Predicting Grizzly Bear (*Ursus arctos*) densities in British Columbia using a multiple regression model

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Prepared for
British Columbia Ministry of Water, Land and Air Protection

BRITISH
COLUMBIA

May 5, 2004

Summary:

We determined the relationships between Grizzly Bear density and ultimate measures of ecosystem productivity and mortality at a landscape scale using multiple linear regression and field based density estimates from Grizzly Bear populations across western North America. We found that Grizzly Bear densities in non-coastal environments were positively related to the mean annual rainfall, to the presence of salmon, and to the proportion of the population's perimeter that was contiguous with other Grizzly Bear populations. Grizzly Bear densities in non-coastal environments were negatively related to human and livestock density, and to the reported mortality rate ($r^2 = 0.62$, $n = 33$). We could not predict Grizzly Bear density on the BC coast because the single Grizzly Bear density estimate on the coast did not appear to be related to the same factors as those in the BC interior or in coastal Alaska. We used the multiple linear regression model to predict Grizzly Bear density and associated confidence limits in 61 Grizzly Bear population sub-units in BC, in areas with few or no salmon. Five of the 61 sub-units (Alta, Atlin, North Cascades, Taiga and Tatshenshini) had unrealistically high predictions. We estimated that the remaining 56 sub-units contained about 14,000 Grizzly Bears, which is a mean density of 16 Grizzly Bears /1000 km^2. The model also accurately predicted zero Grizzly Bears in 5 areas of the province where the species has been extirpated: Lower Mainland, Sunshine Coast, Okanagan, Fraser Plateau, and Peace.

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INTRODUCTION

        The development of aerial survey and genetic identification techniques has facilitated many recent estimates of Grizzly Bear density; however, because of the cost of inventories and the vast areas involved, recent field-based estimates have been restricted to a small portion of the hunted populations. Prior to 2003, in areas where there were no survey data, Grizzly Bear populations were estimated using a subjective extrapolation from areas of known density, without an estimate of confidence that could be placed in the result. The subjective extrapolation estimation method did not test fundamental concepts, such as whether small scale habitat attributes would add up to provide an indication of landscape scale density. Nonetheless, various forms of expert-based models were also being used in the five other jurisdictions where Grizzly Bear hunting occurred: Alberta, Northwest Territories, Nunavut, Yukon Territory, and Alaska.

        Resource selection function (RSF) models that can be weighted to predict spatial density (Boyce and MacDonald 1999) have been proposed as an alternative to expert-based models (Boyce and Waller 2003; Apps *et al*. 2004). But multivariate statistical models, which can be used to predict density within a study area, are usually based on small-scale habitat attributes and animal data collected from a small number of individuals from a single population. These data are influenced by the local availability of resources and the individual behaviours related to regional life history or human activity; as a result, such multivariate statistical models do not necessarily generalize well to other landscapes (Boyce *et al*. 1999; Myserud and Ims 1999; Apps *et al*. 2004). The above factors clearly limit the utility of RSF models as comprehensive predictive tools. Hence, while the empirical RSF models may be statistically explanatory and objective, considerable subjectivity may be required in deciding in which other areas to apply the models (e.g., Boyce and Waller 2003). The model described here could be considered an RSF model based on very large resource units and density, rather than on occurrence.

        Recent work has demonstrated the link between density and measures of prey abundance for carnivores (Carbone and Gittleman 2002), and between density and measures of primary productivity for ungulates (Crete 1999). Ultimate measures of productivity for a species should directly affect density in all environments, allowing the construction of general predictive models once other limiting factors are taken into account. The examination of measures of productivity at the population scale is not confounded by behavioural preferences made by individuals.

        We examined the relationship between existing Grizzly Bear density estimates and ultimate factors representing productivity and mortality. Grizzly Bears are omnivores, and their reliance on animal protein varies greatly across their range (Mattson *et al*. 1991; McLellan and Hovey 1995; Hilderbrand *et al*. 1999; Gau *et al*. 2002). The single largest meat source in their diet is spawning salmon, and all areas of very high Grizzly Bear density offer large numbers of salmon over a significant portion of the non-denning season (Miller *et al*. 1997; Hilderbrand *et al*. 1999). In the continental interior, Grizzly Bears are mainly herbivorous and frugivorous, supplementing their diet with nuts, insects, ground squirrels, anadromous and freshwater fish, and ungulates where available (Mattson *et al*. 1991; McLellan and Hovey 1995; Hilderbrand *et al*. 1999; Gau *et al*. 2002). Grizzly Bears prefer highly digestible plant species and plant parts; because they have a single gut, they are relatively inefficient at digesting plant matter (Welch *et al*. 1997; Rode and Robbins 2000; Rode *et al*. 2001; Felicetti *et al*. 2003). Grizzly Bears in the

interior concentrate their foraging in moist sites; most of their preferred plant species can be considered hydrophilic (McLellan and Hovey 2001; McLoughlin *et al*. 2002). The abundance of berry and mast crops is also likely related to seasonal rainfall.

We considered how measures of connectivity may affect Grizzly Bear density, because where Grizzly Bear populations are isolated from each other, they may exhibit source-sink population dynamics (Proctor *et al*. 2002; Apps *et al*. 2004). We considered the direct and documented mortality of hunting on Grizzly Bears over the previous ten years, and assumed that historic and largely unreported and unrecorded killing of Grizzly Bears by humans would be represented by the surrogate variables: human and livestock density.

METHODS

Recent efforts to predict world agricultural production and the effect of global warming have led to the development of numerous indices of plant productivity, based on satellite sensor data and, in some cases, combined with sophisticated mathematical models. Spatial data to predict rainfall, temperature and sunshine are available (Table 1; Daly *et al*. 1994; Kumar *et al*. 1997), but we could not find digital soils maps that predict nutrient limitation to the resident plant community.

Table 1. Variables extracted from digital databases for this analysis, including a description of the original data used to build the GIS coverage and the spatial resolution (all data were shifted to raster format).

Variable	Source Data	Resolution (km)	Reference
mean annual precipitation	ground station weather data	4	Daly et al. 1994
mean growing season temperature	ground station weather data	55	Leemans and Cramer 1991
actual evapotranspiration (AET)	ground station weather data	55	
normalized differential vegetation index (NDVI)	MODIS satellites	2	MTPE EOS Data Products Handbook Volume 1
non-vegetated land	MODIS satellites	2	MTPE EOS Data Products Handbook Volume 1

Maps are available for several limiting factors of plant productivity across large geographic areas. Evapotranspiration (AET) is a measure of the water balance and energy available in an environment, and is related to primary plant productivity, species diversity and ungulate biomass (Rosenzweig 1968; Currie 1991; Crete 1999). Evapotranspiration is a composite index of the two most limiting resources to photosynthesis: water and solar radiational energy (Rosenzweig 1968). AET can be transformed into a measure of net primary productivity (Leith 1976), and was used as a measure of primary productivity to describe Grizzly Bear life history strategies across North America (Ferguson and McLoughlin 2000).

The normalized differential vegetation index (NDVI) is a measure of plant vigour and can be equated to above ground vegetation productivity and biomass. NDVI is derived from a comparison of a single visible signal to a single near-infrared signal, and is normalized with the measured albedo (James and Kalluri 1993). NDVI is a simplification of the greenness index, which has been found to predict Grizzly Bear habitat selection at finer scales than those analyzed here (Mace and Waller 1999). Many digital indices of primary productivity are based on similar or identical data and are correlated (e.g., the correlation between AET and NDVI in our data was $n = 46$, $r^2 = 0.67$, $P < 0.001$).

We derived indices of ecosystem productivity from raster format spatial databases (Table 1). Study area boundaries were digitized, and mean values for each variable were calculated for each study area, excluding values for large (> 69 km^2) areas of open water. Large water bodies were excluded to keep density estimates unbiased and to maintain consistency with previous estimates made elsewhere. Initial univariate relationships between productivity variables were assessed visually and by using rank correlation.

We used a simple dummy variable to index the presence of salmon in each study area because we did not have measures of salmon availability. Earlier work (Hildebrand *et al*. 1999) documented the relationship between meat, particularly salmon, in the diet and Grizzly Bear density; this is supported by our analysis. Salmon abundance was recorded as: absent (0), present in small numbers (1), or present in large numbers (2), based on the location of the study area and the authors' descriptions. All coastal areas (but no interior areas) had large numbers of salmon available. Terrestrial meat sources also likely influence density (Hildebrand *et al*. 1999), but we excluded this measure from our analysis because it is highly variable, and we felt we could not determine estimates for many of our study areas.

We calculated the connectivity of each population to adjacent populations based on the influences of topography (large rivers, lakes, and glaciers), human factors (multi-lane high traffic highways and dense human settlement), and gaps in Grizzly Bear distribution. This required considerable local knowledge about Grizzly Bear distribution in all southern study areas and the extent of this knowledge varied.

We summarized kill (human-caused Grizzly Bear mortality) for each study area from study results, government records and databases, and published accounts. Accurate records of human-caused mortality have been recorded since at least the mid-1970s for all the jurisdictions in this study. We calculated mean yearly reported human-caused kill density (kills / 1000 km^2) for the ten year period previous to the density estimate. Kill density, as a proportion of observed Grizzly Bear density, was used to index the effect of human-caused kill on observed population density. (This is a simplification of the effect of kill on density, because the effect of kill should be non-linear and populations vary in the rates of human-caused mortality they can sustain.) Because most kill rates were low ($< 3\%$), the kill effect was probably nearly linear over the range of our data.

We developed spatial measures of human and livestock density based on Statistics Canada and US Census Bureau data.

We critically reviewed estimates of Grizzly Bear density in the published and unpublished literature. We were interested in estimates of total Grizzly Bear density (i.e.,

including cubs), for landscapes relevant to a Grizzly Bear population; therefore, we used estimates only where study area size was larger than approximately ten female home ranges. In practice, this meant study areas contained at least 20 resident Grizzly Bears and were > 1500 km^2. We accepted estimates only where authors had corrected for Grizzly Bears that were not detected during fieldwork; generally, this meant the use of mark-recapture analysis but more subjective assessment was accepted in a few cases. Authors also had to explicitly consider the possible bias of geographic closure on their density estimate (White *et al*. 1982). We accepted density estimates from 46 study areas across western North America. Our study areas covered the likely range of densities found in North America and most of the current range of ecosystems occupied by Grizzly Bears (Figure 1). For example, the lowest density occurred in the central Keewatin (3.5 Grizzly Bears / 1000 km^2) and the highest was found on the Alaska peninsula (550 Grizzly Bears / 1000 km^2), where salmon are abundant and available for most of the year.
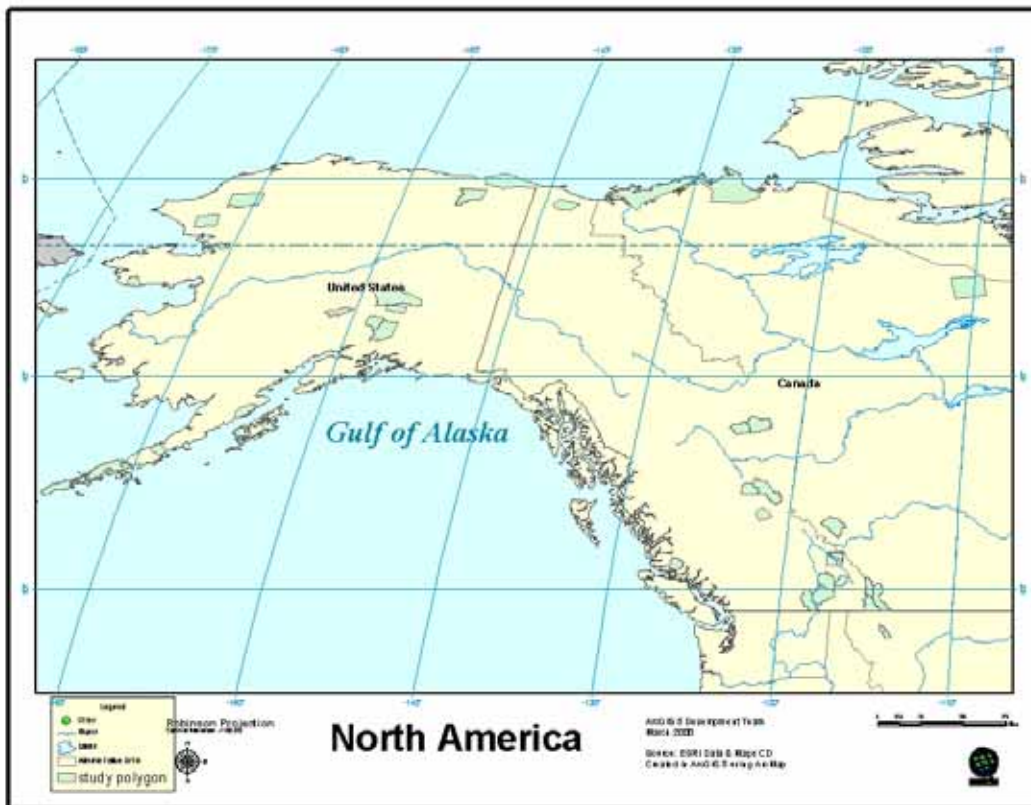
Figure 1. Location of the Grizzly Bear study areas (green polygons) used to develop the multiple regression model.

We used multiple linear regression to relate Grizzly Bear density to factors which might influence density. We checked for outliers with residuals > 2 and examined whether assumptions regarding normality and equality of variances were met by ensuring plots of the multivariate residuals were not clumped or skewed (Tabachnick and Fidell 1996). We selected a final model

for use in predicting density based on: (1) the model fit compared to other potential models (as measured by the overall r^2); (2) the likelihood that the variables in the model indexed known limiting factors; and (3) the need to minimize the number of parameters in the model because our sample size was small.

We applied the model to provincial Grizzly Bear Population Units (GBPUs) except where there were big differences within the GBPUs in precipitation or salmon abundance. In those cases, we divided the GBPUs into more homogeneous subunits along existing ecosection lines or Wildlife Management Unit boundaries (Figure 2, and Table 2). We then calculated the current carrying capacity, which was the population estimate using all the variables while setting the hunting mortality to zero. We used the current carrying capacity to calculate the reported mortality as a percent (i.e., 100 x reported mortality / current carrying capacity). We then re-ran the model with all five variables to determine the current population estimate. This slightly overestimated population size where hunting was high. The BC provincial system for Grizzly Bear conservation and hunting management also requires an estimate of the idealized carrying capacity. To determine the idealized carrying capacity, we ran the model with only the precipitation and salmon variables by setting the other measures, which index human effects, to zero. The current and idealized carrying capacity estimates are referred to as "habitat effectiveness" and "habitat capability," respectively, in the BC Grizzly Bear Harvest Management Procedure (Austin *et al*. 2004).

Figure 2. Grizzly Bear population sub-units considered for application of the multiple regression model. (We did not apply the model to the 16 coastal sub-units outlined in blue or to the 5 sub-units indicated with arrows.)

Table 2. Grizzly Bear population unit and sub-unit population estimates based on the multiple linear regression model for areas with salmon = 0 or 1 (interior areas). Shaded population estimates were considered unreasonable.

Grizzly Bear Population Unit	Grizzly Bear Population Sub-unit	Density Estimate	Population Estimate
Alta		14	419
Babine		35	487
Blackwater-West Chilcotin		9	193
Bulkley-Lakes	Bulkley-Lakes	37	292
Cassiar	Cassiar Central	21	473
Cassiar	Liard Lowlands West	19	105
Cassiar	Southern Lakes	18	152
Central Monashee		23	143
Central Purcell		32	150
Central Rockies		34	235
Central Selkirk		31	178
Columbia	Columbia	40	221
Columbia	Adams	19	175
Edziza-Lower Stikine	Upper Stikine	32	219
Finlay-Ospika		23	689
Flathead		28	97
Francois		17	192
Fraser Plateau		0	0
Georgia Strait		0	0
Hart		20	386
Hyland	Hyland East	18	117
Hyland	Hyland West	19	173
Hyland	Liard Lowlands East	19	35
Kettle-Granby		12	81
Llinaklina-Homathko		42	571
Lower Mainland		0	0
Moberly		23	174
Muskwa	Muskwa	22	679
Muskwa	Liard Lowlands Central	19	96
Nation	Carp	24	255
Nation	Stuart	30	229
North Cascades		23	228
North Purcell		42	228
North Selkirk		44	264
Nulki	Nulki	10	137
Nulki	Bowron West	18	55
Okanagan		0	0

Grizzly Bear Population Unit	Grizzly Bear Population Sub-unit	Density Estimate	Population Estimate
Omineca	Omineca	23	547
Omineca	Takla	33	179
Parsnip	Parsnip	37	160
Parsnip	MacGregor	47	313
Peace		0	0
Quesnel Lake North		35	317
Robson	Robson	34	502
Robson	Bowron East	36	182
Rockies Park Ranges		28	164
Rocky	Rocky NE	19	266
Rocky	Rocky NW	22	226
Rocky	Rocky SE	13	59
Rocky	Rocky SW	19	162
South Chilcotin Range		22	358
South Purcell		23	158
South Rockies		24	201
South Selkirk		21	86
Spatsizi		25	540
Spillamacheen		35	141
Stein-Nahatlatch		52	401
Tagish	Tagish	16	42
Tagish	Atlin	57	199
Taiga		18	622
Tatshenshini		67	864
Tweedsmuir	Tweedsmuir	36	373
Upper Skeena-Nass		39	661
Valhalla		28	96
Wells Gray		29	374
Yahk		16	44

RESULTS

Rainfall explained the greatest proportion of the variance in interior Grizzly Bear densities and also appeared to influence coastal Grizzly Bear densities, but Grizzly Bear densities in coastal areas were much higher than those in interior areas with similar rainfall (Figure 3). Because the only BC coastal study area (Kingcome and Wakeman inlets) had less than one-tenth the expected density, the reasons for which were unclear, we concluded that we could not predict Grizzly Bear density on the BC coast, and therefore restricted our model to the 33 interior Grizzly Bear populations.
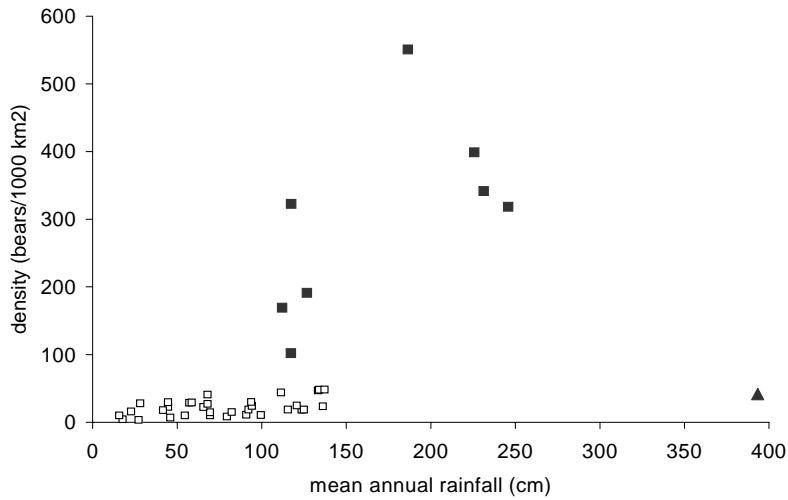
Figure 3. The relationship between Grizzly Bear density and mean annual precipitation for coastal (■) and interior (□) Grizzly Bear populations. The Kingcome population (▲) is an unexplained outlier from coastal British Columbia.

In the interior of the continent, density was related to annual precipitation (Figure 4, and Figure 5A), more weakly related to annual temperature and AET, and not related to NDVI (Figures 5B-D). The presence of salmon appeared to increase density regardless of the variable used to index vegetative carrying capacity (Figure 5).
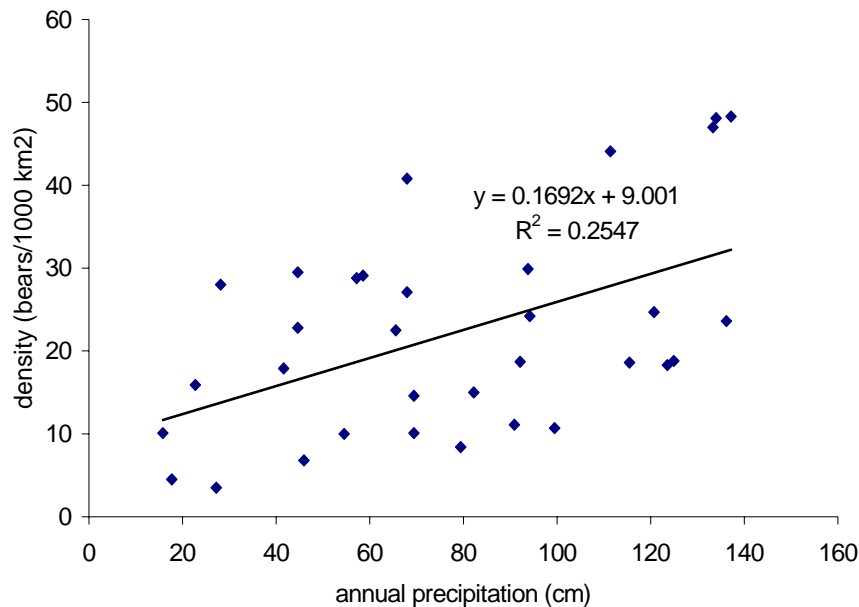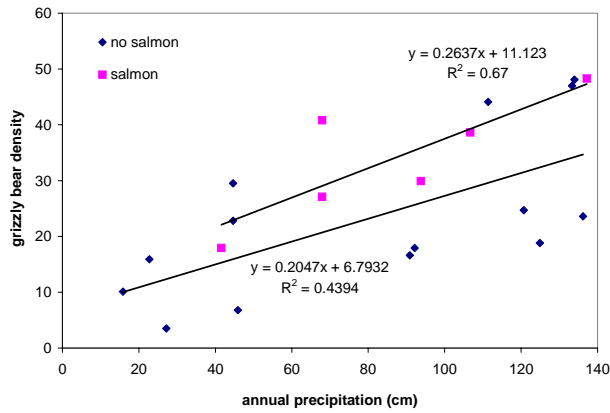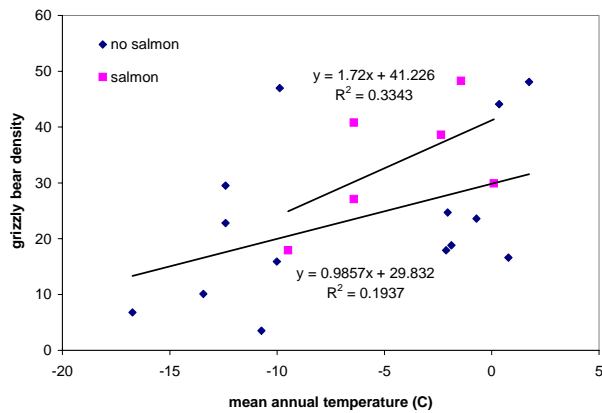

$y = 0.1692x + 9.001$
$R^2 = 0.2547$

Figure 4. The relationship between Grizzly Bear density and mean annual precipitation for 33 interior Grizzly Bear populations.

9

A

B

Figures 5A-D. The relationship between Grizzly Bear density and: (A) mean annual precipitation, (B) mean annual growing season temperature (April-October), (C) annual actual Evapotranspiration (AET), and (D) annual NDVI for grizzly populations where average human-caused kill rate was < 5% of the population and at least 50% of the study area periphery was continuous with adjacent Grizzly Bear populations.
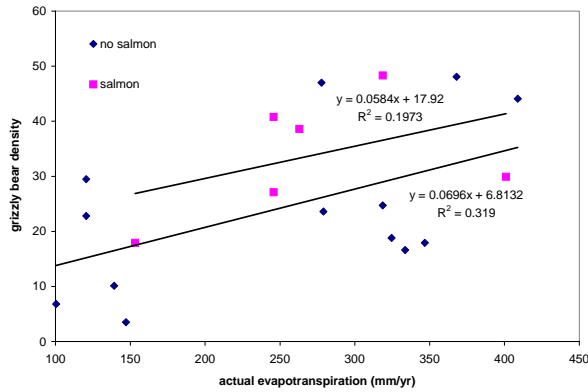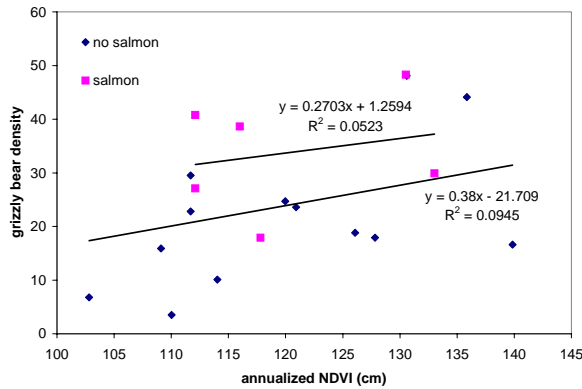
C

D

Figures 5A-D (cont.). The relationship between Grizzly Bear density and: (A) mean annual precipitation, (B) mean annual growing season temperature (April-October), (C) annual actual Evapotranspiration (AET), and (D) annual NDVI for grizzly populations where average human-caused kill rate was < 5% of the population and at least 50% of the study area periphery was continuous with adjacent Grizzly Bear populations.

In our best model, Grizzly Bear density was positively related to mean annual rainfall, to the presence of salmon, and to the proportion of the population's perimeter that was continuous with other Grizzly Bear populations. Grizzly Bear density was negatively related to human and livestock density and to the rate of reported human-caused mortality (Figure 6, and Table 3, $r^2 = 0.62$, $n = 33$).

Table 3. Statistics describing the regression of density on mean annual precipitation, salmon presence, connectivity, 10-year mean per cent recorded hunting mortality, and human plus livestock density.

IV	coefficient	SE	p
Intercept	-10.22	9.028	0.27
Salmon	9.69	3.822	0.02
10-year mean percent kill	-0.64	0.364	0.09
Connectivity	0.17	0.082	0.04
Precipitation	0.23	0.045	0.00
Human + livestock density	-0.64	0.667	0.35

Rainfall explained the greatest proportion of the variance in the interior model, underscoring the ultimate importance of this factor to density (Figure 4, and Table 3). The significance of the binary salmon variable supports the importance of this source of protein even in interior populations where salmon are available in much lower numbers, and for shorter time periods, than they are nearer the ocean. Grizzly Bear density in the interior was also correlated with AET and growing season temperature, but not with NDVI or seasonality (Figure 5). No combination of the other measures of primary productivity improved fit above that of precipitation alone.
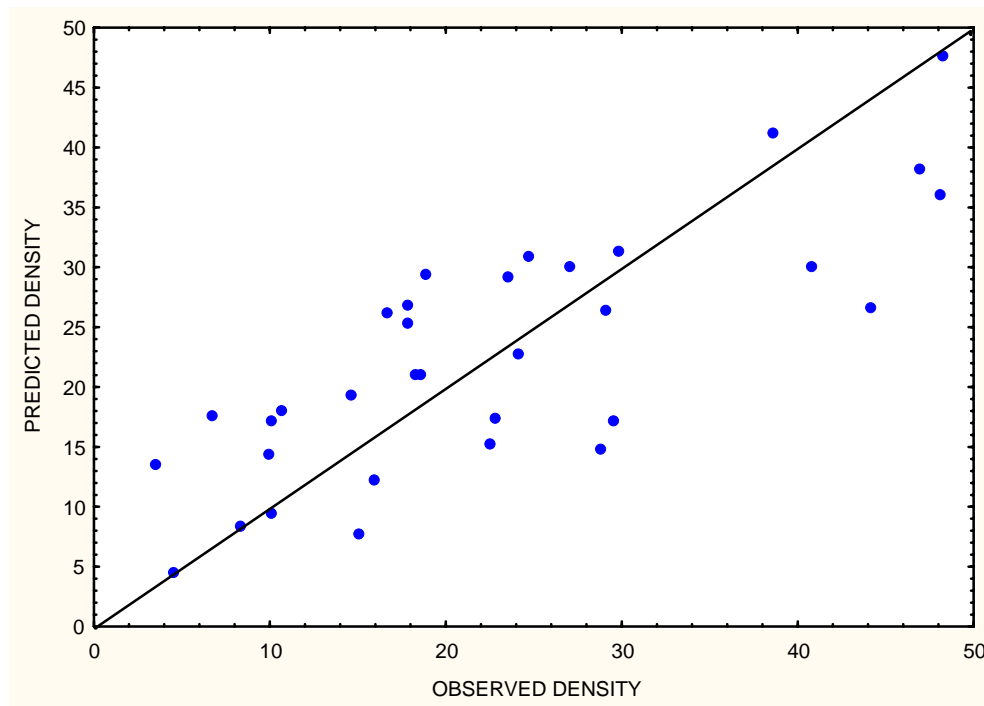

Figure 6. Observed vs predicted Grizzly Bear densities in the 33 study areas using the multiple linear regression model. Line indicates a perfect relationship between observed and predicted densities.

Neither topographic nor human-caused isolation alone were related to Grizzly Bear density. Isolation as measured by gaps in the current distribution of Grizzly Bears, regardless of its causes, was related to bear density. This result, if it is ultimately based on the lack of connectivity and not on other correlates, highlights the value in maintaining continuous distributions in wild populations. Both human and cattle density were weakly correlated with connectivity ($r = -0.40$), and the relationship we observed between density and connectivity may have been more correlative than causative because the lack of Grizzly Bears in an area was likely related to previous human effects (Mattson and Merrill 2002). Further, the connectivity variable was subjectively derived, so the accuracy of the measure would likely vary based on the available local knowledge regarding Grizzly Bear distribution.

We found a relatively small negative effect of reported human-caused mortality on Grizzly Bear density probably because kill rates were almost always very low. Kill rate is more likely to have a greater effect on density as kill increases, especially past the sustainable level, but fit was not improved by transforming this variable (i.e., by adding it in other functional forms like higher order polynomials). The fact that kill is expressed as a rate limits the predictive utility of the model because we need an estimate of density before the effect of kill can be calculated. We attempted to fit other measures of kill, such as kill rate over the past 20 years and kill density, but found no relationship.

Human and livestock densities have long been associated with the decline in the distribution of Grizzly Bears (Mattson and Merrill 2002), and our results suggested that the number of humans and livestock also affected density in areas which still supported Grizzly Bears, even when recorded human-caused mortalities were accounted for. This variable probably indexes habitat displacement and both current and historical non-recorded human-caused mortality.

We used the model to predict Grizzly Bear density, and associated confidence limits in 61 Grizzly Bear population sub-units in BC that have few or no salmon. Five of the 61 sub-units (Alta, Atlin, North Cascades, Taiga and Tatshenshini) had unrealistically high predictions, presumably because the model did not capture significant aspects of the ecology of those populations or of the history of human-caused mortality in those areas. We estimated that the remaining 56 sub-units contained approximately 14,000 Grizzly Bears [90% confidence limits 6000-24,000], a mean density of 16 Grizzly Bears / 1000 km^2 (Table 2). The model also accurately predicted zero Grizzly Bears in 5 areas of the province where Grizzly Bears have been eliminated: Lower Mainland, Sunshine Coast, Okanagan, Fraser Plateau, and Peace).

Confidence limits on the predictions were constant, for a given level of precision, for all density estimates, and were therefore a greater fraction of small estimates than of large ones (see Austin *et al*. 2004).

DISCUSSION

Our approach differs from most analyses of resource selection by animals. We use measures of landscape scale density as the dependent variable rather than presence or abundance of individuals at a site. Density combines all the factors that influence population dynamics in a single measure that allowed us to more directly assess ultimate factors influencing Grizzly Bear

densities. More importantly, density should exclude factors such as individual behavior and regionally-specific life history strategies that influence the outcome of finer scale analyses. Our results were unaffected by the relative abundance of different resources within a study area; it was the total abundance of resources that was reflected in our measure. We considered the scale of our approach to be more appropriate for generating a general model than most resource selection models, because our dependent variable was measured at a similar scale to that which we made predictions, and our model incorporated data across the entire area for which we made predictions.

The absolute width of the confidence interval on the predicted population estimates is not a relevant indicator of the value of this technique for estimating grizzly bear density. The appropriate comparison is how well the multiple regression model predicts Grizzly Bear density relative to alternative techniques. Given that the expert-based model used previously had no measure of uncertainty, its precision could not be assessed; therefore, the expert-based model cannot be statistically compared to the multiple regression approach discussed here. We chose the multiple regression over the expert opinion process (Hamilton and Austin 2004) because it was more objective (i.e., it was based primarily on data). Our choice was not based on how precise the predictions were. Five of the 61 sub-units (Alta, Atlin, North Cascades, Taiga and Tatshenshini) had unrealistically high predictions. Alta and Taiga densities may have been influenced by factors that were not part of the model. The North Cascades appeared to still be depressed from high historic kills not associated with high human or cow density or the topographic isolation of the area. Precipitation in Atlin and Tatshenshini was 70 and 80 cm respectively beyond the range of the modeled data, but more importantly, both areas contain a high proportion of rock and ice that is not Grizzly Bear habitat. The Alta and Taiga units were likely overestimated because the lack or excess of soil drainage in the boreal shield promotes either aquatic or dry-adapted herbs, neither of which is preferred by Grizzly Bears.

We assumed that DNA mark-recapture estimates were unbiased, an assumption that may not be true if capture probability of cubs' DNA was low. Reasons for low capture probability of cubs' DNA could include cubs passing under barbed wire without touching it, thus leaving no hair, or cubs' hair being new and firmly attached, rather than ready to moult, as is generally the case for adults (Mowat *et al*. 2004).

Our model suggests that food availability ultimately limits Grizzly Bear density. This seems reasonable given only young individuals are vulnerable to predation and occasional cannibalism; hence, top down limitation of Grizzly Bear density is unlikely. Ferguson and McLoughlin (2000) demonstrated relationships between several life history traits, evapotranspiration (AET), and seasonality (the coefficient of variation of monthly AET values) for 24 Grizzly Bear populations in North America, but only one weak relationship with density for coastal populations. We found no such relationship between density and AET or seasonality for interior populations ($n = 19$, $P > 0.56$) using the data presented in their paper. Ferguson and McLoughlin (2000) did not consider kill rates or connectivity, so it is possible that some of the populations they examined may have been well below carrying capacity.

Utilizing absolute numbers of salmon would be preferable to a simple binary (presence / absence) variable but those data are rarely available for broad areas. The incorporation of a

measure of ungulate abundance may also improve the predictive power of the model but, we could not acquire or derive those estimates for our study areas.

This model is insensitive to habitat attributes that are considered important by many grizzly bear biologists, and those attributes that are changing most quickly over time (i.e., road building and forest harvesting). This emphasizes that these predictions apply at large temporal and spatial scales. Future model efforts will attempt to better predict the influence of unrecorded human-caused mortality, as well as the influences of time and space. We hope to incorporate rapidly changing landscape measures such as road density and forest openings into future models.

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ACKNOWLEDGEMENTS