

GRIZZLY BEAR DENNING AND POTENTIAL CONFLICT AREAS IN THE GREATER YELLOWSTONE ECOSYSTEM

SHANNON R. PODRUZNY, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA, e-mail: srp@montana.edu

STEVE CHERRY, Department of Mathematical Sciences, Montana State University, Bozeman, MT 59717, USA, e-mail: cherry@math.montana.edu

CHARLES C. SCHWARTZ, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA, e-mail: chuck_schwartz@usgs.gov

LISA A. LANDENBURGER, U.S. Geological Survey, Northern Rocky Mountain Science Center, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA, e-mail: lisa_landenburger@usgs.gov

Abstract: Increasing winter use of steep, high-elevation terrain by backcountry recreationists has elevated concern about disturbance of denning grizzly bears (*Ursus arctos*) in the Greater Yellowstone Ecosystem (GYE). To help identify areas where such conflicts might occur, we developed a spatially explicit model to predict potential denning areas in the GYE. Using a scan area of 630 m around each location, we assigned site attributes to 344 den locations of radio-tracked grizzly bears from 1975–99. Attributes identified as predictors for the analysis included elevation, slope, an index of solar radiation, and forest cover. We used the Mahalanobis distance statistic to model the similarity between sites used by denning bears and each cell in the data layers. We used the final Mahalanobis distance model to produce maps of the study area. Potential denning habitat, based upon the model, is abundant within the GYE. Our results can be used by land management agencies to identify potential conflict sites and minimize effects of regulated activities on denning grizzly bears. We illustrate how the Gallatin National Forest (GNF) used the model to examine the overlap between potential snowmobile use areas and potential denning habitat as part of a Biological Assessment submitted to the U.S. Fish and Wildlife Service.

Ursus 13:19–28 (2002)

Key words: denning, geographic information system, GIS, Greater Yellowstone Ecosystem, grizzly bear, Mahalanobis distance, model, *Ursus arctos*

Grizzly bears are vulnerable to disturbance at their den sites (Linnell et al. 2000). During the denning period, bears survive an extended period of low (or no) food availability by obtaining all energy through metabolism of fat reserves (Folk et al. 1972, Nelson and Beck 1984, Ramsay and Dunbrack 1986, Hissa 1997, Hellgren 1998, Linnell et al. 2000). Production of young and lactation place additional energetic demands on reproductive females (Nelson 1973, Ramsay and Dunbrack 1986, Farley and Robbins 1995, Hellgren 1998, Linnell et al. 2000). Linnell et al. (2000) noted that because of these physiological demands and the importance of the den itself in meeting those demands, disturbance during the denning period may have more negative effects on bears than disturbance during other times of the year when bears are mobile and additional energy sources are available. Potential effects of disturbance to denning bears include elevated energy use associated with increased movements in the den (Reynolds et al. 1986, Schoen et al. 1987), den abandonment (Craighead and Craighead 1972, Reynolds et al. 1976, Harding and Nagy 1980, Schoen et al. 1987), potential loss of cubs (Schoen et al. 1987), and displacement from denning areas (Craighead and Craighead 1972, Schoen et al. 1987). Winter use of the GYE by recreationists has increased in recent years (Greater Yellowstone Coordinating Committee 1999). Public concern over the potential effects of increasing snowmobile activity on grizzly bears has grown. Consequently, the GNF, which has jurisdiction over the northern-most portions of the GYE, was sued over the adequacy of their

Forest Plan (GNF 1987) in addressing the impacts of snowmobiles and off-road-vehicles on grizzly bears (Sierra Club et al. vs. Garber et al. and Cooke City Chamber of Commerce et al. CV 00-12-BU-RWA). The identification of potential denning areas in the GYE would allow managers to address areas of potential conflict and thus minimize displacement or disturbance of bears from denning areas by snowmobiles.

Our primary objective was to identify grizzly bear denning habitat in the GYE. We used a GIS (geographic information system) to manipulate data from satellite imagery and known den locations to create a spatially explicit model. From the model, we mapped potential denning habitat and used those maps to estimate the overlap between snowmobile use areas and potential denning habitat on the GNF.

STUDY AREA

The study area included approximately 90,032 km² of the GYE (Fig. 1), including Yellowstone and Grand Teton National Parks and contiguous lands >1,500 m in elevation (Anderson 1991). The GYE forms the headwaters of 3 major watershed systems: the Missouri, Snake, and Green (Marston and Anderson 1991). The area is topographically diverse; terrain varies from gently sloping lava flows and alluvial outwashes to high-alpine plateaus and glaciated peaks. The central geologic feature of the area is the Yellowstone Caldera and Plateau. Climate in the region is typified by long, cold winters and cool summers

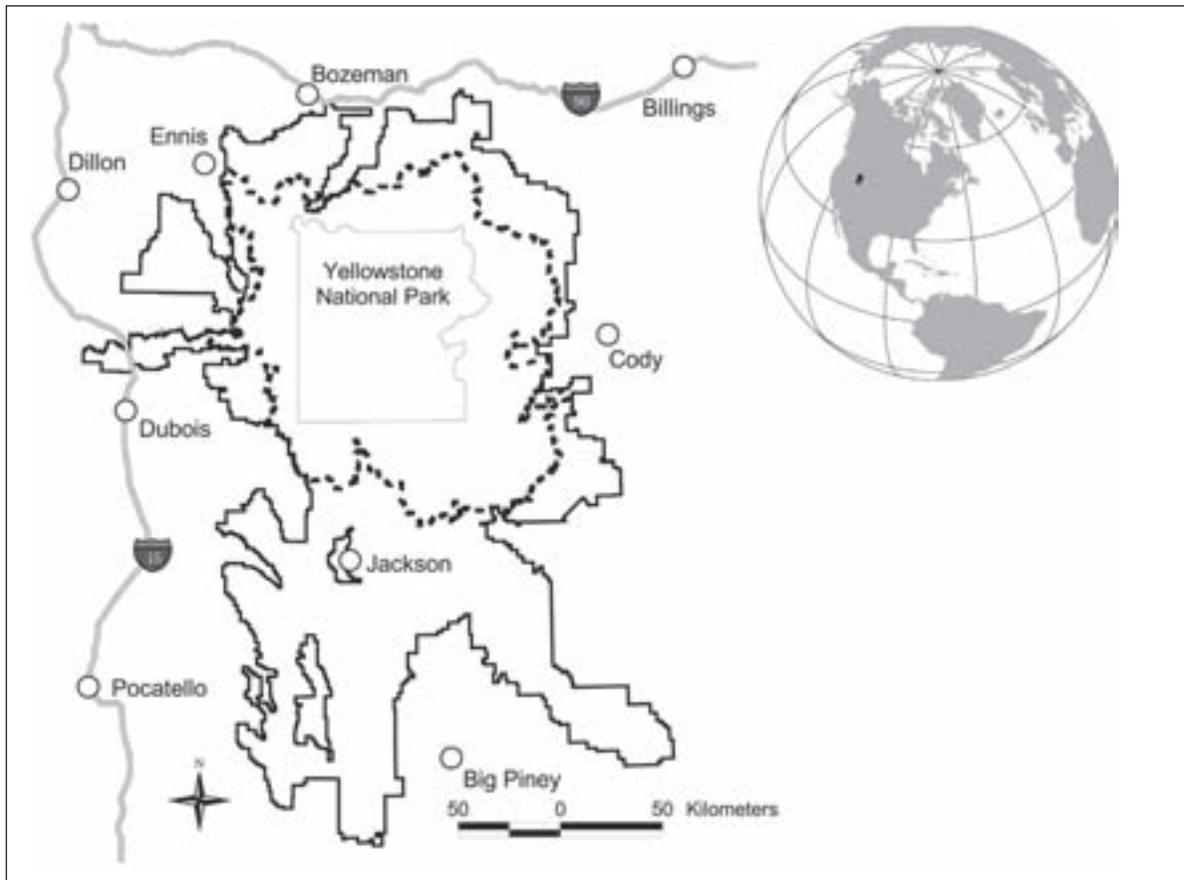


Fig. 1. Location of the Greater Yellowstone Ecosystem (GYE), USA, including contiguous publicly-owned lands (solid outline). Land management guidelines within the Yellowstone Grizzly Bear Recovery Zone (dashed line) emphasize protection of the grizzly bear and its habitat.

(Marston and Anderson 1991). Vegetation generally follows an elevational gradient (Patten 1963, Waddington and Wright 1974, Despain 1991, Romme and Turner 1991), with sagebrush (*Artemisia* spp.) range lands occupying lower elevations (<1,900 m) along the edges of the ecosystem and valley bottoms. Douglas-fir (*Pseudotsuga menziesii*; 1,900–2,200 m) and limber pine (*Pinus flexilis*) forests dominate lower slopes and drier sites, with quaking aspen (*Populus tremuloides*) occurring in the interface. Subalpine forests consist of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Whitebark pine (*Pinus albicaulis*) occurs at higher elevations to timberline (about 2,900 m). The highest elevations include alpine meadows and rock.

Important anthropogenic boundaries exist within the study area. The Yellowstone Grizzly Bear Recovery Zone (YGBRZ, U.S. Fish and Wildlife Service 1993) is centered around Yellowstone National Park and surrounding publicly owned land in the northern 2/3 of the study area. Management practices on federal lands within the YGBRZ

emphasize protection of the grizzly bear population. These lands are managed by 6 National Forests and 3 National Parks. Grizzly bears currently occupy the YGBRZ, and their range extends beyond that boundary, particularly to the south in Wyoming (Schwartz et al. 2002).

METHODS

Telemetry and Location of Den Sites

Grizzly bears were captured and fitted with radio transmitters with techniques described by Blanchard (1985), Knight and Eberhardt (1985), and Blanchard and Knight (1991). Locations of dens were identified by aerial telemetry from 1975–99 (Judd et al. 1986, Blanchard and Knight 1991). Widespread, large-scale fires occurred in the study area in 1988; we did not include den sites from years prior to 1988 that were located in subsequently burned areas. Our estimated telemetry error was approximately 300 m, based on comparisons of aerially estimated coordinates and GPS-acquired locations of retrieved

radiocollars (Interagency Grizzly Bear Study Team, unpublished data).

Modeling Denning Habitat

GIS can be used to model denning habitat. The Mahalanobis distance statistic, coupled with GIS, was used by Clark et al. (1993, 1998) and Knick and Dyer (1997) to model black bear (*Ursus americanus*) and black-tailed jackrabbit (*Lepus californicus*) habitat, respectively, and by Corsi et al. (1999) to model wolf (*Canis lupus*) distribution. We chose to use the Mahalanobis distance statistic rather than other multivariate techniques (e.g., logistic regression) because the technique does not depend on definition of study area or availability boundaries, thus eliminating problems caused by misclassification of available habitats as used or unused (Clark et al. 1993, Knick and Rotenberry 1998). Statistically, the Mahalanobis distance measure eliminates problems of interaction and covariation among variables commonly found in multiple regression techniques (Seber 1984, Knick and Rotenberry 1998). Therefore, we used the technique of Clark et al. (1993, 1998) by calculating the Mahalanobis distance on a landscape scale with a GIS to model potential grizzly bear denning areas in the GYE. The Mahalanobis distance statistic (MHD) is given by:

$$\text{MHD} = (x - \hat{\mu}) \hat{\Sigma}^{-1} (x - \hat{\mu})$$

where x is a vector of habitat characteristics associated with each map cell, $\hat{\mu}$ is the estimated mean vector of habitat characteristics at known den sites, and $\hat{\Sigma}^{-1}$ is the inverse of the estimated covariance matrix computed from the known den sites. We used SPlus (MathSoft, Inc. 1988) to estimate $\hat{\mu}$ and $\hat{\Sigma}$ from habitat variables collected at known den locations.

Attributes identified as predictors for the analysis included elevation (m), slope (in degrees), solar radiation index, and percent forest cover. Because circular measures cannot be used to calculate the Mahalanobis distance statistic, we chose to use the solar radiation index as a substitute for topographical aspect. We created GIS data layers for each of these variables in ARC/GRID format (Environmental Systems Research Institute, Inc. 1993) with 30-m map cells. Because we used spatial data classified from satellite imagery, we were able to map our large study area at this fine resolution. Elevation, slope, and solar radiation were derived from U.S. Geological Survey 30-m digital elevation models. We calculated solar radiation using an adaptation of Iqbal's (1983) equation that calculates hourly extraterrestrial radiation striking an arbitrarily oriented surface (K. Keating, U.S. Geological Survey, Bozeman, Montana, USA, personal commu-

nication, 2000). Lawrence and Parmenter (2001) created the cover type map using 30-m Thematic Mapper imagery acquired in 1993. We re-categorized the original vegetation classifications into "Forest", "Non-Forest", and "No Data" (water, urban areas, etc). No major changes in cover types, particularly within the YGBRZ, occurred between 1993–99. To accommodate telemetry error within our data, we attributed den locations from resampled GRIDs whose cell values were derived from a 630 m x 630 m (or 21 x 21 map cell) scan area of the original data around that cell. Scan areas were assigned mean elevation, slope, solar radiation, and percent of forested cells.

We used step-by-step matrix algebra among the 4 map layers to create a GIS layer of the Mahalanobis distance values for each 30-m map cell of the GYE. These Mahalanobis distance units represent the standardized squared distance in multivariate space between the set of sample variables from the cells of the data layers and an ideal den site represented by the mean values of known den locations (Clark et al. 1993). If the Mahalanobis distance value of a map cell was small, then the attributes of that area were similar to those at sites selected for dens, on average. Conversely, larger values indicated areas that were dissimilar to known den locations.

Defining Potential Denning Habitat

Methods of displaying and interpreting model outputs have not been standardized. Clark et al. (1993) recoded Mahalanobis distances to P -values based on a χ^2 probability distribution. Knick and Dyer (1997) and Knick and Rotenberry (1998) simply rescaled the Mahalanobis distances into 20% quantiles of the distribution for the study areas. We used the Mahalanobis distance values of existing den locations as guidelines and defined potential denning habitat as all cells with values below the highest values of the model at known den sites. Our objective in defining potential denning habitat was to identify where bear-human conflicts might occur. We interpreted map cells having values within the range of those found at known den sites as having the range of habitat characteristics used by denning grizzly bears. For this reason, we produced a map showing potential denning habitat with Mahalanobis distance values less than the 100th percentile of values of known den locations. The 100th percentile map of potential denning habitat would include the original 344 locations known to be used successfully for denning. We also chose to use the 80th percentile to illustrate the change in potential denning habitat as the vector of the Mahalanobis distance statistic decreased toward the mean. We tested the performance of our model by examining modeled values at 67 new grizzly bear den locations observed in 2000–01.

Model Application

The GNF requested that we map overlap between potential denning areas and snowmobile use areas based upon denning habitat maps defined at both the 80th and 100th percentile (M. Cherry, 2001, Biological assessment: the effects of snowmobile use on grizzly bears, Gallatin National Forest, U.S. Forest Service Gallatin National Forest, Bozeman, Montana, USA). In a separate effort, potential snowmobile use areas were mapped and digitized from U.S. Geological Survey topographic quadrangle maps (Greater Yellowstone Coordinating Committee 1999). Maps of designated wilderness and areas in which motorized use was prohibited were overlaid on the denning maps to identify areas that were protected or unprotected. In the final step, we mapped potentially vulnerable habitat by overlaying the map of snowmobile use areas on defined denning habitat open to snowmobiles. Using this approach, we produced output for the GNF management to examine both the quantity and the spatial distribution of overlap (M. Cherry 2001 unpublished report).

RESULTS AND DISCUSSION

Telemetry and Location of Den Sites

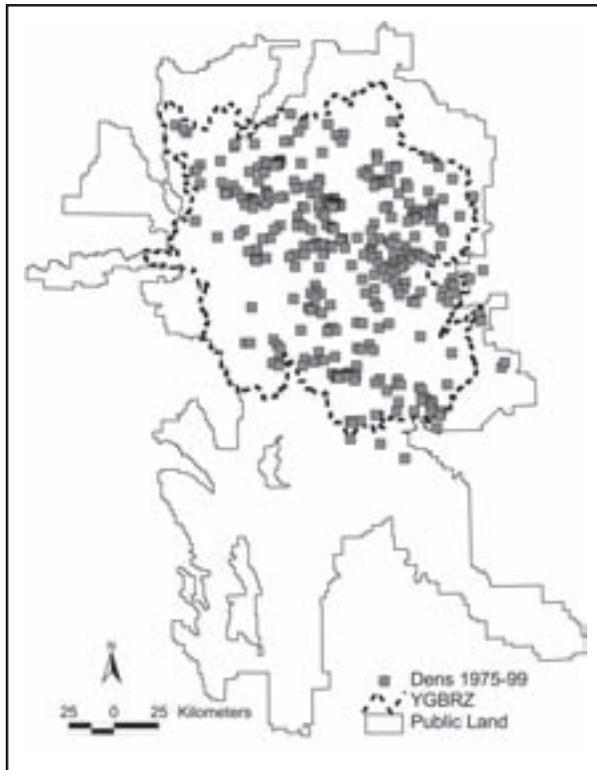


Fig. 2. Locations of 344 grizzly bear dens, Greater Yellowstone Ecosystem, USA, 1975–99. The heavy dashed line indicates the boundary of the Yellowstone Grizzly Bear Recovery Zone (YGBRZ).

We identified 344 den sites for 199 unique grizzly bears from 1975–99 (Fig. 2). We excluded 36 den sites from 1975–87 that were within the 1988 burn. Dens of 115 bears were located in only a single year, dens of 55 bears in 2 years, dens of 11 in 3 years, and dens of 18 in 4–9 years. The sample included 170 den locations of adult females, consisting of 61 with cubs-of-the-year (“cubs”, hereafter), 26 with yearlings, 18 with 2-year-olds, 35 lone adult females, and 30 of adult females of unknown reproductive status. The sample also included 46 den locations of subadult females, 56 of subadult males, and 72 of adult males. Mann-Whitney *U*-tests for differences in individual attributes between each of these groups showed no significant differences (Table 1); therefore, one general model was developed to represent potential denning habitat for all segments of the population.

Modeling Denning Habitat

The digital extent of our model encompassed a 92,032-km² portion of the GYE (Table 2, Fig. 3). This included areas inside and outside of public land boundaries and was limited by the spatial extent of data on the vegetation layer. Mahalanobis distance values from the model ranged from 0.001 to 74.833. The maximum value of the model at a known den location was 18.390 (Fig. 4).

Potential denning habitat appears abundant within the GYE (Table 2, Fig. 3, Fig. 5). According to the model using the 100th percentile as a cutoff, 66% of the GYE has potential for use by denning grizzly bears. Potential denning habitat also appears well distributed across the ecosystem (Fig. 3). The model outputs made biological sense; potential denning habitat appeared most often in places with some slope that would tend to hold snow. Elevation was an important influence on model outcomes; the highest and lowest elevations appear to be excluded from potential denning habitat. When compared to the 100th percentile, the 80th percentile model excluded areas with less forest cover and extreme flatness or steepness of slope, such as larger valleys or alpine peaks (Fig. 5).

We tested the model by comparing areas of potential denning habitat to 67 den locations used during 2000–01 (Fig. 6). Mahalanobis distance values of all 67 den locations fell within the range of previously observed values at den sites. Forty-eight (72%) were located in potential denning areas included in the 80th percentile model; all new dens were located in the 100th percentile model.

Model Application

Applying either of our definitions (i.e., the 80th or 100th percentile models), potential denning habitat is abundant on the GNF. The 80th and 100th percentile models identified 62% and 96%, respectively, of the GNF as potential denning habitat (Table 3). Applying maps of snowmo-

Table 1. Attributes of scan areas around 344 grizzly bear den locations, Greater Yellowstone Ecosystem, 1975–99.

	Elevation (m)		Slope (°)		Solar radiation		Forest (%)	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Pregnant females ^a $n = 61$	2,662	267	19	8.5	0.64	0.12	81	24
Other females $n = 155$	2,637	279	21	8.7	0.64	0.13	78	28
Males $n = 128$	2,621	237	19	8.1	0.63	0.12	86	23
All bears $n = 344$	2,636	261	20	8.2	0.64	0.13	82	25

^a Females emerging from the den with cubs.

Table 2. Area of potential denning habitat from a model based on Mahalanobis distance statistics (MHD) of landscape values at known grizzly bear den locations in the Greater Yellowstone Ecosystem, 1975–99.

Area	Total km ²	Percent potential denning habitat	
		MHD \leq 100 th percentile of den MHDs	MHD \leq 80 th percentile of den MHDs
Study area	92,032	66.0	37.3
Contiguous publicly owned land in the study area	51,072	93.3	58.8
Greater Yellowstone Grizzly Bear Recovery Zone (YGBRZ)	23,5261	95.9	66.3

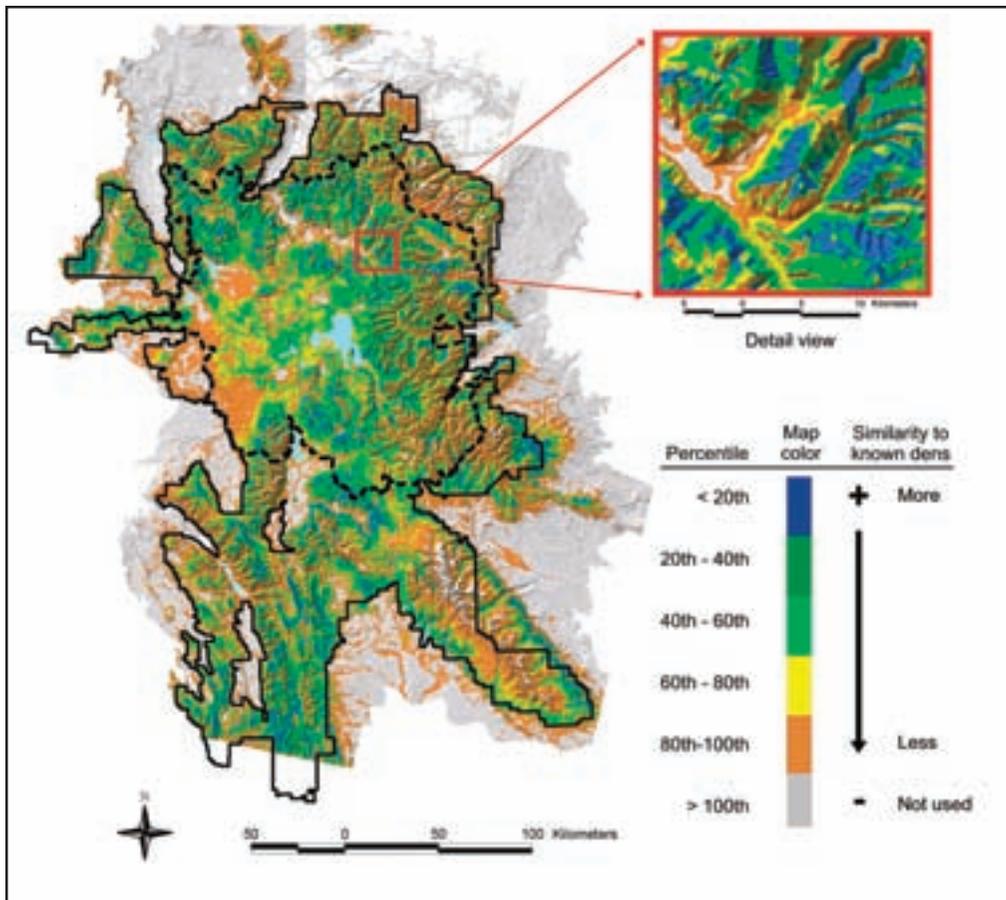


Fig. 3. Map cells of the Mahalanobis distance statistic from the mean habitat vector of habitat associations for grizzly bear dens in the Greater Yellowstone Ecosystem, USA, 1975–99 on public land (heavy, solid line) and in the Yellowstone Grizzly Bear Recovery Zone (dashed line). Map cell values were recoded relative to percentiles of model values at known den locations. Map cells with values greater than the maximum value at a den location were not considered potential denning habitat. The map image was draped over a digital elevation model to show the underlying topography. Major lakes are shown in light blue.

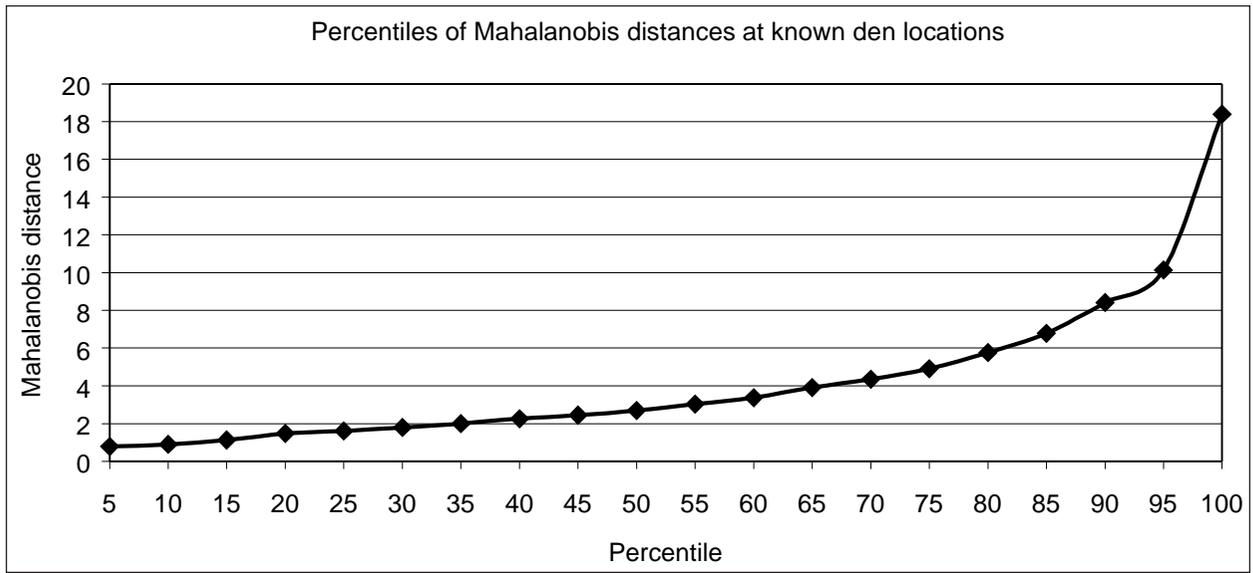


Fig. 4. Percentiles of Mahalanobis distance values from the model at 344 known den locations, in the Greater Yellowstone Ecosystem, USA, 1975–99.

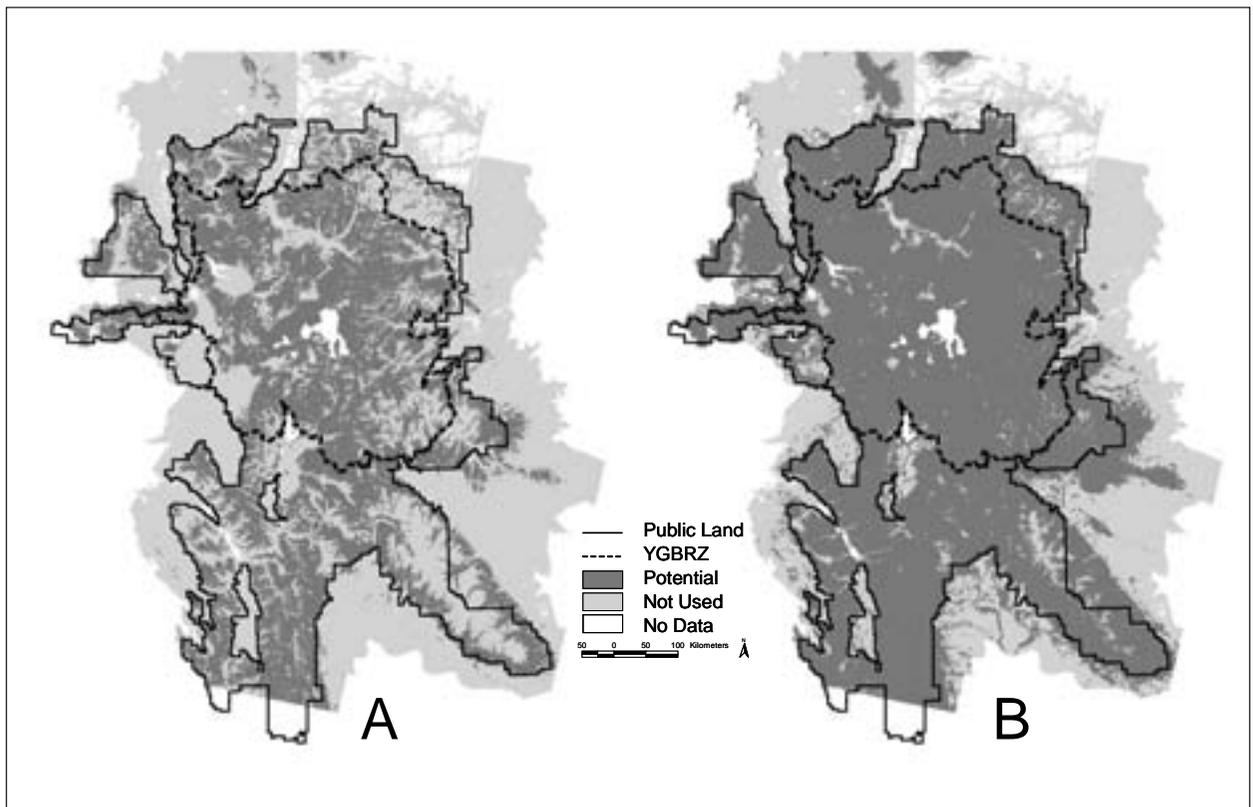


Fig. 5. Potential grizzly bear denning habitat identified using model values at less than the 80th (A) and 100th (B) percentiles of values at known den locations for the Greater Yellowstone Ecosystem, USA, including contiguous public land (solid line) and the Yellowstone Grizzly Bear Recovery Zone (dashed line). Major lakes were given model values of “No Data”.

bile-use areas to the 80th percentile model (Fig. 7) indicated that 57% of the defined denning habitat in unrestricted areas was potentially used by snowmobiles,

whereas only 26% of all potential denning habitat on the GNF was potentially vulnerable to snowmobile use (Table 3). The GNF incorporated these results into a Biological

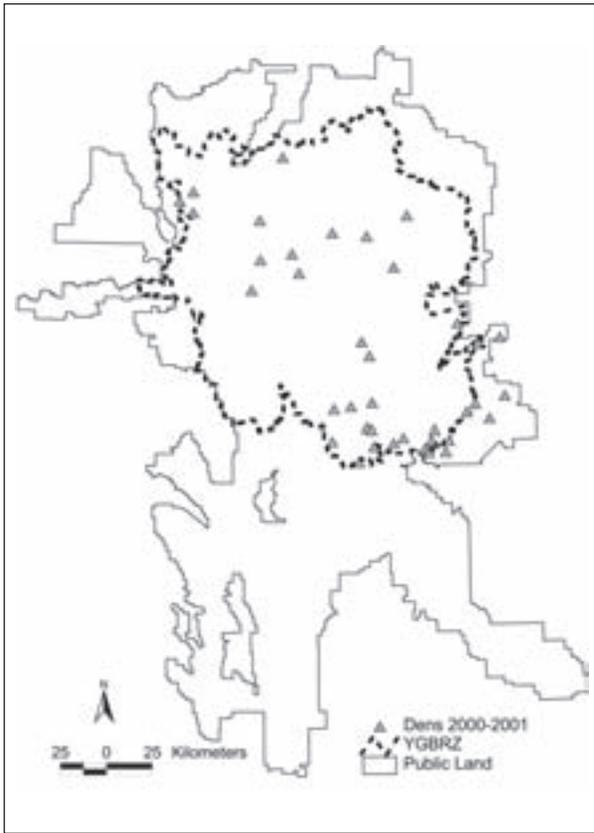


Fig. 6. Locations of 67 grizzly bear dens, Greater Yellowstone Ecosystem, USA, 2000–01. The heavy dashed line indicates the boundary of the Yellowstone Grizzly Bear Recovery Zone (YGBRZ).

Assessment submitted to the U.S. Fish and Wildlife Service (M. Cherry, 2001, unpublished report).

Our results are consistent with field studies of denning grizzly bears in the GYE and other locations. Linnell et

al.'s (2000) review of literature on den site selection by brown bears suggested that brown bears select den sites with stable snow conditions during the denning period. For bears in the Rocky Mountain region, these sites tend to be located at upper–middle elevations with a wide range of site aspects, often protected from the prevailing wind. Typical dens found by Vroom et al. (1976) in Banff National Park, Canada, were located in the upper subalpine–timberline areas on leeward slopes. Mace and Waller (1997) in the Swan Range, Montana, USA, found bears denning at higher elevations (>1,700 m) on steep slopes, and more often on open or open–timbered sites than on heavily forested sites. Judd et al. (1986) found that Yellowstone grizzlies used a wide variety of sites for denning, but dens were most often located on moderately steep, forested slopes with northerly exposures. In an earlier study, Craighead and Craighead (1972), found most dens in Yellowstone National Park, USA, on north–facing slopes at higher elevations (2,400–2,800 m) and often excavated under the roots of a tree. In each of these studies, at least 90% of the dens observed were excavated (Mace and Waller 1997, Linnell et al. 2000).

Our model, mapped at both the 80th and 100th percentiles, performed well when tested with new, independent observations of dens in the year 2000. There were no large-scale changes in the landscape prior to the collection of the new data, and these new dens were well distributed across the geographic range of previously observed dens. Knick and Rotenberry (1998) caution that because the selection function is based on a unimodal mean, any deviation, even if biologically positive, creates larger Mahalanobis distances and lower similarity values. They recommend this technique for mapping use areas when animals are distributed optimally, the landscape is well-sampled to determine the mean habitat vector, and

Table 3. Percent of potential grizzly bear denning habitat (as predicted by 2 classifications of a GIS-based model) open to motorized vehicles and used by snowmobiles on lands managed by the Gallatin National Forest (GNF), Montana, USA.

Geographic boundary	Model ^a	Percent land area			
		Potential denning habitat (PDH)	PDH used by snowmobiles ^b	PDH open to motorized vehicles ^c	PDH open to motorized vehicles used by snowmobiles
GNF ^d (6,628 km ²)	80 th	61.95	26.46	56.35	57.46
	100 th	96.24	24.47	54.79	51.24
GNF within YGBRZ ^e (3,417 km ²)	80 th	73.41	31.16	60.86	75.5
	100 th	96.57	30.65	60.63	72.98
GNF outside YGBRZ (3,211 km ²)	80 th	49.76	19.07	49.26	35.61
	100 th	95.89	17.85	48.53	33.42

^a Model 80th of potential denning habitat included map cells where the Mahalanobis distance value was less than the 80th percentile Mahalanobis distance value at known grizzly bear den locations, 1975–99. Model 100th included Mahalanobis distance values less than the 100th percentile value at den locations.

^b Greater Yellowstone Coordinating Committee (1999).

^c Forest Travel Plan (Gallatin National Forest 1987).

^d Included only portions of the GNF considered occupied grizzly bear habitat (i.e., south of Interstate 90, M. Cherry 2001 unpublished report).

^e Yellowstone Grizzly Bear Recovery Zone (YGBRZ; U.S. Fish and Wildlife Service 1993).



Fig. 7. Application of the 80th percentile potential denning habitat map by the Gallatin National Forest (GNF), Montana, USA. Snowmobile-use and snowmobile-prohibited areas (A) were overlaid on the map of potential denning habitat (B, in gray) to identify potential denning areas which are open to motorized use (C) and potentially used by snowmobiles (D).

distribution of the habitat variable does not change (Knick and Rotenberry 1998). Although the model extends beyond the current range of grizzly bears in the GYE, the topographic and vegetative characteristics of unoccupied areas are similar to occupied areas, and the extent of the model includes the historic range of grizzly bears.

Although we agree with Judd et al. (1986), who concluded that the availability of denning sites in the GYE is not limiting, our model can be used by land managers to identify potential conflict areas and thus minimize potential impacts of winter recreation and other activities on denning bears. Although both potential denning habitat maps included cells with a wide range of Mahalanobis distance values, those cells contained values within the

range of habitat characteristics found at locations used by denning grizzly bears. We can only interpret den sites with large Mahalanobis distance values as being less similar to average den locations than sites with small values. However, the mean vector of the multivariate distribution is not necessarily linked to the effectiveness of a den in meeting physiological and other survival needs. Both superior and inferior den sites may have combinations of variables that are similarly distant in multivariate space. Therefore, choosing lower percentile values (e.g., 50th or 25th) as cut points for defining potential denning habitat might allow managers to focus on areas most like an average den location, but these decisions would be biologically arbitrary. Using lower percentile values could

exclude sites where bears have denned successfully.

Although we can identify the geographic scope of overlap between denning areas and human activities, we lack data to quantify the degree of such disturbance on individuals and the population (Linnell et al. 2000). We do not have data to suggest that females with cubs are more or less susceptible to disturbance while in the den than other segments of the population, but our data suggest that the places they den are not different from those selected by the rest of the population in the GYE. Further research addressing other aspects of the impacts of snowmobiling disturbance to bears is needed. Bears, particularly females with cubs, may have more restricted habitat requirements and be more vulnerable to disturbance by snowmobiles immediately following den emergence than during the denning period (Mace and Waller 1997). Additional research is needed to identify spring habitats of post-emergent bears.

ACKNOWLEDGMENTS

We thank R. Lawrence and A. Hansen of Montana State University for the use of the digital vegetation map, without which the model extent would be limited. M. Haroldson managed the radiolocation database. D. Ouren provided valuable GIS expertise. M. Cherry (U.S. Forest Service) contributed helpful input throughout the project. We especially thank D. Knight (former IGBST leader) and B. Blanchard, retired members of the IGBST, who shepherded the study team from 1973 to 1997. We thank the pilots of the Gallatin Flying Service, Mountain Air Research, Mustang Aviation, and Sky Aviation who flew radiotracking flights and located dens. In particular, pilots D. Stradley, R. Stradley, S. Monger, G. Lust, and R. Hyatt have flown for many years. Personnel who were primarily responsible for bear captures include J. Jonkel, K. Inberg, B. Schleyer, C. Dickinson, M. Lamoreux, M. Haroldson, M. Ternent, M. Biel, K. Gunther, G. Holm, and K. Frey. V. Barnes, J. Clark, S. Knick, K. Podruzny, and K. West provided thoughtful and constructive reviews of the manuscript.

LITERATURE CITED

- ANDERSON, J.E. 1991. A conceptual framework for evaluation and quantifying naturalness. *Conservation Biology* 5:347-352.
- BLANCHARD, B.M. 1985. Field techniques used in the study of grizzly bears. Interagency Grizzly Bear Study Team, Bozeman, Montana, USA.
- , AND R.R. KNIGHT. 1991. Movements of Yellowstone grizzly bears, 1975–87. *Biological Conservation* 58:41–67.
- CLARK, J.D., J.E. DUNN, AND K.G. SMITH. 1993. A multivariate model of female black bear habitat use for a geographic information system. *Journal of Wildlife Management* 57:519–526.
- , S.G. HAYES, AND M. PLEDGER. 1998. Female black bear denning habitat model using a geographic information system. *Ursus* 10:181–185.
- CORSI, F., E. DUPRÉ, AND L. BOITANI. 1999. A large-scale model of wolf distribution in Italy for conservation planning. *Conservation Biology* 13:150–159.
- CRAIGHEAD, F.C. JR., AND J.J. CRAIGHEAD. 1972. Grizzly bear prehibernation activities and denning activities as determined by radiotracking. *Wildlife Monographs* 32.
- DESPAIN, D.G. 1991. *Yellowstone vegetation: consequences of environment and history in a natural setting*. Roberts Rinehart Publishers, Boulder, Colorado, USA.
- ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE, INC. 1993. ArcInfo Version 7.1.2. Redlands, California, USA.
- FARLEY, S.D., AND C.T. ROBBINS. 1995. Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Canadian Journal of Zoology* 73:2216–2222.
- FOLK, G.E. JR., M.A. FOLK, AND J.J. MINOR. 1972. Physiological condition of three species of bears in winter dens. *International Conference on Bear Research and Management* 2:107–124.
- GALLATIN NATIONAL FOREST. 1987. *Forest and Land Management Plan*. U.S. Department of Agriculture, U.S. Forest Service, Bozeman, Montana, USA.
- GREATER YELLOWSTONE COORDINATING COMMITTEE. 1999. *Winter use visitor management: a multi-agency assessment*. Final report of information for coordinating winter recreation in the Greater Yellowstone Area. Yellowstone National Park, Wyoming, USA.
- HARDING, L., AND J.A. NAGY. 1980. Responses of grizzly bears to hydrocarbon exploration on Richards Island, Northwest Territories, Canada. *International Conference on Bear Research and Management* 4:277–280.
- HELLGREN, E.C. 1998. Physiology of hibernation in bears. *Ursus* 10:467–477.
- HISSA, R. 1997. Physiology of the European brown bear (*Ursus arctos arctos*). *Annales Zoologica Fennici* 34:267–287.
- IQBAL, M. 1983. *Introduction to solar radiation*. Academic Press, New York, New York, USA.
- JUDD, S.L., R.K. KNIGHT, AND B.M. BLANCHARD. 1986. Denning of grizzly bears in the Yellowstone National Park area. *International Conference on Bear Research and Management* 6:111–117.
- KNICK, S.T., AND D.L. DYER. 1997. Distribution of black-tailed jackrabbit habitat determined by GIS in southwestern Idaho. *Journal of Wildlife Management* 61:75–85.
- , AND J.T. ROTENBERRY. 1998. Limitations to mapping habitat use areas in changing landscapes using the Mahalanobis distance statistic. *Journal of Agricultural, Biological, and Environmental Statistics* 3:311–322.
- KNIGHT, R.R., AND L.L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. *Ecology* 66:323–334.
- LAWRENCE, R.L., AND A.W. PARMENTER. 2001. Rule-based classification systems using classification and regression tree (CART) analysis. *Photogrammetric Engineering and Remote Sensing* 67:1137–1142.
- LINNELL, J.D.C., J.E. SWENSON, R. ANDERSEN, AND B. BARNES.

2000. How vulnerable are denning bears to disturbance? *Wildlife Society Bulletin* 28:400–413.
- MACE, R.D., AND J.S. WALLER. 1997. Final report: grizzly bear ecology in the Swan Mountains. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA.
- MARSTON, R.A., AND J.E. ANDERSON. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. *Conservation Biology* 5:338–346.
- MATHSOFT, INC. 1988. SPlus Version 5. Cambridge, Massachusetts, USA.
- NELSON, R.A. 1973. Winter sleep in the black bear: a physiologic and metabolic marvel. *Mayo Clinic Proceedings* 48:733–737.
- , AND T.D.I. BECK. 1984. Hibernation adaptation in the black bear: implications for management. *Proceeding of the Eastern Workshop on Black Bear Research and Management* 7:48–53.
- PATTEN, D.T. 1963. Vegetational patterns in relation to environments in the Madison Range, Montana. *Ecological Monographs* 33:375–406.
- RAMSAY, M.A., AND R.L. DUNBRACK. 1986. Physiological constraints on life history phenomena: the example of small bear cubs at birth. *American Midland Naturalist* 127:735–743.
- REYNOLDS, H.V., J.A. CURATOLO, AND R. QUIMBY. 1976. Denning ecology of grizzly bears in northeastern Alaska. *International Conference on Bear Research and Management* 3:403–409.
- REYNOLDS, P.E., H.V. REYNOLDS, AND E.H. FOLLMANN. 1986. Responses of grizzly bears to seismic surveys in northern Alaska. *International Conference on Bear Research and Management* 6:169–175.
- ROMME, W.H., AND M.G. TURNER. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conservation Biology* 5:373–386.
- SCHOEN, J.W., L.R. BEIER, J.W. LENTFER, AND L.J. JOHNSON. 1987. Denning ecology of brown bears on Admiralty and Chichagof islands. *International Conference on Bear Research and Management* 7:293–304.
- SCHWARTZ, C.C., M.A. HAROLDSON, K.A. GUNTHER, AND D. MOODY. 2002. Current distribution of grizzly bears in the Greater Yellowstone Ecosystem, 1990–2000. *Ursus* 13:203–212.
- SEBER, G.A.F. 1984. *Multivariate observations*. Wiley, New York, New York, USA.
- U.S. FISH AND WILDLIFE SERVICE. 1993. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- VROOM, G.W., S. HERRERO, AND T.T. OGLIVE. 1976. The ecology of winter den sites of grizzly bears in Banff National Park, Alberta. *International Conference on Bear Research and Management* 3:321–330.
- WADDINGTON, J.C.B., AND H.E. WRIGHT, JR. 1974. Late Quaternary vegetational changes on the east side of Yellowstone Park. *Quaternary Research* 4:1397–1415.

Received: 28 May 2001.

Accepted: 28 February 2002.

Associate Editor: Barnes.