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Management and Conservation Article

Hazards Affecting Grizzly Bear Survival in the Greater Yellowstone Ecosystem

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ABSTRACT During the past 2 decades, the grizzly bear (*Ursus arctos*) population in the Greater Yellowstone Ecosystem (GYE) has increased in numbers and expanded its range. Early efforts to model grizzly bear mortality were principally focused within the United States Fish and Wildlife Service Grizzly Bear Recovery Zone, which currently represents only about 61% of known bear distribution in the GYE. A more recent analysis that explored one spatial covariate that encompassed the entire GYE suggested that grizzly bear survival was highest in Yellowstone National Park, followed by areas in the grizzly bear Recovery Zone outside the park, and lowest outside the Recovery Zone. Although management differences within these areas partially explained differences in grizzly bear survival, these simple spatial covariates did not capture site-specific reasons why bears die at higher rates outside the Recovery Zone. Here, we model annual survival of grizzly bears in the GYE to 1) identify landscape features (i.e., foods, land management policies, or human disturbances factors) that best describe spatial heterogeneity among bear mortalities, 2) spatially depict the differences in grizzly bear survival across the GYE, and 3) demonstrate how our spatially explicit model of survival can be linked with demographic parameters to identify source and sink habitats. We used recent data from radiomarked bears to estimate survival (1983–2003) using the known-fate data type in Program MARK. Our top models suggested that survival of independent (age ≥ 2 yr) grizzly bears was best explained by the level of human development of the landscape within the home ranges of bears. Survival improved as secure habitat and elevation increased but declined as road density, number of homes, and site developments increased. Bears living in areas open to fall ungulate hunting suffered higher rates of mortality than bears living in areas closed to hunting. Our top model strongly supported previous research that identified roads and developed sites as hazards to grizzly bear survival. We also demonstrated that rural homes and ungulate hunting negatively affected survival, both new findings. We illustrate how our survival model, when linked with estimates of reproduction and survival of dependent young, can be used to identify demographically the source and sink habitats in the GYE. Finally, we discuss how this demographic model constitutes one component of a habitat-based framework for grizzly bear conservation. Such a framework can spatially depict the areas of risk in otherwise good habitat, providing a focus for resource management in the GYE.

KEY WORDS Demography, Greater Yellowstone Ecosystem, grizzly bear, hazard models, known-fate analysis, road density, secure habitat, source–sink dynamics, survival, *Ursus arctos*.

The Greater Yellowstone Ecosystem (GYE) grizzly bear (*Ursus arctos*), listed as a threatened species in 1975, was formally delisted by the United States Fish and Wildlife Service (USFWS) in 2007 (USFWS 2007). The bear was relisted by court order in November 2009. Today, this population of grizzly bears lives in close proximity to humans and is what Scott et al. (2005:384) refer to as a "conservation-reliant species," that is, a species that is at risk from threats so persistent that it requires continuous management to maintain population levels.

Humans are the primary agent of death in grizzly bears. Indeed, rates of human-caused mortality determine the trajectories of most grizzly bear populations (Eberhardt et al. 1994, McLellan et al. 1999, Harris et al. 2006). Accordingly, understanding bear–human relationships and modeling the mortality risk in human-dominated landscapes have received recent attention, leading to development of increasingly comprehensive, spatially explicit hazard models. For example, building on early studies that emphasized the effects of roads on grizzly bear survival (Archibald et al. 1987, McLellan and Shackleton 1988, Mattson and Knight 1991, Mace et al. 1996, Mace and Waller 1997), recent hazard models also consider differences in land management policy, proximity to humans and human developments, terrain features, and vegetation cover, as well as sex, age, and management history of individual bears (Boyce et al. 2001, Merrill and Mattson 2003, Johnson et al. 2004, Nielsen et al. 2004, Haroldson et al. 2006). Moreover, these models have the potential to provide managers with spatially explicit assessments of risks, thereby focusing management activities (Nielsen et al. 2006).

Risk assessments are typically constructed using data from histories of radiomarked individuals or the locations of dead bears (Boyce et al. 2001, Merrill and Mattson 2003, Johnson et al. 2004, Nielsen et al. 2004, Haroldson et al. 2006). Methods to model survival from marked individuals are well established, allow for direct comparisons among habitats where bears survive and where they die, and constitute one component necessary to parameterize demographic models (White and Garrott 1990, White and Burnham 1999). Models using known mortality locations allow for an alternative approach when telemetry data are unavailable. These models compare mortality sites to random or telemetry locations but require assumptions about reporting rates and the spatial accuracy of the death sites (Merrill and Mattson 2003, Nielsen et al. 2004).

Despite progress in modeling grizzly bear mortality risk, important challenges remain. Most notably, in the GYE, a

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hazard model is needed that addresses the full extent and current nature of the management situation. Even the most recent models were limited to Yellowstone National Park (YNP) and the USFWS Grizzly Bear Recovery Zone, which together include only about 61% of the known grizzly distribution in the GYE (Boyce et al. 2001, Johnson et al. 2004, Schwartz et al. 2006*b*). In addition, these models were built using data from a time series (1975 to mid-1990s) spanning the year 1983, a time when management programs affecting grizzly bear survival changed substantially (Schwartz et al. 2006*c*). Thus, although these studies provided valuable insights into causes of grizzly bear mortalities, neither provided an ecosystem-wide, comprehensive assessment of factors potentially affecting survival under current management.

Even the most recent model for grizzly bear survival in the GYE, which used data from a time series (1983–2001) reflecting current management, only addressed one spatial covariate that was jurisdictional in nature (Haroldson et al. 2006). Haroldson et al. (2006) did not model human disturbance or food covariates in a spatial context.

Finally, although previous studies helped explain differences in grizzly bear mortality in all or part of the GYE, none provided a comprehensive approach that considered the full range of effects of jurisdictional management, food availability, and human disturbance. Here, we evaluated an array of spatial covariates, selected a priori, as potential mediators of mortality risk, including those associated with human disturbance, those that quantify habitat quality expressed as the spatial distribution of seasonally important foods, and those depicting differences in jurisdictional management. We modeled monthly survival 1) to determine which landscape features (i.e., foods, land management policies, or human disturbance) best describe the spatial heterogeneity in grizzly bear survival, 2) to depict differences in hazards across the GYE, and 3) to demonstrate how our spatially explicit model of female survival can be linked with additional demographic parameters to identify source and sink habitats (Pulliam 1996) within the GYE because it is well accepted that survival of adult females is the most important factor driving population trajectory of grizzly bears (Eberhardt et al. 1994, Hovey and McLellan 1996, Boyce et al. 2001, Eberhardt 2002, Harris et al. 2006). Based on the literature, we hypothesized that humans and their activities would best describe spatial differences in grizzly bear survival.

STUDY AREA

Grizzly bears occupied approximately 37,000 km^2 in the GYE (Schwartz et al. 2006*b*). Our study area essentially coincided with occupied grizzly bear range (Fig. 1) and included YNP and Grand Teton National Park, portions of 6 adjacent national forests, plus state and private lands in Montana, Wyoming, and Idaho, USA. The GYE, a high-elevation plateau with 14 mountain ranges >2,130 m, contained the headwaters of 3 major continental-scale rivers. Summers were short with most average annual precipitation (50.8 cm) falling as snow. Vegetation transitioned from low-elevation grasslands through conifer forests at midelevations, reaching alpine tundra around 2,900 m. Detailed descriptions of the geography, climate, and vegetation appear in Schwartz et al. (2006*c*).

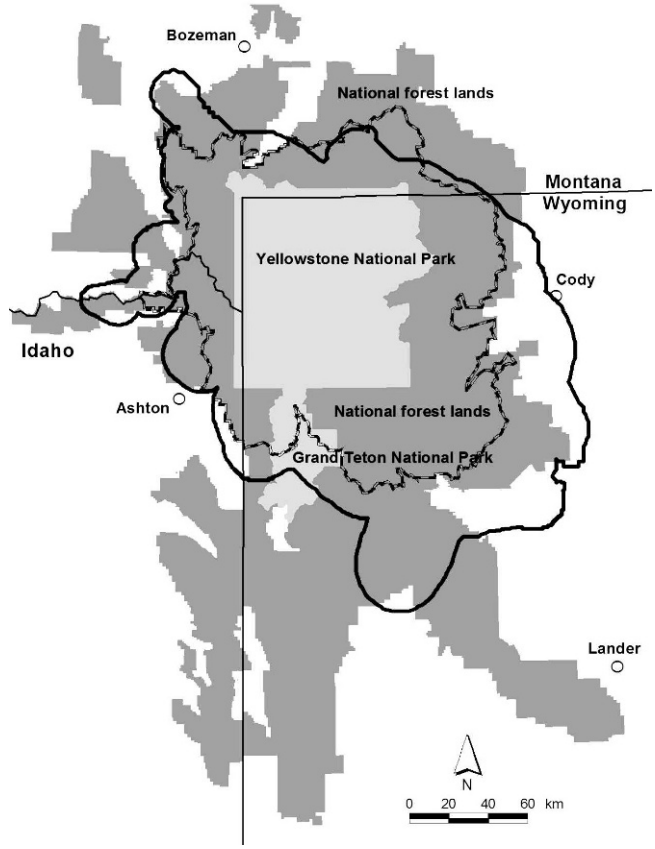

Figure 1. The Greater Yellowstone Ecosystem located in Idaho, Montana, and Wyoming, USA, where we studied hazards to grizzly bear survival from 1983 to 2003. Displayed are national forest lands (dark gray), national park lands (light gray), current distribution of grizzly bears (heavy black line), and the Grizzly Bear Recovery Zone (dashed line).

METHODS

Our trapping and collaring protocols, telemetry flight schedules, sampling design, and animal welfare protocol were previously detailed in Schwartz et al. (2006*c*). We complied with current laws of the United States of America and conducted research in accordance with animal care and use guidelines, and our study was approved by the United States Geological Survey (USGS) Institutional Animal Care and Use Committee. We used the known-fate data type in Program MARK (<warnercnr.colostate.edu/~gwhite/mark/mark.htm>, accessed 14 Feb 2004; White and Burnham 1999) to investigate the influence of covariates on the survival of bears not dependent on their mothers (age $\geq$2 yr), which we refer to as independent bears. We constructed monthly encounter histories from telemetry records for individual bears collared from 1983 to 2003 (Haroldson et al. 2006). Consistent with previous survival analyses, we right-censored data for individuals whose final fate we classed as unexplained or unresolved (Eberhardt et al. 1994, Eberhardt 1995, Boyce et al. 2001; see Haroldson

et al. 2006). We used an information-theoretic approach and selected the best-approximating models using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 1998, 2002).

Haroldson et al. (2006) found differences in survival associated with sex, season, and method of sampling but not with age class (i.e., subadult, ad) for independent bears. We started with a base model that contained 3 parameters: intercept, sex (F = 1, M = 0), and sample category (study sample = 0, conflict sample = 1). We considered bears in the study sample to be a representative sample for making inferences about the GYE population, whereas the conflict sample was a biased subset of problem bears. We used both samples in model building but only discuss results pertaining to the study sample. For details of how we coded individual bears to a sample, see Schwartz et al. (2006*c*). Because Haroldson et al. (2006) also showed seasonal differences in survival, we included 3 seasons (2 parameters: winter and spring–summer; autumn was the reference) in our base model. Following Doherty et al. (2006), we built models using this base model with season and added one additional spatial covariate. We also used AIC_c values to contrast similar covariates and identified the best covariate among them. For example, we knew a priori that road density was an important predictor of grizzly bear survival. We had 4 measures of road density, and although all were selected based on previous research, we wanted to avoid the iterative process of model building (build all possible combinations) discussed by Burnham and Anderson (2002). We, therefore, built simple models and chose the one measure of road density from the model with the lowest AIC_c score as the best measure for explaining survival among those covariates. Finally, we combined individual covariates from models with AIC_c values that were less than that for the base model with season into more complex models to identify the most parsimonious model based on AIC_c scores. To determine whether our models improved upon those of Haroldson et al. (2006, table 14), we reconstructed their top models using our data and contrasted theirs with ours using AIC_c.

In the original top model of Haroldson et al. (2006), season reflected an important effect. Haroldson et al. (2006) defined 3 temporal seasons: denning (1 Nov–31 Mar), spring–summer (1 Apr–31 Jul), and autumn (1 Aug–31 Oct) and treated autumn as the reference. We also built models with these seasons and additional human disturbance covariates. Additionally, we built models with seasonally derived human disturbance covariates that we calculated for 2 seasons: spring–summer (Apr–Jul) and autumn (Aug–Oct). For these covariates, we set winter months to zero in the design matrix and excluded the temporal covariate for spring–summer.

We tested model fit using an receiver operating characteristic (ROC) curve, contrasting recorded mortality sites (true-positive fraction) with very high-frequency telemetry locations for bears that survived (true-negative fraction), excluding locations for bears that died. For mortality sites, we used locations of known and probable mortalities, excluding dependent young and bears wearing active transmitters at death (Craighead et al. 1988). Our mortality data spanned 1983 to 2005 and included all reported mortalities in the GYE; our live-bear telemetry data spanned 1983 to 2003.

We assessed effects of individual covariates on survival from our most parsimonious model by varying each covariate ± 2 standard deviations from the mean while holding all other covariates at their mean. In some cases, this returned values beyond actual data ranges, in which case, we truncated. For example, if a mean number of developed sites within the daily activity radius of a bear was 0.23, but at -2 standard deviations, the value was -0.8, a nonsensical value. In this case, we truncated at zero.

Individual Covariates

We attributed telemetry locations for each bear in each year with spatial covariates. Covariates were binomial (0, 1), discrete, or continuous. Binomials were locations inside or outside an area (e.g., in a national park). Discrete covariates were counts of developed sites, trail heads, and similar sites contained within the average daily activity radius surrounding each telemetry location. We estimated average daily activity radii using data from a subsample of grizzly bears instrumented with Global Positioning System (GPS) collars (Telonics, Mesa, AZ) during 2000 to 2004. We calculated the activity radii from arithmetic centers for individual bears (F = 13, M = 29) for each 24-hour period with ≥ 3 GPS locations (including both 2-dimensional [2D] and 3D fixes) using the program Ranges 6 (version 1.2; Dice and Clark 1953, Kenward et al. 2003). We then calculated 2 mean daily activity radii, one for females and one for males, and used these estimates for all individuals in our sample. Continuous covariates were distance measurements from a point or arc (e.g., campground or road) to a telemetry location. Once we attributed locations, we calculated the mean value of telemetry points for each bear during each season or year, and we used those values as covariates in Program MARK. We assumed telemetry locations represented a random sample of use within the home range of the bear and that the mean represented exposure of the bear to that particular covariate (e.g., road density). We provide covariate details as an electronic supplement (see Table S1 at www.wildlifejournals.org).

We coded telemetry locations by jurisdictional area, including inside national parks (YNP, Grand Teton National Park, and John D. Rockefeller Memorial Parkway), United States Forest Service (USFS) wilderness, and USFS multiple-use lands. We coded telemetry locations in Idaho, Montana, or Wyoming, outside national park boundaries. Finally, to see whether we could improve on the spatial model of Haroldson et al. (2006), we coded locations inside YNP, outside YNP but inside the Recovery Zone, and outside the Recovery Zone.

Studies of the food habits of the Yellowstone grizzly bear have identified 4 major diet items, which include ungulates, cutthroat trout (*Oncorhynchus clarkii*), seeds of whitebark pine (*Pinus albicaulis*), and army cutworm moths (*Euxoa auxiliaris*; Mattson et al. 1991). We coded telemetry

locations as inside or outside of areas that spatially defined distributions of those foods during those periods when bears were expected to be using each of those foods. We used maps for elk (*Cervus elaphus*) and bison (*Bison bison*) range and also combined them to depict an ungulate winter range (Weaver et al. 1986, Dixon 1997, Mattson et al. 2004). We included March–May, months when carcass consumption was greatest. Spawning habitat for cutthroat trout was confined to tributary streams of Yellowstone Lake. We used a map that buffered all known fish spawning streams by 2 km, the area where bears concentrate when foraging on fish (Mattson and Reinhart 1995; Haroldson et al. 2005). We considered May–July to be the months of greatest fish consumption. We used a map of known moth sites and complexes that buffered recorded sightings of grizzly bears actively feeding at insect aggregations by 500 m (Bjornlie and Haroldson 2005). We dissolved borders of overlapping buffers at individual sites to produce single polygons of each site. We considered July–September to be the time of greatest moth-site use. During years of abundant whitebark pine seed crops, grizzly bears tend to be found at higher elevations because whitebark pine generally occurs from around 2,500 m to timberline (Mattson and Reinhart 1994). When whitebark fails to produce a seed crop, grizzlies tend to forage on ungulates and root crops at lower elevations, closer to humans (Picton et al. 1986, Mattson et al. 1992, Felicetti et al. 2003). We coded telemetry locations as either inside or outside mapped whitebark pine stands using a map generated from Landsat 7 Enhanced Thematic Mapper (ETM+) imagery and topographic data, which had an overall classification accuracy of 95.8% (Landenburger et al. 2008). Because grizzly bears use pine seeds during spring and autumn and because use varies with abundance, we built and contrasted models with both annually and seasonally (Aug–Oct) coded locations. We included temporal covariates explored by Haroldson et al. (2006) and included indices of winter severity (a surrogate of carcass availability) and whitebark pinecone production. We also attributed locations with elevation using 1-arc-second (30 m), grid-spacing, digital elevation models from the USGS (2002).

The greatest cause of bear deaths has historically been sanctioned management removals. Many removals have been associated with homes, ranches, and developed recreational sites. We used a map of home distribution on private lands across 20 counties surrounding the GYE from Hernandez (2004). The map recorded number of homes per 2.59 km^2, excluding those in incorporated cities and towns. We filled in cities and towns using housing estimates from the United States Census Bureau (2000) from 1990 and 2000. We used USGS digital, orthographic photos to estimate the footprint of each town at time of census. Based on the distribution of homes in photos, we approximated the proportion of homes per 2.59 km^2. We then multiplied this proportion by the total homes listed for that census and assigned that value to each 2.59-km^2 area within-town footprints. We used total homes present in 1980, 1985, 1990, and 1999 to attribute telemetry data from 1983 to 1985, 1986 to 1990, 1991 to 1995, and 1996 to 2003, respectively. We attributed each location with number of homes within a 2.59-km^2 cell. We also tested the natural log of homes [ln(total homes + 1)], hypothesizing that the effect of change from 1 to 2 homes was much greater on bear survival than changing, for example, from 101 to 102 homes. We also attributed locations based on distance (km) to the nearest section containing the home.

We used Geographic Information System (GIS) maps from cumulative effects models (CEM) to quantify developments, trailheads, and backcountry campsites (Weaver et al. 1986, Dixon 1997, Mattson et al. 2004). We treated each development as a separate site (i.e., point). We treated mapped trailheads and associated parking areas separately from developed sites. In general, most trailheads were simply parking areas from which hikers or hunters embarked on backcountry trips. With few exceptions, trailheads were not associated with attractants. The most notable exception was where outfitters staged, corralled, and fed sweet feed and grain to riding stock. We included such trailheads in our developed-sites layer. Finally, we identified backcountry campsites from the CEM layer. These sites represented camping areas regularly used by hikers and hunters.

These GIS layers quantifying developments, trailheads, and backcountry camp sites were principally from CEM. However, because the spatial extent of CEM was limited to the Recovery Zone, we supplemented maps with additional information outside the Recovery Zone from the Shoshone, Gallatin, and Bridger–Teton national forests; we specifically mapped cabins, campgrounds, campsites, picnic areas, and trailheads. We excluded developments not potentially lethal to bears, which included roadside exhibits, scenic overlooks, boat docks, parking lots, gravel pits, water-treatment plants, viewing areas, interpretive sites, guard stations, radiotowers, and airports. We also reviewed 1:100,000 USGS topographic maps for campgrounds, roadside parks, and similar sites, outside USFS lands. We attributed telemetry points with the number of sites within a daily activity radius for female and male bears. We also attributed each telemetry point with a measure of distance (km) to the nearest point for each layer.

Because roads affect grizzly bear survival, the amount of roadless habitat is considered a measure of security for bears. For the GYE, secure habitat has been defined as any area $\geq$4.05 ha (10 acres) that is >500 m from an open or gated road (Interagency Grizzly Bear Committee 1998, USFWS 2003). We attributed telemetry locations as inside or outside secure habitat.

We compiled a thematic layer of motorized routes for the GYE. We started with the CEM roads layer, which mapped all existing motorized routes within the Recovery Zone. We added motorized routes outside the Recovery Zone using 1:24,000-scale, USGS, level 3, Digital Line Graphs and Topologically Integrated Geographic Encoding and Referencing (TIGER)/Line® data (2005 TIGER/Line Shapefiles, United States Census Bureau, Washington, D.C.). Transportation routes in Grand Teton National Park, the John D. Rockefeller Memorial Parkway, the National Elk Refuge, and private lands near Jackson Hole, Wyoming,

were provided by the Grand Teton National Park. We mapped both total and open roads. We calculated open motorized-route density from those roads open to motorized vehicles (USFWS 1993, Summerfield et al. 2004); CEM classified open-route density into 2 seasons: season 1 = 1 March to 15 July; season 2 = 16 July to 30 November. Total motorized-route density included open roads and roads with restricted or closed motorized access.

We evaluated road density at 2 spatial scales. The USFS uses a 2.59-km^2 (1-$mile^2$) moving window to calculate road densities (Summerfield et al. 2004). Because that scale did not match the scale we used to define secure habitat, we created a second road-density metric. We used a 0.25-km^2 moving window, which was 500 m wide and equivalent in scale to the 500-m distance from a road we used to define secure habitat. We attributed telemetry points with road density at the 30-m pixel scale, considering the 2 CEM seasons for open motorized-route density and no seasonal designation for total route density. The moving-windows protocol counted road segments bisecting each 30-m pixel, and the average length of a segment in 1.4 million pixels in our study area was 25.8 m. We used pixel count in the models and converted counts to road density for presentation here. We also attributed telemetry points with a measure of distance (km) to the nearest open road.

We created 3 spatial maps depicting areas open to elk hunting. One delineated areas open to early season rifle hunting, principally along the boundaries of YNP. Opening dates, lengths, and closing dates varied but typically were within the range of 1 September to 31 October. The second data set mapped areas open to elk hunting during the general rifle season in the 3 states, typically mid-October to November. The third map combined the early and general hunt layers and depicted areas open to hunting during September through November. We attributed grizzly bear locations as inside or outside areas open to hunting and treated them as seasonal covariates.

Trails provided access for hunters into the backcountry, and we hypothesized that bears near trails in areas open to hunting would be exposed to an increased probability of a lethal encounter with a hunter compared with bears living in inaccessible areas. We used the CEM layer for mapped trails (nonmotorized), supplemented with files from the Shoshone, Gallatin, and Bridger–Teton national forests that mapped trails outside the Recovery Zone. We set trail density to zero inside YNP because hikers in the park are unarmed and, therefore, encounters are not lethal. There were no documented mortalities inside the national parks associated with self-defense in our mortality database, supporting our assumption of nonlethal encounters in YNP. We used a moving window at 4 scales (0.25 km^2, 1 km^2, 2 km^2, and 5 km^2) to measure trail density around each telemetry location during the early hunt, the general hunt, and for both hunts. Unsure of what scale to use for trail density, we chose a 0.25-km^2 window because it matched our measure of road density. We chose the 1-km^2 and 2-km^2 windows because they bracketed the daily activity radii for male and female grizzly bears. We chose the 5-km^2 window because it approximated what we presumed to be the distance an average hunter might travel off trail in pursuit of elk. We also measured distance to the nearest trail.

We used USFS maps of livestock allotments on national forests to attribute grizzly bear locations as inside or outside active cattle and sheep allotments. Grazing on national forests is seasonal, with turnout and removal dates dependent on allotment location, grazing program, and type of stock. Lacking data to determine the exact times livestock were present, especially among years and months, we treated all allotments the same and attributed telemetry locations as inside or outside cattle, sheep, or both allotment polygons for June–September, the season when most grazing occurred on public lands.

Our estimated telemetry error was approximately 300 m, based on GPS-acquired locations of retrieved collars (Podruzny et al. 2002). We have no data suggesting errors were directionally biased. For some spatial layers (i.e., rural homes, road density, developed sites), pixel size or scan area accounted for that error. For locations coded as binomial (in or out of area), most polygons were >1 km^2 (e.g., jurisdictional areas, allotments, areas open to hunting), and the probability of error was small and likely offset because the error was random. For distance measurements, exact distances were influenced by telemetry error, but the relative magnitude should have been unaffected (i.e., points close to roads would still have a small value compared with points distant from roads, even with telemetry error).

To model human disturbance, we treated seasonally derived values as one covariate (i.e., they all appeared in one column) in the Program MARK design matrix because coefficient values for each covariate were on the same scale. Our design matrix consisted of 504 rows (21 yr $\times$ 12 months $\times$ 2 groups [sample and conflict]). In the top model from Haroldson et al. (2006), season was an important covariate. Haroldson et al. (2006) defined 3 seasons: denning (1 Nov–31 Mar), spring–summer (1 Apr–31 Jul), and autumn (1 Aug–31 Oct). For seasonal coefficients of human disturbance, we calculated values for 2 seasons: spring–summer (Apr–Jul) and autumn (Aug–Oct). For these, we set winter months to zero in the design matrix. Mean seasonal values were included in one column in the design matrix for each covariate.

Harris et al. (2006) demonstrated with the current GYE rates of reproduction (0.318 F cubs/F/yr) and survival of dependent young (cubs = 0.63, yearlings = 0.817) that lambda $\geq$ 1.0 in 95% of stochastic simulations when adult female survival was = 0.91. We chose this value of female survival to identify source and sink areas in the GYE. We used results from our best hazard model to predict survival of independent females from our study sample for each 30-m^2 pixel in the GYE and classified them as source (survival $\geq$ 0.91) or sink habitats (survival $<$ 0.91) to illustrate how hazard models can be linked with demographic models.

RESULTS

Our data spanned 21 years (1983–2003) and contained 11,888 telemetry records during 6,992 months from 362

Table 1. Models we used to assess the effect of jurisdictional and human disturbance covariates on estimates of grizzly bear survival in the Greater Yellowstone Ecosystem, 1983–2003. We compare results to the best model from Haroldson et al. (2006) and an intercept-only model. Abbreviations: AIC_c, Akaike's Information Criterion adjusted for small sample size; USFS, United States Forest Service; YNP, Yellowstone National Park.

Model no.[a]	Model type	AIC_c	No. of parameters	ΔAIC_c[b]	Deviance
Jurisdictional					
19	Base[c] + 3 seasons[d] + national parks + WY + MT	740.383	8	0.00	724.363
20	Base + 3 seasons + national parks + USFS wilderness + USFS multiple-use lands	741.821	8	1.44	725.801
22	Base + 3 seasons + outside YNP + outside Recovery Zone	748.263	7	7.88	734.220
Human disturbance					
1	Base + winter season + secure habitat + ln(total homes +1) + developed sites + open motorized-route density + distance to homes + distance to developments + distance to roads + open to hunting + elevation + whitebark pine distribution	635.588	11	0.00	613.550
2	Base + winter season + secure habitat + ln(total homes +1) + developed sites + open motorized-route density + distance to homes + distance to developments + distance to roads + open to hunting + elevation	637.073	13	1.49	611.021
3	Base + winter season + secure habitat + ln(total homes +1) + developed sites + open motorized-route density + open to hunting + elevation	637.139	10	1.55	617.108
8	Base + winter season + secure habitat + ln(total homes +1) + developed sites + open motorized-route density + open to hunting + elevation + whitebark pinecone count	639.119	11	3.531	617.081
Haroldson et al. (2006, table 14) top model					
21	Base + 3 seasons + outside YNP + outside Recovery Zone + whitebark pinecone index	745.035	8	109.45[c]	729.014
25	Intercept only	831.448	1	195.86[c]	829.448

[a] Model no. relates to all models constructed (Table S3 at www.wildlifejournals.org).
[b] ΔAIC_c values are comparisons within model types; we compared the top model by Haroldson et al. (2006) and the intercept-only model to model 4, the best complex model we constructed.
[c] The base component of models contained 3 parameters: intercept, sex (F = 1, M = 0), and trap status (sample = 0, conflict = 1).
[d] The 3 seasons were winter, spring–summer, and autumn. Autumn was the reference, therefore, season represented 2 parameters.

bears. Encounter histories contained 1,004 records (bear–yr), with 686 (356 F, 330 M) from the study sample and 318 (167 F, 151 M) from the conflict sample. The average time an individual bear was in our data set was 2.6 years (SD = 1.9), and our sample size increased from a low of 17 bear–years in 1985 to a high of 85 bear–years in 2001. During that time, there were 75 recorded mortalities, 31 (10 F, 21 M) from the study sample and 44 (19 F, 25 M) from the conflict sample. There were 25 encounter histories where the final fate was undetermined and censored. Our estimated average daily activity radius for females was 1.1 km (n = 2,923, SE = 0.02), and for males, it was 1.5 km (n = 3,104, SE = 0.03).

In general, when we added individual covariates to the model with sex and sample (base model), measures of human disturbance were better predictors of survival than were jurisdictional boundaries or spatial distributions of key foods, and seasonal covariates were better predictors than annual covariates (see Table S2 at www.wildlifejournals.org). Based on AIC_c values (670.76), grizzly bear survival was best explained with measures of open, rather than total, motorized route density, using a moving window of 0.25 km^2 rather than 2.59 km^2 (ΔAIC_c = 7.74). Seasonally defined secure habitat was the second-best spatial predictor of survival (AIC_c = 682.63), followed by the number of developed sites within the daily activity radii of grizzly bears (AIC_c = 714.82). Housing density explained differences in bear survival, but the formula ln(total homes + 1) provided the best measure based on AIC_c values. Measures of distance to homes, developments, and roads yielded lower AIC_c models than the base model. The amount of time bears spent in areas open to autumn, ungulate hunting during both the early and general rifle hunts yielded lower AIC_c models than the base mode.

Human disturbance covariates that did not explain differences in bear survival included the density of trailheads (AIC_c = 750.34) and backcountry campsites (AIC_c = 751.34) within the daily activity radii of bears and distances to these point sources ($\Delta AIC_c \geq 74.08$). Differences in survival were not explained by trail density, regardless of scale, measured during the hunting season, or the amount of time bears spent on cattle, sheep, or both allotment types. Of the 75 recorded mortalities for radiocollared bears, only 4 were related to livestock, and 3 were not within a USFS grazing allotment.

Habitat covariates that explained differences in survival included elevation, amount of time bears spent in mapped whitebark pine forest, and annual whitebark pinecone production. Amount of time spent at spawning streams, moth sites, or on ungulate winter range did not explain survival differences.

Our jurisdictional models were an improvement to the top model of Haroldson et al. (2006). Attributing telemetry locations as in or out of national parks, USFS wilderness, USFS multiple-use lands, or outside all these areas (Table 1, model 20) yielded a model that was 3.21 ΔAIC_c units fewer than the best model of Haroldson et al. (2006), where spatial covariates were inside YNP, outside the park but inside the Recovery Zone, or outside the Recovery Zone, plus an index of whitebark pinecone production (model 21).

Table 2. Parameter and beta coefficient estimates from the top model we used to assess the effect of spatial covariates on estimates of grizzly bear survival in the Greater Yellowstone Ecosystem, 1983–2003.

Parameter	β estimate	SE	95% CI Lower	95% CI Upper
Intercept	−0.063	1.553	−3.107	2.982
Sex	0.565	0.260	0.054	1.076
Winter season	6.702	1.605	3.556	9.849
Sample	−0.898	0.257	−1.402	−0.394
Secure	1.235	0.600	0.059	2.412
ln(total homes + 1)	−1.083	0.398	−1.862	−0.304
Developed sites	−0.269	0.088	−0.442	−0.097
Road density[a]	−0.088	0.027	−0.142	−0.034
Open to hunting	−1.217	0.284	−1.774	−0.660
Elevation	1.681	0.608	0.491	2.872

[a] We modeled road density as the no. of 30-m pixels in the 0.25-km^2 moving window containing a road segment.

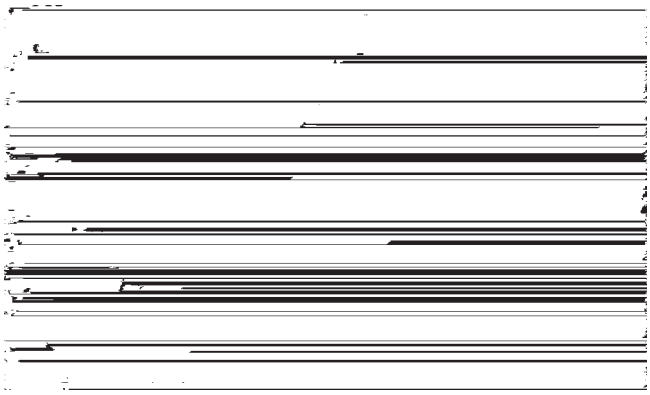

Figure 2. Effects of individual covariates on point estimates of the survival of an independent, female grizzly bear from our study sample in the Greater Yellowstone Ecosystem, USA, 1983–2003. We estimated survival for each covariate while holding all other covariates at their mean and varying the covariate of interest by ±2 standard deviations. Some lines do not span ±2 standard deviations because values were outside the actual range of data and were, therefore, truncated.

Predicted survival was highest in wilderness, followed by national parks, multiple-use land, and nonfederal land. Mean estimates of annual survival for female bears from the study sample were 0.978, 0.958, 0.897, and 0.824, for wilderness, national parks, multiple-use land, and nonfederal land, respectively. The 95% confidence intervals for all 4 estimates overlapped. Likewise, attributing locations as either in a national park or outside a national park but within the states of Idaho (Idaho treated as the reference), Montana, or Wyoming (model 19) yielded a model that was 4.65 ΔAIC_c units lower than the Haroldson et al. (2006) best model (model 21). Predicted survival was highest in national parks, followed by bears residing in Wyoming, then Montana, and finally Idaho. We also built a model by excluding the whitebark pinecone index from model 21 to allow for direct comparisons of jurisdictional covariates alone. That model (model 22) was 7.88 ΔAIC_c units greater than model 19.

We used human-disturbance covariates from our univariate models to develop complex models. Grizzly bear survival was best explained by sex, sample, winter season, open motorized-route density, secure habitat, ln(total homes + 1), developed sites, elevation, open to hunting, distance to homes, distance to developed sites, and distance to roads (model 2, AIC_c = 637.073). Confidence intervals for all β coefficients in the model, with the exception of the 3 distance measures, did not bound zero.

The human-disturbance model with the second-lowest AIC_c value (637.139) contained the same suite of covariates, without the 3 distance measures, and only differed from the top model by 0.066 ΔAIC_c units, effectively making the 2 models equivalent (model 3). Thus, we chose it as our best model built with human-disturbance covariates. This model was also 103.2 ΔAIC_c units fewer than the top jurisdictional model (model 19), 107.9 ΔAIC_c units fewer than the top model by Haroldson et al. (2006; model 21), and 194.3 ΔAIC_c units fewer than an intercept model (model 25).

Adding the covariate describing the amount of time bears spent in whitebark pine (model 1) yielded a model that was 1.6 ΔAIC_c units lower than model 2 and differed by a single parameter. Adding whitebark pinecone counts as a temporal covariate to model 2 yielded a model that was 1.98 ΔAIC_c units greater (model 8). Based on these comparisons, we concluded that the most parsimonious model predicting the spatial probability of grizzly bear survival contained covariates describing human disturbances on the landscape (Table 2). Covariates describing distribution of foods or temporal availability of whitebark pine seed did not contribute to the best model.

A ROC score of 0.72 for our best model suggested a fair fit. When we fit the model excluding hunter-related mortalities during autumn, the ROC score improved to 0.80.

Comparing changes in survival across the range of values for each covariate, while holding all others at their mean, suggested that elevation had the greatest effect on survival (Fig. 2). At +2 standard deviations, predicted survival was 0.980, whereas at −2 standard deviations, predicted survival was 0.922, a difference of 0.058. Similar comparisons contrasting predicted survival for the high values and low values of other covariates revealed that differences were as follows: secure habitat (0.043), open motorized-route density (0.034), developed sites (0.018), open to hunting (0.017), and the natural logarithm of total homes (0.015). The highest correlation among covariates was between open motorized-route density and secure habitat ($r = -0.654$ for spring; $r = -0.616$ for autumn; $P < 0.001$). However, models built excluding road density (model 14; AIC_c = 645.253) or secure habitat effects (model 6; AIC_c = 639.035) had higher AIC_c values when compared with model 2 (AIC_c = 637.139) containing both covariates, demonstrating that each of these covariates contributed important and different information to the model. Varying these 2 factors together suggested that increased road density had a greater effect on predicted survival as secure habitat decreased (Fig. 3).

Model 2 predicted annual survival for an independent female from our study sample as 0.961, with survival in winter, spring–summer, and autumn equal to 0.995, 0.984,

Figure 3. Effects of varying amount of secure habitat and open motorized-route density on point estimates of survival of an independent female grizzly bear from the study sample in the Greater Yellowstone Ecosystem, 1983–2003.

and 0.982, respectively, setting all covariates at their means. Extrapolating results across the GYE illustrated the variation in risk of mortality for a female grizzly bear from the study sample (Fig. 4). Consistent with interpretation of β coefficients (Table 2), mortality was predicted to be greatest in areas near roads and developed sites, with the greatest risk occurring at, and beyond, the interface between public and private lands. Dividing habitats in which female survival was predicted to be ≥ 0.91 (source) and <0.91 (sink) allowed us to reclassify probabilities of survival into these 2 categories (Fig. 5).

DISCUSSION

Our primary objective was to determine what features (landscape, food, land management, or human disturbance) best described hazards to grizzly bears in the GYE. Our results support our hypothesis that measures of human disturbance best explain spatial heterogeneity of grizzly bear mortality. Models built with covariates reflecting differences in management policies (i.e., jurisdictional boundaries) or spatial and temporal distributions of key foods were less informative.

The most important predictors of survival in our best model were the amount of secure habitat within a bear's home range and road densities outside of secure habitat. Both covariates contributed explanatory power because excluding either returned AIC_c scores greater than our best model. It is well known that grizzly bears suffer higher human-caused mortality in heavily roaded portions of their range (McLellan and Shackleton 1988, Mattson and Knight 1991, Mace et al. 1996). Mattson and Knight (1991) estimated that areas near developments, within 3 km from primary roads or 1.5 km from secondary roads, represented 32.9% of the landscape within YNP but accounted for 70.3% of bear mortalities. Our model also suggested that as the amount of secure habitat declines, road density must also decline to maintain high survival. Managing the landscape to reduce hazards to grizzly bears, therefore, requires balancing road density standards with the amount of secure habitat available, something previously not considered when establishing road-density standards on public lands (Summerfield et al. 2004). If road densities become too great, secure areas become isolated islands surrounded by heavily roaded areas. Travel among secure islands then becomes more hazardous, effectively fragmenting the landscape.

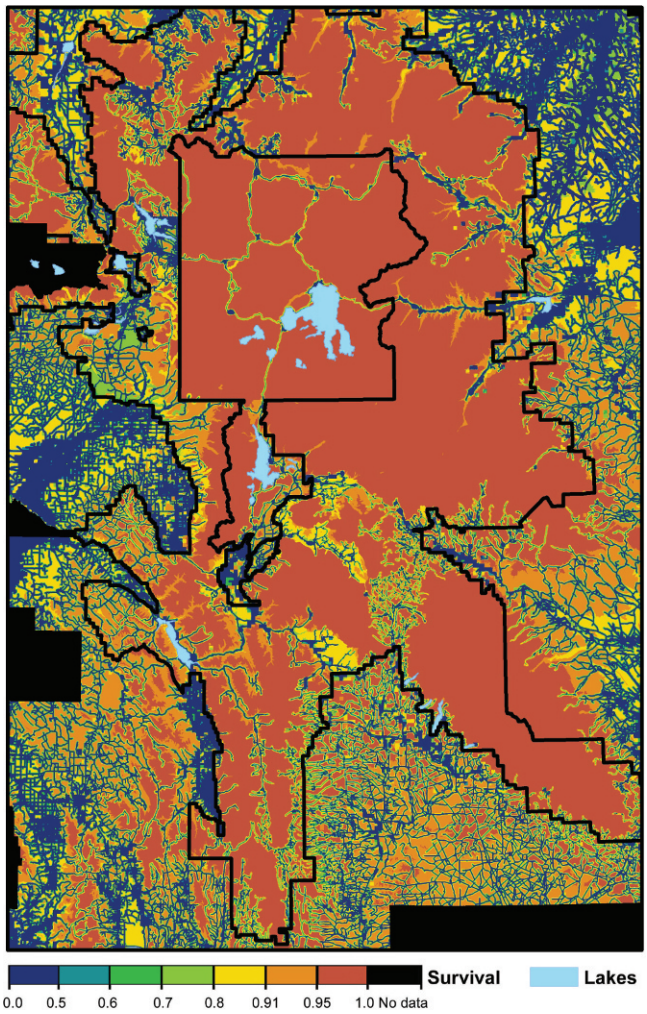

Figure 4. Spatial variation in estimated probability of survival for a female grizzly bear from our study sample in the Greater Yellowstone Ecosystem, 1983–2003. The model (Table 1, model 2) contained covariates describing sex, sample, winter season, open motorized-route density, secure habitat, the natural logarithm of total homes, developed sites, elevation, areas open to elk hunting, and an intercept term. The outer black line is the boundary of national forest lands, whereas the inner black line is the boundary of national park lands.

Of the covariates in our best model, the number of homes per section and the roads associated with those developments were the best predictors of grizzly bear survival on private lands. To our knowledge, this is the first time housing density has been directly linked to grizzly bear survival in a spatial context.

Since 1970, the human population in the 21 counties surrounding the GYE has grown by >60% to approximately 370,000 people (Hernandez 2004), which exceeds 78% of all other counties in the United States (Hansen et al. 2002). The current form of development consists of large-lot, rural subdivisions, and consequently, the area (ha) developed is expected to exceed population growth. Hernandez (2004)

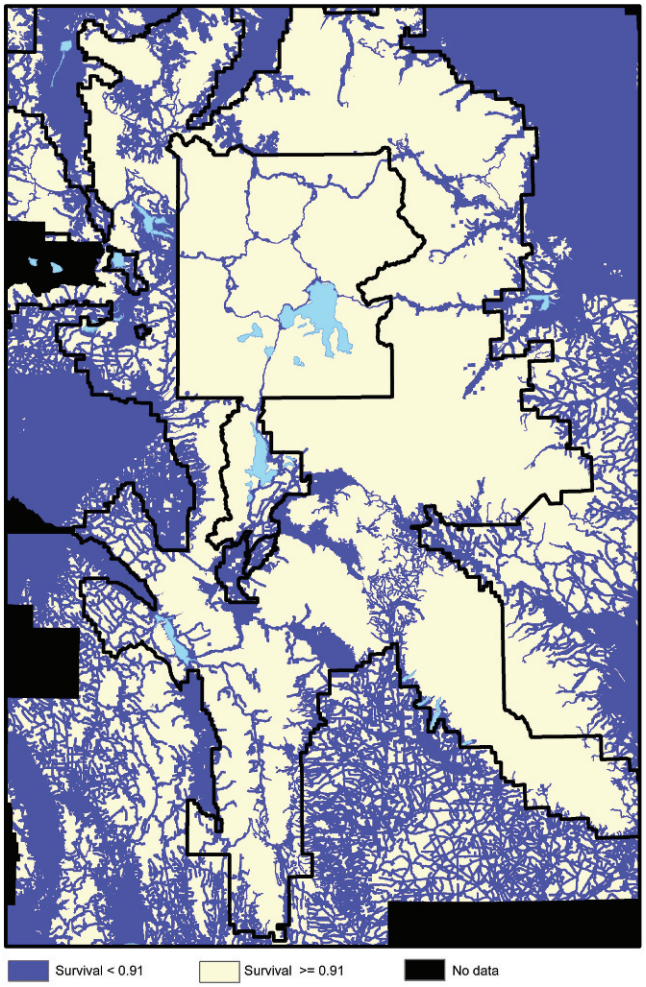

Figure 5. An illustration of the source and sink habitats for the Greater Yellowstone Ecosystem grizzly bear population, 1983–2003. Source habitats (white) are areas where a female grizzly bear survival was ≥ 0.91, and sink habitats (blue) are areas where a female grizzly bear survival was <0.91. The threshold is based on an estimate of sustainable mortality from Harris et al. (2006) that demonstrated population growth (λ) for the Yellowstone bear population ≥ 1.0 with 95% probability when female grizzly bear survival = 0.91. The outer black line is the boundary of national forest lands, and the inner black line is the boundary of national park lands.

concluded rural growth was positively related to the road density, encroaching development, and the education level of the individuals in the area. Growth was negatively related to distance to water, travel time to a hospital, and travel to national park or national forest areas. Modeled growth from 1999 to 2020 forecasted that an additional 7.7% to 10.7% of occupied grizzly bear habitat will be affected by low-growth and boom scenarios, and 8.5% of occupied grizzly bear habitat will be affected if growth progresses at its current rate (Gude et al. 2007). At current rates of development, the conversion of agricultural land to exurban housing density is forecasted to occur in 559 sections, or approximately 1,551 km^2 of the land, by 2020. In the boom scenario, approximately 4,307 km^2 of land will convert to ≥ 1 house/16.2 ha (40 acres; 16 homes/$mile^2$). Regardless of the pace, our model suggests that private lands development will continue to affect grizzly bear survival in the GYE.

Our analyses failed to show a spatial relationship between the distribution of key bear foods and survival, leading us to conclude that the proportion of time an individual bear spends on winter ranges, near fish-spawning streams, on cutworm moth sites, or within mapped stands of whitebark pine is not a good predictor of survival. All these foods are seasonally abundant in some years but not in others. It has been well demonstrated that grizzly bears exhibit dietary plasticity in the GYE and readily shift among habitats accordingly (Mattson et al. 1991; Felicetti et al. 2003, 2004). We conclude that spatial shifts made by grizzly bears associated with changes in food abundance do not predict survival unless the bears shift to habitats with more human disturbance. We explain our rationale for this conclusion using whitebark pine as an example.

It has been well documented that grizzly bear mortality in the GYE is greater during years with little or no autumn whitebark pine seed availability, and bears shifted to lower elevations in years without pine seeds (Blanchard and Knight 1991, Mattson et al. 1992, Blanchard and Knight 1995, Mattson 1998). Surviving bears in our study also used lower elevations in poor seed years, compared with average or excellent seed years, but bears suffering mortality in poor seed years used lower elevations than bears that survived (Fig. 6). Bears suffering mortality in average and excellent pine seed years were, on average, found at lower elevations than bears that survived, but the standard error about the mean was large, so statistical differences were not detectable. Blanchard and Knight (1995) also found a significant shift in elevation between poor and good seed years; independent male and female grizzlies were consistently located at high elevations during autumns of average and excellent nut production but at lower elevations during poor production years.

Results from our model and plots of the distribution of hazards associated with surviving versus dying bears suggested that bears do shift to lower elevations during poor pine seed years, but that this elevation shift does not itself predispose bears to increased mortality. Bears that shift to lower elevations that have been altered by human disturbance (e.g., more roads, developments, homes) are exposed to more risk, whereas bears that shift to lower elevations in habitats that are secure are not subject to increased hazards and thus survive. Bears that survived had more secure habitat, with lower road density, and fewer homes and developed sites within their home ranges during autumn compared with bears that died, regardless of seed abundance (Fig. 6). Standard errors about the means were substantially larger for bears that died, especially in average and excellent seed years, suggesting that even in years when pine seeds were available, some bears tended to remain at lower elevations with higher levels of human disturbance and risk. The large standard error about elevation for dead bears also suggested that some individuals that died remained at higher elevation (i.e., areas with fewer hazards), similar to bears that survived, but still suffered mortality. Of the 30 deaths recorded during the autumn, 10 were hunting related, and the proportion of time bears spent in areas open

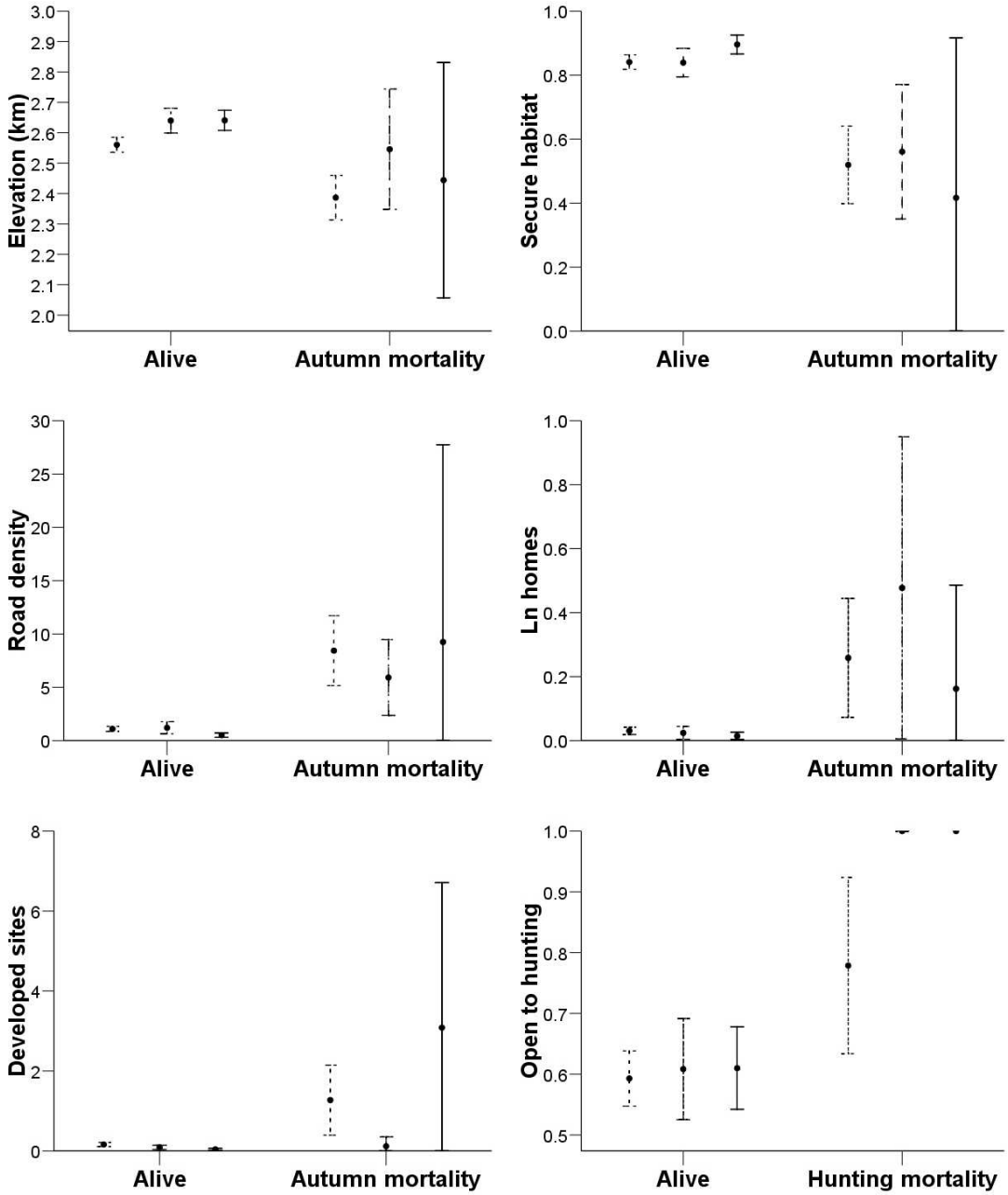

Figure 6. Mean ± 2 standard errors for the seasonal covariates for grizzly bears that lived versus those that died during autumn (Aug–Oct) or during hunting season (Sep–Nov). Error bars are for poor (0–7.5), average (8–13.5), and excellent (14–29) median counts of whitebark pinecones, left to right, respectively. Data are from radiocollared bears in the Greater Yellowstone Ecosystem, 1983–2003.

to hunting was greater and more variable for bears that died than for bears that survived (Fig. 6). Seven additional mortalities during the autumn were classified as poaching or malicious killings and could have been associated with hunting. Some bears in autumn died far from roads and human developments, and those deaths tended to be associated with autumn ungulate hunting.

During autumn, most areas outside national parks are open to ungulate hunting. Haroldson et al. (2004) presented evidence that the distribution of some radiomarked bears changed from use inside YNP to outside YNP with the opening of elk hunting. This use change to outside YNP was attributed to the availability of gut piles left by hunters, which brought hunters and bears into close proximity. About 51% (57 of 112) of the known and probable deaths after August of independent bears in our mortality database were associated with hunters defending a camp, carcass, or themselves when charged by a grizzly. Our best model included the covariate delineating amount of time a bear spent in areas open to elk hunting and predicted the presence of armed humans during autumn increased the risk of mortality by about 1.7% for a bear spending all its time in areas open to elk hunting. On average, bears in our sample spent about 61% of their time in areas open to hunting during hunting season. This slight decline in survival associated with hunting can easily be absorbed by bears

living in habitats fostering high survival (sources) but can result in sink area effects if the addition of hunting mortality results in a nonsustainable rate of survival.

The improvement in our ROC curve scores when we excluded hunter-related mortality indicated that our best model either did not capture all spatial heterogeneity associated with hunter-caused grizzly bear deaths or that there was no strong spatial context to these mortalities. There were 57 hunter-related grizzly bear deaths during autumn in our mortality database. These mortalities occurred in wilderness and nonwilderness areas, and locations did not shift with whitebark pine seed abundance ($\chi^2 = 0.004$; $P = 0.949$), but nearly 2.6 times as many deaths occurred during poor ($n = 41$) versus good ($n = 16$) seed years. Food habits and isotope studies clearly showed grizzly bears, especially females, transitioned from pine seeds to meat when seed availability was poor, and bears moved into areas open to hunting during the hunting season (Mattson et al. 1991, Felicetti et al. 2003, Ruth et al. 2003, Haroldson et al. 2004). In years of good seed production, female bears foraged mainly on pine seeds, thus avoiding direct conflict (aside from surprise encounters) with hunters for carcasses. In poor seed years, female bears shifted to ungulate meat, increasing the probability of conflict with hunters. The energetics of hyperphagia, lack of pine seeds, and the association of ungulate meat with hunters likely compel bears to be less wary (or possibly more aggressive) toward hunters in the search for food, which leads us to conclude that differences in rates of hunter-related mortality in good versus poor seed years is more likely explained by changes in bear behavior, rather than by differences in spatially explicit hazards on the landscape. If true, modeling hunter-related mortality in a spatial context would be difficult, and such a conclusion might also suggest that this dynamic could increase if whitebark pine declines because of the mountain pine beetle (*Dendroctonus ponderosae*) or blister rust (*Cronartium ribicola*), warranting long-term monitoring and possible management intervention (Bockino 2008).

Naves et al. (2003) developed a conceptual framework for classifying European brown bear (*U. a. arctos*) habitat quality that required building separate models addressing factors influencing mortality and reproduction. The mortality model was influenced principally by anthropogenic or human-disturbance factors, whereas important predictors of reproduction were nutritional or natural factors. By linking these 2 models, they were able to classify habitats into 5 categories in 2D space: avoided matrix (no reproduction and very high mortality), sink (low reproduction and high mortality), refuge (low reproduction and low mortality), attractive sink (high reproduction and high mortality), and source (high reproduction and low mortality). Because Naves et al. (2003) lacked adequate data on the spatial heterogeneity of demography, they modeled the relationship among presence–absence and 2 separate sets of explanatory variables comprising human factors (mortality) and natural ones (reproduction), under the assumptions that human factors drive mortality, natural factors determine reproduction, and presence is a surrogate for reproduction and survival. Using historic data from northern Spain, Naves et al. (2003) confirmed that most extinction occurred in matrix habitat, and fewest deaths occurred in source habitat.

Nielsen et al. (2006) followed a similar approach by combining models of occurrence and risk to advance a habitat-based framework for conservation of grizzly bears in Alberta, Canada. Like Naves et al. (2003), Nielsen et al. (2006) conceded that models describing fitness (reproduction and survival) especially across gradients of human disturbance and land cover types would greatly improve management and conservation. However, Nielsen et al. (2006) recognized that few areas possess adequate data to parameterize demographic rates necessary for describing fitness and instead used more commonly available data on occupancy and distribution of mortality locations.

Fortunately, because of the long-term commitment of both state and federal agencies in the GYE, we had adequate data to estimate demographic rates. The duration of monitoring and sample sizes we reported is the largest, to our knowledge, from a single study addressing grizzly bear demographics in North America (McLellan et al. 1999, Schwartz et al. 2003, Haroldson et al. 2006).

Naves et al. (2003) recommended modeling reproductive rate in a spatial context. We chose to treat that rate as a constant when evaluating lambda across the GYE landscape for several reasons. First, although demographic models of reproduction in the GYE have predicted density-dependent effects between litter size and population size, spatially explicit estimates of density did not exist (Schwartz et al. 2006*a*). Second, Schwartz et al. (2006*a*) showed that litter size was asymptotic once their index of population size reached 325–350 bears and that index has been >350 since 1998. Third, Schwartz et al. (2006*a*) demonstrated that in years following abundant seed crops of whitebark pine, female grizzly bears produced more 3-cub litters. Schwartz et al. (2006*a*) incorporated cone counts into their model as a temporal covariate (i.e., each F was assigned the same covariate value in any given yr), so counts were not spatially explicit. Adding spatially explicit covariates for whitebark pine to the top reproduction models of Schwartz et al. (2006*a*) did not improve them (C. Schwartz, USGS, unpublished data). Finally, Harris et al. (2006) showed that reproductive rate only contributed 0.089 to the elasticity of the population growth rate. Consequently, we felt treating reproduction as a constant, estimated at the ecosystem scale, was reasonable. Linking reproduction with our best model of survival allowed us to demographically depict source and sink habitats in a spatial context across the GYE (Fig. 5). To our knowledge, we are the first to use demographic measures to identify source and sink habitats for a large-mammal population.

Population trajectory (λ) can also be viewed as 1 of 2 dimensions in a conservation framework (Naves et al. 2003). We propose that habitat selection constitutes the second dimension. We know bears do not use the landscape uniformly in the GYE; they have shown preferences for areas with high resource value and have shifted their use of elevation according to seasonal and annual food abundance.

Layered upon ecologically driven habitat selection are the influences of humans, their developments, and their activities. Linking population trajectory, a direct measure of "demographic vigour" (Caughley 1977:55), with a model of habitat selection would allow managers to evaluate the current state of grizzly bear habitat at various spatial scales (e.g., bear management unit or subunit, primary conservation area), the consequences of prescribed management activities (i.e., infrastructure development), and the effects of changing food resources on the fecundity or habitat selection in the conservation framework of Naves et al. (2003). Because bears use habitats differently among seasons, we suggest time as a possible third dimension. Clearly, the probability of habitat-specific selection varies among seasons, so selection and use of source or sink habitats by grizzly bears likely changes accordingly (Nielson et al. 2003). These shifts must be considered when prioritizing habitats for protection or management.

MANAGEMENT RECOMMENDATIONS

Those responsible for land management will continue to influence the quality of grizzly bear habitat on public lands. Of all the covariates we examined, the amount of secure habitat and the density of roads in nonsecure habitat on public lands had the greatest effect on grizzly bear survival. We strongly support the continued protection of secure habitats for grizzly bears in the GYE and maintaining road densities in nonsecure habitats at levels necessary to maintain source habitat.

Our models demonstrate that when bears move to lower elevations in poor whitebark pine seed years, survival is dependent on the density of human-related hazards on the landscape. Mature whitebark pine is currently declining in abundance in the GYE because of the mountain pine beetle and blister rust. Should that trend continue, grizzly bears will likely increase their use of lower-elevation habitats, where mortalities are typically higher because lower-elevation habitats tend to be more hazardous. Land management agencies could focus management programs in low-elevation habitats to maintain or improve security for grizzly bears.

Government, nongovernment, and nonprofit organizations have the potential to influence habitat quality on private lands via conservation easements and other programs (Gustanksi and Squires 2000). County governments likewise can influence development adjacent to grizzly bear habitat with land-use planning that minimizes rural sprawl and considers wildlife needs and human safety. Our hazard model can be used to help provide guidance on which parcels are most important; this is particularly true if our hazard model is linked with a habitat-selection model.

Results presented here represent the commitment among agencies for several decades to monitoring the long-term status of the Yellowstone grizzly bear. Without that commitment, this work would not have been possible. Humans will continue to dominate this landscape, and we anticipate future changes in the GYE associated with climate, energy development, and human population growth. Continued long-term monitoring will provide further insight into how these changes might affect grizzly bears and their habitats. We strongly encourage agencies responsible for grizzly bear conservation to continue this support.

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LITERATURE CITED

Archibald, W. R., R. Ellis, and A. N. Hamilton. 1987. Responses of grizzly bears to logging truck traffic in the Kimsquit River Valley, British Columbia. International Conference on Bear Research and Management 7:251–257.

Bjornlie, D., and M. A. Haroldson. 2005. Grizzly bear use of insect aggregation sites documented from aerial telemetry and observations. Pages 39–43 *in* C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone grizzly bear investigations, 2004: annual report of the Interagency Grizzly Bear Study Team. U.S. Geological Survey, Bozeman, Montana, USA.

Blanchard, B. B., and R. R. Knight. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41–67.

Blanchard, B. B., and R. R. Knight. 1995. Biological consequences of relocating grizzly bears in the Yellowstone ecosystem. Journal of Wildlife Management 59:560–565.

Bockino, N. K. 2008. Interactions of whitebark pine blister rust, host species, and mountain pine beetle in whitebark pine ecosystems in the Greater Yellowstone. Thesis, University of Wyoming, Laramie, USA.

Boyce, M., B. M. Blanchard, R. R. Knight, and C. Servheen. 2001. Population viability for grizzly bears: a critical review. International Association for Bear Research and Management Monograph Series 4, Knoxville, Tennessee, USA.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, New York, USA.

Craighead, J. J., K. R. Greer. R. R. Knight. and H. I. Pac. 1988. Grizzly bear mortalities in the Yellowstone Ecosystem 1959–1987. Montana Department of Fish, Wildlife and Parks; Craighead Wildlife Institute; Interagency Grizzly Bear Study Team; and National Fish and Wildlife Foundation, Bozeman, Montana, USA.

Dice, L. R., and P. J. Clark. 1953. The statistical concept of home range as applied to the recapture radius of deer mouse (*Peromyscus*). University of Michigan Contributions to the Laboratory of Vertebrate Biology 62, Ann Arbor, Michigan, USA.

Dixon, B. G. 1997. Cumulative effects modeling for grizzly bears in the Greater Yellowstone Ecosystem. Thesis, Montana State University, Bozeman, USA.

Doherty, K. E., D. E. Naugle, B. L. Walker, and J. M. Graham. 2006. Greater sage-grouse winter habitat selection and energy development. Journal of Wildlife Management 72:187–195.

Eberhardt, L. L. 1995. Population trend estimates from reproductive and survival data. Pages 13–19 *in* R. R. Knight and B. M. Blanchard, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Study Team, 1994. National Biological Service, Bozeman, Montana, USA.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Eberhardt, L. L., B. M. Blanchard, and R. R. Knight. 1994. Population trend of the Yellowstone grizzly bear as estimated from reproductive and survival rates. Canadian Journal of Zoology 72:360–363.

Felicetti, L. A., C. C. Schwartz, R. O. Rye, K. A. Gunther, J. G. Crock, M. A. Haroldson, L. Waits, and C. T. Robbins. 2004. Use of naturally occurring mercury to determine the importance of cutthroat trout to Yellowstone grizzly bears. Canadian Journal of Zoology 82:493–504.

Felicetti, L. A., C. C. Schwartz, R. O. Rye, M. A. Haroldson, K. A. Gunther, D. L. Phillips, and C. T. Robbins. 2003. Use of sulfur and nitrogen stable isotopes to determine the importance of whitebark pine nuts to Yellowstone grizzly bears. Canadian Journal of Zoology 81:763–770.

Gude, P. H., A. J. Hansen, and D. A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. Ecological Applications 7:1004–1018.

Gustanksi, J. A., and R. H. Squires. 2000. Protecting the land: conservation easements past, present, and future. Island Press, Washington, D.C., USA.

Hansen, A. J., R. Rasker, B. Maxwell, J. J. Rotella, A. Wright, U. Langner, W. Choen, R. Lawrence, and J. Johnson. 2002. Ecology and socio-economics in the New West: a case study from Greater Yellowstone. BioScience 52:151–168.

Haroldson, M. A., K. A. Gunther, D. P. Reinhart, S. R. Podruzny, C. Cegelski, L. Waits, T. Wyman, and J. Smith. 2005. Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA. Ursus 16:167–180.

Haroldson, M. A., C. C. Schwartz, S. Cherry, and D. S. Moody. 2004. Possible effects of elk harvest on fall distribution of grizzly bears in the Greater Yellowstone Ecosystem. Journal of Wildlife Management 68:129–137.

Haroldson, M. A., C. C. Schwartz, and G. C. White. 2006. Survival of independent grizzly bear in the Greater Yellowstone Ecosystem, 1983–2001. Pages 33–42 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Harris, R. B., C. C. Schwartz, M. A. Haroldson, and G. C. White. 2006. Trajectory of the Yellowstone grizzly bear population under alternative survival rates. Pages 44–57 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Hernandez, P. C. 2004. Rural residential development in the Greater Yellowstone: rates, drivers, and alternative future scenarios. Thesis, Montana State University, Bozeman, USA.

Hovey, F. W., and B. N. McLellan. 1996. Estimating population growth of grizzly bears from the Flathead River drainage using computer simulations of reproduction and survival rates. Canadian Journal of Zoology 74:1409–1416.

Interagency Grizzly Bear Committee. 1998. Grizzly bear/motorized access management. Interagency Grizzly Bear Committee task force report, revised 1998. Interagency Grizzly Bear Committee, Missoula, Montana, USA.

Johnson, C. J., M. S. Boyce, C. C. Schwartz, and M. A. Haroldson. 2004. Modeling survival: application of the multiplicative hazards model to Yellowstone grizzly bear. Journal of Wildlife Management 68:966–978.

Kenward, R., A. South, and S. Walls. 2003. Ranges 6 v1.2: for the analysis of tracking and location data. Anatrack, Wareham, United Kingdom.

Landenburger, L., R. L. Lawrence, S. Podruzny, and C. C. Schwartz. 2008. Mapping regional distribution of a single tree species: whitebark pine in the Greater Yellowstone Ecosystem. Sensor 8:4983–4994.

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, USA.

Mace, R. D., and J. S. Waller, T. L. Manley, L. J. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads and habitat in the Swan Mountains, Montana. Journal of Applied Ecology 33:1395–1404.

Mattson, D. J. 1998. Changes in mortality of Yellowstone's grizzly bears. Ursus 10:129–138.

Mattson, D. J., K. Barber, R. Maw, and R. Renkin. 2004. Coefficients of productivity for Yellowstone's grizzly bear habitat. U.S. Geological Survey, Biological Resources Discipline, Biological Science Report UGSG/BRD/BSR–2002–2007, Lafayette, Louisiana, 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., B. M. Blanchard, and R. R. Knight. 1992. Yellowstone grizzly bear mortality, human habituation, and whitebark pine seed crops. Journal of Wildlife Management 56:432–442.

Mattson, D. J., and R. R. Knight. 1991. Effects of access on human-caused mortality of Yellowstone grizzly bears. U.S. National Park Service, Bozeman, Montana, USA.

Mattson, D. J., and D. P. Reinhart. 1994. Whitebark pine on the Mount Washburn massif, Yellowstone National Park. Pages 106–117 *in* W. C. Schmidt and K. J. McDonald, compliers. Proceedings of the symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, General Technical Report INT-270, Ogden, Utah, USA.

McLellan, B. N, and F. W. Hovey, R. D. Mace, J. G. Woods, D. W. Carney, M. L. Gibeau, W. L. Wakkinen, and W. F. Kasworm. 1999. Rates and causes of grizzly bear mortality in the interior mountains of British Columbia, Alberta, Montana, Washington, and Idaho. Journal of Wildlife Management 63:911–920.

McLellan, B. N, and D. M. Shackleton. 1988. Grizzly bears and resource extraction industries: effects of roads on behavior, habitat use and demography. Journal Applied Ecology 25:451–460.

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.

Naves, J., T. Wiegand, E. Revilla, and M. Delibes. 2003. Endangered species constrained by natural and human factors: the case of brown bears in Northern Spain. Conservation Biology 17:1276–1289.

Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2003. Development and testing of phenologically driven grizzly bear habitat models. Ecoscience 10:1–10.

Nielsen, S. E., S. Herrero, M. S. Boyce, R. D. Mace, B. Benn, M. L. Gibeau, and S. Jevons. 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem, Canada. Biological Conservation 120:101–113.

Nielsen, S. E., G. B. Stenhouse, and M. S. Boyce. 2006. A habitat-based framework for grizzly bear conservation in Alberta. Biological Conservation 130:217–229.

Picton, H. D., D. M. Mattson, B. M. Blanchard, and R. R. Knight. 1986. Climate, carrying capacity and the Yellowstone grizzly bear. Pages 129–135 *in* G. P. Contreras and K. E. Evans, compilers. Proceedings of the grizzly bear habitat symposium. U.S. Forest Service, General Technical Report INT-207, Ogden, Utah, USA.

Podruzny, S. R., S. Cherry, C. C. Schwartz, and L. A. Landenburger. 2002. Grizzly bear denning and potential conflict areas in the Greater Yellowstone Ecosystem. Ursus 13:19–28.

Pulliam, H. R. 1996. Sources and sinks: empirical evidence and population consequences. Pages 45–69 *in* O. E. Roades, R. K. Chesser, and M. S. Smith, editors. Population dynamics in ecological space and time. University of Chicago Press, Chicago, Illinois, USA.

Ruth, T. K, D. W. Smith, M. A. Haroldson, P. C. Buotte, C. C. Schwartz, H. B. Quigley, S. Cherry, K. M. Murphy, D. Tyers, and K. Frey. 2003. Large-carnivore response to recreational big game hunting along the Yellowstone National Park and Absaroka–Beartooth Wilderness boundary. Wildlife Society Bulletin 31:1150–1161.

Schwartz, C. C., M. A. Haroldson, and S. Cherry. 2006*a*. Reproductive performance for grizzly bears in the Greater Yellowstone Ecosystem, 1983–2002. Pages 18–24 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Schwartz, C. C., M. A. Haroldson, K. A. Gunther, and D. Moody. 2006*b*. 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. 2006*c*. Study area and methods for collecting and analyzing demographic data on the Yellowstone grizzly bear. Pages 9–17 *in* C. C. Schwartz, M. A. Haroldson, G. C. White, R. B. Harris, S. Cherry, K. A. Keating, D. Moody, and C. Servheen, authors. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

Schwartz, C. C., S. D. Miller, and M. A. Haroldson. 2003. Grizzly/brown bear. Pages 556–586 *in* G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. Wild mammals of North America: biology, management, and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Scott, J. M., D. D. Goble, J. A. Wiens, D. S. Wilcove, M. Bean, and T. Male. 2005. Recovery of imperiled species under the Endangered Species Act: the need for a new approach. Frontiers in Ecology and the Environment 3:383–389.

Summerfield, B., W. Johnson, and D. Roberts. 2004. Trends in road development and access management in the Cabinet–Yaak and Selkirk grizzly bear Recovery Zones. Ursus 15:115–122.

U.S. Census Bureau. 2005. American fact finder. <http://factfinder.census.gov>. Accessed 15 Apr 2005.

U.S. Fish and Wildlife Service [USFWS]. 2003. Draft final conservation strategy for the grizzly bear in the Greater Yellowstone Area. Interagency Conservation Strategy Team, Missoula, Montana, USA.

U.S. Fish and Wildlife Service [USFWS]. 2007. Final rule designating the GYA population of grizzly bears as a Distinct Population Segment and removing the Yellowstone Distinct Population Segment of grizzly bears from the Federal List of Endangered and Threatened Wildlife. 72 FR 14866. <http://www.fws.gov/mountain-prairie/species/mammals/grizzly/yellowstone.htm>. Accessed 15 Dec 2009.

U.S. Geological Survey [USGS]. 2000. National elevation dataset: the national map seamless server. <http://seamless.usgs.gov/>. Accessed 15 Jan 2002.

Weaver, J., R. Escano, D. Mattson, T. Puchlerz, and D. Despain. 1986. A cumulative effects model for grizzly bear management in the Yellowstone Ecosystem. Pages 234–246 *in* G. P. Contreras and K. E. Evans, compilers. Proceedings of the grizzly bear habitat symposium. Intermountain Research Station, U.S. Forest Service General Technical Report INT-207, Ogden, Utah, USA.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(suppl): S120–S139.

White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

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