Defining landscape suitable for restoration of grizzly bears Ursus arctos in Idaho

Article *in* Biological Conservation · February 1999

DOI: 10.1016/S0006-3207(98)00057-3

ELSEVIER

Biological Conservation 87 (1999) 231–248

BIOLOGICAL
CONSERVATION

Defining landscapes suitable for restoration of grizzly bears *Ursus arctos* in Idaho

Troy Merrill[a], David J. Mattson[b,*], R. Gerald Wright[c], Howard B. Quigley[d]

[a]*LTB Consulting, 415 East 7th, Moscow, ID, 83843, USA*
[b]*U.S.G.S. Forest and Rangeland Ecosystem Science Center and Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID, 83844-1136, USA*
[c]*U.S.G.S. Idaho Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID, 83844-1136, USA*
[d]*Hornocker Wildlife Institute, University of Idaho, Moscow, ID, 83844-3228, USA*

Received 7 April 1997; received in revised form 17 April 1998; accepted 20 April 1998

Abstract

Informed management of large carnivores depends on the timely and useful presentation of relevant information. We describe an approach to evaluating carnivore habitat that uses pre-existing qualitative and quantitative information on humans and carnivores to generate coarse-scale maps of habitat suitability, habitat productivity, potential reserves, and areas of potential conflict. We use information pertinent to the contemplated reintroduction of grizzly bears *Ursus arctos horribilis* into central Idaho to demonstrate our approach. The approach uses measures of human numbers, their estimated distribution, road and trail access, and abundance and quality of bear foods to create standardized indices that are analogues of death and birth rates, respectively; the first subtracted from the second indicates habitat suitability (*HS*). We calibrate *HS* to sightings of grizzly bears in two ecosystems in northern Idaho and develop an empirical model from these same sightings based on piece-wise treatment of the variables contained in *HS*. Depending on whether the empirical model or *HS* is used, we estimate that there is 14 800 km^2 of suitable habitat in two blocks or 37 100 km^2 in one block in central Idaho, respectively. Both approaches show suitable habitat in the current Evaluation Area and in an area of southeastern Idaho centered on the Palisades Reservoir. Areas of highly productive habitat are concentrated in northern and western Idaho and in the Palisades area. Future conflicts between humans and bears are most likely to occur on the western and northern margins of suitable habitat in central Idaho, rather than to the east, where opposition to reintroduction of grizzly bears is currently strongest. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Carnivores; Conservation design; Dispersal; Human impacts; Roads; Scale

1. Introduction

Managers of large carnivores often make decisions without access to information derived from detailed empirical data. This is especially true of managers charged with planning and executing reintroduction programs. Some guidance is available in the tenets of risk management and decision theory (*cf.* Berger, 1980). However, there are currently few approaches to organizing and displaying quantitative *and* qualitative information in ways that are useful to scientists and managers under such conditions of uncertainty.

Several issues are important to integrating well-developed qualitative information with sparse empirical data so that the products are useful to the development of conservation strategies. Conceptual models are vital to clarifying biological relations that are, in turn, critical to achieving conservation aims (Walters, 1986; Williams, 1997). In most cases these models focus on factors that affect survival and reproduction of the species of interest. Information about factors thus high-lighted is critical, including information on trends and spatial variation in their abundance. Finally, timeliness is important. Conservation-relevant regional analyses can easily become mired by the collection of unnecessarily detailed data, while critical management issues languish without input of relevant biological information (*cf.* Ludwig et al., 1993). This is not to say that detailed

---

* Corresponding author: Tel.: 001-208-885-3589; fax: 001-208-885-3618; e-mail: matt7281@novell.uidaho.edu

PII: S0006-3207(98)00057-3

information is unimportant but, rather, the tempo of most conservation issues requires that managers use existing information to improve current management (Walters, 1986; Clevenger et al., 1997).

Grizzly bear *Ursus arctos horribilis* conservation in the central part of Idaho, USA (US) (Fig. 1), is an exemplar of situations where managers require timely, relevant, and otherwise useful information to help cope with uncertainty and human conflict. Grizzly bears are currently absent or exist only in very small numbers in central Idaho and there is very little information on the biology of resident bears, historical or contemporary. Conservation of grizzly bears in central Idaho has been a policy priority only in recent years. In 1850 grizzly bears occupied almost all of Idaho [Fig. 2(a)]. By 1920, humans had purposefully eliminated grizzly bears from most of the state [Fig. 2(b)] (Merriam, 1922) and, by 1970, grizzly bears were extirpated from 97% of their

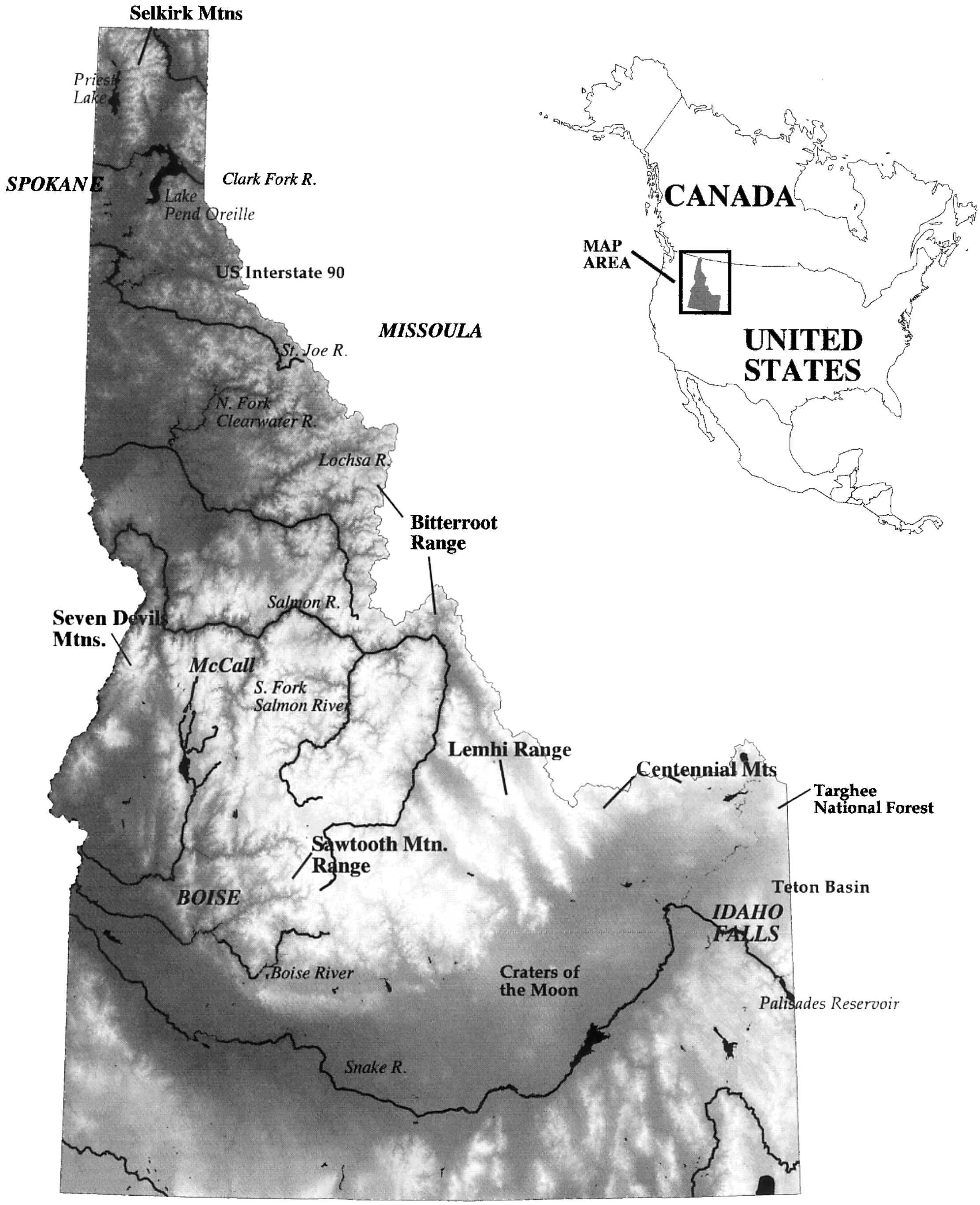


Fig. 1. The state of Idaho, showing rivers, topography, and place names mentioned in the text. Lower elevations are shown as progressively darker shading. Boise, Missoula and Spokane are the largest cities in the analysis area.

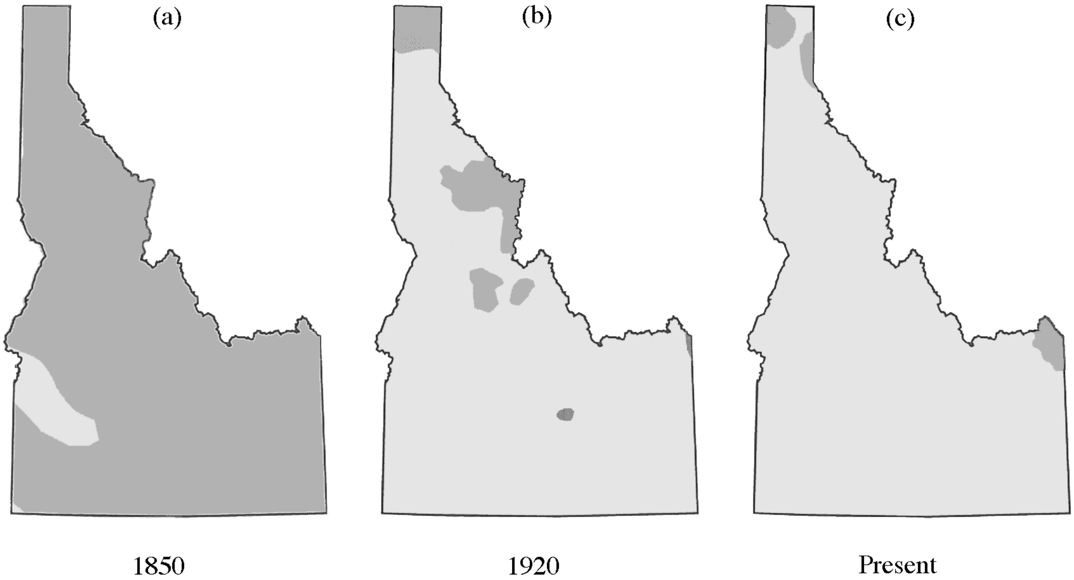


Fig. 2. Estimated distributions of grizzly bears in Idaho (dark gray) in (a) 1850, (b) 1920, and (c) the present.

former range [Fig. 2(c)]. Recent conservation plans have included central Idaho as a recovery area for grizzly bears (US Fish and Wildlife Service, 1993). However, controversy arising from plans to reintroduce or augment bears in this region has high-lighted uncertainties about the productivity, security and overall suitability of habitat in and around the designated Evaluation Area.

We illustrate an approach to marshaling information that is attentive both to the issues of grizzly bear conservation in Idaho and to the more general issues of timeliness and conceptual relevance. We emphasize the suitability of habitat for grizzly bears and extend a method developed by Clevenger et al. (1997) for brown bears *U. a. arctos* in Spain. Our approach builds on well-developed conceptual models regarding the conservation and demography of grizzly bears in North America (Mattson et al., 1996a,b). Unlike many previous habitat-suitability models, our procedure focuses on human-related factors because most grizzly bears in the contiguous US die because humans kill them (Mattson et al., 1996a).

2. Methods

Our method is comprised of five parts: (1) development of an index of habitat productivity; (2) development of an index for the presence of humans, equivalent to the inverse of habitat effectiveness for grizzly bears, comprised of potential human activity, modified by road and trail density; (3) a means of generalizing the landscape to a scale commensurate with the size of grizzly bear life-time ranges; (4) a means of calibrating an index of habitat suitability and of deriving an empirical model from observations of grizzly bears in northern Idaho; and (5)secondary analyses designed to aid conservation design and the development of management strategies. Although the digital data that we used were available at different resolutions, and several of our preliminary calculations used pixels <1 km^2 in size, our final results are presented at a resolution of 1 km^2.

*2.1. Index of habitat productivity (*HP*)*

Habitat productivity was derived from information on the regional diets of grizzly bears, the occurrence and abundance of bear foods within coarse-scale vegetation types, and the distribution of these vegetation types in Idaho. Seasonal coefficients for each bear food (Table 1) were calculated as the sum of all instances where a given species was recorded as a food in a study of bear diet (i.e. occurrence in one study corresponded to a count of 1), weighted by whether it was frequent (generally $>15\%$, ='3'), common (1–15%, ='2'), or incidental ($<1\%$, ='1') among the collected feces (Appendix A). Data were obtained from 14 studies of black *U. americanus* and grizzly bears in habitat similar to that found in Idaho. Vegetation types were scored based on the occurrence of bear foods, weighted by their abundances and seasonal coefficients (Table 1; Appendix A). Information on the occurrence and abundance of plant species in each of 66 vegetation types was obtained from Caicco (1989).

We assumed that greater topographic complexity would result in greater habitat productivity for grizzly bears, first, because unit area productivity would be elevated as an artifact of greater actual surface area per unit area projection and, second, because greater

Table 1
Seasonal coefficients (Wgt_{ik}) used to weight the contribution of different plants in the diet of grizzly bears to calculations of grizzly bear habitat productivity for Idaho vegetation types

Species	Species Weight		
	Spring	Summer	Fall
Grazed foods			
Graminoids	38	26	26
Angelica spp.	20	15	3
Castilleja spp.	2	2	0
Cirsium (*scariosum*) [a]	3	2	0
Claytonia (*lanceolata*)	14	0	0
Equisetum (*arvense*)	37	9	8
Erythronium grandiflorum	18	0	0
Heracleum lanatum	33	19	11
Hieracium spp.	4	2	0
Hydrophyllum capitatum	2	2	0
Lathyrus (*ochroleuca*)	3	2	1
Ligusticum (*canbyi*)	11	0	0
Osmorhiza (*chilensis*)	24	0	0
Senecio (*triangularis*)	10	6	0
Taraxacum (*officinale*)	20	10	3
Trifolium spp.	15	16	7
Vicia (*americana*)	4	5	0
Excavated foods			
Hedysarum spp.	4	5	11
Lomatium spp.	7	10	8
Melica spp.	2	2	2
Fruits and seeds			
Amelanchier alnifolia	1	20	8
Arctostaphylos uva-ursi	10	4	14
Berberis repens	0	8	4
Chimaphila umbellata	0	3	0
Cornus stolonifera	0	13	10
Crataegus (*douglasii*)	0	7	5
Disporum spp.	0	1	0
Fragaria (*virginiana*)	4	6	0
Juniperus spp.	2	0	3
Lonicera spp.	5	7	2
Oplopanax horridum	0	4	5
Pinus albicaulis	5	3	12
Prunus virginiana	0	4	4
Rhamnus alnifolia	2	14	4
Rosa spp.	0	6	6
Rubus (*parviflorus*/*idaeus*)	2	7	2
Sambucus racemosa	0	8	6
Sheperdia canadensis	3	14	10
Sorbus spp.	0	15	20
Vaccinium caespitosum	3	7	2
V. globulare/*membranaceum*	0	34	27
V. scoparium	0	8	8

[a] Specific epithets in parentheses indicate species that comprised the majority of this observed use, although use of other species of the same genus was also recorded.

complexity commonly begets greater vegetation diversity (Rosenzweig, 1995). Habitat productivity scores for each map pixel based on vegetation type were therefore adjusted to account for the effects of topographic complexity. Complexity was calculated as the number of different elevations in a 9×9 cell neighborhood of 93 m^2 cells using a digital elevation model (DEM) produced by the US Geological Survey. This parameter was scaled to range from 0.5 to 1.0 so that it would modify no more than one-half the raw score of a given pixel. Extreme modifications within vegetation types were rare because most types were associated with similar topography throughout their range.

Ungulates are known to be important to many grizzly and brown bear populations, especially during the spring when bears scavenge winter-killed animals (Mattson, 1997a). Spring productivity scores were therefore multiplied by 1.5 if winter elk *Cervus elaphus* densities were above the state median (densities were provided by the Idaho Department of Fish and Game on the basis of $7\frac{1}{2}'$ US Geological Survey quadrangles). This ungulate-based multiplier was taken from the grizzly bear cumulative effects model for the Yellowstone ecosystem (Grizzly Bear Cumulative Effects Analysis Working Group, 1990) given that central Idaho contains elk densities comparable to those found in Yellowstone (Davis and Butterfield, 1991). Deer *Odocoileus* spp. densities were not considered because deer are seldom used by grizzlies, even when abundant (Mattson, 1997a).

Seasonal scores were standardized to the maximum for each season so that they ranged from 0 to 1000. These scaled values (HP) were used in the final calculation of 'habitat suitability' and to identify areas of overlap between highly productive habitat and high levels of human activity (see below).

2.2. *Index of habitat effectiveness (*HE*)*

An index of grizzly bear habitat effectiveness was calculated as a function of local human population size and proximity to populated places ($WDIST$), the proclivity of human residents to use back-country areas (RVD), and road and trail density ($ACCESS$). The smaller the local human population, the further the grid cell from towns and cities, and the lower the density of access routes, the higher would be grizzly bear habitat effectiveness.

2.2.1. *Recreation visitor days and regional population size (RVD)*

The US Forest Service collects data on recreation visitor days (RVD) and inventories roadless and designated wilderness areas. The US Census Bureau provides human censuses, by county and town, at 10-year intervals. We used these data to empirically describe a relationship between local human population size (during 1990) and RVDs on local National Forests, controlling for effects of nearby National Parks and total roaded area (Appendix A). RVD was thus expressed as number of visitor days/km^2 for National Forest areas not near National Parks. We used data for 23 National Forests in the northern Rocky Mountains of Montana, Idaho, northwest Wyoming, and northeast Oregon. We calculated local population size as the sum for all counties containing parts of a given National Forest. This roughly corresponded to an area 80 km in radius from a point near the center of the forest.

Although absolute levels of human activity per unit area of roaded landscape may be higher on National Forests compared to private lands, we were primarily interested in describing in general terms how the number of local human residents translated into level of activity in the backcountry. This relationship was curvilinear, with backcountry activity increasing at a lower rate than increases in local population size. We emphasized the form rather than the exact magnitude of this relationship by standardizing *RVD* to be ≤ 1 (Appendix A).

2.2.2. The effects of distance to and size of a population center (WDIST)

The previous analysis provided us with a relationship between local human population size and *RVD*s at the scale of a National Forest, but did not describe how this use depended upon the distance to populated places or the number of residents there. We used a method called inverse distance weighting interpolation (Philip and Watson, 1982; Watson and Philip, 1985) to specify the effects of distance and the population size of towns (from 1990 US Census data) on potential human activity in a given grid cell. This method calculates a value for each grid cell based upon the population sizes of all surrounding censused towns, its averaged distance from those populated places, and a function that describes how levels of human activity decline with increasing distance from a place of residence.

The rate at which human activity declined as a function of distance from place of residence was governed by a single parameter that we estimated from general information on the behavior of recreationists involved in activities typical of the northern Rockies (Wallwork et al., 1980; Smith, 1983; McLaughlin et al., 1989). We specified a curve describing frequency of trip distances from places of residence that was of a negative exponential form (Smith, 1983). We then calculated the power parameter describing this function (-1.45) for use in the inverse distance weighting interpolation. *WDIST*, the result of this calculation, was scaled to be 0–1.

2.2.3. Potential human activity (H')

An estimate of potential human activity in each grid cell (H) was obtained by multiplying *WDIST* and *RVD* (Appendix A). This measure ranged in value from 0 to 0.9 but skewed toward low values. H was therefore normalized by taking the natural log of $H \times 1000$, standardized to the maximum observed value. This transformed value, H', approached 0 in the mountains of central Idaho and 1 in the two largest cities of our analysis area. The degree to which the potential for human activity indicated by H' was realized, however, depended on local road and trail densities.

2.2.4. Density of road and trail access (ACCESS)

Density of roads and trails (in km/km^2) was calculated for a 25-km^2 area centered on each grid cell using digital data provided by the US Geological Survey. Trails were weighted by a factor of 0.35 (Mattson, 1993). These data substantially under-represented true road densities, especially in contrast to more comprehensive inventories such as those made by Mace et al. (1997) for their study of grizzly bears in the state of Montana. Mace et al. (1997) also calculated densities for an area of *c.* 3 km^2, which, given the same road network, predictably results in higher maximum road densities compared to our approach. Comparison of road densities presented here with road densities calculated in other study areas should be mindful of these differences in method and data.

2.2.5. Habitat effectiveness for grizzly bears (HE)

Habitat effectiveness (*HE*, ranging from 0 to 1000) was a function of H' and *ACCESS* (Appendix A). The primary relationship between *HE* and *ACCESS* was nonlinear, with the rate of decline in *HE* lessening with each unit increase in *ACCESS* (negative geometric; Mace et al., 1997). The slope of this primary relationship steepened as values of H' increased. In other words, habitat effectiveness declined as human access increased, but the rate of this decline accelerated as human activity on a given density of roads increased (see McLellan, 1990).

2.2.6. Habitat suitability for grizzly bears (HS)

Habitat suitability (*HS*) was the difference between habitat productivity (*HP*, the analogue of potential birth rate) and the actualized human presence (1000-*HE*; the analogue of death rate) (Appendix A).

2.3. Scaling habitat suitability

Habitat suitability needs to be depicted at a scale that is appropriate to management issues and the organism that is being managed (Ruggerio et al., 1994). Grizzly bears occupy large home ranges that vary in size with habitat productivity. For example, annual home ranges of adult females in northwest Montana (123 km^2) are about one-half the size of ranges in the Yellowstone ecosystem (281 km^2) (Blanchard and Knight, 1991; Mace and Manley, 1993). This difference is likely the result of greater precipitation and related greater berry production in areas such as northwest Montana that have a greater maritime climatic influence (Canfield and

Harting, 1987). *HS* and *HP* were therefore recalculated for each grid cell as the average of a surrounding life home range-sized area that increased from north (300 km^2) to south (900 km^2) in accordance with diminishing precipitation (the latter value is roughly the size of an adult female life home range in the Yellowstone ecosystem [Blanchard and Knight, 1991]). These smoothed values of *HS* and *HP* were used for mapping purposes and in all subsequent analyses.

2.4. Calibration and empirical modeling

2.4.1. Data for calibration

Maps of grizzly bear observations in northern Idaho from Layser (1978), Zager (1983), and Kasworm and Thier (1994) were used for calibration and confirmation of our models [Fig. 3(a)]. We intersected the digitized observations with 1-km^2 grid cells and recorded for each cell whether it contained 0 or ≥ 1 observation. The core and peripheral-most sightings of grizzly bears in each of the Selkirk and Cabinet–Yaak ecosystems were also circumscribed by eye [Fig. 3(a)]. We assumed that these delineations depicted core and peripheral ranges for these populations.

2.4.2. Analysis

The proportion of cells that were outside of grizzly bear range or in core or peripheral range were summarized for increasing values of *HS*. We observed at what value of *HS* the probability that a cell was located in core range exceeded the probability that it was located in any other category. Furthermore, we noted whether this result held for increasing values of *HS* and whether it was consistent between the Selkirk and Cabinet–Yaak ecosystems.

Autologistic regression analysis (Demaris, 1992; Augustin et al., 1996) was used to calibrate *HS* to the grizzly bear observations. The probability (p) that each cell contained 0 or $\geqslant 1$ grizzly bear observations, modeled as a logit ($\ln[p/(1-p)]$), was related to annually-averaged *HS*, the number of adjoining cells with bear observations (0–8), and whether the cell was located in the Selkirk or Cabinet–Yaak ecosystems. We included grid cells that were within the radius of a standard life home range beyond the peripheral-most bear range [Fig. 3(a)]. Parameters were estimated by maximum likelihood and models were compared by the Akaike Information Criterion (*AIC*; Akaike, 1973). Counts of occupied adjoining cells were included to account for

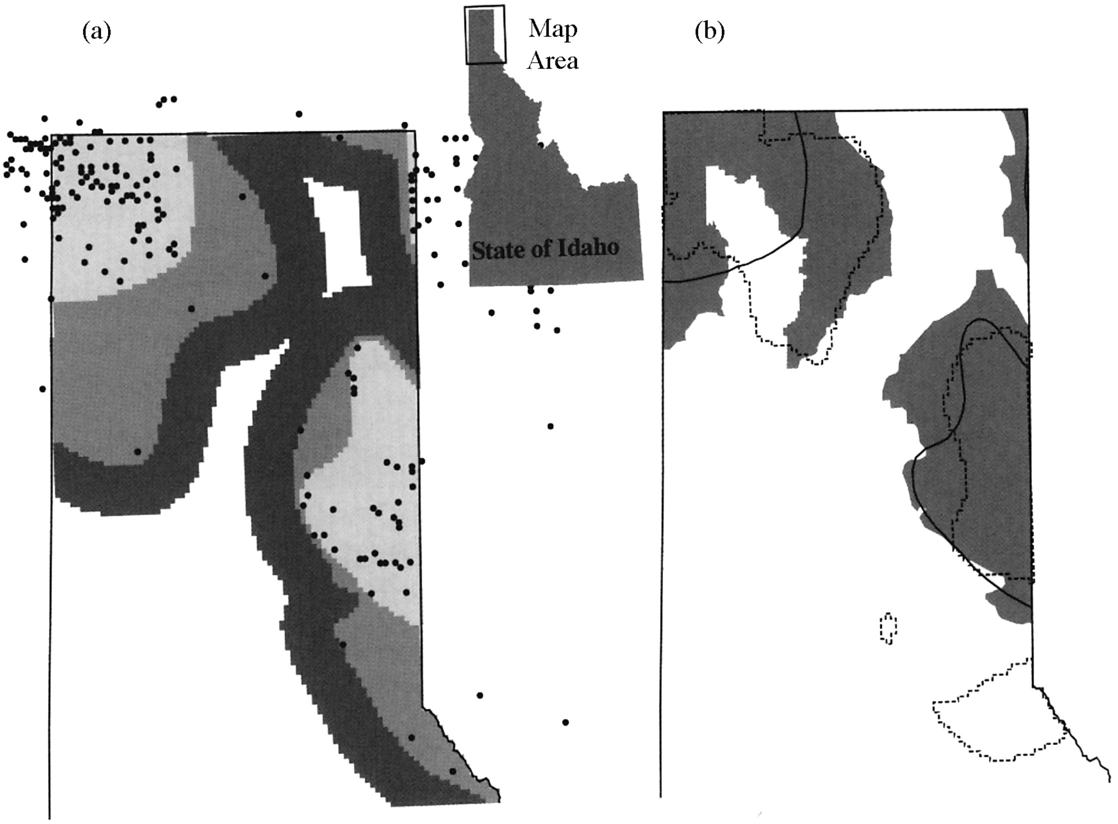


Fig. 3. Grizzly bears and grizzly bear range in northern Idaho: (a) observations of grizzly bears and their sign (●), delineations of core and peripheral grizzly bear range (light and medium gray, respectively), and the surrounding buffer (dark gray) defining the extent of the analysis area used for calibrating *HS* and developing the piece-wise empirical model. (b) Delineation of core grizzly bear habitat by eye (—), delineation of suitable habitat by $HS = 625$ (- - -), and location of officially-designated grizzly bear Recovery Areas (dark gray).

first-order spatial correlation of sightings (Augustin et al., 1996). Ecosystem identification was included as a class variable to test whether there were differences attributable to ecosystem.

Autologistic regression was also used to develop an empirical model based on separate, piece-wise treatment of the variables (*ACCESS*, *HP*, *RVD*, and *WDIST*) otherwise subsumed in *HS*. Furthermore, multiple linear regression was used to empirically relate *HS* to each of its constituent variables. The partial correlations from this relationship were compared with standardized coefficients calculated for each factor in the empirical model to identify differences in the relative weighting of variables between the conceptual and empirical approaches.

2.4.3. Data issues

Using grizzly bear observations to calibrate *HS* and develop an empirical model was potentially problematic. Differences in record keeping between ecosystems could affect results and required tracking of ecosystem identity during model development. Foremost of the problems, though, was the likelihood that observations of grizzly bears and their sign would be complexly related to measures of human activity and access (*ACCESS*, *RVD*, and *WDIST*). The probability that a bear would be active in a given cell might decline with human activity, but the probability that its presence would be detected might simultaneously increase. The relationship of grizzly bear observations to human-related factors was therefore likely to be hump-shaped and best modeled by a polynomial. Even so, while a polynomial might provide the best empirical fit, it would not best describe the biological relationship between grizzly bear activity and human-related factors. When using models to predict suitable grizzly bear habitat in Idaho we therefore did not use forms that included polynomials even though they fit the observational data better.

2.5. Conservation design

We conducted several subsidiary analyses to aid the design and management of conservation areas. These analyses were used to identify blocks that were either individually large or collectively part of a complex within range of potential reciprocal dispersal. Other blocks were identified, not likely to contribute to conservation efforts, that were both smaller than a life-range and beyond conceivable dispersal from a 'source' block. These procedures also high-lighted areas between blocks where the benefits of habitat rehabilitation (e.g. closing roads) would potentially be the greatest.

We first inspected the relationships of *HS* to the observational data and to the delineations of grizzly bear range in northern Idaho to identify thresholds or inflections in the probability that a grizzly bear would be present or that the cell would be in core range. We then used the conceptual and empirical models to delineate all areas in Idaho where annually averaged *HS* or a specified *p* exceeded the identified threshold value. This extrapolation was contingent on our assumption that areas coinciding with core range or a high probability of observing grizzly bears in northern Idaho represented 'suitable' habitat, where grizzly bears were likely to survive (*cf.* Wielgus et al., 1994). However, threshold values could be based on other assumptions about the suitability of existing habitat conditions in northern Idaho.

We superimposed a circular life home range-sized area on each block of composite 'suitable' habitat, drawn around the centroid of the defining polygon. We used this graphical-quantitative comparison to identify blocks where at least one female grizzly bear could likely meet her life-time requirements without ranging into 'unsuitable' habitat (e.g. into areas where mortality risk was presumably greater than the level needed to achieve long-term conservation goals).

We created two buffers around each block greater than one life-range in size. The first buffer was *c.* one-half as wide (20 km) and the other *c.* equal to the minimum distance that subadult males are likely to disperse from maternal ranges (from Blanchard and Knight, 1991). We assumed that any area capable of supporting a female for her life-time was also a potential source of young bears that would disperse as far as 20–40 km. Depending upon the considerations (i.e. genetic or directly demographic), other buffers could be added that reflect shorter dispersal distances such as those of subadult females.

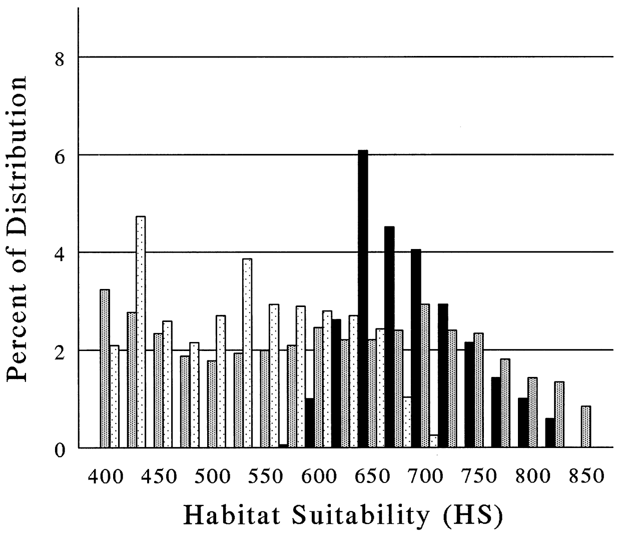
Our final analysis was used to identify areas where the potential for human-grizzly bear conflicts was likely to be highest assuming that all of Idaho's suitable grizzly bear habitat was occupied by bears. We first identified a threshold value for habitat productivity (*HP*) that corresponded with the first inflection in its logistic relationship to grizzly bear observations in northern Idaho. All areas exceeding this value were considered to be 'highly productive.' We next intersected highly productive summer–fall habitat with areas of above-average human activity ($1-HE$), restricted to areas that were in or within potential dispersal distance of suitable grizzly bear habitat. We assumed that, all else equal, the greatest potential for conflict lay in the juxtaposition of the most productive habitats with areas also heavily used by humans, and that most conflicts would occur in the fall and late summer (Mattson, 1990; Gunther, 1994; Riley et al., 1994; Blanchard and Knight, 1995).

3. Results

3.1. Calibration of the conceptual model

The probability that a given 1-km^2 cell in the Selkirk and Cabinet–Yaak ecosystems of northern Idaho would be in core grizzly bear range tended to increase with increasing values of habitat suitability (*HS*) (Fig. 4). This was most marked in the Cabinet–Yaak ecosystem. In both ecosystems, the probability of being in core range first exceeded the probability of being anywhere else when *HS* exceeded 625. The probability of being core range continued to be greater at all higher values of *HS* in the Cabinet–Yaak ecosystem, but dropped below the probability of being in peripheral range at *HS* values > 725 in the Selkirk ecosystem. This latter result can be ascribed to the inherently high probability of any cell being in peripheral range given the considerable extent of this range type in the Selkirk ecosystem [Fig. 3(a)].

(a) Selkirks



(b) Cabinet-Yaak

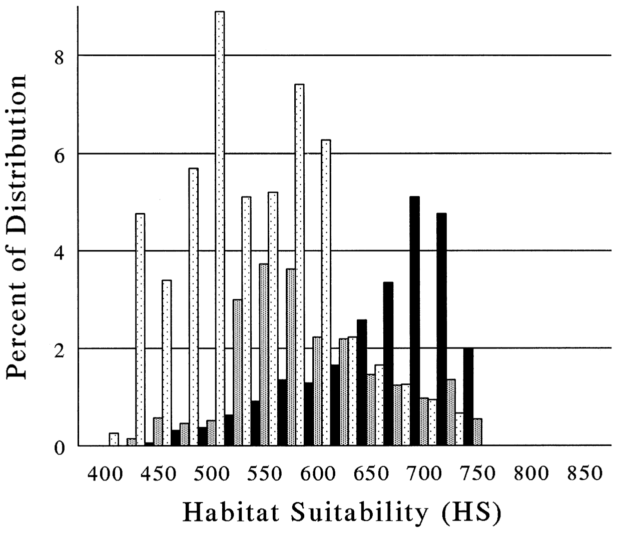


Fig. 4. Relative frequency of 1-km^2 grid cells by grizzly bear habitat suitability (*HS*) for cells contained within core range (black bars), peripheral range (bars with fine stippling), and the outside buffer (coarse stippling) for the (a) Selkirk and (b) Cabinet–Yaak grizzly bear ecosystems.

Habitat suitability, as calculated by the conceptual model (*HS*), was related to the probability that a grizzly bear or its sign had been observed in a given km^2 in northern Idaho (*PROB*) (Fig. 5). As expected, this relationship was best described by a polynomial for the Selkirk ecosystem. There was also an abrupt increase in *PROB* at values of HS > 600. In contrast, the relationship in the Cabinet–Yaak ecosystem appeared to be monotonic and continuous. However, when data were pooled, there was no effect attributable to ecosystem (Wald $\chi^2 = 0.60$, $p = 0.437$) and a model consisting of the number of adjoining cells that contained grizzly bear observations (*COUNT*) and a polynomial comprised of HS^2 and HS^3 best described the relationship of *PROB* to *HS*. The *G*-test for these three independent variables was significant (d.f. $= 3$, $G = 184.3$, $p < 0.001$), $R_L{}^2$ (Demaris, 1992) for the model = 0.16, and Somers' $D = 0.664$. Standardized estimates for the coefficients of *COUNT*, HS^2, and HS^3 were 0.224, 3.45, and −2.83, respectively.

The model by which we translated *HS* to a spatial representation of *PROB* did not include HS^3 (see Methods):

$$\text{Logit}(PROB) = -6.63 + 0.971 \times COUNT + 0.00000558 \times HS^2.$$

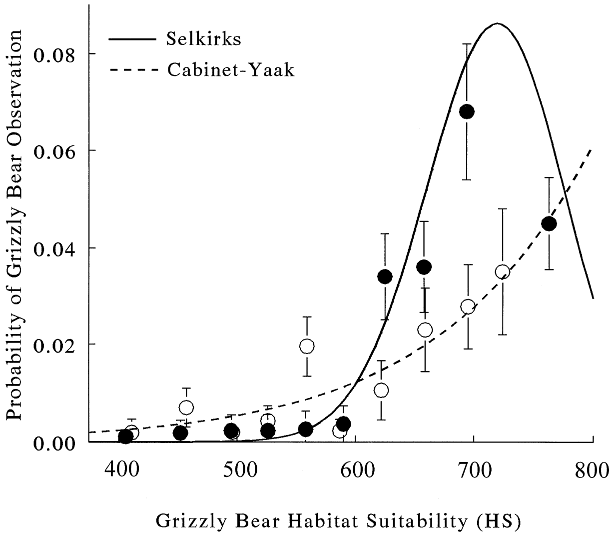


Fig. 5. Relation between the probability of observing a grizzly bear or its sign and grizzly bear habitat suitability (*HS*) for the Selkirk (—) and Cabinet–Yaak (- - -) ecosystems. Means and associated standard errors were calculated for percentiles defined by approximately equal sample sizes and intervals of *HS* and are displayed to illustrate goodness-of-fit.

The *AIC* for this model was 1024.5, in contrast to the previous polynomial model where $AIC = 1011.1$; the coefficient for HS^2 was significant (Wald $\chi^2 = 44.2$, $p < 0.001$) and $R_L{}^2 = 0.14$. We set the effect of *COUNT* to 0 when applying this model. Based on the relationship between *PROB* and *HS*, and other results presented above, we used $HS = 625$ as a threshold for delineating 'suitable' grizzly bear habitat, corresponding to $PROB = 0.012$. This delineation corresponded well with the subjectively-drawn boundary of grizzly bear range in northern Idaho based on distributions of grizzly bear observations [Fig. 3(b)].

3.2. The empirical model

We dropped *RVD* from consideration for the empirical model because of its correlations with *WDIST* (Pearson $r = -0.413$) and *HP* ($r = -0.312$). All other *r*' s were $< | 0.250 |$. Values of *WDIST* and *ACCESS* were transformed (square root and squared, respectively) to achieve a better fit to the logistic function. Habitat productivity (*HP*), inverse distance to townsites, weighted by town population size (*WDIST*), and access density (*ACCESS*) all exhibited strong individual relationships to *PROB*.

The relationship between *PROB* and *HP* [Fig. 6(a)] was positive, monotonic, and consistent between the Selkirk and Cabinet–Yaak ecosystems. Of particular interest was a marked increase in *PROB* in both ecosystems at values of *HP c.* 110. We interpreted this as a threshold effect and so used 110 to demarcate highly productive grizzly bear habitat in subsequent analyses.

The primary relationships of *PROB* to the two human-related factors, *WDIST* and *ACCESS*, were negative, but exhibited the expected secondary positive relationships only in the Selkirk ecosystem [Fig. 6(b) and 6(c)]. As discussed above (see Methods), the hump-shaped relationships evident in the Selkirk ecosystem are probably artifacts of declines in detection of grizzly bears and their sign by humans in the most remote areas, even when levels of grizzly bear activity were high. The Cabinet–Yaak ecosystem also differed from the Selkirk ecosystem in exhibiting lower values of *PROB* at low values of *WDIST* and *ACCESS*. However, given the consistency of the relationship between *PROB* and *HP* between the two ecosystems and a lack of related *a priori* hypotheses, explanation of this discrepancy can only be highly speculative.

The empirical model containing *COUNT*, *HP*, $ACCESS^2$, and $WDIST^{0.5}$ was more likely ($AIC = 843.2$) than the model used to predict *PROB* from *HS*, although $R_L{}^2$ and Somers' *D* for this model (0.17 and 0.681, respectively) were comparable to values of each for the model based on *HS*. As in the model based on *HS*, there was no effect attributable to ecosystem (Wald $\chi^2 = 0.17$, $p = 0.679$). Collectively, the four

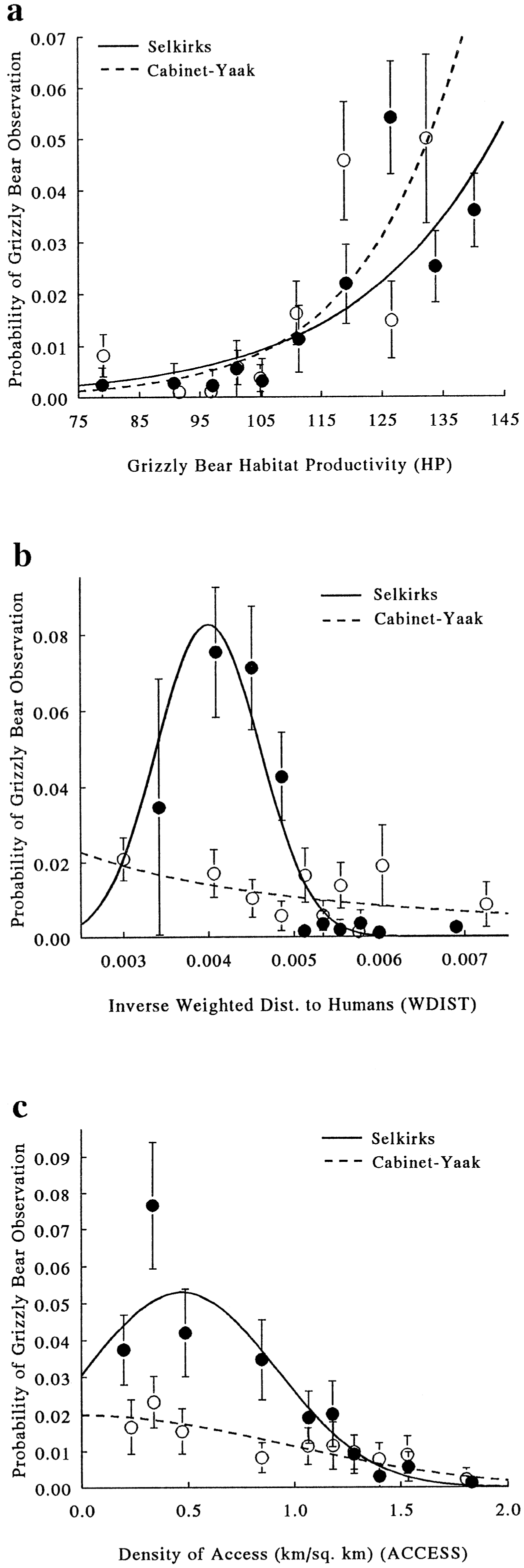


Fig. 6. Relations between the probability of observing a grizzly bear or its sign and (a) grizzly bear habitat productivity (*HP*), (b) inverse weighted distance from humans (*WDIST*), and (c) density of road and trail access (*ACCESS*), for the Selkirk (—) and Cabinet–Yaak (- - -) ecosystems. Means and associated standard errors were calculated for percentiles defined by approximately equal sample sizes and intervals of these variables and are displayed to illustrate goodness-of-fit.

independent variables were significantly related to *PROB* (d.f. = 4, $G = 166.4$, $p < 0.001$). The model used to predict *PROB* was:

$$\begin{aligned}\text{Logit}(PROB) = {} & -4.32 + 0.849 \times COUNT \\ & + 0.040 \times HP - 66.7 \times WDIST^{0.5} \\ & - 0.400 \times ACCESS^2.\end{aligned}$$

We again used $PROB = 0.012$ as a threshold for depicting 'suitable' grizzly bear habitat by this model and set the effect of *COUNT* to 0.

Standardized coefficients for *COUNT*, *HP*, $ACCESS^2$, and $WDIST^{0.5}$ in the empirical model were 0.196, 0.419, −0.228, and −0.295, respectively; i.e., *HP* had a positive effect on *PROB* while *ACCESS* and *WDIST* had comparable negative effects, together somewhat greater than the effect of *HP*. Based on the results of multiple linear regression, *HS* more strongly reflected the effects of *ACCESS* (partial $R^2 = 0.39$) than the effects of *WDIST* (partial $R^2 = 0.02$), especially compared to the empirical model. The effect of *HP* on *HS* (partial $R^2 = 0.36$) was comparable to its effect in the empirical model.

3.3. Current habitat suitability

Depending on the model, the amount of currently suitable grizzly bear habitat in Idaho varied from 18 600 km^2 (the empirical model) to 45 100 km^2 (the conceptual model) (Fig. 7). The two models were in greatest agreement in their depiction of suitable habitat in northern Idaho (2690 and 3290 km^2, for the empirical and conceptual models, respectively) and the Palisades area east-southeast of Idaho Falls (2220 and 2750 km^2). The congruence of results in northern Idaho is not surprising given that estimation and calibration of the empirical model and conceptual models, respectively, were based on data from this area.

The two models diverge most substantially in their representation of suitable habitat in central Idaho. The conceptual model estimates that there is a large 37 130 km^2 block of contiguous suitable habitat whilst the empirical model estimates there are two widely separated blocks of 5030 km^2 in the north and 9740 km^2 in the south, together amounting to only 14 770 km^2.

3.4. Conservation design

According to the conceptual model, suitable grizzly bear habitat in Idaho is characterized by the large block in central Idaho, five smaller blocks located in the Panhandle, and an additional five small blocks located peripheral to the southern half of the large central block [Fig. 8(a)]. An additional block is located in the Palisades area east of Idaho Falls (see Fig. 1 for locations). All of the blocks within currently designated Idaho recovery areas are larger than an estimated life home range. Outside of designated recovery areas, the block bounded by the Coeur d'Alene and St. Joe Rivers in northern Idaho and the block centered on the Lemhi Range in southern Idaho also meet this criterion. However, isolated blocks in the Seven Devils Mountains, immediately south of the Clarks Fork River, and at the southern terminus of the Bitterroot Range are smaller than a life home range. Even so, all but two of these

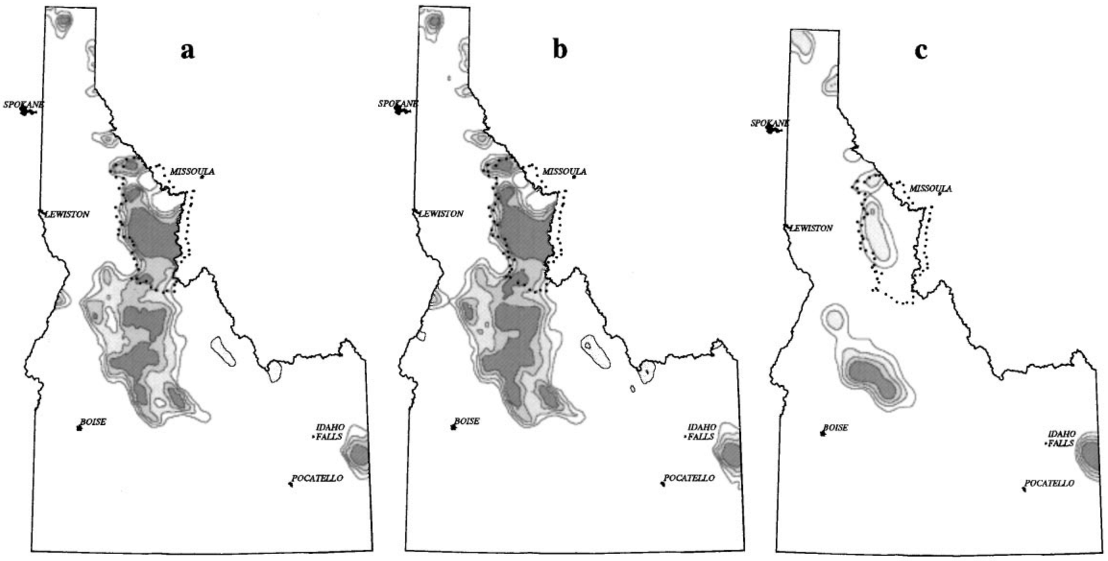


Fig. 7. Distribution of suitable grizzly bear habitat in Idaho defined by (a) $HS = 625$, (b) *HS* equivalent to $PROB = 0.012$, and (c) $PROB = 0.012$ for the empirical model. Isopleths delineate increasingly suitable grizzly bear habitat. The dotted line delineates the Evaluation Area initially chosen to consider locating reintroduced grizzly bears in central Idaho.

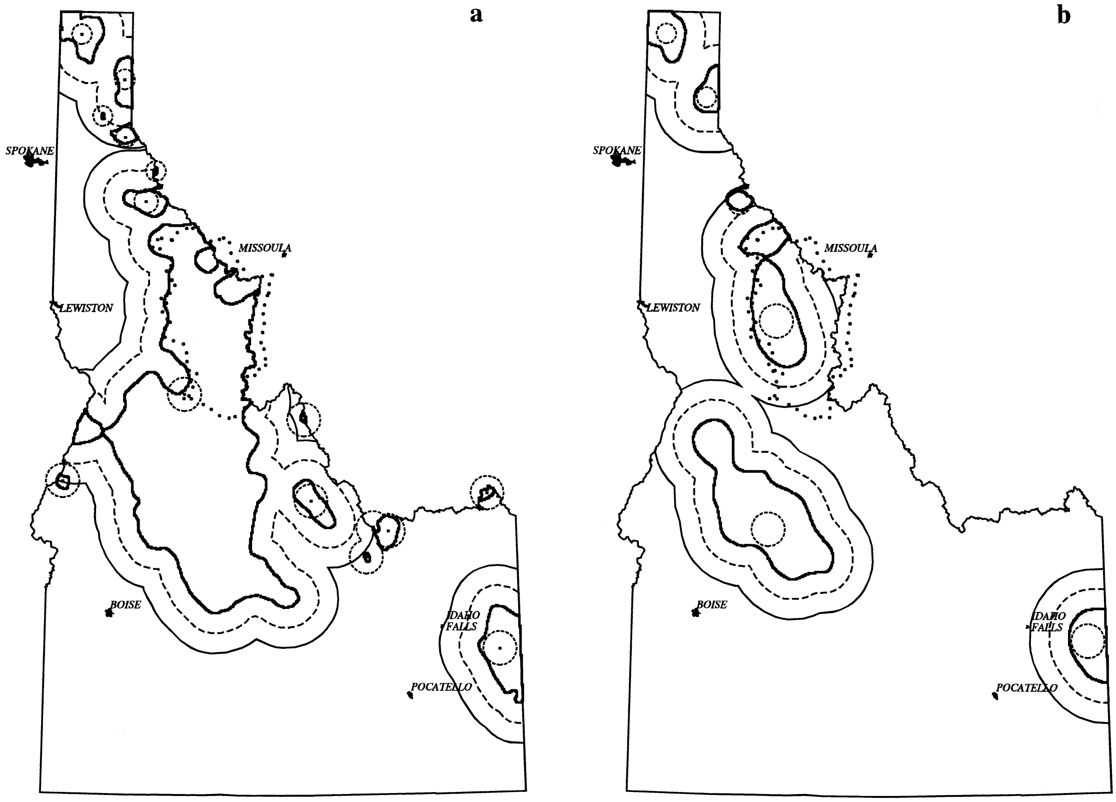


Fig. 8. Delineations of suitable grizzly bear habitat by (a) *HS* equivalent to $PROB = 0.012$ and (b) $PROB = 0.012$ for the empirical model. Each block of suitable habitat is shown with a circle approximately the size of an adult female life home range superimposed. Each block greater in size than the superimposed range is also shown buffered by lines 20- and 40-km distance from the outer boundary. These buffers delineate areas into which subadult male grizzly bears might disperse from maternal ranges under conditions where all of the identified suitable range is fully occupied by grizzly bears.

smaller blocks are within likely dispersal distances from areas that exceed the size of one life range. The block east of Idaho Falls is probably also contiguous with other 'suitable' habitat in Wyoming.

In short, according to the conceptual model, the largest contiguous block of suitable habitat in central Idaho is potentially connected to other Recovery Areas to the north by a series of 'demographic stepping stones' (*cf.* Mattson et al., 1996a), and the remaining suitable habitat in southeastern Idaho is potentially accessible to bears in the Yellowstone Recovery Area. These conclusions are, of course, contingent upon the validity of the assumptions used in the conceptual model and the related ability of dispersing grizzlies to survive intervening inhospitable habitat.

According to the empirical model, there is much less potential for conservation and recovery of grizzly bears in Idaho under existing conditions. All current grizzly bear recovery areas, as well as the block of suitable habitat in the Palisades area, still contain contiguous blocks of suitable habitat that are greater than one female life home range in size [Fig. 8(b)]. However, this model predicts that there is no block centered on the Lemhi Range with potential for grizzly bear conservation and that there is much less potential for persistence and dispersal of grizzly bears between the Cabinet–Yaak and current Selway–Bitterroot recovery areas. In addition, dispersal between the two relatively large central Idaho blocks is only marginally likely under this model.

3.5. Distribution and availability of productive habitat

We examined distributions of the most productive 40 000 km^2 of grizzly bear habitat in Idaho, by season (Fig. 9). Our results suggest that Idaho's grizzly bear habitat is naturally fragmented, most evidently during the spring [Fig. 9(a)]. Small blocks are scattered throughout the state during this season, with the two largest blocks centered on the Boise River and Palisades Reservoir (see Fig. 1 for place locations). During summer and fall, productive habitat is more contiguous [Fig. 9(b) and 9(c)]. Even so, there is a major discontinuity between productive habitat south and north of the main Salmon River and another potential discontinuity between US Interstate 90 and Lake Pend Oreille.

Delineations of suitable habitat by both models encompassed most of the habitat in Idaho where annually averaged *HP* was >110 (Fig. 10). Inclusion

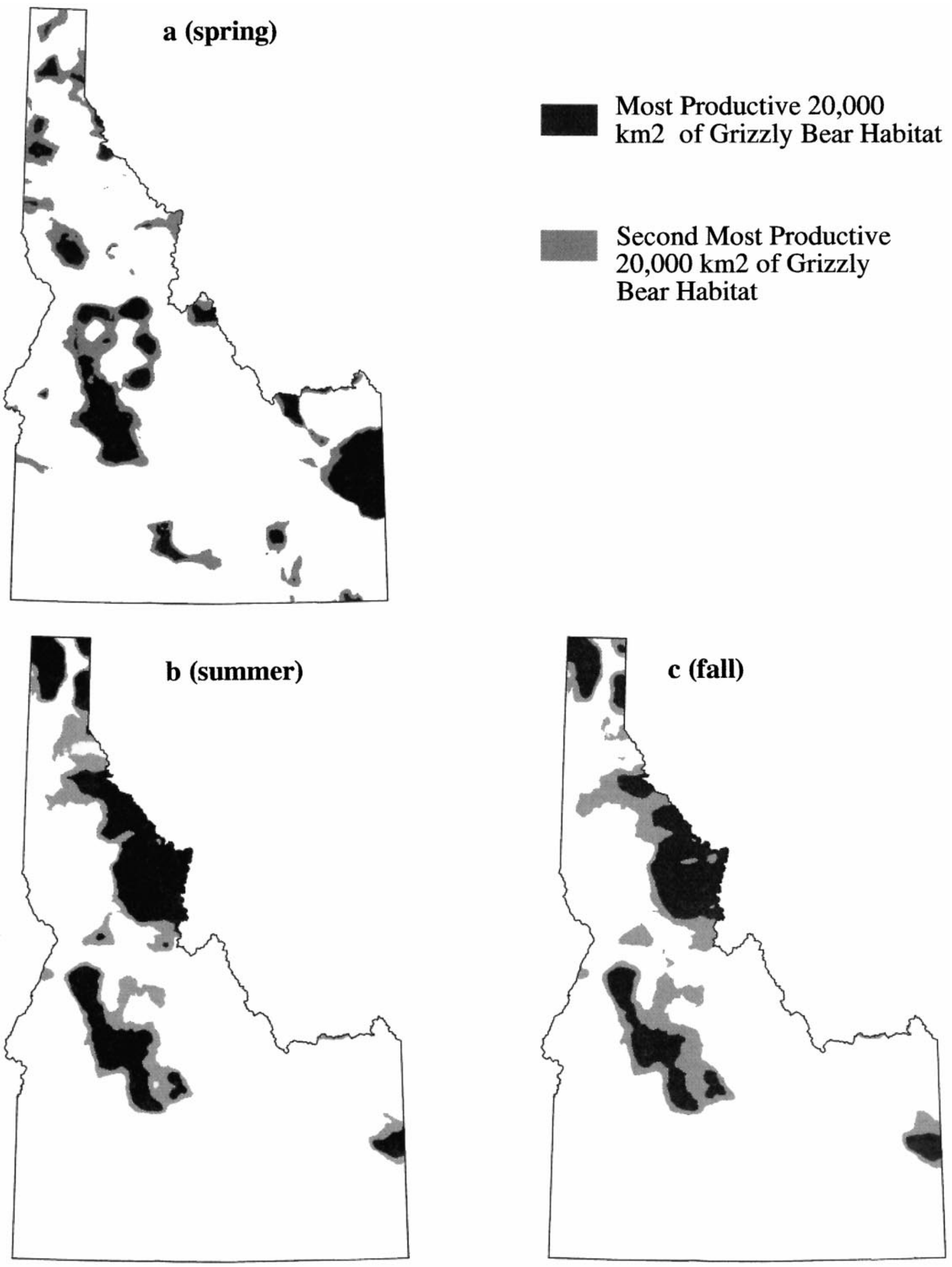


Fig. 9. Distribution of productive grizzly bear habitat in Idaho during (a) spring, (b) summer, and (c) fall, distinguished by being, successively, the most productive 20,000 and 40,000 km^2 for each season.

was somewhat greater for results of the conceptual model (82%) compared to the empirical model (74%). On the other hand, results of the empirical model were almost wholly comprised of the most productive grizzly bear habitat in Idaho (95%), compared to results of the conceptual model that were comprised of only 46% habitat where $HP > 110$. Under both models, the greatest area of highly productive habitat existed outside of suitable habitat in northern Idaho, especially in the Selkirk ecosystem. These areas of disjunction are best interpreted as highly productive grizzly bear habitat that is currently precluded from use by bears because of high levels of human access or numbers of resident humans.

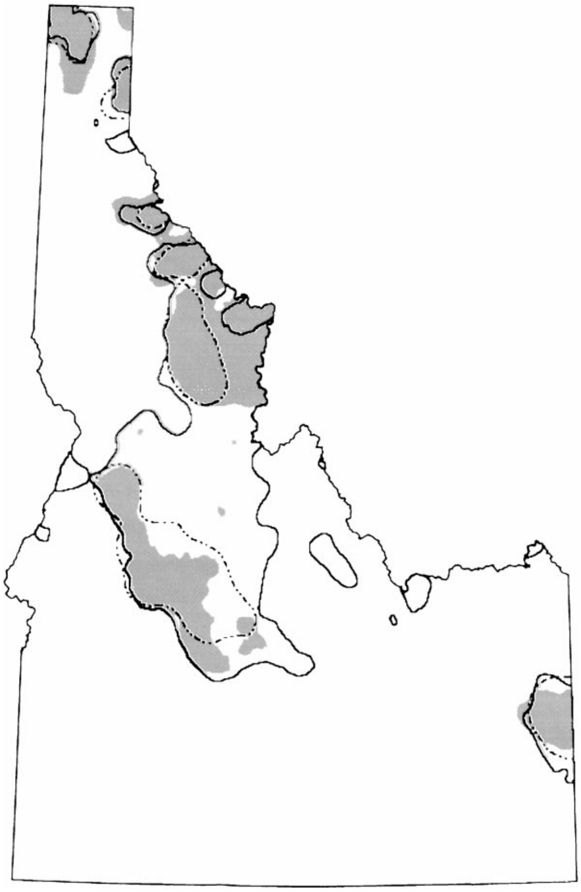


Fig. 10. The most productive grizzly bear habitat in Idaho (gray), averaged for summer and fall, superimposed with delineations of suitable grizzly bear habitat by *HS* (—) and by the empirical model (- - -).

3.6. Sites of potential conflicts

During summer and fall the most likely sites of potential conflict between humans and grizzly bears are concentrated primarily in the Lochsa and North Fork of the Clearwater drainages and around Priest Lake and the southern terminus of the Selkirk Mountains (Fig. 11; see Fig. 1 for place locations). Other potential conflict sites are clustered between Featherville and McCall and in the Teton Basin and Swan Valley. Sites of potential conflict in central Idaho are concentrated to the north and west, rather than to the east, where opposition to reintroduction of grizzly bears is currently strongest.

4. Discussion

4.1. The benefits of an explicit approach

We know that humans have major impacts on the survival and behavior of grizzly bears (Mattson et al., 1996a). However, in central Idaho there are no data obtained from grizzly bears that scientists can use to specify the details of human–grizzly bear relations. There are also no data describing the details of human behavior and distributions, nor are there the means for obtaining these data in the near future. Does this mean that managers and scientists are only able to employ assessments of vegetation composition or general statements of broad principles in their plans for management of grizzly bears in places like central Idaho?

We demonstrate an approach that systematically translates qualitative information and sparse quantitative data into spatial representations of grizzly bear habitat based on a conceptual model. Other scientists could have specified a different model based on the same qualitative information; and this different model could have exhibited a sufficient degree of correspondence with the empirical evidence. However, our situation is different only in degree rather than kind from that confronting different scientists analyzing the same set of empirical data (Burnham and Anderson, 1992).

All management decisions employ certain assumptions about the state of the world or the managed resource, but rarely do decision-making processes require an explicit divulgence of these critical presuppositions (Young, 1982). Our approach benefits by being explicit, thereby revealing assumptions for examination and allowing for comparison with other models based on different premises (Botkin, 1990; Shrader-Frechette and McCoy, 1993). We do not claim definitive results. However, we argue that this type of an approach improves the basis for management decisions under conditions where empirical data are rare but qualitative understanding is well advanced.

4.2. Suitability of Idaho grizzly bear habitat

4.2.1. Central Idaho

Assuming that habitat within the Selkirk and Cabinet–Yaak Recovery Areas is ‘suitable,’ there is a large area capable of supporting grizzly bears in Idaho. Most of this suitable habitat is concentrated in the roadless central mountains. This is not unexpected, given that scientists who study grizzly bears have long emphasized the importance of roadless areas to grizzly bear survival (Craighead, 1980; Peek et al., 1987; Mattson, 1990; Craighead et al., 1995). Even so, the different models predict more than a two-fold difference, ranging from 14 800 to 37 100 km^2, in the amount of suitable grizzly bear habitat in central Idaho.

This discrepancy probably stems partly from the problems of extrapolation, especially for the empirical model, and partly from differences in the extent to which the two models weight human landscape features (*ACCESS* and *WDIST*). There are reasons to have confidence in both models. Both have some degree of empirical corroboration in their statistical relationships to the distribution of grizzly bear sightings in northern Idaho. However, we remain uncertain about how grizzly

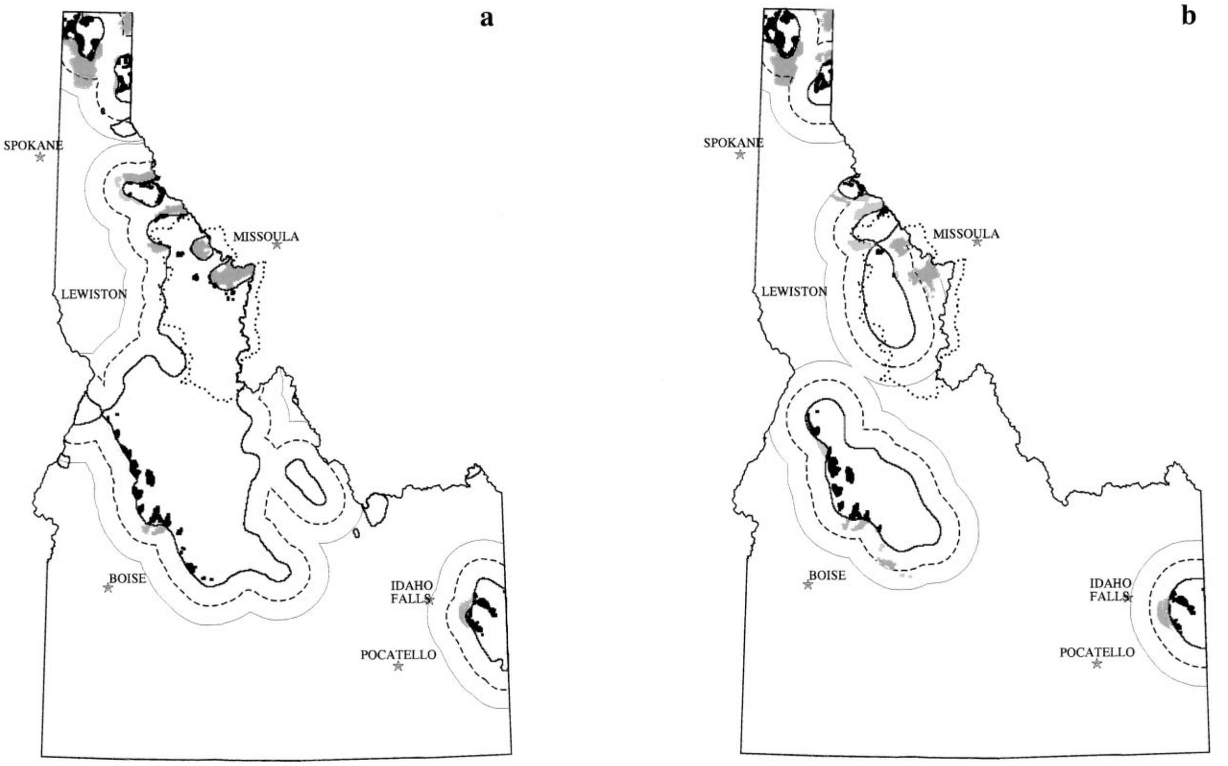


Fig. 11. Areas of greatest (black) and next greatest (gray) potential for conflict between humans and grizzly bears during summer and fall based on delineations of suitable habitat by (a) *HS* and (b) the empirical model, assuming that all suitable habitat is fully occupied by grizzly bears. These areas of potential conflict are shown superimposed on delineations of suitable habitat and buffers defining the area where subadult male grizzly bears might disperse. The dotted line delineates the Evaluation Area initially chosen to consider locating reintroduced grizzly bears in central Idaho. Conflict areas are enlarged to improve illustration.

bear sightings are related to the distribution and numbers of bears (Mattson, 1997b). Empirical relationships may also change with changes in the larger biophysical context and therefore may not be extrapolated with confidence. These factors recommend cautious use of the empirical model. On the other hand, the conceptual model requires further confirmation. Given these considerations, the two models probably depict the bounds of suitable habitat in central Idaho and together suggest that grizzly bears have the greatest chances of surviving and reproducing in western portions of the current Reintroduction Evaluation Area and in the area stretching from the Sawtooth Mountain Range to the South Fork of the Salmon River.

This robust result holds only if bears in central Idaho are accorded protection from direct mortality comparable to that provided bears in other recovery areas. Our model does not account for variation in lethality of human–bear contact that could result from variation in legal protection (Mattson et al., 1996a,b). We emphasize frequency of human–bear contact and essentially hold human behavior constant. Any greater mortality risk from encounters with humans than currently exists in northern Idaho (our base-line) would lead to a more pessimistic prognosis concerning the amount of 'suitable' (e.g. allowing for population persistence) habitat.

Grizzly bear habitat management has traditionally emphasized road access. However, the number of human residents in a given area (*WDIST*) explained substantial variation in sightings of grizzly bears in northern Idaho with an effect in the empirical model equal to that of road density. This highlights the potential importance of managing not just road and trail access, but also numbers of people in or near carnivore conservation areas; or, if management of human numbers is not feasible, management of human access may be required to compensate for increases in human populations (McLellan, 1990; Mattson et al., 1996b).

Given the results of our two models, it is intriguing that grizzly bears were extirpated in central Idaho but survived elsewhere in the state. Much of the answer to this paradox lies in understanding conditions at the time most grizzly bears were extirpated in the contiguous US between 1850 and 1920. By 1920, grizzly bear range had been reduced to three small remnants in the central mountains of Idaho (Merriam, 1922) [Fig. 2(b)]. By contrast, grizzly bears in the Panhandle and far southeastern Idaho were part of populations that occupied contiguous ranges *c.* 30 000 km^2 in size. In fact, grizzly bears only survived between 1920 and 1970 where they had been part of these two largest ranges (Mattson et al., 1995). The key question is therefore, why had grizzly bears in central Idaho been reduced to such small fragmented populations as early as 1920?

The answer to this question can only be speculative, but there is reason to be believe it involves salmon *Oncorhynchus* spp. Anecdotal (Wright, 1909) and recent scientific (Hilderbrand et al., 1996) evidence suggests that grizzly bears in central Idaho made heavy use of spawning salmon. Even in Yellowstone Park, where bears have access only to the smaller cutthroat trout *O. clarki*, grizzly bears from a large part of this ecosystem concentrate to use spawners (Mattson and Reinhart, 1995). These bears experience disproportional mortality from humans who are also concentrated along lake shores and near spawning streams. We hypothesize that predictable heavy use of spawning salmon in riparian areas rendered grizzly bears in central Idaho highly vulnerable to human-caused mortality. Whether by intent or by accident, humans were probably better able to find or more likely to encounter grizzly bears under these conditions. For example, Wright (1909) describes personally killing more than 25 grizzly bears in areas near spawning streams in *c*. 12 years. If our hypothesis is correct, this historical extirpation is anomalous relative to current conditions given that salmon are currently absent from most of central Idaho. However, if salmon recover to near historic numbers, spawning reaches may become a critical consideration in modeling and managing grizzly bear habitat (Mattson and Reinhart, 1995).

4.2.2. *Yellowstone Recovery Area*

Our results corroborate concerns about the potentially precarious status of grizzly bears in the Idaho portion of the Yellowstone Recovery Area. Except for a small area in the Centennial Range, none of the Targhee National Forest in the Yellowstone Recovery Area was contained within the most liberal delineation of suitable habitat. This is consistent with recent poor success trapping grizzly bears in this area (one bear in 5 years of more-or-less intensive trapping; M. Haroldson, Interagency Grizzly Bear Study Team, pers. comm.), few grizzly bear sightings (Blanchard et al., 1992), high levels of human access, and the prevalence of low productivity habitat.

4.2.3. *Corridors and habitat rehabilitation*

Although our analysis does not encompass the entire Northern Rockies, it does provide some preliminary insight into prospects for either the existence or creation of corridors in Idaho between designated grizzly bear recovery areas. In particular, the existence of good spring habitat in the southernmost Bitterroot Range notwithstanding, there is no reason to expect that currently suitable conditions connect central Idaho grizzly bear habitat with the Yellowstone Recovery Area. This is consistent with previous observations regarding the isolation of Yellowstone's grizzly bear population, including the absence of any observed emigration or immigration during >30 years of intensive grizzly bear research (Mattson and Craighead, 1994; Craighead et al., 1995). By contrast, there seem to be greater prospects for continuity north of central Idaho, either under existing conditions or with habitat rehabilitation.

Two inclusions of low suitability habitat intrude into otherwise highly suitable conditions in the northeastern part of the current central Idaho Evaluation Area [Fig. 10(a)]. These areas of low suitability follow upper reaches of the Lochsa and North Fork of the Clearwater rivers, represent areas where there is high potential for human–bear conflict because productive bear habitat is juxtaposed with high levels of human access (Fig. 11), and adjoin otherwise highly suitable conditions. If habitat rehabilitation were a policy option, these two areas are obvious candidates for such an effort. One of these watersheds has, in fact, been independently prioritized for rehabilitation (Bader and Bechtold, 1996).

4.3. *Sites of potential conflicts*

Our results regarding the location of potential conflict sites need to be understood in context. We are not suggesting, given the nearby presence of a grizzly bear population, that conflicts at these locations are inevitable. Rather, a combination of circumstances (i.e. highly productive habitat, high levels of human activity, and nearness to otherwise highly suitable grizzly bear habitat) makes conflict more likely. Grizzly bear management elsewhere has demonstrated that effective control of foods and odors that would otherwise attract grizzly bears to humans can substantially reduce the level of realized conflict under conditions that we have considered (Gunther, 1994). Also, our assessment does not include conflicts that may arise from the presence of big game hunters inside occupied grizzly bear habitat. These conflicts are less predictable, or occur at a scale that we cannot address.

Acknowledgements

We thank the Idaho GAP Project for providing us with digital vegetation maps for Idaho; the US Geological Survey for digital elevation and road and trail maps; the US Census Bureau for data on human population size and location; and the Idaho Fish and Game Department for information on elk numbers. We thank Drs. James Peek, Torbjörn Ebenhard and Stephen Herrero for their helpful reviews.

Appendix

Scores for each vegetation type j and each season k (spring, summer, and fall) $= \sum Ab_{ij} \times Wgt_i$ where Ab_{ij} = the abundance of species i in type j, and Wgt_i = the seasonal weight given to each species i, applicable to all types j. Species abundance was taken from Caicco (1989), where if a species was present and 'diagnostic' it was given a value of 2, and if present and 'other' it was given a value of 1. Some commonly used bear foods (*e.g. Trifolium* spp., *Lathyrus ochroleuca*, *Vicia americana*, and *Erythronium grandiflorum*) were not included in these lists, although all berry-producing species were accounted for. Other features of site and stand that might influence berry production were not considered. Weights for graminoids were modified for application to the species tables in Caicco (1989). Bear food habits studies typically combine all graminoids, while Caicco (1989) lists graminoid species separately. Therefore, we apportioned the aggregate graminoid weight to each species, proportional to the number of graminoid species listed in Caicco (1989) that were available and known to be used by bears during a given season. Vegetation types were based on pre-existing US Forest Service schemes for regional mapping. We used digital maps of these types created for the GAP project—a program designed to identify gaps in the protection of biodiversity using vegetation-based models of species' distributions (Scott et al., 1993).

The empirical model relating recreation visitor days (RVD) to local human population size ($LOCAL$) and the extent of roaded area (km^2) in a given National Forest ($ROAD$) was:

$$RVD' = 4.82 + 0.170 \times LOCAL' + 0.642 \times ROAD' - 0.588 \quad (1A)$$

where RVD' = the natural log of $RVD/1000$, $LOCAL'$ = the natural log of local population size, $ROAD'$ = the square root of total roaded area (km^2), and '−0.588' was the 'non-park' effect. Statistics for the complete model were: d.f. = 4/19, $F = 1325$, $p < 0.001$, $R^2 = 0.44$. Total roaded area was calculated as the difference between total National Forest area and total area of the forest in wilderness and RARE II units. Controlling for the effects of National Parks (we attributed a 'park effect' to all National Forests bordering Glacier and Yellowstone National Parks by using 'near park' or 'not near park' as a covariate), and setting roaded area effects at the regional average, this model reduced to:

$$RVD' = 5.04 + 0.170 \times LOCAL' \quad (2A)$$

We back-transformed the result and scaled the value ≤1 for use in later calculations:

$$RVD = e^{(5.04 + 0.170 \times LOCAL')}/1276 \quad (3A)$$

where '1276' was the maximum value observed for any grid cell in Idaho, and $LOCAL$ was calculated on the basis of all townsites within 80 km. We used a regionally-averaged roaded area because this effect was of extraneous interest to our analysis; it merely pro-rated visitor days to unit area, assuming that most human activity was concentrated on roads. This model characterized a relationship between human activity and local population size that had two critical features: (1) an intercept >0 (i.e. there was substantial human activity predicted, despite very small local populations); and (2) human activity that increased at a lesser rate than increases in local population.

Other calculations used in our method were:

$$H = RVD \times WDIST \quad (4A)$$

$$H' = \ln(H \times 1000) \quad (5A)$$

The base relationship of HE to $ACCESS$ was described for an area where H' approximately equaled 0. This rare to non-existent situation was described so that HE would approach zero at the highest access densities calculated for Idaho (3.2 km/km^2):

$$HE = 1 - M \times (0.56 \times ACCESS^{0.5}) \quad (6A)$$

M was the multiplier derived from H', that steepened the slope of this relationship as H' increased:

$$M = 1 + 15 \times H'^6 \quad (7A)$$

This relationship satisfied the condition that human impacts would be substantial, but little varied, at low values of *H'*, and escalate rapidly only at high levels of potential human activity. The parameter for *H'* was derived so that HE would fit conditions (i.e.; rate of grizzly bear population increase) observed in the Yellowstone ecosystem (Pease and Mattson, 1998), and the drainages of the South Forks and North Forks (Hovey and McLellan, 1996) of the Flathead River in Montana and adjacent British Columbia, Canada.

$$HS = HP - (1000 - HE) \quad (8A)$$

References

Akaike, H., 1973. Information theory and an extension of the maximum principle. In: Pertran, B.N., Csaki, F. (Eds.), Second International Symposium on Information Theory. Akademiai Kiadi, Budapest, Hungary, pp. 267–281.

Augustin, N.H., Mugglestone, M.A., Buckland, S.T., 1996. An autologistic model for the spatial distribution of wildlife. Journal of Applied Ecology 33, 339–347.

Bader, M. and Bechtold, T., 1996. The conservation biology alternative for grizzly bear population restoration in the Greater Salmon–Selway region of central Idaho and western Montana. Alliance for the Wild Rockies Special Report no. 8, Missoula, MT.

Berger, J., 1980. Statistical Decision Theory: Foundations, Concepts, and Methods. Springer–Verlag, New York.

Blanchard, B.M., Knight, R.R., 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58, 41–67.

Blanchard, B.M., Knight, R.R., 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal of Wildlife Management 59, 560–565.

Blanchard, B.M., Knight, R.R., Mattson, D.J., 1992. Distribution of Yellowstone grizzly bears during the 1980s. American Midland Naturalist 128, 332–338.

Botkin, D.B., 1990. Discordant Harmonies: A New Ecology for the Twenty-First Century. Oxford University Press, Oxford.

Burnham, K., Anderson, D.R., 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. In: McCullough, D.R., Barrett, R.H. (Eds.), Wildlife 2001: Populations. Elsevier, Amsterdam, pp. 16–20.

Caicco, S.L., 1989. Manual Accompanying the Map of Existing Vegetation of Idaho. College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, ID.

Canfield, J., Harting, A.L., 1987. Movements and behavior. In: LeFranc, Jr., M.N., Moss, M.B., Patnode, K.A., Sugg, III, W.C. (Eds.), Grizzly Bear Compendium. Interagency Grizzly Bear Committee, Denver, CO, pp. 27–46.

Clevenger, A.P., Purroy, F.J., Campos, M.A., 1997. Habitat assessment of a relic brown bear *Ursus arctos* population in northern Spain. Biological Conservation 80, 17–22.

Craighead, J.J., 1980. A proposed delineation of critical grizzly bear habitat in the Yellowstone region. International Conference on Bear Research and Management Monograph 1, 1–20.

Craighead, J.J., Sumner, J.S., Mitchell, J.A., 1995. The Grizzly Bears of Yellowstone: Their Ecology in the Yellowstone Ecosystem, 1959–1992. Island Press, Washington, DC.

Davis, D., Butterfield, B., 1991. The Bitterroot Grizzly Bear Recovery Area: A Report to the Bitterroot Technical Review Team. Clearwater National Forest, Orofino, ID and Mountain West Ecology, Moscow, ID.

Demaris, A., 1992. Logit Modeling: Practical Applications. SAGE, Newbury Park, CA.

Grizzly Bear Cumulative Effects Analysis Working Group, 1990. CEM—A Model for Assessing Effects on Grizzly Bears. US Forest Servive Grizzly Bear Habitat Coordinator's Office, Missoula, MT.

Gunther, K., 1994. Bear management in Yellowstone National Park, 1960–93. International Conference on Bear Research and Management Monograph 9, 549–560.

Hilderbrand, G.V., Farley, S.D., Robbins, C.T., Hanley, T.A., Titus, K., Servheen, C., 1996. Use of stable isotopes to determine diets of living and extinct bears. Canadian Journal of Zoology 74, 2080–2088.

Hovey, F.W., McLellan, B.N., 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Canadian Journal of Zoology 74, 1409–1416.

Kasworm, W.F., Thier, T.J., 1994. Cabinet–Yaak Ecosystem Grizzly Bear and Black Bear Research 1993 Progress Report. US Fish and Wildlife Service, Grizzly Bear Recovery Coordinator's Office, Missoula, MT.

Layser, E., 1978. Grizzly bears in the southern Selkirk Mountains. Northwest Science 52, 77–91.

Ludwig, D., Hilborn, R., Walters, C., 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science 260, 17–18.

Mace, R.D., Manley, T.L., 1993. South Fork Flathead River Grizzly Bear Project: Progress Report for 1992. Montana Department of Fish, Wildlife, and Parks, Helena.

Mace, R.D., Waller, J.S., Manley, T.L., Lyon, L.J., Zuring, H., 1997. Relationships among grizzly bears, roads, and habitat in the Swan Mountains. Montana. Journal of Applied Ecology 33, 1395–1404.

Mattson, D.J., 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 8, 33–56.

Mattson, D.J., 1993. Background and Proposed Standards for Managing Grizzly Bear Habitat Security in the Yellowstone Ecosystem. Cooperative Park Studies Unit, College of Forestry, Wildlife, and Range Sciences, University of Idaho, Moscow, ID.

Mattson, D.J., 1997a. Use of ungulates by Yellowstone grizzly bears *Ursus arctos*. Biological Conservation 81, 161–177.

Mattson, D.J., 1997b. Sustainable grizzly bear mortality calculated from counts of females with cubs-of-the-year: an evaluation. Biological Conservation 81, 103–111.

Mattson, D.J., Craighead, J.J., 1994. The Yellowstone grizzly bear recovery program: uncertain information, uncertain policy. In: Clark, T.W., Reading, R.P., Clarke, A.L. (Eds.), Endangered Species Recovery: Finding the Lessons, Improving the Process. Island Press, Washington, DC, pp. 101–130.

Mattson, D.J., Reinhart, D.P., 1995. Influences of cutthroat trout (*Oncorhynchus clarki*) on behaviour and reproduction of Yellowstone grizzly bears (*Ursus arctos*), 1975–1989. Canadian Journal of Zoology 73, 2072–2079.

Mattson, D.J., Wright, R.G., Kendall, K.C., Martinka, C.J., 1995. Grizzly bears. In: LaRoe, E.T., Farris, G.S., Puckett, C.E., Doran, P.D., Mac, M.J. (Eds.), Our Living Resources: A Report To The Nation on the Distribution, Abundance, and Health of US Plants, Animals, and Ecosystems, US National Biological Service, Washington, DC, pp. 103–105.

Mattson, D.J., Herrero, S., Wright, R.G., Pease, C.M., 1996a. Designing and managing protected areas for grizzly bears: how much is enough? In: Wright, R.G. (Ed.), National Parks and Protected Areas: Their Role in Environmental Protection. Blackwell Science, Cambridge, MA, pp. 133–164.

Mattson, D.J., Herrero, S., Wright, R.G., Pease, C.M., 1996b. Science and management of Rocky Mountain grizzly bears. Conservation Biology 10, 1013–1025.

McLaughlin, W.J., Harris, C.C., Tynon, J.F., Timko, S.E., 1989. The 1987 Leisure Travel and Recreation Study: Analysis for Region II—Final Report. Department of Wildland Recreation Management, University of Idaho, Moscow, ID.

McLellan, B.N., 1990. Relationships between human industrial activity and grizzly bears. Int. Conf. Bear Res. and Manage. 8, 57–64.

Merriam, C.H., 1922. Distribution of grizzly bears in US. Outdoor Life 54, 405–406.

Pease, C.M., Mattson, D.J., 1998. Demography of the Yellowstone grizzly bears. Ecology, in press.

Peek, J.M., Pelton, M.R., Picton, H.D., Schoen, J.W., Zager, P., 1987. Grizzly bear conservation and management: a review. Wildlife Society Bulletin 15, 160–169.

Philip, G.M., Watson, D.F., 1982. A precise method for determining contoured surfaces. Australian Petroleum Exploration Assoc. J. 22, 205–212.

Riley, S.J., Aune, K., Mace, R.D., Madel, M.J., 1994. Translocation of nuisance grizzly bears in northwestern Montana. International Conference on Bear Research and Management 9, 567–573.

Rosenzweig, M.L., 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge, UK.

Ruggerio, L.F., Hayward, G.D., Squires, J.R., 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. Conservation Biology 8, 364–372.

Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, D'Erchia, S.F., Edwards, T.C., Jr, Ulliman, J., Wright, R.G., 1993. GAP analysis: a geographic approach to protection of biological diversity. Wildlife Monograph 123, 1–41.

Shrader-Frechette, K.S., McCoy, E.D., 1993. Method in ecology: strategies for conservation. Cambridge University Press, Cambridge, UK.

Smith, S., 1983. Recreation Geography. Longman, New York.

US Fish and Wildlife Service, 1993. Grizzly Bear Recovery Plan. US Fish and Wildlife Service, Missoula, MT.

Wallwork, S.S., Lenihan, M.L., Polzin, P.E., 1980. Montana Outdoor Recreation Survey. Bureau of Business and Economic Research, School of Business Administration, University of Montana, Missoula, MT.

Walters, C., 1986. Adaptive management of renewable resources. Macmillan, New York.

Watson, D.F., Philip, G.M., 1985. A refinement of inverse distance weighted interpolation. Geo-Processing 2, 315–327.

Wielgus, R.B., Bunnell, F.L., Wakkinen, W.L., Zager, P.E., 1994. Population dynamics of Selkirk mountain grizzly bears. Journal of Wildlife Management 58, 266–272.

Williams, B.K., 1997. Logic and science in wildlife biology. Journal of Wildlife Management 61, 1007–1015.

Wright, W.H., 1909. The Grizzly Bear: The Narrative of a Hunter-naturalist. Charles Scribner's Sons, New York.

Young, O.R., 1982. Resource Regimes: Natural Resources and Social Institutions. University of California Press, Berkeley, CA.

Zager, P., 1983. Grizzly bears in Idaho's Selkirk Mountains: update. Northwest Science 57, 299–309.