Models of grizzly bear density for conservation design in the North **American Rocky Mountains**

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Abstract

We investigated relations between estimated grizzly bear Ursus arctos horribilis densities in 12 Rocky Mountain study areas and several potentially predictive or explanatory variables that included tassled cap transformed Thematic Mapper (TM) satellite imagery, the extent of whitebark pine Pinus albicaulis range, diet energy concentration, remoteness from humans, and study area size. Our objective was to develop models for predicting potential grizzly bear population sizes in areas currently unoccupied by bears, or supporting small and vulnerable populations. To test our models, we examined goodness of fit of predicted and observed densities in 5 additional study areas and determined whether predicted densities were spatially correlated with observations of grizzly bears in 2 regions. We also determined whether key predictive metrics correlated positively with a direct measure of habitat productivity in the Yellowstone region. Our best model included a single variable (Wetness from tasseled cap transformed TM imagery). This model optimized parsimony and fit and produced density predictions that correlated well with distributions of grizzly bear observations and fit observed densities in the 5 independent test areas. TM Wetness was also positively correlated with habitat productivity in the Yellowstone region. Based on this model, and without considering limiting human effects, we predicted that former 1850s range in Arizona and New Mexico could support 1905 bears (0-5059 prediction interval), that currently unoccupied but potential habitat in central Idaho could support 615 bears (443–757), and that habitat currently occupied by a very small (<40) and vulnerable population in northwestern Montana could support 362 bears (286-428).

1. Introduction

Grizzly bears (Ursus arctos horribilis) in the western USA were extirpated from most of their range and otherwise reduced in numbers during 1850-1970 (Mattson & Merrill, 2002). Protections offered by the U.S. Endangered Species Act halted declines and, in places, allowed for apparent increases (Mattson & Merrill, 2002). However, several populations remain small (<100 animals) and well below carrying capacity (the North Cascades, Cabinet-Yaak, and Selkirk ecosystems; U.S. Fish & Wildlife Service, 1993; Mattson & Merrill, In review). Potential habitat in central Idaho and elsewhere also remains unoccupied (Merrill et al., 1999; Carroll, Noss & Paquet, 2001a; Carroll et al., 2001b; Merrill & Mattson, 2003). There is an imperative to increase the small populations (U.S. Fish & Wildlife Service, 1993) and restore grizzly bears to areas with biophysical potential (U.S. Fish & Wildlife Service, 2000; Dugelby et al., 2001). However, the success of such endeavors is often contingent on

predicting potential grizzly bear densities. To do so requires robust coarse-grained models motivated by data that are consistent for the geographic scope of potential applications.

Several studies have modeled the relative capability or "quality" of grizzly bear habitat with the intent of appraising the potentiality of areas outside currently occupied range. Merrill et al. (1999), Carroll et al. (2001a, 2001b) and Noss et al. (2002) developed models that produced dimensionless indices of habitat capability or effectiveness. Merrill & Mattson (2003) predicted source areas based on death rate modeled as a function of management jurisdictions and remoteness from humans. Carroll et al. (2001a, 2001b) and Noss et al. (2002) used tasseled cap transformed Thematic Mapper (TM) satellite imagery (Crist & Cicone, 1984) to represent biophysical habitat conditions, showing generally positive relations with Greenness and negative relations with Wetness. Other finer-scale studies of grizzly bear habitat selection have also shown a positive Greenness effect

(Mace et al., 1999; Nielsen et al., 2002). None of these previous studies directly modeled or predicted grizzly bear density.

In this paper we present models of potential grizzly bear density that are broadly applicable within the North American Rocky Mountains. We based the models on existing density estimates, using study area as the unit of observation. We only included study areas with published information on diet because of our interest in the potential relation between bear density and estimated diet quality. We considered explanatory and predictive metrics that were consistent among study areas and regions of potential model application. These metrics included Greenness, Wetness, and Brightness (from TM tasseled cap transformed satellite imagery), location in or out of whitebark pine (*Pinus albicaulis*) range, and remoteness from humans. We considered whitebark pine range because of the documented effects of this food source on grizzly bear demographics (Pease & Mattson, 1999; Mattson, 2000; Mattson & Merrill, 2002), and remoteness to control for potential human effects on estimated grizzly bear densities. Our objective was to develop models that could predict potential grizzly bear densities in the absence of major human impacts or, at least, correlate well with the distribution of grizzly bear habitat capability. We judged our models by goodness of fit, the match between predicted and observed densities in study areas not used for model development, the strength of spatially-explicit relations between predicted densities and distributions of grizzly bear observations in 2 test regions, and the strength of relations between predictive metrics and a direct measure of grizzly bear habitat productivity.

2. Study Area

The study areas from which we obtained estimates of grizzly bear density and diet energy were in the North American Rocky Mountains and associated interior mountain ranges (Fig. 1). Mean latitudes ranged from 44º N (Yellowstone) to 53º N (Jasper). The climate was cold continental, with greater maritime influence progressively west of the main Rocky Mountain crest (Bryson & Hare, 1974). Conifer forests covered most of each study area. Engelmann spruce Picea engelmanni, subalpine fir Abies bifolia, Douglas-fir Pseudotsuga menziesii and lodgepole and whitebark pines, Pinus contorta and P. albicaulis, were common forest dominants throughout. Western larch Larix occidentalis, grand fir Abies grandis, western hemlock Tsuga heterophylla, and western red cedar Thuja plicata were abundant in areas with greater winter precipitation (Peet, 1988).



The 5 study areas that we used to examine goodness-of-fit between predicted and observed densities were all located in British Columbia, Canada, between 49– 58° N latitude and 116–124° W longitude (Fig. 1; Hamilton & Austin, 2002). Two of these study areas (Prophet and Parsnip) were located north and west of the study areas used for model development. Climatic and vegetation conditions in the test study areas resembled those of the modeled study areas except that the 2 northern-most test areas included boreal forest vegetation typified by extensive white spruce (Picea glauca), black spruce (P. mariana) and aspen (*Populus tremuloides*) forest cover.

The study areas we used to test relations between predicted grizzly bear densities and distributions of grizzly bear observations were located at 48° N latitude in northwestern Montana (the Cabinet-Yaak; U.S. Fish & Wildlife Service, 1993) and between 32-37º N latitude in former grizzly bear range of Arizona and New Mexico. The Cabinet-Yaak study area was located near (<50 km from) 2 study areas used to develop the density models and had similar vegetation and climate. It was defined as the aggregate area within 9.8 km of grizzly bear observations obtained in this region during 1959–2000 (17,554 km²; Mattson & Merrill, 2004). The Arizona/New Mexico study area was defined by estimated grizzly bear range in 1850 (352,050 km²; Brown, 1996; Mattson & Merrill, 2002). Most of this area was vegetated by conifer forest, piñon pine (*P. edulis*) and juniper (*Juniperus* spp.) woodland, oak (Quercus spp.) and manzanita (Arctostaphylos spp.) shrubland, and desert grassland (Brown, 1994). The climate was typified by a bimodal peak in precipitation, including late summer "monsoonal" rainfall (Bryson & Hare, 1974).

Table 1. Sources of grizzly bear density estimates and fecal content analyses for study areas used in this analysis. Density estimate method (as described in text), feces sample size, and years of feces sample coverage are also given.

Study area	Density estimate (n/100 km²)	Density estimate method	Feces sample size	Number of years of feces collection	Density reference	Fecal content reference
Jasper	1.07	Enumeration	320	3	Russell et al. (1979)	Russell et al. (1979)
Banff	0.83	Sighting rate	418	5	Vroom (1974)	Hamer & Herrero (1983)
Kananaskis	1.60	Mark-recapture	288	3	Mowat & Strobeck (2000)	Wielgus (1986)
Glacier, BC	2.60	Sighting rate	54	2	Mundy (1963)	Mundy (1963)
N. Fk. Flathead	6.40	Modified enumeration	1,100	13	McLellan (1989)	McLellan & Hovey (1995)
Waterton	1.50	Mark-recapture	119	3	Mowat & Strobeck (2000)	Hamer et al. (1991)
Glacier, MT	2.00	Mark-recapture	1,484	9	Mowat & Strobeck (2000)	Kendall (1986)
Selkirk/Cabinets	2.30	Enumeration	108	8	Wielgus et al. (1994) & Servheen (1983)	Kasworm & Their (1991)
Mission Mtns	2.04	Enumeration	177	1	Servheen (1983)	Servheen (1983)
East Front	1.53	Enumeration	1,094	10	Aune & Kasworm (1989)	Aune & Kasworm (1989)
Scapegoat	1.53	Enumeration	282	5	Aune & Kasworm (1989)	Craighead et al. (1982)
Yellowstone	1.50	Mark-recapture	3,423	11	Eberhardt & Knight (1996)	Mattson et al. (1991)

3. Methods

3.1. Data and explanatory variables

Our data for developing models of grizzly bear density consisted of published point estimates from 12 study areas (in bears/100 km²; Table 1). The methods used to develop these estimates included enumeration of known individuals, enumeration of home ranges of known individuals, excluding individuals proportional to the extent that their ranges extended beyond study area boundaries, sighting rates, and mark-recapture based on genetic or radio marks (Table 1). All of the methods were potentially biased, either by lack of population closure (enumeration, resighting, and mark-recapture techniques; Boulanger et al., 2002) or failure to detect individuals (enumeration techniques). For some models we treated the density estimate from the North Fork of the Flathead (McLellan 1989) as an outlier because, at 6.4 bears/100 km², it was >2x higher than any other density estimate obtained for a population of Rocky Mountain grizzly bears. Methods used to estimate grizzly bear densities in the 5 test areas were based on mark-recapture analysis of individuals identified by DNA obtained from hair (Boulanger et al., 2002; Hamilton & Austin, 2002). Our measure of diet net digested energy (see below) was based on estimates of proportional grizzly bear fecal content from the same study areas or others nearby those that provided point estimates of bear density (Table 1). Fecal sample sizes varied among study areas, as did coverage of annual variation in diet (Table 1).

We used study area-specific summary statistics as explanatory variables in our modeling of bear densities. We averaged Wetness, Greenness, and Brightness for each study area using July 19–26, 2000, 8-day composite MODIS Level 3 images for calculations. We represented whitebark pine abundance as the percent of each study area within whitebark pine range (Critchfield & Little, 1966), deleting areas where whitebark pine was sparse or functionally extinct owing to mortality caused by white pine blister rust (*Cronartium ribicola*; > 40% mortality and >50% of remaining trees infected; Kendall, 1995). To control for potential human effects on estimates of grizzly bear density, we also calculated an average index of remoteness from humans for each study area. This index accounted for local densities of roads and modeled levels of human activity on them as a function of censused human numbers and distance from places of human residence. The index is described by Merrill et al. (1999) and has shown strong correlations with observed distributions of both live (Merrill et al., 1999) and dead (Merrill & Mattson, 2003) grizzly bears. We obtained digital data on numbers and distributions of humans from U.S. Census Bureau TIGER files for the U.S. 1990 census (updated for 1994) and Statistics Canada Enumeration Areas for the Canadian 1996 census. We obtained digital data on distributions of roads from William Haskins (The Ecology Center, Missoula, MT), assembled from U.S. Census Bureau Tiger files at a 1:100,00 scale, Alberta and British Columbia NTS mapsheet data at a 1:50,000 scale, British Columbia TRIM data at a 1:20,000 scale, and British Columbia Provincial Recreation Maps at a scale of 1:250,000.

We used a spatially-explicit index of habitat productivity for grizzly bears in the Yellowstone region to test the biological basis of key variables selected for inclusion in our models of grizzly bear density. We viewed the imagery-based variables, in particular, as crude but easily measured surrogates for putative biological features (Crist & Cicone, 1984). We were interested in determining whether these crude surrogates correlated with a more direct measure of unit area grizzly bear habitat productivity. The habitat productivity index that we used is described in detail by Mattson et al. (2003). It is based on observed densities of habitat use by radio-



marked grizzlies, weighted by indexed net digested energies associated with observed activities. Habitat we used diet item-specific correction factors reported by Hewitt & Robbins (1996; Cfi) to estimate ingested volumes

energies associated with observed activities. Habitat productivity was calculated for habitat types that were mapped for a 162,300 km² study area centered on Yellowstone National Park (Merrill & Mattson, 2003).

The data we used for relating predicted densities to distributions of grizzly bear observations consisted of observations from the Cabinet-Yaak study area and former grizzly bear range in Arizona and New Mexico (Fig. 2). The Cabinet-Yaak observations (n = 863) were collected during 1959–2000 and were compiled and made available by Wayne Kasworm of the U.S. Fish & Wildlife Service (Kalispel, MT). The Arizona/New Mexico observations (n = 92) were published in newspapers, journals, and government reports during 1850–1935 and were compiled by Brown (1996). These data represent grizzly bear observations at 2 different scales (a 20x difference in area) and for 2 different time periods (contemporaneous versus during early European settlement under USA auspices). For this test, we calculated explanatory variables as the average for 300km² (Cabinet-Yaak) or 900-km² (Arizona/New Mexico) buffers around random points or grizzly bear observations (see below).

3.2. Calculation of diet energy index

We calculated an index of unit volume net digested energy (Dtnetj) for each study area (j) based on adjustments to average proportional fecal contents. We first calculated population-average fecal content for all years and seasons for each study area (i.e., Ff_{ij} = the proportion of diet item i in feces from study area j). Next,

e We selected our models of grizzly bear density by Akaike's Information Criterion, corrected for small sample size effects (AICc; Burnham & Anderson, 1998). We used maximum likelihood to estimate model parameters (Weisberg, 1985) and type I linear regression because of our interest in predictive applications (Zar, 1984). We calculated type I P-values for regression parameters by randomization of residuals (Manly, 1990). As noted

244 to 293 and averaged 259.0.

3.3. Modeling strategy

randomization of residuals (Manly, 1990). As noted above, we considered Wetness, Greenness, Brightness, remoteness from humans, and extent of whitebark pine range as potential explanatory variables. We also considered the effects of Dtnet and study area size because of our interest in, for Dtnet, the potential effects

from the fecal remains (i.e., Fc_{ij} = Ff_{ij} x Cf_i). These factors accounted for the effects of differential digestibilites and

detectabilities. We then multiplied proportional ingested

energy (Net_i; Mattson et al., 2003) to calculate the relative

contribution of each item to total diet net digested energy (i.e, $Fn_{ii} = Fc_{ii} \times Net_i$). The index of total unit volume net

digested energy for each study was the sum, across all

energy (i.e., Dtnetj = Σ Fn_{ij}). Values ranged from 244 to

304 and averaged 262.8 across the 12 study areas. We

based on a priori knowledge of comparative study area

conditions. Excluding Jasper, Dtnetj values ranged from

treated Jasper as an outlier (the highest value at 304)

diet items, of their contributed relative net digested

volumes by diet item-specific indices of net digested

of diet energy concentration and, for study area size, the potential bias introduced in estimates of animal densities (Smallwood & Schonewald, 1996; Silva, Brimacombe & Downing, 2001).

We also used linear regression to determine the relation between mapped indexed habitat productivity in the Yellowstone region and imagery-derived variables included in our models of grizzly bear density. We calculated mean productivity values and mean values for imagery-derived variables for each of 181 grid cells overlain on the 162,300 km² Yellowstone test area (see above; Merrill & Mattson, 2003). Each cell was 30 km on a side (900 km²) to approximate the size of a female life range in the Yellowstone region (Mattson & Merrill, 2002; 2004). We regressed productivity on the imagery-based variables. To account for first-order spatial autocorrelation, we included mean productivity of the 8 adjoining cells as an independent effect.

We judged the predictive performance of each candidate density model by calculating differences between observed point density estimates and point predictions in the 5 test areas and by testing the hypothesis (H₀) that mean differences did not differ from 0. We also calculated Pearson regression coefficients (r) between observed and predicted densities for the 5 test areas. We considered "significance" to be α = 0.10. We obtained observed density estimates for the test areas from Hamilton & Austin (2002). These density estimates averaged 2.4 bears/100 km² and ranged from 1.6 (Prophet study area) to 3.0 (Parsnip study area) bears/100 km². Density estimates in Hamilton & Austin (2002) for the Parsnip study area were differentiated by "plateau" and "mountain." We calculated a weighted average density for the Parsnip study area based on the proportions of "plateau" (0.56) and "mountain" (0.45) determined from a map and description in Ciarniello, Boyce & Beyer (2002). We used a density estimate for the West Slope study area that was the mean of the 3 estimates in Hamilton &

Austin (2002) obtained during 3 different years using adjacent or overlapping sample areas. We did not use study areas in Hamilton & Austin (2002) that were used in our original model development, in coastal areas with spawning salmonids, or known to contain at-risk populations that were well below carrying capacity.

We used logistic regression to determine the relation between grizzly bear density, as predicted by candidate models, and the spatial distribution of grizzly bear observations in the Cabinet-Yaak and Arizona/New Mexico test areas. These logit-based models expressed the probability that a location would be a bear observation versus a random point as a function of predicted bear density. We judged relative model fit by the cumulative area under the Receiver Operating Characteristic (ROC) curve (Hosmer & Lemeshow, 2000) and by $R_{\rm L}^2$ (Menard, 2002). We judged significance by the Score statistic (Hosmer & Lemeshow, 2000; Menards, 2002). As noted above, we calculated mean predicted densities for a circular buffer centered on each bear observation or random point. Buffers were 300-km² in size in the Cabinet-Yaak area and 900-km² in size in the Arizona/New Mexico area. These buffers accounted for potential error in the location of bear observations, and roughly corresponded to the size of female ranges in each area (Mattson & Merrill, 2002). We used a number of random points that was equal to the number of bear observations, but with both random points and bear observations half-weighted so that total model degreesof-freedom equaled number of bear observations. This approach produced models that reflected the level of information imparted by bear observations alone, as opposed to an arbitrary number of random points. Model results were also easily interpreted in that backtransformed logits >0.5 indicated an instance where a bear observation was more likely to have been obtained than by chance, whereas values <0.5 indicated the opposite.

Table 2. Candidate models for explaining and predicting densities $(n/100 \text{ km}^2)$ of grizzly bears in the North American Rocky Mountains. For all models, n = 11 and the dependent variable is density squared; i.e., predicted densities are obtained by taking the square root of model results. Parameter estimates, with standard errors in parentheses, are given for variables included in each model, along with overall model statistics. Greenness (*Grn*) and Brightness (*Brght*) are squared in all models, extent of whitebark pine range (*Wbp*) is transformed by its square root (sqrt), and *Dtnet* and Wetness (*Lweti*) are transformed by their natural logs (In). Details of the *Lweti* transformation are explained in the text. Models are ordered by AIC_c values. The final table entry is for a model with the intercept term only.

		Model statistics											
Model	Intercept	Lweti	Grn ²	Brght ²	ln(<i>Dtnet</i> +1)	sqrt(Wbp)	F	Р	R ²	AIC _c			
Den ₁	-20.3 (7.7)	3.14 (0.24)	0.015 (0.003)	_	5.08 (1.41)	_	10.5	< 0.0001	0.97	4.87			
Den₂	8.32 (0.93)	2.76 (0.47)	_	_	_	_	34.9	<0.0001	0.79	4.96			
Den₃	7.42 (0.75)	2.82 (0.35)	0.014 (0.005)	_	_	_	14.7	< 0.0001	0.90	5.17			
Den ₄	-2.26 (0.45)	0.038+ (0.002)	0.044 (0.003)	0.0061 (0.0004)	_	3.28 (0.48)	119.5	< 0.0001	0.99	6.22			
Den₅	5.36 (1.05)	2.63 (0.29)	0.026 (0.006)	0.0015 (0.0006)	_	_	10.9	< 0.0001	0.94	7.07			
_	3.07 (0.54)	_	_	- · · ·	_	-	_	_	0.00	9.60			
†The par	⁺ The parameter was estimated for $-1 \times Wet^2$ rather than <i>Lweti</i> .												

4. Results

4.1. Models of grizzly bear density

We identified 5 candidate models to predict grizzly bear density (Table 2). All predict density squared. In developing these models, we considered linearizing transformations of most candidate effects (Weisberg, 1985), including squared values of Greenness (Grn) and Brightness (Brght), the square root of whitebark pine range (Wbp), and natural log transformed values of Dtnet and Wetness (Wet). Because Wet was a negative value, we first multiplied by -1, took the natural log of the resulting value +1, and then multiplied the result again by -1 to retain the original directional meaning of this metric. We called the resulting variable Lweti.



Of all the candidate factors, Lweti exhibited consistently the strongest relation to grizzly bear density (Fig. 3a). Of the imagery-derived variables, Grn2 showed the second strongest relation, but only in combination with Lweti (Fig. 3b). The best model included Lweti, Grn2, and natural log transformed Dtnet, with Dtnet having the weakest effect of the 3 variables. However, this "best" model was of only explanatory value because Dtnet is not available for most predictive applications. Study area size and remoteness from humans were not included in any candidate model. The coefficient of determination (r2) between Lweti and Grn2 was virtually nil (= 0.003), whereas the r2 between sqrt(Wbp) and ln(Dtnet + 1) was 0.22.

4.2. Relation between Wetness and Yellowstone habitat productivity

As the strongest variable in all of our models of grizzly bear density, we tested for a relation between Wet and habitat productivity (Prod) in the Yellowstone region, controlling for potential spatial autocorrelation by including the mean productivity of adjacent cells (Mprod) as an independent effect. The resulting model was:

sqrt(Prod) = 0.13 + 0.92sqrt(Mprod) +
0.047Lweti;

where 'sqrt' indicates a square root transformation. Overall model statistics were n = 222, df = 2/219, F = 436.5, P < 0.0001, and $R^2 = 0.80$. T-values for coefficients of Mprod and Lweti were 17.8 and 5.7, respectively, with P-values for both <0.0001. Because Lweti and Mprod were highly collinear (tolerance = 0.55), we also specified a model that included Lweti alone:

sqrt(Prod) = 0.47 + 0.076sqrt(Wet).

Statistics for this model were df = 1/220, F = 236.1, P < 0.0001, and $r^2 = 0.52$. In contrast to the strong relation between Prod and Wet, the coefficient of determination (r2) for the relation between Prod and the best fitting transformation of Greenness (ln[Grn + 1]) was only 0.09.

We were also interested in calibrating the Yellowstone habitat productivity metric to bear density as predicted by model Den2. Again, we accounted for potential first order spatial autocorrelation by including the mean of predicted densities for the 8 cells adjoining each focal cell (Mden). The resulting model was:

 $Den2^{2} = -10.9 + 43.5Mden^{2} + 971ln(Prod + 1);$

where Den2 and Mden were squared. Model statistics were n = 222, df = 2/219, F = 231.2, P < 0.0001, and R^2 = 0.68. T-values for Mden and Prod were 9.7 and 6.8, respectively, with P-values for both <0.0001. Again, because Mden and Prod were highly collinear (tolerance = 0.51), we also specified a model that included Prod alone:

 $Den2^{2} = -54.9 + 792sqrt(Prod).$

Statistics for this model were df = 1/220, *F* = 283.7, <u>P</u> < 0.0001, and r^2 = 0.56.

4.3. Correspondence between predicted & observed densities in test study areas

None of the mean differences between observed grizzly bear densities and densities predicted by the 4 candidate models differed significantly ($\alpha = 0.10$) from 0, including and excluding the Parsnip study area (Table 3). We only considered 4 of the 5 models (Den2–Den5) because, as noted above, Den1 was not suitable for predictive applications. We also calculated results excluding the Parsnip study area because, of all the test areas, the observed density here was consistently the highest relative to predictions, and because the point estimate that we used was based on a weighted average of uncertain reliability. Of the models, Den2 produced results that were the most discrepant, with a tendency to underestimate densities by about 0.2-0.3 bears/100 km2. The model based on Wetness, Greenness, Brightness, and whitebark pine range (Den4) produced predictions that were, on average, the least different from observed densities. On the other hand, Den2 was the only model that produced predictions that were substantially positively correlated with observed point estimates.



4.4. Relations between predicted densities & distributions of bear observations

The best fit to distributions of grizzly bear observations in both the Cabinet-Yaak and Arizona/New Mexico test areas was obtained using the density model based on Lweti alone (Den2). The relation was strong and statistically significant (< α = 0.10) in both cases, but especially so for the Arizona/New Mexico data (Fig. 4). The model for the Cabinet-Yaak area was:

where Logit(p) is the logit transformed probability that a location was that of a grizzly bear versus a random point, and model statistics were n = 863, df = 1, Score statistic = 26.1, P < 0.0001, area under the ROC curve = 0.60, and R_L^2 = 0.13. By comparison, area under the ROC curve for models Den3, Den4, and Den5 were 0.55, 0.52, and 0.54, respectively.

The model for Arizona and New Mexico was:

$$Logit(p)AZ/NM = -2.97 + 4.80ln(Den2 + 1).$$

Model statistics were n = 92, df = 1, Score statistic = 26.2, P < 0.0001, area under the ROC curve = 0.80, and $R_L^2 = 0.24$. Densities predicted for the Cabinet-Yaak area were higher and included a much narrower range (1.8–2.5 bears/100 km²) compared to densities predicted for Arizona and New Mexico (0–2.0 bears/100 km²). Area under the ROC curve for models Den3, Den4, and Den5 were 0.75, 0.70, and 0.74, respectively.

4.5. Predicted densities in the Cabinet-Yaak, Arizona/New Mexico, and central Idaho areas

We used the density model based on Lweti alone (Den2) to predict potential populations of grizzly bears in the Cabinet-Yaak study area, 1850s grizzly bear range in Arizona and New Mexico, and potential habitat in central Idaho (Merrill et al., 1999). These predictions did not consider limiting human effects, and expressed current biophysical habitat potential. For purposes of calculating 90% prediction intervals, we used the following statistics: n = 11, $\Sigma xi2 = 42.8$, $\square = -1.90$, and t = 0.90(2) = 1.83 (Zar, 1984). Estimates were as follow: (1) the Cabinet-Yaak (with the 90% prediction interval in parentheses): 362 (286-428); (2) 1850s range in Arizona/New Mexico: 1,905 (0–5,059); and (3) potential habitat in central Idaho: 615 (443–757). The large prediction interval for Arizona and New Mexico arose from the large difference between Lweti for this area and the mean of Lweti for values used in model estimation.

5. Discussion

Our analysis suggests that models based on natural log-transformed Wetness (i.e., Lweti) are suitable for predicting grizzly bear densities throughout the central and perhaps southern North American Rocky Mountains, from Arizona north to northern Alberta and adjacent British Columbia. Given the data, the model based on Wetness alone was jointly the most parsimonious and best fitting predictive model (i.e., it minimized AIC_c). Predicted densities also were not significantly different from observed densities in the 5 independent test areas and correlated well with meso-scale distributions of grizzly bear observations collected under quite different regimes in two study areas characterized by distinctly different climates and vegetation. Moreover, Wetness correlated well with an independent and direct measure of grizzly bear habitat productivity in the Yellowstone region of Wyoming, Montana, and Idaho.

Our models are applicable at macro (i.e., population) and meso (i.e., life range) scales. The models were developed using populations as the unit of analysis, but nonetheless produced results spatially correlated with observations of individual bears at the scale of putative life ranges. The grizzly bear observations from both meso-scale test areas, but especially from Arizona and New Mexico, were probably primarily single observations of individuals (Brown, 1996; Mattson and Merrill, 2004). Representing landscapes at the grain of life ranges represents conditions affecting bears over a lifetime, which is logically the minimum useful grain for analyzing and representing multi-annual bear density (Smallwood, 1999). This grain contrasts with virtually all other analyses of grizzly bear habitat relations to date, which have used day-specific locations of individual bears as primary units of analysis, considering only data from a single population (e.g., Mattson, Knight and Blanchard, 1987; Mace et al., 1996, 1999; Nielsen et al., 2002).

We were surprised that Wetness was the best predictor of grizzly bear density and, used alone, produced the best correlations with distributions of coarse-grain bear observations. Previous research has shown strong positive relations between Greenness and the distribution of bear observations, and weaker negative relations with Wetness (Mace et al., 1999; Nielsen et al., 2002; Noss et al., 2002). This discrepancy could have arisen from the finer-grained nature of previous analyses compared to the work presented here. Even so, there is no compelling a priori argument why Wetness should be a better predictor than Greenness, even at coarser grains. Of the three imagery-derived metrics, Wetness is the most sensitive to soil and plant moisture. It also tends to be most sensitive to forest conditions and standing water. By contrast, Greenness is correlated with features such as canopy closure, leaf area, and fresh biomass (Crist and Cicone, 1984; Crist, Laurin

and Cicone, 1986). It could be that Wetness conveyed the importance of forested conditions and available water to broad-scale potentiality of grizzly bear habitat. Given that we used July imagery, Wetness also could have been a surrogate for mid-summer precipitation. That said, little is known about broad-scale determinants of grizzly bear habitat productivity, other than the importance of spawning salmonids and oaks and the inhospitability of deserts (Miller et al., 1997; Mattson and Merrill, 2002).

Our presumed measure of diet net digested energy concentration (Dtnet) explained comparatively little variation in bear density. This could have been because the measure was biased and otherwise inaccurate. Its' minor contribution also could have arisen from perhaps the minor effect of diet energy concentration on bear density, in contrast to unit area density of food biomass. Total dietary digested energy is a function of volumetric passage rate and concentration of digestible energy (Pritchard and Robbins, 1990). Our measure of diet energy was more likely a measure of the latter rather than the former parameter. In this context, Wetness and Greenness would have been surrogates for unit area food abundance. In other words, our models can be interpreted as suggesting that food quality, per se, is less important than food quantity in determining grizzly bear densities.

Our predictions of potential grizzly bear population size for the Cabinet-Yaak, central Idaho, and Arizona and New Mexico areas have conservation implications. Although currently unoccupied by grizzly bears, central Idaho could potentially support a very large number of bears. Achieving this potential would require restoration of a successfully reproducing population (U.S. Fish and Wildlife Service, 2000), with the prospect of perhaps increasing the number of grizzly bears in the contiguous USA by nearly ½ again as many (U.S. Fish and Wildlife Service, 1993). Our model suggests that, biophysically, the Cabinet-Yaak region could support many more grizzly bears than the current 35 estimated to live there (Kasworm, Carriles and Radandt, 2000). High human densities and lethality are very likely imposing major limits on recovery of this very small population (Mattson and Merrill, 2004). Finally, compared to currently occupied Rocky Mountain grizzly bear range, former range in Arizona and New Mexico probably supported generally lower densities of bears. This lesser potential contributes to explaining the comparatively rapid loss of grizzly bears in this region during 1850–1920 compared to Montana and Wyoming (Mattson and Merrill, 2002). That said, there are still areas in the Southwest that, biophysically, could probably support grizzly bears at densities comparable to those in extant Rocky Mountain populations.

Our density predictions should be considered conservative. Although remoteness from humans statistically did not explain variation in estimated bear densities, it is unlikely that grizzly bears existed at the maximum numbers biophysically possible in any of the study areas used in this analysis. Negative human effects are pervasive in the Rocky Mountains, especially because humans cause almost all deaths of mature bears (Mattson et al., 1996; McLellan et al., 1999). Although we use the term "potential" in representing our model results, this potential should be understood to include some chronic level of human impact. The model that we used for our predictions (Den2) also produced results that tended to be biased low, at least with respect to densities that were observed in our test study areas.

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