# DISTRIBUTION OF GRIZZLY BEARS IN THE GREATER YELLOWSTONE ECOSYSTEM, 1990–2000

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, email: chuck\_schwartz@usgs.gov MARK A. HAROLDSON, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Forestry Sciences Lab, Montana State University, Bozeman, MT 59717, USA, email: mark\_haroldson@usgs.gov KERRY A. GUNTHER, Bear Management Office, Yellowstone National Park, WY 82190, USA, email: kerry\_gunther@nps.gov DAVE MOODY, Trophy Game Section, Wyoming Game and Fish Department, 260 Buena Vista, Lander, WY 82520, USA, email: dmoody@missc.state.wy.us

Abstract: The Yellowstone grizzly bear ( $Ursus\ arctos\ horribilis$ ) has been expanding its range during the past 2 decades and now occupies historic habitats that had been vacant. A current understanding of the distribution of grizzly bears within the ecosystem is useful in the recovery process and to help guide the state and federal land management agencies and state wildlife agencies of Idaho, Wyoming, and Montana as they prepare management plans. We used kernel estimators to develop distribution maps of occupied habitats based on initial sightings of unduplicated females (n = 300) with cubs-of-the-year, information from radiomarked bears (n = 105), and locations of conflicts, confrontations, and mortalities (n = 1,235). Although each data set was constrained by potential sampling bias, together they provided insight into areas within the Greater Yellowstone Ecosystem (GYE) currently occupied by grizzly bears. The current distribution (1990–2000) extends beyond the recovery zone identified in the U.S. Fish and Wildlife Service (USFWS) Recovery Plan. Range expansion is particularly evident in the southern portion of the ecosystem in Wyoming. A comparison of our results from the 1990s to previously published distribution maps show an approximate increase in occupied habitat of 48% and 34% from the 1970s and 1980s, respectively. We discuss data biases and problems implicit to the analysis.

Ursus 13:203-212 (2002)

Key words: distribution, grizzly bear, kernel density, range analysis, Ursus arctos, Yellowstone ecosystem

Prior to European settlement, the grizzly bear had an extensive distribution on the North American continent (Rausch 1963). With the advance of settlement, the grizzly bear was relegated to <2% of this historic range within the continental United States (USFWS 1993, Mattson et al. 1995). Today, the grizzly bear exists as 5 remnant populations south of Canada; only the Northern Continental Divide and GYE populations contain >350 individuals (Servheen 1999).

The Yellowstone grizzly bear was listed as a threatened species in 1975 (USFWS 1993). Since that listing, efforts to move toward recovery of the species have included preparation and multiagency implementation of 2 versions of a Recovery Plan (USFWS 1982, 1993). One of the tasks in the 1993 Recovery Plan was the preparation of the Conservation Strategy for the grizzly bear in the Greater Yellowstone Ecosystem; a draft was released in 2000 (USFWS 2000a). In addition, the States of Idaho, Wyoming, and Montana are currently developing state management plans that would apply if grizzly bears were delisted.

The Recovery Plan defined a recovery zone as "the area in each grizzly bear ecosystem within which the population and habitat criteria for achievement of recovery will be measured" (USFWS 1993:17). The recovery zone was not intended to include all areas of grizzly bear occupancy, and "bears can and are expected to exist outside the recovery zone lines in many areas" (USFWS 1993:18). When the recovery zone for the Yellowstone grizzly was established in 1982, it contained the known distribution of bears at that time. This area, renamed the Primary Con-

servation Area (PCA) in the Draft Conservation Strategy (USFWS 2000*a*), encompassed 23,833 km². The PCA was defined as the area that contained the seasonal habitat components needed to support a recovered population within the GYE (USFWS 2000a:22). However, grizzly bear range currently extends beyond the PCA. Range expansion is particularly evident in the southern portion of the ecosystem in Wyoming.

Counts of unduplicated females with cubs-of-the-year (Knight et al. 1995) serve as an estimate of minimum population size in the Recovery Plan (USFWS 1993). Counting females with cubs-of-the-year in a 16-km (10-mile) perimeter area surrounding the recovery zone is part of this recovery criterion (UFSWS 1993), and these counts have been ongoing since 1993. Counting known humancaused mortalities in the 16-km zone has also been in place since 1993 as per directions of the USFWS (C. Servheen, USFWS, Missoula, Montana, USA, personal communication, 2001). The 16-km area was established to accommodate females living in the recovery zone that had home ranges extending beyond this zone. These criteria were included in the Draft Conservation Strategy but were met with confusion and resistance, particularly among a committee of citizens appointed by the governors of Idaho, Montana, and Wyoming to review the document (USFWS 2000b). This committee recommended removal of these criteria.

Understanding the current distribution of bears within the ecosystem is useful in the recovery process and can provide guidance to federal land managers and managers from Idaho, Montana, and Wyoming as they prepare their management plans. Here, we present range distribution maps for the grizzly bear in the GYE during the 1990s. We compare our results with previously published distribution maps from the 1970s and 1980s and discuss data biases and problems implicit to the analysis.

#### STUDY AREA

The study area encompasses the GYE, which includes Yellowstone and Grand Teton National Parks and adjacent federal, state, and private lands in portions of Montana, Wyoming, and Idaho. The GYE is geographically defined as the Yellowstone Plateau and surrounding mountain ranges either above 2,130 m (Marston and Anderson 1991) or 1,500 m (Anderson 1991, Patten 1991). We prefer the 1,500 m elevation because all 10,022 radiorelocations of grizzly bears in the GYE (1975–2000) range between 1,584 and 3,656 m in elevation.

The GYE contains the headwaters of 3 major continental-scale river systems: the Missouri–Mississippi, Snake–Columbia, and Green–Colorado. Aspects of the underlying geology, hydrology, climate, and elevation are described by Marston and Anderson (1991). Long, cold winters and short summers characterize the climate of the Yellowstone Plateau. Precipitation generally increases with elevation and is typically greatest on the windward sides of mountain ranges. Precipitation occurs throughout the year (Baker 1986), with a peak in late spring at lower elevations and drier conditions during summer and fall (Weaver 1980). The highest elevations have a distinct winter peak in precipitation, particularly in western portions of the ecosystem (Despain 1987).

Patterns of precipitation and temperature produce predictable vegetation patterns (Marston and Anderson 1991). At low elevations, foothill grasslands or shrub steppes occur. With increasing moisture, open stands of Rocky Mountain juniper (Juniperus scopulorum), limber pine (Pinus flexilis), and Douglas-fir (Pseudotsuga menziesii) occur. Douglas-fir forms the lowest-elevation forest community at around 1,900-2,200 m (Patten 1963, Waddington and Wright 1974, Romme and Turner 1991). Lodgepole pine (Pinus contorta) dominates the extensive Yellowstone Plateau at mid-elevations, where poor soils formed from rhyolite predominate (Despain 1990). With increasing elevation, spruce-fir or subalpine forests dominate. Engelmann spruce (Picea engelmannii) and whitebark pine (Pinus albicaulis) form the upper tree line (2,600-2,900 m) around 2,900 m (Patter 1963, Waddington and Wright 1974, Despain 1990). Alpine tundra occurs at the highest reaches of all major mountain ranges.

#### **METHODS**

## **Data Sources**

We used locations of grizzly bears from 1990–2000 to generate current distribution maps. Data sources included: (1) initial observations of unduplicated females with cubsof-the-year, (2) relocations of radiocollared bears, and (3) locations of conflict and confrontations between grizzly bears and humans and locations of documented grizzly bear mortalities (hereafter referred to as conflicts).

Unduplicated Females.—In 1973, the Interagency Grizzly Bear Study Team (IGBST) began documenting observations of females with cubs-of-the-year to record quasi-quantitative data on the population (Knight et al. 1995). Family groups are more readily observed because they spend more time in open habitats during daylight hours than other bears (Blanchard and Knight 1991). Family groups also have more distinguishing characteristics than single bears, such as number of young, size differentials, and color markings. Although the process is subjective, standard criteria to distinguish unique groups have been established (Knight et al. 1995). Tallies of females with cubs-of-the-year may include repeated observations of the same family. Here, we only used the initial sighting of unique females with cubs-of-the-year (hereafter referred to as unduplicated females), thus giving equal weight to all individuals.

Radiotelemetry Locations.—Each year, members of the IGBST radiomarked a sample of bears for research and monitoring purposes. Additionally, some bears associated with bear-human conflicts were trapped (management bears) and transported or released on site. All of these bears, with the exception of dependent young, were also collared. Each year, from 1990-2000, there were 35 to 84 ( $\bar{x} = 59$ ) bears wearing radiotransmitters. We used radio-relocations from grizzly bears captured for research and management purposes to generate a distribution. Rather than construct a single distribution using all relocations from all bears, we constructed home ranges for each bear with cumulatively ≥30 relocations, giving equal weight to bears rather than relocations. We did this because some individuals were radiotracked over several years, whereas others were tracked for shorter durations. Individual home ranges constructed for each bear were then overlaid and the outermost boundary produced by the resulting composite polygon was used to delineate the distribution.

Home ranges of individual bears included all locations collected during the time that an individual wore a transmitter. Our sample only included individuals who were alive during the decade of the 1990s (n = 105), although

we included relocations prior to 1990 for bears alive during the 1990s. For bears captured in research sampling, we used all locations with the exception of den sites, where only 1 location was used per site. For bears that were transported for management purposes, we used locations taken after the bear had established a new home range (>1 year after relocation) or had returned to an established home range known to us. For individuals with data collected before and after transport, with obviously distinct ranges, we divided their locations into 2 groups and constructed kernel ranges for each group with ≥30 relocations. We did this because the single kernel range constructed from all locations had a bimodal shape and included area between the 2 clusters of points likely unused by the bear.

Conflict Reports.—Prior to 1992, records of grizzly bear-human conflicts, confrontations, and mortalities in the GYE were dispersed among many agencies and individuals (Gunther et al. 1993). The Yellowstone Ecosystem Subcommittee and the Interagency Grizzly Bear Committee recognized the need to consolidate and standardize the collection of conflict data and assigned the duty to Yellowstone National Park. Since 1992, conflict information has been collected and recorded in a standard format (Gunther et al. 1993). We used conflict records (1992–2000) reported by Gunther et al. (1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000, 2001). Each record in the database represents a bear-human conflict, confrontation, or mortality on a single day. Consequently, the conflict report does not differentiate individual bears at conflict sites with the exception of mortalities. We used only 1 observation where multiple conflicts occurred in the same area (identical coordinates), thus giving equal weight to each location.

Historic Distribution.—Both Basile (1982) and Blanchard et al. (1992) used observations of females accompanied by young of all ages to map distribution for the 1970s and 1980s, respectively. We initially attempted to construct a map for the 1990s using similar data. However, our dataset was less complete because observers did not report females with young larger than cubs-of-theyear as they did when bears were more rare. Reporting interest to a large degree has waned over time. Consequently, we used initial observations of unduplicated females for comparisons. Of all the data sets, observations of unduplicated females were collected most consistently through time. We constructed range distributions by decade to evaluate changes in distribution and for comparison to previously published results. We used data from observations of unduplicated females collected from 1973 to 2000 to illustrate comparative changes in distribution through time. We divided this data set into 3 periods, 1973-79, 1980-89, and 1990-2000. We used the 197379 and 1980–89 periods because 2 previously published papers (Basile 1981, Blanchard et al. 1992) used them. We also investigated more equal intervals (1973–82, 1983–91, and 1992–2000), but this did not change the interpretation.

# Spatial Analyses

Field studies commonly record data on the locations of organisms, and such observations can be used to describe the home ranges of individuals or the distribution of taxa (Seaman and Powell 1996, Powell 2000). Previous research has demonstrated that kernel methods can provide more accurate estimates of home range than the harmonic mean or the minimum convex polygon models (Naef-Daenzer 1993, Worton 1995, Seaman and Powell 1996, Swihart and Slade 1997). Kernel methods estimate the utilization distribution, which is the distribution of an animal's position on a plane (Worton 1989).

Kernel estimators are nonparametric, thus avoiding assumptions about normality. However, no method exists to approximate sample sizes because they lack associated variance estimators (White and Garrott 1990). Recent studies by Seaman et al. (1999) evaluated issues of sample size relative to accuracy of range size prediction. They concluded that the fixed kernel with smoothing selected by least-squares cross-validation (LSCV) provides the least biased and lowest surface fit error estimates of the 95% home range area. Bias of the inner contours is greater than bias of the 95% contour. The general trend for adaptive kernel estimates is opposite. The adaptive kernel with LSCV smoothing is satisfactory up to the 80% contour but overestimates areas at the 95% contour. Hence fixed kernels more accurately define the surface area of use, whereas adaptive kernels more accurately define areas of high use. Additionally, the fixed kernel with LSCV has the lowest frequency and magnitude of poor estimates. Large relative mean squared errors occur most frequently with very small sample sizes (10–20) and are rare (<0.3%of replicates) for fixed kernel with LSCV when sample sizes are ≥30. Seaman et al. (1999) recommend a minimum sample size of 30 observations when using LSCV.

Based on these findings, we calculated the 95% utilization distribution using the fixed kernel estimator with LSCV as the smoothing parameter, with a sample size ≥30. We used the software package Animal Movements (Hooge and Eichenlaub 1997), which is available as an ArcView® GIS program extension at http://www.absc.usgs.gov.gistools/animal\_mvmt.htm. The LSCV follows Silverman (1986).

Autocorrelation, resulting from a short sampling interval (Swihart and Slade 1985), was not a problem with the data used for this analysis. Observations of unduplicated females and mortalities represented different individuals

and were hence uncorrelated. Radio-relocation data were collected every 7–10 days on average, thus reducing problems with autocorrelation. It was more difficult to determine autocorrelation for conflict reports. Bear–human conflict records could represent repeated conflicts of the same bear on subsequent days. Consequently, we used only 1 conflict from any specific area (no matching Universal Transverse Mercator coordinates), thus eliminating multiple events in the same location. This restriction should make conflicts nearly independent of each other with the exception of an individual bear creating conflicts on subsequent days in slightly different areas. Autocorrelation in a small number of these conflicts would underestimate the distribution (Swihart and Slade 1985).

Because we constructed range maps using 3 databases, and each was expected to be slightly different, we also constructed a range map showing overlap among them. We did this by converting each of the 3 range estimates into grids with 30- x 30-m pixels. These grids were then combined to depict overlap.

## **RESULTS**

#### Current Distribution

The fixed kernel range constructed from observations

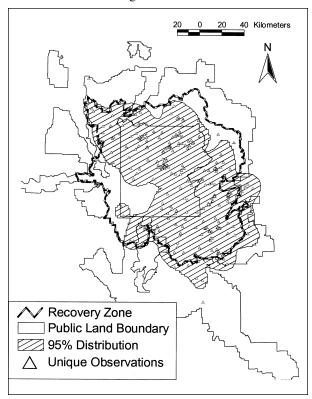


Fig. 1. Fixed kernel distribution constructed with unique observations (n = 300) of female grizzly bears with cubs-of-the-year in the Greater Yellowstone Ecosystem, 1990–2000.

(n = 300) of unduplicated females (Fig. 1) during 1990–2000 encompassed 22,904 km<sup>2</sup>, with 83% and 98.7% within the recovery zone and the 16-km perimeter area, respectively. Only 1.3% (299 km<sup>2</sup>) was outside the 16-km perimeter area (Table 1).

The fixed kernel range constructed from radiotelemetry relocations (n = 107 home ranges, 105 individuals; Fig. 2) approximated the distribution defined by unduplicated females but encompassed more area (26,573 km²) and showed that grizzly bears in the GYE extend beyond the recovery zone, particularly in the southeastern and southern portions of the ecosystem. The recovery zone and the 16-km perimeter area encompass 77.4% and 95.3% of the defined area, respectively.

The distribution map (Fig. 3) constructed from conflict locations (n=1,235) encompassed 30,652 km², with 65.8% and 87.2% contained within the recovery zone and the 16-km perimeter, respectively. Some conflicts, both on public and private land, occurred beyond the distribution boundaries, especially on the Beaverhead, Targhee, and Gallatin National Forests (Fig. 3). The distribution based on conflict locations was greater than both unduplicated female and radiotelemetry ranges.

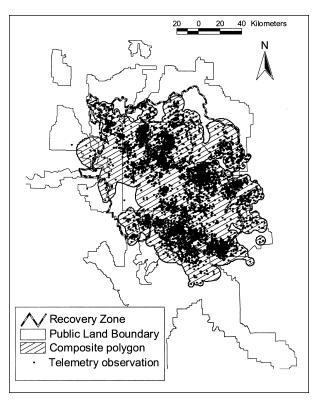


Fig. 2. Distribution of grizzly bears in the Greater Yellowstone Ecosystem, 1990–2000, constructed from 105 unique radiocollared bears with ≥30 relocations/individual. Fixed kernel ranges for each bear were overlaid and the outermost boundary produced by the composite polygon are presented here.

Table 1. Area (km²) of grizzly bear distribution based on fixed kernel range estimators in the Greater Yellowstone Ecosystem, 1990–2000. The merged range was developed from the union of the outer boundary of the overlaid distributions. See text and Fig. 5 for details.

Data source	No. of locations	Total area (km²)	Area within Recovery Zone (%)	Area within Recovery Zo 16-km perimeter (%	
Unduplicated females	300	22,904	83.0	98.7	
Telemetry	6,445	26,573	77.4	95.3	
Conflicts	1,235	30,652	65.8	87.2	
Merged distributions (outer union)		34,416	65.5	87.7	

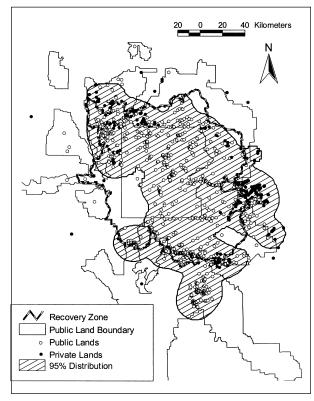


Fig. 3. Fixed kernel distribution constructed with locations of grizzly bear-human conflicts, confrontations, and mortalities in the Greater Yellowstone Ecosystem, 1992–2000.

# Comparisons with Historic Distributions

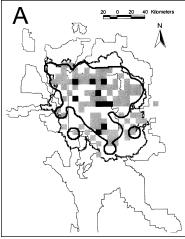
Distribution maps constructed with observations of unduplicated females during the 1990s (n = 300) encompassed 22,904 km², whereas those constructed for the 1980s (n = 148, 1980–89) and 1970s (n = 84, 1973–79) encompassed 17,086 km² and 15,424 km², respectively. This reflects an 11% and 34% increase in occupied range from the decade of the 1970s to the 1980s and 1980s to the 1990s, respectively; occupied range increased 48% from the 1970s through the 1990s (Fig. 4). Comparisons among periods showed an expansion of bears into the southeastern portion of the GYE into the Washakie Wilderness area on the Shoshone National Forest. Additional

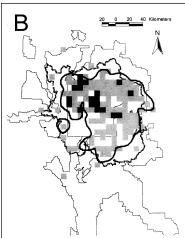
expansion occurred south into the Teton Range and the Gros Ventre and Green River drainages. During this same period, observations of unduplicated females have not declined within Yellowstone National Park (i.e., core of the recovery zone; IGBST, unpublished data).

#### DISCUSSION

The distribution maps presented here vary in size and shape depending upon which data were used to construct the distribution. The unduplicated female data set represents the smallest distribution. By definition it excluded males, which tend to have larger home ranges and more exploratory movements than females, resulting in a conservative estimate of distribution. The unduplicated female data were collected in a consistent manner during the past decade. Their main application was to estimate the minimum number of adult females within the population (Knight et al. 1995). The criteria for distinguishing unique females have evolved since 1975, but were standardized around 1986. The number of observations in any given year may be influenced by food abundance (Picton et al. 1986), survey effort (Mattson 1997), and the proportion of females with cubs. Observation flights were conducted annually by the IGBST to document unduplicated females. Observation effort increased through time (Mattson 1997), and survey areas beyond the recovery zone were added in 1998 (Schwartz 1999). However, most effort has focused on the recovery zone. As a consequence, one would expect more sightings within this area of the ecosystem and fewer on the perimeter. During the 1970s and likely through the first half of the 1980s, grizzly bear distribution was contained within the recovery zone. As bears began to expand into unoccupied habitats beyond the recovery zone during the 1990s, our knowledge of their distribution likely lagged behind actual occupancy. Such a lag in information and sighting effort beyond the recovery zone, particularly for unduplicated females, would result in an underestimation of range expansion and current distribution during the 1990s.

Basile (1982) and Blanchard et al. (1992) used these data in combination with observations of females with older young to depict bear distribution, providing impor-





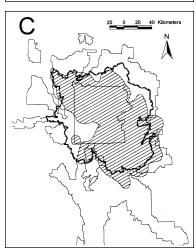


Fig. 4. Distribution maps for grizzly bears in the Greater Yellowstone Ecosystem for (A) 1973–79, (B) 1980–89, and (C) 1990–2000. Shaded squares (100-km² cells) are from Basile (1982) for the 1970s and Blanchard et al. (1992) for the 1980s. Gray cells indicate occupancy in <50% of years studied, whereas black cells represent occupancy in >50% of years studied. We constructed the distributions (polygons) shown on all 3 maps based on fixed kernel ranges of unique observations of females with cubs-of-the-year.

tant baseline data for comparison. Because we only used the initial observation of unique females with cubs-of-the -year, we did not expect our depictions of historic distribution to match what they identified. Although our distribution maps constructed from observations of unduplicated females during the 1970s and 1980s are not identical to the maps constructed by Basile (1982) and Blanchard et al. (1992), they approximate each other visually (Fig. 4). Additionally, our coverages for the 1970s and 1980s included 84 of 102 (83%) 100-km² cells identified by Basile (1982) and 91 of 110 (87%) cells identified by Blanchard et al. (1992), respectively. We feel confident that our kernel estimates of ranges by decade depict approximate range expansion from the 1970s through the 1990s.

The range map constructed from radiotelemetry locations included a sample of bears marked for research and management monitoring. The IGBST trapped throughout the ecosystem, but efforts were confined primarily to the recovery zone. Effort during the 1990s extended beyond the recovery zone, especially in Wyoming on the southern boundary. Some areas in the GYE were either not trapped or trapping efforts were unsuccessful. These areas included the northern portion of the Absaroka Beartooth Wilderness, the Pitchstone Plateau, and the Centennial, Gravelly, and Tobacco Root mountains. Efforts were made during 1992-94 to trap and mark bears on the Madison and Pitchstone Plateaus with very limited success (1 bear collared). The Centennial Mountains were trapped during 1991, with no grizzly bears captured. Consequently, the distribution based on telemetry locations may not represent some areas occupied by bears where none were radiocollared.

Research trapping was supplemented by management efforts because some problem bears were captured and radiocollared. Some of these bears were released on site (primarily non-target individuals), but others were translocated to more secure habitats within ecosystem. Many translocated bears returned to their capture origin (Blanchard and Knight 1995). Most management trapping occurred outside the national parks and wilderness areas, either on lands managed by the Forest Service or in private ownership. Consequently, several areas on the perimeter of the ecosystem were sampled, which would tend to make the telemetry coverage more inclusive. However, there were likely areas occupied by grizzlies that we did not identify.

The distribution constructed from conflict locations was the largest. We anticipated this because many conflicts occurred on the periphery of the ecosystem or outside some habitats considered suitable for grizzly bears. The conflict data did not represent a random sample from an unknown bear distribution. Rather, the distribution from which they were drawn was actually a mixture of the distribution of human activity and the bear distribution. Areas within this distribution represented places ranging from high human use (towns and subdivisions) with low bear use to areas having high bear use with low human use (backcountry). Some conflicts reflected dispersing subadults and bears lured into unsuitable habitats. Additionally, conflict distributions were influenced by past management actions implemented within the recovery zone in the mid-to-late 1980s in an effort to minimize bearhuman conflict and mortality (Mattson 1990, Gunther 1994). These included garbage management, implementation of backcountry food storage requirements, and removal of domestic sheep grazing allotments. Conflicts have since been reduced within the recovery zone (Gunther 1994, Gunther et al. 2003). Similar management actions have not been implemented outside the recovery zone where many conflicts currently occur. Consequently, locations of conflicts and mortalities are often our first indication of grizzly bears occupying new habitats; they also identify areas where managers should implement or develop new programs.

There is considerable interest in knowing the current distribution of grizzly bears in the GYE, and many managers would prefer a single map. However, it is difficult to clearly define what constitutes a "distribution". For example, should exploratory forays by subadult males be given equal weight to areas habitually used by adult females? The analytical methods we used here provide precise estimates such as the 95% distribution from a given data set. However, these methods are statistical estimators and make no judgments about habitat quality, security, or other needs of bears. As such, they can and do include areas unused by bears and exclude areas used by bears. For example, the peripheral areas often have the fewest data, and our ability to provide accurate estimates in these regions is limited (Seaman et al. 1999). Consequently, no single distribution represents the best depiction of occupied grizzly bear habitat in the GYE. Each is a different shape and size depending upon sample size and sample distribution; they measure different aspects of distribution. Overlaying the 3 distributions identified areas of intersection and an outermost perimeter (Fig. 5). This outer perimeter encompassed 34,416 km<sup>2</sup>, with 65.5% and 87.7% contained within the recovery zone and 16km perimeter area, respectively (Table 1, Fig. 6). Interpretations of occupancy near the edge of this polygon must be made with caution in light of data and analytical biases. Occupancy near this boundary must be interpreted as an approximation. Additional supportive evidence should be considered when making judgments about occupied habitat near this edge.

Additional research is needed to determine if some habi-

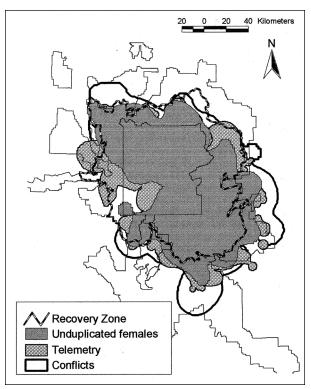


Fig. 5. Grizzly bear distribution in the Greater Yellowstone Ecosystem, 1990–2000. Map depicts overlap of distributions constructed using fixed kernel from: (1) observations of unique unduplicated females with cubs-of-the-year, (2) relocations of radiocollared bears, (3) locations of grizzly bear–human conflicts, confrontations, and mortalities.

tats outside of this polygon are occupied. These areas include: (1) the Gravelly Mountain Range, (2) northern portions of the Gallatin National Forest, particularly on the Boulder Plateau, (3) that portion of Custer National Forest contained within the GYE, and (4) portions of the Targhee National Forest on the Pitchstone Plateau and the Centennial Mountains.

Bader (2000) constructed distribution maps for the major grizzly bear populations in the U.S. portion of the Northern Rockies. His methods and data were different from ours, precluding direct comparisons; his estimated distribution of the grizzly bear in the Greater Yellowstone Ecosystem is larger than ours and identified areas of occupancy that are not identified here (i.e., Tobacco Root Mountains in the northwest GYE).

Although our depiction of grizzly bear distribution in the GYE during the 1990s is not exact, we did use a rigorous process and the best available data. It is evident from our analysis that grizzly bears have expanded into previously vacant range. This is confirmed from our ranges constructed with unduplicated female observations (11% and 34% increase from 1970s to 1980s and 1980s to 1990s, respectively) and by comparisons with previously pub-

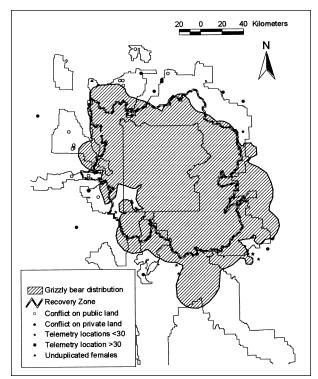


Fig. 6. Grizzly bear distribution in the Greater Yellowstone Ecosystem, 1990–2000. Map represents the outer edge of a composite polygon constructed by overlaying fixed kernel ranges constructed from (1) observations of unique unduplicated females with cubs-of-the-year, (2) relocations of radiocollared bears, (3) locations of grizzly bear-human conflicts, confrontations, and mortalities. Visible points represent data not contained within this coverage.

lished data. It is not our intention to focus on reasons for such an expansion, but we can speculate that it is likely a product of improved management practices (Mattson 1990, Gunther 1994), a series of good food years (Mattson 1998), and a population increase (Eberhardt and Knight 1996, Boyce et al. 2001).

Our range maps also show that occupied habitats in the GYE extend beyond the current recovery zone. Such information could be viewed in 2 ways. One could argue that it emphasizes the need to increase the size of the existing recovery zone. However, when the original recovery zone was identified, it included all known areas occupied by bears (USFWS 1982). Constructing a new zone to encompass current bear range could result in a similar exercise in the future should bears continue to expand. Additionally, the recovery zone was not intended to include all areas of grizzly bear occupancy (USFWS 1993:18). Alternatively, one could view occupancy outside the recovery zone as vital information to state and federal land management agencies and state wildlife agencies for their planning efforts. For these plans to be effective, criteria ensuring long-term survival of bears beyond the PCA need to be considered. This is particularly relevant because 17% to 34% (depending upon which coverage is used) of currently occupied habitat is not covered by any specific habitat standards or guidelines associated with the Fish and Wildlife Service Conservation Strategy (USFWS 2000*a*).

Current recovery standards and the Conservation Strategy include population monitoring and mortality limits on lands contained within the recovery zone and the 16-km perimeter area. If recommendations of the Governors' Round Table (USFWS 2000b) are followed, the 16-km perimeter area will be discarded. If recovery of the Yellowstone grizzly bear population is premised on the health of the existing population, the states will need to establish demographic standards and mortality limits for that portion of the population living outside the recovery zone. These could differ from those in the recovery zone, but must ensure the long-term health of the entire population. Grizzly bears in the GYE are effectively a single population and sound conservation practices must focus on all occupied habitats.

#### **ACKNOWLEDGMENTS**

A number of people contributed to this work. We thank L. Eberhardt for recognizing the need for this analysis and M. Taper for providing guidance on the application of fixed kernel ranges. S. Podruzny and L. Landenburger provided valuable assistance with ArcView programming and analyses and K. West provided helpful editorial suggestions. A number of individuals have been involved in data collection. We especially thank D. Knight and B. Blanchard, retired members of the IGBST, who shepherd the study team from its inception in 1973 through 1997. We thank pilots D. Stradley, R. Stradley, S. Monger, G. Lust, and R. Hyatt, who have flown grizzly bear radiotracking flights in the GYE for many years. Personnel who were primarily responsible for bear capture include J. Jonkel, K. Inberg, B. Schleyer, C. Dickinson, M. Lamoreux, M. Ternent, M. Biel, and G. Holm. K. Frey, M. Bruscino, H. Pac, and A. Dood provided data and assistance with grizzly bear mortalities. We also thank the many individuals who provided information on sightings of unduplicated females, conflicts, and mortalities. Finally, we thank F. van Manen, Associate Editor, and the 2 anonymous reviewers for making this a better manuscript.

#### LITERATURE CITED

Anderson, J.E. 1991. A conceptual framework for evaluating and quantifying naturalness. Conservation Biology 5:347–352.

BADER, M. 2000. Distribution of grizzly bears in the U.S. Northern Rockies. Northwest Science 74:325–334.

- Baker, R.G. 1986. Snagamonian and Wisconsin paleoenvironments in Yellowstone National Park. Geological Society of America Bulletin 97:717–736.
- Basile, J.V. 1982. Grizzly bear distribution in the Yellowstone area, 1973–79. U.S. Forest Service Research Note INT-321.
- BLANCHARD, B.M., AND R.R. KNIGHT. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41–67
- ———, AND ———. 1995. Biological consequences of relocating grizzly bears in the Yellowstone Ecosystem. Journal of Wildlife Management 59:560–565.
- ——, , , AND D.J. MATTSON. 1992. Distribution of Yellowstone grizzly bears during the 1980's. American Midland Naturalist 128:332–338.
- Boyce, M.S., B.M. Blanchard, R.R. Knight, and C. Servheen. 2001. Population viability for grizzly bears: a critical review. International Association of Bear Research and Management, Monograph Series Number 4.
- Despain, D.G. 1987. The two climates of Yellowstone National Park. Proceedings of the Montana Academy of Science 47:11–20.
- ——. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Roberts Rinehart Publishing Company, Boulder, Colorado, USA.
- EBERHARDT, L.L., AND R.R. KNIGHT. 1996. How many grizzlies in Yellowstone? Journal of Wildlife Management 60:416–421.
- Gunther, K.A. 1994. Bear management in Yellowstone National Park, 1960–93. International Conference on Bear Research and Management 9(1):549–560.
- ——, A.K. Aune, S. Cain, T. Chu, and C.M. Gillin. 1993. Grizzly bear—human conflicts in the Yellowstone Ecosystem 1992. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- ——, ——, ——, AND R.R. KNIGHT.

  1994. Grizzly bear–human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 1993. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- Grizzly bear-human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 1994. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- Grizzly bear-human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 1995. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- Grizzly bear-human conflicts, confrontations, and

- management actions in the Yellowstone Ecosystem, 1996. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- ———, M. BRUSCINO, S. CAIN, T. CHU, K. FREY, M.A. HAROLDSON, AND C.C. SCHWARTZ. 1998. Grizzly bear-human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 1997. Interagency Grizzly Bear Committee, Yellowstone Ecosystem, 1997. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- , \_\_\_\_, J. COPELAND, K. FREY, M.A. HAROLDSON, AND C.C. SCHWARTZ. 1999. Grizzly bear—human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 1998. Interagency Grizzly Bear Committee, Yellowstone Ecosystem Subcommittee Report. U.S. Department Interior, National Park Service, Yellowstone National Park, Wyoming, USA.
- —, —, —, —, —, , —, , —, , AND ——. 2000. Grizzly bear–human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 1999. Pages 55–108 *in* C.C. Schwartz and M.A. Haroldson, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team 1999. U.S. Geological Survey, Bozeman, Montana, USA.
- ———, ———, J. COPELAND, K. FREY, M.A. HAROLDSON, AND C.C. SCHWARTZ. 2001. Grizzly bear–human conflicts, confrontations, and management actions in the Yellowstone Ecosystem, 2000. Pages 65–126 *in* C.C. Schwartz and M.A. Haroldson, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team 2000. U.S. Geological Survey, Bozeman, Montana, USA.
- —. 2003. Grizzly bear–human conflicts in the Yellowstone Ecosystem. Ursus 14:In Press.
- HOOGE, P.N., AND B. EICHENLAUB. 1997. Animal movement extension to arcview. Version 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.
- KNIGHT, R.R., B.M. BLANCHARD, AND L.L. EBERHARDT. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the year. Wildlife Society Bulletin 23:245–248.
- Marston, R.A., and J.E. Anderson. 1991. Watersheds and vegetation of the Greater Yellowstone Ecosystem. Conservation Biology 5:338–346.
- Mattson, D.J. 1990. Human impacts on bear habitat use. International Conference Bear Research and Management 8:33–56.
- . 1997. Sustainable grizzly bear mortality calculated from counts of females with cubs-of-the-year: an evaluation. Biological Conservation 81:103–111.
- ——. 1998. Changes in mortality of Yellowstone's grizzly bears. Ursus 10:129–138.
- ——, R.G. WRIGHT, K.C. KENDALL, AND C.J. MARTINKA. 1995. Grizzly bears. Pages 103–105 *in* E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, editors. Our living

- resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of Interior, National Biological Service, Washington D.C., USA.
- NAEF-DAENZER, B. 1993. A new transmitter for small animals and enhanced methods of home-range analysis. Journal of Wildlife Management 57:680–689.
- PATTEN, D.T. 1963. Vegetational pattern in relation to environments in the Madison Range, Montana. Ecological Monographs 33:375–406.
- ——. 1991. Defining the Greater Yellowstone Ecosystem. Pages 19–25 in R.B. Keiter and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage. Yale University Press, New Haven Connecticut, USA.
- PICTON, H., D. MATTSON, B. BLANCHARD, AND R. KNIGHT. 1986. Climate, carrying capacity, and the Yellowstone grizzly bear. Pages 129–135 in G. Contreras and K. Evans, compilers. Proceedings: grizzly bear habitat symposium. U.S. Forest Service General Technical Report INT-207, Missoula, Montana, USA.
- POWELL, R.A. 2000. Animal home ranges and territories and home range estimators. Pages 65–110 in L. Boitani and T.K. Fuller, editors. Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, New York, USA.
- RAUSCH, R.L. 1963. Geographic variation in size of North American brown bears, *Ursus arctos* L., as indicated by condylobasal length. Canadian Journal of Zoology 41:33– 45.
- 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.
- Schwartz, C.C. 1999. Evaluation of a capture—mark—recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 13–22 *in* C.C. Schwartz and M.A. Haroldson, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 1998. U.S. Geological Survey, Bozeman, Montana, USA.
- SEAMAN, D.E, J.J. MILLSPAUGH, B.J. KERNOHAN, G.C. BRUNDIGE, K.J. RAEDEKE, AND R.A. GITZEN. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.
- ——, AND R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis.

- Ecology 77:2075-2085.
- Servheen, C. 1999. Status and management of the grizzly bear in the lower 48 United States. Pages 50–54 *in* C. Servheen, S. Herrero, and B. Peyton, compilers. Bears, status survey and conservation action plan. IUCN/SSC Bear and Polar Bear Specialist Groups, Gland, Switzerland and Cambridge, United Kingdom.
- SILVERMAN, B.W. 1986. Density estimation for statistics and data analysis. Chapman & Hall, London, United Kingdom.
- SWIHART, R.K., AND N.A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. Journal of Wildlife Management 49:1019–1025.
- ———, AND ———. 1997. On testing for independence of animal movements. Journal of Agricultural, Biological, and Environmental Statistics 2:1–16.
- U.S. FISH AND WILDLIFE SERVICE. 1982. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Denver, Colorado, USA.
- ——. 1993. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- 2000a. Draft conservation strategy for the grizzly bear in the Yellowstone area. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- ——. 2000b. Summary of public comments on the draft conservation strategy for the grizzly bear in the Yellowstone area. U.S. Fish and Wildlife Service, Missoula, Montana, USA.
- WADDINGTON, J.C.B., AND H.E. WRIGHT, JR. 1974. Late Quaternary vegetational changes on the east side of Yellowstone Park, Wyoming. Quaternary Research 4:175– 184.
- WEAVER, T. 1980. Climates of vegetation types of the northern Rocky Mountains and adjacent plains. American Midland Naturalist 103:392–398.
- WHITE, G.C., AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA
- WORTON, D.J. 1989. Optimal smoothing parameters for multivariate fixed and adaptive kernel methods. Journal of Statistical Computation and Simulation 32:45–57.
- ——. 1995. Using Monte Carlo simulation to evaluate kernelbased home range estimators. Journal of Wildlife Management 59:794–800.

Received: 28 May 2001.

Accepted: 26 December 2001.

Associate Editor: Van Manen.