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Author(s): David J. Mattson and Troy Merrill

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A model-based appraisal of habitat conditions for grizzly bears in the Cabinet–Yaak region of Montana and Idaho

David J. Mattson^{1,3} and Troy Merrill^{2,4}

¹U.S. Geological Survey Southwest Biological Science Center, Colorado Plateau Research Station,
P.O. Box 5614, Northern Arizona University, Flagstaff, AZ 86011-5614, USA

²LTB Institute of Landscape Ecology, 208 South Main, Suite 7, Moscow, ID 83843, USA

Abstract: We used a broad-scale model based on observations of grizzly bears (*Ursus arctos*) or their sign, calibrated to reported putative death rate, to appraise current habitat conditions in the Cabinet–Yaak region of Montana. Habitat capability (i.e., potential grizzly bear densities) and regional human population sizes had the greatest effects in this model. We predicted the effects of (1) human population increases (+150% anticipated by 2023), (2) changes in lethality of humans (i.e., the probability that a human would kill a bear given an encounter), and (3) differences in the ratio of unknown to known bear deaths on the extent and location of potential source areas. We predicted densities of 1.0 and 2.1 grizzly bears/100 km² with and without human impacts, respectively. Under our baseline scenario (3% sustainable mortality and 1:1 ratio of unknown to known bear deaths), we predicted that 2 source areas totaling 9,156 km² and potentially supporting 123 bears occurred in our study area. With projected human population increases, potential source areas and bear populations declined by 33% and 45%, respectively. A spatially uniform increase of 1% in annual death rate (as a surrogate for increased human lethality) reduced potential source areas and bear numbers by 41% and 36%. Source areas and bear numbers declined by 39% and 34% if the ratio of unknown to known grizzly bear deaths was 2:1 versus 1:1. We obtained the best match with current population estimates (about 35 bears) assuming a 2:1 ratio of unknown to known deaths and a very low sustainable death rate of 2%. This implies either high levels of illegal human-caused mortality and low birth and recruitment rates or a population smaller than currently estimated. We conclude that human numbers and human lethality will likely govern the fate of grizzly bears in this region.

Key words: Cabinet–Yaak, density, grizzly bears, habitat suitability, Montana, *Ursus arctos*

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The grizzly bear population in the Cabinet–Yaak region of far northwestern Montana is small. A total of 30–40 grizzly bears are estimated to live there, with <15 bears residing in the Cabinet Mountains, relatively isolated from the remainder of the population in the Yaak drainage north of U.S. Highway 2 (Kasworm et al. 2000). Estimates of population size have not changed during the last 15 years (Servheen et al. 1987, U.S. Fish and Wildlife Service 1993, Kasworm et al. 2000), although a recent estimate of growth rate (Wakkinen and Kasworm 2004) ostensibly includes the possibilities of population decline to about 6 or increase to about 63 animals within the last decade (i.e., the 95% CI for λ [finite rate of population growth] = 0.84–1.06). The

potential for demographic rescue by populations of grizzly bears elsewhere is impaired by intervening human barriers (Servheen et al. 1998, Proctor et al. 2002). Assuming isolation, 35 and 63 individuals roughly equate to effective populations (N_e) of 7 and 13, respectively (Allendorf and Ryman 2002). Whether judged by census population size or N_e , these numbers do not insure population viability for even 10 generations of bears (i.e., about 100 years; Suchy et al. 1985, Reed and Bryant 2000, Allendorf and Ryman 2002).

Managers have advocated increasing the number of grizzly bears in the Cabinet–Yaak region, primarily in response to prescriptive requirements of the U.S. Endangered Species Act (U.S. Code 1531–1544, U.S. Fish and Wildlife Service 1993). Humans cause most grizzly bear deaths in northwestern Montana and adjacent Idaho (Knick and Kasworm 1989, McLellan et al.

³David_Mattson@usgs.gov ⁴troy@moscow.com

1999, Manley 2001). Because of this, management has focused on reducing human-caused mortality, which has been deemed the primary factor limiting population growth (U.S. Fish and Wildlife Service 1993). Efforts to boost population size have included augmenting the Cabinet Mountains' population with 4 subadult females transplanted from British Columbia, Canada (Kasworm et al. 1998).

Efforts to recover grizzly bears in the Cabinet–Yaak region have been hampered by limited information about the bears and their habitat. Small populations of secretive animals are intrinsically difficult to study and monitor. This is highlighted by the substantial uncertainty regarding vital rates of Cabinet–Yaak grizzly bears, despite many years of intensive data-collection efforts (Wakkinen and Kasworm 2004). Lack of data makes it very difficult to directly estimate population status and trend or analyze relations between vital rates and habitat. Moreover, there will probably never be enough resources to remedy these deficits. Yet, effective management action requires insight about limiting factors, current habitat capability, and the implications of foreseeable habitat trends.

Explanatory spatial models based on crude demographic indicators (e.g., *ad hoc* observations of bears or their spore) or extrapolated from areas where demographic data are more abundant can generate useful insights. All management actions are based on models, whether they are implicit, highly personal, and undisclosed or explicit and subject to collective scrutiny (Cork et al. 2000). The question is not whether to use models, but rather which ones, and by what standards (Brulle 2000, Brunner and Colburn 2002).

In this paper, we use explanatory spatial models based on *ad hoc* observations of grizzly bear sign to appraise: (1) the current extent and location of potential source areas in the Cabinet–Yaak region, (2) the effects of foreseeable human population increases, (3) the effects of changes in lethality of humans, and (4) the effects of different ratios of unknown to known grizzly bear deaths. There is increasing evidence that numbers of humans and human lethality (i.e., the odds that a person will kill a bear during an encounter) have as much or more effect on grizzly bears as do amounts of road access, a traditional focus of management (McLellan 1990, Mattson et al. 1996a, Merrill et al. 1999, Mattson and Merrill 2002). Although not well understood (Mattson 1998a, McLellan et al. 1999), the ratio of unknown to known grizzly bear deaths is also important in assessing the status of grizzly bear populations and their habitat (Mattson 1997a).

Study area

Our study area is centered on the Cabinet–Yaak Grizzly Bear Recovery Area in northwestern Montana and adjacent Idaho (U.S. Fish and Wildlife Service 1993), between 47° and 49°N latitude and 114° and 117°W longitude (Fig. 1). The northern part of the Recovery Area encompasses much of the Yaak River drainage and is bounded to the west by the Purcell Mountains. The southern part of the Recovery Area is centered on the Cabinet Mountains, which contain the 381-km² Cabinet Mountain Wilderness Area. Elevations range from about 500 to 2,700 m. The climate is wet temperate and subalpine, with 100 to 150 cm of precipitation falling primarily as winter snow.

The study area is mostly forested, with ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) dominant on warm, dry sites and grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) dominant on undisturbed wetter sites. Subalpine fir (*Abies bifolia*), Englemann spruce (*Picea engelmannii*), and mountain hemlock (*Tsuga mertensiana*) are abundant above about 1500 m. Berry-producing shrubs include hawthorn (*Crataegus douglasii*), serviceberry (*Amelanchier alnifolia*), and chokecherry (*Prunus virginiana*) in riparian bottoms or on dry slopes, buffaloberry (*Shepherdia canadensis*) under open forest stands, and huckleberry (*Vaccinium* spp.) shrub fields in old burns or recent clearcuts that were broadcast burned to reduce slash.

During the 2000 census, about 252,000 people resided in counties in Montana and Idaho that contained our study area (<http://quickfacts.census.gov/qfd>). The largest nearby cities were Troy, Libby, Eureka, and Thompson Falls in Montana, and Bonners Ferry and Sandpoint in Idaho. About 90% of the Recovery Area is in federal ownership administered by 3 National Forests. Private lands and human settlements are concentrated at lower elevations, in valley bottoms, with the exception of private industrial forests owned by Plum Creek Timber Company, which occur at all elevations. Kasworm et al. (2000) and Wakkinen and Kasworm (2004) provide additional details on the study area.

Methods

Our appraisal was based on 2 models, one used to estimate potential grizzly bear density and described in detail elsewhere (Mattson and Merrill, 2003, Models of grizzly bear density for conservation design in the North American Rocky Mountains, USGS Southwest Biolog-

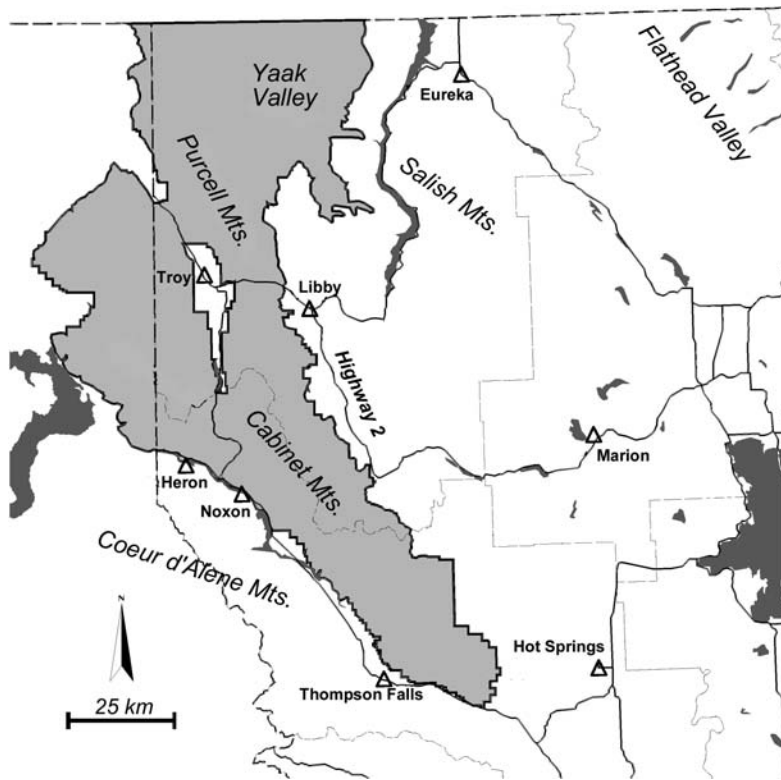


Fig. 1. The Cabinet–Yaak region of northwestern Montana and northern Idaho, USA. Cities and towns are denoted by open triangles. The U.S. Fish and Wildlife Service Grizzly Bear Recovery Area is shaded gray.

ical Science Center, Flagstaff, Arizona, USA) and one specified in this paper based on data from the Cabinet–Yaak region. We calibrated the second model to produce results interpretable as a measure of death rate. These models and related calibrations are described in the following sections.

Potential grizzly bear density

Mattson and Merrill (unpublished report 2003) describe models for estimating potential grizzly bear densities (*Density*) based on current biophysical habitat conditions. In essence, these models predict densities in an area with minimal human effects based on study areas ($n = 12$) throughout the North American Rocky Mountains with estimates of grizzly bear densities and diet. A number of variables were considered to explain variation in densities, including study area sizes, which ranged from 291–23,957 km². Other variables (e.g., tasseled cap transformed Wetness, Greenness, and Brightness from MODIS satellite data) represented values averaged

for each study area. The model we used for our analysis here was based only on Wetness (i.e., *Wet*) and provided the best fit to spatial distributions of grizzly bear observations in the Cabinet–Yaak study area (Mattson and Merrill [unpublished report 2003]; see the following section for a description of the observations data set):

$$\text{Density}^2 = 8.3 + 2.8(\ln[(-\text{Wet}) + 1]) \quad (1)$$

Wetness is known to correlate with standing water, soil and plant moisture, and other forest conditions (Crist and Ciccone 1984).

We rescaled predicted densities so they would be at the resolution of an average female grizzly bear range (i.e., 300 km²) rather than the resolution of our map data (i.e., 1 km²). We did this by averaging values within a 300-km² circle centered on each map pixel (i.e., by using a “moving window”). Multi-year animal ranges are the maximum logical scale for representing multi-year population densities (Merrill et al. 1999, Mattson and Merrill 2002). Female grizzly bear ranges from the Cabinet–Yaak region are about the size of the window used in our

analysis. Adult females in the Swan Mountains, Montana, had a mean 95% range size of 124 km² (Mace and Manley 1993), which is roughly equivalent to a female life range size of 370 km² (Mattson 1993). Mean size of 100% female ranges for the season of maximum movements (spring) was 243 km² in the same study area (Mace et al. 1996).

Cabinet–Yaak bear sign

We used methods based on information theory to develop a logistic regression model that explained differences between the distributions of 806 random points and $n = 505$ observations of grizzly bears or their sign in the Cabinet–Yaak region (“observation” subsequently), 1985–2000 (Fig. 2). Parameter estimates were by maximum likelihood methods, and model selection was based on minimizing the sample-size-corrected version of Akaike’s Information Criterion (AIC_c; Burnham and Anderson 1998, Hosmer and Lemeshow 2000). We judged the relative importance

of variables by the change in AIC_c (i.e., ΔAIC_c) with deletion of each variable, in turn, from the model (Burnham and Anderson 1998).

We obtained locations of observations of grizzly bears or grizzly bear sign (i.e., tracks, feces, hair, or excavations) from W. Kasworm (U.S. Fish and Wildlife Service [USFWS], Libby, Montana, USA). These observations were obtained by the USFWS primarily from personnel of wildlife and land management agencies (Kasworm and Manley 1988, Kasworm et al. 2000). Many of the observations were recorded on sighting forms sent by the USFWS to agency personnel. Observations were verified by qualified agents whenever possible and rated on a scale of 1 to 5 for reliability. We used all rankings of reliability for this analysis. We generated random points within a sample area defined by the aggregation of 10-km radius buffers around these observations of grizzly bears or grizzly bear sign (Fig. 2). This constrained random points to an area likely used by the bears that contributed to the observations.

We weighted random points and grizzly bear observations so that their summed weights equaled the number of grizzly bear observations ($n = 505$), and so that random points and bear observations contributed equally to model specification. The resulting logits, when transformed back to probabilities, were thus subject to straight forward interpretation; that is, any value < 0.5 indicated a site where the odds of observing grizzly bears or their sign was less than by chance, whereas any value > 0.5 indicated the opposite. Total degrees of freedom also directly reflected the number of bear observations rather than the arbitrary number of random points used for this analysis. We generated a relatively large number of random points, and then down-weighted their contribution to model specification, so as to ensure good coverage and stable parameter estimates.

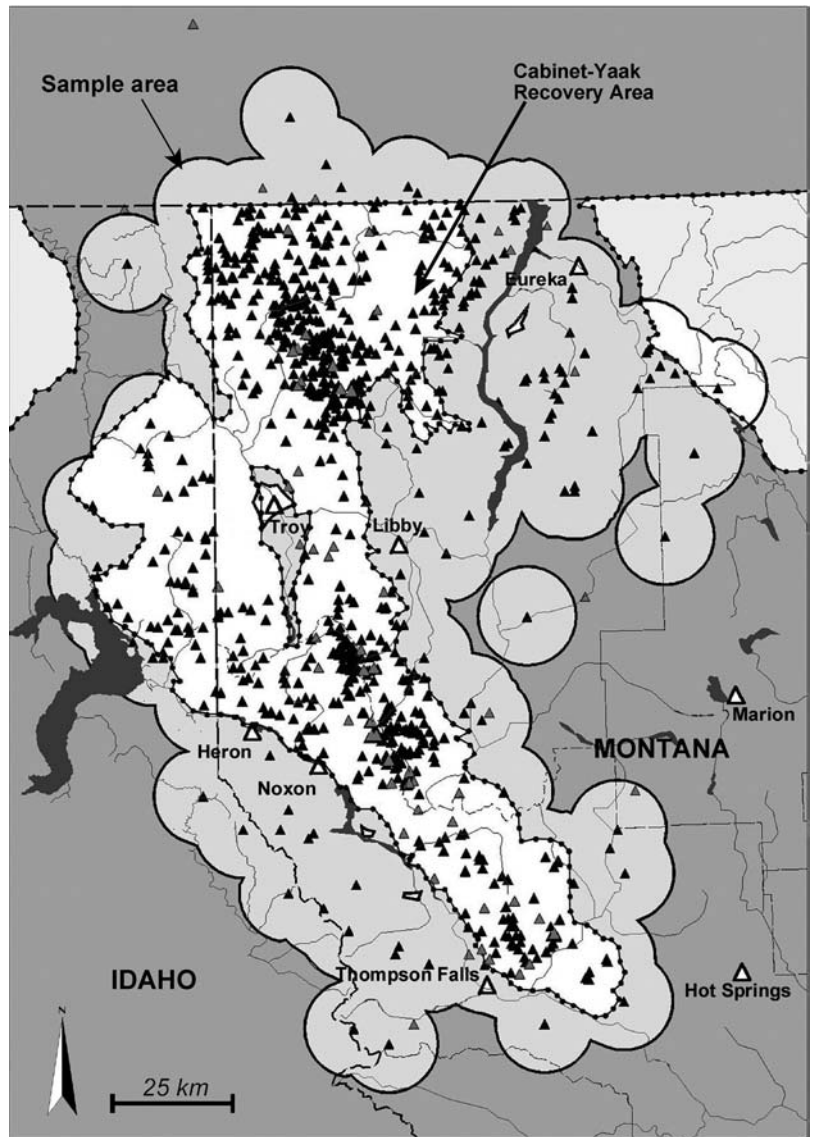


Fig. 2. Location of grizzly bear observations (small black triangles, 1985–2000) and deaths (small gray triangles, 1985–2000) and the sample area used to generate random points (thick solid line) in the Cabinet–Yaak region. Large open triangles denote cities and towns. The Grizzly Bear Recovery Area is delineated by a dotted line. Lakes and major drainages are also shown. Data were provided by W. Kasworm, U.S. Fish and Wildlife Service, Libby, Montana, USA.

We also reweighted bear observations so that newer data contributed more to model specification than did older data; that is $weight = year\ of\ observation - 1984$. We scaled these weights so that degrees of freedom were not changed. We accounted for elapsed time to give greater weight to more recent observations, assuming

that newer observations reflected contemporaneous conditions better than older observations, and that recent conditions were of most interest to managers. Recent observations also were a better temporal match to the dates of roads and human census data that we used in our analysis (see below).

We considered potential explanatory variables that related primarily to frequency of contact between humans and grizzly bears. These variables included the number of people counted during the last census within 20, 40, 60, and 100 km of a point (i.e., regional population), road density, potential level of human activity (i.e., *Wdist*, a measure based on number of people [from census blocks] and their nearness [based on census block centroids], weighted by a decay function; Merrill et al. 1999), predicted level of human activity (i.e., *Remote*, a metric that combined road density and *Wdist*; Merrill et al. 1999), and potential grizzly bear density (from model [1]). We increased the “grain” of these measures for consideration in model specification by averaging their values for a 300-km² area around each random point or observation of a grizzly bear or grizzly bear sign. We did this for 2 reasons: (1) to account for potential error in the spatial location of bear observations, and (2) to account for the broader-scale influences of habitat conditions on the odds that a bear would be present and detected by a human.

We obtained human census information from the U.S. Census Bureau (<http://www.census.gov/geo/www/tiger/tiger2k>) and Statistics Canada (<http://www12.statcan.ca/english/census01/products/standard/popdwell>) and information on roads from W. Haskins of The Ecology Center, Inc. (TECI), Missoula, Montana, USA. The roads data included roads of all management types, including open, closed, and restricted. We did not differentiate management status because comprehensive information of this sort was not readily available for most of our study area.

Delineating potential source areas

Calibration to pseudo-death rate. We rescaled or “calibrated” the bear sign model (above) to pseudo-death rate by relating model outputs to the distribution of known grizzly bear deaths ($n = 16$) from the Cabinet–Yaak region for 1985–2000 (a 16 yr period; Kasworm et al. 2000, 2002). These deaths did not include 1 that occurred outside our study area. We also treated instances where cubs died with their mother as one observation. Five of the 16 deaths were of radiomarked individuals, 4 deaths were from unknown causes, 5 were in defense of life or property (DLP), 3 were illegal, 1 was

a management removal, 1 was a mistaken identity, 1 was a trapping related death, and 1 was deemed natural.

We considered both a 1:1 and 2:1 ratio of unknown to known deaths in our calculations. We initially chose a 1:1 ratio because it represented a reasonable mid-point of results from studies that investigated this relation. These results included 0.8:1 (Dood et al. 1986), approximately 1:1 (Knight and Eberhardt 1985), 1:1–1.2:1 (McLellan et al. 1999), and 1.2:1 (Cherry et al. 2002), and invoked different assumptions about whether radiomarked bears were considered in the calculations. We additionally considered a 2:1 ratio because our modeled results (see below) based on a 1:1 ratio did not come close to matching current estimates of grizzly bear population size in the Cabinet–Yaak region and were apparently too optimistic. Our intent was to determine which assumption regarding the ratio of unknown to known bear deaths was most consistent with current information about demography of grizzly bears in the Cabinet–Yaak region rather than to make *a priori* judgments about which ratio should apply.

We were able to represent potential *per capita* death rate by accounting for factors associated with potential bear density (i.e., the bear sign model) and by weighting the observations used in model development so that the modeled probability corresponded to deaths as a proportion of total bear-years. As for the bear sign model, we weighted recent deaths more heavily than older ones in model specification. Assuming a constant population of 35 bears, there were $35 \times 16 = 560$ bear years for the 16 years of 1985–2000. Assuming a 1:1 ratio of unknown to known deaths, $2 \times 16 = 32$ bears died during this time. Assuming a 2:1 ratio, $3 \times 16 = 48$ died. Thus, assuming a 1:1 ratio, the weights used in model specification for dead bears and random points ($= 860$) were 2 and $(560 - 32)/860 = 0.614$, respectively. Assuming a 2:1 ratio, these weights were 3 and $(560 - 48)/860 = 0.595$. The weights of 2 and 3 assigned to a dead bear were the multipliers required to obtain total number of dead bears from the number of dead bears that were recorded (see above). This approach assumed a stable population of 35 bears (Kasworm et al. 2000) and that the spatial distributions of unknown and known grizzly bear deaths were not functionally different.

We used our pseudo-death rate model to identify potential source areas. A source area was where our model predicted that birth rates exceeded death rates (i.e., death rate was “sustainable”). Because of uncertainties arising from the assumptions used in our model of pseudo-death rate, and because of our interest in matching model predictions to current estimates of

population size and growth rate in the Cabinet–Yaak region, we defined source areas using different assumed sustainable death rates, or cutpoints. Potential source areas were identified as all areas where modeled pseudo-death rate was less than the cutpoint (excluding patches less than 300 km² [Merrill et al. 1999]).

We adopted a baseline cutpoint of 3% for sustainable death rate in this analysis. This cutpoint was within the range of sustainable female death rates calculated by Eberhardt (1990) for grizzly bears, although at the low end of the spectrum associated with a short life span, late age of first reproduction, or poor survival to age 5. We did not use this cutpoint as a definitive representation of sustainable death rate in the Cabinet–Yaak region. Rather the 3% cutpoint produced a good initial match between predicted source areas and current representations of core range (Kasworm et al. 2000) and provided a basis of comparison for scenarios that invoked different assumptions about human lethality. All of the death rate cutpoints that we examined in this analysis applied to both males and females. This application is consistent with using deaths of both genders for our calculations and assumes that females and males are of equal importance for sustaining a small population such as this one.

Accounting for variation in human lethality. The death rate model that we applied to this analysis only accounted for factors affecting frequency of encounter between humans and grizzly bears (i.e., remoteness) and did not account for factors associated with human lethality (i.e., the probability that a human would kill a bear during a given encounter; Mattson et al. 1996a). We used differences in the extent of source areas, delineated using different cutpoints for sustainable death rate, to represent the potential spatial effects of changes in human lethality. In our model, changes in spatial extent that were associated with decreasing the cutpoint (i.e., positing that bears could only sustain a lower death rate) were equivalent to positing that human lethality was higher than expected. This equivalence was correct to the extent that the higher lethality resulted in an increase in annual death rates equal to the difference in cutpoint levels. By contrast, changes associated with increasing the cutpoint corresponded to the spatial gains predicted by our model if human lethality was lower than the 3% baseline.

Results

Potential grizzly bear density

Predicted potential grizzly bear densities (model [1]) were consistently highest in far northwestern Montana

and along the Idaho–Montana border and lowest in the Flathead Valley (Fig. 3). In Idaho, potential densities were generally >2.0 bears/100 km², and to the south, in the Coeur d’Alene Mountains, they were about 2.5 bears/100 km². Potential densities for the entire sample area averaged 2.1 bears/100 km², and ranged from 1.6 to 2.5 bears/100 km². The model predicted that, without human impacts, the 17,554-km² sample area (Fig. 2) could support about 362 grizzly bears. With human impacts (using model [4], below, and assuming current human lethality), that number would be reduced by 52%, to 174 (1.0 bear/100 km²).

Bear sign model

The model we chose to explain differences between the distributions of random points and grizzly bear observations (i.e., the logit-transformed probability that a point was a bear observation versus a random point [$\text{Logit}(p)_{\text{bs}}$]) was biologically interpretable and had the lowest AIC_c score (601.4) of all the models we considered. This model was:

$$\begin{aligned} \text{Logit}(p)_{\text{bs}} &= 0.32 - 0.44 \ln(\text{Cent} + 1) - 7.2 \ln(\text{Rdden} + 1) \\ &\quad + 6.3 \sqrt{\text{Rdden}} - 0.12 \text{Hpop60}^2 \\ &\quad - 1.9 \ln(\text{Hpop100} + 1) + 1.5 \text{Density}^2 \end{aligned} \quad (2)$$

where *Cent* was distance to the centroid of grizzly bear observations (in m), *Rdden* was road density (in km/km²), *Hpop60* was density of resident humans within 60 km (in number/km²), *Hpop100* was density of resident humans within 100 km, and *Density* was potential grizzly bear density (in number/100 km²) as predicted by model (1) (Mattson and Merrill, unpublished report 2003; see Methods). Statistics for model (2)’s goodness-of-fit were $n = 505$, 1×10^3 df, $G^2 = 587$, and $P = 1.00$. Area under the Receiver Operating Characteristic (ROC) Curve was 0.76, which indicates acceptable discrimination (Hosmer and Lemeshow 2000).

As indicated by ΔAIC_c (in parentheses), the relative importance of each variable was: *Density* (24.0), *Cent* (18.0), *Hpop60* (17.4), *Hpop100* (9.3), first term *Rdden* (3.9), and second term *Rdden* (3.9). Based on random points, the coefficient of determination (r^2) between *Hpop60* and *Hpop100* was 0.28; between *Hpop60* and *Rdden*, 0.004; between *Hpop60* and *Density*, 0.08; between *Hpop100* and *Rdden*, 0.009; between *Hpop100* and *Density*, 0.09; and between *Rdden* and *Density*, 0.10.

We fit relations between $\text{Logit}(p)_{\text{bs}}$ and each of the variables included in model (2), treated separately, to

graphically examine and display the nature of these univariate relations (Fig. 4). The relation with *Rdden* (Fig. 4b) suggested that, on average, the probability of observing bear sign was >0.48 only at road densities <1.1 km/km². Similarly, probabilities of observing bear sign were >0.48 only in areas with human densities <2.6 and <3.4 people/km² within 60 and 100 km, respectively (Fig. 4a), or where there were potentially >2.1 bears/100 km² (Fig. 4c). We used a threshold probability of 0.48 because this value corresponded to the threshold annual death rate of 3%, assuming a 1:1 ratio of unknown to known deaths (see below).

For purposes of prediction, we consolidated the effect of *Cent* and the second (positive) *Rdden* term into the intercept of model (2) by adding the value of their coefficient-weighted means (1.2) to the intercept. We did this because we interpreted these variables as controls for bias that were spurious to our primary interest in representing grizzly bear habitat potential. More specifically, we interpreted *Cent* as a measure of broad-scale spatial autocorrelation among bear observations. We interpreted the second *Rdden* term as a measure of increasing probability of sign detection with increasing road access rather than as some fundamental relation between bears and their habitat (Merrill et al. 1999). Thus, the model we used to predict source areas was:

$$\begin{aligned} \text{Logit}(p)_{bs} = & 1.6 - 7.2 \ln(Rdden + 1) - 0.12Hpop60^2 \\ & - 1.9 \ln(Hpop100 + 1) + 1.5Density^2 \end{aligned} \quad (3)$$

We also derived a model (i.e., *Density_{adj}*) to account for the negative effects of *Rdden*, *Hpop60*, and *Hpop100* on *Density*. We did this by solving model (3) for *Density*, given $\text{Logit}(p)_{bs}$:

$$Density_{adj} = \text{sqrt}[(\text{Logit}(p)_{bs} + 1.6)/1.5]. \quad (4)$$

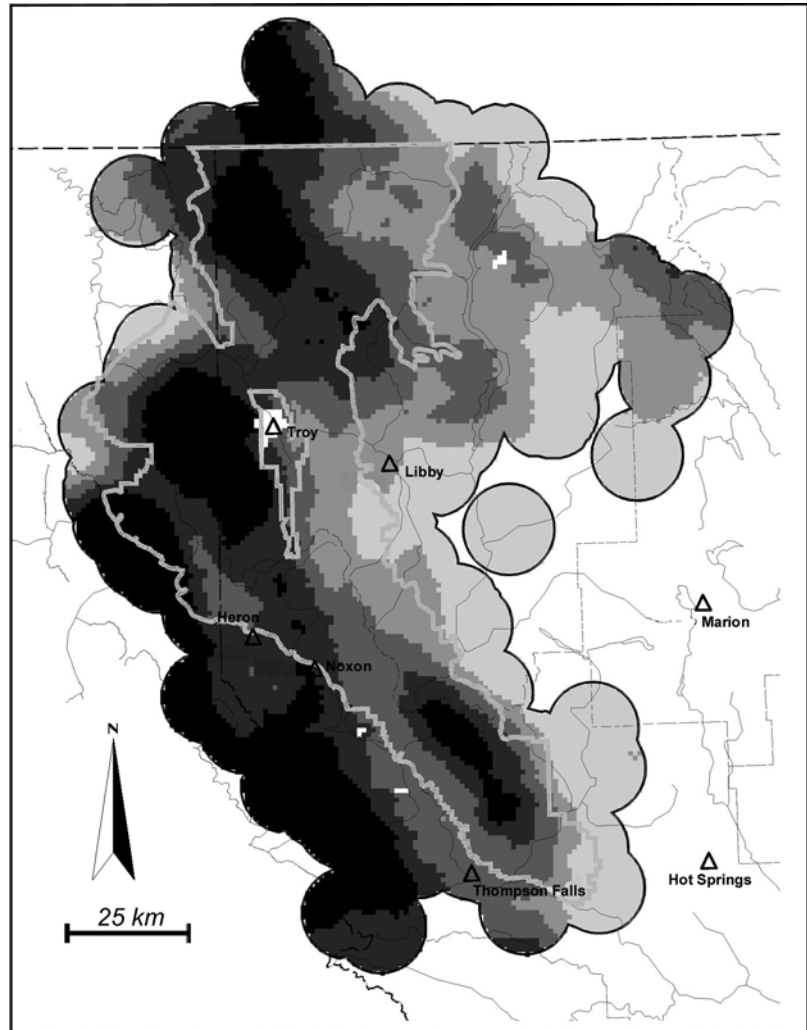


Fig. 3. Potential grizzly bear densities ($n/100$ km²) in the Cabinet-Yaak region, without human impacts. Darker shading denotes higher densities, lighter shading lower densities. Triangles denote cities and towns and the gray line delineates the Grizzly Bear Recovery Area.

Pseudo death rate model

For relating model (2) to a measure of pseudo-death rate, we transformed the response of model (2) ($\text{Logit}(p)_{bs}$) from a logit to a probability (P_{bs}), as follows: $P_{bs} = e^{\text{Logit}(p)_{bs}} / (1 + e^{\text{Logit}(p)_{bs}})$. Assuming a 1:1 ratio of unknown to known grizzly bear deaths, P_{bs} was related to the logit of pseudo-death rate ($\text{Logit}[DR_{1:1}]$) as follows:

$$\text{Logit}(DR_{1:1}) = -1.8 - 7.0P_{bs}^2. \quad (5)$$

P_{bs} was squared in this model and in model (6) below because it improved fit, assuming a logistic response

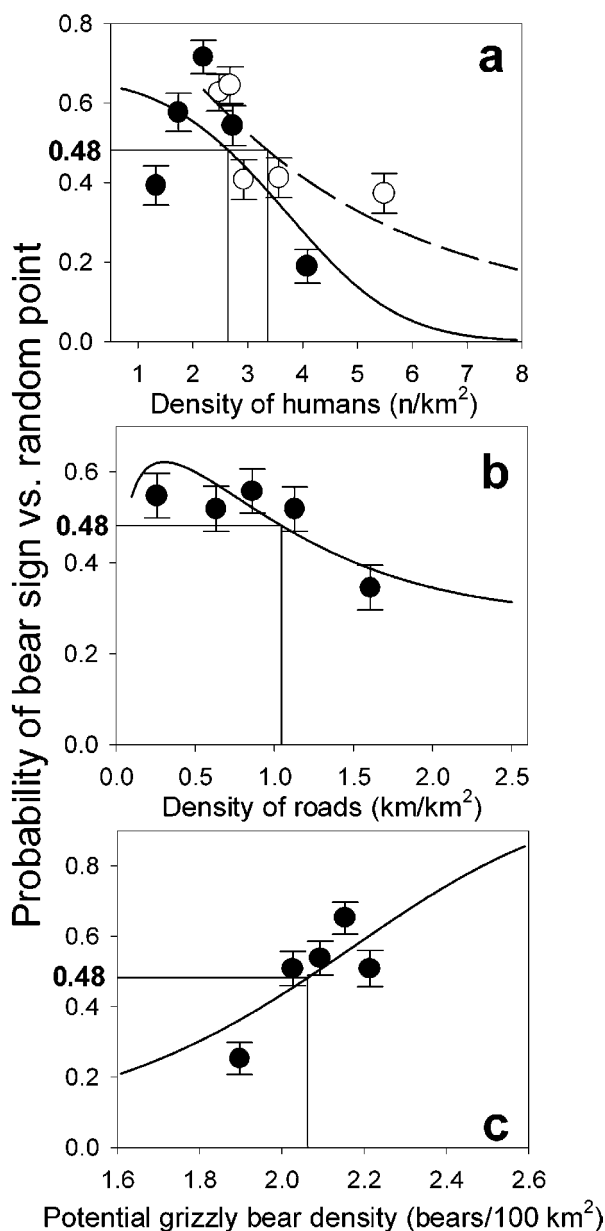


Fig. 4. Univariate relations between the probability that a location was a grizzly bear observation versus a random point and (a) human densities within 60 km and 100 km (solid line and circles versus dashed line and open circles, respectively), (b) road density, and (c) potential grizzly bear density, for the Cabinet–Yaak region. Lines denote the modeled relation. Circles and SE bars are for quintiles of data from 1985–2000 and illustrate goodness-of-fit.

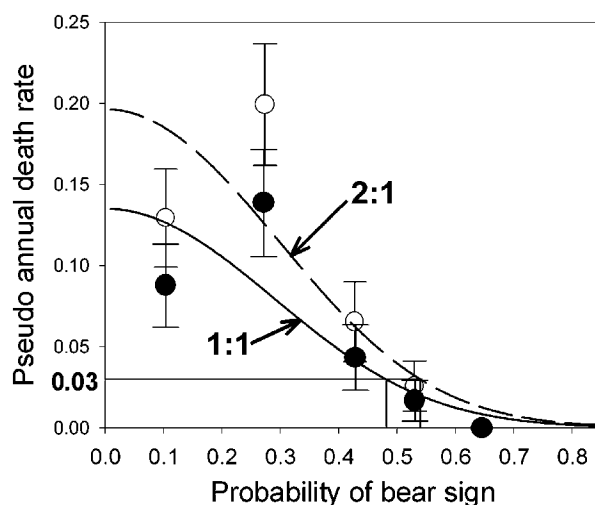


Fig. 5. Univariate relations between the probability that a location was a grizzly bear death versus a random point, calibrated to represent pseudo-death rate, for the Cabinet–Yaak region. Lines denote the modeled relation. Circles and SE bars are for quintiles of data from 1985–2000 and illustrate goodness-of-fit. The solid line and circles represent a 1:1 ratio of unknown to known deaths; the dashed line and open circles represent a 2:1 ratio.

(Hosmer and Lemeshow 2000). Area under the ROC Curve for model (5) was 0.66, which is on the cusp of acceptable and unacceptable discrimination (Hosmer and Lemeshow 2000).

Assuming a 2:1 ratio of unknown to known grizzly bear deaths, P_{bs} was related to $\text{Logit}(DR_{2:1})$ as follows:

$$\text{Logit}(DR_{2:1}) = -1.4 - 7.1P_{bs}^2. \quad (6)$$

Area under the ROC Curve for model (6) was also 0.66.

We converted $\text{Logit}(DR_{1:1})$ and $\text{Logit}(DR_{2:1})$ (both denoted as $\text{Logit}[DR_{x:1}]$ in the following text) to probabilities ($DR_{x:1}$, our measure of pseudo-death rate) as follows: $DR_{x:1} = e^{\text{Logit}(DR_{x:1})} / (1 + e^{\text{Logit}(DR_{x:1})})$. Relations between $DR_{x:1}$ and P_{bs} are shown in Fig. 5. We used values of $DR_{x:1}$ to map potential source areas.

Potential source areas

Assuming a 3% sustainable death rate and 1:1 ratio of unknown to known bear deaths, predicted source areas comprised 9,156 km² of the sample area. This source habitat consisted of 2 patches separated by a corridor along U.S. Highway 2 (Fig. 6a). The southern patch included a relatively extensive, largely unoccupied,

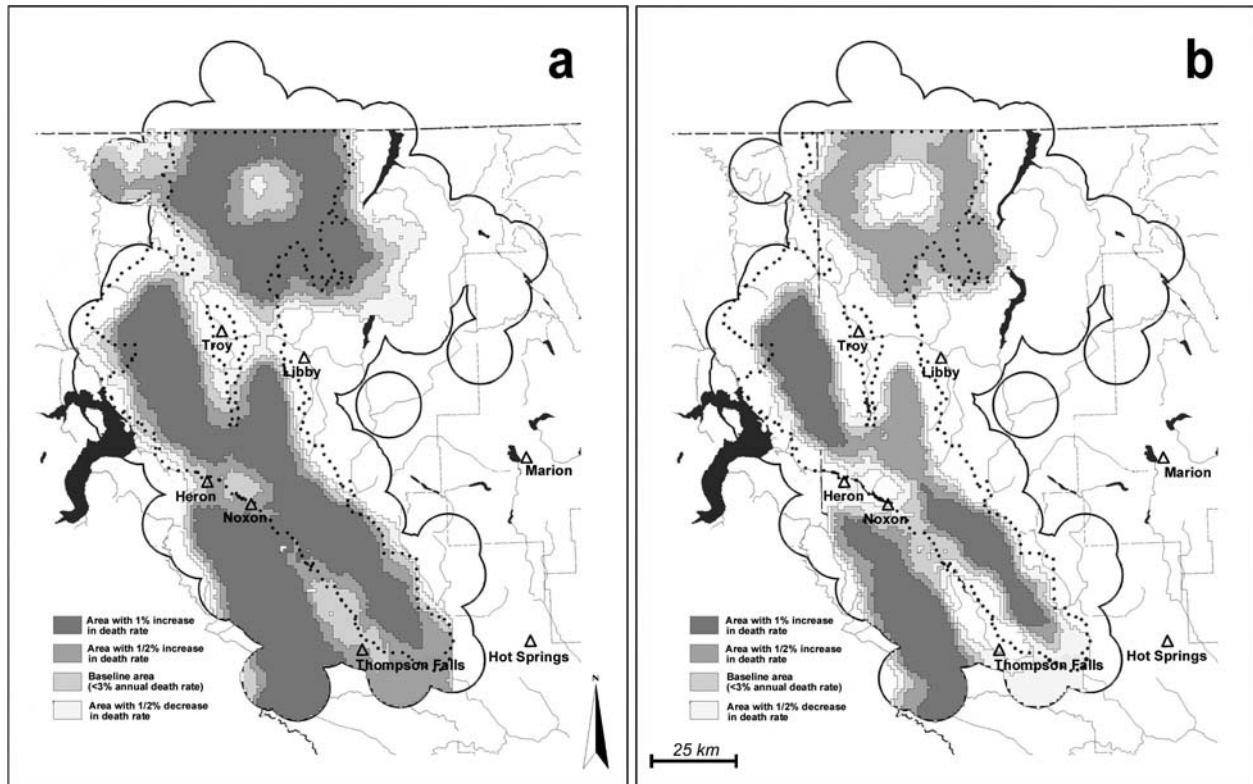


Fig. 6. The predicted current (circa 2000) location and extent of source areas in the Cabinet–Yaak region (a) assuming a 1:1 ratio of unknown to known grizzly bear deaths, and (b) assuming a 2:1 ratio of unknown to known deaths. Darker gray shading corresponds to increasingly restrictive assumptions about sustainable mortality or human lethality. The Recovery Area is delineated by a dotted line. The solid black line delineates the sample area.

source area to the south of Heron and Noxon in the Coeur d'Alene Mountains. This patch was outside of the current Recovery Area. Accounting for human impacts, model (4) predicted that existing source areas could support 123 bears under our baseline scenario.

The extent and configuration of predicted source areas changed with projected increases in human populations and with different assumptions about the ratio of unknown to known bear deaths. Assuming a uniform 150% increase in human populations and 1:1 ratio of unknown to known deaths, source areas were reduced by 33% to 2 patches totaling 6,148 km² and potentially supporting 68 bears (Fig. 7a). Assuming the ratio of unknown to known bear deaths was 2:1 rather than 1:1, source areas were reduced by 39% to 5,548 km² potentially supporting 81 bears (Fig. 6b). Using the 2:1 assumption, projected human population increases reduced source areas by 77% to 1,265 km² potentially supporting 18 bears (Fig. 7b).

Predicted source areas also changed with differences in putative human lethality. Assuming a spatially uniform 0.5% increase in annual death rate owing to an assumed increase in human lethality, source areas were reduced by 18% to 7,512 km² potentially supporting 106 bears (see baseline scenario, Fig. 6a). Assuming a 1% increase, source areas were reduced by 41% to 5,386 km² potentially supporting 79 bears. By contrast, an assumed 0.5% decrease in annual death rate increased source areas by 13% to 10,371 km² potentially supporting 134 bears (Fig. 6a).

Source areas (2,840 km²) capable of supporting about 50 bears and a total area (5,493 km²) capable of supporting 100 bears (the approximate recovery goal for this ecosystem) roughly correspond to our 2.5% sustainable death rate scenario assuming a 2:1 ratio of unknown to known deaths (Figs. 7a and 8a). If we assume a population of three-quarters ($N = 75$) rather than half ($N = 50$) of the 100 bears needed to reside in source

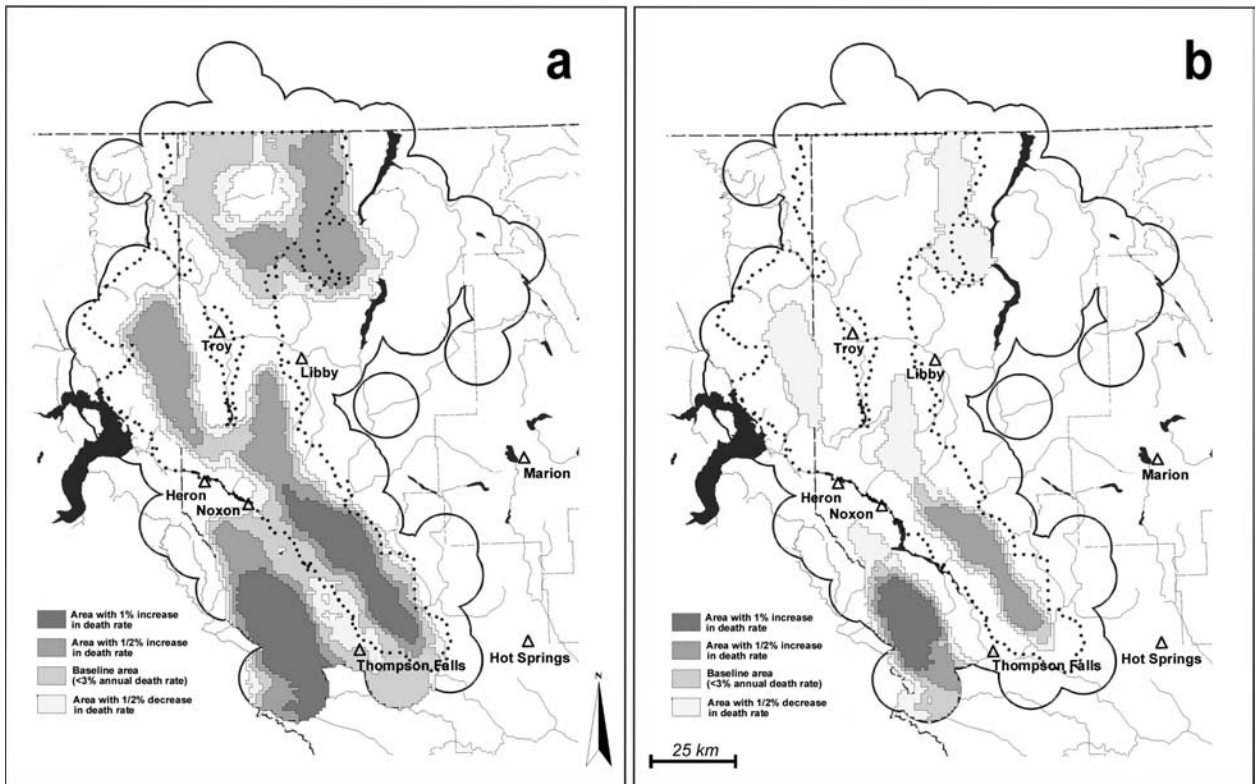


Fig. 7. The predicted location and extent of source areas in the Cabinet–Yaak region with a uniform human population increase of $1.5\times$ assuming (a) a 1:1 ratio of unknown to known grizzly bear deaths, and (b) a 2:1 ratio of unknown to known deaths. Darker gray shading corresponds to increasingly restrictive assumptions about sustainable mortality or human lethality. The Recovery Area is delineated by a dotted line. The solid black line delineates the sample area.

areas, source areas would need to be 50% larger and total $4,260\text{ km}^2$ (Fig. 8b). Both scenarios still result in a major gap between grizzly bear range in the Cabinet and Yaak portions of the study area and include a sizable source area outside the current Recovery Area boundary in the Coeur d'Alene Mountains.

These recovery scenarios differ substantially from the one that best matches the current population estimate of approximately 35 bears within the official Recovery Area. A population of this size is most closely approximated by a 2:1 ratio of unknown to known bear deaths and a 2% sustainable death rate, which yields a total $1,862\text{ km}^2$ of source areas containing about 16 bears. For this determination we assumed that about half the bears in a stable population live within source areas, as would be expected with high rates of movement between source and sink habitats (Doak 1995).

Discussion

The models presented here are based on *ad hoc* data and explanatory variables that are surrogates for parameters of more direct and fundamental interest: the frequency and lethality of contact between grizzly bears and humans (Mattson et al. 1996a). The logistics of directly measuring frequency of contact between humans and bears, and the likelihood that a human would kill a bear given an encounter, are enormous. The surrogates that we used to explain distributions of grizzly bear observations (roads and human densities) have well established effects on grizzly bear behavior and demography (McLellan 1990, Mattson et al. 1996b, Merrill et al. 1999, Woodroffe 2000, Mattson and Merrill 2002, Merrill and Mattson 2003), which is why we chose them for consideration. Road densities and assumed levels of human activity also potentially explained detection bias that undoubtedly affected the data used in this analysis.

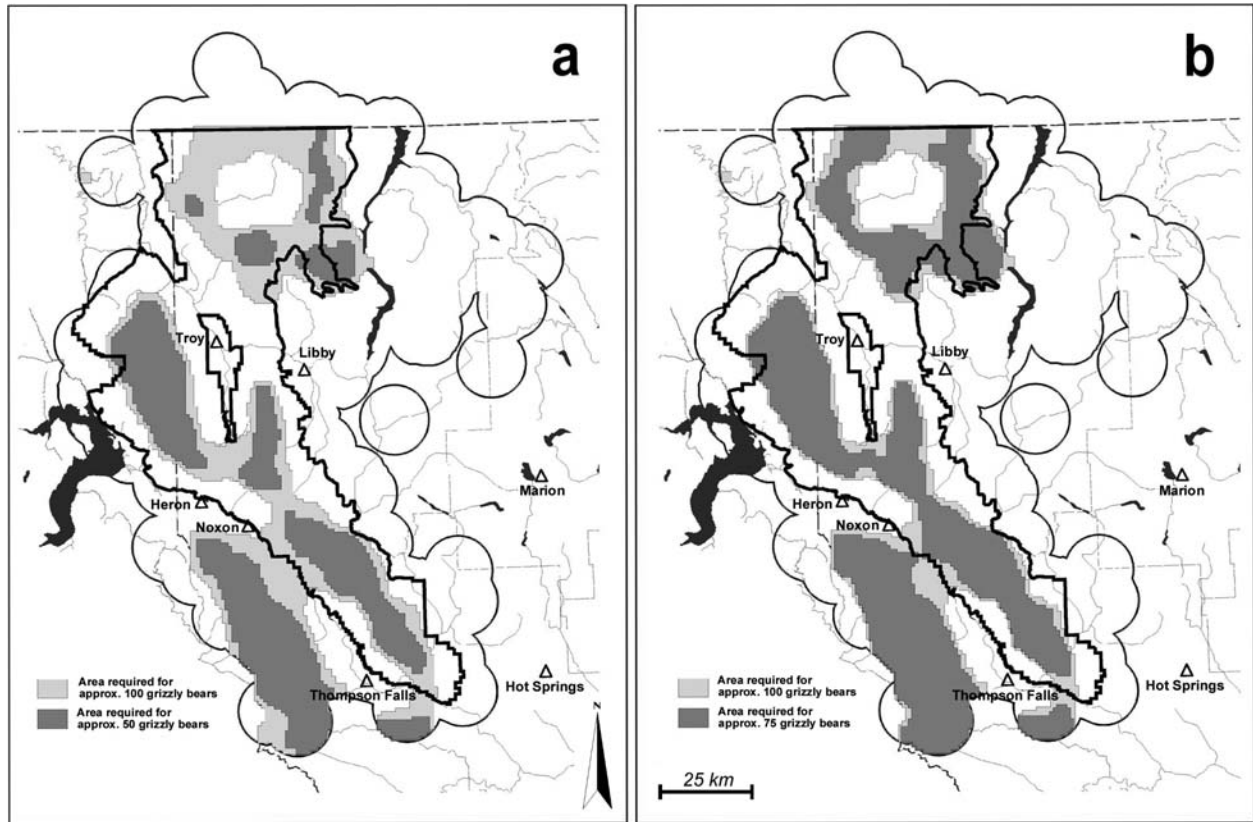


Fig. 8. The predicted location and extent of grizzly bear source areas and adjacent range capable of supporting 100 bears in the Cabinet–Yaak region, assuming a 2:1 ratio of unknown to known grizzly bear deaths and otherwise compatible levels of human lethality, (a) with source areas containing 50 bears and (b) with source areas containing 75 bears. The Recovery Area is delineated by a dotted line.

In fact, the positive polynomial effect of road density in our bear sign model very likely represented this bias.

Our results are consistent with a small range and small population of grizzly bears in the Cabinet–Yaak region. Within the 17,554 km² sample area, predicted total source area varied 5.6× in size, from 1,862 km² to 10,371 km², depending on assumptions about levels of human lethality and, relatedly, ratios of unknown to known deaths. These source areas, even if fully protected and fully occupied by grizzly bears (roughly 30 to 123 bears), are mostly well below the size thresholds commonly viewed as necessary to sustain grizzly bear populations (Woodroffe and Ginsberg 1998, Mattson and Merrill 2002, Wielgus 2002). Moreover, even under the most optimistic assumptions, and consistent with current observations (Kasworm et al. 2000), our model shows relatively complete isolation of grizzly bears in the Yaak region from conspecifics further south in the Cabinet Mountains.

The closest match of predicted bear numbers to the 30–40 estimated to exist in the Cabinet–Yaak region was obtained assuming a 2:1 ratio of unknown to known grizzly bear deaths and a sustainable annual death rate of about 2%. This was based on the related assumption that with $\lambda \approx 1$, about half of 35 bears would exist in source areas versus sinks (Doak 1995). This relatively pessimistic result could have been caused, mathematically, by an over-estimate of population size in the Cabinet–Yaak region (i.e., N is <35). If not, then this result implies several things. For one, the ratio of reported to unknown deaths may be lower than is currently thought (i.e., $<1:1$; McLellan et al. 1999, Kasworm et al. 2000). This, in turn, suggests that illegal human-caused grizzly bear deaths, which are rarely reported (Mattson 1998a, McLellan et al. 1999), may be relatively common. For another, a low sustainable death rate suggests that birth and recruitment rates may be low (Eberhardt 1990),

which is intriguing given the apparent richness of bear habitat and relatively high potential grizzly bear densities in the Cabinet–Yaak region. Female reproduction could be low simply because of problems finding a mate in this small, low-density population (i.e., the Allee effect; Stephens and Sutherland 1999).

High levels of competition with sympatric American black bears (*Ursus americanus*) could also cause low birth and recruitment rates among grizzly bears in this region. Grizzly bears can dominate, and occasionally kill, black bears in head-to-head competition (Ross et al. 1988, Mattson et al. 1992, Smith and Follmann 1993). However, our proposed explanation does not entail direct competition, but rather, scramble competition for food resources. Grizzly bears and American black bears exhibit considerable dietary overlap, probably because each species evolved in isolation from the other until the relatively recent evolutionary past (Herrero 1978, Mattson 1998b). In general, to the extent that meat is available, grizzly bears, especially adult males, eat more meat than do black bears (Mattson 1997b, Mattson 1998b, Jacoby et al. 1999). However, grizzly bears in the Cabinet–Yaak region are among those that eat the least meat (Jacoby et al. 1999). As a consequence, the diets of grizzly bears and black bears in this region are virtually indistinguishable and characterized by reliance on huckleberries (*Vaccinium* spp.; Kasworm and Their 1991). This common reliance on berries predictably puts grizzly bears at a disadvantage in scramble competition because of (1) the lower efficiencies of use associated with their larger average body size (Welch et al. 1997), and (2) the comparatively very high densities of black bears. The capture rate for black bears in the Cabinet–Yaak region (i.e., captured bears/trap night) has been about 10× greater than the capture rate for grizzly bears (Kasworm et al. 2000).

More optimistically, our model suggests some connectivity between the Cabinet–Yaak grizzly bear population and populations to the north, in Canada, or potential grizzly bear habitat to the south, in Idaho. The presence of a large block of potential but largely unoccupied grizzly bear habitat along the Idaho border is consistent with the results of different models used by Merrill et al. (1999) and Mattson and Merrill (2002). Even so, Proctor et al. (2002) suggest that potentially connective populations along the Canadian border are substantially isolated from large contiguous populations of grizzly bears farther north in British Columbia. Potential habitat to the south is similarly isolated by a major highway.

With the potentially critical exception of the patch to the south in the Coeur d'Alene Mountains, our results confirm the logic of recovery area boundaries in the Cabinet–Yaak region. Virtually all existing predicted source areas plus those needed to meet ecosystem-specific recovery goals are within the official Recovery Area. However, the patch in the Coeur d'Alene Mountains outside the Recovery Area could be critical to meeting longer-term recovery goals for grizzly bears in the contiguous United States. These goals include connectivity between potential grizzly bear habitat in central Idaho and occupied grizzly bear habitat in the Cabinet–Yaak region of both the U.S. and Canada (Shaffer 1992, Bader 2000). Central Idaho is, in turn, the most likely bridge to the currently isolated Yellowstone grizzly bear population (Mattson and Merrill 2002, Merrill and Mattson 2003).

Our analysis emphasizes the potential importance of regional human population sizes and local human activity to grizzly bear conservation, at least among factors influencing levels of contact between humans and grizzly bears. Of the human-related variables included in the bear sign model, regional human population sizes were the most important. This result is consistent with a growing body of evidence showing that number of people, as much as or more than road densities, govern the fate of grizzly bear populations (McLellan 1990, Merrill et al. 1999, Woodroffe 2000, Mattson and Merrill 2002, Merrill and Mattson 2003). Assuming this is so, our results suggest that it becomes much more difficult to sustain grizzly bear populations once local (i.e., within 60 km) human densities exceed 2.6 people/km², at least in regions similar to our study area. Our results also suggest that road access negatively impacts bears in the Cabinet–Yaak region, especially when total road densities exceed about 1.1 km/km².

The major effect of human numbers on the extent of predicted source habitat is significant because management attention has historically focused on road access and has almost altogether neglected the implications of human population growth for management strategies and mitigation. Looking back from the year 2000, it took 29 years for human populations in the Cabinet–Yaak region to grow 150%. At current growth rates, the population could increase by another 150% within 21 years. Unless other factors compensate for increased numbers of people, our results suggest that this growth could cause the loss of all source habitat in the Yaak area along with potential connectivity to Canadian bear populations.

Perhaps the most hopeful result of this analysis is the indicated importance of human lethality to determining

conditions for grizzly bears in the Cabinet–Yaak region. Human lethality is very difficult to directly measure. Even so, results of the source area model show that small changes in death rate or changes in the ratio of unknown to known bear deaths, both potentially attributable to variation in human lethality, could induce substantial changes in the sizes of grizzly bear source areas. This sensitivity may be unique to the configuration of habitat conditions in the Cabinet–Yaak region. Even so, our results suggest that levels of human lethality could largely determine the fate of the Cabinet–Yaak grizzly bear population. Certainly, it is in reducing levels of human lethality that there is greatest promise for mitigating the effects of prospective human population increases.

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