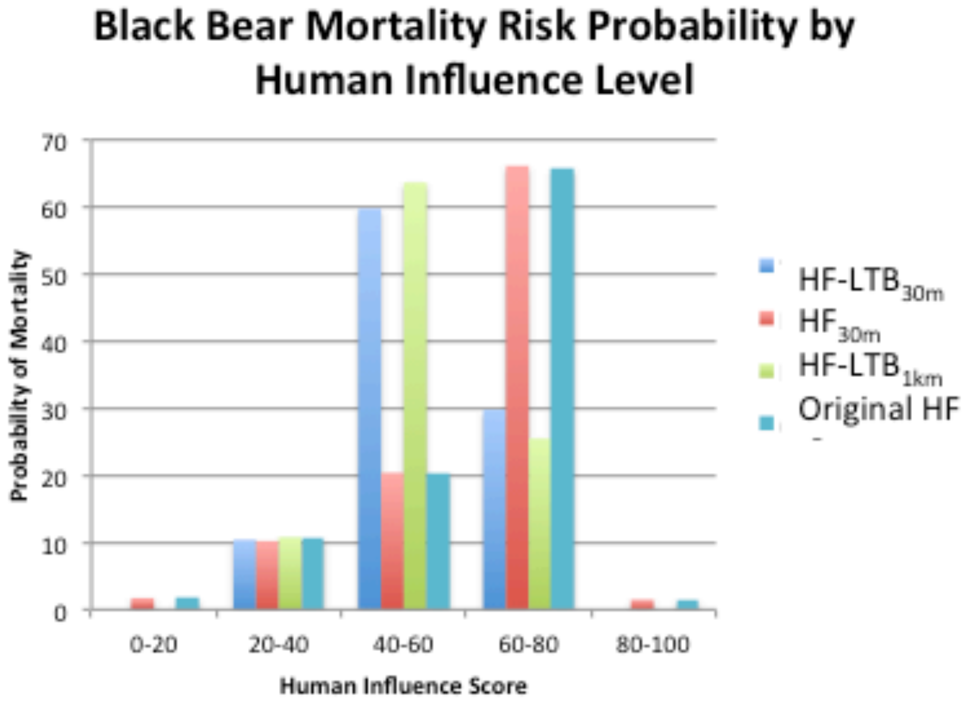
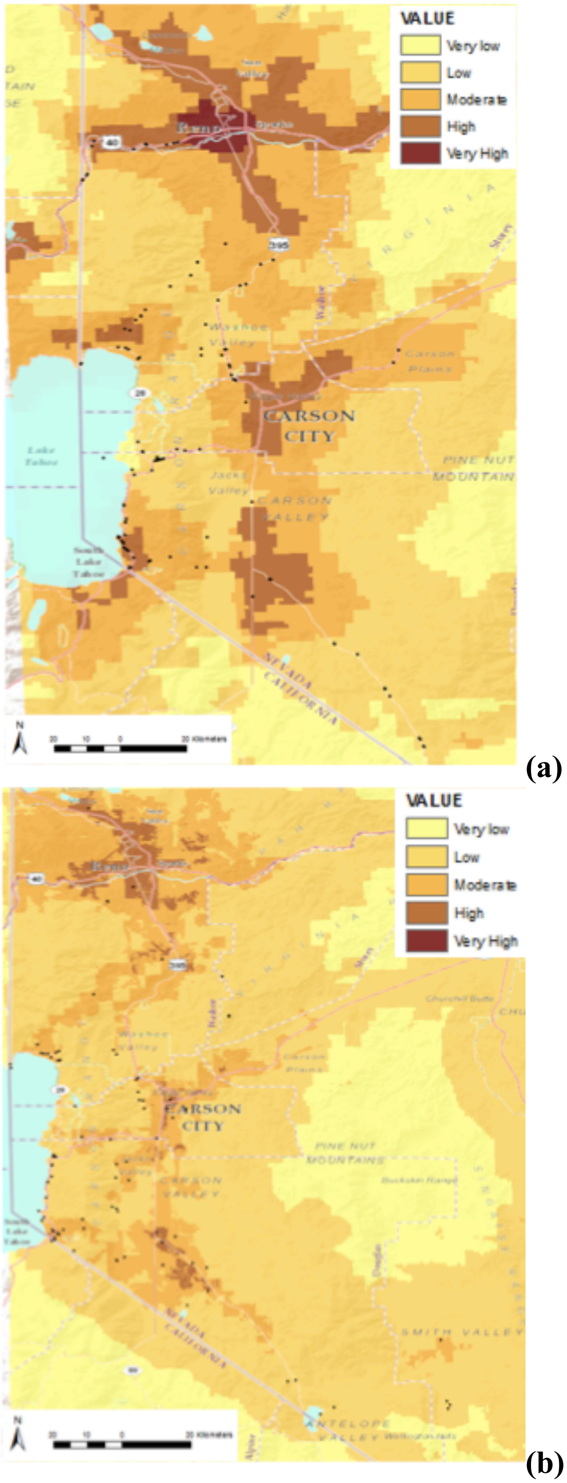


FIGURE 7. Map of mortality locations against HF values in the WGB and western Great Basin from the Original HF (a) and the HF-WGB$_{30m}$ (b).



TABLES

TABLE 1. Parameters used in construction of the original HF and the HF-WGB$_{30m}$.

Original HF Parameters	**HF-WGB$_{30m}$ Parameters**
Distance to Major Road	Distance to Major Road
Distance to Navigable River	Distance to Dirt Roads and Hiking Trails
Distance to Rail	Distance to Rail
Urban Polygons	Urban Polygons
Distance to Coastline	Recreation Sites
Human Population Density (km^2)	Human Population Density (km^2)
Nighttime Artificial Light Intensity	Communication lines/towers
Landcover	Landcover

TABLE 2. Classifications of the WGB landscape binned into HF categories for the original HF and the HF-WGB$_{30m}$.

HF Level	**Percentage (%) of landscape in original HF**	**Percentage (%) of landscape in HF-WGB$_{30m}$**
Very low (<20)	41.6	25.2
Low (20-40)	39.8	67.1
Moderate (40-60)	14.1	6.6
High (60-80)	4.3	1.2
Very high (80-100)	0.3	0

CHAPTER FIVE

Integrating mortality risk and habitat selection information to evaluate habitat suitability of a large carnivore in a human-dominated landscape

Abstract

The black bear population in Western Nevada including the Lake Tahoe Basin (WGB) and western Great Basin is small (<400 individuals), but growing. Simultaneously, human dominance of the landscape is increasing and leading to increased habitat fragmentation and human-driven bear mortality, mostly from vehicle collisions and human-bear conflict. Bears generally avoid human development, but can be attracted to human food resources in the region. As a result of this, increasingly pervasive human presence across the landscape will eventually lead to barriers to growth and threaten long-term persistence of the population. Early indicators of threats to future population expansion include incidence of human-bear conflict and human-induced mortality.

Spatially explicit habitat suitability models that reflect variation in habitat quality across a landscape allow the accurate estimation of functional habitat connectivity for the growing black bear population. Biologists can combine habitat selection probability and mortality risk models into a framework that identifies a landscape gradient from habitat sink/low quality to safe/high quality areas. We construct such models for black bears in the WGB and western Great Basin by using mortality risk and habitat selection models,

and create a map of bear habitat quality across the landscape. We classify the landscape into five habitat states reflecting habitat selection probability and mortality risk level, identifying patches of habitat with high selection probability and low mortality risk (12% of the landscape). These areas were almost entirely adjacent to areas of high selection probability and high mortality risk (5% of the landscape), creating a potentially dangerous matrix for black bear dispersal. Although the majority of the study area was of moderate selection probability and low-moderate mortality risk, patches of high selection probability and high mortality risk severely fragment the landscape. Additionally, this modeling exercise allows us to make recommendations for adapting strategic conservation tools for local application.

Introduction

Understanding the factors that influence individual habitat selection, and how the decisions of individuals generate population-level patterns of distribution and abundance, is a critical area of study in ecology. Such an understanding is also an important foundation for conservation planning, enabling conservationists and managers to manage habitat, and ensure connectivity of habitat patches across a landscape (Johnson 1980, Chetkiewicz and Boyce 2009, Braaker, Moretti et al. 2014). Modeling habitat selection gives us key insights into wildlife ecology; however, these efforts do not fully address how landscape heterogeneity may be linked to individual fitness (Nielsen, Stenhouse et al. 2006, Roever, van Aarde et al. 2013).

The study of how individual animals move across a landscape is complicated by systems where human influence on the landscape may impact multiple aspects of a species' ecology (May, Gorini et al. 2012, Rich, Mitchell et al. 2012, Pigeon, Nielsen et al. 2014). Maladaptive habitat selection, for example, may occur when animals have high probability of selection for habitat with desirable resources, but that also has characteristics of anthropogenic activity (such as roads or agricultural fields) that increase the likelihood of human-wildlife conflict, and in extreme cases, mortality risk (Schlaepfer, Runge et al. 2002, Battin 2004). Hence, when classifying habitat quality, mortality costs must be included to offset other desirable habitat attributes as attractive population sinks differ greatly in their impact on population persistence from those habitats that share a high probability of selection (preferred habitat from the perspective of the individual), but have extremely low risk of mortality or conflict.

Uncovering the relationship between a species' life history characteristics and habitat is also relevant for ecologists interested in the implications of novel ecosystems for a species' persistence. Although recent literature has largely focused on the novelty of ecosystems with high degrees of human modification, it is arguable that landscapes with heterogeneous patterns of type and magnitude of human activity can also be considered "novel" to populations of wildlife sharing these spaces (Hobbs, Higgs et al. 2014). For example, in certain systems, humans may have a pervasive, but subtle, influence on the landscape, expanding recreational activity into areas that are otherwise relatively undisturbed (Reed, Hilty et al. 2014). Even though this type of activity does not involve the same landscape transformation as urban areas, such activity can take place at low levels over a vast area. Documented impacts to the wildlife that selects these areas include increased risk of mortality (Goodrich and Berger 1994, Ruth, Smith et al. 2003, Musiani, Anwar et al. 2010, Costello, Cain et al. 2013, Reed, Hilty et al. 2014). In these cases, thorough analyses of habitat suitability that include fitness proxies should identify the trade-offs for wildlife in these regions.

Information on how the characteristics of habitat patches influence an individual's mortality risk is crucial in landscape classification (Nielsen, Stenhouse et al. 2006). In many landscapes with pervasive human activity, building habitat selection and mortality risk models with a suite of anthropogenic variables further sets the stage for an informed classification of habitat quality in response to human pressures. Combining the information generated by these models allows for a unique classification of the landscape reflecting accurate indications of whether an area will threaten the persistence of a population, while also informing analyses of suitable habitat connectivity (Nielsen, Stenhouse et al. 2006). Although ideally the information relating an individual's fitness potential to a habitat type would be precise calculations of survival and reproductive potential, it is often extremely difficult to gather these data, especially for the large-bodied, wide-ranging mammals that often use landscapes at a coarse spatial scale (Linke, McDermid et al. 2013, Roever, van Aarde et al. 2013). In light of these limitations, building mortality risk indices using locations of mortality incidents across a landscape allows ecologists to approximate risk associated with habitat types, which advances understanding of an important part of the wildlife-habitat relationship (Nielsen, Herrero et al. 2004, Ciarniello, Boyce et al. 2007, Basille, Van Moorter et al. 2013).

The Nevada portion of the Lake Tahoe Basin (WGB) and western Great Basin is a dynamic ecosystem that has undergone rapid human development since the 1940s, leaving a highly heterogeneous landscape in terms of forest cover and type and magnitude of human activity (Raumann and Cablk 2008, Manley, Parks et al. 2009) (Figs. 1&2). The population of black bear (*Ursus americanus)* that shares this landscape is recolonizing historic habitat, after being extirpated from the region in the early twentieth century (Lackey, Beckmann et al. 2013). The rapid spatial expansion and increased densities of bears have occurred simultaneously with human landscape transformation. This confluence of events has driven increased incidents of human-bear conflict in the region, affecting the welfare of both humans and wildlife.

Habitat selection analyses conducted at both coarse ($1km^2$) and fine ($30m^2$) spatial resolutions have shown that black bears avoid areas with high human activity (Reynolds-Hogland, Mitchell et al. 2007, Merkle, Krausman et al. 2011, Johnson, Breck et al. 2015). Similarly constructed mortality risk models suggest that heightened mortality is related to a variety of human land use types (Ryan, Pack et al. 2007, Obbard and Howe 2008, Mitchell, Pacifici et al. 2009). The interrelated nature of these ecological patterns and the potential for conservation management to address the conflicts makes it particularly important to quantify how habitat suitability varies between patches of habitat in the WGB.

Using Resource Selection Probability Functions, we modeled habitat selection from black bear location data collected with GPS collars. We then created an index of habitat selection probability by bears in the WGB and western Great Basin study area. Following a similar protocol, we modeled the relative probability of black bear mortality using locations of black bear carcasses as well as locations of human-bear conflicts that resulted in on-site euthanizing of the animal. Combining the relatively probability of selection and mortality indices, we then defined areas of high selection probability and low mortality risk as primary habitat, and areas of high selection probability and high mortality risk as primary sink areas, both of which deserve conservation attention. We continued the protocol to define areas of secondary habitat and secondary sinks on the landscape, as well as non-critical habitat (Nielsen, Stenhouse et al. 2006). This method of habitat suitability classification, while not a direct measure of demographic sources and sinks, does provide unique insights for the prioritization of conservation actions and can inform connectivity analyses for the region.

Methods

Study Area

The study area in western Nevada incorporated an area of roughly 130,794 ha.

Study area boundaries to the west and east coincide with the Sierra Nevada and Sweetwater mountain ranges, respectively (Fig. 1). The National Forest Service protects 60,702 ha of the study area, and much of the additional land area is public and managed by state agencies. Frequent rainfall, thick woody vegetation, and pine forests characterize the western Sierra Nevada, while the rain shadow effect provides for a more arid, shrubland ecosystem in the more eastern regions (Manley, Murphy et al. 2004, Raumann and Cablk 2008). Reno, in the northeastern part of the study area, is the largest urban center, and except for Carson City in the center of the study area, other human settlements occur in small towns clustered in the more fertile regions of the landscape. Permanent human settlements are prohibited in protected areas; however ski lodges, campsites, and park offices are located within park boundaries.

The WGB is home to over 60 mammal species (Schlesinger, Ramsos 2000), including a small population of American black bear (*Ursus americanus*) with subpopulations inhabiting different areas of the basin, often geographically separated by mountain ranges (Beckmann 2002, Beckmann and Berger 2003, Lackey 2004). In this shared human-bear landscape, complaints of human-bear conflict, as well as incidents of human-induced mortality of bears is on the rise (Lackey 2004, Beckmann and Lackey 2008). Increases in conflict are linked to an omnivorous diet that allows black bears in the WGB to benefit from anthropogenic resources (i.e. garbage, livestock) found in areas with high human activity (Beckmann, Karasin et al. 2008). Black bears in the WGB are known to forage on privately-owned fruit orchards, raid garbage in commercial and residential sites, and cross busy roads in search of resources, thus putting humans in proximity to these wild animals, resulting in elevated risk of mortality for bears

(Beckmann and Lackey 2008). An annual hunting season for black bears was initiated in Fall 2011 and occurs from September-December, where up to 20 animals can be harvested each season.

Black Bear Habitat Selection Data

We used GPS location data that were collected by the Nevada Department of Wildlife (NDOW) and Wildlife Conservation Society's (WCS) North America Program (Jon Beckmann and Carl Lackey, pers. comm.). From May-November of 2005-2010, GPS collars were attached to 7 male and 17 female black bears captured in back country regions of the Carson and Pinenut Mountain Ranges or at the urban-wildland interface. Only adult animals were collared. GPS collars by Vectronics were set up to transmit location signals every 4 hours and emit a mortality signal when an animal did not move for 48 hours. Location data were collected in a database shared by NDOW and WCS project investigators and updated at the end of each field season. From May-November of 2011-2013, we set baited barrel and snare traps for black bears in remote forested regions of the Carson, Pinenut, and Sweetwater Mountain Ranges to capture and attach GPS collars to additional bears in backcountry areas with nominal human development but low to moderate human recreational activity.

Black Bear Mortality Location Data

We used black bear mortality reports that were collected by the NDOW and WCS from 1997-2013. During this time period, authorities from NDOW responded to incidents of vehicle collisions with bears along local roadways as well as calls from residents about bear-related public safety concerns. Detailed reports for both of these issues were recorded upon response to the incident, and included a full description of the location and often an associated address. Hunters with a tag for bear harvest are required by law to record the precise location of where they took down the animal and report this information along with delivering the animal carcass to NDOW authorities before they can process the animal. This information was also entered into the mortality database. Information on rarely occurring illegal black bear mortalities were gathered opportunistically from anonymous phone calls or tips from local residents.. Prior to analyzing the data for mortality risk analyses, we visited the location of each mortality report and recorded a precise GPS location.

Records of “sport hunt” mortalities begin from 2011when the state of Nevada implemented a legal black bear hunting season for the first time in the state’s history. “Illegal” mortalities have only been documented on three occasions (2001, 2007, and 2011) and are likely from local residents who have faced severe property damage in the past from bears. “Public safety” mortalities occured when NDOW trapped and euthanized black bears using areas with humans present and appear to not be afraid of humans (e.g. inside a home). Almost all bears that are captured by NDOW as a result of human-bear conflicts are caught and experience deterrent techniques (i.e. rubber bullets, Karelian bear dogs, etc) to discourage their use of an area. However, in relatively rare cases some bears are lethally removed due to public safety concerns

Modeling black bear locations

We generated nine spatial data layers in a GIS (ESRI ArcMap 10.2.2) representing environmental features and the anthropogenic landscape in the WGB and western Great Basin (Table 1). Although certain anthropogenic variables are often found in similar studies of wide-ranging large carnivores, such as distance to road and urban centers, we also used parameters that are specific to the WGB landscape with biological support for their impact to large carnivore behavioral ecology, such as distance to recreation site, distance to trail, distance to railway, and human population density (Goodrich and Berger 1994, Markovchick-Nicholls, Regan et al. 2008, Merenlender 2008, Burt and Rice 2009, Musiani, Anwar et al. 2010). The landcover layer was generated by specialists at NDOW specifically for biodiversity assessments in the WGB and projected at 1-meter resolution. We used nearest neighbor tools in ArcMap to reclassify the layer to $30m^2$ (fine) and $1km^2$ (coarse) resolutions for multi-scale analyses. Feature layers representing major water bodies, railways, recreation sites, stream and road systems, and trails were acquired from NDOW and the Douglas County open access GIS resources. These were transformed in ArcMap to find Euclidian distance from the nearest feature. These layers were also reclassified for projection at both $30m^2$ and $1km^2$ spatial resolutions. Feature layers representing urban polygons and human population density were available from the USDA's Lake Tahoe Basin Management Unit. These were also manipulated in ArcMap with nearest neighbor tools to classify and project them at $30m^2$ and $1km^2$ spatial resolution for analyses.

Due to the large quantity of data points and to avoid bias from autocorrelation of locations, for habitat selection analyses, we took a random sample of one-third of the total male and female GPS location points (male n= 2186 location points; female n= 5000 location points) and created shapefiles of male and female locations using ArcMap. We then used the Buffer tool to create circular buffers around each location point in accordance with the home range sizes of male and female black bears. This distance was conservatively set at 80km^2 for male home range and 20km^2 for female home range based on home range kernel estimates from previous data from the long-term study of the black bear population in the WGB and western Great Basin (Beckmann and Berger 2003). We generated 4372 random locations in ArcMap inside of the buffered male black bear "used" points to represent "available" resource units. This process was repeated for the buffered female black bear points to generate 10,000 randomly selected "available" locations. Each "available" location was within a buffer distance deemed to be the average distance a black bear can travel within a day (Cooper & Millspaugh, 1999; Compton et al., 2002; Boyce, 2006; Buskirk & Millspaugh, 2006; Ciarniello et al., 2007).

For mortality risk analyses, we took the GPS location points of mortality incidents (n= 366 location points) and created shapefiles using ArcMap. We then used the Buffer tool to create 5km^2 circular buffers around each location point (Treves, Martin et al. 2011). 732 random locations were generated in ArcMap inside of the buffered "used" mortality points to represent "available" resource units.

We developed resource selection probability function (RSPF) models for two levels of spatial analysis using the coarse and fine scale landscape parameters and both habitat selection and mortality black bear location data collected over the course of the study period. Resource selection analysis employed a logistic regression approach, using the logit command to compare characteristics of black bear "used" sites with "available" sites in the study region (Manly 2002, Sawyer and Brashares 2013).

For our logistic regression-based RSPF model, a black bear habitat selection or mortality "used" GPS location was considered a "success" and given a value of 1, where an “available” resource unit was given a value of 0, and the nine variables used as predictor variables. The RSPF is assumed to take the form:

$$w^*(x) = \exp(\beta o + \beta_1 x_1 + ... \_ \beta_p x_p)/1 + \exp(\beta_0 + \beta_1 x_1 + ... + \beta_p x_p)$$

where $x = (x_1, x_2, ..., x_p)$ holds the values for the X variables that are measured on a unit. Maximum likelihood estimates of the β parameters in the equation was calculated. We used chi-squared tests on deviances to assess whether there is any evidence that the probability of use of a location is related to a combination of the variables being considered.

For both spatial scales, we tested for collinearity of candidate variables using Pearson correlation coefficients, and variables with a correlation coefficient (r) > 0.7 were not included together in the models (Ciarniello, Boyce et al. 2007, Sawyer and Brashares 2013). We used AICc values to select relevant variables (Burnham & Anderson, 1998; Zielinski et al., 2004; Harris et al., 2008; Horne et al., 2008; Kirk & Zielinski, 2009), and we considered models comparable if the delta AIC was < 2.0 (Ciarniello et al., 2007). For models with similar AICc values, we chose the model with fewer terms (Quinn & Keough, 2002).

We assessed the predictive capability of each model using a Spearman’s rank correlation based on 5-fold cross validation (Boyce et al. 2002). In this procedure, we estimated an RSPF model using a random draw of 80% of the data. We then used this model to predict the frequency of occurrence in the withheld 20% of the data using 10 RSPF bins, and repeated the process 5 times, replacing the withheld 20% and removing the next 20% (Boyce et al. 2002). For our study, a model that had strong predictive capabilities would have a higher number of locations in bins with the highest RSPF scores. Once the final RSPF was derived, we used ArcMap 10.2 (ESRI, 2013) to map the probability of habitat selection over the entire study area.

Identifying Habitat States

We followed the methods of Nielsen, Stenhouse et al. (2006) to define five habitat states based on combining black bear habitat selection probability (see Chapter 1) and mortality risk probability (see Chapter 2). Values for habitat selection and mortality risk probability were binned in categories from 1-10 with 1 representing the lowest probability and 10 representing the maximum probability. Non-critical habitat was considered as those areas with low habitat selection probability and any degree of mortality risk. Secondary habitat had moderate selection probability and low mortality risk, while primary habitat represented areas with high habitat selection probability and low mortality risk. Secondary sink areas had moderate habitat selection with high mortality risk levels, and primary sink areas had both high habitat selection values and high mortality risk (Fig. 3). We followed the methods of Nielsen, et al. (2006) to set threshold levels of mortality risk and habitat selection probability to distinguish the values associated with each habitat category. Non-critical habitat encompassed habitat selection values less than 5, no matter the value of mortality risk, while all other habitat categories had habitat selection values of 5 or greater. The divide between primary or secondary habitat and primary or secondary sink occurred at the mortality risk value threshold of 5. Primary sink or habitat versus secondary sink or habitat was distinguished by a habitat selection probability threshold value of 7. We then calculated the percentage of the study area that reflected each habitat type, to ascertain the proportion of effective habitats present within each area.

Results

Male and female black bears have significantly different home range sizes (Beckmann 2003), so models for male and female animals were constructed separately. Nonetheless, the results of our analyses were relatively similar for both sexes. RSPF results for female black bears suggested that eight input variables significantly influence habitat selection either negatively or positively (Table 2; see Chapter 1 for full model results). Results for male black bears showed that six input variables were significant predictors of habitat selection probability (Table 3; see Chapter 1 for full model results).

Female black bears were most likely to select habitat at moderately low human population densities (between 30-40 people/km^2; see Chapter 1)). Preferred vegetation types were Great Basin Semi-Desert Chaparral, Mediterranean California Red Fir Forest and Woodland, and Rocky Mountain Subalpine-Montaine Riparian Woodland. Female bears strongly avoided arid and semi-arid grasslands, areas at high elevations, and those with landcover classification indicating human development. Overwhelmingly, female bears selected habitat at least 5km from a road and at least 20km from a recreation site. Higher habitat selection probability was also associated with short distance to a permanent water body, stream, and short distance to unpaved trails.

Male bears were most likely to select habitat with the lowest human population density (0.8 people/km^2; see Chapter 1). Male black bears had the highest probability of selecting Mediterranean California Ponderosa-Jeffrey Pine Forest and Woodland, followed by Rocky Mountain Subalpine-Montane Riparian Woodland, Mediterranean California Red Fir Forest and Woodland, and Northern Pacific Mesic Subalpine Woodland. Similar to female bears, areas with lowest probability of selection are characterized as being at high elevations, arid and semi-arid land, and all areas classified as having human activity (low and medium-high intensity human development, agriculture, and areas recently burned or mined).

Male bears had a high probability of selecting habitat within 5 kilometers of a major road, and within 5 kilometers of a recreation site. Overwhelmingly, there was high selection probability for habitat less than 1 kilometer from a water body, less than 2 kilometers from a trail, and within 5 kilometers of a permanent or seasonal stream. While both male and female bears primarily selected habitat with low human population densities, male bears had a 70% probability of selecting the habitat with the lowest (0.8pp/km^2) population density.

Mortality risk models using landscape data at fine spatial resolutions identified a suite of anthropogenic variables, as well as distance to water and landcover as the best predictors of mortality risk (χ^2=205.8871, p<0.0001) for black bears in the WGB (Table 2; Chapter 2).

Based on our classification of habitat states, data from male and female black bears yielded similar results for habitat suitability across the WGB and western Great Basin landscape. Around 12% of the study area comprised primary habitat for both sexes of bears, while 7% of habitat was primary sink for male bears, and 4% for female bears (Fig. 4). Secondary habitat, which had low mortality risk and moderate habitat selection probability, comprised around 47% of the study area, whereas secondary sink areas, with high mortality and moderate habitat selection probability, composed 6%. Overall, about 32% of the study area was classified as non-critical habitat for both male and female bears. The majority of non-critical habitats were found in the very arid regions, those at high elevations, and areas in the easternmost part of the study area with very few records of black bear occurrence. Primary habitat appears to be most concentrated in the forested, fertile parts of the WGB closest to permanent water sources. Secondary habitat dominated the Great Basin regions between the Sierra Nevada mountain range and the central Pinenut Range. Primary and secondary sink areas, although constituting only a small part of the landscape, appear to disrupt connectivity of primary habitat, especially in areas nearest Lake Tahoe (Figs. 5 & 6).

Discussion

Our study area in the WGB is a heterogeneous matrix of protected forestland, developed areas, and many other types of human land use. Because national parks and protected forest have greater restrictions on land-use practices, it is often assumed that these areas will pose a lower risk of mortality and more secure habitat for animals than would areas with fewer restrictions. However, this is not always the case in systems with pervasive human activity where popularity of human recreation in or near park boundaries and idiosyncrasies of animal sensitivity to human presence may increase incidences of human-wildlife conflict or human-induced mortality to animals (Burt and Rice 2009, Goldstein, Poe et al. 2010, Musiani, Anwar et al. 2010).

We found that primary habitat with the densest forest cover and often with protected status were fragmented by primary sink habitat for male and female black bears (Fig. 5). However, the protected designation of an area likely had less influence on black bear mortality than did the location of the protected area in relation to type and magnitude human activity. Therefore, as human activity in the WGB rapidly extends into backcountry forested areas, it creates novel habitat for black bears that can potentially become primary or secondary sinks (Hobbs, Higgs et al. 2009, Morse, Pellissier et al. 2014).

Primary habitat is important for the protection and persistence of the black bear population in the WGB and western Great Basin, yet constitutes only about 12% of the landscape. Given the relative scarcity of such habitat, it is essential that these areas receive considerable conservation and management attention. A no net-loss approach to these habitat patches would ensure their ability to support the black bear population, and constitute important forested sections of dispersal corridors (Cushman 2006). Results of the modeling efforts also show that secondary habitat constitutes a majority of the WGB landscape. Conservation-based management efforts should be concentrated on maintaining very low mortality risk in these regions, as they have considerable potential to maintain the black bear population and support its persistence and possible expansion, in light of such limited primary habitat (Fig. 5).

Although only around 6% of the study area, patches of primary sinks may be a threat to the connectivity of suitable habitat in the region and further study is necessary to determine whether their existence can potentially impact the population growth of black bears in the region (Kanda, Fuller et al. 2009). Conservation managers should investigate whether strategies to reduce mortality risk of bears are possible in these areas, focusing on both wildlife deterrent techniques and changing human behavior to reduce conflict (Conover 2001, Treves and Karanth 2003, Woodroffe, Thirgood et al. 2005).

Habitat selection models are often used to guide the management and conservation of wildlife; however, misinterpreting maladaptive habitat selection by wildlife can result in the protection of habitats that fail to support the local persistence of the species. By including models of mortality risk using empirical data, we can better define habitat suitability for a particular species. In systems with high levels of human activity or human-wildlife conflict, it is also especially important to construct these habitat selection and mortality risk models with a variety of anthropogenic variables to properly identify the various drivers of habitat suitability patterns for the focal species. One of the next steps of this project is to determine if these habitat selection and mortality risk models relate to demographic responses by the population to determine if these areas of primary and secondary risk truly act as attractive sinks or evolutionary traps (Roever, van Aarde et al. 2013).

Because black bears have such large home ranges, habitat-based management should focus on large areas to account for the heterogeneity that characterizes shared human-wildlife landscapes. To inform management, our analyses can project information gathered from trends in the study area to other, larger regions. Although our study region in western Nevada is relatively small in spatial extent, it is a portion of the larger Great Basin, which stretches across 477,000 km^2 and four states and is home to an expanding population of black bears in the western Great Basin (Lackey, Beckmann et al. 2013). We intend to use the information generated from these analyses to model the potential for connectivity of suitable habitat and aid in the design of corridors to insure the ability of the black bear population in the WGB to expand and recolonize historic habitat across the western regions of the Great Basin (Lackey, Beckmann et al. 2013).

The methods put forth by Nielsen et al. (2006) to combine habitat selection and mortality risk probability to better classify habitat suitability have served as an important step for conservation efforts of large mammals worldwide (Chetkiewicz and Boyce 2009, Nielsen, McDermid et al. 2010, Roever, van Aarde et al. 2013). However, habitat suitability predictions may be enhanced by a more nuanced approach to categorizing the five habitat states. As opposed to relating thresholds of mortality risk and habitat selection probability to arbitrary delineations of source-sink potential, these categories can instead be based on the life history characteristics of the species in question, as well as population trends gathered from the empirical data. For example, for some species with extremely low reproductive rates or very small population sizes, setting the parameters for primary habitat may involve classifying areas with the lowest levels of mortality risk (i.e. at values of 1 or 2), to be able to adequately preserve the population. Similarly, for habitat generalists like the black bear, habitat selection probabilities at low or moderate values may be misclassified as non-critical habitat when in fact these areas may be adequate for species use and persistence. We recommend that future users of this modeling framework think critically about their focal species and study system to properly use this conservation tool to reach informed understanding about the relationships between landscape heterogeneity and wildlife population persistence.

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FIGURES

FIGURE 1. The Lake Tahoe Basin (WGB) and part of the US Great Basin study system.

FIGURE 2. Gross change in area (ha) by landcover class from 1940-2002 in the southern WGB (Adapted from Raumann *et al*. 2008).

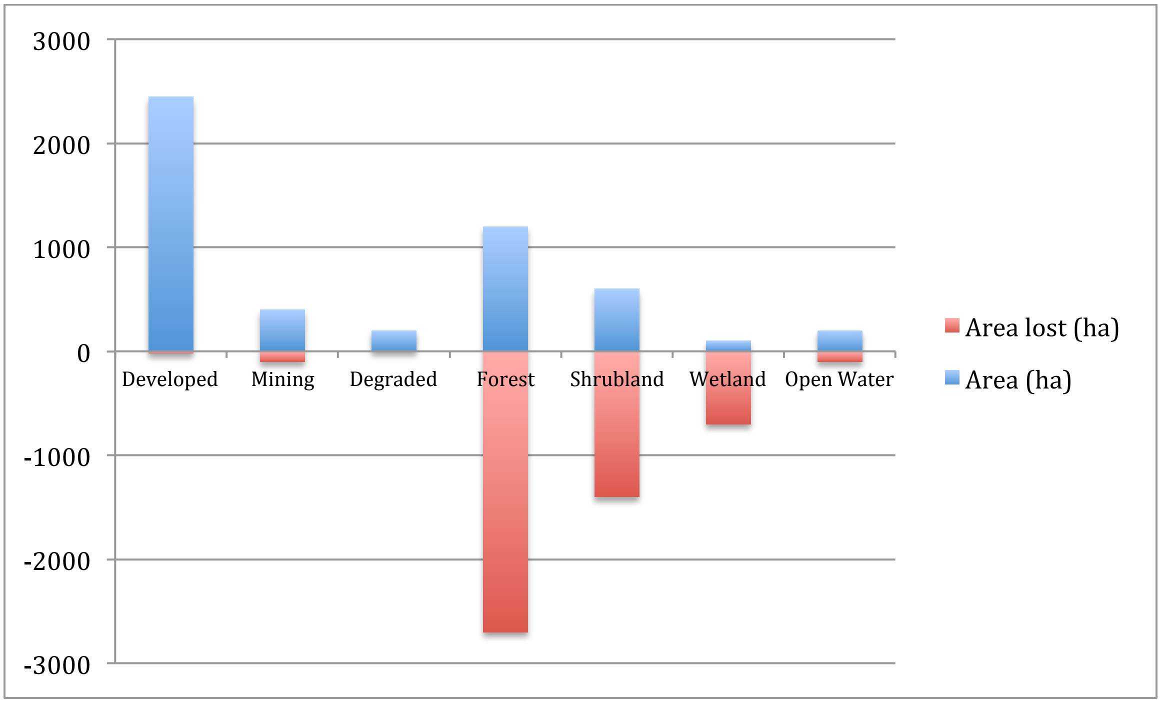


FIGURE 3. Five Habitat States categorized based on probability of habitat selection (10 ordinal bins from 1-low to 10-high) and relative probability of mortality (10 ordinal bins from 1-low to 10-high) for black bears in the WGB. This figure was adapted from Nielsen *et al.* (2006).

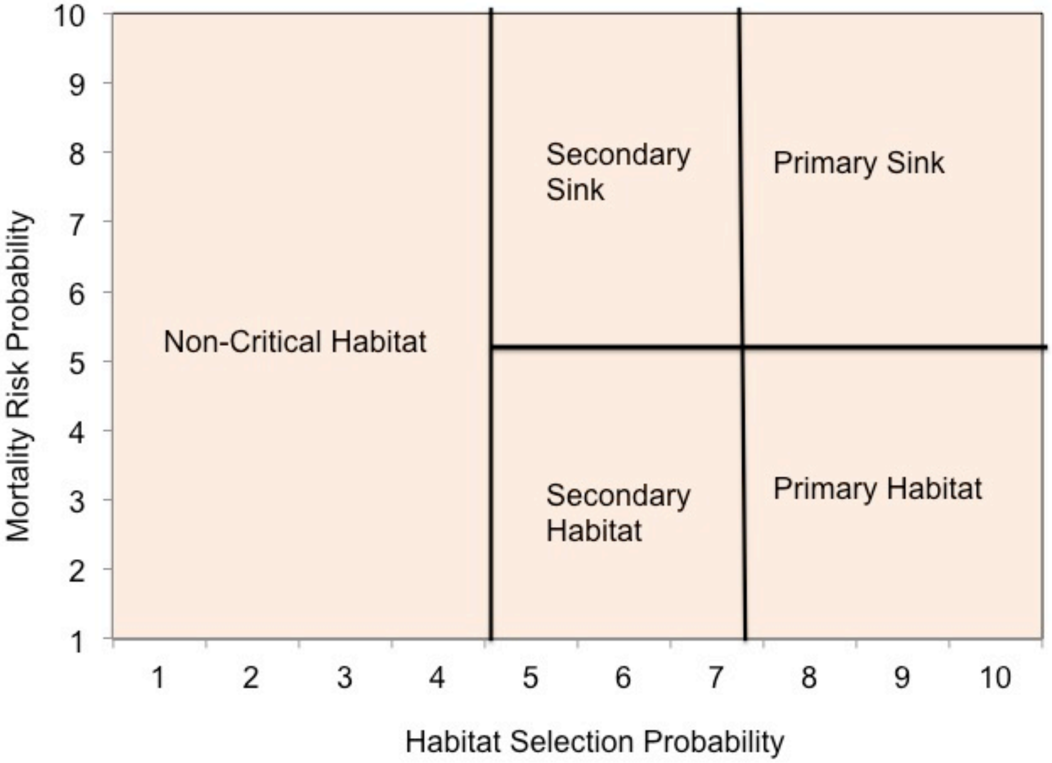


FIGURE 4. Percentage of WGB landscape falling into the five Habitat States of habitat suitability in the WGB for male (a) and female (b) black bears

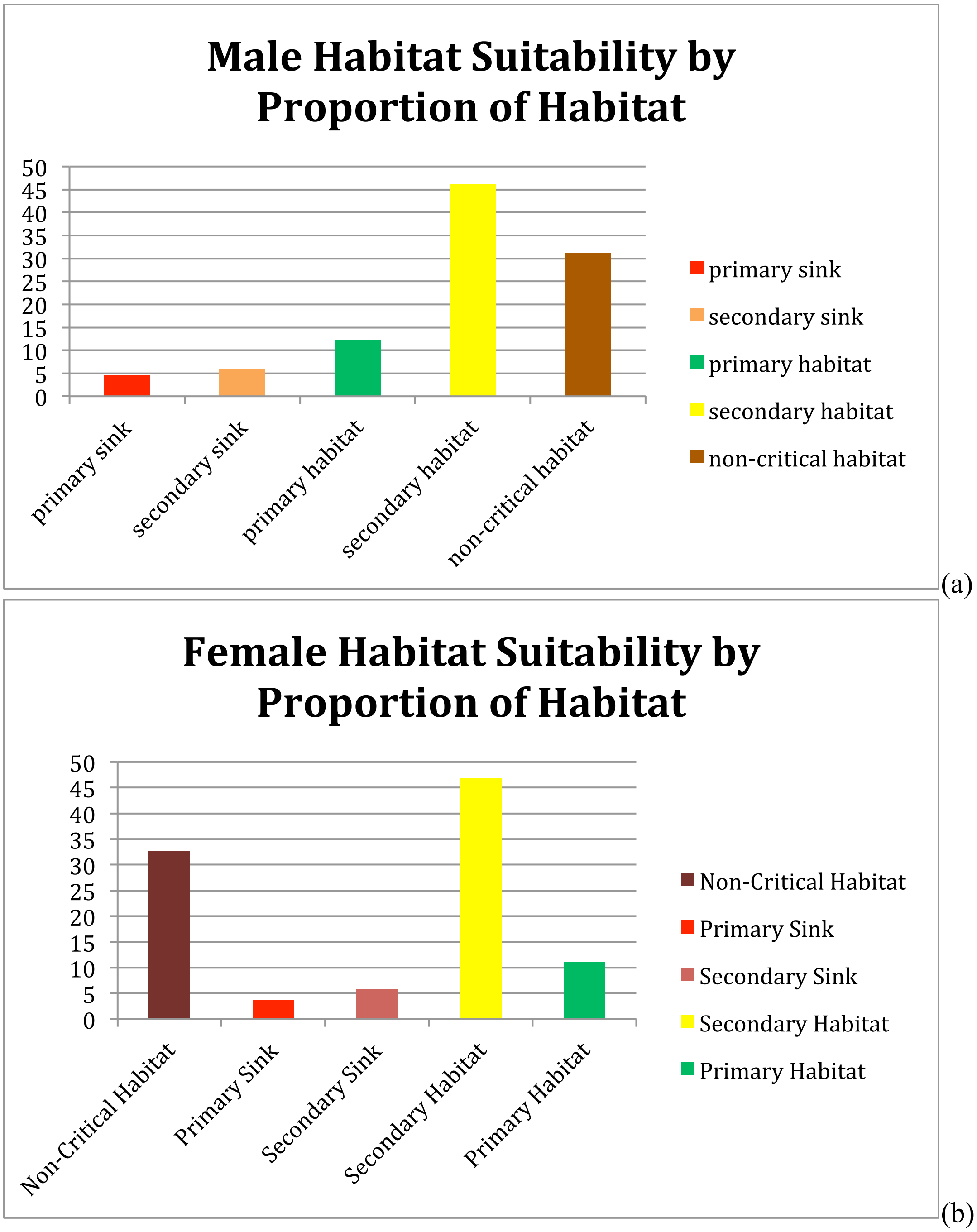
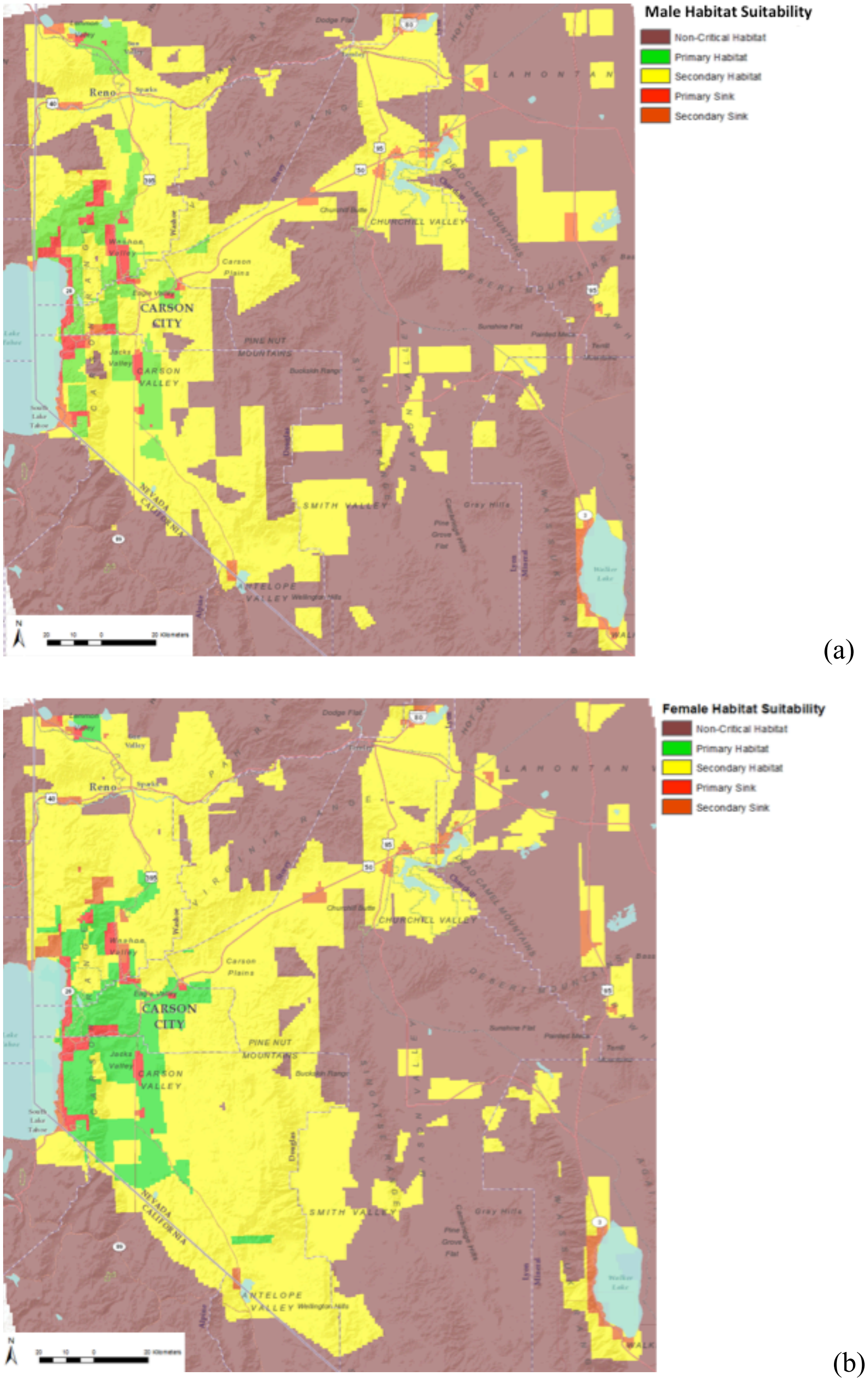


FIGURE 5. Maps of five Habitat Categories of suitability for black bears in the WGB and western Great Basin for male (a) and female (b) bears.



(a)

(b)

TABLES

TABLE 1. Parameters used in construction of the habitat selection and mortality risk models for black bears in the WGB.

Landcover	Categorical	29 vegetative and anthropogenic landcover categories
Distance to Road	Continuous	Straight-line distance to nearest road in kilometers
Distance to Water Body	Continuous	Straight-line distance to nearest large water body in kilometers
Distance to Stream	Continuous	Straight-line distance to nearest permanent or seasonal stream in kilometers
Distance to Trail	Continuous	Straight-line distance to nearest hiking trail in kilometers
Distance to Rail	Continuous	Straight-line distance to nearest Amtrak or regional railroad line in kilometers
Urban Polygon	Categorical	Census-defined urban areas measured in km^2
Human Population Density	Categorical	2010 census-defined human population density by zip code in persons/km^2
Distance to Recreation Site	Continuous	Straight-line distance to nearest recreation site, trail head, camp site, or ski lodge in kilometers

TABLE 2. The most parsimonious RSPF models for habitat selection probability for male and female black bears in the WGB.

F	Distance to water + urban polygon + distance to stream + distance to road + distance to recreation site + human population density + landcover	14255	<.0001
M	Urban polygon + distance to stream + distance to road + distance to recreation site + human population density + landcover	3416.55	<.0001

TABLE 3. The most parsimonious RSPF model for mortality risk for black bears in the WGB.

Model	**AIC**	**P**
Distance to water + distance to road + landcover + urban polygon + human population density + distance to recreation site	956.032	<0.0001

CHAPTER SIX

Summary and Conclusions

In this dissertation, I investigated the role of characterizing human activity in the Western Nevada including the Lake Tahoe Basin (WGB) and portions of the western Great Basin, by incorporating findings into estimations of habitat use, mortality risk, and habitat suitability in a large carnivore, the American black bear (*Ursus americanus*). The specific aims of this dissertation were to answer the following questions: 1) How do anthropogenic landscape patterns impact large carnivore ecology? 2) How do analyses at different spatial resolutions affect our understanding of human influence on carnivore behavioral patterns? 3) How can general conservation tools and analyses be applied to local and/or species-specific issues?

To answer these questions, I used over 19,000 GPS location points collected for 24 black bears from 2005-2011, 366 black bear mortality locations from 1997-2013, and multi-resolution landscape data representing anthropogenic and environmental habitat heterogeneity in the WGB. I analyzed these data using Resource Selection Probability Functions (RSPF). Chapter 2 explores how a variety of anthropogenic and environmental landscape variables appear to affect black bear habitat use. Chapter 2 also investigates how refining the spatial resolution of landscape variables influences the results of habitat selection analyses. Chapter 3 similarly explores how anthropogenic and environmental landscape variables at multiple spatial and temporal resolutions predicted mortality risk of black bears in the WGB. Chapter 4 describes the impact of manipulating the Human Footprint index (Sanderson, Jaiteh et al. 2002) for modeling species-specific land use dynamics in the WGB. Chapter 5 combined RSPF model results from Chapters 2 and 3 to estimate habitat suitability for black bears in the WGB.

In Chapter 2, I hypothesized that the inclusion of anthropogenic variables in habitat selection analyses would demonstrate a response of black bears to heterogeneous types and magnitudes of human activity in the WGB. I also hypothesized that estimating habitat selection at a fine (30m^2) spatial resolution would demonstrate nuances of habitat use that would be overlooked by analyses at a coarse (1km^2) resolution. Indeed, model results showed that a variety of anthropogenic landscape variables are significant predictors of black bear habitat use. However, I found that there was no significant difference in the predictive power of analyses of habitat selection conducted with variables modeled at fine and coarse spatial resolutions. These results support earlier findings, that were only conducted at coarse spatial resolutions, that large carnivore habitat selection is influenced by human activity, and observed at coarse spatial resolutions (Roever, Boyce et al. 2008, Tucker, Clark et al. 2008, Lesmerises, Dussault et al. 2012) and suggest that finer scale analyses are not critical to understanding patterns of habitat choice in large carnivores.

In Chapter 3, I hypothesized that including a variety of anthropogenic and environmental landscape variables in analyses would be important to properly understand drivers of human-induced mortality to black bears in the WGB. These findings were supported by the model results, which showed that many metrics of human activity were significant predictors of black bear mortality risk. I also hypothesized that estimating mortality risk using variables measured at a fine (30m^2) spatial resolution would demonstrate nuances of mortality risk overlooked by analyses using variables measured at a coarse ($1km^2$) resolutions. Our results also supported this hypothesis, showing a significant difference between model results using variables at both resolutions. Variables at fine spatial resolutions had more predictive power when estimating the landscape characteristics driving black bear mortality risk. These results contribute to a growing body of evidence suggesting that large carnivores are vulnerable to multiple types of disturbance from human activities, which can fragment their habitat (Cherry, Haroldson et al. 2002, Ciarniello, Boyce et al. 2007, Linke, McDermid et al. 2013). Our results would be greatly enhanced by additional data regarding demographic trends of black bears in the WGB and western Great Basin, allowing us to estimate the impacts of rate and distribution of black bear mortality on population persistence.

In Chapter 4, I explored manipulating The Human Footprint (HF) (Sanderson, Jaiteh et al. 2002), a well-recognized spatial index summarizing gradients of human influence on the environment, for use in modeling large carnivore landscape use in a local and species-specific context. I expected that altering the anthropogenic variables used to construct the HF from global to regional- and species-specific would yield significantly different characterizations of the HF in the WGB, and would lead to different results when used to model black bear population dynamics. Similarly, I expected that reducing the spatial resolution from a coarse $1km^2$ to a finer $30m^2$ would significantly alter the way the HF was characterized across the WGB landscape, and would yield significantly different results when applied to modeling black bear population dynamics. Our manipulations of the HF showed that although reducing the spatial resolution of the landscape variables used to construct the index did not significantly alter results, the recalculation of the HF with regional and species-specific variables yielded significantly different interpretations of both the spatial composition of the HF in the WGB and the impact of the HF on models of black bear habitat use and mortality risk. These findings are in line with studies suggesting the HF requires adaptation of variables for use at ecoregional extents (Woolmer, Trombulak et al. 2008), and advances this concept by suggesting further modifications reflecting the life history characteristics of the study species be employed when using the HF to estimate ecological patterns related to specific species.

In Chapter 5, I incorporated results from Chapters 1 and 2 into an integrated use-mortality model that characterizes the type and spatial arrangement of habitat suitability for black bears in the WGB. Because of the high rates of human-carnivore conflict in our study region, I felt it was important to include elements of maladaptive habitat selection in classifying habitat quality in the landscape. I found that although primary and secondary sinks comprise a small amount of the total WGB landscape, their spatial arrangement fragments areas of important primary and secondary habitat, which may ultimately threaten habitat connectivity. These analyses contribute to a growing body of literature demonstrating the usefulness of combining habitat selection and mortality risk models to predict the influence of habitat suitability on species population persistence (Nielsen, Stenhouse et al. 2006, Falcucci, Ciucci et al. 2009, Roever, van Aarde et al. 2013).

Implications of this work

In addition to the conservation and management implications of this study as discussed in Chapters 2-5, this dissertation has many implications for future studies of ecological processes and conservation in landscapes with heterogeneous human influence. In particular, these results contribute to the understanding of how commonly used ecological and conservation methods can be best adapted for local or species-specific studies. Although RSPF models are widely used to model habitat selection patterns of wildlife (Boyce 2006, Johnson, Nielsen et al. 2006, Chetkiewicz and Boyce 2009), it is often difficult to collect data that accounts for frequency of habitat use. The long-term dataset of black bear GPS location points used in Chapter 2 allowed us to use high-quality and fine-scale empirical data to investigate behavioral trends of a wide-ranging large carnivore. Similarly, wildlife studies are often limited to modeling mortality risk using locations of animal carcasses, opportunistically discovered on the landscape (Nielsen, McDermid et al. 2010, Rich, Mitchell et al. 2012, Roever, van Aarde et al. 2013), or using estimations of areas that may pose mortality threats (Nielsen, McDermid et al. 2010, Rich, Mitchell et al. 2012). Chapter 3 used a robust dataset with the locations of multiple types of black bear mortality collected over a 14-year study period, allowing for more accurate estimates of mortality risk based on actual mortality locations.

The results of Chapter 4 allow us to make recommendations for using indices like the HF for applied conservation efforts. Based on our data on a population of large carnivores that frequently experiences human-wildlife conflict, I was able to construct a HF index that reflected detailed patterns of human influence on the environment in our study region. Applying this framework to a different species, however, would require an investigation of the literature to determine which types of anthropogenic activities likely have an impact to the species and at which scale.

The results of Chapter 5 also enhance our understanding of how to apply conservation tools to specific objectives. Although I support the Nielsen, Stenhouse et al. (2006) rationale for combining habitat selection and mortality risk information to inform habitat suitability models, I argue that the methods should always be tailored to accurately reflect the life history characteristics and the location of the species or population in question. For example, researchers should ideally use information on mortality, fecundity, and immigration rates to set thresholds for defining habitat states in terms of source or sink potential.

This dissertation also adds to an expanding literature base that evaluates the dual role of ecological as well as social drivers of human-wildlife conflict (Howe, Obbard et al. 2010, Musiani, Anwar et al. 2010, Rasmussen and Arler 2010, Baruch-Mordo, Breck et al. 2011, Merkle, Krausman et al. 2011, Kojola and Heikkinen 2012). I found that our results allowed us to identify the types of human activity that influence carnivore ecology, including habitat avoidance and/or selection or mortality for a large carnivore. However, as human social dynamics are a simultaneous driver of human-wildlife conflict (Knight 2000, Conover 2001, (IUCN) 2003, Naughton-Treves, Grossberg et al. 2003, Treves and Karanth 2003, Merkle, Krausman et al. 2011, Kojola and Heikkinen 2012), our study sets a framework for further study evaluating the social differences of areas with varying degrees of conflict.

This study is one of the first to incorporate such a large variety of anthropogenic landscape parameters into models of large carnivore habitat use and mortality risk. This demonstrates the nuances of large carnivore tolerance to human activity, especially in forested, backcountry areas. The study is one of few to investigate the impact of spatial resolution on the predictive power of these models. Although scale is often addressed in similar studies, it usually refers to observing patterns across spatial extent as opposed to spatial resolution (Sawyer and Brashares 2013, Waller, Belant et al. 2013, Yan, Zeng et al. 2013, Gilroy, Medina Uribe et al. 2014). The study shows that although large carnivores use landscapes at a coarse spatial resolution, some human threats operate on the landscape at finer resolutions and thus, understanding (and potentially avoiding) human-driven mortality of large carnivores may require such a fine-resolution analysis. Uncovering these trade-offs can help inform conservation management plans.

The HF has been used to look at the persistence of wildlife, and in particular carnivores, at a continental scale (Laliberte 2004) or the scale of a species range (Yackulic, Sanderson et al. 2011), rescaled and recalculated HF indices have not previously been used to evaluate the influence of human activity on carnivore ecology and conservation strategies at the local scale. Our research provides a framework for using this tool in future evaluations of human impacts to wildlife.

Because human development and landscape heterogeneity are expected to play increasingly central roles in wildlife conservation (Wikramanayake, McKnight et al. 2004, Woolmer, Trombulak et al. 2008, Harju, Dzialak et al. 2011, Inman, Brock et al. 2013), these approaches used in the dissertation may become more common as researchers strive to understand the influence of landscape heterogeneity on ecological processes, and also to project the influence of these trends into the future. Examining the response of wildlife to human activity in changing landscapes will allow us to better understand the potential to manage human-wildlife interactions in areas that may become novel ecosystems (Hobbs, Higgs et al. 2009, Threlfall, Law et al. 2012).

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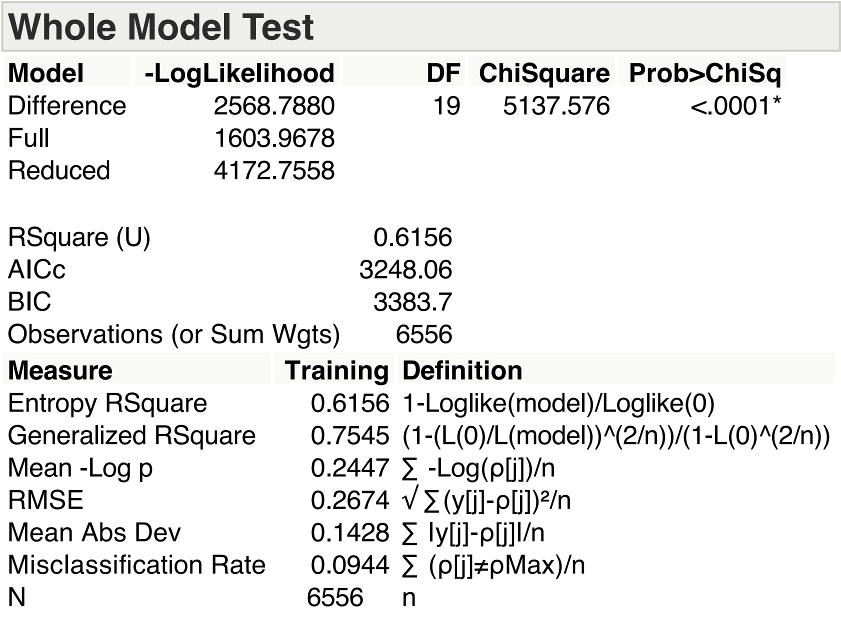
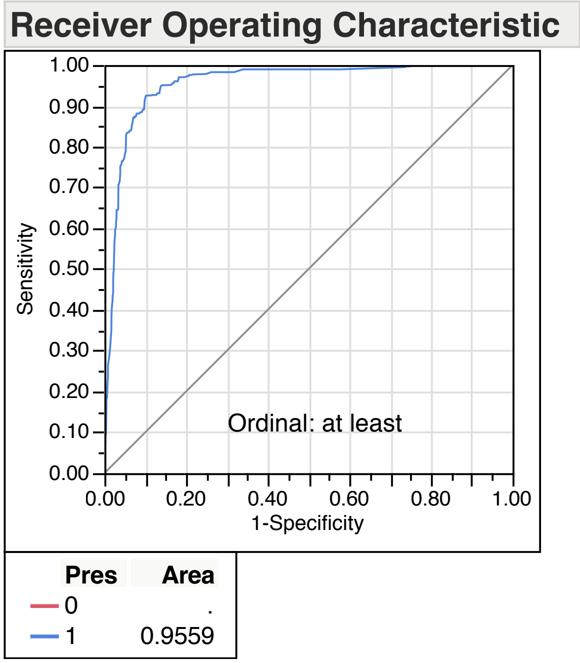
Appendix

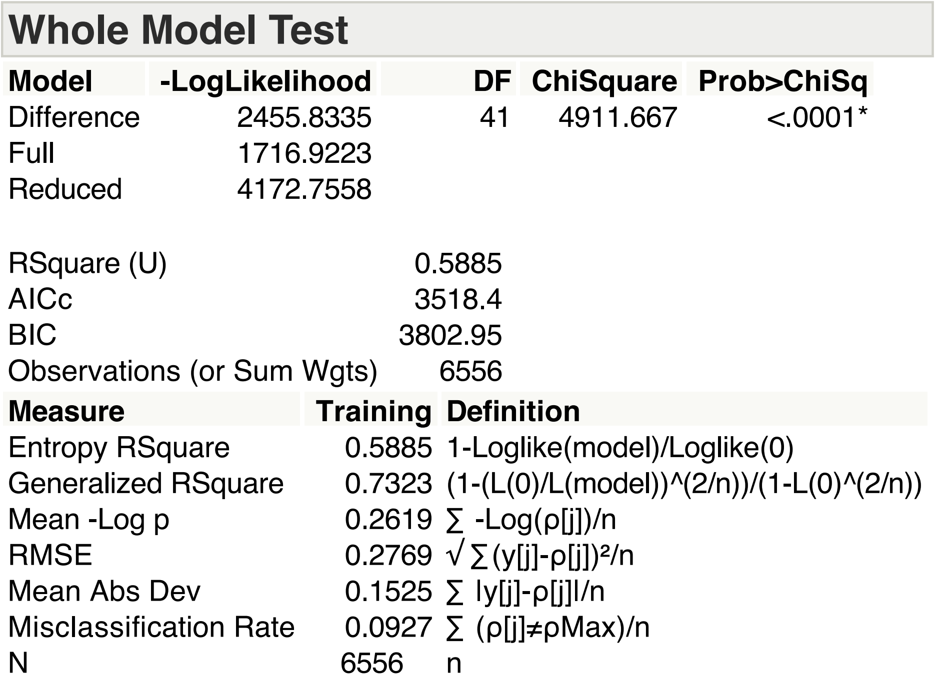
Supplementary Table S1. Whole model test and ROC results for male black bear RSPF habitat selection model (Chapter 1) with coarse-resolution variables.



```
Whole Model Test

Model        -LogLikelihood        DF   ChiSquare   Prob>ChiSq
Difference        2568.7880        19    5137.576      <.0001*
Full              1603.9678
Reduced           4172.7558

RSquare (U)                       0.6156
AICc                             3248.06
BIC                               3383.7
Observations (or Sum Wgts)          6556

Measure                  Training  Definition
Entropy RSquare            0.6156  1-Loglike(model)/Loglike(0)
Generalized RSquare        0.7545  (1-(L(0)/L(model))^(2/n))/(1-L(0)^(2/n))
Mean -Log p                0.2447  ∑ -Log(ρ[j])/n
RMSE                       0.2674  √∑(y[j]-ρ[j])²/n
Mean Abs Dev               0.1428  ∑ |y[j]-ρ[j]|/n
Misclassification Rate     0.0944  ∑ (ρ[j]≠ρMax)/n
N                         6556     n
```



Supplementary Table S2. Whole model test results for male black bear RSPF habitat selection model (Chapter 1) with fine-resolution variables.



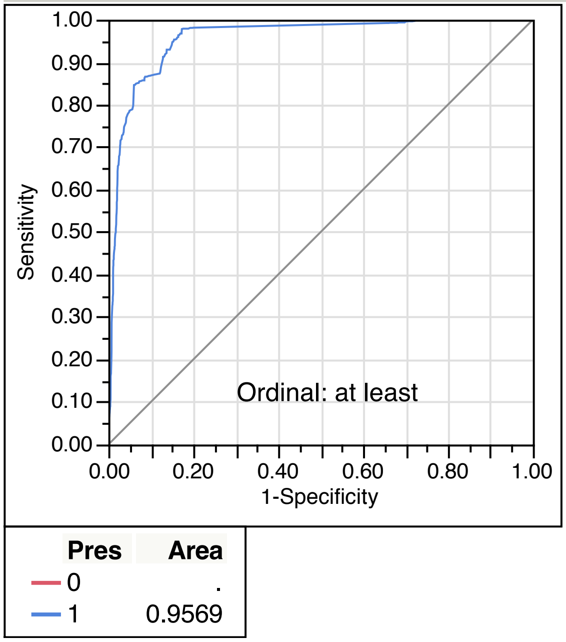
Whole Model Test

Model	-LogLikelihood	DF	ChiSquare	Prob>ChiSq
Difference	2455.8335	41	4911.667	<.0001*
Full	1716.9223			
Reduced	4172.7558			

RSquare (U)	0.5885
AICc	3518.4
BIC	3802.95
Observations (or Sum Wgts)	6556

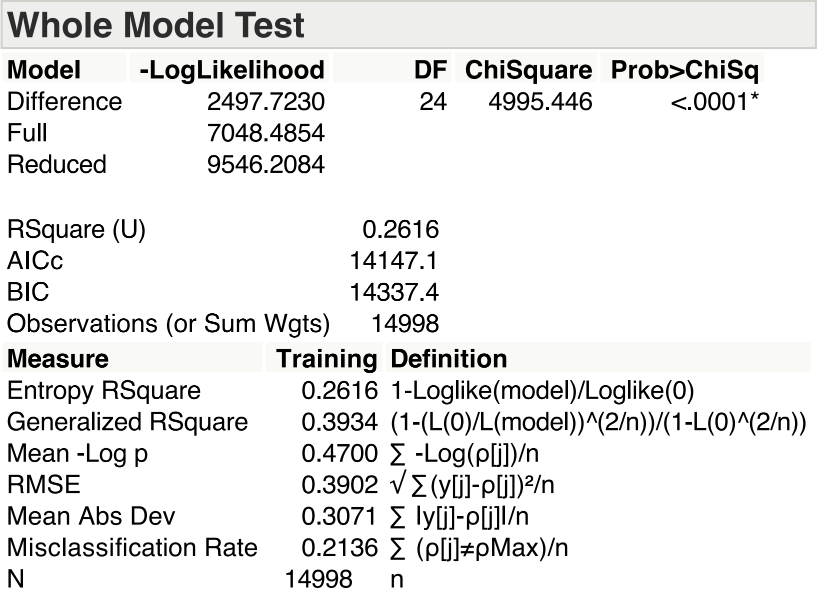
Measure	Training	Definition
Entropy RSquare	0.5885	1-Loglike(model)/Loglike(0)
Generalized RSquare	0.7323	(1-(L(0)/L(model))^(2/n))/(1-L(0)^(2/n))
Mean -Log p	0.2619	∑ -Log(ρ[j])/n
RMSE	0.2769	√ ∑(y[j]-ρ[j])²/n
Mean Abs Dev	0.1525	∑ |y[j]-ρ[j]|/n
Misclassification Rate	0.0927	∑ (ρ[j]≠ρMax)/n
N	6556	n

Receiver Operating Characteristic



Pres	Area
🟥 0	.
🟦 1	0.9569

Supplementary Table S3. Whole model test results for female black bear RSPF habitat selection model (Chapter 1) with coarse-resolution variables.



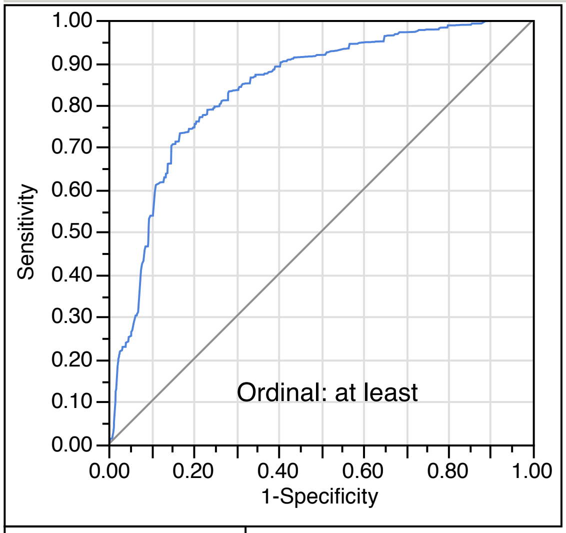
Whole Model Test

Model	-LogLikelihood	DF	ChiSquare	Prob>ChiSq
Difference	2497.7230	24	4995.446	<.0001*
Full	7048.4854			
Reduced	9546.2084			

RSquare (U)	0.2616
AICc	14147.1
BIC	14337.4
Observations (or Sum Wgts)	14998

Measure	Training	Definition
Entropy RSquare	0.2616	1-Loglike(model)/Loglike(0)
Generalized RSquare	0.3934	(1-(L(0)/L(model))^(2/n))/(1-L(0)^(2/n))
Mean -Log p	0.4700	∑ -Log(ρ[j])/n
RMSE	0.3902	√∑(y[j]-ρ[j])²/n
Mean Abs Dev	0.3071	∑ Iy[j]-ρ[j]I/n
Misclassification Rate	0.2136	∑ (ρ[j]≠ρMax)/n
N	14998	n

Receiver Operating Characteristic



Pres	Area
🟥 0	.
🟦 1	0.8362

Supplementary Table S4. Whole model test results for female black bear RSPF habitat selection model (Chapter 1) with fine-resolution variables.

Whole Model Test

Model	-LogLikelihood	DF	ChiSquare	Prob>ChiSq
Difference	3169.6634	43	6339.327	<.0001*
Full	6376.5450			
Reduced	9546.2084			

RSquare (U)	0.3320
AICc	12841.4
BIC	13176.2
Observations (or Sum Wgts)	14998

Measure	Training	Definition
Entropy RSquare	0.3320	1-Loglike(model)/Loglike(0)
Generalized RSquare	0.4788	(1-(L(0)/L(model))^(2/n))/(1-L(0)^(2/n))
Mean -Log p	0.4252	∑ -Log(ρ[j])/n
RMSE	0.3712	√ ∑(y[j]-ρ[j])²/n
Mean Abs Dev	0.2768	∑ Iy[j]-ρ[j]I/n
Misclassification Rate	0.1878	∑ (ρ[j]≠ρMax)/n
N	14998	n

Receiver Operating Characteristic