
Extirpations of Grizzly Bears in the Contiguous United States, 1850–2000

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Abstract: *We investigated factors associated with the distribution of grizzly bears (*Ursus arctos horribilis*) in 1850 and their extirpation during 1850–1920 and 1920–1970 in the contiguous United States. We used autologistic regression to describe relations between grizzly bear range in 1850, 1920, and 1970 and potential explanatory factors specified for a comprehensive grid of cells, each 900 km² in size. We also related persistence, 1920–1970, to range size and shape. Grizzly bear range in 1850 was positively related to occurrence in mountainous ecoregions and the ranges of oaks (*Quercus* spp.), piñon pines (*Pinus edulis* and *P. monophylla*), whitebark pine (*P. albicaulis*), and bison (*Bos bison*) and negatively related to occurrence in prairie and hot desert ecoregions. Relations with salmon (*Oncorhynchus* spp.) range and human factors were complex. Persistence of grizzly bear range, 1850–1970, was positively related to occurrence in the Rocky Mountains, whitebark pine range, and local size of grizzly bear range at the beginning of each period, and negatively related to number of humans and the ranges of bison, salmon, and piñon pines. We speculate that foods affected persistence primarily by influencing the frequency of contact between humans and bears. With respect to current conservation, grizzly bears survived from 1920 to 1970 most often where ranges at the beginning of this period were either larger than 20,000 km² or larger than 7,000 km² but with a ratio of perimeter to area of <2. Without reductions in human lethality after 1970, there would have been no chance that core grizzly bear range would be as extensive as it is now. Although grizzly bear range in the Yellowstone region is currently the most robust of any to potential future increases in human lethality, bears in this region are threatened by the loss of whitebark pine.*

Extirpaciones de Osos Pardos en el Territorio Contiguo de los Estados Unidos, 1850–2000

Resumen: *Investigamos los factores asociados con la distribución de los osos pardos (*Ursus arctos horribilis*) en 1850 y su extirpación durante los períodos 1850–1920 y 1920–1970 en el territorio contiguo de los Estados Unidos. Utilizamos regresión autológica para describir las relaciones entre el rango de distribución del oso pardo en 1850, 1920 y 1970 y los posibles factores que podrían explicar las diferencias utilizando una red amplia de celdas de 900 km² de tamaño cada una. También relacionamos la persistencia para el periodo 1920–1970, con el tamaño y la forma del rango. El rango del oso pardo en 1850 estuvo positivamente correlacionado con la presencia de ecoregiones montañosas y los rangos del roble (*Quercus* spp.), los pinos de piñón (*Pinus edulis* y *P. monophylla*), el pino de corteza blanca (*P. albicaulis*) y el bisonte (*Bos bison*) y estuvo negativamente relacionado con la presencia de ecoregiones de praderas y desiertos calurosos. Las relaciones con el rango de salmones (*Oncorhynchus* spp.) y con los factores humanos fueron complejas. La persistencia del rango del oso pardo, 1850–1970, estuvo positivamente correlacionada con la presencia de las montañas Rocallosas, el rango del pino de corteza blanca y el tamaño local del rango del oso pardo al inicio de cada período, y estuvo negativamente relacionado con el número de humanos y los rangos de bisontes, salmones y pinos de piñón. Especulamos que los alimentos eran los principales factores que afectaron la persistencia al influir en la frecuencia de contacto entre humanos y osos. Con respecto a la conservación actual,*

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los osos pardos sobrevivieron de 1920 a 1970 más frecuentemente en aquellos rangos donde, al inicio del período, el tamaño excedía los 20,000 Km² o los 7,000 Km² pero con una proporción de perímetro al área <2. Sin reducciones en la letalidad humana después de 1970 no hubiera habido ninguna posibilidad de que los rangos-núcleo del oso pardo fueran tan extensos como lo son ahora. A pesar de que el rango del oso pardo en la región de Yellowstone es actualmente la más robusta de todas frente a incrementos futuros de letalidad por humanos, los osos en esta región están amenazados por la pérdida del pino de corteza blanca.

Introduction

Grizzly bears (*Ursus arctos horribilis*) in the contiguous United States die primarily because humans kill them. This is true now and has apparently been true since widespread contact with European settlers began in the mid-1800s. Storer and Tevis (1955) and Brown (1985) document the details of persecution and subsequent declines of grizzly bear populations in the southwestern United States. Mattson et al. (1996a) provide evidence from bears radiotracked in the northern Rocky Mountains that pervasive human-caused mortality continues. Even so, some grizzly bear populations survive. It is unclear what biophysical features of grizzly bear range are associated with the highest probabilities of persistence. Granting that humans are the primary cause of grizzly bear extirpations, we speculated that likelihood of extirpation was also affected by topography, vegetation, and the presence of livestock and croplands.

Mattson et al. (1996a, 1996b) offer a conceptual framework for thinking about grizzly bear extirpations. The number of grizzly bears killed by humans depends on the frequency and lethality of contact. Although affected by the particulars of grizzly bear behavior (e.g., habituation to humans), frequency of contact with humans is likely most affected by the number of humans residing in an area, especially in the time before motorized vehicles and well-maintained road systems allowed for greater mobility. The extent of vegetation cover, the complexity of local topography, and the juxtaposition of rich bear habitats with those favored by humans also have a high likelihood of affecting the frequency of contact between bears and humans.

Lethality of contact is probably determined by many factors, especially those identified with human behavior and values. The presence of livestock and agricultural crops, the associated displacement of native foods, and the predictable escalation of depredations by bears have often substantially elevated the per capita lethality of humans to grizzly bears (Storer & Tevis 1955; Brown 1985). On the other hand, in instances where humans have been disinterested or benign, livestock or crops provided supplemental food for bears and may have led to ephemeral increases in population size (Storer & Tevis 1955; Mattson 1990). Finally, and perhaps most important, changes in human value systems, world views, and legal

protections can substantially change the lethality of grizzly bear encounters with humans (Kellert et al. 1996).

It is possible that indigenous humans also affected the distribution of grizzly bears prior to settlement of western North America by Europeans. Native Americans killed grizzly bears for prestige, oil, and body parts (Ewers 1958; Mathews 1961; Hans 1964; Clark & Casey 1992). The Lewis and Clark expedition did not observe any grizzly bears in 1804–1806 along the Missouri River in areas occupied by maize-cultivating tribes such as the Mandans (Burroughs 1961), suggesting that along the west-east trending rivers of the Great Plains, sedentary tribes curtailed the distribution of grizzly bears (Mattson 1998). On the other hand, grizzly bears coexisted with and perhaps dominated numerous tribes in what is now California (Storer & Tevis 1955). Such interactions undoubtedly would have been modified by the nature and abundance of important bear foods such as ungulates or acorns and pine seeds.

These considerations guided our examination of grizzly bear extirpations between 1850 and 1970 in the contiguous United States. We investigated relations between landscape features and persistence of grizzly bears during two periods, 1850–1920 and 1920–1970. We chose 1850 and 1920 as the years that begin and delimit these two time periods because historical data did not allow us to confidently delineate ranges prior to 1850, and because a unique map of grizzly bear range was available for 1920 (Merriam 1922). We also examined the likelihood of extirpation for 1920–1970 in terms of conventional theories regarding the effects of range size and shape (Diamond 1975). We hypothesized that (1) the 1850 distribution of grizzly bears was negatively associated with hot deserts, the highest densities of Native Americans, and the distribution of sedentary Native American cultures that cultivated maize and was positively associated with vegetation that provided high-energy-content foods, including acorns from oaks (*Quercus* spp.), seeds from piñon or whitebark pines (*Pinus monophylla*, *P. edulis*, and *P. albicaulis*), and tissue from bison (*Bos bison*) and salmon (*Oncorhynchus* spp.). We also hypothesized that (2) increased human densities, decreased topographic complexity, and decreased annual moisture were associated with decreased likelihood of grizzly bear persistence. We were unsure of the relationship between persistence and area of croplands

or numbers of livestock, although (3) a negative partial relationship seemed most likely. Finally, we hypothesized that (4) increased range size and increased ratio of area to edge increased likelihood of persistence.

Our objective was to understand the history of grizzly bear extirpations well enough to derive both general and specific implications relevant to current and future conservation of grizzly bears. Based on this analysis, we describe features that render grizzly bear ranges robust to deterioration of human conservation values for periods as long as several decades; appraise the status of current ranges and recovery areas relative to these features; and describe characteristics that will likely enhance prospects of restoration in regions where we currently have no grizzly bears to inform us through direct study.

Methods

Delineating Grizzly Bear Range

We delineated grizzly bear range in the western United States for the years 1850, 1920, and 1970. Most previous delineations of grizzly bear range for the early 1800s show grizzly bears distributed throughout most of the western United States, east nearly to the Mississippi

River (Servheen 1990). Detailed faunal records indicate, however, that grizzly bears were absent or rare in large parts of this area. We thus revised the range of grizzly bears circa 1850 to correspond with published regional or state-by-state analyses of faunal records (Bailey 1905, 1931, 1936; Seton 1937; Over & Churchill 1941; Warren 1942; Hall 1946; Storer & Tevis 1955; Burroughs 1961; Ingles 1965; Long 1965; Armstrong 1972; Leopold 1972; Stebler 1972; Turner 1974; Bee et al. 1981; Jones et al. 1983, 1985; Brown 1985; Gowans 1986; Lyman 1986; Zeveloff & Collett 1988) (Fig. 1a). These published sources included regional or state-wide delineations of historical grizzly bear range and/or descriptions and records of grizzly bear occurrence, including dates of extirpation for local populations.

We delineated grizzly bear range circa 1920 based on a map made by C. H. Merriam (1922). This map was hand-drawn, however, and needed to be spatially rectified for geographic information system analysis. We thus modified the location of some populations according to geographic features labeled on Merriam's map, original information contained in reports of the U.S. Bureau of Biological Survey (Bailey 1905, 1926, 1931, 1936; Cary 1911), and records from circa 1920 reported by Storer and Tevis (1955) and Brown (1985) (Fig. 1a). We also delineated a small population overlooked by Merriam in

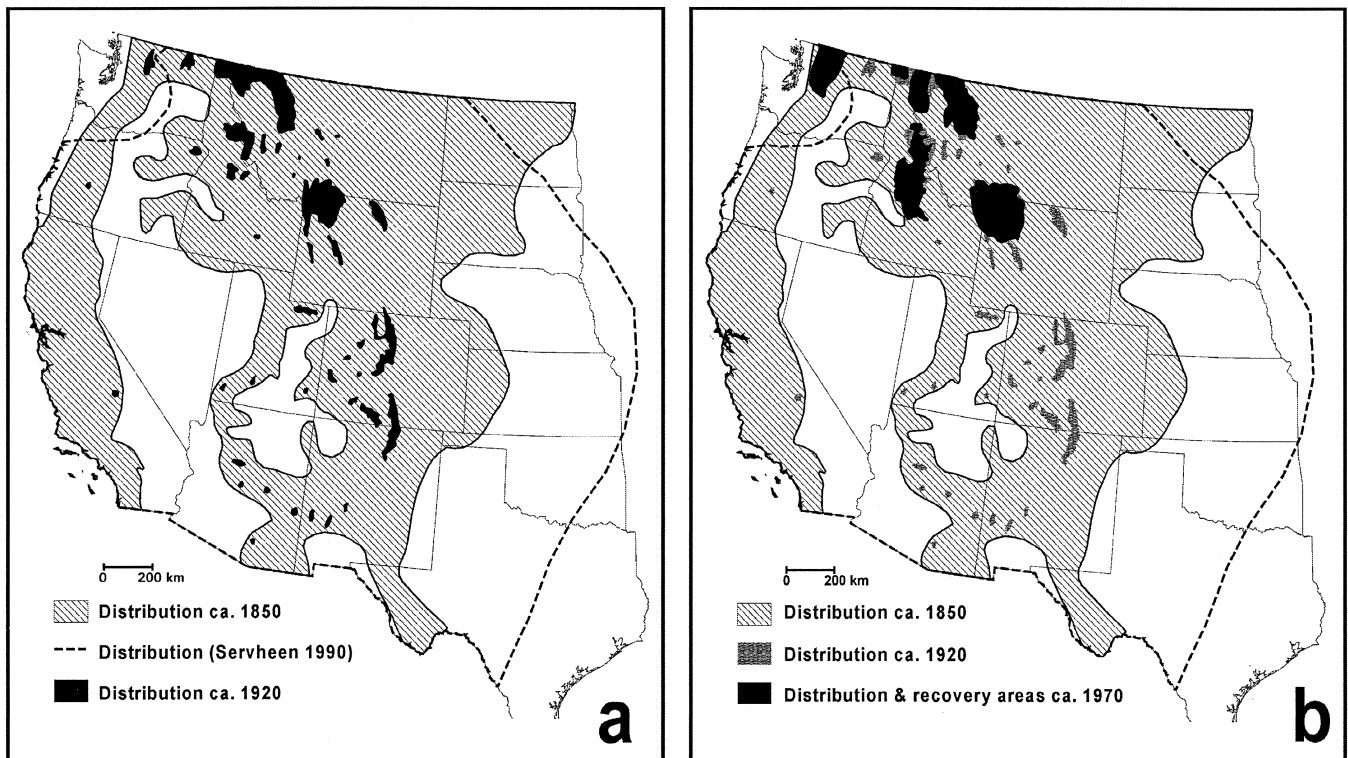


Figure 1. Ranges of grizzly bears in the western contiguous United States in (a) 1850 and 1920 and in (b) 1850 and 1970. The dashed line is a typical delineation of grizzly bear range before European settlement (Servheen 1990) prior to our more detailed reconstruction. State boundaries are thin lines.

the southern Sierra Nevada of California based on post-1920 records of grizzly bears in this area (Grinnell et al. 1937). We assumed that Merriam did not detect and delineate bear range circa 1920 in a way that was biased with respect to our explanatory variables. We delineated grizzly bear range circa 1970 according to contemporary records of grizzly bear sightings (Layser 1978; Zager 1983; McDonald et al. 1988; Aune & Kasworm 1989; Blanchard et al. 1992; Almack et al. 1993; Kasworm & Thier 1994; Merrill et al. 1999) (Fig. 1b).

Explanatory Variables

We used maps of estimated densities of Native Americans and of maize (*Zea mays*) cultivation from Driver (1969). These maps were electronically scanned and edited to delete information we did not need. High densities were defined as ≥ 60 people/100 km², moderate densities as 25–59 people/100 km², and low densities as < 25 people/100 km². We took distributions of oak-dominated vegetation types from Küchler (1964). We used the distributions of whitebark and piñon pines from Critchfield and Little (1966) and bison and salmon range from Haines (1970) and Taylor (1999), respectively.

We obtained post-1850 distributions of humans, cattle (*Bos taurus*), and maize and wheat (*Triticum aestivum*) croplands from official U.S. government sources (U.S. Census Bureau and U.S. Department of Agriculture). This information was depicted in iso- or choropleth maps that we electronically scanned and edited. We were unable to locate nationwide maps of distributions of domestic sheep (*Ovis aries*). Because we did not include distributions of sheep in our analysis, and because there is ample contemporary evidence for the effects of sheep husbandry on survival of grizzly bears (Knight & Judd 1983), we were unable to fully test hypothesis 3. Even so, distributions of sheep and cattle were probably broadly similar, because areas of low primary productivity, or those with most biomass concentrated on trees, would have supported low densities of both.

We described broad-scale differences in vegetation and related differences in climate and topography through an adaptation of Bailey's ecoregions of the United States (Bailey 1995). We consolidated Bailey's classification for our study area into eight types similar in topography and vegetation and consistent with our hypotheses 1 and 2. This step was taken to reduce the otherwise prohibitive number of parameters introduced by using all of Bailey's types in our analysis.

Framework of Analysis

We overlaid a map of the western United States east to the Mississippi River with a grid comprised of 30 × 30 km cells. Each cell of this grid constituted an observation for our analysis and was assigned the following values:

counts of all choropleth dots or isopleth zones contained within cell boundaries each for humans and cattle, corn and wheat croplands; square kilometer of maize and zones of different densities for Native Americans; square kilometer of each intersected ecoregion, treated as eight separate variables; square kilometer of oak vegetation types and piñon pine, whitebark pine, bison, and salmon ranges; square kilometer of grizzly bear range at the beginning and end of each period, treated as two separate variables; and square kilometer of grizzly bear range at the end and beginning of each period, summed over the focal cell and eight adjoining cells. We assumed that all areas in Canada were occupied by grizzly bears, but we used an explicit map of grizzly bear range extending into Mexico (Leopold 1972) to specify adjacent range in cells bordering these two countries. Given the limitations of our information, the assumption that all of Canada adjoining occupied range in the United States was also occupied by grizzly bears in 1850 and 1920 seemed more defensible than assuming that grizzly bears were absent.

We chose the size of cells, the spatial boundaries of analysis, and the date of measurement for independent variables based on considerations of grizzly bear biology. The 900 km² of each grid cell approximated the size of the life range of a female grizzly bear in the single study where this parameter was estimated (Blanchard & Knight 1991). Although the sizes of annual grizzly bear ranges vary with habitat conditions (Canfield & Harting 1987), we concluded that use of life-range dimensions was desirable in an analysis that emphasized phenomena transpiring over decades rather than single years and that 900 km² was probably applicable to most of the western United States based on our knowledge of historical ecological conditions.

We defined the spatial boundaries of analysis for each period to include all cells occupied by grizzly bears at the beginning of each transition and all adjoining unoccupied cells. We assumed that this definition would mitigate the effects of potential error in range delineations by not representing bear range as exact boundaries but rather as categorized percentages of occupancy by cell. This delineation also encompassed all the area potentially available to resident or dispersing grizzly bears at the beginning of each transition. For the analysis relating grizzly bear range circa 1850 to human and biophysical factors, we included the entire area of any ecoregion that contained grizzly bear range.

We related the probability of persistence to data on humans, cattle, and croplands collected near the midpoint of each period—in 1889–1890 and 1950. Availability of data dictated that we use these dates rather than exact midpoints. We assumed that terminal states in 1920 and 1970 would reflect conditions 20–30 years earlier better than conditions at any other time due to lags in demographic and behavioral responses by bears to changes in human features of the landscape. This was

based on theory (Doak 1995) and case histories of the responses of grizzly bear populations to human-induced perturbations (e.g., Craighead et al. 1995).

Analysis

We used logistic regression to model the probability of persistence as a logit (Demaris 1992), analyzing the likelihood that a given cell occupied by or available to grizzly bears at the beginning of each period was occupied by bears at the end. We defined occupancy by two standards: 25% and 99% of a given cell in grizzly bear range. The second standard identified what we considered "core" range. We thus developed two models for each of two periods, one each for each of the two standards. We also developed four models for core range in 1850: one for the entire range and one each for ranges in three aggregate regions of hot desert and piñon-juniper, grassland and prairie, and coastal mountain and lowland. This approach allowed us to evaluate the effects of using different cutpoints to determine occupancy and, in the case of 1850, differences in effects of factors among regions.

We considered the effects of first-order spatial autocorrelation in each model by including the extent of adjacent grizzly bear range at the beginning of each period as an independent variable (Augustin et al. 1996). We did not consider higher-order spatial correlation (i.e., the effects of grizzly bear range in cells farther away than those adjacent to a focal cell) because of problems with interpretation and the likelihood that any higher-order effects would be multiplicative rather than additive.

We used Akaike's information criterion (AIC) to select models containing a reduced subset of candidate effects (Burnham & Anderson 1998) and R_L^2 and Somer's D to judge the predictive efficiency of the model (Demaris 1992). We considered models with a lower AIC to be more likely descriptions of the data, and, contingent on AIC, models with a higher R_L^2 or D to be more predictive and explanatory. Parameters were estimated by maximum likelihood. Where needed, we transformed independent variables to conform with the assumption of a logistic response. We evaluated the relative importance of individual independent variables by the change in AIC (Δ), obtained by deleting each variable in turn from the best model and based on our knowledge of biological relations (Burnham & Anderson 1998). For purposes of display, we described univariate relations for factors of biological interest or with the strongest effects on persistence.

We did not use p values or tests of hypotheses to reach conclusions in our analysis. We mapped response and explanatory variables, ostensibly providing a complete representation of the population and its environment. We were therefore not sampling or making inductive inferences from a sample to a population. Under such conditions, error entered into the analysis primarily

through unknown inaccuracies in the maps. We used statistical models as means of accounting for the structure of the covariance matrix. We assumed that representing conditions at the scale of life ranges imparted an appropriate level of information to the analysis. The number of observations used in information-based model selection and parameter-estimation procedures had a biological basis, as did values of the response and explanatory variables for each observation.

Predictions

We used data from circa 1990 in conjunction with the model that described 1920–1970 extirpations of core range to predict the location and extent of core ranges in 2000. In addition to using updated information on humans, cattle, and croplands, we also edited the map of whitebark pine distribution to account for the fact that by 1990 this species had been virtually extirpated by a pathogen in much of its former range. Based on the map provided by Kendall (1995), we treated whitebark pine as extirpated in all areas where 41–100% of the trees were dead and 51–100% of the remaining live trees were infected. We undertook this exercise to project what might have happened between 1970 and 2000 if the lethality of humans to grizzly bears observed during 1920–1970 had not changed. By using the model to control for changes in the biophysical environment, we interpreted differences between observed and predicted core ranges in 2000 as measures of change in human lethality arising from actions such as the institution in 1975 of legal protections for grizzly bears under the U.S. Endangered Species Act (U.S. Fish and Wildlife Service 1993).

We predicted probabilities on a cell-by-cell basis. We raised these probabilities to the 0.6 power to account for the fact that the 1920–1970 model described extirpations for 50 years, whereas we were predicting the same for only 30. We used a 900-km² moving window to create isopleths of probability by 25% intervals and calculated the resulting total area with a >75% probability for each grizzly bear range. We used this value as an index of robustness to short-term (i.e., several decades) increases in human lethality. We also calculated the aggregate probability that core range would have existed where it did in 2000 if 1920–1970 effects had persisted. We obtained this value for each range by multiplying predicted probabilities for all grid cells that were core in 2000.

Results

Grizzly Bear Range circa 1850

Ecoregion provided much of the explanation for range-wide distribution of grizzly bears in 1850 (Table 1). Griz-

Table 1. Parameters (β) and change in Akaike's information criterion (Δ) for models describing the relation between core grizzly bear range in 1850 (>99% of a grid cell in grizzly bear range) and explanatory variables.^a

Explanatory variable	Entire range		Hot desert & piñon-juniper ecoregions		Coastal ecoregions		Grassland & prairie ecoregions	
	β	Δ	β	Δ	β	Δ	β	Δ
Constant	-0.15		-0.67		-0.77		2.4	
Ecoregions								
Rocky Mountain	0.92 ^b	656	1.2 ^b	164				
coastal mountain	0.0034	116	0.71 ^a	81	0.0024	44		
coastal lowland	0.39 ^b	75			0.29 ^b	30		
sagebrush desert	0.0024	117						
prairie	-0.0034	487					-0.0056	264
hot desert	-0.22 ^b	145	-0.21 ^b	47				
grassland							-0.0026	52
Food ranges								
oaks	0.61 ^b	219	0.50 ^b	114	0.88b ^a	51		
piñon pines	0.0024	42	0.0030	38				
whitebark pine	0.0058	23			0.0070	18		
bison	0.0013	99					0.0010	54
salmon	0.0020	6						
salmon (ln transformed)	-0.55	33						
Human factors								
humans	0.00067	24	-0.00036	29			0.00092	95
humans (squared)	-8.3×10^{-6}	18						
maize culture	0.00050	11	0.33 ^a	140			-0.14 ^b	31
Model R_L^2		0.45		0.44		0.49		0.30
Model Somer's D		0.79		0.80		0.64		0.68
n		4942		1312		682		1968

^aModels are described for the entire 1850 range and for each of three constituent aggregate ecoregions.

^bParameter is for natural log (ln)-transformed values of the independent variable.

zly bear range was strongly positively associated with the Rocky Mountains, coastal mountains, and sagebrush desert and was negatively associated with hot desert and prairie (Fig. 2). Of the foods, grizzly bear range was most strongly positively associated with ranges of oak-dominated vegetation types and bison. Human factors were of relatively minor importance. Grizzly bear range was positively associated with maize cultivation and nonmonotonically related to densities of Native Americans.

Many of the range-wide relations were repeated at the level of aggregate ecoregions (Table 1). Within hot desert and piñon-juniper ecoregions, grizzly bear range was strongly positively associated with oak-dominated vegetation (Fig. 3) and areas transitional to the coastal and Rocky Mountains. The association of grizzlies with piñon pines was substantially weaker than the association with oaks (Fig. 3). Grizzly bears here also tended to occur where there were fewer humans, except when those humans were engaged in maize cultivation. Within coastal regions, the strong positive association of grizzly bears with oaks was reiterated (Fig. 3), whereas relations with human factors were absent. Grizzly bears apparently occupied the prairies and grasslands only where there were bison (Fig. 3) or humans not engaged in maize cultivation. Relations between grizzly bear range

and human factors were reversed here compared with the desert and piñon-juniper ecoregions.

Extirpations, 1850–1920

The persistence of grizzly bears until 1920 in range they occupied in 1850 was most likely within Rocky Mountain ecoregions and the range of whitebark pine (Table 2; Fig. 4). Persistence was also more likely where grizzly bear range had been locally extensive within the surrounding 7200 km² during 1850. Extirpation was most likely where grizzly bears had been associated with bison, piñon pine, and salmon in 1850 and where there were high densities of humans. Persistence was more likely where there were higher densities of cattle. These relations were evident regardless of which cutpoint defined occupancy by grizzly bears, although R_L^2 increased for the model of core range. The only change between models was the inclusion of sagebrush desert and the exclusion of wheat cropland in the model for core range versus total range.

Simply by occurring mostly within a Rocky Mountain ecoregion, a given cell had a nearly 30% chance of containing some ($\geq 10\%$) grizzly bear range in 1920. If no part of a cell occurred in this type, the chance that grizzly bears persisted dropped to nearly zero. Similarly,

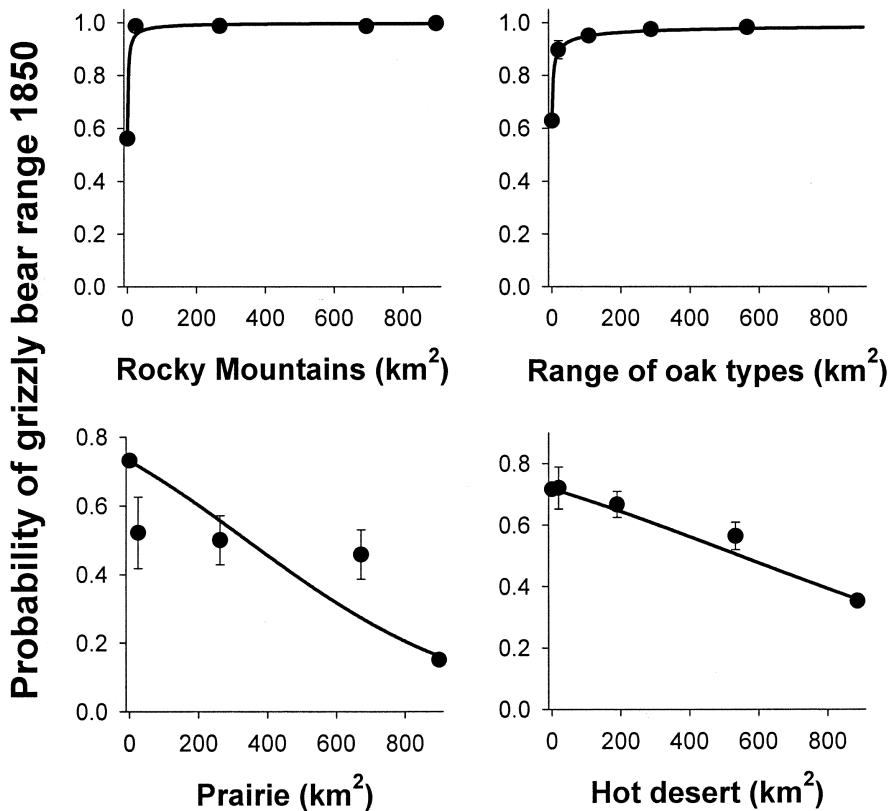


Figure 2. Probability that a grid cell was core grizzly bear range in 1850 as a function of the extent of Rocky Mountain ecoregions, oak vegetation types, prairie, or hot desert in the grid cell. Lines depict univariate relations for each factor. Points and associated standard deviations are shown for quintiles of the data to illustrate goodness of fit.

probability of persistence approached 100% in areas mostly or completely contained within the range of whitebark pine (Fig. 4). Probability of persistence also escalated markedly where grizzly bear range within an 8100-km² area including the focal grid cell exceeded 8000 km² in 1850 (Fig. 4).

Extirpations and Predictions, 1920–2000

EFFECTS OF ENVIRONMENTAL VARIABLES

Ecoregion dropped out as an explanatory variable after 1920, simply because all but two remaining grizzly bear populations circa 1920 occurred in only one type, the Rocky Mountain ecoregion. Considering the remaining variables, probability of persistence was most strongly related to whitebark pine range (Table 2; Fig. 4). As in the previous period, this relation was positive. Secondly, persistence was more likely where the grid cell was associated with extensive grizzly bear range in the surrounding and inclusive 8100 km² during 1920. Probability of persistence escalated markedly where the 1920 range was >7000 km² in size. As during 1850–1920, probability of persistence declined as the density of people increased, although—in contrast to the previous transition—probability of persistence also declined with increasing density of cattle.

The relation of persistence to human densities during 1920–1970 resembled a negative exponential (Fig. 4). The probability that a cell was core grizzly bear range in 1970 dropped to near zero at human densities of >7/km² (i.e., 6000 humans in a 900-km² area). By contrast, probability of persistence was markedly higher at human densities of <0.5/km² (i.e., 350 humans in a grid cell). Probability of persistence also approached 60–80% where a grid cell was almost entirely within range of whitebark pine (Fig. 4).

PROJECTION OF 1920–1970 EFFECTS THROUGH 2000

With biophysical conditions as they were circa 1990 and effects of these conditions the same as during 1920–1970, there was virtually no chance that there would have been core grizzly bear range in all of the places that it existed in 2000 (Fig. 5). The aggregate probability that there would have been as much core range as existed in 2000 if 1920–1970 effects had persisted was $<1 \times 10^{-18}$, each, for the Northern Continental Divide, Cabinet-Yaak, and Yellowstone ranges. The probability was 0.038 for the Selkirk grizzly bear range.

We used the model explaining 1920–1970 extirpations to calculate within each existing or potential grizzly bear range the area that had a >75% probability of containing core range if 1920–1970 effects had persisted to the present (Fig. 5). We interpreted this value as an

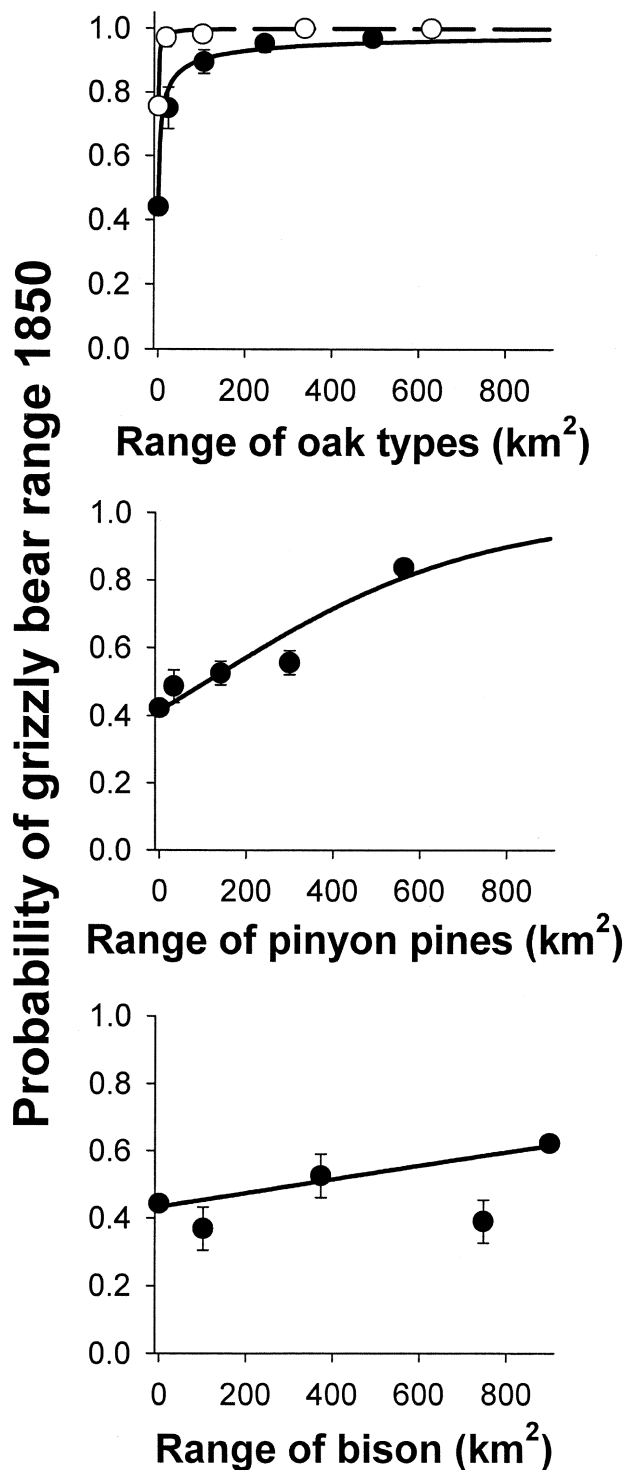


Figure 3. Probability that a grid cell was core grizzly bear range in 1850 as a function of the extent of oak vegetation types in desert-piñon juniper ecoregions (solid line) and coastal ecoregions (dashed line), extent of piñon pine range in desert-piñon juniper ecoregions, and extent of bison range in grassland-prairie ecoregions. Lines depict univariate relations for each factor. Points and associated standard deviations are shown for quintiles of the data to illustrate goodness of fit.

index of robustness for these existing or potential ranges. Nowhere in the current Cabinet-Yaak or Selkirk grizzly bear ranges was there a >75% probability of core range existing if 1920–1970 effects had persisted. The Northern Continental Divide and Yellowstone ranges contained 1523 and 5993 km², respectively, that surpassed this threshold. Potential grizzly bear range in the Bitterroot and North Cascades regions contained 3140 and 158 km², respectively, where probability of core range was >75% under this pessimistic scenario. When we modeled probabilities without whitebark pine present in the Northern Continental Divide or Yellowstone ranges—assuming total extirpation of this food—there were no cells where probability of persistence was >50%.

RELATION TO RANGE SIZE AND SHAPE

The only populations that remained large (>200 bears) in 1970 (those of the Yellowstone and Northern Continental Divide regions) were those that had occupied contiguous ranges >20,000 km² in size in 1920 (Fig. 6a). In addition, all ranges containing even a few grizzly bears in 1970 were larger than 2,500 km² in 1920. None of the numerous ranges less than the size of a single adult female life range (approximately 900 km²) in 1920 contained any grizzly bears in 1970. Of the 1920s ranges >7,000 km² in size, the two with the highest ratio of perimeter to area (>2.0) were also without grizzly bears in 1970.

Of current ranges, only those of the Yellowstone and Northern Continental Divide grizzly bear populations exceed 20,000 km² and have a ratio of perimeter to area of <2.0 (Fig. 6b). The Bitterroot and North Cascades grizzly bear recovery areas (Almack et al. 1993; U.S. Fish and Wildlife Service 1993) approach 20,000 km² in size, but currently have few or no grizzly bears. All other ranges or recovery areas are <7,000 km². Aside from size- and shape-related considerations, densities of humans in or near all current grizzly bear ranges or recovery areas are <7/km², but none are <0.5/km² (Bitterroot = 2.9, Cabinet-Yaak = 2.9, Northern Continental Divide = 3.2, Selkirks = 3.2, Yellowstone = 2.0).

Discussion

1850s Range

Our results are consistent with aspects of hypothesis 1 that humans and biophysical factors affected where grizzly bears lived even before European settlers were a major cause of mortality. Grizzly bears apparently were absent from or rare in desert areas, especially those with hotter climates. This is consistent with an aversion to daytime activity during the summer and the selection of ameliorated sites for daytime bedding by bears at lower latitudes (Schleyer 1983).

Table 2. Parameters (β) and change in Akaike's information criterion (Δ) for models describing the relation between persistence of grizzly bears in 1850–1920 and 1920–1970 and explanatory variables.^a

Explanatory variable	1850–1920				1920–1970			
	total range		core range		total range		core range	
	β	Δ	β	Δ	β	Δ	β	Δ
Constant	–6.5		–7.3		–26		–3.1	
Ecoregions								
Rocky Mountain sagebrush desert	0.39 ^b	570	0.45 ^a	482				
Food ranges								
piñon pines	–0.0019	37	–0.0027	51	–0.33 ^b	6		
whitebark pine	0.0041	102	0.0032	73	0.50 ^b	134	0.64 ^a	100
bison	–0.0017	77	–0.0018	46				
salmon	–0.12 ^a	29	–0.00083	20				
Human factors								
humans	–0.00015	13	–0.00024	20			–0.80 ^a	14
cattle	0.0032	23	0.0027	12	–0.25 ^b	18	–0.32 ^a	14
wheat	–0.097 ^b	4			0.005	2		
corn					0.66 ^b	2	1.4 ^a	10
Previous range size								
range in 1850	0.00058	34	0.00058	12				
range in 1920					2.8 ^b	55	0.00059	34
Model R_L^2	0.51		0.64		0.65		0.80	
Model Somer's D	0.77		0.82		0.87		0.92	
n	3481		3481		926		926	

^aModels are described for total range (>25% of a grid cell in grizzly bear range) and core range (>99% of a grid cell in grizzly bear range) at the end of each interval.

^bParameter is for natural log (\ln)-transformed values of the independent variable.

Availability of oaks and bison also positively affected the location of core grizzly bear range in 1850. This is consistent with the current importance of acorns to black bears (*U. americanus*) in places such as southern Colorado (Beck 1991) and central Arizona (LeCount et al. 1984) and of bison to grizzly bears in the Yellowstone region, especially where other high-quality foods are scarce (Green et al. 1997; Mattson 1997a). The weaker relations between grizzly bear range and the ranges of large-seeded pines were plausible, given what was probably the less favorable energetics of using pine seeds compared with those of larger acorns or tissue from a bison.

The weak, nonmonotonic relation of grizzly bear range with salmon was ambiguous with respect to hypothesis 1. Core 1850 grizzly bear range was unlikely to occur where the range of spawning salmon was most extensive, yet salmon were a high-quality bear food of historical importance to grizzly bears in the northwestern United States (Hilderbrand et al. 1996). Human competition and predation potentially explain this paradox. Native Americans killed grizzly bears and also apparently dominated the most productive salmon spawning streams (Ewers 1958; Mathews 1961; Hans 1964; Clark & Casey 1992; Taylor 1999). A food like spawning salmon that was highly aggregated and that concentrated would-be consumers would predictably heighten competition between grizzlies and humans.

In the east, grizzly bear range was truncated where Native Americans cultivated maize and resided in semi-permanent villages concentrated along rivers and streams (Holder 1970). Although we cannot be certain how grizzly bears used the Great Plains, evidence suggests that they concentrated their activities along rivers and streams, where food and cover were more abundant (Dodge 1959; Burroughs 1961; Stebler 1972; Gowans 1986; Aune & Kasworm 1989). If humans and black bears also concentrated their activities in riparian habitats, then interference or scramble competition and increases in deaths caused by humans could have limited dispersal of grizzly bears across the Great Plains into eastern deciduous forests. *Ursus arctos* can flourish in temperate deciduous forests, as in Europe, but they exhibit considerable dietary overlap with black bears in the same habitats (Mattson 1998). The impediment of interspecific competition can help explain why grizzly bears, arriving in temperate latitudes at about the same time as human progenitors of Clovis-point technology, did not spread further east or south when, at the same time, these technologically advanced humans spread to all of North and South America.

In 1850, grizzly bears in desert and piñon-juniper ecoregions of the Southwest were more likely present where humans cultivated maize and absent where there were high densities of nonmaize-growing Native Americans. Unlike in the Great Plains, maize cultivation in the

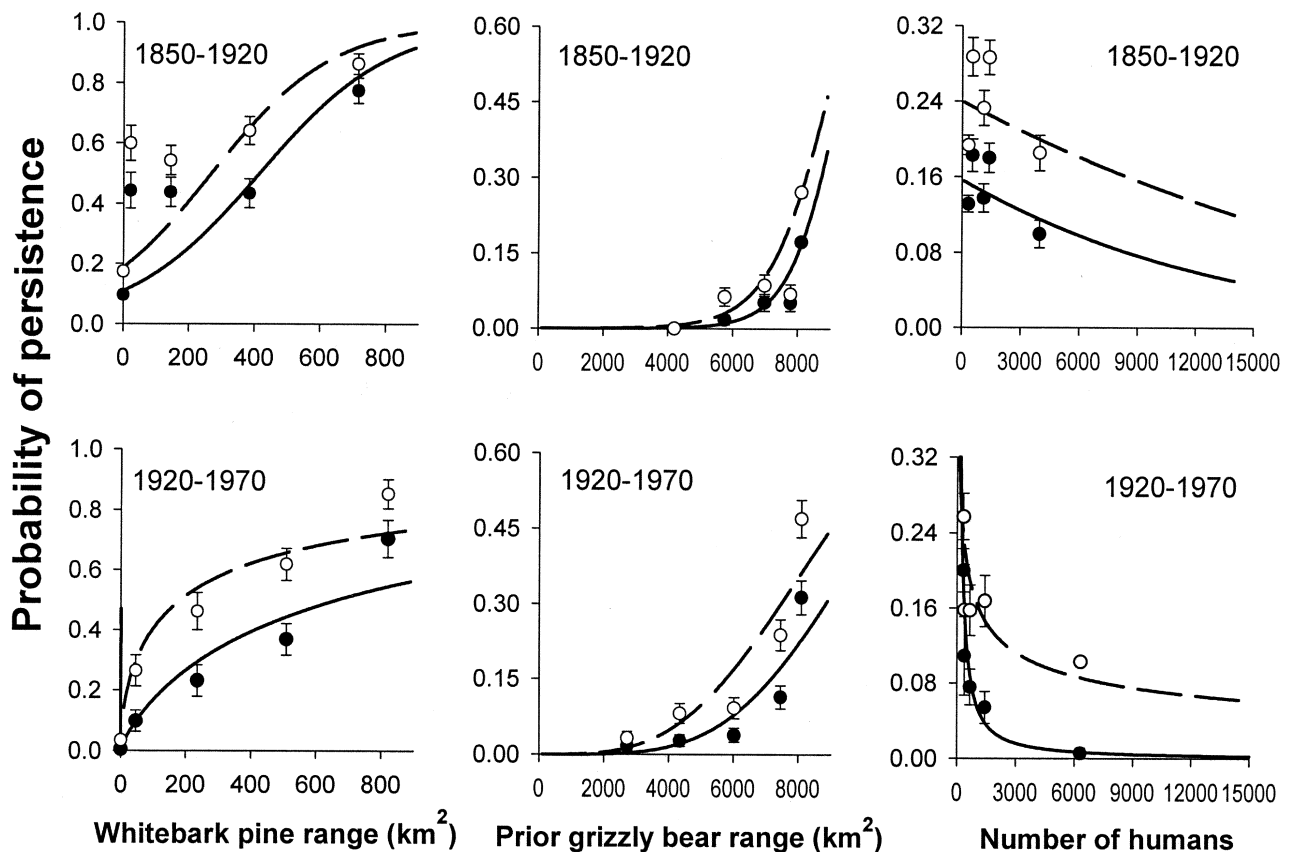


Figure 4. Probability that grizzly bears persisted in a grid cell in 1850–1920 and 1920–1970 as a function of the extent of whitebark pine range and number of humans in the grid cell and the extent of grizzly bear range in the focal and surrounding eight cells. Solid lines show relations for persistence of core range (99%) and dashed lines relations for persistence of at least 25% grizzly bear range within the cell. Points and associated standard deviations are shown for quintiles of the data to illustrate goodness of fit. Filled circles represent core range and open circles total range.

Southwest was more dispersed, especially relative to potentially important grizzly bear foods such as acorns and piñon pine seeds (Glassow 1980). Even so, pine seeds and acorns were also important foods of southwestern Native Americans (Dunmire & Tierney 1997). As in areas with salmon, where high densities of southwestern Native Americans relied more exclusively on wild foods such as pine seeds, acorns, and ungulates, competition between grizzly bears and humans may have been more stringent and the occurrence of core grizzly bear range less likely.

Extirpations

European settlers had a major detrimental effect on grizzly bears in the United States. The effects of European settlement changed over time, however, owing to the modification of effects of human numbers by intervening factors. Given the negative relations between grizzly bear persistence and numbers of resident humans dur-

ing both 1850–1920 and 1920–1970, our results are consistent with hypothesis 2 that humans caused the decline of grizzly bears. Even so, and consistent with other aspects of hypothesis 2, ecoregion had a dominant intervening effect during the first period, and key foods, sizes of bear ranges, and presence of cattle and croplands had effects during both the first and second periods.

The positive association of grizzly bear persistence with the Rocky Mountains during 1850–1920 could have several root causes. Grizzly bears may have existed here at densities higher than anywhere else. Although this may be true in contrast to grass-, sagebrush-, and juniper-dominated ecoregions, it is unlikely the case in contrast to most coastal lowlands, where grizzly bears could exist at exceptionally high densities (Storer & Tevis 1955). Assuming comparable densities, grizzly bears may have been more dispersed in the Rocky Mountains, especially in contrast to drier ecoregions where, as pointed out before, there is evidence that grizzly bears concentrated along watercourses. Given that European settlers also

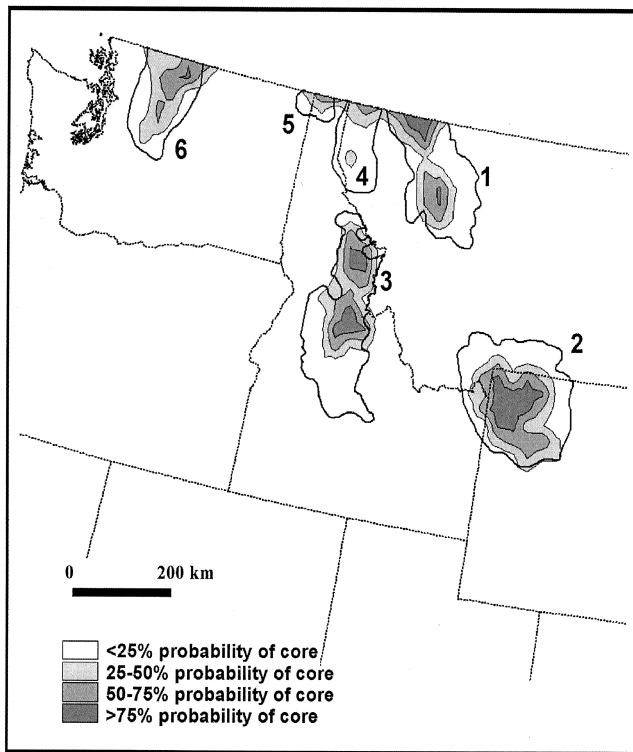


Figure 5. Isopleths depicting predicted probabilities of core grizzly bear range in 2000, given biophysical conditions circa 1990 and assuming the persistence of 1920–1970 effects (i.e., human lethality). Thick solid lines delineate either existing or potential grizzly bear ranges in the (1) northern Continental Divide, (2) Yellowstone, (3) Bitterroot, (4) Cabinet-Yaak, (5) Selkirk, and (6) North Cascades regions. Thin lines are state boundaries.

tended to travel and reside in riparian areas (Hafen et al. 1970), grizzly bears may have been especially vulnerable to extirpation in drier than in wetter ecoregions.

With respect to hypothesis 3, the relation between grizzly bear persistence and cattle changed between 1850–1920 and 1920–1970 from positive to negative. This reversal probably reflected a shift in the relative balance between cattle as a beneficial food and cattle as a catalyst of lethal conflict with humans. Cattle are good grizzly bear food (Murie 1948; Knight & Judd 1983). There is evidence that the flood of cattle into California and the Southwest not only replaced native ungulates lost to overharvest, but also led to short-term increases in numbers of grizzly bears, which profited by preying on livestock at a time when husbandry was lax and predator extermination programs unorganized (Storer & Tevis 1955; Brown 1985). There is direct evidence from the turn of the nineteenth century that grizzly bears in the Southwest obtained much of their energy from meat, most likely from cattle (Jacoby et al. 1999). By the end

of the 1800s, contact with cattle increasingly precipitated lethal responses from increasingly effective predator-control agents and increasingly attentive owners (Storer & Tevis 1955; Brown 1985).

The presence of bison, salmon, or piñon pines in 1850 was associated with accelerated loss of grizzly bear range in 1850–1920. These effects probably had as much to do with interactions between humans and grizzly bears as with nutrition. Some foods more than others predictably brought grizzly bears into more frequent, predictably lethal, contact with Europeans by concentrating bears at predictable times and places at lower elevations nearer humans. Salmon, rather than contributing to persistence, likely hastened the demise of grizzly bears by luring them into harm's way (Merrill et al. 1999). Although piñon pine seeds and bison carcasses might have been spatially more dispersed than salmon, bison carcasses were often abundant along riparian areas (Burroughs 1961; Haines 1970), and piñon pines were abundant at lower elevations nearer where Europeans settled and were active (Brown 1994). Compounding this, bison, perhaps one of the most important foods of grizzly bears on the Great Plains, were nearly extirpated from 1850 to 1920.

In contrast to areas with bison, salmon, and piñon pine, grizzly bears survived well in whitebark pine range. Again, the explanation probably has more to do with interactions between humans and grizzly bears than with nutrition. Whitebark pine grows only at high elevations, distant from most human settlements (Mattson et al. 2001). When whitebark pine seeds are abundant, grizzly bears are attracted to the remote whitebark pine forests, where they are killed by humans at a much lower rate (Mattson et al. 2001). Thus, the presence of whitebark pine can induce a refuge effect.

Oak-dominated vegetation was probably intermediate between whitebark pine and other foods in its effects on levels of contact between humans and grizzly bears. Oak forests were typically not concentrated at low elevations or in riverine habitats and did not occur at high elevations (Brown 1994). Thus, the neutral effect of oak-dominated vegetation on extirpations between 1850 and 1920 is not surprising, despite the fact that acorns produced in these forests were probably a high-quality bear food that positively influenced distributions of grizzly bears in 1850.

Range Collapse and Dimensions

Grizzly bear range in North America collapsed from one margin (southern) toward another (northern). The explanation is straightforward. Humans have been and continue to be sparser in Canada and Alaska, the current strongholds for grizzly bears, compared with the contiguous United States. At the broadest scale, extirpation

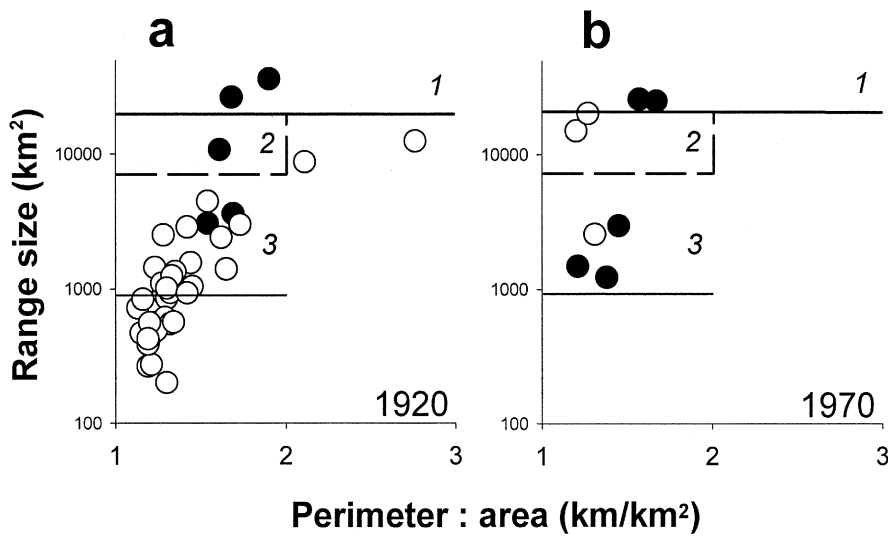


Figure 6. Grizzly bear ranges in 1920 and 1970 plotted against size (log scale) and ratio of perimeter to area. Filled circles are ranges with surviving grizzly bears in 1920 or 1970. Open circles are ranges where grizzly bears did not persist in 1920 or ranges or recovery areas where grizzly bears were absent or rare but managed for restoration in 1970. Areas with a 1 define conditions associated with the best prospects for persistence; with a 2 conditions associated with moderate prospects for persistence, where range shape is a greater consideration; and with a 3 conditions under which persistence is highly unlikely. The horizontal line about one-third of the way up from the bottom corresponds with 900 km²—the hypothetical size of a female life range used for this analysis.

was a deterministic event that tracked spatial patterns of elevated human-caused mortality.

Even so, this pattern of grizzly bear extirpations in North America is consistent with the first principles of island biogeography theory. Although the reduction of grizzly bear range was characterized by a broad retreat, at a finer scale, range collapse in the contiguous United States exhibited a classic pattern of fragmentation followed by extirpations of the smallest populations. Whether or not one argues that this is merely part of the larger pattern of habitat loss, consistent with hypothesis 4, small size and, to a lesser extent, attenuated shape predisposed grizzly bear populations to extirpation.

Implications for Contemporary Conservation

The long-term survival of grizzly bears in the contiguous United States was enhanced by the existence of ranges >20,000 km² in size with proportionately little edge and few people within. This is consistent with the results of Woodroffe and Ginsberg (1998), who found that grizzly bear populations require protected areas of about 4000 km² and 50,000 km² in size to have a 50% and 90% chance, respectively, of surviving. Hitherto, there has been little basis other than anecdote for stating how large a range should be or how few people should be within to ensure the persistence of any large carnivore. This lack of information has contributed to the establishment of goals for grizzly bear recovery in the contiguous United States that neglect the effects of human density

altogether and that simply reflect perceptions of status quo habitat capacity and social acceptance (U.S. Fish and Wildlife Service 1993). If grizzly bears are restricted to ranges smaller than 20,000 km², as is the case for all but the Northern Continental Divide and Yellowstone recovery areas, extensive restrictions on access and armaments or widespread modification of human behavior likely will be required if bears are to survive (Mattson 1997b; Mattson et al. 1996a).

Our results show that changes in human attitudes and behavior have been critical to the survival of grizzly bears from 1970 to the present. In essence, models of grizzly bear extirpation depicted how the physical presence of humans translated through intervening effects into losses of occupied grizzly bear range. Thus, the discrepancy between current grizzly bear range and that predicted by the model for extirpations between 1920 and 1970 was an effect attributable to changes in human lethality since 1970. Without major favorable changes in the behavior of humans living in and near grizzly bear ranges, there is no chance that these ranges would be as extensive as they are now given the biophysical conditions that existed in 1990. This is direct evidence for the dramatic beneficial effect of conservation policies enacted through legislation such as the U.S. Endangered Species Act (ESA).

There are no guarantees that humans will continue to be as protective of grizzly bears in the contiguous United States as they were during 1970–2000. There have been proposals to revise the ESA to make its pro-

tections less stringent. There have also been proposals to remove ESA protections from the Yellowstone grizzly bear population. **Our results suggest that under current biophysical conditions Yellowstone's grizzly bear range would be the most robust of any to increased human lethality lasting two to three decades. The mostly unoccupied Bitterroot range, with bears fully restored, would be the second-most robust. Otherwise, grizzly bears in the Cabinet-Yaak, Selkirk, and North Cascade ranges stand little chance of surviving even short-term increases in human lethality. Assuming an objective of long-term persistence, these results argue for continued stringent protection of grizzly bears in the Cabinet-Yaak, Selkirk, and North Cascade ranges and high-priority restoration of bears to the Bitterroot Range.**

The apparent robustness of Yellowstone's grizzly bear range is deceptive. Whitebark pine seeds are currently one of the two most important grizzly bear foods in the Yellowstone region (Mattson et al. 1991). Virtually all the whitebark pine in this system is projected to be lost either to an exotic pathogen or to global climate warming (Kendall 1995; Mattson et al. 2001). Like Mattson et al. (2001), our results suggest that the apparent robustness of Yellowstone's grizzly bear range is contingent on the presence of abundant whitebark pine. Such vulnerability emphasizes the need for concern over loss of this food and argues for the inadvisability of removing any legal protections for this population.

More positively, our results contribute to identifying areas where there are good prospects for restoring grizzly bears extirpated between 1850 and 1970. Ideal restoration areas would be larger than 20,000 km² and would contain <7 humans/km². Extensive core areas would also exist where there are <0.5 humans/km². Greater topographic relief would be an asset, but only where key foods dispersed bears away from human activity. The presence of bison and extensive communities of oaks such as *Quercus gambelii* or *Q. turbinella* would also enhance prospects for restoration by providing high-quality bear food. The identification of such areas, if they exist, is a necessary next step toward ensuring the long-term survival of grizzly bears in the contiguous United States.

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