The extent and location of habitat biophysically suitable for grizzly bears in the Yellowstone region

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Abstract: We appraised the extent of potential core and source areas in a 162,300-km^2 study area centered on the current range of Yellowstone's grizzly bears (about 37,600 km^2). We modeled habitat productivity based on habitat types defined by differences in grizzly bear foraging behavior and associated coefficients of productivity. We coupled habitat productivity with a previously defined model of remoteness from humans to model habitat suitability. We defined core areas as patches >900 km^2 where habitat suitability values were >1 SD above the study area mean. We also modeled the distribution of grizzly bear deaths in the Yellowstone region, 1989–99, as a function of explanatory landscape features and used this model to identify potential source areas. This model suggested that grizzly bears died primarily as a function of (1) frequency of contact with humans and (2) whether humans were encountered in lethal settings such as public-land grazing allotments or areas outside National Parks. We identified 27,032 km^2 of core areas and 47,807 km^2 of potential source habitat. Core areas were 98% contained by source areas. The Wind River (3,358 km^2), Palisades (2,036 km^2), and Centennial (1,691 km^2) core areas occurred largely outside current grizzly bear range. The existence of potential source habitat along and north of the Centennial Mountains suggests that the prospects for eventual connectivity between the Yellowstone grizzly bear population and potential grizzly bear range in central Idaho are better than previously thought.

Key words: core areas, grizzly bears, habitat productivity, habitat suitability, lethality, remoteness, source areas, *Ursus arctos horribilis*, Yellowstone

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The trend, distribution, and size of Yellowstone's grizzly bear (*Ursus arctos horribilis*) population have been studied intensively during the last 25 years. Although there is disagreement about the magnitude and causes of trends, there is consensus that the population declined between the early 1970s and mid-1980s and generally increased thereafter until the present (Knight and Eberhardt 1985, 1987; Eberhardt et al. 1994; Pease and Mattson 1999; Boyce et al. 2001). During this same period the distribution of grizzly bear observations expanded outward, primarily to the south and east, from a core area centered on Yellowstone National Park (Basile 1982; Blanchard et al. 1992; Schwartz et al. 2002). The most recent published estimate of population size, based on data collected during 1989–94, gave 90% confidence limits of 280 to 610 bears (Eberhardt and Knight 1996). This contrasts with an estimated population size of about 230 bears in the 1960s (Craighead et al. 1974, National Research Council 1974). By all indications, the Yellowstone grizzly bear population has increased in size and occupied a larger area since the mid-1980s, primarily in the Absaroka Mountains of Wyoming.

This begs the question of sufficiency. Whatever the size, trend, and range of the current population, is it enough? The U.S. Fish and Wildlife Service (USFWS) Grizzly Bear Recovery Plan (USFWS 1993) delineates the official Recovery Area for Yellowstone's grizzly bear population and states criteria for determining recovery. Yet there are those who have argued that the Recovery Area and associated recovery criteria are impractical or insufficient to achieve long-term demographic and genetic viability (Reid and Gehman 1986, Mattson and Reid 1991, Shaffer 1992, Craighead et al. 1995, Craighead 1998, Willcox 1999, Bader 2000*a*). Recovery standards are partly expressions of

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values (Mattson and Craighead 1994, Mattson et al. 1996*a*), and the documents espousing different recovery criteria are largely value statements. Even so, there is little doubt that more bears spread over larger areas have greater odds of surviving. There is also little doubt that connected, rather than isolated, populations of grizzly bears in the northern U.S. Rocky Mountains have greater odds of surviving habitat change and of retaining evolutionary potential (Mattson and Reid 1991, Craighead and Vyse 1996, Mattson et al. 1996*a*, Craighead et al. 1999). Assuming that the goal of grizzly bear conservation is robust populations, there is an imperative to identify unoccupied areas adjacent to or near occupied range that, under existing conditions, could serve as demographic sources. At a minimum, this identification allows for the conscious preservation of potential source characteristics or, if desired, for the conscious, rather than unintentional, choice to degrade this potential.

By definition, source grizzly bear habitat occurs where birth rates exceed death rates. Because humans cause virtually all the deaths of weaned grizzly bears in the Yellowstone region (Mattson 1998, Boyce et al. 2001), remoteness from humans is an important feature of source grizzly bear habitat (Craighead 1980, Knight 1980, Peek et al. 1987). In most appraisals remoteness has been equated with designated or *de facto* wilderness (e.g., Bader 2000*b*). However, Merrill et al. (1999) modeled remoteness in terms of densities of roads and trails, local and regional human population sizes, and distance from townsites. In concept, grizzly bear survival is positively related to remoteness from humans (Merrill et al. 1999, Pease and Mattson 1999). By contrast, population-level reproductive output is, in concept, positively related to habitat productivity (Merrill et al. 1999). Productivity has been a difficult feature to model and typically has been represented by satellite imagery (e.g., greenness, wetness, brightness; Mace et al. 1999, Carroll et al. 2001).

Human attitudes and behaviors also determine the numbers of grizzly bears that die. Together with frequency of contact, the lethality of humans to grizzly bears largely determines grizzly bear death rates in places like the Yellowstone region (Mattson et al. 1996*a*,*b*). However, there are not yet published accounts of the effects of spatial variation in *per capita* risk of mortality from humans in appraisals of potential grizzly bear habitat. There are strong indications that grizzly bear death rates are greater in non-park versus park jurisdictions in the Yellowstone region (Mattson et al. 1996*a*, Boyce et al. 2001), plausibly owing to restrictions on uncased and loaded firearms in U.S. National Parks (Mattson et al. 1996*a*,*b*). There are also strong indications that big game hunters and sheepherders, *per capita*, pose a greater risk to grizzly bears than any other class of humans (Mattson 1998, Boyce et al. 2001). Within grizzly bear range, sheepherders are spatially associated with grazing allotments, whereas big game hunters are spatially associated with non-park public lands. There is thus good reason to expect that mortality risk in the Yellowstone region differs between park and non-park public lands, and between areas inside and out of grazing allotments.

Grizzly bears can survive and reproduce outside the official Recovery Area (Hoak et al. 1981, Reid and Gehman 1986, Blanchard et al. 1992, Bader 2000*a*, Schwartz et al. 2002). However, as yet, no systematic appraisals of the location and extent of this potentiality have focused on the Yellowstone region. Merrill et al. (1999) examined only a small part of this area occurring in Idaho. Moreover, they used a model of productivity weighted toward conditions with greater maritime climatic influences typical of areas farther north and west of Yellowstone. Carroll et al. (2001) included the Yellowstone region in their appraisal of suitable grizzly bear habitat in the Rocky Mountains of Canada and the United States. However, the resolution of their mapped results was much finer than the scale of grizzly bear movements (*cf.* Merrill et al. 1999). They also used a model of productivity that was based on results from a climatically different study area in northwestern Montana (Mace et al. 1999) and used thresholds based on quantiles of the modeled response rather than demographic relations. Neither of these previous studies considered landscape features potentially associated with human lethality.

In this study we appraise the extent and location of potential source and core grizzly bear habitat in the Yellowstone region, including areas well outside the designated Recovery Area. We employ a model of habitat productivity derived from observations of grizzly bears in the Yellowstone region (Mattson et al. 2003) and generalize modeled results to the scale of lifetime or annual grizzly bear movements. We calibrate our metrics to records of grizzly bear deaths in the Yellowstone region, considering landscape features plausibly associated with differences in human lethality. Finally, we apply to identified source areas size criteria that are based on grizzly bear ecology and historical records of grizzly bear extirpations (Mattson and Merrill 2002). Our objective is to systematically identify potential core and source areas in a conceptually defensible way so that a more informed debate can occur among those making value-based claims about grizzly bear conservation in this region (see Merrill et al. 1999, Cork et al. 2000).

Study area

Our Yellowstone-centered study area includes currently occupied grizzly bear range plus surrounding area extensive enough to contain potential nearby or adjacent core habitat, but not so large as to exceed what we consider bounds of legitimate extrapolation of models based on Yellowstone data. Current grizzly bear range in the Yellowstone region is about 37,600 km^2 (Bader 2000*a*, Schwartz et al. 2002) and about 60% contained within official Recovery Area boundaries centered on Yellowstone National Park (Schwartz et al. 2002). Our study area encompasses 162,300 km^2 in the states of Wyoming, Montana, and Idaho, between 108°05′W and 114°00′W longitude and 41°47′N and 47°25′N latitude (Fig. 1a). To the east, the study area is bounded by the Bighorn and lower Wind rivers, to the south by the transition between foothills of the Wind River and Salt River mountain ranges and the high desert of Wyoming, to the west by the Continental Divide and the scarp of the Island Park Plateau, and to the north by the crest of the Little Belt Mountains.

Our study area is topographically diverse, but typified by alternating steep mountains and high-elevation valleys. To the east and southwest this high-relief topography transitions to high-elevation (>1,350 m) plains. The study area contains head-waters of the Missouri, Yellowstone, Green, and Snake rivers, as well as major mountain ranges including, counter-clockwise from the west, the Teton, Salt River, Wind River, Absaroka, Crazy, Big Belt, Gallatin, Madison, Gravelly, Pioneer, and Centennial ranges (Fig. 1b). Central parts of the study area are dominated by high-elevation (>2,000 m) plateaus, including the Island Park, Yellowstone, and Beartooth plateaus.

The study area climate is continental with large geographic differences in annual precipitation and

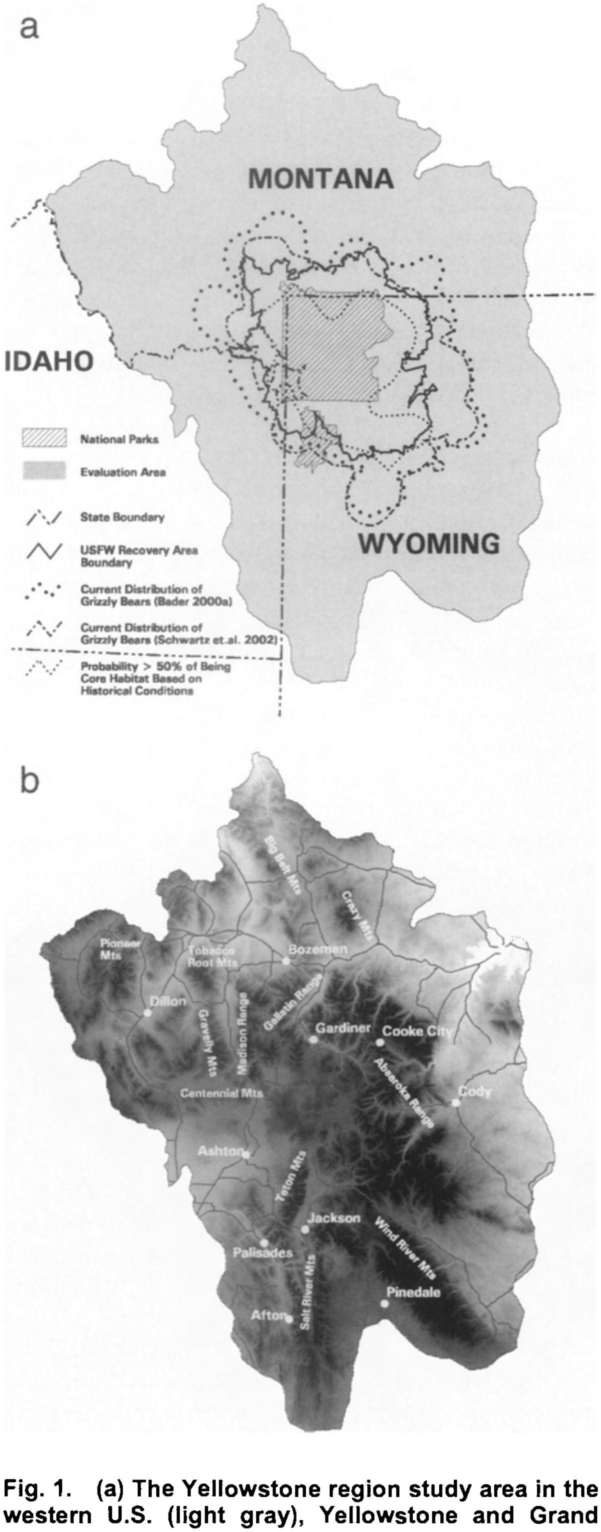

Fig. 1. (a) The Yellowstone region study area in the western U.S. (light gray), Yellowstone and Grand Teton National Parks (cross-hatching), and boundaries of the USFWS grizzly bear Recovery Area (dark solid line), current distribution of grizzly bears (Bader 2000*a*: large dots; Schwartz et al. 2002: dashes), and core habitat predicted by Mattson and Merrill (2002) assuming hunting and lack of Endangered Species Act (16 U.S. Code 1531–1544) protection (small dots). (b) The Yellowstone region study area showing major towns and cities, rivers, and mountain ranges. Higher elevations are denoted by darker shading.

temperature (National Oceanic and Atmospheric Administration 1983). Average annual precipitation varies from 15–35 cm at the lowest elevations to 60–75 cm at the highest. Average annual snowfall varies from 400–600 cm at high elevations in western parts of the study area to 50–100 cm at low elevations, especially to the north and east. In the wettest areas snow cover persists from October to May, whereas in the driest areas snow is present only sporadically during the winter. In general, proportionally more precipitation falls during winter to the south and west in contrast to a spring peak farther north and east. Average annual temperatures decline from about 7–8°C at the lowest elevations to <0°C at the highest.

The center of the study area is dominated by conifer forests, with non-forest vegetation increasingly prevalent toward the periphery, especially at lower elevations (Küchler 1964). Below 1,800 m elevation, Douglas-fir (*Pseudotsuga menziesii*) is the most common dominant tree. At mid elevations, lodgepole pine (*Pinus contorta*) is pervasive, especially on sites burned within the last 100–200 years, whereas sub-alpine fir (*Abies bifolia*) and Engelmann spruce (*Picea engelmannii*) are dominant on wet, cold, or less recently disturbed sites. Above 2,500 m, whitebark pine (*Pinus albicaulis*) is abundant and replaced at upper treeline near 3,100 m by alpine vegetation. Lower-elevation non-forest vegetation is dominated by grasses, most commonly Idaho fescue (*Festuca idahoensis*) and bluebunch wheatgrass (*Pseudoroegneria spicatum*, and by shrubs, most commonly subspecies of big sagebrush (*Artemisia tridentata*). More details about study area vegetation can be found in Barbour and Billings (1988) and Despain (1990).

The density of permanent human residents in the study area is relatively low—about 2 people/km^2 (U.S. Department of Commerce Census Bureau 2002). Most of the 337,000 residents are concentrated in or near towns and cities located in the valleys and plains. The largest towns in the study area are Bozeman (26,500), Livingston (6,900), and Dillon (3,800) in Montana; Cody (8,800), Jackson (8,600), and Powell (5,400) in Wyoming; and Rexsburg (17,300) and St. Anthony (3,300) in Idaho (Fig. 1b).

Methods

We used 2 models to identify potential source and core areas for grizzly bears. Conceptually, we defined source areas as places where death rate was sustainable (i.e., on a sustained basis, birth rates exceeded death rates). Sink areas (i.e., "sinks") were the opposite. We defined core areas as the most productive and remote places in the Yellowstone region. We provide more exact definitions below.

The model that we used to identify core areas was based on methods described by Merrill et al. (1999) and produced dimensionless indices of remoteness and overall suitability. The model that we used to identify source areas was derived from relations between historical grizzly bear deaths and explanatory landscape features and predicted a surrogate measure of death rate. We describe these 2 modeling approaches and our method for calculating habitat productivity in the following sections.

Calculating habitat productivity

The Interagency Grizzly Bear Study Team and agencies responsible for managing grizzly bear habitat in the Yellowstone region developed vegetation categories based on classification systems that were mapped in detail for the USFWS grizzly bear Recovery Area (Mattson and Despain 1985). The Yellowstone Grizzly Bear Cumulative Effects Model (CEM) uses this map for calculating human impacts. Mattson et al. (2003) consolidated this detailed classification into 16 aggregate habitat types based on similarities of grizzly bear foraging behavior. Using 20 years of data on the foraging behavior of grizzly bears in the Yellowstone region, Mattson et al. (2003) calculated coefficients of habitat productivity for each of the 16 habitat types for each of 4 seasons. The seasons were: spring (den emergence–15 May), estrus (16 May–15 July), early hyperphagia (16 July–30 August), and late hyperphagia (1 September–advent of denning). Productivity values were adjusted to account for whether an area was in ungulate winter range, within 100 m of a forest edge, or in the north, east, south, or west quadrants of the Recovery Area. We used these coefficients to calculate productivity for our study area from maps of the 16 habitat types (Mattson et al. 2003). For purposes of this analysis, we converted coefficients from the absolute values given in Appendix 10 of Mattson et al. (2003) to a relative index scaled from 0 to 1.

The CEM vegetation map covers only the USFWS Recovery Area (Fig. 1a). Because we wanted to evaluate the suitability of areas outside the Recovery Area, we used maps based on satellite imagery to extend the CEM-based map of aggregate habitat types to the entire study area. High-resolution (30-m pixel) maps of the vegetation of Idaho, Montana, and Wyoming were developed from Landsat Thematic Mapper (TM) imagery by the USGS (U.S. Geological Survey) Gap

Analysis Project and various U.S. Forest Service projects. Because the maps were created separately for each state, they had different vegetation classifications. C. Carroll (Director, Klamath Center for Conservation Research, Orleans, California, USA) 'cross walked' the state-specific classifications into a common scheme for the Yellowstone region. The resulting standardized map of vegetation for southeast Idaho, western Wyoming, and southwest Montana had 69 vegetation types (Noss et al. 2002). Based on dominant plant species, elevation, and location in the region, we reclassified these 69 vegetation types into the 16 aggregate habitat types used for calculating grizzly bear habitat productivity (Mattson et al. 2003).

Defining core habitat by the habitat suitability model

Our model of habitat suitability (Merrill et al. 1999) is based on the assumption that a population will persist if, on average, its birth rate is greater than its death rate. Because there is a relationship between birth rates in the Yellowstone population and productivity of its habitat (Mattson 2000), we treated modeled habitat productivity as a surrogate for birth rate. Because most weaned grizzly bears in the Rocky Mountains die because they are killed by humans, partly as a function of how often they encounter people (Mattson et al. 1996*a*,*b*), we treated the inverse of remoteness from humans as a partial surrogate for death rate. Our mapped suitability metric was the standardized index of productivity minus the standardized index of inverse remoteness—a spatially explicit surrogate for potential population growth rate.

Remoteness from humans. We modeled remoteness by methods described in Merrill et al. (1999). In general terms, remoteness was a function of access and potential human activity. We used updated 1990 U.S. Department of Commerce Census Bureau data, spatially referenced by topologically integrated geographic encoding and referencing (TIGER) file census block group centroids, to calculate 2 indices that together predicted potential human activity. For the first index we used an inverse distance weighting (IDW) algorithm available in the Arc Info™ (Environmental Systems Research Institute, Redlands, California, USA) Grid module to interpolate population sizes between census block group centroids. The decay function of the IDW algorithm, or the rate at which the influence of a point decreased, was based on a generalized distribution of trip distances expected for recreationists in the northern Rockies (Wallwork et al. 1980, Smith 1983, McLaughlin et al. 1989). The second index described the relation between local human population size and number of recreation visitor days (RVD) on national forests. This relation was curvilinear, with backcountry use increasing at a lower rate than increases in the local population. We combined these 2 indices to create a single index of potential human activity.

Realized levels of human activity were calculated as a positive function of potential human activity and road density in km^2/km. Habitat effectiveness (HE) was the inverse of realized human activity. HE declined as road density increased, with the rate of decline accelerating as potential human activity increased. We obtained data on linear access features from TIGER files, supplemented with digital maps of roads provided by the Forest Supervisor's Office of each national forest in the region.

Environmental variation and scale of grizzly bear movements. The productivity of grizzly bear habitat in the Yellowstone region varies substantially annually and seasonally (Mattson et al. 2003). We did not explicitly model this variability, but rather accounted for these effects indirectly. To account for seasonal variation we averaged productivity among the 4 seasons. To account for annual variation and the scale of bear movements, we assigned to each pixel the average suitability score calculated for a surrounding area the approximate size of a female life range in the Yellowstone region (about 900 km^2; Blanchard and Knight 1991). Compared to a map at the resolution of data used in our calculations, the result of this moving window analysis was a much smoother topology that aggregated areas of uniformly high and low suitability.

Thresholds for transitional and core habitat. We defined 2 categories of suitable habitat: core and transition. We set the cut point for suitable habitat as the mean of the suitability metric for our study area. We designated habitats having a suitability value greater than the mean but less than the mean plus 1 standard deviation (SD) as transitional. We defined habitats having a suitability value greater than the mean plus 1 SD, in blocks $>900 \text{ km}^2$ as core.

Confirming the habitat suitability model. We compared our definition of core habitat with the USFWS Recovery Area and the current distribution of grizzly bears (Bader 2000*a*, Schwartz et al. 2002). By policy, the USFWS Recovery Area contains enough high-quality habitat to support a recovered population (U.S. Fish and Wildlife Service 1993) and, in fact, includes most of the current distribution of grizzly bears (Schwartz et al. 2002). Bader (2000*a*) used the locations of grizzly bear deaths to define a range that was substantially larger than the Recovery Area. This range plausibly represented the extent of areas used by bears, but not necessarily areas where bears had a good chance of surviving and reproducing.

We also tested our definition of core habitat by comparing it with the results of independent models. Within context of this study, we compared results of the suitability modeling with results of the landscape mortality risk modeling (see below). We also compared our results to those of Mattson and Merrill (2002). Mattson and Merrill (2002) examined historical extirpations of grizzly bear populations in the contiguous United States over 2 periods—1850 to 1920 and 1920 to 1970. They used relations between the probability that grizzly bears had persisted during 1920–70 and landscape features such as food availability and human population density to predict the probability that an area would be core grizzly habitat in 2000, assuming humans remained as lethal to grizzly bears during 1970–2000 as they were during 1920–1970. This definition of core habitat was quite conservative in that it assumed continued sport hunting of grizzly bears and the absence of endangered species protections. We expected that this prediction of core habitat based on historical trends would be smaller, and contained within, our modeled reckoning of suitability based on current conditions.

Defining source habitat by the landscape mortality risk model

We modeled the probability (y) that a location was that of a dead bear killed by a human versus a random point (transformed as a logit $[\ln(y/[1-y])]$; Hosmer and Lemeshow 2000) as a function of explanatory landscape features. We used the measures of remoteness and habitat productivity described above as candidate explanatory variables, in addition to distance from the centroid of all bear deaths and whether a bear death or random point were located in or out of a National Park or grazing allotment. We selected our best model by the sample-size-corrected version of Akaike's Information Criterion (AIC_c; Burnham and Anderson 1998), estimated parameters by maximum likelihood, and described model fit by Somer's D and R_L^2 (Hosmer and Lemeshow 2000, Menard 2000). We did not employ traditional statistical inference because of the "contaminated" nature of use (= death) versus availability data (Boyce et al. 2002), and provide P values only as a conventional point of reference.

We chose variables for consideration in our analysis on the basis of their likely ability to explain the distribution of bear deaths and to control for nuisance effects in our use of this model to identify putative source areas. We interpreted National Parks and grazing allotments as surrogates for spatial variation in human lethality (see introduction). We interpreted productivity and remoteness as surrogates for the joint probability that humans and grizzly bears would be active in an area (i.e., frequency of contact). Finally, we interpreted distance from the centroid of bear deaths as a surrogate for the diminishing odds that, all else equal, bears would be active in areas further from the core of grizzly bear range. Together, productivity and distance from the centroid served as surrogates for population-level exposure to conditions at any given spatial point (i.e., exposure time).

Information used in this analysis came from published sources and federal agencies. We obtained information on grizzly bear deaths in the Yellowstone region for 1989–99 from data compiled by the Interagency Grizzly Bear Study Team (Knight et al. 1990, 1991, 1992; Gunther et al. 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000). We obtained digital boundaries of administrative units from the National Park Service, the U.S. Department of Agriculture Forest Service, and the Bureau of Land Management, and digital boundaries of grazing allotments from the Forest Supervisor's office of each of the National Forests within our study area.

Calculating the number of random points. We used a non-arbitrary number of random points to specify this model. We chose a number that would yield model outputs that could be crudely interpreted as a spatially explicit death rate. To achieve this end, we construed random points as the total number of bear years that yielded the observed number of dead bears, minus the number of bears known to have died during that period by human causes. Thus, we calculated total number of random points as $(334 \times 11 = 3{,}674) - 138$; where 334 is the most likely recent historical estimate of grizzly bear population size in the Yellowstone region (Eberhardt and Knight 1996), 11 is the number of years of data used in this analysis, and 138 is the total number of bears known to die by human causes during this period (69), times 2. In other words, we calculated the total number of bear years (3,674) yielding the mortality data, minus the total of number of bear years that resulted in a known human-caused bear death (138). Thus, the resulting modeled value, back-transformed from a logit, could be interpreted as the crude annual probability of human-caused death as a function of landscape features. We multiplied the number of human-caused deaths by 2 for reasons explained below.

Weighting observations. In general, about half of all human-caused deaths are reported in areas like the

Yellowstone region (McLellan et al. 1999). Even so, some human-caused deaths are almost certain to be recorded (deaths by accident or by management intervention), especially compared to deaths caused by poachers, hunters, and livestock caretakers (Mattson 1998). We dealt with this complexity by differentially weighting human-caused deaths so that the weights summed to 138 ($2 \times n$), yet with deaths by accident or management removal weighted by '1' and other deaths by a larger factor (*wgt*). We calculated *wgt* ($= 2.47$) from the following conditionality: $22 + 47 \times wgt = 69 \times 2 = 138$; where 22 is the number of bears that died by accident or management removal, 47 is the number of bears known to have died from other, less detectable, human causes, 69 is the total number of known human-caused deaths, and 138 is the estimated total number of human-caused deaths, known and unknown. These weights were used in our model specification. Thus, each death by human causes other than management removal or accident was imparted roughly 2.5× the information content, or 'importance', as other human-caused deaths. This assumed that among the less detectable deaths, associated landscape features did not differ between those that were and were not recorded ("known").

Scope and scale of modeling and predictions. We restricted the distribution of random points used in explanatory modeling to the current distribution of grizzly bears in the Yellowstone region as defined by Bader (2000*a*). We generalized our results to the scale of the average annual rather than lifetime range of an adult female (about 300 km^2; Blanchard and Knight 1991) because we were modeling an annual phenomenon (annual probability of death).

Threshold for potential source habitat. We delineated potential source habitat as areas where, jointly, predicted annual probability of human-caused death was <0.06 (Eberhardt 1990, U.S. Fish and Wildlife Service 1993) and scaled (0–1) productivity was >0.015. Potential sink habitat was productive habitat where putative death rate was ≥ 0.06. The productivity threshold masked areas where, in theory, bears would be unable to find enough food to survive and reproduce. We set the productivity threshold by examining mapped productivity in the Yellowstone region and identifying productivity values that, based on experience, delimited areas we judged to be too unproductive to support bears (e.g., broadscale sagebrush desert typified by *Artemisia tridentata tridentata* and *A. t. wyomingensis*).

Results

Remoteness and productivity

The most remote parts of our study area were concentrated in the eastern portions of Yellowstone National Park (YNP), southeast of YNP, and in the Wind River Range (Fig. 2a). The most productive parts of the study area were concentrated in mountain ranges to the north and east of YNP and to the south in the Wind River and Salt River Ranges (Fig. 2b).

Core areas defined by the habitat suitability model

Location and extent of core areas. A total of 27,426-km^2 of potential core grizzly bear habitat existed in the Yellowstone region (Fig. 3). After deleting 2 patches of core habitat <900 km^2 in size, the total was reduced to 27,032 km^2. This core habitat was distributed in 4 major blocks: Central Yellowstone with 20,146 km^2, the Centennials to the west with 1,691 km^2, the Palisades to the south with 2,036 km^2, and the Wind Rivers to the southeast with 3,358 km^2. These core areas were surrounded by and connected to each other by transitional habitat (Fig. 3). The Centennial, Palisades, and Wind River core areas were 20 km, 44 km, and 30 km distant, respectively, from the nearest point of the Central Yellowstone core area.

Overlap of core areas with other delineations. Potential core grizzly bear habitat in the Yellowstone region overlapped substantially with the 4 other delineations of grizzly bear range (Table 1). YNP and the surrounding USFWS Recovery Area were at the center of our delineation of core grizzly bear habitat. Even so, only 62% of the 27,032 km^2 we defined as core habitat and only 12% of the 45,330 km^2 that we defined as transitional habitat were contained by the Recovery Area (Fig. 4a, Table 1). The boundary of currently occupied range (Schwartz et al. 2002) contained somewhat more of the suitable areas defined by our analysis: 17,841 km^2 (66%) of core habitat and 9,519 km^2 (21%) of transitional habitat (Fig. 4c, Table 1). As we expected, the area predicted to be core habitat if there were no U.S. Endangered Species Act protections (Mattson and Merrill 2002) was mostly within core habitat defined in this analysis (Fig. 4d, Table 1). In general, discrepancies between our delineation of core habitat and either the Recovery Area or currently occupied range were primarily attributable to non-overlap with peripheral, mostly unoccupied, core habitat in the Palisades and Wind River areas.

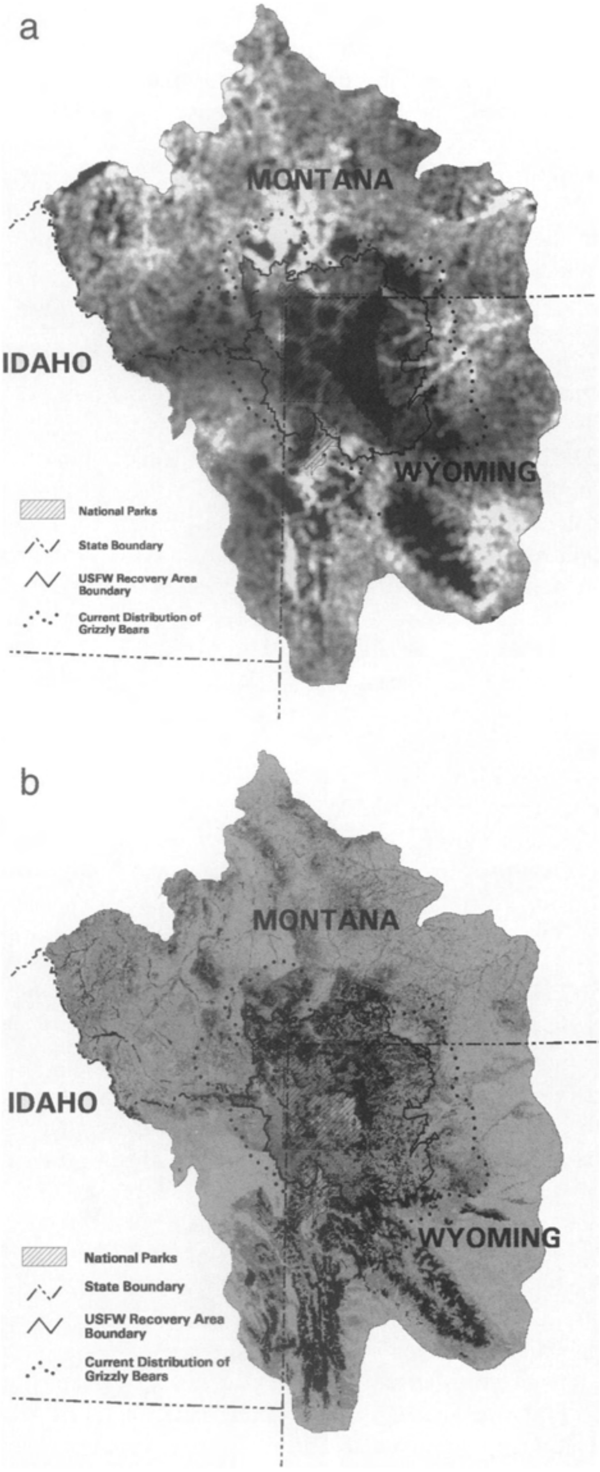

Fig. 2. Distribution of (a) remoteness from humans and (b) productivity for grizzly bears in the Yellowstone region study area, western U.S. More productive or more remote areas are denoted by darker shading.

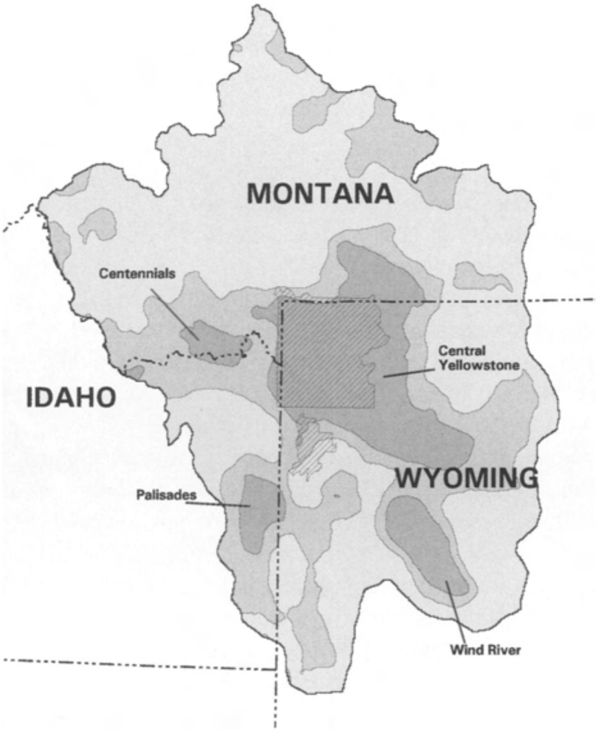

Fig. 3. The location of core (dark gray) and transitional (medium gray) grizzly bear habitat in the Yellowstone region as delineated by the habitat suitability model. The 4 major core areas, each >900 km^2, are labeled

Source areas defined by the landscape mortality risk model

Estimated landscape mortality risk model.

The logit-transformed probability (logit[p]) that a location was that of a dead bear versus a random point was best explained by the following model:

$$\begin{aligned} Logit(p) = &-1.46 + 132\ln(PROD + 1) - 110PROD \\ &- 2.23REMOTE^2 - 0.00002DIST \\ &+ 0.49ALLOT - 1.36PARK; \end{aligned}$$

where *PROD* was the index of productivity, *REMOTE* was the index of remoteness, *DIST* was the distance from the centroid of bear range (in m), *ALLOT* was whether the location was in (1) or out (0) of a livestock allotment, and *PARK* was whether the location was in (1) or out (0) of a National Park. *PROD* was included as a polynomial because of its non-monotonic relation to the modeled outcome (see below); a "1" was added prior to taking the natural log transformation of the first

Table 1. Total areas of grizzly bear core habitat, source areas, range, and the Recovery Area delineated by different models or policies in the Yellowstone region study area (diagonal cells), and percent overlap among all combinations of these delineations (off-diagonal cells). Percent values are for the relative amounts of delineations denoted by rows contained within delineations denoted by columns.

	Delineation					
Delineation	**Core areas by habitat suitability model**	**Source areas by landscape mortality risk model**	**Current grizzly bear range (Schwartz et al. 2002)**	**Current grizzly bear range (Bader 2000*a*)**	**Recovery Area designated by USFWS**	**Core area without ESA predicted by Mattson and Merrill (2002)**
Core areas by habitat suitability model	100% (27,032 km^2)	98%	66%	76%	62%	48%
Source areas by landscape mortality risk model	55%	100% (47,807 km^2)	47%	56%	40%	29%
Current grizzly bear range (Schwartz et al. 2002)	49%	62%	100% (36,306 km^2)	92%	62%	41%
Current grizzly bear range (Bader 2000*a*)	48%	63%	79%	100% (42,285 km^2)	57%	37%
Recovery Area designated by USFWS	69%	80%	94%	100%	100% (23,959 km^2)	71%
Core area without ESA predicted by Mattson and Merrill (2002)	84%	90%	97%	100%	95%	100% (15,440 km^2)

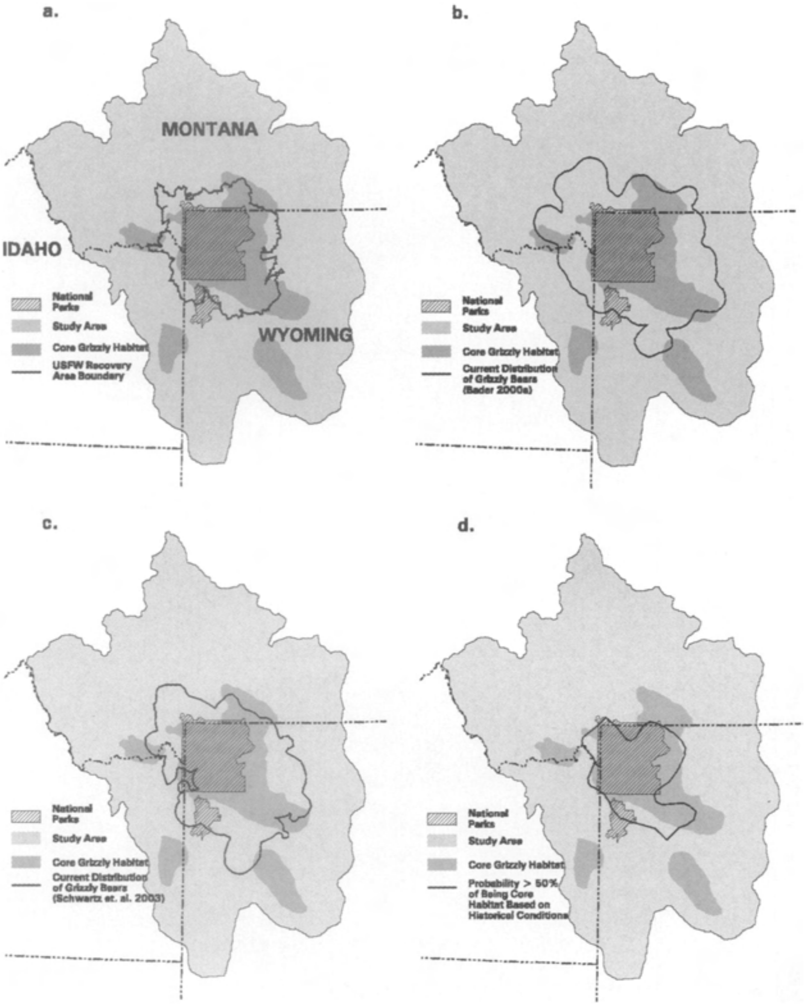

Fig. 4. Overlap of core habitat predicted by the habitat suitability model (dark gray) and (a) the USFWS grizzly bear Recovery Area, (b) the current distribution of grizzly bears (Bader 2000*a*), (c) the current distribution of grizzly bears (Schwartz et al. 2002), and (d) core habitat predicted by Mattson and Merrill (2002) assuming hunting and lack of ESA protection.

positive term because *PROD* included 0 values. The change-in-AIC$_c$ (Δ) with deletion of each variable in turn from the model, pooling both *PROD* effects, was 29.3, 29.8, 27.8, 3.5, and 12.5 for *PROD*, *REMOTE*, *DIST*, *ALLOT*, and *PARK*, respectively. The statistics for the model were: 4×10^3 df, $G^2 = 1061$, $P = 1.00$, $R^2_L = 0.79$, Somer's $D = 0.42$. Considered univariately, the probability of a dead bear peaked at habitat productivity values near 0.17 (Fig. 5a), whereas this probability declined monotonically with increasing remoteness (Fig. 5b). By this model, bears were most likely to die outside of national parks and on grazing allotments, in moderately productive habitat near people (Fig. 6).

To apply the model for predictive purposes, we set *DIST* and *PROD* to mean values (80,000 and 0.079, respectively) calculated for the grizzly bear range delineated by Bader (2000*a*). We did this to control for the extraneous effects of habitat productivity and distance from the centroid of grizzly bear range. *PROD* and *DIST* functioned in the explanatory model as surrogates for expected levels of bear activity or population-level "exposure." Controlling for these effects in the predictive model translated the results from a surrogate of unit area probability of death to a surrogate of per bear probability of death. Thus, the predicted logit-transformed probability of putative annual per bear death rate was:

$$
\begin{aligned}
Logit(p) = {} & -1.71 - 2.23REMOTE^2 \\
& + 0.49ALLOT \\
& - 1.51PARK
\end{aligned}
$$

Location, extent, and overlap of potential source areas. We judged about 21%, or 33,664 km^2, of the study area to be unproductive for grizzly bears. Of the remaining 128,632 km^2, the landscape mortality risk model identified 47,807 km^2 as potential source areas (i.e., areas where the back-transformed logit was <0.06; Fig. 7a). These potential source areas encompassed all of the core areas defined by the habitat suitability model and were more extensive (Table 1, Fig. 7b). According to landscape mortality risk, the Central Yellowstone and Centennial source areas were contiguous and, together, 34,209 km^2 in size. The Palisades and Wind River source areas were 8,480 km^2 and 4,115 km^2, respectively. The Palisades and Wind River source areas also were 7 km and 15 km distant, respectively, at their closest points from the Central Yellowstone source area.

One potential source area was delineated near the Little Belt Mountains on the Lewis and Clark National

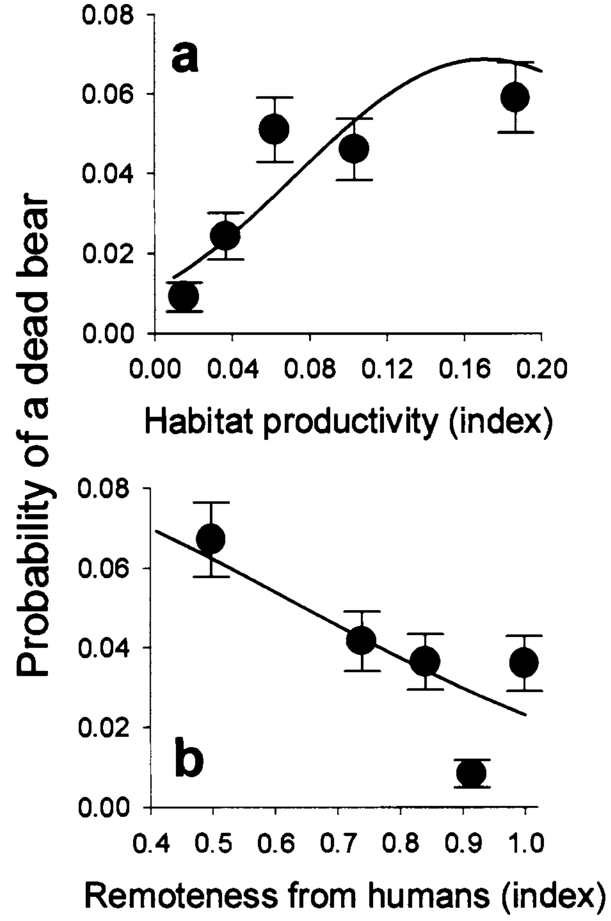

Fig. 5. Relation between the probability that a location was that of a dead grizzly bear versus a random point and (a) habitat productivity and (b) remoteness from humans, for the Yellowstone region, 1989–99. Points and error brackets are means and SE's for quintiles and are shown to illustrate goodness of fit.

Forest. This source area was 3,959 km^2 in size, 72 km distant from the nearest USFWS Recovery Area, and did not overlap with any core area or any other delineation of grizzly bear habitat (Fig. 7b). However, about 2,729 km^2 of this source area overlapped with transitional habitat defined by the habitat suitability model.

The landscape mortality risk model also identified 80,825 km^2, or almost 50% of the study area, as grizzly bear population sinks (Fig. 7c). Population sinks ringed the central Yellowstone source area, preventing range expansion to the north and separating the Central Yellowstone area from the Palisades area and the Palisades area from the Wind River area. Population sinks also constricted access between the Central Yellowstone and Wind River source areas.

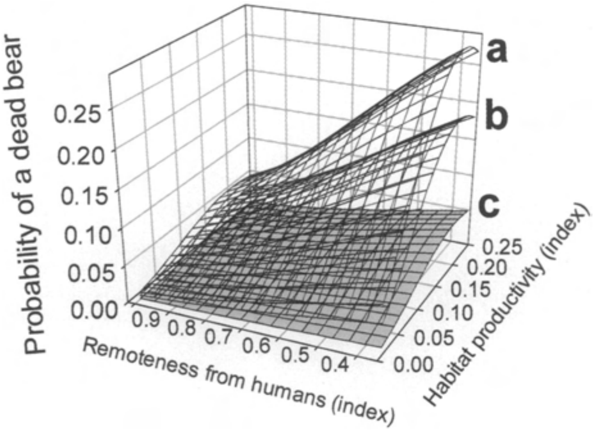

Fig. 6. Relation between the probability that a location was that of a dead grizzly bear versus a random point and, jointly, remoteness from humans and habitat productivity, for the Yellowstone region, western U.S., 1989–99 for areas outside a National Park, but inside a grazing allotment (a); for areas outside allotments and National Parks (b); and for areas inside National Parks (c).

Discussion

Interpreting core areas

The habitat suitability model used to define core areas in this analysis has been confirmed by grizzly bear demographic data elsewhere. Merrill et al. (1999) found a strong relation between the habitat suitability metric and observations of grizzly bear sign in northern Idaho. Our measure of remoteness from humans was also confirmed by explaining much of the variation in distributions of grizzly bear observations in this same study area (Merrill et al. 1999). Because of its logic and apparent robustness, Carroll et al. (2001) adopted the remoteness metric to map potential grizzly bear habitat for the Rocky Mountains of Canada and the U.S.

In a broad sense, there was agreement between delineations of core areas by the habitat suitability model and other delineations of grizzly bear range in the central part of our study area. However, confirmation of the Central Yellowstone core area by other delineations of grizzly bear range was compromised by that fact that there was not a conceptual one-to-one correspondence between core areas and these other definitions. The USFWS grizzly bear Recovery Area was significantly affected by human social and political factors (Primm 1992). Even so, the habitat suitability model suggested that much of what was included in the Recovery Area was, in fact, some of the highest quality grizzly bear habitat in the region. This held as well for results of the

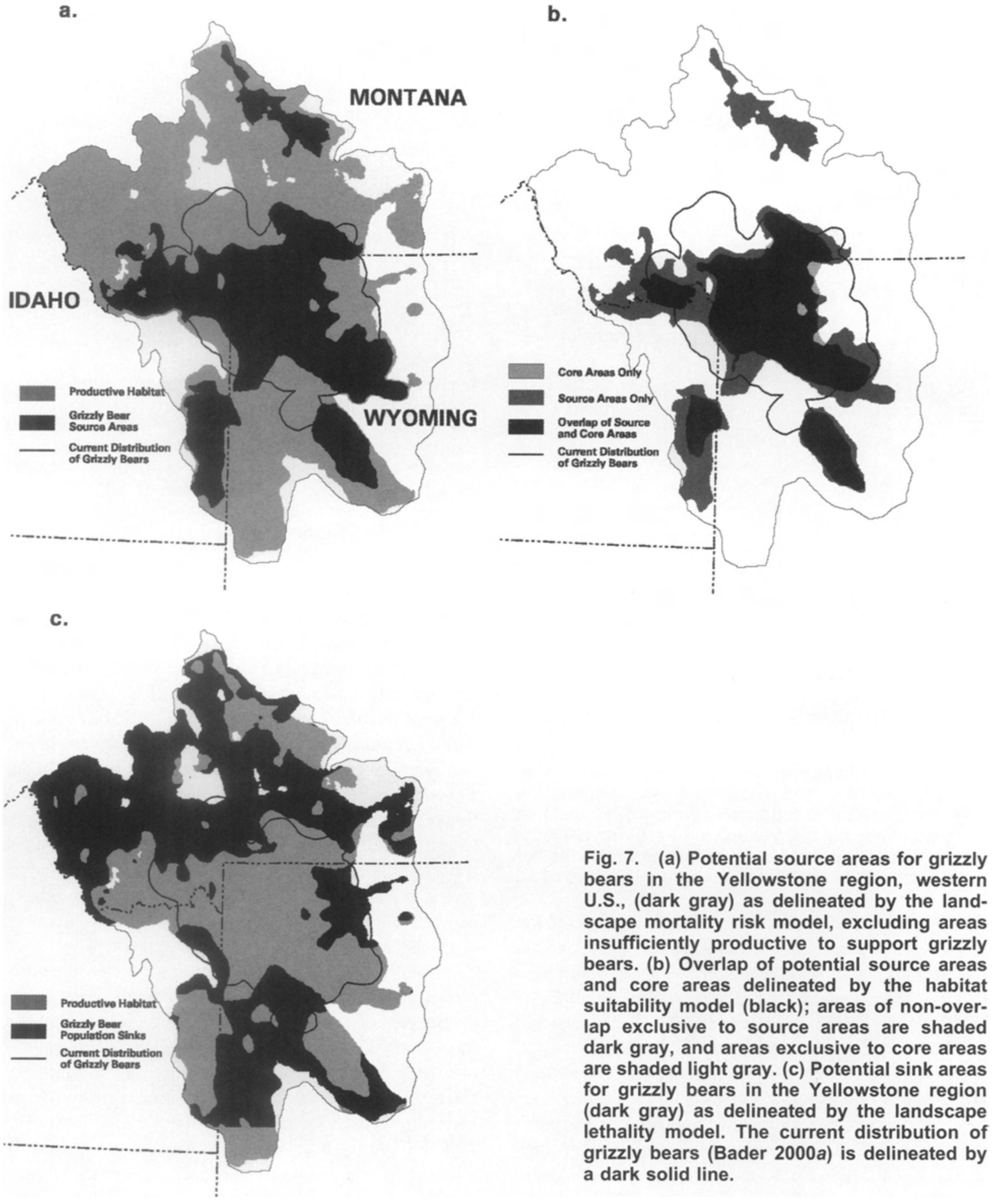

Fig. 7. (a) Potential source areas for grizzly bears in the Yellowstone region, western U.S., (dark gray) as delineated by the landscape mortality risk model, excluding areas insufficiently productive to support grizzly bears. (b) Overlap of potential source areas and core areas delineated by the habitat suitability model (black); areas of non-overlap exclusive to source areas are shaded dark gray, and areas exclusive to core areas are shaded light gray. (c) Potential sink areas for grizzly bears in the Yellowstone region (dark gray) as delineated by the landscape lethality model. The current distribution of grizzly bears (Bader 2000*a*) is delineated by a dark solid line.

landscape mortality risk model. The current distribution of grizzly bears was also compromised as a basis for comparison because it only delineated areas where grizzly bears were present long enough to be killed, rather than areas where grizzly bears stood a good chance of surviving and reproducing. Nonetheless, there was congruence between the Central Yellowstone core area and current grizzly bear range in that the latter formed a roughly concentric ring around the former.

Exceptions to this general pattern occurred on the Beartooth Plateau to the north and in the southern-most reaches of the Absaroka range to the southeast. In both places the habitat suitability and landscape mortality risk models suggested that favorable conditions for grizzly bears extended somewhat beyond current range as described by Schwartz et al. (2002). In the southeast, predicted core habitat may be occupied in the near future if the apparent trend toward range extension continues in this region (Blanchard et al. 1992, Schwartz et al. 2002). In the Beartooth Plateau, the discrepancy between core or source habitat and documented range could have arisen from model bias or bias in field methods. The Beartooth Plateau has consistently been less intensively trapped and monitored than other areas in the Yellowstone region (e.g., Schwartz and Haroldson 2002).

Core areas were insufficient for appraising the extent of conditions capable of supporting grizzly bears because they were delineated by an arbitrary criterion; i.e., by suitability values >1 SD above the mean. The evaluation of grizzly bear range by Carroll et al. (2001) was similarly limited. This lack of demographically-based thresholds was a major reason why we were interested in confirming core areas by comparison with other delineations of grizzly bear range. Even so, core areas can be interpreted as "the best of the best"—areas containing the most productive and most remote grizzly bear habitat in the Yellowstone region. Because the Central Yellowstone core area appeared to be a more conservative delineation of grizzly bear range than either the USFWS Recovery Area or current range based on bear deaths, we judged delineations of core areas outside of current grizzly bear range to be similarly robust and conservative.

Implications of the landscape mortality risk model

The landscape mortality risk model confirmed our expectations about factors having a major effect on rates of human-caused grizzly bear deaths in the Yellowstone region. Productivity and remoteness had a dominant effect on numbers of deaths. Taken together, these measures were surrogates for frequency of contact between humans and grizzly bears by virtue of their assumed correlation with densities of bears and humans, respectively. The strong relations of productivity and remoteness to spatial distributions of grizzly bear deaths also confirmed the biological merits of these measures in our model of habitat suitability. Consistent with results of Boyce et al. (2001), inclusion of effects related to grazing allotments and management jurisdiction also confirmed our expectations regarding spatial variation in *per capita* human lethality, although these lethality-related effects were much smaller than effects related to putative frequency of contact between humans and bears.

The landscape mortality risk model not only highlighted the importance of certain landscape features to grizzly bear survival, it also clarified management actions with the greatest promise for either restoring or preserving demographically beneficial elements of grizzly bear habitat. Consistent with previous recommendations by the National Research Council (1974), Johnson and Griffel (1982), and Knight and Judd (1983), and especially pertaining to domesticated sheep, minimizing numbers of livestock and associated human caretakers would benefit grizzly bears. Increasing the extent of jurisdictions, like National Parks, where loaded and accessible firearms were prohibited would also help. But, minimizing the amount of human activity in grizzly bear range would perhaps be of greatest importance. That said, socio-political factors largely determine opportunities to implement these perhaps obvious measures beneficial to grizzly bears (Primm 1992, Mattson and Craighead 1994).

Interpreting source and sink areas

Unlike the threshold for core areas, the threshold for potential sources and sinks was based on an explicit demographic relation (the landscape mortality risk model) and a criterion directly linked to sustainability (6% annual chance of death). Compared to core areas, source areas were thus a better basis for identifying the extent of conditions in the study area where the average grizzly bear was likely able to survive long enough to replace itself in the population. However, the landscape mortality risk model was somewhat compromised by lacking the effects of habitat productivity on reproductive success of females. Reproductive output of female grizzly bears in the Yellowstone region varies, spatially and temporally, primarily depending on the availability of whitebark pine seeds (Mattson 2000). The habitat suitability model was thus superior to the landscape mortality risk model insofar as it incorporated the effects of habitat productivity in determinations of the very best grizzly bear habitat.

Our delineation of source areas was based on the assumption that 6% is, in fact, the threshold for sustainable mortality in the Yellowstone region. Real conditions could invalidate this assumption for several reasons. Local variation in *per capita* risk from humans could result in either a higher or lower threshold. Eberhardt (1990) only considered female death rates in calculating sustainable mortality, whereas we used deaths of males and females in constructing our mortality risk model. At the very least, this introduces uncertainty in the relation between our threshold and Eberhardt's work. Finally, the 6% human-caused rate adopted by the USFWS Recovery Plan (U.S. Fish and Wildlife Service 1993) assumes a greater rate of natural mortality than is probably currently the case among Yellowstone grizzly bears. This potential discrepancy would make our delineation of source areas conservative relative to their true extent.

Are there unoccupied but biophysically suitable source areas?

Based on this analysis, we conclude that there are extensive and productive potential source areas peripheral to and nearby the current distribution of Yellowstone grizzly bears. The USFWS Recovery Area contained 40% and current grizzly bear range and 56% of all potential source habitats identified in our study area. By all indications there are 3 sizable, largely unoccupied, source areas in the Yellowstone region: one in the Wind River Mountains to the southeast of current range, a second to the south, centered on the Palisades region of Idaho, and a third to the west, along the Centennial Mountains, primarily in Montana. A source area centered on the Wind River Mountains is consistent with a marked increase in grizzly bear sightings and sheep-related conflicts in recent years, especially along the west slopes of this range (e.g., Gunther et al. 2000). The Palisades source area coincides with an area of suitable conditions identified by Merrill et al. (1999) in their appraisal of potential grizzly bear habitat in Idaho. A potential source area here is also consistent with the presence of grizzly bears as recently as 1979. During July of that year a sheepherder killed a grizzly bear near Bald Mountain (Craighead et al. 1988). On the other hand, the potential source area along and to the north of the Centennial Mountains was not identified in Idaho by Merrill et al. (1999). However, this discrepancy may be attributable to the location of this source area largely outside of Idaho, in Montana. If the presence of this source area is confirmed, then prospects for connectivity between the Yellowstone region and potential grizzly bear habitat in central Idaho may be greater than suggested by Merrill et al. (1999).

At least 2 of the peripheral source areas are separated from the Central Yellowstone core–source area by intervening sinks. The map of source habitat paints a more optimistic picture than the map of core areas. For reasons stated above, source areas are a better basis than core areas for depicting fragmentation. The Centennial potential source area is contiguous with the main grizzly bear source area centered on YNP, whereas the Palisades and Wind River potential source areas are quite close by way of Grand Teton NP and the southeast extremity of the Absaroka Range, respectively. The Palisades and Wind River potential source areas are too small by themselves to support a robust grizzly bear population (Mattson and Merrill 2002). Their relatively small size and attenuated shape probably account for the apparent extirpation of grizzly bears here during historical times when humans were much more lethal (Mattson and Merrill 2002). However, with protections offered by the U.S. Endangered Species Act, a substantial number of grizzly bears could probably live in these peripheral source areas, contingent on periodic augmentation by bears dispersing from areas closer to YNP. Assuming equal densities in occupied and potential grizzly bear range (about 1.6 bears/100 km^2; Eberhardt and Knight 1996; Schwartz et al. 2002), the current Yellowstone grizzly bear population could be increased by about 115 grizzly bears if they were allowed to occupy the Wind River, Palisades, and Centennial potential source areas.

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