



Tools and Technology

Methods to Estimate Distribution and Range Extent of Grizzly Bears in the Greater Yellowstone Ecosystem

DANIEL D. BJORNIE,¹ *Large Carnivore Section, Wyoming Game & Fish Department, 260 Buena Vista, Lander, WY 82520, USA*

DANIEL J. THOMPSON, *Large Carnivore Section, Wyoming Game & Fish Department, 260 Buena Vista, Lander, WY 82520, USA*

MARK A. HAROLDSON, *United States Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715, USA*

CHARLES C. SCHWARTZ, *United States Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, 2327 University Way, Suite 2, Bozeman, MT 59715, USA*

KERRY A. GUNTHER, *Bear Management Office, Yellowstone Center for Resources, Yellowstone National Park, P.O. Box 168, Yellowstone National Park, WY 82190, USA*

STEVEN L. CAIN, *National Park Service, Grand Teton National Park, P.O. Box 170, Moose, WY 83012, USA*

DANIEL B. TYERS, *United States Forest Service, 2327 University Way, Suite 2, Bozeman, MT 59715, USA*

KEVIN L. FREY, *Bear Management Office, Montana Fish, Wildlife and Parks, 1400 S 19th Avenue, Bozeman, MT 59718, USA*

BRYAN C. ABER, *Idaho Department of Fish & Game/United States Forest Service, 3726 Highway 20, Island Park, ID 83429, USA*

ABSTRACT The distribution of the Greater Yellowstone Ecosystem grizzly bear (*Ursus arctos*) population has expanded into areas unoccupied since the early 20th century. Up-to-date information on the area and extent of this distribution is crucial for federal, state, and tribal wildlife and land managers to make informed decisions regarding grizzly bear management. The most recent estimate of grizzly bear distribution (2004) utilized fixed-kernel density estimators to describe distribution. This method was complex and computationally time consuming and excluded observations of unmarked bears. Our objective was to develop a technique to estimate grizzly bear distribution that would allow for the use of all verified grizzly bear location data, as well as provide the simplicity to be updated more frequently. We placed all verified grizzly bear locations from all sources from 1990 to 2004 and 1990 to 2010 onto a 3-km × 3-km grid and used zonal analysis and ordinary kriging to develop a predicted surface of grizzly bear distribution. We compared the area and extent of the 2004 kriging surface with the previous 2004 effort and evaluated changes in grizzly bear distribution from 2004 to 2010. The 2004 kriging surface was 2.4% smaller than the previous fixed-kernel estimate, but more closely represented the data. Grizzly bear distribution increased 38.3% from 2004 to 2010, with most expansion in the northern and southern regions of the range. This technique can be used to provide a current estimate of grizzly bear distribution for management and conservation applications. © 2013 The Wildlife Society.

KEY WORDS ArcGIS, distribution, Greater Yellowstone Ecosystem, grizzly bear, kriging, range extent, *Ursus arctos*.

The importance of accurately measuring the distribution and range extent of species is a frequent topic in ecological studies and fundamental to wildlife conservation and management (Buckland and Elston 1993, Guisan and Zimmerman 2000, Rushton et al. 2004, Sargeant et al. 2005, Gaston and Fuller 2009). However, the effectiveness of methods to estimate distribution and range extent can vary depending on data type, data quantity, and sampling regime (Seaman et al. 1999, Segurado and Araujo 2004, Borger et al. 2006, Hernandez et al. 2006). Accurately delineating distribution can be especially important for species listed as

threatened or endangered by the U.S. Fish and Wildlife Service under the Endangered Species Act (ESA). Underestimating distribution may leave some populations vulnerable; whereas, overestimating may lead to unnecessary restrictions in areas where the species does not occur or assumptions regarding population size that may result in inappropriate management decisions. These estimations of distribution and range extent may also have implications for the delisting process, because demonstrating population increases and associated range expansions are essential in documenting recovery.

Grizzly bears (*Ursus arctos*) had an extensive distribution throughout North America prior to European settlement, spanning multiple ecoregions and latitudinal gradients (Rausch 1963, Craighead et al. 1995, Schwartz et al. 2003). Through direct and indirect perturbations of

Received: 14 March 2013; Accepted: 1 July 2013

¹E-mail: dan.bjornlie@wyo.gov

grizzly bear populations and habitats, the distribution was reduced to <2% of its historical extent within the continental United States south of Canada by the mid-20th century (Mattson and Merrill 2002, Schwartz et al. 2003). Grizzly bears in the conterminous 48 states have been reduced to 5 remnant populations, with only the Northern Continental Divide Ecosystem and Greater Yellowstone Ecosystem populations containing >100 individuals (Proctor et al. 2012). In 2007, the Greater Yellowstone Ecosystem grizzly bear population was removed from the list of threatened species under the ESA. However, in 2009 the Greater Yellowstone Ecosystem grizzly bear population was returned to the ESA list of threatened species because of concerns regarding its persistence in response to increased mortality of whitebark pine trees (*Pinus albicaulis*), which produce nuts that provide an important autumn food source for grizzly bears (USFWS 2013). The grizzly bear population in the Greater Yellowstone Ecosystem remains listed in 2013, further stressing the importance of ample and rigorous grizzly bear population and distribution data collection and analysis.

Since population lows in the late 1960s and early 1970s (Craighead et al. 1995), the distribution of the Greater Yellowstone Ecosystem grizzly bear population has continued to expand into areas and habitats unoccupied since the early 20th century (Schwartz et al. 2002, 2006). Up-to-date information on the area and extent of this distribution is crucial for federal, state, and tribal wildlife and land managers to make informed decisions regarding grizzly bear management. Developing a standard protocol for estimating distribution that utilizes all available grizzly bear location data and can be regularly updated is needed to provide accurate and current distributional boundaries.

Grizzly bear location data in the Greater Yellowstone Ecosystem has been collected from multiple sources over several decades and has resulted in numerous approaches to delineating distributional boundaries. Basile (1982) and Blanchard et al. (1992) used radiotelemetry locations and locations of verified observations of female grizzly bears with young to map grizzly bear distribution in the 1970s and 1980s, respectively. Schwartz et al. (2002, 2006) used a fixed-kernel density estimator to develop utilization distributions of radiomarked individual bears as well as composite kernels of locations of conflicts, mortalities, and female grizzly bears with cubs-of-the-year. However, the latter method has a number of drawbacks. It excludes observations or verified evidence of unmarked bears other than females with cubs-of-the-year (Schwartz et al. 2002). It also requires aggregation and fixed-kernel density estimator analyses of each of the multiple data types (individual bears, conflicts, mortalities, females with cubs-of-the-year), which are then overlaid and dissolved to create the final estimated distribution. Therefore, this method is complex and computationally time-consuming, making analysis difficult to conduct annually. In addition, the abundance of locations collected by Global Positioning System (GPS) radiocollars makes

fixed-kernel density estimator analysis problematic for the creation of distribution maps due to issues of spatial autocorrelation and high variability in densities of locations among data sources (Girard et al. 2002, Hemson et al. 2005).

Our objective was to develop a technique to generate an ecosystem-wide grizzly bear distribution map that would allow for the use of all grizzly bear telemetry locations and verified observations of grizzly bears or grizzly bear sign, and could be frequently updated as grizzly bear distribution changes. We compared results of this new technique with previous efforts of Schwartz et al. (2006) to evaluate the efficacy and accuracy of the model. Finally, we used this new technique to evaluate changes in grizzly bear distribution since 2004.

STUDY AREA

The study area encompassed the Greater Yellowstone Ecosystem, an approximately 75,000 km² area including Yellowstone and Grand Teton National Parks, and adjacent federal, state, private, and tribal lands in Montana, Wyoming, and Idaho, USA. Mattson et al. (1991) and Schwartz et al. (2002) provide detailed descriptions of the study area.

METHODS

Data Sources

To directly compare area and extent of grizzly bear distribution calculated by our new method to those of Schwartz et al. (2002, 2006), we used the identical raw location data from 1990 to 2004 used by Schwartz et al. (2006) in our initial analysis. We then used all verified location data obtained during 1990–2010 to create an updated distribution map for grizzly bears in the Greater Yellowstone Ecosystem. Verified data included the following: all GPS and very high frequency telemetry locations, locations of observations or tracks reported or verified by experienced agency personnel, locations associated with grizzly bear–human conflicts, mortalities, and scats or hair samples attributed to grizzly bears via DNA analysis.

Spatial Analyses

We used a geographic information system (ArcGIS v. 10.0) to place a 3-km × 3-km grid over an area containing all verified grizzly bear locations in the Greater Yellowstone Ecosystem. Grid-cell size was based on the mean daily activity radius of 1.5 km for male grizzly bears (Schwartz et al. 2010). We overlaid the 1990–2004 and 1990–2010 locations on the grid and assigned grid cells containing ≥1 location a value of 1 and unoccupied cells a value of 0. To account for unoccupied cells resulting from missing data within known grizzly bear distribution, we performed zonal analysis for each grid cell. We summed the value of the target cell and all 8 adjacent cells; thus, each cell had a potential zonal sum ranging from 0 to 9.

Following the zonal analysis, we generated a centroid point for each cell and attributed it with the zonal sum of that cell for both data sets. We used ordinary kriging in the

Geostatistical Analyst extension in ArcGIS to develop a predicted surface of zonal analysis values (Johnston et al. 2001). We modified the resulting surface to display only areas with predicted values of ≥ 1.0 . We visually compared the area and extent of the kriging surface produced from the 1990–2004 data set with the original data and to the distribution estimate produced by Schwartz et al. (2006). We then compared the kriging surface created from both data sets to evaluate changes in grizzly bear distribution from 2004 to 2010.

Lastly, to investigate the impact of annually adding new locations to the existing data set without censoring data from the beginning of the period, we removed 1990–1995 locations to create a 1996–2010 data set. This 15-year span is comparable to that evaluated by Schwartz et al. (2006). We conducted the same analysis using this censored data set and compared it with the 1990–2010 estimated distribution.

RESULTS

Using the 1990–2004 locations ($n = 45,629$) from Schwartz et al. (2006) and ordinary kriging, we created an estimated distribution of 36,364 km², 2.4% smaller than the estimate from Schwartz et al. (2006; Table 1). The extent of the 2004 kriging distribution extended marginally beyond Schwartz et al. (2006) on the northern and western sides, and receded slightly on the southern and eastern edges of the distribution (Fig. 1).

The estimate of distribution produced from verified grizzly bear locations from 1990 to 2010 ($n = 293,660$) and ordinary kriging generated a 2010 distribution area of 50,280 km² (Table 1), an increase of 13,916 km² (38.3%) from the 2004 kriging estimate. Much of this expansion is associated with suitable habitat connecting previously occupied areas (Fig. 2; Merrill and Mattson 2003).

There was very little impact on 2010 distribution by removing 1990–1995 location data, because the majority of cells containing 1990–1995 locations also contained locations from 1996 to 2010, thus remaining in the analysis as occupied. The estimated area of distribution decreased by 232 km², from 50,280 km² to 50,048 km² (0.46%).

DISCUSSION

Geostatistical analysis has introduced new methods for the estimation of species distribution (Walker et al. 2008). Kriging is a geostatistical technique that interpolates a

prediction surface based on known values of surrounding points (Johnston et al. 2001). Kriging utilizes the spatial autocorrelation of location data to infer predicted values of an interpolated surface (Johnston et al. 2001) and produce an objective prediction surface without the variability due to sampling effort (Girard et al. 2002) or necessary fitting of fixed-kernel density estimator smoothing factors (White and Garrott 1990, Borger et al. 2006). Although normally distributed data are necessary to obtain probability maps using ordinary kriging (Walker et al. 2008), normality is not required to predict an interpolated surface (Johnston et al. 2001). The combination of a generalized grid, summarized using zonal analysis, and a surface interpolated from the resulting grid values provides the most parsimonious balance of inclusion and exclusion of low-density peripheral locations and allows for annual updates of grizzly bear distribution and analysis of range expansion.

The slight difference in overall distribution between the 2004 fixed-kernel density estimator and kriging maps reflects the idiosyncrasies of each technique. Fixed-kernel density estimator methods were developed to estimate the intensity of utilization and are thus more focused on core areas of use, rather than peripheral boundaries (Hemson et al. 2005). Fixed-kernel home-range estimators tend to overestimate home-range size (Girard et al. 2002), which likely explains the slightly larger distribution estimated by Schwartz et al. (2006). Because this distribution used a variety of data sets to create and merge multiple overlapping fixed-kernel home ranges, there was considerable variability in kernel estimation. High-density locations of GPS-collared bears created tight, compact home ranges; while composite kernels of lower density locations, such as those derived from mortalities, conflicts, and females with cubs-of-the-year, extrapolated to a greater extent (Schwartz et al. 2002). In many cases, these composite kernels defined the outer edge of the grizzly bear distribution (Schwartz et al. 2002). Kriging was able to address a number of these issues by evaluating all data locations equally. The zonal analysis of 3-km grid cells limited the distance kriging could extrapolate the distribution past any verified grizzly bear location. Consequently, this analysis resulted in a slightly smaller estimated distribution that more closely tracks the data.

Although some attempts to define the distribution of rare or cryptic species are predictions based on areas of suitable habitat (Guisan and Zimmerman 2000), we had the ability to use abundant species-location data to estimate distribution.

Table 1. Comparison of area and percent of total area of grizzly bear (*Ursus arctos*) distribution by method and jurisdiction in the Greater Yellowstone Ecosystem, USA, 1990–2004 and 1990–2010. Locations from 1990 to 2004 are from Schwartz et al. (2006) for both methods.

Jurisdiction	1990–2004				1990–2010	
	Schwartz et al.		Kriging		Kriging	
	Area (km ²)	Percent of total	Area (km ²)	Percent of total	Area (km ²)	Percent of total
ID	2,697	7.2	2,033	5.6	4,508	9.0
MT	6,528	17.5	7,673	21.1	11,970	23.8
WY	17,599	47.2	16,533	45.5	21,843	43.4
National Park System	9,683	26.0	9,566	26.3	10,237	20.4
Wind River Reservation	751	2.0	559	1.5	1,722	3.4
Total	37,258		36,364		50,280	

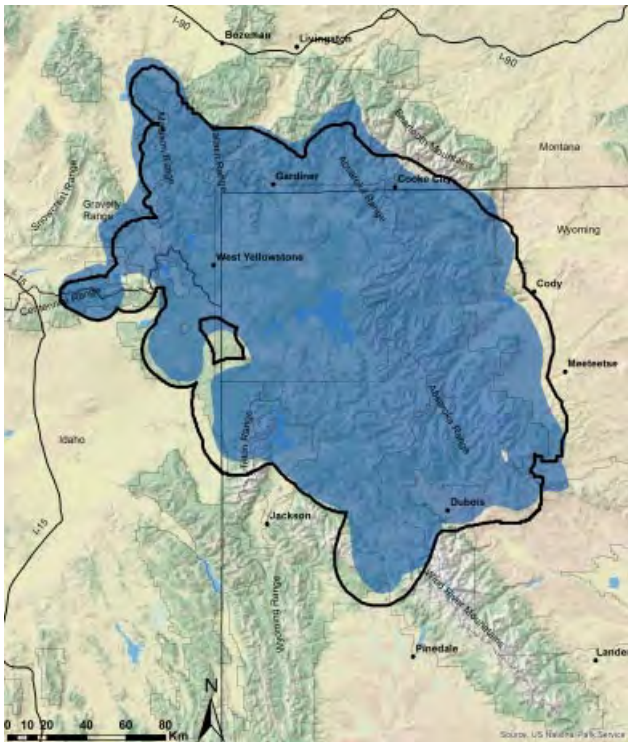


Figure 1. Comparison of 1990–2004 grizzly bear (*Ursus arctos*) distribution in the Greater Yellowstone Ecosystem, USA. The dark line represents the grizzly bear distribution calculated by Schwartz et al. (2006). The blue shaded area represents the grizzly bear distribution calculated using ordinary kriging and the location data from Schwartz et al. (2006).

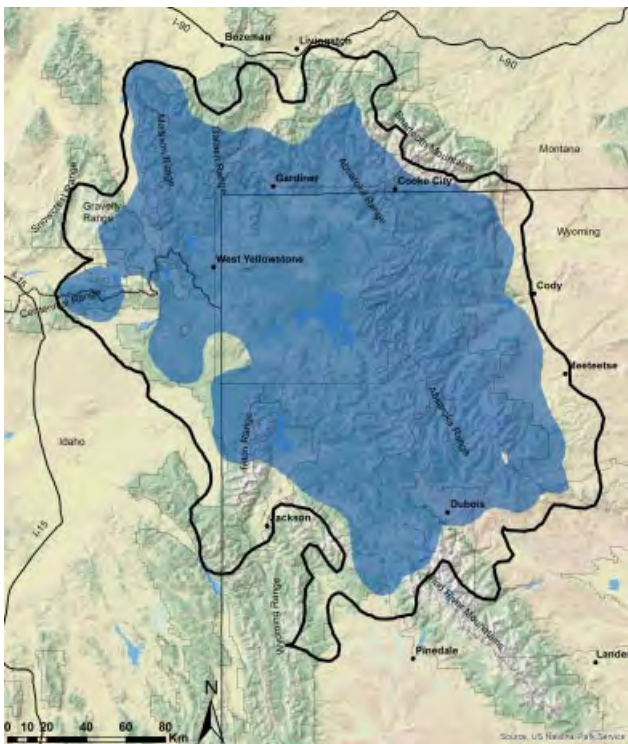


Figure 2. Grizzly bear (*Ursus arctos*) distribution in the Greater Yellowstone Ecosystem, USA, 1990–2004 and 1990–2010, calculated using ordinary kriging. The blue shaded area represents the 1990–2004 distribution. The dark line represents the 1990–2010 distribution.

The uniform evaluation of all data locations allowed us to use a larger sample of grizzly bear locations from a variety of sources. Although agency grizzly bear research and monitoring efforts throughout the Greater Yellowstone Ecosystem supply abundant radiotelemetry locations, many verified grizzly bear locations are obtained by numerous other means in areas where radiocollared bears do not reside. In the past, these locations were not used to calculate grizzly bear distribution. However, the technique presented here aggregated >293,000 verified grizzly bear locations from a variety of sources, including all radiotelemetry locations, conflicts, mortalities, DNA samples, and locations of observations or tracks verified by experienced personnel. The grid system and zonal analysis attenuated the influence of duplicate points and high-density GPS locations by distilling those points to one grid-cell value ranging from 0 to 9, regardless of the number of locations within that cell. The range of these zonal analysis values also provided weight to core areas within the distribution with a higher likelihood of occupancy.

Most of the range expansion observed from 2004 to 2010 occurred in areas with the highest potential for range expansion (Merrill and Mattson 2003). Further range expansion in the eastern edge of the ecosystem is likely limited by open, sagebrush vegetation cover with more human activity. On the western side, expansion appears to be limited along the Continental Divide in the Centennial Mountains by a combination of open landscape and Interstate 15, which likely serves as a barrier to dispersal because there has been no increase in that area since 2004 (Fig. 2). Along the northern region, expansion has occurred across the Gravelly Range to the eastern slopes of the Snowcrest Range and has occurred in most cover types from the northern extent of the Madison Range to the northern areas of Absaroka Range. Although we have verified documentation of grizzly bears in the Beartooth Mountains in the northeastern corner of the Greater Yellowstone Ecosystem, this area still remains the only largely unoccupied area of the northern portion of the ecosystem. Despite this northern expansion in recent years, it appears that, besides expansion into areas such as the Beartooth Mountains and the northern Gallatin Range south of Bozeman, Montana, further expansion to the north may be limited by open landscape and the increasingly human-dominated corridor along Interstate 90 (Fig. 2).

The potential for increased grizzly bear expansion to the south, however, is much higher. Grizzly bear locations are becoming increasingly common in the northern portion of the Wyoming Range and, in 2011, 2012, and 2013, verified grizzly bear photos were taken by remote cameras at black bear (*U. americanus*) bait sites at the southern extent of the Wind River Mountains. Although still uncommon in the southern reaches of these ranges, confirmed evidence of grizzly bear presence is likely to increase as grizzly bears continue to expand their southern distribution into these mountain ranges.

Ordinary kriging requires adequate spatial and temporal sampling to provide necessary data, especially at the edge of

the distribution. Radiocollaring and aerial observations of grizzly bears at their range periphery as part of routine monitoring, documentation of verified observations from around the Greater Yellowstone Ecosystem, and the use of remote cameras can contribute significant data for distribution mapping. However, future Greater Yellowstone Ecosystem grizzly bear distribution analyses should also consider the appropriate time span for analysis. The imperceptible change in 2010 distribution as a result of removing 1990–1995 locations further demonstrates the robustness of the technique. As new locations are added to the data set, points in the center of the distribution will have little effect on the margin, while points at the perimeter will contribute to an updated estimate of range extent. Because grizzly bears are a relatively long-lived species and radiocollaring efforts cannot annually encompass the entire Greater Yellowstone Ecosystem, including additional years will ensure that the resulting distribution is an accurate representation of grizzly bear range extent with little danger of bias from inclusion of too many years of location data. We recommend 15–20-year data sets to maintain a sufficient sample size while ensuring that a surplus of data does not result in failure to detect potentially contracting distributions.

MANAGEMENT IMPLICATIONS

Our technique can be applied on a more frequent basis to provide the most current estimation of grizzly bear distribution for use in grizzly bear management and conservation, as well as provide for improved public safety with up-to-date information on areas of probable grizzly bear occupancy. Clearly, not all grizzly bears in the Greater Yellowstone Ecosystem are radiocollared or otherwise detected, and this is especially true of lone bears inhabiting the edges of the main distribution. Consequently, our estimate should be considered a minimum known area of occupancy, not an extent of occurrence, because we have many outliers that are not included in the main grizzly bear distribution map. Thus, this map should not be used as a presence–absence boundary, because grizzly bears undoubtedly occur outside this line. Continued population monitoring will ensure adequate location data to further improve our understanding of the distribution and expansion of Greater Yellowstone Ecosystem grizzly bear population.

ACKNOWLEDGMENTS

Grizzly bears captured for telemetry studies were handled in accordance with each agency's animal care and use guidelines under permit from the U.S. Fish and Wildlife Service. We wish to thank the many field personnel from member agencies of the Interagency Grizzly Bear Study Team (IGBST) who contributed to the collection of grizzly bear location data used in these analyses. Member agencies of the IGBST include the Northern Rocky Mountain Science Center of the U.S. Geological Survey; Wyoming Game and Fish Department; Montana Fish, Wildlife, and Parks; Idaho Fish and Game; National Park Service; U.S. Forest Service; U.S. Fish and Wildlife Service; and the Wind

River Fish and Game of the Shoshone and Arapahoe Tribes. We thank pilots S. Ard, N. Cadwell, G. Hyatt, G. Lust, S. Monger, K. Overfield, T. Schell, A. Spencer, D. Stinson, R. Stradley, D. Stradley, and C. Tyrrel, for conducting observation and telemetry flights. We thank N. Cudworth for a very thorough review of the first draft of this manuscript. We also thank Dr. M. Higgs, Department of Mathematical Science, Montana State University, for helpful suggestions regarding methods used. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Basile, J. V. 1982. Grizzly bear distribution in the Yellowstone area, 1973–1979. U.S. Forest Service Research Note INT-32, Ogden, Utah, USA.
- Blanchard, B. M., R. R. Knight, and D. J. Mattson. 1992. Distribution of Yellowstone grizzly bears during the 1980s. *American Midland Naturalist* 128:332–338.
- Borger, L., N. Franconi, G. De Michele, A. Gantz, F. Meschi, A. Manica, S. Lovari, and T. Coulson. 2006. Effects of sampling regime on the mean and variance of home range size estimates. *Journal of Applied Ecology* 75:1393–1405.
- Buckland, S. T., and D. A. Elston. 1993. Empirical models for the spatial distribution of wildlife. *Journal of Applied Ecology* 30:478–495.
- Craighead, J. J., J. S. Sumner, and J. A. Mitchell. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992. Island Press, Washington, D.C., USA.
- Gaston, K. J., and R. A. Fuller. 2009. The sizes of species' geographic ranges. *Journal of Applied Ecology* 46:1–9.
- Girard, I., J. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on GPS telemetry on home range size estimations. *Journal of Wildlife Management* 66:1290–1300.
- Guisan, A., and N. E. Zimmerman. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135:147–186.
- Hemson, G., P. Johnson, A. South, R. Kenward, R. Ripley, and D. Macdonald. 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross validation. *Journal of Wildlife Management* 74:455–463.
- Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29:773–785.
- Johnston, K., J. M. Ver Hoef, K. Krivoruchko, and N. Lucas. 2001. Using ArcGIS geostatistical analyst. Environmental Systems Research Institute, Redlands, California, USA.
- Mattson, D. J., B. M. Blanchard, and R. R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69:1619–1629.
- Mattson, D. J., and T. Merrill. 2002. Extirpations of grizzly bears in the contiguous United States, 1850–2000. *Conservation Biology* 16:1123–1136.
- Merrill, T., and D. J. Mattson. 2003. The extent and location of habitat biophysically suitable for grizzly bears in the Yellowstone region. *Ursus* 14:171–187.
- Proctor, M. F., D. Paetkau, B. N. McLellan, G. B. Stenhouse, K. C. Kendall, R. D. Mace, W. F. Kasworm, C. Servheen, C. L. Lausen, M. L. Gibeau, W. L. Wakkenin, M. A. Haroldson, G. Mowat, C. D. Apps, L. M. Ciarniello, R. M. R. Barclay, M. S. Boyce, C. C. Schwartz, and C. Strobeck. 2012. Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs* 180.
- 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* 41:33–345.
- Rushton, S. P., S. J. Ormerod, and G. Kerby. 2004. New paradigms for modeling species distributions? *Journal of Applied Ecology* 41:193–200.
- Sargeant, G. A., M. A. Sovada, C. C. Slivinski, and D. H. Johnson. 2005. Markov chain estimation of species distribution: a case study of the swift fox in western Kansas. *Journal of Wildlife Management* 69:483–497.

- Seaman, D. E., J. J. Millsaugh, 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.
- Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2002. Distribution of grizzly bears in the Greater Yellowstone Ecosystem, 1990–2000. *Ursus* 13:203–212.
- Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2006. Distribution of grizzly bears in the Greater Yellowstone Ecosystem in 2004. *Ursus* 17:63–66.
- Schwartz, C. C., M. A. Haroldson, and G. C. White. 2010. Hazards affecting grizzly bear survival in the Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 74:654–667.
- Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly bear. Pages 556–586 in G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, editors. *Wild mammals of North America: biology, management, and conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Segurado, P., and M. B. Araujo. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography* 31:1555–1568.
- United States Fish and Wildlife Service [USFWS]. 2013. Grizzly bear recovery: Yellowstone. U.S. Fish and Wildlife Service, Missoula, Montana, USA. < <http://www.fws.gov/mountain-prairie/species/mammals/grizzly/yellowstoneindex.html> >. Accessed 2 Feb 2013.
- Walker, J. S., R. C. Balling, Jr., J. M. Briggs, M. Katti, P. S. Warren, and E. A. Wentz. 2008. Birds of a feather: interpolating distribution patterns of urban birds. *Computers, Environment, and Urban Systems* 32:19–28.
- White, G. C., and R. A. Garrott. 1990. *Analysis of wildlife radio-tracking data*. Academic Press, London, United Kingdom.

Associate Editor: Glenn