

MODELING SURVIVAL: APPLICATION OF THE ANDERSEN–GILL MODEL TO YELLOWSTONE GRIZZLY BEARS

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Abstract: Wildlife ecologists often use the Kaplan–Meier procedure or Cox proportional hazards model to estimate survival rates, distributions, and magnitude of risk factors. The Andersen–Gill formulation (A–G) of the Cox proportional hazards model has seen limited application to mark–resight data but has a number of advantages, including the ability to accommodate left-censored data, time-varying covariates, multiple events, and discontinuous intervals of risks. We introduce the A–G model including structure of data, interpretation of results, and assessment of assumptions. We then apply the model to 22 years of radiotelemetry data for grizzly bears (*Ursus arctos*) of the Greater Yellowstone Grizzly Bear Recovery Zone in Montana, Idaho, and Wyoming, USA. We used Akaike’s Information Criterion (AIC_c) and multi-model inference to assess a number of potentially useful predictive models relative to explanatory covariates for demography, human disturbance, and habitat. Using the most parsimonious models, we generated risk ratios, hypothetical survival curves, and a map of the spatial distribution of high-risk areas across the recovery zone. Our results were in agreement with past studies of mortality factors for Yellowstone grizzly bears. Holding other covariates constant, mortality was highest for bears that were subjected to repeated management actions and inhabited areas with high road densities outside Yellowstone National Park. Hazard models developed with covariates descriptive of foraging habitats were not the most parsimonious, but they suggested that high-elevation areas offered lower risks of mortality when compared to agricultural areas.

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Relocation data collected from free-ranging animals can be used to estimate survival and cause-specific mortality (White and Garrott 1990). A common application is the Kaplan–Meier procedure (Kaplan and Meier 1958) modified by Pollock et al. (1989a) to estimate survival distributions for radiomarked animals that enter the study at different times. Researchers also have applied the Cox proportional hazards model but with the added flexibility of addressing continuous covariates and multivariable relationships (Riggs and Pollock 1991, Conroy et al. 1996). The A–G formulation of the Cox proportional hazards model is a more flexible approach to modeling survival distributions (Andersen and Gill 1982). The Cox model is suitable only for right-censored data, but the A–G formulation will accommodate left- and right-censored observations, continuous and categorical covariates that may vary during monitoring, and discontinuous intervals of risk. Numerous examples of the A–G

model exist in the health sciences, but A–G has been used infrequently in wildlife biology and ecology (but see Boyce et al. 2001).

Scientists have used radiotelemetry to monitor grizzly bears in the Greater Yellowstone Grizzly Bear Recovery Zone since the early 1970s. This work addressed questions of population dynamics and survival, but no previous research focused on the spatial variation in risk factors across the recovery zone (e.g., Knight and Eberhardt 1985, Knight et al. 1988, Eberhardt et al. 1994, Eberhardt and Knight 1996). Pease and Mattson (1999) modeled survival based on numerous demographic and nonspatial habitat variables, but they employed a complex project-specific maximum likelihood procedure that may have resulted in faulty statistical inference (Eberhardt and Cherry 2000). In contrast to Pease and Mattson’s (1999) methods, the A–G model is easy to interpret, available in many statistics packages, and can accommodate spatial covariates that correlate with grizzly bear behavior.

We illustrate use of A–G models with an application to a subset of radiotelemetry data for grizzly bears of the Greater Yellowstone Grizzly Bear Recovery Zone. We used AIC_c to assess a small

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number of ecologically plausible predictive models relative to explanatory covariates for demography, human disturbance, and habitat (Burnham and Anderson 1998). Because the A–G model has been cited only rarely in the wildlife literature, we provide a brief explanation of data structure, interpretation of results, assessment of assumptions, and compare our results to previous survival analyses of Yellowstone grizzly bears. Also, we present a map of the hazard function across the recovery zone highlighting areas of potentially high-mortality “sink” areas for grizzly bears (Knight et al. 1988).

METHODS

Andersen–Gill Model

The A–G model, a derivation of the Cox proportional hazards model as a counting process, accommodates left- and right-censored data, time-dependent covariates, measurements on covariates over a large number of time intervals, multiple events, and discontinuous intervals of risk (Fleming and Harrington 1991, Therneau and Grambsch 2000). For an accessible introduction to the Cox model see Klein and Moeschberger (1997). Left-censored observations result from subjects entering the study at different times. When the fate of marked subjects is unknown, right-censored data occur. If uncorrected, right- and left-censored data bias survival estimates. Time-dependent covariates accommodate effects that may vary in magnitude with time. The ability of the A–G model to accommodate multiple events per individual is irrelevant to studies assessing survival but has application to other areas of wildlife research such as infection rate or natality. Discontinuous intervals of risk are the product of missed observations or measurements; for example, disappearance, but eventual relocation of a radiomarked animal would constitute a discontinuity in the risk measurement.

Data for the A–G model are structured so that each animal is treated as 1 to many observations (rows in spreadsheet). The interval of risk for each observation is defined by variables describing the start and end times of successive relocations. An event variable is coded as “1” for mortality or “0” for right-censored intervals. Right-censored intervals are not considered as incomplete data, but as subjects whose event counts are still 0. Any number of continuous or categorical variables represents the behavior or condition of the animal during the corresponding interval of risk. A stratum

variable, if included, represents group membership and allows the calculation of a unique baseline hazard for each stratum.

Statistical Assumptions

Several types of residuals are available to assess model fit and identify poorly predicted subjects and influential points. Deviance residuals are analogous to the Pearson residual of generalized linear models and, when plotted, reveal individual cases that fit the survival model poorly. A uniform distribution of residuals around 0 also suggests good model fit to the sample data. Score residuals can be derived from Schoenfeld residuals and used to assess each subject’s leverage on parameter estimates (Therneau et al. 1990).

As with the Cox model, the principal assumption of the A–G approach is that the hazard or risk ratio is proportional over time. The hazard ratio represents the proportionate change in the mortality rate due to a unit change in the respective covariate. Proportional hazards are maintained if the influence of some treatment or other independent variable remains consistent across the duration of the study (i.e., $\beta_j(t) = \beta$ for all t). The assumption can be assessed using plots of the logarithms of the estimated cumulative hazard functions for different treatment groups (Andersen 1982). Convergence of curves indicates that the hazard function has a different effect on each group across time. For variables that are continuous or have many levels, a more powerful technique is to plot the scaled Schoenfeld residuals for each variable against time (Grambsch and Therneau 1994). Following inspection of residuals for a uniform distribution, a line can be fit to the plot and tested for a nonzero slope. A significant fit suggests rejection of the proportional hazards assumption.

STUDY AREA

Our study area was constrained to the nearly 24,000-km² Greater Yellowstone Grizzly Bear Recovery Zone that includes Yellowstone National Park and extends across portions of southern Montana, northern Wyoming, and eastern Idaho, USA (U.S. Fish and Wildlife Service 1993). The central portion of the recovery zone is rolling plateau surrounded by mountainous terrain with elevations ranging from 1,600 to 4,200 m. Lodgepole pine (*Pinus contorta*) is the dominant canopy species across forested areas. Forest stands consisting of Douglas-fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), subalpine

Table 1. Independent variables and categorical coding used to describe variation in survival of grizzly bears of the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA, 1975–1997.

Variable	Description and categorical code
Demography/season	
Age + Age ²	Quadratic function for age of bear at time of location
Sex	Male (1) or female (0)
Human disturbance	
(Distance to development) + (Distance to development) ²	Quadratic function describing distance (m) of bear relocation to major development (e.g., town, park facility)
No. of management actions	Cumulative number of management actions experienced by a bear at time of radiotelemetry location
In park	Bear location inside (1) or outside (0) Yellowstone National Park
(Road density) + (Road density) ²	Quadratic function describing density of high-use roads (1-km ² area)
Trail density	Density of trails (1-km ² area)
Habitat	
Agriculture	Low-elevation agricultural lands
High-elevation open habitats	Rocky convex lithic ridges, talus and scree, and high-elevation forest openings
Low-elevation open and forested habitats	Low-elevation dry and mesic meadows, grasslands, forest openings, marshes, fens and stands of Douglas-fir, lodgepole pine, and spruce
Whitebark pine	High-elevation sites dominated by whitebark pine
High-elevation fir/whitebark	High-elevation sites dominated by subalpine fir with a component of whitebark pine
Mid-elevation fir/pine	Mid-elevation stands of subalpine fir, lodgepole pine, and whitebark pine
Other	All habitat classes found across the study area, but not coded with unique identifiers
In elk winter range	Bear location inside (1) or outside (0) elk winter range
In bison winter range	Bear location inside (1) or outside (0) bison winter range
In trout spawning	Bear location inside (1) or outside (0) area associated with spawning trout

fir (*Abies lasiocarpa*), or whitebark pine (*Pinus albicaulis*) also occur but are less widespread. Non-forest grass and shrublands occur below 2,125 m and often contain Idaho fescue (*Festuca idahoensis*), big sagebrush (*Artemisia tridentata*), and bluebunch wheatgrass (*Agropyron spicatum*; see Blanchard and Knight [1991] for further description and references). Fire is a natural disturbance agent of both grassland and forested ecosystems with the largest contemporary event occurring in 1988 when approximately 5,600 km² were burned. The recovery area supports some of the highest ungulate densities in North America (Mattson 1997). Elk (*Cervus elaphus*) and bison (*Bison bison*) are the most widespread and abundant species followed by smaller, more localized populations of mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and bighorn sheep (*Ovis canadensis*).

Animal Capture and Monitoring

From 1975 to 1997, researchers captured 101 female and 123 male grizzly bears and fitted them with VHF radiocollars. Some bears were caught through research activities (research bears) while other individuals were actively sought and radiomarked following a bear–human interaction (management bears). After radiomarking, researchers relocated bears once every 7 to 14 days via fixed-wing aircraft. For survival analyses, we excluded all observations associated with bear

capture, transport, and release as well as all locations recorded for den sites and dropped collars; we included only “known” and “probable” mortalities (Craighead et al. 1988). We calculated movement distances and speeds for successive relocations in an effort to identify incorrectly recorded data.

Spatial Descriptors of Survival

We developed Geographic Information System (GIS) routines or used available spatial data to identify environmental and human activity features that may influence the survival of grizzly bears across the recovery zone (Table 1). Many of the spatial attributes were taken from the Yellowstone Cumulative Effects Model (CEM) spatial database (Dixon 1997). We conducted GIS analyses with Idrisi32 (Clark Labs 2002) and ArcView (Environmental Systems Research Institute 2000).

Habitat Type.—We used digital maps of habitat type from the Yellowstone CEM spatial database (Dixon 1997). These maps were developed from aerial photographs and detailed field investigations and were updated using satellite imagery following the fires of 1988. We used pre- and post-fire maps to assign habitat attributes to bear locations according to their date of location. Mattson et al. (1999) redefined the many original habitat types into 18 super classes. We used knowledge of grizzly bear mortality factors to consolidate the

habitat classes identified by Mattson et al. (1999) into 7 new classes (Table 1). We defined these 7 classes with the objective of investigating bear mortality relative to variation in the elevation of habitats, and thus distance from human contact, and the availability of whitebark pine seeds, which are associated with the movements and behaviors of bears. We used deviation coding to parameterize habitat type as a single categorical variable. Deviation coding differs from indicator coding in that the effect of each variable in the set is contrasted against the overall effect of the independent variable, not an arbitrary reference class (Menard 1995).

Ungulate Winter Range.—Maps of elk and bison winter range were taken from the Yellowstone CEM. Those spatial data did not quantify ungulate density or fine-scale distribution patterns but represented the generalized spatial extent of elk and bison populations during the winter over a number of years (Dixon 1997). Bear locations were coded as inside (1) or outside (0) each of the winter ranges.

Cutthroat Trout.—Spawning habitat for cutthroat trout (*Onchorhynchus clarki*) is restricted to tributaries of Yellowstone Lake. Past researchers (e.g., Mattson and Reinhart 1995) identified and investigated bear behavior in those areas and that information was spatially collated within the supplemental habitat data used for the Yellowstone CEM (Dixon 1997). During the spawning season, Mattson and Reinhart (1995) reported that bears concentrated within 2,000 m of trout-bearing streams. We buffered the inland shoreline of spawning streams 2,000 m to represent the larger zone of influence of trout on bear behavior. Bear locations were coded as inside (1) or outside (0) those buffered areas. We also included an interaction term representing the linear distance of bears and bear mortalities from major human developments located within the buffered trout spawning areas.

Human Access.—We used a moving-window algorithm to generate spatial surfaces of road and trail density. The final maps represented the number of pixels of linear features within 1-km² portions of the study area. The road and trail data were taken from spatial coverages developed for the Yellowstone CEM (Dixon 1997). Linear features from that database were classified according to amount and type of use. We generalized the classification system to a road layer of relatively high use (>1 vehicle/day) and all trails used for non-motorized activities. In the case of roads, separate

coverages were used to represent seasonal closures. Road and trail access and use changed over the 22 years of bear monitoring, but we did not have sufficient data to represent that variation.

Major Human Developments.—Major human developments were defined as any concentration of human activity that included ≥30 facilities or the capacity for ≥100 persons to overnight within a 1-km radius of the source (Mattson et al. 1999). Those locations were taken from the Yellowstone CEM spatial database (Dixon 1997). We assessed bear survival relative to the distance from the nearest major human development.

Location within Yellowstone National Park.—We assessed the location of each bear and mortality record relative to the boundary of Yellowstone National Park. A categorical variable was used to code all bear locations or mortality sites that occurred within (1) or outside (0) the boundary of the park.

Model Development and Assessment

We developed A–G models from 11 categorical and 5 continuous behavioral and demographic variables that we assumed explained variation in survival among bears (Table 1). We structured data so that each row represented 1 relocation interval for an animal and columns described the interval length in days, whether a mortality (i.e., event) occurred, and the demographic characteristics and habitat and disturbance features of the relocation interval. Mortality events occurred at the end of each radiotelemetry interval, thus we attributed each relocation interval with the GIS or demographic values for that end location. Covariates, particularly spatial covariates, likely varied with bear movements and could in theory be sampled at any point during the relocation interval. We developed 2 additional datasets to assess the sensitivity of the analyses to our sampling protocol. We repeated our analyses for covariate values queried from locations at the beginning of the observation interval and for locations selected randomly from a circular area centered on the first location in the interval with a radius equal to the distance between successive locations. For the latter 2 datasets, we maintained the end location as the most sensible query point for intervals in which mortalities were recorded. We truncated all intervals >30 days and considered those as discontinuous intervals of risk. We used the exact partial likelihood method to partition deaths with tied mortality times between competing risk pools (Therneau and Grambsch 2000).

The large number of independent variables and the potential for thousands of explanatory models required that we develop models based on a priori knowledge of bear behavior and what we assumed to be causative factors. We developed subsets of models according to 3 explanatory themes: grizzly bear demography, human activity, and habitat. Sample size limitations prevented evaluation of models with the full suite of variables. Thus, we made comparisons among the 3 explanatory themes, but we do not suggest that we captured the full range of model possibilities. Because we recorded few deaths, we calculated the corrected AIC_c for small sample sizes (Anderson et al. 2000). We calculated Akaike weights (w) and interpreted those values as the approximate probability that each model is the best model of the set of proposed models. Although we had some prior knowledge to suspect a nonlinear effect, we initially used AIC_c to assess hazard as a quadratic function of distance to development and road and trail density (Carroll et al. 2001, Boyce and Waller 2003). Thus, our models should be considered exploratory. We used tolerance scores to assess variables within each model for excessive collinearity (<0.1 ; Menard 1995). Collinear polynomial terms were transformed; each case was represented by the difference from the mean value for that variable for both the linear and squared term.

We provide likelihood ratio χ^2 statistics for assessment of goodness-of-fit for the most highly parameterized model for each explanatory theme. We plotted deviance residuals versus time to assess the fit of the sample data to the corresponding model and to identify aberrant cases. We statistically and graphically evaluated the proportional hazards assumption for each variable and aggregate model. We used the Receiver Operating Characteristic (ROC) to assess the predictive capacity of the most parsimonious models (Fielding and Bell 1997). We had insufficient data to cross-validate the ROC analysis, and therefore the ROC score represents a liberal assessment of classification accuracy.

We graphically presented the A-G model as a map of risk. We applied the β coefficients generated with the A-G models to a logistic equation and then calculated the predicted relative probability of mortality at each 30×30 -m cell of the recovery zone. The probability of mortality varied according to habitats and disturbance at each cell and the strength and sign of the respective β coefficient. Instead of using β coefficients from

the single most parsimonious model, we used Akaike weights (w) to calculate aggregate coefficients for all covariates contained within models with $w > 0$ (i.e., multi-model inference; Anderson et al. 2000). We also adjusted standard errors for variance due to uncertainty in model selection. We truncated all continuous GIS data (e.g., roads, distance to developments) to values equal to maximum observed bear behaviors (e.g., highest road density occupied by a bear) and thus prevented extrapolation of model results beyond the data used to estimate coefficients. All statistical analyses were performed with Stata (Stata Corporation 2002) and S-Plus 2000 (Mathsoft 2001).

RESULTS

Model Fit

We recorded 63 grizzly bear mortalities and 9,485 monitoring intervals, and we used those data to fit 13 A-G models (Table 2). Intervals had a median duration of 6 days for right-censored and 5 days for mortality observations. Of the models relating grizzly bear survival to demographic factors, the model including a term for sex and both linear and quadratic terms for age had the lowest AIC_c score and was statistically significant ($\chi^2 = 15.55$, $df = 3$, $P = 0.001$; Table 2). The linear and quadratic terms for age were highly correlated, and therefore we used a mean age of 8 to transform that variable. The A-G models describing the effects of human developments and disturbance on bear survival had small AIC_c scores and therefore provided best inference of the set of candidate models (Table 2). The most highly parameterized model of that set was statistically significant ($\chi^2 = 125.60$, $df = 10$, $P < 0.001$). Corrected Akaike weights suggested model-selection uncertainty when choosing between the model consisting of terms for road density, number of management actions, sex, and age ($AIC_c w = 0.558$) and the larger model consisting of the former covariates and location of bears relative to Yellowstone National Park, major developments, and trail density ($AIC_c w = 0.442$). We used the mean distance of bear locations from major developments (10,992 m) to reduce collinearity between the linear and squared terms for the distance to major development variable. Both models had large areas under their ROC curves (0.807, $SE = 0.033$; 0.858, $SE = 0.026$) suggesting good predictive capacity for identifying high-risk areas of the recovery zone. The best of the set of habitat models controlled for differences in sex

Table 2. Candidate Andersen–Gill models, number of parameters (*K*), log-likelihood, Akaike's Information Criterion (AIC_c) scores, differences among AIC_c scores (Δ), and AIC_c weights (*w*) for subsets of demographic, human disturbance, and habitat variables for grizzly bears of the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA, 1975–1997.

Model	<i>K</i>	Log-likelihood	AIC_c	ΔAIC_c	<i>w</i>
Demography					
Age ^{2a} + Sex	3	-165.18	336.77	92.70	<0.001
Sex	1	-169.37	340.81	96.74	<0.001
Age ²	2	-168.47	341.14	97.07	<0.001
Human disturbance					
(Road density) ² + (No. of management actions) + Sex + Age ²	6	-115.29	244.07	0	0.558
(Road density) ² + (No. of management actions) + (Outside park) + (Distance to development) ² + (Trail density) + Sex + Age ²	10	-110.15	244.54	0.47	0.442
(Distance to development) ² + (No. of management actions) + Sex + Age ²	6	-129.95	273.40	29.33	<0.001
(Outside park) + (No. of management actions) + Sex + Age ²	5	-138.17	287.40	43.33	<0.001
(Trail density) + (No. of management actions) + Sex + Age ²	5	-144.55	300.16	56.09	<0.001
(No. of management actions) + Sex + Age ²	4	-146.09	300.87	56.80	<0.001
Habitat					
Vegetation + Sex + Age ²	10	-153.06	327.52	83.45	<0.001
Vegetation + (Winter range) + (Trout spawning) + (Distance to development × Trout spawning) + Sex + Age ²	13	-147.56	328.55	84.48	<0.001
(Trout spawning) + (Distance to development × Trout spawning) + Sex + Age ²	11	-161.19	333.43	89.36	<0.001
(Winter range) + Sex + Age ²	4	-162.44	335.93	91.86	<0.001

^a Squared term represents full quadratic function inclusive of a linear term.

and age while quantifying variation in survival associated with occupancy of patches of the 6 habitat types (ROC = 0.705, SE = 0.036) but had a much larger AIC_c score ($\Delta AIC_c = 83.45$) than models including covariates representative of human presence. The most complex of the habitat models was statistically significant ($\chi^2 = 50.79$, *df* = 13, *P* < 0.001).

The exponentiated linear coefficients from an A–G model are interpreted as risk ratios relating the magnitude of a covariate to grizzly bear survival. Using multi-model inference, the weighted aggregate coefficients from the set of disturbance models suggested that the risk of dying was 3.4 ($\exp[4 \times 0.302]$) times greater for bears with 4 management actions when compared to bears with no recorded human interaction (Table 3). Similarly, when statistically controlling for other variables in the model, bears were 1.5 times more likely to die when ranging outside the park, and male bears experienced a risk of death 1.8 times greater than that for females. Quadratic terms revealed that bears experienced greater risks of mortality as road density increased, but mortality decreased at very high densities (>11.7 km/km²). A convex response curve illustrated that mortality was greatest near and far from major human developments. Likewise, the quadratic relationship with age was J-shaped indicating that younger and older bears experienced higher rates of mortality.

Although not the most parsimonious of the complete set of models, we generated Akaike weights for the habitat models (Table 2) and calculated aggregate coefficients adjusted for model selection uncertainty. When controlling for sex and age, bears experienced the greatest risk of mortality when occupying agricultural lands and the lowest risk when inhabiting patches of high elevation whitebark pine (Table 4). Confidence interval coverage for the other habitat covariates

Table 3. Coefficients, standard errors, and 95% confidence intervals of Andersen–Gill models representing the effects of demography and human disturbance on survival of grizzly bears radiomarked in the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA, 1975–1997. Akaike weights were used to adjust coefficients and variance for model selection uncertainty.

Variable	Coefficient ^a	SE	95% CI
No. of management actions	0.302	0.107	0.092 to 0.512
In park	-0.410	0.507	-1.404 to 0.584
Distance to development	-0.020	0.030	-0.078 to 0.038
(Distance to development) ²	0.001	0.002	-0.002 to 0.005
Road density	1.440	0.307	0.839 to 2.041
(Road density) ²	-0.124	0.033	-0.188 to -0.059
Trail density	0.159	0.236	-0.305 to 0.622
Age	-0.026	0.035	-0.094 to 0.043
Age ²	0.009	0.004	0.002 to 0.017
Sex	0.606	0.334	-0.049 to 1.260

^a Positive coefficient indicates increased hazard for categorical variables coded as 1 vs. 0.

Table 4. Coefficients, standard errors, and 95% confidence intervals of Andersen-Gill models representing the effects of habitat occupancy on survival of grizzly bears radiomarked in the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA, 1975–1997. Akaike weights were used to adjust coefficients and variance for model selection uncertainty.

Variable	Coefficient ^a	SE	95% CI
Agriculture	2.334	0.815	0.738 to 3.931
High-elevation open habitats	-1.405	0.762	-2.899 to 0.089
Low-elevation open and forested habitats	-0.514	0.293	-1.088 to 0.060
Whitebark pine	-1.202	0.485	-2.154 to -0.251
High-elevation fir/whitebark	0.587	0.639	-0.667 to 1.840
Mid-elevation fir/pine	-0.421	0.311	-1.031 to 0.189
Trout spawning	0.833	1.088	-1.300 to 2.967
Trout spawning × Distance to develop	-0.094	0.135	-0.358 to 0.170
Bison winter range	0.222	0.357	-0.477 to 0.921
Elk winter range	0.124	0.246	-0.358 to 0.607
Sex	0.568	0.294	-0.008 to 1.145
Age	-0.043	0.032	-0.105 to 0.020
Age ²	0.010	0.003	0.003 to 0.016

^a Positive coefficient indicates increased hazard for categorical variables coded as 1 vs. 0.

included risk ratios of 1 suggesting imprecise estimates and weak inference.

Survival curves illustrate variation in risk as a function of model covariates (Therneau and Grambsch 2000). As an example, a 3-year-old

male grizzly bear with 3 management actions inhabiting habitats with road densities of 1.25 km/km² experiences much higher risks of mortality than a 10-year-old female bear with 1 management action occupying areas of the recovery zone with no roads (Fig. 1). The A-G model predicts a mean survival time of 13.6 years (SE = 3.89) for the female bear experiencing good conditions for survival and 2.6 years (SE = 0.09) for the male bear subjected to less favorable conditions.

Figure 2 illustrates spatial variation in survival across the recovery zone according to the covariates and corresponding aggregate coefficients fitted to the most parsimonious model for human disturbance while controlling for demography (Table 3). Consistent with interpretation of coefficients from those models, the highest probability of mortality is predicted to occur in areas with many roads outside Yellowstone Park (Fig. 2). However, based on our knowledge of grizzly bear survival, the quadratic term for distance to major development appeared to overpredict the risk of mortality in the Absaroka Wilderness found in the southeastern corner of the recovery zone.

Testing Model Assumptions

Global tests of nonzero slopes in Schoenfeld residuals were nonsignificant for each model suggesting that our data did not violate the proportional hazards assumption (maximum $\chi^2 = 8.87$, $df = 9$, $P = 0.45$).

In accordance with those results, plots of scaled Schoenfeld residuals versus time for each independent variable illustrated little variation in predicted β values during the study. Plots of deviance residuals were symmetrical about zero and revealed no poorly predicted bear locations or mortalities. We observed small differences in aggregate coefficients (i.e., multi-model inference) and corrected 95% confidence intervals among the 3 datasets generated from the end location, start location, and a random location of each nonmortality

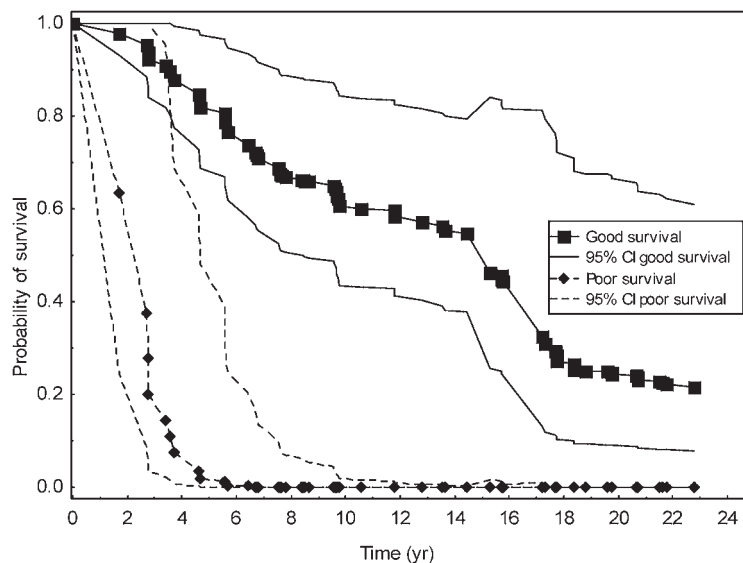


Fig. 1. Expected survival and 95% confidence intervals for 2 hypothetical grizzly bears with different levels of risk: a 10-year-old female bear residing inside Yellowstone National Park, Idaho, Wyoming, and Montana, USA, across habitats with no roads or trails (good conditions) and a 3-year-old male bear found outside the park in areas with road and trail densities of 1.25 km/km².

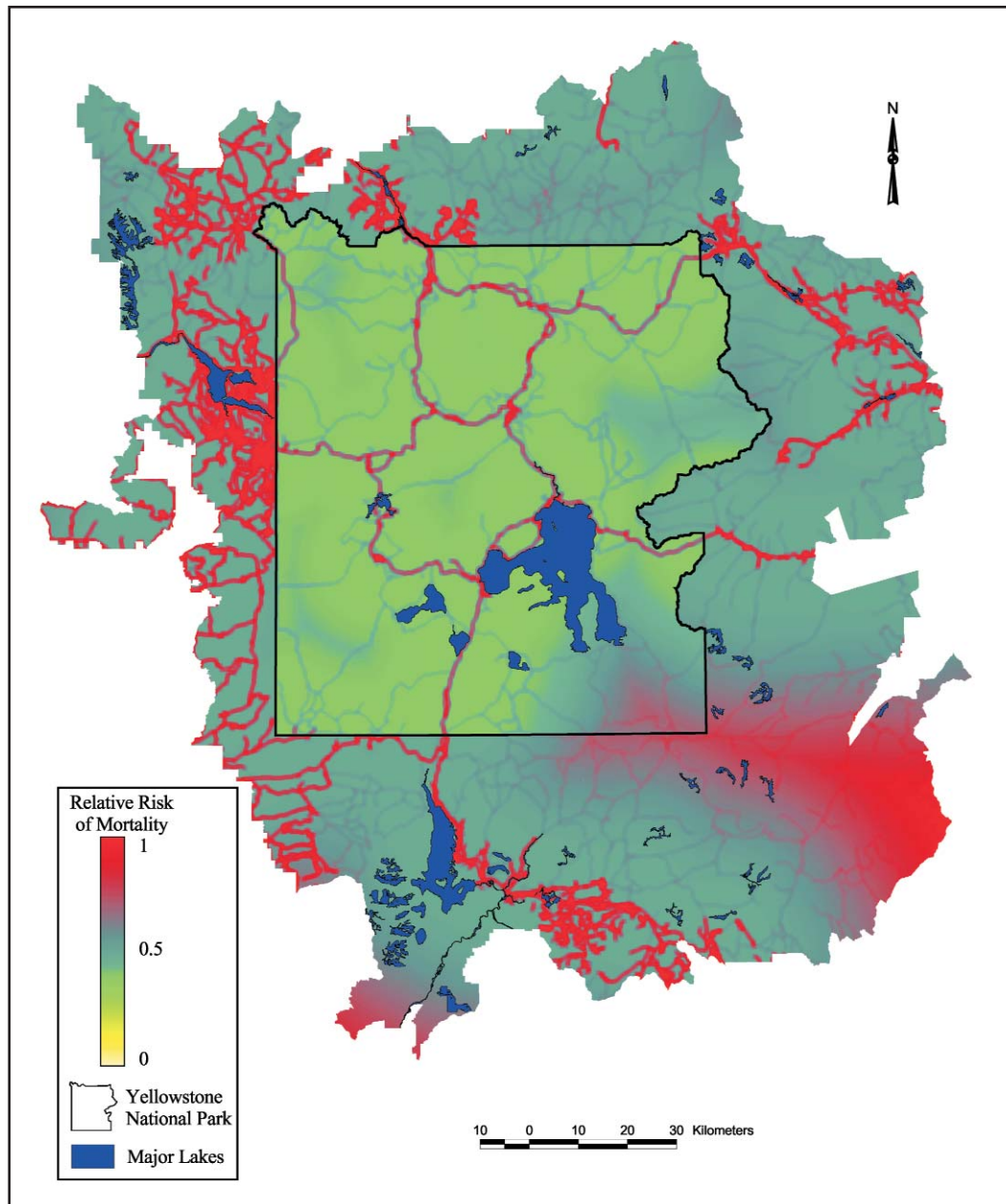


Fig. 2. Spatial variation in the predicted relative risk of mortality for an 8-year-old female grizzly bear according to location across the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA. Weighted coefficients were generated using Andersen-Gill models representing human disturbance covariates.

ty interval (Figs. 3, 4). Differences in coefficients were inconsistent in direction for both the human disturbance and habitat models. As expected, spatial covariates demonstrated a greater range of variability than aspatial covariates such as age.

DISCUSSION

Model Inference

Past efforts at understanding the mortality patterns of Yellowstone grizzly bears largely agree with our findings, but these studies were encum-

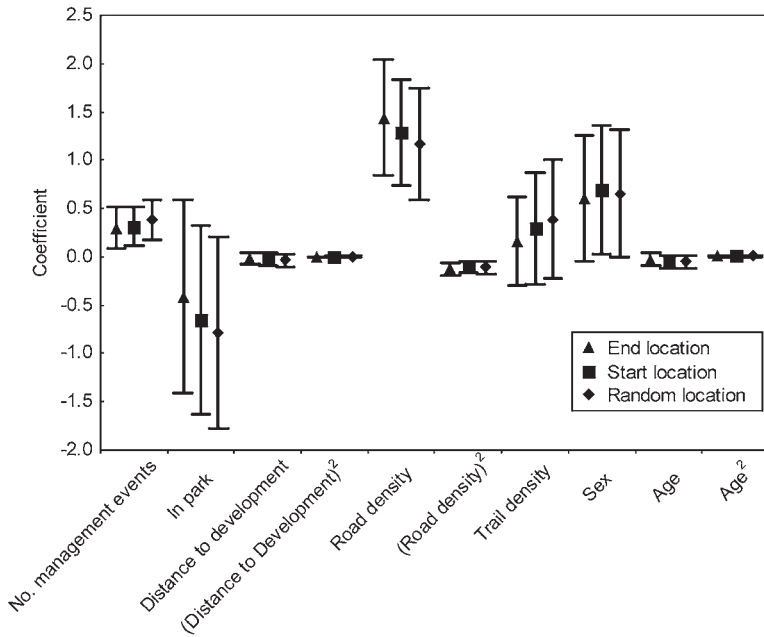


Fig. 3. Influence of sampling protocol on strength of weighted β coefficients representing human disturbance and demography covariates for grizzly bears of the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA. For non-death intervals, covariate values were queried from locations at the end of the observation interval, the beginning of the interval, and for locations selected randomly within the interval.

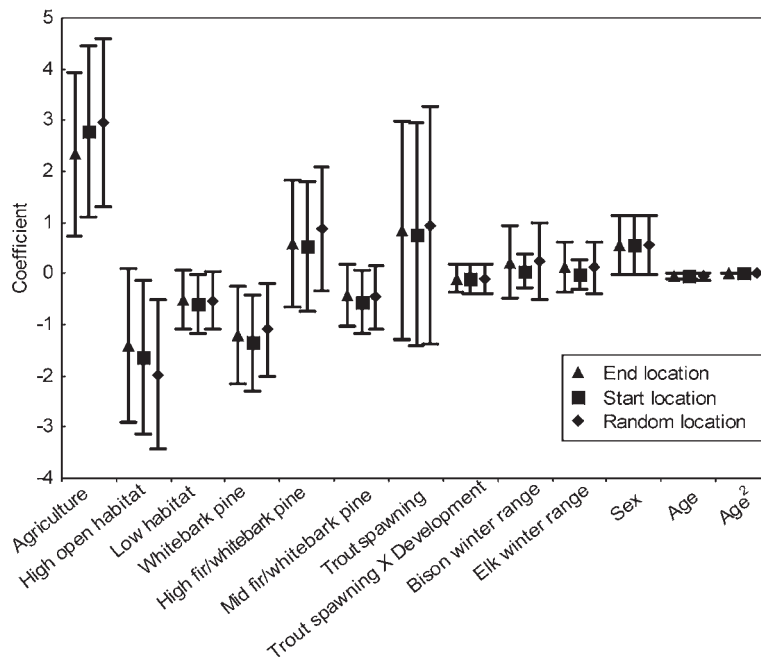


Fig. 4. Influence of sampling protocol on strength of weighted β coefficients representing habitat and demography covariates for grizzly bears of the Greater Yellowstone Grizzly Bear Recovery Zone in Idaho, Wyoming, and Montana, USA. For non-death records, covariate values were queried from locations at the end of the observation interval, the beginning of the interval, and for locations selected randomly within the interval.

bered by multiple univariate methods, are difficult to reproduce, or failed to represent spatial variation in risk factors. For example, Pease and Mattson (1999) used a study-specific maximum likelihood procedure to identify a relationship between rates of bear mortality and, in order of importance, sex, management-trapping status, and age (but see Eberhardt and Cherry 2000). Mattson et al. (1992) adopted a univariate statistical approach and concluded that mortality was related to sex, management trappings, and proximity of bears to roads and human developments. Applying the A-G model to a similar dataset, Boyce et al. (2001) reported that demographic factors, number of management actions, occupancy of Yellowstone National Park, and bear density were related to mortality. Using program MARK, Haroldson et al. (unpublished report) found lower survival during years of poor whitebark pine cone production and for management trapped bears, male bears, and bears with a higher proportion of annual locations outside Yellowstone National Park.

Our results also support the widely held assertion that grizzly bear mortality and persistence is directly related to human presence (Mattson and Merrill 2002). Areas of high road densi-

ty were correlated with recorded grizzly bear mortalities or management removals from the recovery zone. In general, road density is positively related to human access and facilities increased bear–human interactions (Mace et al. 1996). Human activities associated with facilities, roads, and trails had a negative affect on bear survival across the recovery zone, but the type of human–bear interaction or the resulting response favored bears that resided inside Yellowstone National Park. Those bears had less exposure to livestock, other human attractants, and illegal hunting (see Knight et al. 1988).

Our models of bear mortality and habitat use were not the most parsimonious of the total set, but they had good predictive power and provided insight into spatial variation in grizzly bear survival. In agreement with our understanding of cause-specific mortality, bears that occupied agricultural areas experienced greatly increased likelihood of human encounter and overall risk (Knight et al. 1988). Alternatively, bears at high elevations foraging on foods such as army cutworm moths (*Euxoa auxiliaris*) or whitebark pine seeds had fewer opportunities to interact with humans and lower mortality relative to occupancy of other habitat types (Mattson et al. 1991, 1992; Table 4). Inference and prediction generated from the majority of habitat coefficients is limited, however, by considerable sampling variance and model-selection uncertainty.

Maps representing risk of mortality can be used to plan or prioritize remediation or other management activities designed to enhance survival, a major limiting factor for grizzly bear populations (McLellan et al. 1999). Maps of risk also can be compared with maps of selection to identify habitats or features of the landscape that are attractant sinks for bears (Mace and Waller 1998, Mattson and Merrill 2002). In addition, review of risk maps may illuminate the predictive limitations of models. For example, we believe that the disturbance model overpredicted the risk of mortality to bears occupying the Absaroka Wilderness in the southeastern portion of the recovery zone (Fig. 2). Although the predictions are consistent with the convex function suggesting that mortality was greatest near point sources of human contact and less developed portions of the recovery zone where hunting occurs, little mortality has been recorded for either radiomarked or unmarked bears in the Absaroka Wilderness (Knight et al. 1988, Schwartz et al. 2002). We suspect that an interaction term of distance to human develop-

ments and elk hunting areas would better represent the nonlinear relationship.

One limitation of the A–G model is that it does not accommodate covariates that are invariant across mortality intervals. When a subject is monitored frequently, we expect short time intervals and little variation in covariates that change only over larger periods. Andersen–Gill models statistically control for inter-pool variation but do not allow estimation of a corresponding coefficient. As examples, we attempted to fit variables that assessed the effects of season and size of whitebark pine seed crop on survival, but those data were invariant across the 63 risk pools (i.e., recorded bear deaths). Researchers have reported decreased survival during periods when bears are most active and when bears are attracted to low-elevation habitats; typically, those behaviors occur during late summer and autumn and during years of small seed crops (Mattson et al. 1992; Pease and Mattson 1999; Haroldson et al., unpublished report).

Management policies and ecological conditions across the park and the wider recovery zone changed considerably over the 22 years of data collection (Gunther 1994, Murphy and Kaeding 1998). We treated many of our spatial covariates (e.g., roads, trails) as constant, but their influence likely varied in location and effect across the duration of the study. Our review of the proportional hazards assumption suggested that our models were robust to temporal variation in the factors that we assumed influenced bear survival. We suggest caution, however, when our models are used to predict bear survival into the future. Ongoing recovery efforts and anticipated ecosystem change may influence grizzly bear survival in ways that are not comparable to the historical conditions and management regimes reflected by the coefficients in our models (Reinhart et al. 2001).

Model Strengths, Application, and Assumptions

For many short-duration studies (e.g., 2 yr), complexity of hypothesized models and power of statistical tests will be limited by sample size (Conroy et al. 1996). Our dataset included an unusually large number of radiomarked animals (226) over a long period (22 yr), yet we recorded only 75 mortalities while animals were being monitored, 63 of which occurred in the recovery zone. In the context of the A–G model, the number of events—mortalities in our case—determines sample size. For studies of long-lived species, adequate sample sizes may be a problem. An approx-

imate indicator of poor power is large risk ratios (>2 or <0.5) coinciding with confidence interval coverage that bounds 1 (Riggs and Pollock 1991). Schoenfeld (1983) provides a formula to calculate the number of subjects necessary to identify statistically significant differences in treatment effects (i.e., power analysis). Application, however, is limited to trials where subjects can be randomized to different treatment groups.

Where large effect sizes or liberal α indicate sufficient power, parameter estimates may be compromised by too many covariates for the available sample. We are unaware of any literature directly discussing the implications of too few data for Cox or A-G models, but some guidelines exist for conventional logistic regression. In general, little is known about the small-sample behavior of maximum likelihood estimators, but a rule of thumb is that true estimates of standard errors require 10 events per model parameter (Peduzzi et al. 1996, Hosmer and Lemeshow 2001). Because spatial databases offer researchers a large number of potential variables and sample sizes may be low for survival models, we encourage practitioners to carefully consider the number of covariates included in their models. We violated that rule in an effort to more fully describe grizzly bear survival and control for confounding factors, but we avoided fitting hypothetical models with the potential for 22 covariates. Deviance residuals and consistency of coefficients from the 3 datasets suggested that our set of models was stable.

The A-G approach offers a great deal of flexibility, but a number of data-related issues should be considered during study design, data preparation, model development, and interpretation. Of primary concern is the identification of a monitoring interval that is sensitive to the behavior of interest. Some covariates such as age or sex will change infrequently or not at all during a sampling interval or the course of a study. Other covariates such as occupancy of a habitat patch or distance from an object, such as roads, may change frequently or continuously within a sampling interval. For each interval of risk, we chose the radiotelemetry location marking the end of the interval as representative of behavior across the entire interval. Sensitivity analyses consisting of alternative sampling protocols did not reveal systematic bias or dramatic variation in coefficients (Figs. 3, 4). However, we recognize that frequent animal locations generated with Global Positioning System collars would provide a more precise assessment of mortality factors.

Animal monitoring need not be at regular intervals, but infrequent relocations may lead to an inaccurate time of death or censoring. Consistent overestimation of time to death or censoring will bias survival curves and falsely inflate mean survival times. Survival data also should be evaluated to ensure censoring mechanisms are random and are correctly identified (Pollock et al. 1989b). Biased coefficients may arise if specific age or sex classes are more likely to drop radiocollars or certain mortality causes, such as illegal hunting, correspond with perceived radiotransmitter failure. Other more general sampling considerations are discussed by Pollock et al. (1989a) and include random sampling of individuals within each demographic class and ensuring that capture and monitoring efforts do not influence future survival.

MANAGEMENT IMPLICATIONS

Although our primary objective was illustration of the A-G method, our results provide some guidance for managers implementing recovery plans for the Yellowstone grizzly bear population. With the exception of high-elevation and agricultural areas, differential use of vegetative habitat and bison and elk winter ranges was not strongly related to bear survival. In agreement with previous research for the Yellowstone and other populations of bears, mortality was most strongly associated with places where bears and humans interacted. Considering only the suite of variables we modeled and the limitations of the data, our results suggest that bear survival would be enhanced if management practices reduced bear-human interactions in areas of concentrated human use.

The flexibility of the A-G model provides opportunities to link habitat use with survival. With few exceptions (e.g., Hines 1987, Klinger et al. 1989, Loegering and Fraser 1995), researchers have failed to relate animal distribution to limiting factors more directly associated with birth and death processes. The A-G model can be used to understand and predict survival and, when combined with models of resource selection (Manly et al. 2002), identify locations on landscapes with both a high likelihood of animal occurrence and mortality. Grizzly bears in Yellowstone National Park demonstrated such risk-prone behaviors in favor of accessing good foraging habitats (Knight et al. 1988, Mattson et al. 1992). Conservation efforts would be best focused at identifying and mitigating risks at those locations.

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