Updating and Evaluating Approaches to Estimate Population Size and Sustainable Mortality Limits for Grizzly Bears in the Greater Yellowstone Ecosystem

Photo courtesy of John Way

10 September 2012

Interagency Grizzly Bear Study Team (IGBST)

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Report summarizing discussion of issues and analyses during workshops at Bozeman, Montana, February 3–4, 2011; July 11–12, 2011; and February 1–2, 2012

Report prepared by
Richard B. Harris

Workshop participants
(in alphabetical order):

BRYAN ABER, Carnivore Biologist, Idaho Department of Fish and Game, Island Park, Idaho

DANIEL D. BJORNLIE, Large Carnivore Biologist, Wyoming Game and Fish Department, Lander, Wyoming

MARK BRUSCINO, Large Carnivore Section Supervisor, Wyoming Game and Fish, Cody, Wyoming

STEVEN L. CAIN, Senior Wildlife Biologist, Grand Teton National Park, Jackson, WY

STEVE CHERRY, Associate Professor of Statistics, Department of Mathematical Sciences, Montana State University, Bozeman, Montana

JOSEPH D. CLARK, Research Ecologist, U.S. Geological Survey, Leetown Science Center, Southern Appalachian Research Branch, Knoxville, Tennessee

KEVIN FREY, Wildlife Management Specialist, Montana Fish, Wildlife and Parks, Bozeman, Montana

DAVID L. GARSHELIS, Bear Project Leader, Minnesota Department of Natural Resources and Conservation, Grand Rapids, Minnesota

KERRY A. GUNTHER, Bear Management Program Leader, Bear Management Office, Yellowstone National Park, Wyoming

MARK A. HAROLDSON, Supervisory Wildlife Biologist, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Bozeman, Montana

RICHARD B. HARRIS, Adjunct Research Associate Professor, Department of Ecosystem and Conservation Sciences, College of Forestry and Conservation, University of Montana, Missoula, Montana

MEGAN D. HIGGS, Assistant Professor of Statistics, Department of Mathematical Sciences, Montana State University, Bozeman, Montana

LISA A. LANDENBURGER, Geographer, U.S Geological Survey, Northern Rocky Mountain Science Center and U.S. Forest Service, Bozeman, Montana

RICHARD D. MACE, Wildlife Biologist, Montana Fish, Wildlife, and Parks, Kalispell, Montana

DARYL MEINTS, Regional Wildlife Manager, Idaho Department of Fish and Game, Idaho Falls, Idaho

STERLING D. MILLER, Senior Wildlife Biologist, National Wildlife Federation, Missoula, Montana

SHANNON R. PODRUZNY, Ecologist, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Bozeman, Montana

CHARLES C. SCHWARTZ, Supervisory Research Wildlife Biologist, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Montana State University, Bozeman, Montana (retired)

CHRISTOPHER SERVHEEN, Grizzly Bear Recovery Coordinator, U.S. Fish and Wildlife Service, University of Montana, Missoula, Montana

DAN TYERS, Grizzly Bear Habitat Coordinator, U.S. Forest Service, Bozeman, Montana

FRANK T. VAN MANEN, Supervisory Research Wildlife Biologist, U.S. Geological Survey, Northern Rocky Mountain Science Center, Interagency Grizzly Bear Study Team, Bozeman, Montana

GARY C. WHITE, Professor, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado (retired)

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Cover photo: Female grizzly bear with cub-of-the-year near the Madison River, Montana, May 2012. Photo by John Way.

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Executive Summary and Management Recommendations

1. Workshop objectives: Our objectives were to 1) revise current protocols for estimating population size of the Greater Yellowstone Ecosystem (GYE) grizzly bear population, 2) reevaluate current mortality limits as necessary based on this revised estimate of population size and updated demographic analyses, and 3) discuss possibility of zoning the ecosystem for mortality limits given the expanding population.

2. Background: To aid the reader in understanding the context of this workshop and the differences between management recommendations contained herein and those arising from previous workshops (see Interagency Grizzly Bear Study Team 2005, 2006), a summary of analyses and protocols underlying previous population estimates and management recommendations is provided. We include schematic diagrams of the processes involved in population estimation and derivation of mortality limits, and graphs indicating how uncertainty is accounted for.

3. Improving estimation of population abundance: Following up on the results of Schwartz et al. (2008), which demonstrated biases inherent in the existing method of indexing population size using unduplicated counts of females with cubs-of-the-year (F_{COY}) and the associated rule set of Knight et al. (1995), the group made efforts to consider alternative approaches. We considered, but ultimately abandoned, a clustering algorithm combined with Bayesian methods and ancillary data resampling to estimate the number of true F_{COY} using existing data on bear movements. We found that, although the method had considerable promise, it was quite complex, and depended on assumptions of the true spatial juxtaposition of female bears on the landscape, for which information is currently lacking. Instead, the group recommends transitioning from the current protocol for indexing abundance to a mark-resight estimator using systematic flight observation data collection since 1997. The mark-resight estimator yields an estimate of the number of F_{COY} present based on 1) the presence of a radio-marked sample, and 2) two systematic observation flights/year, during which all F_{COY} observed are recorded and, following observation, checked for marks (i.e., radio collar). This mark-resight estimator solves many of the problems inherent in the Knight et al. (1995) approach, but suffers from 1) low precision, because of small numbers of F_{COY} marked and observed, and 2) biases from geographic heterogeneity in the availability and detection probabilities of marked bears relative to unmarked bears. Ways to substantially reduce bias associated with the second disadvantage is the subject of ongoing research and analysis.

4. Preliminary analyses to update our understanding of grizzly bear vital rates from telemetry data: Mortality limits currently in place are based on demographic analyses using data from 1983 through 2001. Monitoring results from 2011 triggered a demographic review under existing protocols. Therefore, the team re-evaluated survival and fecundity of GYE grizzly bears for the time period 2002–2011, independent of previous analyses (but using consistent analytical approaches). These analyses are currently being refined, finalized, and prepared for a peer-reviewed

publication. Preliminary data suggest, however, that the rate of growth seen during the 1983–2001 period has slowed. The proximate cause of this slower growth was lower survival rates among the yearling, and possibly, cub age-classes. Survival of adult females did not change between the two time-periods. Data indicate survival of adult males increased from the earlier to the later time period. Fecundity (female cubs produced/adult female/year) declined slightly. Based on these vital rates, asymptotic population growth of the GYE grizzly bear population during 2002–2011 ranged from 0% (using a conservative assumption that unresolved fates of independent females represented mortality) to 2.2% (based on censoring data of independent females with unresolved fates). Similar to the 1983–2001 period, population growth based on grizzly bear vital rates suggested greatest vigor within the Recovery Zone but outside of Yellowstone National Park, followed by the area encompassed by Yellowstone National Park. Although population growth rates remained lowest in the area outside the Recovery Zone, this rate increased compared with the 1983–2001 period. Consequently, population growth rates are now more similar across these 3 zones of the ecosystem.

   5. Preliminary analyses of intrinsic and extrinsic factors associated with grizzly bear vital rates: Preliminary analyses using Program MARK (White and Burnham 1999) and an information-theoretic framework indicated 1) density dependence and 2) resource effect hypotheses (i.e., losses of whitebark pine, WBP) are both supported by the data. WBP indices were prominent in top models estimating the transition probabilities for the proportion of females with cubs. However, indices of population density effects were better supported in models estimating juvenile survival. Thus, our conclusions regarding the primary drivers for the change in population trajectory were mixed, in part because the effects of density dependence on grizzly bear vital rates may be similar to those resulting from a reduction in food supply and may be temporally confounded as well. Analyses are ongoing and will be submitted to a peer-review journal for publication.

   6. Recommended revisions to sustainable mortality limits: Based on the updated demographic rates and a deterministic analysis of population growth yielding stability, the team recommends that managers adopt a new threshold of 7.6% mortality (from all causes) for independent (2 years or older) female grizzly bears. This differs from the previously recommended threshold of 9% because 1) juvenile survival rates (and fecundity) seem to be lower during 2002–2011 than the 1983–2001 period, and 2) the team feels comfortable in recommending a strategy focused on a goal of stability rather than growth. Similar to existing protocols, the team recommends the mortality threshold of 7.6% also be adopted for dependent offspring, counting human causes only. We note that despite a reduction of the mortality threshold for independent females and dependent offspring to 7.6%, the corresponding mortality limit may represent a greater number of bears compared with previous years because of greater size of the GYE grizzly bear population and because new techniques, such as the mark-resight estimator, may reduce the low bias of current population estimates based on the Knight et al. (1995) rule set. The team recommends the existing mortality threshold for independent males (15% from all causes) be retained.

The team also recommends that a revision of the existing boundary defining Suitable Habitat be adopted as the area within which grizzly bear mortalities counting against the mortality threshold be tallied. Under this change, some grizzly bear mortalities in areas where long-term occupancy or expansion is likely unsustainable would not be counted against the mortality threshold. This change would also correct a currently existing inconsistency, under which bear mortalities are counted over a much larger area than where systematic data collection efforts occur.

1. Workshop Objectives

When initially organized in late 2010, this workshop had 3 major objectives:
1. Review and revise the rule set of Knight et al. (1995) used to determine the unique number of females with cubs-of-the-year, which has been the foundation for determining population size, with the goal of reducing bias in the estimate.
2. Evaluate current mortality limits as necessary based on an updated population estimate.
3. Discuss the possibility of zoning the ecosystem for mortality limits given the expanding population.

Subsequent to the first workshop in February 2011, population monitoring results collected during 2011 (Haroldson 2012) triggered a demographic review under existing protocols (U.S. Fish and Wildlife Service 2007*a*). This necessitated two additional tasks:

4. Evaluate current mortality limits as necessary in light of newly updated estimates of demographic (vital) rates for the GYE grizzly bear population for 2002–2011 (i.e., results of the demographic review). This time period was selected because it 1) represented an independent data set from the previous analyses based on data from 1983–2001 and 2) reflected the time period when whitebark pine began noticeably declining.

5. Produce an initial investigation of intrinsic and extrinsic factors potentially associated with changes in grizzly bear vital rates.

Results of this workshop will be used to re-evaluate the basis for, and application of, rules for sustainable mortality limits. As per the commitment of all involved management agencies, our goal is to ensure that mortality management of the Greater Yellowstone Ecosystem grizzly bear population is based on the best available science to maintain long-term population viability. We expect a number of peer-reviewed publications to result from investigations conducted as part of these workshops, and when published, they should supplant this document as an authoritative source. This report is provided now so that stakeholders can be informed of our deliberations and necessary decisions and actions can be taken using the best available science.

2. Background

The GYE grizzly bear population was listed as threatened under the Endangered Species Act in 1975. A concerted and coordinated effort by federal, state, tribal, and private land managers led to the development and implementation of conservation measures with the primary purpose to reduce grizzly bear mortality and manage for suitable and secure habitat. During the decades of the 1980s and 1990s, the Interagency Grizzly Bear Study Team documented an increase of the GYE grizzly bear population, growing from approximately 200–350 bears in the mid-1980s (Eberhardt and Knight 1996) to at least 600 in 2012.

The U.S. Fish and Wildlife Service submitted a final rule to delist the GYE grizzly bear population in March 2007. This delisting rule was challenged in court and the Federal District Court in Missoula, Montana ordered to reverse the delisting in September 2009; protections under the Endangered Species Act were reinstated in March 2010. The District Court decision was appealed on two primary issues: 1) adequacy of regulatory mechanisms after delisting (i.e., the Conservation Strategy) and 2) potential threat of whitebark pine decline on the GYE grizzly bear population. The 9th Circuit Court of Appeals rendered a decision in November 2011 and reversed the District Court decision regarding the adequacy of protections provided under the Conservation Strategy but upheld the District Court decision that the U.S. Fish and Wildlife Service had not sufficiently articulated that whitebark pine decline was not a threat to the GYE grizzly bear population.

We provide here a capsule summary of protocols in use from adoption of the 1993 Grizzly Bear Recovery Plan until 2007, when the Revised Demographic Recovery Criteria for the Yellowstone Ecosystem were implemented (U.S. Fish and Wildlife Service 2007*a*), and from 2007 through the present time. This background (Section 2) can be skipped, but may be useful for reference in understanding options for improving the protocols presented in this document. Readers wishing to examine only the considerations and results of the current (year 2011–2012) workshop should go to Section 3.

2.1. Protocol in place prior to 2007

Management guidelines were set to assure that:

- A minimum of 15 females accompanied by cubs-of-the-year (F_{COY}, hereafter) were documented over a running 6-year average, inside the Recovery Zone plus a 10-mile perimeter immediately surrounding the Recovery Zone.
- 16 of 18 Bear Management Units (BMUs) were to be occupied by females with young (cubs, yearlings, or 2-year-olds) for a running 6-year sum of observations, with no 2 adjacent BMUs unoccupied.
- Known human-caused mortality was not to exceed 4% of the conservative, minimum population size index based on the most recent 3-year sum of unduplicated F_{COY}.

- o This rule was amended in 2000 to include probable human-caused mortalities, and cubs accompanying known and probable human-caused female deaths.
- No more than 30% of the 4% mortality were to be females (i.e., 1.2% of the minimum population size index).
- These mortality limits were not to be exceeded during any 2 consecutive years for recovery to be achieved. The threshold was based on a 6-year running average of mortality contrasted with the annual limit established from the 3-year sum of F_{COY}.

The population size and allowable numbers of human-caused mortalities were calculated as a function of the number of unique F_{COY} observed. Identification and separation of F_{COY} followed methods reported by Knight et al. (1995; these protocols came to be known colloquially as the "Knight rule set"). We summarize the protocols suggested by Knight et al. (1995) to distinguish unique individual F_{COY} seen in any given year from duplicate observations of the same F_{COY} in Appendix A.

Following determination of the number of F_{COY} observed in any year, the next step was to produce a conservative index of the number of adult females present. This was achieved by summing the number of F_{COY} seen during a 3-year period and subtracting the number of adult female mortalities recorded during this time period (Equation 1):

$$\hat{N}_{min,t} = \sum_{i=t-2}^{t} \frac{\hat{N}_{obs,i} - d_i}{0.274}, \tag{1}$$

where

$\hat{N}_{min,t}$ = a conservative index of total population size in year (*i*-2)

$\hat{N}_{obs,i}$ (following notation of Keating et al. 2002) = number of unique F_{COY} observed in year *i* (as per Knight et al. [1995]), and

d_i is the number of known and probable human-caused mortalities of adult females (age >4) in year *i*.

To extrapolate to the number of all bears present, this value was divided by the estimated proportion of adult females in the population (0.274), assuming a stable age distribution.

This extrapolation made no claims to being an unbiased estimate of actual population size. Because the 3-year sum of F_{COY} was based on an observed number of unduplicated individuals (as described by Knight et al. [1995]), it provided a very conservative index of population size (i.e., an extrapolation from bears actually seen), rather than a true estimate of population size. As such, it undoubtedly underestimated both total population size and sustainable mortality limits. Nor did it permit calculation of valid confidence bounds.

Mortality limits were set at 4% of $\hat{N}_{min,t}$ with no more than 30% of this 4% (1.2% of the population) to be females. The 4% total mortality and 30% female values came from

simulation work conducted by Harris (1986), suggesting that a population of grizzly bears similar to those in the U.S. Northern Rockies sustaining approximately 6% added human-caused mortality (to an assumed background level of natural mortality) would have a very low probability of decline (on average, 70% of simulated mortalities were of males). Further, to account for the likelihood that not all dead bears would be known and thus enter the calculations, it was assumed that 1 additional bear died for each 2 that were documented. This was accomplished by further reducing the mortality limit from 6% to 4% annually. These steps are summarized in Figure 1.1.
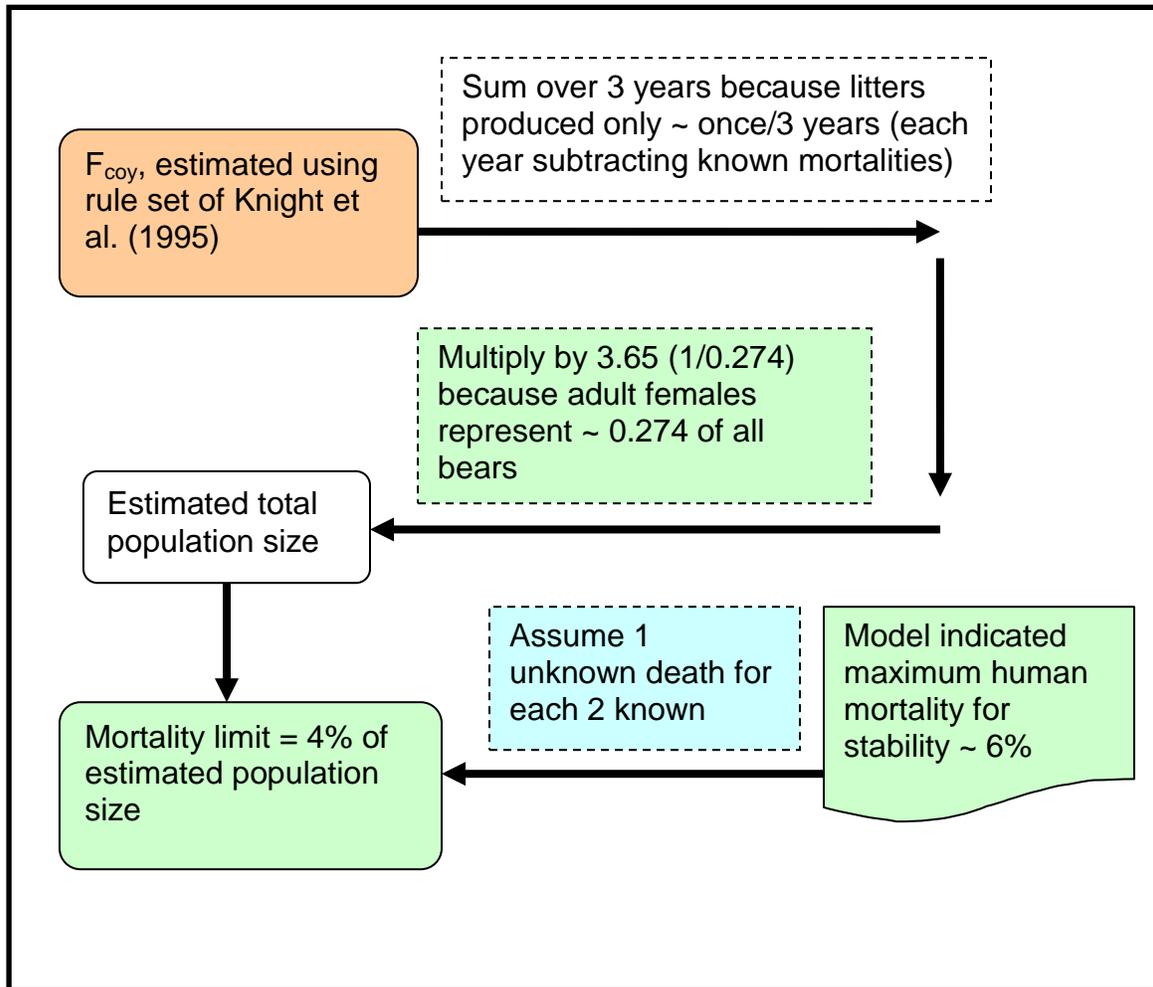
Figure 1.1. Flow chart of the protocol in place during 1993–2007 for estimating the number of grizzly bears in the Greater Yellowstone Ecosystem and limits to mortality.

This protocol had a number of characteristics, some of which could be seen as deficiencies, others as benefits:

- The 30-km rule set developed by Knight et al. (1995) to distinguish unique F_{COY} was designed to minimize Type I errors (i.e., reduce probability of mistakenly identifying sightings of the same F_{COY} as a different F_{COY}) and thus was designed to be conservative (i.e., some F_{COY} will not be identified as unique because they are too close to other F_{COY}).

- The protocol was conservative in that mortality limits were based on a conservative index of population size.

- The protocol was in place until 2007. During the 1983–2001 period, point estimates of the rate of increase of the GYE grizzly bear population ranged between 4% and 7% per year (4% if survival of independent females was calculated based on the assumption that unresolved fates represented mortalities and 7% if records of independent females with unresolved fates were censored; Harris et al. 2006: Table 18; Harris et al 2007:172). During this same period, grizzly bear distribution expanded (Schwartz et al. 2002, 2006*c*, lending additional support to a growing population.

- The constant 0.274 (Eberhardt and Knight 1996:417) represented the proportion of adult females in the population, defined as bears ≥5 years of age (U.S. Fish and Wildlife Service 1993: Appendix C:156; Eberhardt et al. 1994: Table 2:362). Because some 4-year-old females produce cubs (Eberhardt and Knight 1996, Schwartz et al. 2006*b*), their inclusion into the above equation could result in an overestimation of total population size because the constant 0.274 represents only females ≥5 years of age. Additionally, not all females of age class 5 produce first litters, as some delay reproduction until ages 6–8 (Eberhardt and Knight 1996: Table 1:361; Schwartz et al. 2006*b*). Consequently, the proportion used to extrapolate F_{COY} to total population size contained an unknown amount of error. Also, this proportion was based on the assumption of a stable age distribution, which may not be the case.

- The protocol assumed that on average, adult female grizzly bears produced a litter once every 3 years. Deviations from this assumption could overestimate (interval <3 years) or underestimate (interval >3 years) population size. The estimated proportion of F_{COY} in any given year based on a sample of radio-collared bears (age >3) ranges from 0.05 to 0.60. During this period (1983–2001), the Study Team monitored 352 females and documented 110 cub litters. This equated to 0.315 litters/female/year or 3.2 years between litters (1/0.315), suggesting that summing over 3 years generates a downward bias in estimating population size.

- Mortality limits were based on original work by Harris (1984), which was developed using input from a generic grizzly bear population for the continental U.S. These values were not specific to the GYE population. More recent ecosystem-specific data are now available.

During 2004–2006, scientists and managers involved with the GYE grizzly bear population had arrived at a consensus that newer, peer-reviewed scientific information (Cherry et al. 2002; Keating et al. 2002; Haroldson et al. 2006; Harris et al. 2006; Schwartz et al. 2006*a*, *b*, *d*) existed that should be used to improve these methods, develop new methods for these management approaches, or both.

2.2 Protocol adopted in 2007 and currently in place ("Knight-Chao2" protocol)

Following considerable analyses during the years 2000–2005, consideration of options, and input and review from both scientists and general public, a new protocol for estimating population size and mortality limits was proposed in 2005 (see Interagency Grizzly Bear Study Team 2005, 2006), and incorporated into the final Conservation Strategy for Grizzly Bears in the Greater Yellowstone Ecosystem published in 2007 (Interagency Conservation Strategy Team 2007) and the Revised Demographic Recovery Criteria for the Yellowstone Ecosystem (U.S. Fish and Wildlife Service 2007*a*). This remains the protocol in use as of the writing of this document.

2.2.1. Independent females

2.2.1.1. Estimating population size of females.—The earlier conservative index of population size has been replaced by a population estimate, albeit one that still has its roots in the method of delineating unique F_{COY} using the Knight et al. (1995) rule set. Counts of unduplicated F_{COY} and sighting frequencies continue to follow methods outlined by Knight et al. (1995). However, unlike prior to 2007, an attempt is made to estimate the total number of F_{COY} present from the distribution of the frequencies of sighting of individual F_{COY}. As implemented by Cherry et al. (2007), observed count frequencies are used to estimate a preliminary, year-specific total number of F_{COY} using the Chao2 estimator (Chao 1989) (hereafter $\hat{N}_{FCOY\text{-}Chao2}$).

F_{COY} are assumed to be ≥4 years of age because female grizzly bears in the GYE almost never produce cubs prior to this age. The total number of females ≥4 years of age in the entire population (i.e., with and without cubs-of-the-year) is estimated by dividing $\hat{N}_{FCOY\text{-}Chao2}$ by 0.289; this number is the estimated proportion of F_{COY} in the entire population of females ≥4 years of age and is based on transition probabilities calculated from the telemetry sample (see Appendix C of Interagency Grizzly Bear Study Team [2005] and for details see Schwartz and White [2008]). Thus, the resulting estimate represents, on average, the total number of females ≥4 years of age in the GYE population.

In turn, this number is divided by 0.77699, the estimated proportion of female bears ≥4 years of age in the population of females that are ≥2 years of age. The resulting value represents an estimate of total independent female bears (age ≥2 years) in the GYE. It is this, the number of females aged 2 and above that serves as the reference for mortality limits, as estimated by Harris et al. (2006).

2.2.1.2. Derivation of sustainable mortality limit.—The mortality limit for independent female bears is set at 9% of the population estimate for females ≥2 years old based on Harris et al. (2006; equivalent to a survival rate of 91% for these age classes). All mortalities are counted including: (1) agency-sanctioned management removals, (2) loss of radio-marked bears, (3) reported deaths from all causes (i.e., human, natural, and undetermined causes), and (4) an estimate of unknown and unreported losses. The 9% mortality threshold was chosen because

simulations suggested that given fecundity and survivorship for dependent offspring estimated for 1983–2001, when survival of independent-aged females was ≥0.91, the annual growth rate (λ) of the population would be ≥1.0 in 95% of simulations (Harris et al. 2006, Schwartz et al. 2006*a*).

       2.2.1.3. Application of allowable mortality limits.—To dampen variability and provide managers with inter-annual stability in the threshold, allowable mortality limits are based on a smoothed estimate of the number of F_{COY} present in the population in each year, using past years' data and estimates. Linear and quadratic regression models of the natural log of $\hat{N}_{FCOY\text{-}Chao2}$ with year are fitted as an initial estimate of trend for $\hat{N}_{FCOY\text{-}Chao2}$. Support for linear versus quadratic models is assessed using an information-theoretic analysis approach based on Akaike's Information Criterion (AIC_c; Burnham and Anderson 2002). Respective AIC_c weights of the linear and quadratic models are then used to obtain model-averaged estimates of $\hat{N}_{FCOY\text{-}Chao2}$. The model-averaged endpoint in the time series is used as the most appropriated estimate for number of F_{COY} in the population. The method described in 2.2.1.1 is applied to the model-averaged estimate of F_{COY}, and it is this estimate from which sustainability of annual mortality is assessed.

       2.2.1.4. Unknown and unreported mortality.—Unknown and unreported mortality are estimated based on the method of Cherry et al. (2002). This method assumes that all deaths associated with management removals (sanctioned agency euthanasia or removal to zoos) and deaths of radio-marked bears are known. It estimates the number of reported and unreported mortalities based on counts of reported deaths from all other causes.

2.2.2. Dependent offspring

       2.2.2.1. Estimating the number of dependent offspring.—The number of cubs in the annual population estimate is based on estimates of the model-averaged number of F_{COY} ($\hat{N}_{FCOY\text{-}Chao2}$, see section 2.2.1.1.). We use an average litter size of 2.04 cubs (Schwartz et al. 2006*b*). The number of yearlings in the population is estimated from the number of cubs the previous year that survived. We assume cub survival to be 0.638 (Schwartz et al. 2006*d*). Thus, we estimate the number of yearlings in the population in any given year by multiplying the estimated number of cubs the previous year by 0.638.

       2.2.2.2. Sustainable mortality limit of dependent offspring.—Just as for independent females, the mortality limit for dependent bears of both sexes be set at no more than 9% of the total estimate of dependent offspring in the population. The rationale for using the same mortality limit as for independent females is explained in IGBST (2005:36). However, unlike for independent females, only human-caused deaths (both reported known and probable) are tallied against the threshold (Interagency Grizzly Bear Study Team 2006).

2.2.2.3. Application of allowable mortality limit.—To dampen variability and provide managers with inter-annual stability, estimates for numbers of dependent offspring are derived from the model-averaged estimate of F_{COY} based on Chao2 and allowable mortality limits are a 9% annual limit from human causes only.

2.2.2.4. Unknown and unreported mortality.—We lack empirical data to estimate unknown and unreported mortality for dependent offspring (Interagency Grizzly Bear Study Team 2006).

2.2.3. Independent males

2.2.3.1. Population estimate for males.—An estimate of independent males (age ≥2 years old) depends on the estimate of independent females and modeled sex ratio of the population (Harris et al. 2006, Interagency Grizzly Bear Study Team 2006). Based on estimates of reproduction and survival, the sex ratio based on projections from the stable age distribution is 0.388:0.611 M:F. Therefore the male segment represents 63.5% (0.388/0.611 = 0.635) of the female population (i.e., there are 0.635 male bears for every female bear).

2.2.3.2. Sustainable mortality limit.—Based on Harris et al. (2006), the mortality limit for independent male bears is set at 15% of the population estimate for males ≥2 years old. Similar to mortality limits for independent female bears, all mortalities are counted, including: (1) agency-sanctioned management removals; (2) loss of radio-marked bears; (3) reported deaths from all causes (i.e., human, natural, and undetermined causes); and (4) an estimate of unknown and unreported losses. The 15% mortality threshold was chosen because it approximates what occurred in the GYE from 1983–2001 (Haroldson et al. 2006), a period when population was estimated to have increased around 4–7% per year (Harris et al. 2006).

2.2.3.3. Application of allowable mortality limits.—To dampen variability and provide managers with inter-annual stability in the mortality threshold, the allowable annual mortality limit is 15% of the estimate of males ≥2 years old as derived from the estimate of females ≥2 years old (see section 2.2.1.1.). For example, the 2004 estimate of females ≥2 years old was 214 bears. The number of independent males (age ≥2 years) is estimated at 136 (214 x 0.635 = 136). The 15% limit based on this estimate = 20 (136 x 0.15 = 20) male bears. Therefore, estimated total mortality for independent-aged males in 2004 (23 mortalities; Cherry et al. 2002) was 3 bears above the allowable mortality limit of 20.

2.2.3.4. Unknown and unreported mortality.—Estimates of unknown and unreported mortality for independent males are based on the method of Cherry et al. (2002), as for females.

All steps are summarized in Fig. 2.1.

2.2.4. Total population size
Total population size is estimated annually based on the sum of estimates for independent female, independent male, and dependent bears.

2.2.5. Uncertainty
Unlike the protocol in place prior to 2007, most (but not all) steps involved in this protocol contain statistically valid measures of sampling error, and thus confidence limits can be calculated for individual steps. At the least, these provide information on how certain we are of any given step along the way. In some cases, they provide explicit bases for calibrating risk, by allowing for more or less conservative management guidelines based on a range of plausible outcomes rather than a single point estimate. However, uncertainty in each step is not incorporated into subsequent steps, making it difficult to understand the degree of certainty in final estimates.

Table 2.1 summarizes the steps illustrated in Fig. 2 that begin with counting the number of F_{COY} seen yearly to estimates of mortality limits, indicating the function of each, whether the expectation of the calculation is unbiased or not, whether uncertainty of the estimator is explicitly estimated, and, if so, whether it is carried through to the next step in the process and in what way. Most steps leading up to this estimate of population size are biased towards underestimating the population. Accordingly, use of these population estimates to obtain sustainable mortality rates likely result in conservative mortality thresholds.
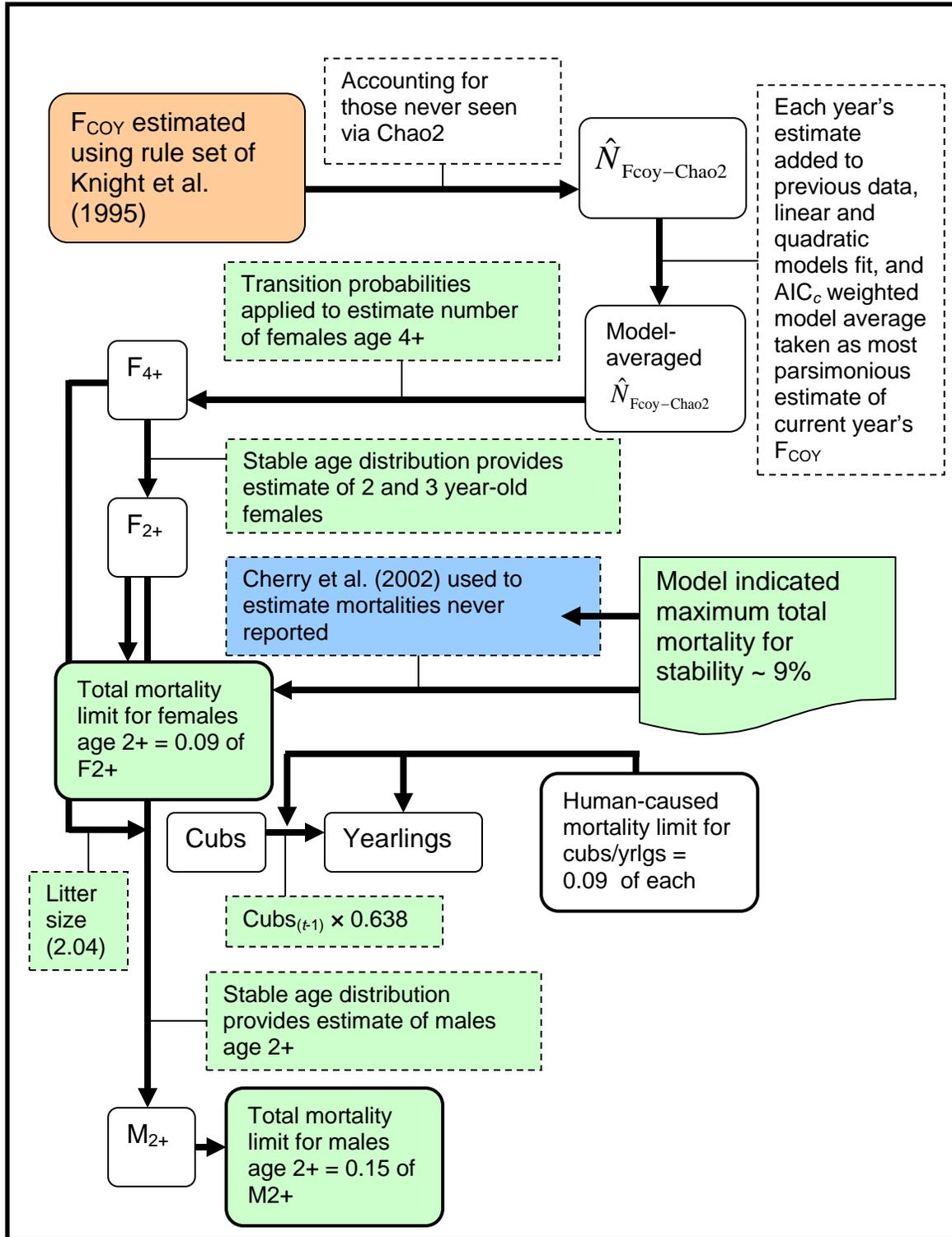
Figure 2.1. Flow chart of the protocols in place since 2007 for estimating the number of grizzly bears in the Greater Yellowstone Ecosystem and assessing sustainable mortality limits.

Table 2.1. Current protocol (in place since 2007), showing expected biases at each step, whether or not uncertainty (from sampling error) can be estimated, and whether (or how) this uncertainty is carried through to final estimates of population size and sustainable mortality of grizzly bears in the Greater Yellowstone Ecosystem.

Step in process	Function	Is expectation of result unbiased (U) , biased low (L), or biased high (H) and implications of this	Is uncertainty available from estimation procedure? (Y or N)	Is uncertainty carried through to the final management indicator? (Y or N)
1. Knight et al. rule set	Provide an index of the number of unique F_{COY} seen from observations	L (increasing negative bias with increasing population size)	N	N
2. Chao2	Estimate number of F_{COY} ($\hat{N}_{Fcoy-Chao2}$) in the GYE from observed number	L (slight negative bias depending on assumptions and sampling frequency, bias decreases as effort increases)	Y	N
3. Estimate taken from model-averaged regression (linear and quadratic)	Smoothen annual fluctuations in estimates of total number of F_{COY}	Expectation is U, but in any given year could be L or H; consequence of smoothing is delay in response to true process change	Y	N
4. Transition probability calculation	Estimate number of females 4+ from estimate of total number of F_{COY}	U	Y	N
5. Stable age distribution	Estimate number of females 2+ from estimate of females 4+	U	Y	N
6.Model sustainable mortality rate for females 2+ using stochastic simulation	Use 'assumed dead' survival rates	Slightly L (sustainable rates conservative)	Y	Y^a (use survival rate associated with 5% probability of 10-yr decline)
	m_x unadjusted for den emergence time	Slightly L (more cubs probably produced than suggested by this approach)		
	All unaccompanied yearlings assumed dead	Slightly L (more yearlings may have survived than estimated)		
	Use mean λ over 10-yr interval	Slightly L (declines more likely in 10 years than during shorter time span)		
7. Use Cherry et al. (2002)	Estimate total number of deaths from documented deaths	Slightly L (slightly more deaths may have occurred than estimated because heterogeneity in data greater than accounted for in estimator; effect would lead to underestimating total mortality)	Y	N

[a] Uncertainty because of deviation from stable age distribution is not accounted for.

3. Improving the current approach to population estimation

The group spent considerable time discussing two alternatives to estimate size and trend of the GYE grizzly bear population. The first alternative estimates the number of F_{COY} from unduplicated sightings in the ecosystem yearly (i.e., the same raw data set currently used in the Knight et al. [1995] approach) using a sequential clustering algorithm and simultaneously estimates the F_{COY} population size using an approach called ancillary data resampling (ADR). The simultaneous estimation of the minimum number of F_{COY} sighted and population size carries uncertainty in assigning unduplicated sightings through to the population estimate. The second alternative uses more traditional mark-resight methods to estimate population size of F_{COY}, bypassing the estimate of the number sighted each year used in all previous methods. The mark-resight approach uses only data from systematic aerial surveys conducted twice yearly and radio-marked animals known to be alive and in the population, as opposed to all sightings of F_{COY} used in previous methods. The consensus of the group is that the second of these two alternatives is preferred, for reasons explained below. Methods for both alternatives are described in this section, following a review of why current methods based on the Knight et al. (1995) rule set are problematic and a better approach is desirable.

3.1. Assessing the Knight et al. (1995) rule set

It has long been recognized that the rule set established by Knight et al. (1995) to distinguish unique F_{COY} from a set of yearly observations of unmarked F_{COY}, while useful for the purposes it had initially been designed for, suffers from two flaws that permeated the entire protocol: 1) there is no way to quantify uncertainty, and 2) it is known to produce population estimates that are biased low and the magnitude of this bias increases with true population size. Thus, if measuring an increasing population, it would underestimate the rate of increase. Similarly, it would also underestimate the magnitude of the reduction in a population that was truly declining.

Schwartz et al. (2008) wrote a computer program to automate application of the Knight et al. (1995) rule set by developing algorithms that accurately replicated manual application of the rule set. They then used data from radio-marked F_{COY} to simulate performance of the rule set under various hypothetical but realistic levels of known population abundance. To accomplish the latter, radio-locations of bears from multiple years were overlaid on a map of the ecosystem as if they had all been produced in a single year, and bears were then randomly sampled from this "superpopulation" of observable bears. Sets of known (radio-marked) F_{COY} locations were placed on the map in ways that would populate areas in which few, if any, radio-marked females had been located (livetrapping bears is difficult in some geographic regions) but were known to be occupied by adult female bears. The result was a rather uniform distribution of bear locations for the simulations to evaluate the Knight et al (1995) rule set, with the goal of producing realistic inter-sighting distances and times, which are crucial components of the rule set. Repeated samples (*n* = 500 simulations) of 10, 20, 40, 80, and 100 true F_{COY} were taken from this superpopulation to represent variability in samples obtained by chance through the sampling protocol.

The result of most relevance from Schwartz et al. (2008) was that the rule set returned increasingly negatively biased results as simulated number of unique F_{COY} (and thus density) increased. With 10 true F_{COY}, the rule set was negatively biased by 12%; this bias increased to 48% for a true population of 100 F_{COY} (Fig. 3.1). Stochastic simulations of any populations with true F_{COY} of 20 or greater failed to produce a single estimate that exceeded the hypothesized population size.
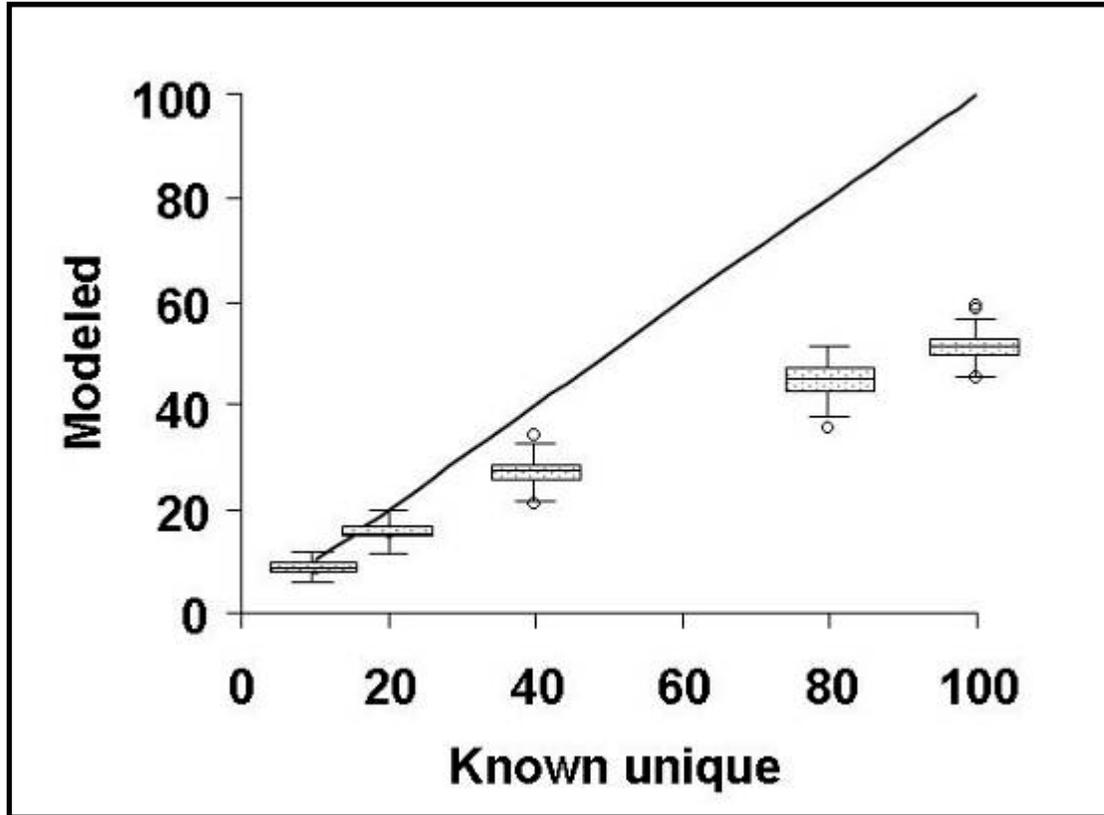
Figure 3.1. Side-by-side box plots of the simulated number of unique female grizzly bears with cubs-of-the-year (F_{COY}) in the Greater Yellowstone Ecosystem using the Knight et al. (1995) rule set to distinguish among telemetry locations for radio-collared F_{COY} sampled over a superpopulation of 10 to 100 unique sighted. In each case, n = 500 simulations. Adapted from Schwartz et al. (2008), except that reference F_{COY} line (solid line) has been corrected from that published in their paper.

One might ask if these biases resulted from errors in the way the Knight et al. (1995) rule set was conceived or executed, or alternatively, whether they are inherent in any similar attempt to distinguish unique animals from a set of unknown animals. We believe that obtaining an unbiased estimate of the true number of animals from unduplicated counts is difficult because it becomes increasingly challenging to distinguish unique animals from duplicates as density increases. Under the current methods for obtaining sightings of F_{COY}, there are few ways in which 2 sightings can be judged as representing distinct individuals, and they generally depend on such factors as number of cubs (1, 2, or 3) and the interaction of distance and time interval between sightings (summarized in Appendix A). The rule set was designed to reduce the probability of erroneously categorizing 2

sightings of a single animal as being from multiple animals but Schwartz et al. (2008) clearly showed there is a trade-off as population density increases (Fig. 3.1).

In light of these known biases, a group met in October 2007 to devise a research direction with the goal of producing a method to address these problems (Interagency Grizzly Bear Study Team 2008) and that would explicitly account for the uncertainty in estimating the number of unique F_{COY} sighted. The proposed strategy at the time was to develop a probabilistic model using a hierarchical Bayesian framework that would distinguish unique F_{COY} based on data from known (i.e., radio-marked) animals, while simultaneously estimating F_{COY} population size using methods similar to those in Wright et al. (2009). It was recognized at the outset that developing a model of true F_{COY} spatial distribution in the GYE would be required, and that this represented a substantial challenge.

3.2. Alternative #1: Sequential clustering algorithm combined with ancillary data resampling (ADR) to simultaneously estimate number sighted and F_{COY} population size

Dr. Megan Higgs, Department of Mathematical Sciences at Montana State University in Bozeman was contracted to pursue this modeling effort. She presented her preliminary results to the group on February 2 and 3, 2011, and further simulation results on July 11 and 12, 2011. Although the group ultimately concluded that they would not recommend using this approach as part of a revised management protocol, considerable time and effort was spent examining and assessing it. The following section provides a brief overview of the method Dr. Higgs developed and presented. A more detailed description is provided in Appendix B. Dr. Higgs plans to submit this work for publication in peer-reviewed literature at a later date.

The method has several steps and relies heavily on historic radio-telemetry and GPS data of F_{COY} in the study area. The method simultaneously estimates the minimum number of F_{COY} sighted (in place of the Knight et al. [1995] rule set) and the F_{COY} population size (in place of the Chao2 method) using a Bayesian model.

Stage 1: Estimate the minimum number of F_{COY} sighted (n) from all sightings within a year
      Part 1: A logistic regression model fit to historic data is used to predict the probability that two sightings are from the same bear and this is used as the basis for a sequential clustering algorithm resulting in an estimated number of unique F_{COY} sighted.
      Part 2: A cut-off value is obtained through an iterative process to remove most of the bias displayed in Fig. 3.1. Uncertainty in the estimate is quantified by repeatedly applying a sequential clustering algorithm to simulated data obtained by re-sampling from a superpopulation created from historic radio-telemetry and GPS data, similar to the strategy Schwartz et al. (2008) used to quantify uncertainty in the rule set

Stage 2: Estimate the number of F_{COY} in the population given the results from Stage 1

Part 1: This again relies on resampling from a superpopulation created from historic radio-telemetry and GPS data. Repeated sampling from the superpopulation consistent with the actual sampling protocol provides the method by which uncertainty is quantified.

Part 2: The superpopulation can be created based on combining historic data with hypotheses about the spatial distribution of F_{COY} on the landscape. We created three such superpopulations representing different assumptions about the distribution of F_{COY} within the GYE.

Part 3: Repeated sampling from each superpopulation scenario (i.e., ancillary data re-sampling) using the steps described in Appendix B resulted in quantification of the relative likelihood of different values of population size given the total number of observed sightings and the results for the minimum number of F_{COY} sighted obtained in Stage 1.

Model assessment: A simulation study was conducted to assess the performance of the models under violations of the spatial distribution assumptions. This allowed quantification of the magnitude of possible mistakes that could be made if we, for example, assume F_{COY} are preferentially distributed in high sightability areas when really they are distributed more uniformly across the region.

3.2.1 Benefits
1. The method uses all data (ground and flight data).
2. The method provides an estimate of the number of unique F_{COY} sighted.
3. Assumptions regarding the spatial distribution are based on real data from the study area and are readily visualized through plots of the superpopulations.

3.2.2. Limitations
1. The method is computationally intensive
2. The method involves many steps, which make it difficult to explain and understand.
3. The study team deemed the choice of a particular superpopulation to represent the spatial distribution assumption to be subjective.

3.2.3. Discussion
Because of the level of complexity involved in the entire method and computational time, the group decided against using this method. Also, lack of knowledge about the spatial distribution of F_{COY} across the region caused concerns regarding the choice of a particular superpopulation.

3.3. Alternative #2: Mark-resight to estimate number of F_{COY} from standardized aerial surveys

This approach takes advantage of the fact that, beginning in 1997, standardized aerial surveys have been flown twice per summer by experienced pilots and observers, whose

tasks have been to 1) count all bears observed without the aid of telemetry, taking special care to ensure the presence of cubs-of-the-year and number of cubs-of-the-year were correctly documented, and 2) when a F_{COY} is observed, use telemetry receivers to determine whether or not that particular female is wearing a radio collar. These data naturally form the basis for mark-resight estimation of population size, pioneered by Rice and Harder (1977; see White 1996), and subsequently elaborated and extended by other investigators (Miller et al. 1997). In short, the total number of animals of interest (population size) is estimated by considering their detection probability. In this case detection probability is estimated by the distribution of number of re-sightings of the marked (radio-collared) F_{COY} (whose number is known exactly). The maximum number of re-sightings per year in this case is two (i.e., one during each set of observation flights).

Normally, an estimate would be produced for each sampling period (for large mammals, sampling typically occurs once per year) during which the number of marks is known and a set number of resighting surveys occurs. However, in the case of GYE grizzly bears, both the number of marked F_{COY} and the number subsequently observed during the observation flights are smaller than needed for standard yearly application of mark-resight methods (in 6 of the 15 years, no marked F_{COY} were re-sighted, which would make estimates in those years impossible; Table 3.1). Indeed, the Interagency Grizzly Bear Study Team previously studied the feasibility of this technique using all radio-marked bears with 1998–1999 data and concluded that resighting probabilities were too low, and uncertainty of population estimates too great, to apply the technique (Schwartz 1998, 1999).

However, if the assumption can be made that the probability a marked F_{COY} will be seen 0, 1, or 2 times during the 2 observation flights is generally similar from year to year (i.e., the yearly frequencies are manifestations of a single, underlying multinomial distribution), then the entire 15-year data set can be used to generate the probability of detection. Under this assumption, the number of marked F_{COY} in the population and the number of unmarked F_{COY} seen during observation flights varies yearly, but rather than using that individual year's distribution to model resighting probability, the overall resighting probability based on the 15-year aggregated sightings of F_{COY} is applied to each individual year.

Any approach using these data also assumes that the population of F_{COY} is closed within each sampling period (i.e., no deaths of F_{COY} between the first and second flights). Given the high survival rate of adult females (see later sections), this assumption seems biologically acceptable.

One additional assumption underlying use of this method is that the probability of observing a radio-marked F_{COY}, without using telemetry, does not differ from the probability of observing an unmarked F_{COY}. This assumption could be violated if marked F_{COY} differ from unmarked F_{COY} in behavior, habitat preference, pilot knowledge of their whereabouts, or geographic distribution. Study team members were unable to imagine any reasonable situation that would lead to either behavioral or habitat differences

between collared and uncollared F_{COY}. Bears are not collared from aircraft, and thus recently collared bears are unlikely to react to them differently than uncollared bears. Further, F_{COY} are rarely captured and radio-marked in the year they have cubs; most collared F_{COY} wear collars that were attached in earlier years. The study team also indicated it is very unlikely that pilots and observers more readily find marked (radio-collared) F_{COY} than unmarked F_{COY} because they so rarely observed them visually (~10% of the time), even during telemetry flights. Pilots are under strict protocol not to locate F_{COY} using telemetry during observation flights.

With the exception of one characteristic of the data, study team scientists felt that the geographic distribution of collared female bears is generally representative of the geographic distribution and relative density of female bears in the population. The exception was that uncollared F_{COY} are more likely to use army cutworm moth sites for feeding in late summer than collared F_{COY}. Previous work has shown that a subset of bears in the GYE population typically spends 6 to 10 weeks in late summer (mid-July to late September) of most years feeding in alpine scree slopes on these moths (Mattson et al. 1991, Bjornlie and Haroldson 2011). These bears are thus highly visible and have constituted a substantial proportion of bears seen during observation flights. However, capturing and marking bears has been particularly difficult in these portions of the GYE. Early in the season, these remote and high-elevation areas are typically snow-covered, access is difficult, and ground-trapping has rarely occurred. Later in the season, when access improves, most of the bears that would be the subject of capture efforts have already begun feeding on army cutworm moths and are difficult to attract to capture sites. Thus, the proportion of radio-marked F_{COY} among those feeding on these high-visibility sites is lower than in the remainder of the ecosystem because of sampling limitations.

Table 3.1. Number of marked female grizzly bears with cubs-of-the-year (F_{COY}) known to be in the Greater Yellowstone Ecosystem population, number observed once or twice during twice-yearly observation flights, and total number of unmarked F_{COY} (i.e., not wearing operating radio collars) observed each year, 1997–2011.

Year	Marked F_{COY} available	Marked F_{COY} observed once	Marked F_{COY} observed twice	Unmarked F_{COY} observed
1997	6	2	0	16
1998	4	2	0	26
1999	6	1	0	7
2000	7	0	0	16
2001	9	5	0	32
2002	5	0	0	65
2003	4	1	0	25
2004	4	2	0	35
2005	3	0	0	22
2006	8	0	1	43
2007	6	3	0	45
2008	5	1	1	42
2009	6	0	0	28
2010	3	0	0	38
2011	3	1	0	28

Were mark-resight estimates to be applied ecosystem-wide without considering moth sites, the results would be positively biased (the probability of observing uncollared bears in this area is actually much greater than suggested by the proportion of marked bears that are re-sighted). However, the study team was able to identify moth sites and animals observed on them during each year. Thus, the study team proceeded with a preliminary mark-resight estimator that omitted any bears (marked or unmarked) observed at moth sites. In the remainder of the ecosystem, the assumptions of equal observability among marked and unmarked bears seems reasonable, thus the group viewed this approach as providing an unbiased estimator of the yearly number of F_{COY} within the GYE, excluding areas where bears feed on moths.

There are several alternative estimators for use with mark-resight data that differ in their generality (e.g., how well they handle heterogeneity of individual resighting probabilities) and assumptions. Megan Higgs and Gary White presented the group with the results of 3 different estimators:

      1) a Bayesian approach, in which uncertainty in the probabilities of re-sightings obtained from data on marked animals is incorporated to obtain the posterior distribution for F_{COY} population size for areas of the GYE covered by observation flights, excluding the moth sites. Higgs et al. (in review) present several methods, exact and approximate, to obtain the appropriate posterior distribution for this problem.

      2) the Poisson-log normal approach of McClintock et al. (2009), which has recently been incorporated into Program MARK, provides similar results to those obtained by Higgs et al. (in review); and

      3) the generalized binomial model of Bowden and Kufeld (1995), which is available in Program NOREMARK.

Although the latter two are considered approximations, it is noteworthy that both accommodate heterogeneity in resighting probabilities (although the Bowden estimator is designed for situations in which resighting is without replacement within each occasion).

All estimators returned point estimates and confidence (or credible) intervals that did not differ practically, reducing the team's concern regarding the choice of modeling approach.

Preliminary estimates of the number of F_{COY} based on this method suggest they will generally be greater than the numbers returned by the "Knight-Chao2" approach. Because of small sample sizes, confidence intervals surrounding each point estimate are wide. A formal manuscript was submitted in March 2012 to a peer-reviewed journal by Megan Higgs, Gary White, Mark Haroldson, and Dan Bjornlie, which is currently in review.

3.3.1. Benefits

If an unbiased correction factor can be developed for the problem of observations at moth sites, this approach can provide an unbiased estimate of the number of F_{COY} within the GYE, from which population estimates can be projected based on proportions of animals in each age-class (as in the current protocol). Unlike the current procedure, trends reflected in this estimate should reflect true trends,

because there is no known density-associated bias. As currently implemented, it requires no additional research effort, because it uses animals that would be captured and collared in any case (for marked animals) and observation flights that have been consistently conducted since 1997 (for resightings).

3.3.2. Limitations

As currently implemented, the approach yields imprecise estimates (i.e., confidence intervals are large). In particular, the estimator produced with currently available data is somewhat sensitive to the small number of marked F_{COY} observed during both flights (most marked F_{COY} were never observed during flights, Table 3.1.). It also produces annual estimates of F_{COY} that vary considerably. Thus, a smoothing technique, such as regression on time, would be useful to better discern trends, rather than management responding to annual variation of estimates. To be used indefinitely in the future, a well-distributed sample of adult females must be radio-marked and, importantly, the larger this sample is, the more precise the estimator will be. Annual observation flights, similar to those conducted beginning in 1997, must be continued.

3.3.3 Work still to be done

3.3.3.1. Refine and update the geographic area to be excluded because of moth sites.—During the workshop, study team members provided an initial analysis that excluded marked F_{COY} resightings and sightings of unmarked F_{COY} within areas designated as moth feeding sites. A formal and objective procedure for defining areas inhabited by bears that use the moth sites during the period of observation flights is being developed. The downward bias resulting from excluding the moth sites entirely may be alleviated should it be possible to devise an additional estimate for moth sites only. To accomplish this, counts of F_{COY} during observation flights of confirmed moth sites will be conducted and evaluated for an annual moth-only addition to the mark-resight estimate. The accuracy of aerial observations of F_{COY} at moth sites will be evaluated based on simultaneous aerial and ground observations.

3.3.3.2. Work on an appropriate smoothing function.—The current protocol calls for fitting both linear and quadratic terms to series of F_{COY} estimates returned by the "Knight-Chao2" approach, with the single-best estimate in each year taken as the model-averaged mean using AIC_c weights. A similar approach could be applied to the series of estimates from the mark-resight approach. However, this approach may yet be improved by considering additional plausible models beyond the linear and quadratic. The quadratic model imposes a declining trend during later years of a series, thus not allowing for the possibility of population size becoming stable. Functions that include an asymptote would impose stability, thus not allowing for the possibility of a true decline. Because an a priori way to select among these possibilities does not exist, a larger array of candidate models of trend on time, weighted using AIC_c or similar information-theoretic methods, would offer the most objective assessment of recent population trends. We note that fitting smoothing functions will require several years as

counts of F_{COY} based on moth-only observation flights could not be backcast but will only accumulate with additional years of data.

3.3.3.3. Power analysis.—Power analysis would estimate the ability of this monitoring protocol to correctly detect a specified change in state (e.g., increase to decline), given existing estimates of process and sampling variation and specified time frames. A similar analysis was already published for the "Knight-Chao2" approach (Harris et al 2007:174). The anticipated time frame to complete these power analyses is the end of 2012.

3.3.3.4. Improve the precision of mark-resight estimates by expanding it to all females with dependent offspring.—Protocols for aerial observation flights require pilots, upon finding a $F_{COY,}$ to determine whether bears are radio-marked. However, unlike in the "Knight-Chao2" protocol, which depends on the unique nature of F_{COY} to discriminate one individual from another, it may be possible to expand the subset of the population estimated beyond F_{COY}. For the GYE, sample size of marked and unmarked animals would approximately double (assuming a roughly 3-year reproductive cycle) if all observations of adult females with any offspring were considered. This would require little or no additional investment of time on the part of pilots and observers, or reconsideration of the areas to exclude from moth sites (see 3.3.3.1, above). In extrapolating to the total number of females (and from there, to total population size), transition probabilities would still be used, but the ratio to use would be all females except those in the "no offspring" state. However, this approach could fail if the detection probability of females with yearlings or 2-year-olds differs from that of females with cubs-of-the-year. Additionally, aerial observations of females with unrelated, young males could potentially be misclassified as females with offspring or vice versa. Because of these 2 limitations, the study team will first conduct analyses to examine the feasibility of improving precision based on increasing the sample size of marked females. Completion of these analyses is anticipated by the end of 2012.

3.4. Other alternative approaches to population estimation

Both the core study team members and larger group represented at the workshops were mindful of alternative approaches that exist to estimate the population size and trend of bears. Retrospective analyses using statistical population reconstruction (e.g., Gove et al. 2002) may be a potential avenue worth exploring and some simpler population reconstructions have already been completed. These would primarily be useful in either supporting or casting doubt on estimates obtained yearly because inference would lag behind management needs by a few years.

The group was also aware of, and had direct research experience, with mark-recapture estimators using either ingested marks (e.g., tetracycline, Garshelis and Visser 1997, Garshelis and Noyce 2006) or DNA from hairs (Woods et al. 1999, Kendall et al. 2009, Clark et al. 2010). These approaches had previously been considered by GYE managers and deemed currently impractical for budgetary reasons.

3.5. Discussion

The primary motivation for exploring alternative estimation techniques was the desire to obtain unbiased estimates of population size. The group clearly sees the mark-resight approach as the single best available alternative from which to estimate the number of adult females in the GYE (and thus total population size). As preliminary results have shown (Higgs et al., in review), there is an expectation that this technique will produce population estimates that are ≥ than those produced by the Knight-Chao2 approach. The mark-resight technique, unlike the Knight-Chao2 approach, is not increasingly biased low as population size increases (Higgs et al., in review). Although evaluations sofar indicate precision of the mark-resight estimator is low, we note that uncertainty associated with the Knight-Chao2 estimates likely is understated (Higgs et al., in review). We take the view of Paulik (1963) and other population biologists that an approximately unbiased estimate with low precision is always better than a highly precise but biased estimate. We thus conclude the mark-resight technique meets the first workshop objective (see Section 1). However, the group also discussed that 3 issues be further evaluated: (1) low precision, (2) correction factor for F_{COY} observed at moth sites, and (3) trend estimation.

3.5.1 Low precision
Precision of mark-resight estimates of F_{COY} would increase if additional females could be radiomarked. Field sampling constraints limit opportunities to increase sample size of marked females so it is important to determine trade-offs between sample size and precision. Analyses will be conducted to examine the effect of increased sample size on precision, with final evaluations expected by the end of 2012

3.5.2 Correction for F_{COY} observed at moth sites
The current estimate of the zone of influence around army cutworm moth sites for F_{COY} (5,000 m from moth site boundary, based on telemetry data of independent females that used moth sites) is being evaluated by the study team. Evaluation of the effectiveness of this correction is based on comparison of F_{COY} from simultaneous ground and aerial observations (8 flights at 5 different sites) during 2012. Congruence of >95% between ground and aerial estimates would indicate a separate census of F_{COY} at moth sites is feasible, and would serve to adjust the mark-resight estimate. This issue should be addressed by the end of 2012.

3.5.3 Trend estimation
Power analyses are planned to determine the effectiveness to track changes in population trends under different scenarios of population size and change. Final evaluations are expected by the end of 2012. Application of this technique to develop and evaluate trend data, however, will take several years; whereas mark-resight estimates excluding moth feeding sites will be backcast to 1997, estimates that are corrected for F_{COY} using moth sites started in 2012. Therefore, trend data of F_{COY} estimates including moth sites require accumulation of additional years of data.

Because final evaluation of the mark-resight estimator is pending, there was consensus that data required for the "Knight-Chao2" estimator continue to be collected, and these estimates be updated and reported annually.

4. Preliminary analyses to update our understanding of grizzly bear vital rates from telemetry data

The study team has completed preliminary demographic analyses of the GYE grizzly bear population that update those published by Schwartz et al. (2006*e*). That publication examined the population during the years 1983–2001 (with an additional year for reproduction only). New analyses covered the period 2002–2011. Most of these new analyses use Program MARK to estimate rates of survival (cubs, yearlings, subadults, adult females, and adult males) and transition rates among reproductive classes of females (which, in combination with litter sizes, yield fecundity).

With two exceptions, analytical approaches and assumptions followed closely those of Schwartz et al. (2006*e*). The two exceptions were:

      1) Whereas the data set of 1983–2001 provided no basis for recognizing a distinct category of subadult females (aged 2–4) whose survival differed from adult females (aged ≥5 years), model selection procedures applied to the 2002–2011 data in which animals with unresolved fates were assumed to have died supported such a classification (although model selection for 2002–2011 data in which animals with unresolved fates were censored at last contact did not). Thus, subsequent models under the former assumption incorporated 4 age-classes for females: cubs, yearlings, 2–4 years-olds (subadults), and 5+ years old (adults).

      2) Schwartz et al (2006*b*) made no adjustment for the raw reproductive rate (m_x) estimated from multiplying litter size by probability of an adult female being in the "with cubs" state. The updated analyses for 2002–2011 adjusted m_x to account for the discrepancy between the dates on which litter sizes were first documented and the date on which cub survival was modeled as beginning. Schwartz et al. (2006*b*:20) pointed out that the reproductive rate (at cub emergence) later used in population projections ($m_x = 0.318$) was likely biased low by approximately 13% because the mean date of first litter size documentation was 65 days later than the date on which cub survival was estimated. The study team's new analysis adopted the alternative procedure of Mace et al. (2012:122), which is more appropriate when combining m_x with cub survival rates as part of a life-table or matrix-based estimation of a rate of increase.

Results of these preliminary analyses are summarized in Table 4.1., which are provided here as a work in progress. Readers are cautioned that these analyses are ongoing, have not yet been thoroughly vetted or peer-reviewed, and that further work could result in revisions. Nonetheless, the broad outlines of changes in the demographic characteristics of the GYE grizzly bear population during the 2 periods (1983–2001 vs. 2002–2011; see Fig. 4.2) appear robust and are of sufficient importance to management that we believe these tentative results should be shared and considered at this time.

Table 4.1. Demographic rates of the Greater Yellowstone Ecosystem grizzly bear population, 2002–2011, as estimated from preliminary (as yet unpublished) analyses, compared with analogous results from 1983–2001 (Schwartz et al. 2006e). For each vital rate, the point estimate is provided above, and 95% confidence limits are provided below.

Vital rate	2002–2011		1983–2001[a]	
	Point Estimate	95% CI	Point Estimate	95% CI
Cub survival	0.553	0.421-0.667	0.640	0.443-0.783
Yearling survival	0.539	0.346-0.698	0.817	0.489-0.944
Subadult (age 2-4) survival[b]	0.948	0.917-0.968	0.950	0.926-0.965
Subadult (age 2-4) survival[c]	0.887	0.803-0.937	0.922	0.857-0.959
Adult (5+) female survival[b]	0.948	0.917-0.968	0.950	0.926-0.965
Adult (5+) female survival[c]	0.943	0.910-0.964	0.922	0.857-0.959
Adult (5+) male survival[b]	0.948	0.917-0.968	0.874	0.810-0.920
Adult (5+) male survival[c]	0.943	0.910-0.964	0.881	-
Fecundity (adjusted)	0.336	0.264-0.409	0.362	-
Fecundity (unadjusted)[d]	0.286	0.227-0.345	0.318	0.277-0.359

[a] Rates were estimated using a combined subadult and adult age class.

[b] Animals with unresolved fates were censored at last contact; no sex or age-class effect was observed.

[c] Animals with unresolved fates were assumed dead for this analysis; an age-class effect was observed.

[d] These reproductive rates are considered to be biased low for the 1983–2001 period (thus biasing λ low); adjusted fecundity was used in analogous estimations done by the study team for the 2002–2011 period (Table 4.2.)

Table 4.2. *Point estimates (and, where calculated, 95% confidence intervals) of the rate of growth of the Greater Yellowstone Ecosystem grizzly bear population, λ (and bears within spatial subsets of it, weighted by the proportion of time spent in each), during the current period of analysis (2002–2011) and the previous period of analysis (1983–2001). A. Survival rates of independent females estimated with unresolved fate animals censored at last contact. B. Survival rates of independent females estimated with unresolved fate animals assumed dead (entire GYE only).*

Geographic area	2002–2011	95% CI	1983–2001	95% CI
A.				
Entire GYE	1.022	0.966–1.060[a]	1.076	1.008–1.115[b]
YNP [c]	1.022	-	1.054	-
Beyond YNP but within recovery zone [c]	1.041	-	1.121	-
Beyond recovery zone [c]	0.965	-	0.887	-
B.				
Entire GYE	1.003	- [d]	1.041	0.972–1.096[b]

[a] Confidence interval based on techniques presented in Harris et al. (2007).

[b] Harris et al. (2007:172).

[c] We provide these separate λ estimates for each zone because of their management implications, but note that evidence for differences among zones was weak: confidence intervals for the untransformed covariate "zones" overlapped zero.

[d] We did not calculate confidence interval for this scenario; based on scenario A., the 95% confidence interval would likely be similar in width and bound 1.0.

Final analyses have yet to be completed but a few notable points were stressed by the study team and are relevant to the group's deliberations regarding revision of mortality limits:

1) Although confidence intervals for the two time periods overlapped (thus a formal statistical test may fail to show strong evidence of difference), the consensus among the scientific group was that evident declines in cub and yearling survival rates were real.

2) Subadult survival also seems to have declined (although again, a rigorous statistical test might not support this) because AIC_c supported a model for the 2002–2011 data in which age class was included as a covariate, which was not the case for the 1983–2001 period. However, this was only evident when independent survival was based on the scenario in which bears with unresolved fates were assumed dead; no difference was detected for survival of subadult and adult bears when bear with unresolved fates were censored.

3) The point estimate for fecundity was only slightly lower for the later period compared with the earlier period. Mean observed litter size during 2002–2011 was 2.12 cubs, similar to the mean observed during 1983–2002 of 2.04 cubs. Therefore, The

asymptotic proportion of a 4+ female having cubs-of-the-year was 0.269 during the latter period, compared with 0.289 during the earlier period.

4) Survival of adult males appeared to have increased between the 2 time periods.

5) Taken together, these vital rates yielded an estimated asymptotic λ very close to 1.0 during the 2002–2011 period (treating bears with unresolved fates as having died at last contact, estimated λ was 1.003; treating bears with unresolved fates as censored at last contact, estimated λ was 1.022; Table 4.2). Thus, the population increase that occurred during 1983–2002 had evidently slowed or stopped during 2002–2011. Because true vital rates during the 10-year period 2002–2011 may have changed, we cannot pinpoint when the change in trend occurred, or whether the population trajectory in future years will change from that estimated during this time period.

6) As during the earlier period, population growth rates during 2002–2011 were highest when modeled for the population living within the Recovery Zone but beyond the boundary of Yellowstone National Park, lowest beyond the Recovery Zone boundaries, and intermediate within Yellowstone National Park. However, divergence in these trends appeared to narrow during the latter period because there was little support for models with a zone covariate. The growth rate of bears as modeled within the Recovery Zone but outside of Yellowstone National Park declined markedly from the earlier to the later period; the growth rate within Yellowstone National Park declined slightly, and the (negative) rate of growth for bears outside the Recovery Zone actually increased from the earlier to the later period (Table 4.2).

5. Preliminary analyses of intrinsic and extrinsic factors associated with grizzly bear vital rates

The study team completed a number of preliminary analyses with the objective of improving our understanding of the reasons population growth has slowed in recent years. In particular, the team has employed linear models, both in Program MARK and other statistical software, to examine the strength of evidence for various hypotheses relating indices of population density and measure of whitebark pine abundance to vital rates in recent years. In recognition of the fact that vital rates (as well as measured physiological parameters) are likely also functions of sex, age, and other plausible environmental factors (e.g., proportion of time spent within the Recovery Zone boundary), these were also considered in models.

These analyses are currently being refined and re-checked; specific analyses are not yet available for publication in this report. However, the consensus among the assembled group, upon considering the preliminary analyses conducted thus far, is that these data are consistent with both the hypothesis of density-dependence (i.e., the population has grown with respect to a relatively stable carrying capacity, i.e., $N/K \approx 1$) and the hypothesis of adverse effects associated with resource changes, such as whitebark pine decline (i.e., K has declined). These two potential mechanisms are confounded to a large extent. The grizzly bear population has grown by 4% to 7% during the 1980s and 1990s up until ~2002, after which density-dependent effects would be expected to manifest themselves. However, the lower population growth of 0% to 2% during 2002–2011 also coincides with the period in which availability of whitebark pine seeds and other food resources (e.g., cutthroat trout in tributary streams of Yellowstone Lake) declined. Obtaining a better understanding if, and how, these two processes (density dependence and changing food resources) may have contributed to changes in population growth, and their relative contribution, is challenging and is currently the primary research focus for the Interagency Grizzly Bear Study Team. A synthesis report regarding whitebark pine decline, density dependence, and ecological plasticity of grizzly bears in the GYE will be finalized by October 2013. The consensus among the group is the GYE bear population remains healthy and stable at this time and there are no indications the grizzly bear population has entered a prolonged declining trend.

6. Recommended revisions to sustainable mortality limits

The existing protocol uses the results of modeling conducted by Harris et al. (2006) to estimate that, with the GYE exhibiting vital rates similar to those documented during 1983–2001, total mortality of adult females at 9% or below would have a very low probability of inducing a population decline. With the updated analysis of GYE grizzly bear vital rates during 2002–2011 (particularly those indicating possible reductions in cub and yearling survival in recent years), these limits require re-examination.

6.1. Revised limits

6.1.1. Independent females

As an initial approximation, we recommend that mortality limits applicable to independent females be 7.6% of the annual population estimate for independent-aged females. This is a revision of the currently-used 9% (Section 2.2.1.2.), and is based on 1) the revised estimates of vital rates for female grizzly bears during 2002–2011, and 2) a deterministic life-history projection that produces $\lambda \approx 1.0$ with these updated fecundity and survival rates for dependent offspring, and an independent female survival of 0.924. Thus, if survival rates for dependent offspring and fecundity remain similar to those estimated during 2002–2011, mortality (regardless of source) leading to annual survival of independent-aged females of ≥ 0.924 (i.e., annual mortality rate of 0.076 or 7.6%) would, on average, not produce a declining trend. We note that in addition to this mortality limit being based on updated vital rates from 2002–2011, it differs conceptually from the previously adopted one of 9% in being based on a deterministic model, rather than on the independent female survival rate yielding annual population growth rate of $\lambda \geq 1.0$ in 95% of simulations (Harris et al. 2006). The workshop attendees agreed that this conceptual shift was appropriate because wildlife populations in general, and grizzly bears in particular, cannot be managed for growth in perpetuity, especially when the boundary of suitable habitat is generally well defined because of limits on available habitat and incompatibility with human activities beyond this boundary (see Section 6.2). Thus, a change in management objective from one of population growth for recovery to maintenance of a stable grizzly bear population (i.e., $\lambda \approx 1.0$) is biologically logical and desirable, and compatible with management objectives of state and federal agencies charged with managing grizzly bears in the GYE. Secondly, we note that despite the lower mortality threshold of 7.6%, the number of female bears representing that mortality limit may be greater than previous years because population size has increased and because new techniques, such as the mark-resight estimator, may reduce the low bias of current population estimates based on the Knight et al. (1995) rule set.

As in the current protocol (Section 2.2.1.4.), as part of estimating the number of unmarked bears dying, we recommend that unknown and unreported mortality be estimated based on the method of Cherry et al. (2002). This method assumes that all deaths associated with management removals (sanctioned agency euthanasia or

removal to zoos) and deaths of radio-marked bears are known. It estimates the number of unreported mortalities based on counts of reported deaths from all other causes.

6.1.2. Dependent offspring
Just as for independent females, we recommend the mortality limit for dependent bears be set at no more than 7.6% of the total estimate of dependent offspring in the population. The rationale here is similar to Section 2.2.2.2. (i.e., based on IGBST 2005:36), albeit using this revised number. As currently, and unlike for independent females, only human-caused deaths (both reported known and probable) would be tallied against the threshold.

6.1.3. Independent males
As in the previous protocol (Section 2.2.3.2.), no data exist that could be used to inform a sustainable mortality limit for males, because population trajectory is generally independent of male survival rates. Our recommendation therefore is that the current mortality limit of 15% of the annual population estimate of independent males be retained, which is a conservative criterion.

As in the current protocol (Section 2.2.3.4.), we recommend that estimates of unknown and unreported mortality for independent males be based on the method of Cherry et al. (2002).

The suggested protocol is illustrated in Fig 6.1., whereas Table 6.1. illustrates these steps with additional information on uncertainty and bias.
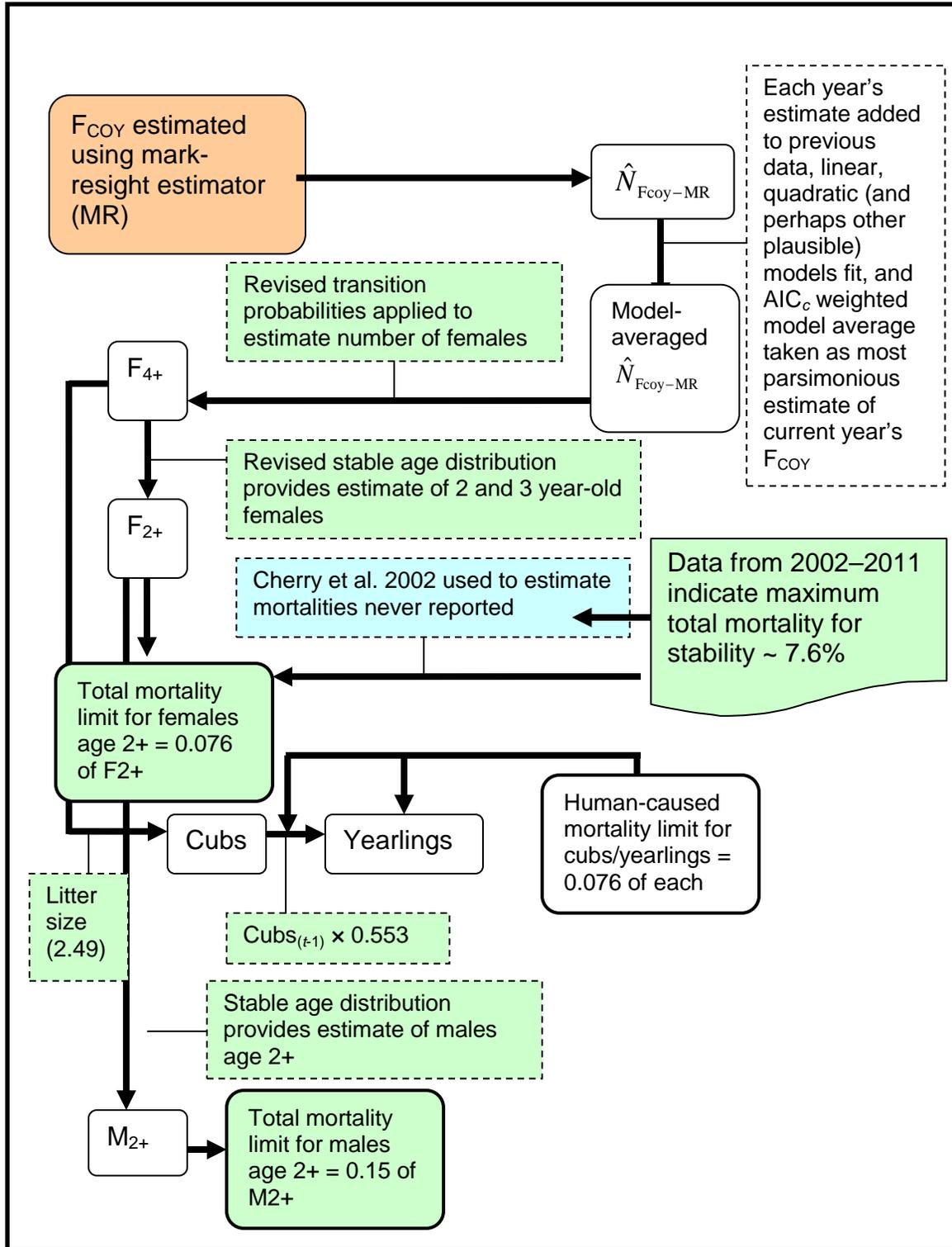
Figure 6.1. Recommended revised flow chart of protocols for estimating the number of grizzly bears in the Greater Yellowstone Ecosystem and limits to mortality.

Table 6.1. Recommended protocol (2012), showing expected biases at each step, whether or not uncertainty (from sampling error) can be estimated, and whether (or how) this uncertainty is carried through to final estimates of grizzly bear population size and sustainable mortality in the Greater Yellowstone Ecosystem.

Step in process	Function	Is expectation of result unbiased (U), biased low (L), or biased high (H) and implications of this	Is uncertainty available from estimation procedure? Y or N)	Is uncertainty carried through to the final management indicator? (Y or N)
1. Mark-resight	Estimate total number of F_{COY} in the GYE from observation flights and marked F_{COY}	U (if satisfactory correction factor for moth site issue can be developed)	Y	N
2. Estimate taken from model-averaged regression (linear, quadratic, other plausible models)	Smoothen annual fluctuations in estimates of total number of F_{COY}	Expectation is U, but in any given year could be L or H; consequence of smoothing is delay in response to true process change	Y	N
3. Transition probability calculation	Estimate number of females 4+ from estimate of total number of F_{COY}	U	Y	N
4. Stable age distribution	Estimate number of females 2+ from estimate of females 4+	U	Y	N
5. Estimate sustainable mortality rate for females 2+ from new demographic analyses	Use survival rates where animals with unresolved fates are censored at last contact	U	Y	N (this differs from 2007 protocol, in which mortality limit had built-in conservative feature because was based on a model suggesting <10% probability of decline; under proposed rate, expected probability of decline = 50%)
	All unaccompanied yearlings assumed dead	Slightly L (slightly conservative because more yearlings may have survived than estimated)	N	
	Use fecundity (m_x) adjusted for date of emergence	U (Note change from previous protocol where this was labeled 'L', i.e., conservative)	Y	
6. Use Cherry et al. (2002)	Estimate true number of deaths from documented deaths	Slightly L (slightly more deaths may have occurred than estimated because heterogeneity in data greater than accounted for in estimator; effect would lead to underestimating total mortality)	Y	N

6.2. Revision of area within which mortality limits apply

Under the existing protocol, grizzly bear mortality limits apply to the entire Conservation Strategy Management Area (U.S. Fish and Wildlife Service 2007*a*). All mortalities occurring within this area are counted and total mortality is estimated (Cherry et al. 2002) to assess whether mortality limits have been exceeded or if a Biology and Monitoring Review is necessary under the Conservation Strategy implementation protocol. As the bear population in the GYE has increased in size and geographic extent, an increasing proportion of these mortalities have occurred outside the Recovery Zone boundary (Fig. 6.2); many of these have occurred in areas of private land ownership where the team consensus is that permanent occupation by grizzly bears is biologically and socially inappropriate or unlikely. Many mortalities are occurring in peripheral areas where the potential to support future maintenance or growth of the GYE grizzly bear population is limited.
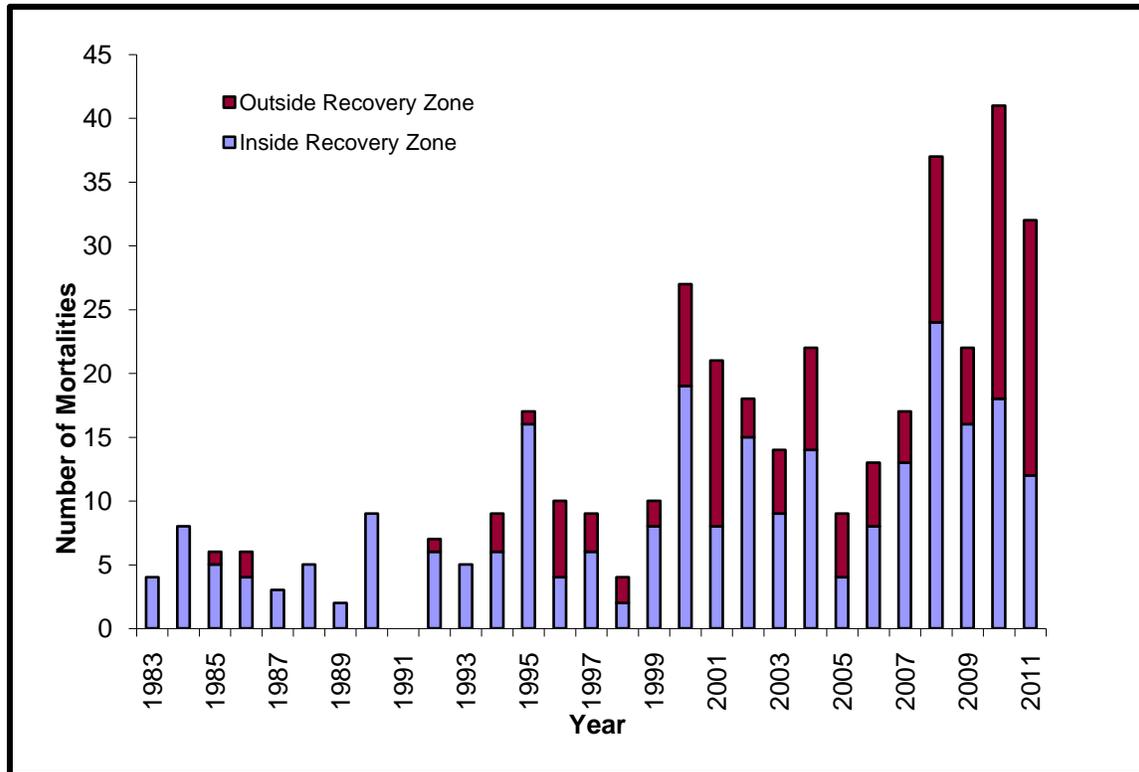
Figure 6.2. Number of mortalities of independent-aged grizzly bears inside and outside the Recovery Zone, Greater Yellowstone Ecosystem, 1983–2011.

In the grizzly bear recovery plan, the Recovery Zone (Fig. 6.3) is defined as the area "within which the population and habitat criteria for achievement of recovery will be measured" (U.S. Fish and Wildlife Service 1993:17). Whereas this may be true, maintenance of an increased bear population in numbers and distribution outside the Recovery Zone helps ensure long-term viability of this population. There is valuable habitat outside the Recovery Zone on public land, grizzly bears currently occur in many of these areas, and grizzly bears have a management future in these areas. Therefore, the

group agreed that mortalities occurring beyond the Recovery Zone boundary on these public lands should be subject to mortality management.

Figure 6.3. Greater Yellowstone Ecosystem, showing proposed boundary beyond which grizzly bear mortalities would not be counted against formalized mortality limits. This boundary is based on U.S. Fish and Wildlife Service Suitable Habitat designation (derived from ecoregions; U.S. Fish and Wildlife Service 2007b) and inclusion of narrow areas along valleys bounded mostly by suitable habitat that could act as potential mortality sinks (see text) for a total area of 49,928 km^2 . The purple line delimits the existing Recovery Zone (23,828 km^2) (termed the "Primary Conservation Area" in the conservation strategy), within which recovery criteria are required. Yellowstone National Park Boundary shown for reference only.
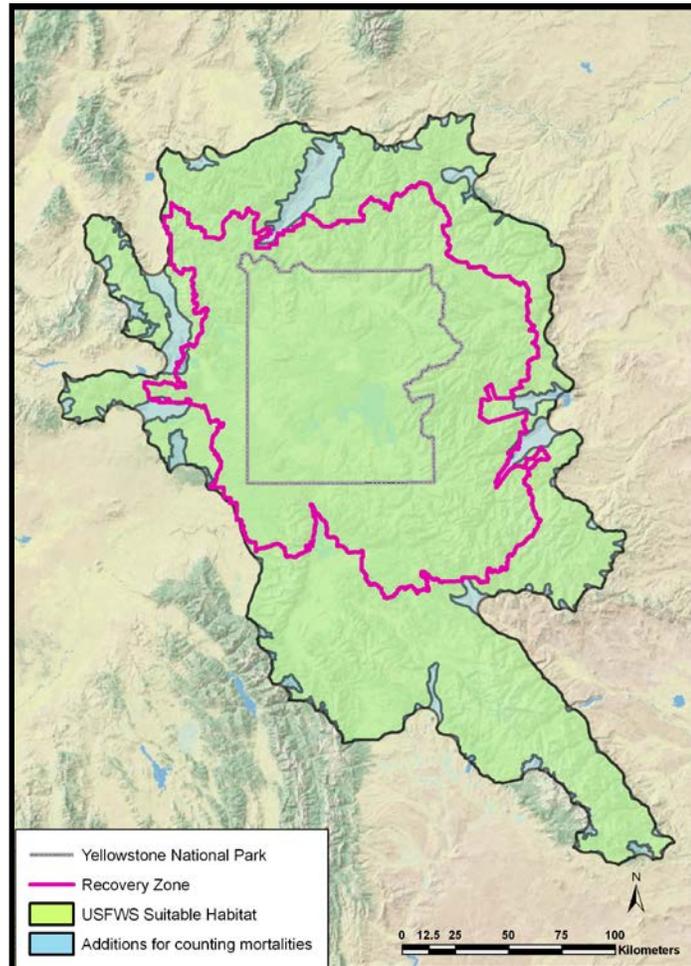
To achieve mortality management in the area appropriate to the long-term conservation of the Yellowstone population and to assure that the area of mortality management was the same as the area where the population estimates are made, the group considered using the boundary developed in 2007 by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 2007*b*) for what was termed "suitable habitat" as a reasonable way to define areas where mortality are managed (Fig. 6.3). There was general agreement that this suitable habitat boundary (enclosing a total area of 46,035 km^2) is sufficiently large to support a viable population in the long term, such that mortalities beyond it could be excluded from consideration. Importantly, this area closely resembles the area in which unique F_{COY} are surveyed and for which population size is estimated. This area is thus most appropriate for applying mortality limits. The study team noted, however, that because the suitable habitat boundary was drawn using mountainous ecoregions, there were narrow, linear areas along valley floors that did not meet the definition of suitable habitat and where population sinks may be created. This phenomenon, in which the quantity and quality of suitable habitat is diminished because of interactions with surrounding, less suitable habitat, is known as an "edge effect" (Lande 1988, Yahner

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1988, Mills 1995). Edge effects are exacerbated in small habitat patches with high perimeter-to-area ratios (i.e., those that are long and narrow) and in wide-ranging species such as grizzly bears because they are more likely to encounter surrounding, unsuitable habitat (Woodroffe and Ginsberg 1998:2126). Mortalities in these areas would be outside suitable habitat but could have disproportionate effects on the population generally contained within the suitable habitat zone, potentially acting as mortality sinks. The study team recommends considering an alternative boundary that includes these narrow areas outside suitable habitat, but largely bounded by it (Fig. 6.3). During 2002–2011, 25 of 225 mortalities (11%) of independent-aged bears occurred outside the boundary of this composite area (Fig. 6.4). An additional issue with the U.S. Fish and Wildlife Service suitable habitat line was that the Recovery Zone occurs outside it in several small areas. This issue can be resolved by using suitable habitat plus the potential sink areas for a boundary that has the greater extent The so altered suitable habitat boundary plus potential sink areas would contain approximately 49,928 km^2 (see Fig. 6.4)

Figure 6.4. Known and probable mortalities of independent grizzly bears (2 years or older) during 2002– 2011 (n = 225) and their occurrence relative to the U.S. Fish and Wildlife Service Suitable Habitat designation (U.S. Fish and Wildlife Service 2007b), Greater Yellowstone Ecosystem. Recommended alternative boundary includes narrow areas bordered mostly by suitable habitat that can potentially function as mortality sinks (blue polygons). Of 225 mortalities of independent-aged bears during this period, 25 occurred outside the modified suitable habitat line (9 females, 16 males). The Recovery Zone (termed the "Primary Conservation Area" in the conservation strategy) represents the area within which recovery criteria are required. Yellowstone National Park Boundary shown for reference only.
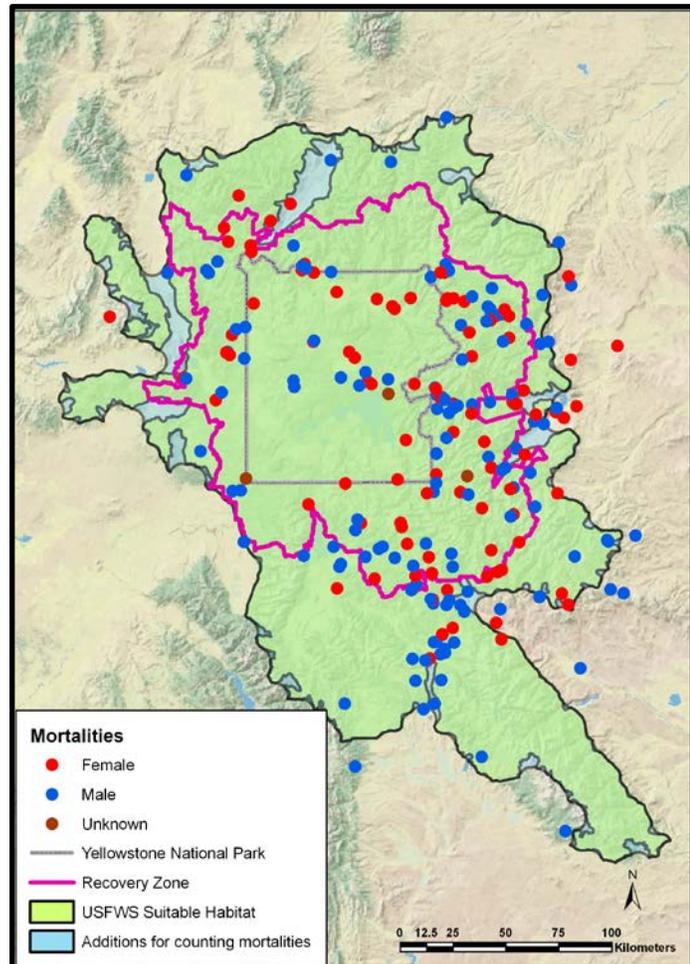
6.3. Alternatives considered but not recommended

6.3.1. Use rates leading to sustainability other than those suggested from demographic analyses

In response to several managers who expressed a desire for more flexibility in handling conflict bears, the group considered whether higher mortality limits (e.g., >9% for independent females) could be justified. Several members noted that, despite occasionally exceeding the mortality limits, the GYE population steadily increased from 1983 until the recent (2002–2011) stagnation of population growth. They also noted the 9% mortality limit incorporates a number of conservative decision points within the protocol (Table 1.1), and that even under the current situation of lower population growth, adult female survival remains high. Following presentation of the provisional demographic analyses from 2002–2011 (summarized in Section 4), this alternative was not pursued further.

6.3.2. Discount mortalities for individuals in some way that reflects their value to future population growth

Similarly (see section 6.3.1.), the group initially considered the suggestion that, because some sex-age classes of grizzly bears are known to exert much less influence on population trajectory than others, mortality quotas might reasonably be varied to reflect these. Analyses could potentially be pursued using either elasticities (from Leslie matrices) or reproductive values (from life-table analyses). The group elected not to pursue this possibility because of the complexity of implementing variable mortality limits based on age and sex.

Report Preparation

We prepared this report to document our review, discussions, and recommendations. We further recommend that results contained here be presented to state and federal managers for discussion, modification, and acceptance and to the general public for comment. Once this task is complete, we also recommend that these methods be presented to the Yellowstone Ecosystem Subcommittee of the Interagency Grizzly Bear Committee for endorsement.

Literature Cited

BJORNLIE, D., and M. A. HAROLDSON. 2011. Grizzly bear use of insect aggregation sites documented from aerial telemetry and observation. Pages 33–35 *in* C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team, 2010. U.S. Geological Survey, Bozeman, Montana, USA.

BOWDEN, D. C., AND R. C. KUFELD. 1995. Generalized mark-sight population-size estimation applied to Colorado moose. Journal of Wildlife Management 59:840–851.

BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

CHAO, A. 1989. Estimating population size for sparse data in capture–recapture experiments. Biometrics 45:427–438.

CHERRY, S., M. A. HAROLDSON, J. ROBISON-COX, AND C. C. SCHWARTZ. 2002. Estimating total human-caused mortality from reported mortality using data from radio-instrumented grizzly bears. Ursus 13:175–184.

CHERRY, S., G. C. WHITE, K. A. KEATING, M. A. HAROLDSON, AND C. C. SCHWARTZ. 2007. Evaluating estimators of the number of females with cubs-of-the-year in the Yellowstone grizzly bear population. Journal of Agricultural, Biological, and Environmental Statistics 12:195–215.

CLARK, J. D., R. EASTRIDGE, AND M. J. HOOKER. 2010. Effects exploitation on black bear populations at White River National Wildlife Refuge. Journal of Wildlife Management 74:1448–1456.

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.

EBERHARDT, L.L., AND R. R. KNIGHT. 1996. How many grizzlies in Yellowstone? Journal of Wildlife Management 60:416–421.

GARSHELIS, D. L., and K. V. NOYCE. 2006. Discerning biases in a large scale mark-recapture population estimate for black bears. Journal of Wildlife Management 70(6):1634–1643.

GARSHELIS, D. L., and L. G. VISSER. 1997. Enumerating megapopulations of wild bears with an ingested biomarker. Journal of Wildlife Management 61(2):466–480.

GOVE, N. E., J. R. SKALSKI, P. ZAGER, AND R. L. TOWNSEND. 2002. Statistical models for population reconstruction using age-at-harvest data. Journal of Wildlife Management 66:310–320.

HAROLDSON, M. A. 2012. Assessing trend and estimating population size from counts of unduplicated females. Pages 10–15 *in* C. C. Schwartz, M. A. Haroldson, and K. West, editors. Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team 2011. U.S. Geological Survey, Bozeman, Montana, USA.

HAROLDSON, M. A., C. C. SCHWARTZ, AND G. C. WHITE. 2006. Survival of independent grizzly bear in the Greater Yellowstone Ecosystem, 1983–2001. *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. 1984. Harvest age structure as an indicator of grizzly bear population status. Thesis, University of Montana, Missoula, Montana, USA.

HARRIS, R. B. 1986. Modeling sustainable harvest rates for grizzly bears. Appendix K *in* A. Dood, R. Brannon, and R. Mace, editors. The grizzly bear in northwestern Montana. Final programmatic environmental impact statement. Montana Department of Fish, Wildlife and Parks, Helena, Montana, USA. Unit Publication, Missoula, Montana, USA.

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. *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., G. C. WHITE, C. C. SCHWARTZ, AND M. A. HAROLDSON. 2007. Population growth of Yellowstone grizzly bears: uncertainty and future monitoring. Ursus 18: 167–177.

HIGGS, M., G. C. WHITE, M. A. HAROLDSON, AND D. J. BJORNLIE. Mark-resight analysis for female grizzly bears with cubs-of-the-year: sparse data and a latent multinomial model. Journal of Agricultural and Biological Statistics (in review).

INTERAGENCY CONSERVATION STRATEGY TEAM. 2007. Conservation Strategy for Grizzly Bears in the Greater Yellowstone. Working document, downloaded from http://www.fws.gov/mountain-prairie/species/mammals/grizzly/yellowstone.htm

INTERAGENCY GRIZZLY BEAR STUDY TEAM. 2005. Reassessing methods to estimate population size and sustainable mortality limits for the Yellowstone grizzly bear. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA. Downloaded from http://www.fws.gov/mountain-prairie/species/mammals/grizzly/yellowstone.htm

INTERAGENCY GRIZZLY BEAR STUDY TEAM. 2006. Reassessing methods to estimate population size and sustainable mortality limits for the Yellowstone grizzly bear: workshop document supplement. U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University. Downloaded from http://www.fws.gov/mountain-prairie/species/mammals/grizzly/yellowstone.htm

INTERAGENCY GRIZZLY BEAR STUDY TEAM. 2008. Reassessing methods to distinguish unique females with cubs-of-the-year in the Greater Yellowstone Ecosystem. Interagency Grizzly Bear Study Team, U.S. Geological Survey, Northern Rocky Mountain Science Center, Montana State University, Bozeman, Montana, USA.

KEATING, K. A., C. C. SCHWARTZ, M. A. HAROLDSON, AND D. MOODY. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. Ursus 13:161–174.

KENDALL, K. C., J. B. STETZ, J. BOULANGER, A. C. MACLEOD, D. PAETKAU, AND G. C. WHITE. 2009. Demography and genetic structure of a recovering grizzly bear population. Journal of Wildlife Management 73:3–17.

KNIGHT, R. R., B. M. BLANCHARD, AND L. L. EBERHARDT. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23:245–248.

LANDE, R. 1988. Genetics and demography in biological conservation. Science 241:1455–1460.

MACE, R. D., D. W. CARNEY, T. CHILTON-RADANDT, S. A. COURVILLE, M. A. HAROLDSON, R. B. HARRIS, J. JONKEL, M. MADEL, T. L. MANLEY, C. C. SCHWARTZ, C. SERVHEEN, J. S. WALLER, AND E. WENUM. 2012. Grizzly bear population vital rates and trend in the Northern Continental Divide Ecosystem, Montana. Journal of Wildlife Management 76:119–128.

MATTSON, D. M., C. M. GILLIN, S. A. BENSON, AND R. R. KNIGHT. 1991. Bear use of alpine insect aggregations in the Yellowstone ecosystem. Canadian Journal of Zoology 69:2430–2435.

McCLINTOCK, B. T., G. C. WHITE, M. F. ANTOLIN, AND D. W. TRIPP. 2009. Estimating abundance using mark-resight when sampling is with replacement or the number of marked individuals is unknown. Biometrics 65:237–246.

MILLER, S. D., G. C. WHITE, R. A. SELLERS, H. V. REYNOLDS, J. W. SCHOEN, K.TITUS,V. G. BARNES, R. B. SMITH, R. R. NELSON, W. B. BALLARD, AND C. C. SCHWARTZ. 1997. Brown and black bear density estimation in Alaska using radiotelemetry and replicate mark-resight techniques. Wildlife Monograph 133.

MILLS, L. S. 1995. Edge effects and isolation: red-backed voles on forest remnants. Conservation Biology 9:395–403.

PAULIK, G. J. 1963. Estimates of mortality rates from tag recoveries. Biometries 19:28–57.

RICE, W. R., AND J. D. HARDER. 1977. Application of multiple aerial sampling to a mark-recapture census of white-tailed deer. Journal of Wildlife Management 41:197–206.

SCHWARTZ, C. C. 1998. Evaluation of a capture-mark-recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 13–20 *in* C. C. Schwartz, and M. A. Haroldson, editors. Yellowstone Grizzly Bear Investigations: annual report of the Interagency Grizzly Bear Study Team, 1998. U.S. Geological Survey, Bozeman, Montana, USA.

SCHWARTZ, C. C. 1999. Evaluation of a capture-mark-recapture estimator to determine grizzly bear numbers and density in the Greater Yellowstone Area. Pages 15–18 *in* C. C. Schwartz, and M. A. Haroldson, editors. Yellowstone Grizzly Bear Investigations: annual report of the Interagency Grizzly Bear Study Team, 1999. U.S. Geological Survey, Bozeman, Montana, USA.

SCHWARTZ, C. C., R. B. HARRIS, AND M. A. HAROLDSON. 2006*a*. Impacts of spatial and environmental heterogeneity on grizzly bear demographics in the Greater Yellowstone Ecosystem: a source–sink dynamic with management consequences. *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, AND S. CHERRY. 2006*b*. Reproductive performance for grizzly bears in the Greater Yellowstone Ecosystem, 1983–2002. *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, S. CHERRY, AND K. A. KEATING. 2008. Evaluation of rules to distinguish unique female grizzly bears with cubs in Yellowstone. Journal of Wildlife Management 72:543–554.

SCHWARTZ, C. C., M. A. HAROLDSON, K. A. GUNTHER, AND D. MOODY. 2002. Distribution of grizzly bears in the Greater Yellowstone Ecosystem, 1990–2000. Ursus 13:203–212.

SCHWARTZ, C. C., M. A. HAROLDSON, K. A. GUNTHER, AND D. MOODY. 2006*c*. Distribution of grizzly bears in the Greater Yellowstone Ecosystem, 1990–2004. Ursus 17:63–66.

SCHWARTZ, C. C., M. A. HAROLDSON, AND G. C. WHITE. 2006*d*. Survival of cub and yearling grizzly bears in the Greater Yellowstone Ecosystem, 1983–2001. *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, G. C. WHITE, R. B. HARRIS, S. CHERRY, K. A. KEATING, D. MOODY, AND C. SERVHEEN. 2006*e*. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. Wildlife Monographs 161.

SCHWARTZ, C. C., AND G. C. WHITE. 2008. Estimating reproductive rates for female bears: proportions versus transition probabilities. Ursus 19:1–12.

U.S. FISH AND WILDLIFE SERVICE. 1993. Grizzly bear recovery plan. U.S. Fish and Wildlife Service, Missoula, Montana, USA. Available from: http://www.fws.gov/mountain-prairie/species/mammals/grizzly/Grizzly_bear_recovery_plan.pdf

U.S. FISH AND WILDLIFE SERVICE. 2007*a*. Grizzly Bear Recovery Plan supplement: revised demographic criteria for the Yellowstone Ecosystem. Federal Register 72:11377. Available from: http://www.fws.gov/mountain-prairie/species/mammals/grizzly/Grizzly_Bear_Recovery_Plan_Supplement_Demographic.pdf

U.S. FISH AND WILDLIFE SERVICE. 2007*b*. Grizzly bears; Yellowstone distinct population; Notice of petition finding; Final rule. Federal Register 72:14865. Available from: http://www.fws.gov/mountain-prairie/species/mammals/grizzly/FR_Final_YGB_rule_03292007.pdf

WHITE, G. C. 1996. NOREMARK: population estimation from mark–resighting surveys. Wildlife Society Bulletin 24:50–52.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:120–139.

WOODROFFE, R., AND J. R. GINSBERG. 1998. Edge effects and the extinction of populations inside protected areas. Science 280:2126–2128.

WOODS, J. G., D. PAETKAU, D. LEWIS, B. L. MCLELLAN, M. PROCTOR, AND C. STROBECK. 1999. Genetic tagging free-ranging black and brown bears. Wildlife Society Bulletin 27:616–627.

WRIGHT, J. A., R. J. BARKER, M. R. SCHOFIELD, A. C. FRANTZ, A. E. BYROM, and D. M. GLEESON. 2009. Incorporating genotype uncertainty into mark-recapture-type models for estimating abundance using DNA samples. Biometrics 65:833–840.

YAHNER, R. H. 1988. Changes in wildlife communities near edges. Conservation Biology 2: 333–339.

Appendix A

Summary of 'rule set' for identifying unique individual females with cubs-of-the-year (Knight et al. 1995)

Knight et al. (1995) developed a rule set used to distinguish sightings of unique females from repeated observations of the same female. Females were judged to be unique based on 3 criteria: (1) distance between sightings, (2) family group descriptions, and (3) dates of sightings. Minimum distance for 2 groups to be considered distinct was based on annual ranges, travel barriers, and typical movement patterns. A movement index was calculated using standard diameter of annual ranges (Harrison 1958) of all radiomarked F_{COY} were monitored 1 May–31 August (Blanchard and Knight 1991). The mean standard diameter for all annual ranges of F_{COY} was 15 km (SD = 6.7 km). They estimated the average maximum travel distance as twice the standard diameter, or 30 km, and used this distance to distinguish sightings of unique F_{COY} from repeat sightings of the same female.

Family groups within 30 km of each other were distinguished by other factors. The Grand Canyon of the Yellowstone, from the lower falls to the confluence of Deep Creek, was considered a natural barrier. Females on either side of this canyon were considered unique. Knight et al. (1995) also discussed paved highways as impediments to travel and cite data presented by Mattson et al. (1987), which showed that grizzlies tended to stay >500 m from roads during spring and >2 km during summer. They provided one example where 2 families considered unique were separated by 2 major highways and were <30 km apart (see Knight et al. 1995:Table 1). Family groups were also distinguished by size and number of cubs in the litter. Once a female with a specific number of cubs was sighted in an area, no other female with the same number of cubs in that same area was regarded as distinct unless (1) the 2 family groups were seen by the same observer on the same day, (2) the 2 family groups were seen by 2 observers at different locations but similar times on the same day, or (3) 1 or both of the females were radiomarked. Because of the possibility of cub mortality, no female with fewer cubs was considered distinct in an area unless (1) she was seen on the same day as the first female, (2) both were radiomarked, or (3) a subsequent observation of a female with a larger litter was made. Knight et al. (1995) assumed that all cubs in a litter were observed and correctly counted. This assumption was strengthened by only considering observations from qualified agency personnel. Observations from the air were only included if bears were in the open and easily observed. Ground observers watched family groups long enough to insure all cubs were seen; observers reported any doubt. Finally, Knight et al. (1995) reference a time-distance criteria but did not provide specific rules for its application. The only example they provided was the separation of 2 sightings of 2 family groups observed 1 day apart and 25 km apart.

This protocol was later criticized by Craighead et al. (1995) as unproven, and later by Mattson (1997), who pointed out ways in which the number of F_{COY} might be influenced by search effort or other annual factors unrelated to true abundance. Methods to identify

unique F_{COY} that are similar in spirit to Knight et al. (1995), if necessarily slightly different in the particular rule set, have also been applied in the Banff ecosystem of Alberta, Canada (Brodie and Gibeau 2007), and the Cantabrian Mountains of Spain (Palomero et al. 1997). Brodie and Gibeau (2007) pointed out, however, that estimates of population trend based on this approach were quite imprecise. The application of the approach to the Cantabrian Mountain grizzly bear population in Spain was also criticized for reasons similar to those articulated by Mattson (1997) by Fernández-Gil et al (2010; see also Palomero et al. 2010; Ordiz et al. 2007).

Schwartz et al. (2008) provided a detailed analysis of the behavior of the Knight et al. (1995) rule set in the Greater Yellowstone Ecosystem. These findings are discussed in the main body of this report.

Literature Cited (Appendix A)

BLANCHARD, B., AND R. KNIGHT. 1991. Movements of Yellowstone grizzly bears. Biological Conservation 58:41–67.

BRODIE, J. F., AND M. L. GIBEAU. 2007. Brown bear population trends from demographic and monitoring-based estimators. Ursus 18:137–144.

CRAIGHEAD, J. J., J. S. SUMNER, AND J. A. MITCHELL. 1995. The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem, 1959–1992. Island Press, Washington, D.C., USA.

FERNÁNDEZ-GIL, A., A. ORDIZ, AND J. NAVES. 2010. Are Cantabrian brown bears recovering? Ursus 21:121–124

HARRISON, J. L. 1958. Range of movement of some Malayan rats. Journal of Mammalogy 38:190–206.

KNIGHT, R. R., B. M. BLANCHARD, AND L. L. EBERHARDT. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23:245–248.

MATTSON, D. M. 1997. Sustainable grizzly bear mortality calculations from counts of females with cubs-of-the-year: an evaluation. Biological Conservation 81:103–111.

MATTSON, D. M., R. R. KNIGHT, AND B. M. BLANCHARD. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. International Conference on Bear Research and Management 7:259–273.

ORDIZ, A., J. NAVES, A. FERNANDEZ, D. HUBER, P. KACZENSKY, Y. MERTZANIS, A. MUSTONI, S. PALAZON, P. QUENETTE, G. RAUER, AND C. RODRIGUEZ. 2007. Distance-based criteria to identify minimum number of brown bear females with cubs in Europe. Ursus 18:157–166.

PALOMERO, G., F. BALLESTEROS, C. NORES, J. C. BLANCO, J. HERRERO, AND A. GARCÍA-SERRANO. 2007. Trends in number and distribution of brown bear females with cubs-of-the-year in the Cantabrian Mountains, Spain. Ursus 18:145–157.

PALOMERO, G., F. BALLESTEROS, C. NORES, J. C. BLANCO, J. HERRERO, AND A. GARCÍA-SERRANO. 2010. Are brown bears recovering in the Cantabrian Mountains? Reply to Fernández-Gil et al. Ursus 21:125–127

SCHWARTZ, C. C., M. A. HAROLDSON, S. CHERRY, AND K. A. KEATING. 2008. Evaluation of rules to distinguish unique female grizzly bears with cubs in Yellowstone. Journal of Wildlife Management, 72:543–554.

Appendix B

The ADR approach presented by Dr. Megan Higgs, Montana State University[a]

1. Logistic regression for classification of sightings of individual bears to identify correlates of multiple sightings being of a single individual.

Ancillary data resampling (ADR) approaches the problem of distinguishing unique F_{COY} by relying strictly on empirical data from GYE grizzly bears (in contrast to Knight et al. 1995 which used rules of thumb coarsely derived from those data). Similarly to Schwartz et al. (2008), the ADR approach uses radio-telemetry data from previously marked F_{COY} (both conventional VHF radio-collars and GPS collars) as the basis for all inference. A map of the GYE is "populated" with a "superpopulation" of bear locations. Each location is from a real bear and retains its spatial and temporal orientation with regard to other locations from the same bear, as well as information on litter size. Simulations then proceed from randomly selecting from the desired number of bears from this superpopulation.

The first stage of the ADR approach begins by using logistic regression to quantify the probability that any given two observations of unknown F_{COY} were of the same bear. Logistic regression is a well-known statistical approach to using a series of explanatory variables to describe or predict a phenomenon that exists on a binary scale. In this case, the phenomenon of interest is whether two sightings of F_{COY} are of the same animal or not. Working with Interagency Grizzly Bear Study Team biologists, Dr. Higgs identified the following variables as useful in predicting the probability of two sighting being of the same bear:
  1) distance between locations,
  2) whether the number of cubs was the same,
  3) if different, whether number of cubs and increased or decreased,
  4) whether both observations occurred during March–April,
  5) whether both observations occurred during May,
  4) whether both observations occurred during June,
  5) whether both observations occurred during July,
  6) whether both observations occurred during August,
  7) an interaction term between distance (variable 'a') and whether both observations were made during March–April (variable 'd'),
  8) a similar interaction term between variable 'a' and variable 'e',
  9) a similar interaction term between variable 'a' and variable 'f',
  10) interaction between 'a' and 'g',
  11) interaction between 'a' and 'h',
  12) an interaction term involving the distance between locations ('a') and whether the time interval between the 2 observations was <3 days;

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[a] A more technical and detailed description of this approach is available from Dr. Megan Higgs, Department of Mathematical Sciences, Montana State University, Bozeman, Montana.

13) an interaction term involving whether the number of cubs seen was the same ('b'), and whether the time interval between the 2 observations was < 3 days.

These predictor variables were all selected based on a prior knowledge of the data set consisting of many years of F_{COY} observations; all make intuitive sense and are similar conceptually to the variables used in the Knight et al. (1995) rule set. For example, it should be obvious that two observations from very distant locations are less likely to be of the same F_{COY} than of two different F_{COY}. Similarly, observations of F_{COY} with same number of cubs are more likely to be of a single bear than observations in which number of cubs differed (note, however, that cubs sometimes die, so an observation of a F_{COY} with *n* cubs could represent the same animal as a subsequent observation of a F_{COY} with *n*-1 or even *n*-2 cubs). Because F_{COY} move at different rates as the non-denning season progresses, the timing (i.e., month) of observations was also found to be a useful predictor. Exploratory data analyses also revealed that, whereas the time interval between observations was important, an important distinction could be made based on whether the intervals between observations was <3 days.

Various logistic regression models were developed based on a data set consisting of all pairwise comparisons of observations of known (e.g., radiomarked) F_{COY} during 1976–2003. The final model was that which minimized AIC. Coefficients for this predictive model are presented in Table 2. For example, the negative sign for distance (variable 'a') indicates that as distance between observation increased, probability of the F_{COY} being the same animal decreased; the positive sign for litter size being the same indicates that, when true, it was more likely that the observations were of a single animal than when false. The strongly negative coefficient for litter size increasing with time reflects the implausibility of litter size increasing with time. Some coefficients have signs (positive vs. negative) that are counter-intuitive because of the interactive effect of all when combined together (i.e., signs predicting the probability that 2 observations were of a single F_{COY} might have differed had they been entered into a single-variable model).

Using a logistic regression model to predict the probability that any 2 observations of unknown F_{COY} has the beneficial property of having been developed by objective, statistical methods, and being based on a large sample of known bears. It is useful in clarifying and quantifying relationships suspected to exist between correlates of observations and truth.

Table 2. Selected (best-fitting) logistic regression model of the probability that any 2 grizzly bear observations were from a single female with cubs-of-the-year (F_{COY}), based on radio-marked F_{COY} monitored in the Greater Yellowstone Ecosystem, 1976–2003. Standard errors of slopes are not shown because they were developed from non-independent data, and because they were not used in the resulting clustering algorithm.

Variable label and description	Parameter estimate
a Distance between locations	−0.143
b Whether number of cubs same	3.356
c Whether number of cubs and increased	−4.514
d Whether both observations occurred during March–April	0.744
e Whether both observations occurred during May	0.921
f Whether both observations occurred during June	0.786
g Whether both observations occurred during July	0.001
h Whether both observations occurred during August	−0.196
i Interaction: a X d	−0.191
j Interaction: a X e	−0.147
k Interaction: a X f	−0.080
l Interaction: a X g	−0.032
m Interaction: a X h	−0.009
n Interaction: a X time interval between observations <3 days	−0.163
o Interaction: b X time interval between observations <3 days	2.218

2. Choosing optimal cut-off values for the probability of being same bear for that number of observations

Unfortunately, even the best-fitting logistic regression model only gets us part-way to the desired end-point. This is because it provides only a *probability* of two observations being of the same individual F_{COY}, whereas what we require is a *classification* algorithm; i.e., one that "decides", for each observation of a F_{COY}, whether it should be considered to represent a unique individual or not.

Thus, the next step in the ADR procedure is an algorithm that aggregates observations of F_{COY} into clusters representing sightings of the same animal, using the predicted probabilities generated from the logistic regression model (each pair of observations of F_{COY} is associated with the series of variables required by the logistic regression model and summarized in Table 2). The clustering itself is briefly described in the next section, and depends on selection of a cut-off value along the probability scale (0,1) to move from quantifying to categorizing. To retain constant bias (or lack thereof) across the range of number of Fcoy sighted, the cut-off value must change as the number of unique animals sighted changes. For example, the figure similar to Fig. 3.1 would require a different cut-off value for each value on the x-axis. Thus, through the cut-off specification determined through simulation, the method attempts to solve the bias problem of the rule set shown in Fig. 3.1.

The algorithm calls for finding cut-off values to minimize bias in identifying unique F_{COY} over the range of plausible values of the number of F_{COY} observations each year

(which will be known) and the true number of F_{COY} present (which will be unknown). That is, cut-off values are selected so that the median of the distribution of the number of unique F_{COY} observed based on the sequential clustering algorithm is equal to the number known (from the telemetry data) to have been observed.

3. Clustering algorithm

Dr. Higgs concluded that a sequential clustering algorithm was both the simpler computationally and closer to the way data are actually accumulated than algorithms that attempt to find the most likely clusters from all possible groupings of that year's F_{COY} observations. Thus, the algorithm begins with the first observation of F_{COY} in that year, and considers this known. The 2nd observation is taken in chronological order, the coefficients from Table 2 applied to the pair of observations to calculate a probability of the 2nd observation being the same F_{COY} as the 1st observation; it is classified as either the same or a unique F_{COY}, based on a comparison of the cut-off value with this probability. This process continues chronologically, observation by observation. Where a cluster of >1 observations has been identified by the algorithm, probabilities of the new observation are calculated for each observation within the cluster, and the mean of those probabilities is taken as the value for that cluster. The cut-off value is then used to classify the new observation as either a unique bear, or, if not unique, as belonging to the cluster with the highest probability.

4. Quantifying uncertainty in the estimate of minimum number sighted using re-sampling from historic data.

To quantify uncertainty in the estimate (obtain a posterior distribution) of the minimum number sighted, Dr. Higgs used a Monte Carlo re-sampling approach modeled after the work in Schwartz et al. (2008) that initially demonstrated and quantified the low bias in the previously used methods. For many re-samples under a known true number of sighted animals, the sequential clustering algorithm is applied to obtain a distribution of estimates that can then be compared with the true value. Dr. Higgs presented the group with evidence that, based on simulations analogous to those conducted in Schwartz et al. (2008) showing the low bias of the previous method, this procedure is capable of predicting an unbiased distribution of F_{COY} present from sets of unidentified F_{COY} observations, over the true range of F_{COY} 10 to 100. Using the superpopulation of bears previously developed by Schwartz et al. (2008) from radio-marked bears as a reasonable approximation to the GYE situation and cut-off values optimized to reduce bias, the ADR procedure produced clusters that, on balance, replicated the number of F_{COY} known to be present.

5. Repeat for different maps (because true density or distribution are not known)

Had this had been all that was required, the group consensus might well have been that this approach provided a convincing and defendable alternative to estimating minimum number of F_{COY} sighted in a year as an alternative to the Knight et al. (1995) rule set. Unfortunately, all inference (i.e., moving from unknown F_{COY} observations to unbiased

number of F_{COY} clusters representing the number of unique F_{COY} observed) depended on the particular "superpopulation" of bears that served as the basis for simulations. Although bear locations came from real bears and each retained known spatial and temporal associations with other locations from the same real bear, the group identified additional areas in which a single, GYE superpopulation, such as used by Schwartz et al. (2008) might fail to reflect reality:

1) F_{COY} captured and marked for radiotracking (or GPS tracking) likely did not reflect an unbiased geographic distribution of all F_{COY} available for observation. This was relevant because the spatial orientation of observations is a critical part of the clustering procedure;

2) The process of relocating a bear using radio-telemetry or GPS collars (i.e., data underlying the likelihood function used in the clustering) may not accurately reflect the process of observing a bear visually. Visibility varies within the GYE, as functions both of vegetation and access to human eyes (relatively few telemetry relocations were associated with a visual observation of the F_{COY}). Even if only the subset of radio-locations were used on which a visual observation was made, this process may also differ from how observations unaided by telemetry are made.

Without knowing the true distribution of F_{COY} in the ecosystem, or how visible any might be given where it lived, the decision was made to develop 3 alternative models of distribution. Each would form the basis for alternative "superpopulations" of bears, which, in turn, would be the basis for the re-sampling that provided the foundation for quantifying uncertainty (obtaining posterior distributions) for minimum number of individuals sighted *and* Fcoy population size using the ADR method (discussed in Section 5):

1) *Uniform scenario.*—A rather uniform spatial distribution scenario, in which the GYE was populated by F_{COY} locations without regard to geography or to the spatial juxtaposition of observations made during 1997–2010 (this latter was developed by Mark Haroldson by applying fixed kernel density methods to non-telemetry observations of F_{COY} from both ground and aerial observers; this was initially labeled "medium" during the workshop). The implicit assumption here was that F_{COY} are distributed and can be observed relatively uniformly within the GYE, and that the irregularities in spatial configuration seen among radio-marked bears resulted from inability to capture bears equally throughout the system, or to monitor them once marked;

2) *Proportional sighting scenario.*—A rather peaked spatial distribution scenario, in which the GYE was populated by F_{COY} locations in a way that followed the spatial distribution suggested by historic sightings of Fcoy without the aid of telemetry (this was initially labeled "high" during the workshop). In other words, this represents the situation where Fcoy have greater density in areas where they are most often sighted. This is thought to be plausible because of associations between habitat type and sightability;

3) *Inverse sighting scenario.*—An inversely concentrated spatial distribution scenario, in which F_{COY} locations were deliberately concentrated in areas where relatively few had actually been observed (this was initially labeled "low" during the workshop).

Note that each scenario was built relative to a spatial distribution of historic F_{COY} observations, but this distribution was itself an unknown mixture of true F_{COY} distribution and detection probability given true presence (which itself was likely a function of vegetation cover and human density in the area).

6. Estimate the number of F_{COY} actually present from those estimated to have been observed using ancillary data resampling (ADR).
As described in the section on the Knight et al. (1995) rule set, we need to be able to estimate the Fcoy population size in any year, not merely the number seen (to avoid yearly heterogeneity caused by variable sighting effort and conditions, i.e., Mattson 1997, others). The current algorithm does this by way of a frequency-of-capture approach (Chao2; see Keating et al. 2002, Cherry et al. 2007). The ADR approach avoids the 2-step nature of this process by directly estimating the number of F_{COY} actually present (i.e., accounting for those never seen in any given year) in a hierarchical Bayesian framework that simultaneously assesses the posterior distribution of F_{COY} observed and those truly present. In any case, these relationships will depend on the assumed spatial juxtaposition of F_{COY}, and thus will vary depending on which of the underlying scenarios is used to develop it. Because 3 different scenarios (i.e., superpopulations) were developed, 3 slightly different versions of the model are considered.

7. Preliminary tests of the ADR approach
It was deemed appropriate to test how the method would perform using data generated under a model different from the one being fit (i.e. supposing the assumed superpopulation describing the spatial distribution is incorrect). During the July 2011 meetings, Dr. Higgs presented the preliminary results of the method when applied to the 3 alternative "superpopulations" of bears from which samples were taken. Each superpopulation reflected an alternative hypothesis about the true spatial distribution of F_{COY} (not just those observed) within the GYE relative to distribution evident from only radio-marked bears.[a] Simulation provides an easy and intuitive way to evaluate the performance of the models under known data-generating models. With 3 models specifying the possible relationships among the known and unknown factors, and 3 sampling scenarios, we had 9 sets of simulation results to examine for any given postulated true number of F_{COY} in the population.

Results of these simulations yielded the following conclusions:

1) Bias in the predicted number of F_{COY} observed was negligible when sampling from the same scenario as the model used to develop it, except when the distribution was based on the high scenario, in which case it was always biased low, by about 8–10%.

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[a] In all 3 scenarios, locations of F_{COY} marked using conventional VHF telemetry collars were retained in their original spatial positions. Because F_{COY} marked using GPS collars had many more locations from which to sample, these locations were the ones that were used to "fill-out" the superpopulations, and were placed on the landscape according to an algorithm that objectively reflected the assumptions of each scenario.

2) Widths of approximate 95% credibility intervals of the means of posterior distributions of observed F_{COY} were 11 to 13% of the mean when population size was small, and 7 to 11% of the mean when population size was large;

3) Bias in the predicted number of F_{COY} actually present was rather large and depended greatly on the data underlying the model generation and the scenario used for data sampling under the ADR. For example, when applying a model developed under the proportional sighting scenario to data sampled using the inverse sighting scenario (Table 6, first line), bias was about -23%; when applying a model developed under the inverse sighting scenario to data sampled using the uniform scenario, bias was +31%. We note that the inverse sighting scenario was chosen to assess the influence of an extreme superpopulation. Therefore, these estimates of bias are likely exaggerated.

4) Widths of approximate 95% credibility intervals of the means of posterior distributions of estimated F_{COY} actually present were large, often exceeding 100% of the true number. For example, when the true number of F_{COY} was 55, and the model using the uniform scenario was applied to samples selected from the inverse sighting scenario, the 95% credibility interval of the number of F_{COY} predicted, although almost unbiased, ranged from 38 to almost 78.

We have no way of knowing which of the scenarios used to develop the superpopulations was close to the true superpopulation and, in fact, do not know if a different scenario altogether may be more representative of the true superpopulation. Therefore, we have no way of choosing among the models or superpopulations for resampling. Although the method was shown to be potentially unbiased and to track population trends reliably when applied to a single hypothetical map (e.g., that produced by Schwartz et al. 2008), it was not consistently unbiased nor precise when applied to an array of data that represented hypotheses we felt must be considered given our uncertainty about the true spatial distribution of F_{COY} on the GYE landscape.

Literature Cited (Appendix B)

CHERRY, S., G. C. WHITE, K. A. KEATING, M. A. HAROLDSON, AND C. C. SCHWARTZ. 2007. Evaluating estimators of the number of females with cubs-of-the-year in the Yellowstone grizzly bear population. Journal of Agricultural, Biological, and Environmental Statistics 12:195–215.

KEATING, K. A., C. C. SCHWARTZ, M. A. HAROLDSON, AND D. MOODY. 2002. Estimating numbers of females with cubs-of-the-year in the Yellowstone grizzly bear population. Ursus 13:161–174.

KNIGHT, R. R., B. M. BLANCHARD, AND L. L. EBERHARDT. 1995. Appraising status of the Yellowstone grizzly bear population by counting females with cubs-of-the-year. Wildlife Society Bulletin 23:245–248.

MATTSON, D. M. 1997. Sustainable grizzly bear mortality calculations from counts of females with cubs-of-the-year: an evaluation. Biological Conservation 81:103–111.

SCHWARTZ, C. C., M. A. HAROLDSON, S. CHERRY, AND K. A. KEATING. 2008. Evaluation of rules to distinguish unique female grizzly bears with cubs in Yellowstone. Journal of Wildlife Management, 72:543–554.

Appendix C

Counts of known and probable mortalities by categories for independent aged female grizzly bears under alternative count lines, Greater Yellowstone Ecosystem, 1986–2010. Sustainability is set at 9% of the estimated population size for independent-aged females.

Year	Inside USFWS suitable habitat (proposed)				Inside USFWS conservation management area (current)				Difference (proposed - current)
	Sanctioned removal	Radioed	Reported	Total	Sanctioned removal	Radioed	Reported	Total	
1986	1	2	1	4	1	2	1	4	0
1987	1	0	1	2	1	0	1	2	0
1988	0	1	0	1	0	1	0	1	0
1989	0	0	0	0	0	0	0	0	0
1990	1	2	3	6	1	2	3	6	0
1991	0	0	0	0	0	0	0	0	0
1992	0	1	0	1	0	1	0	1	0
1993	0	1	2	3	0	1	2	3	0
1994	0	2	1	3	0	2	1	3	0
1995	3	0	5	8	3	0	5	8	0
1996	1	1	2	4	1	1	2	4	0
1997	0	0	3	3	0	0	3	3	0
1998	0	0	1	1	0	0	1	1	0
1999	0	0	1	1	0	0	1	1	0
2000	0	1	6	7	1	1	6	8	-1
2001	2	3	1	6	5	3	1	9	-3
2002	2	2	4	8	2	2	4	8	0
2003	0	0	5	5	0	0	5	5	0
2004	3	1	5	9	4	1	5	10	-1
2005	0	0	2	2	0	0	2	2	0
2006	0	1	1	2	1	1	1	3	-1
2007	3	2	6	11	3	2	6	11	0
2008	3	1	10	14	3	1	10	14	0
2009	0	3	6	9	0	2	7	9	0
2010	3	2	5	10	6	2	5	13	-3
Total	23	26	71	120	32	25	72	129	-9

Appendix D

Counts of known and probable mortalities by categories for independent aged male grizzly bears under alternative count lines, Greater Yellowstone Ecosystem, 1986–2010. Sustainability is set at 15% of the estimated population size for independent-aged males.

Year	Inside USFWS suitable habitat (proposed)				Inside USFWS conservation management area (current)				Difference (proposed - current)
	Sanctioned removal	Radioed	Reported	Total	Sanctioned removal	Radioed	Reported	Total	
1986	0	0	1	1	1	0	1	2	-1
1987	1	0	0	1	1	0	0	1	0
1988	2	1	1	4	2	1	1	4	0
1989	0	1	1	2	0	1	1	2	0
1990	0	1	2	3	0	1	2	3	0
1991	0	0	0	0	0	0	0	0	0
1992	0	5	1	6	0	5	1	6	0
1993	0	2	0	2	0	2	0	2	0
1994	4	1	1	6	4	1	1	6	0
1995	2	3	4	9	2	3	4	9	0
1996	2	0	2	4	2	1	3	6	-2
1997	1	1	3	5	1	1	4	6	-1
1998	0	1	0	1	2	1	0	3	-2
1999	2	2	5	9	2	2	5	9	0
2000	1	2	14	17	2	3	14	19	-2
2001	4	2	3	9	7	2	3	12	-3
2002	3	1	5	9	4	1	5	10	-1
2003	1	3	3	7	2	3	4	9	-2
2004	2	2	5	9	3	2	7	12	-3
2005	1	1	2	4	4	1	2	7	-3
2006	1	3	3	7	1	3	3	7	0
2007	1	1	4	6	2	1	4	7	-1
2008	6	5	11	22	7	5	11	23	-1
2009	2	3	5	10	3	2	6	11	-1
2010	8	1	11	20	11	2	13	26	-6
Total	44	42	87	173	63	44	95	202	-29

Appendix E

Yearly results for sustainability of independent females under the current 9% mortality limit (red horizontal line), Greater Yellowstone Ecosystem, 1986–2010. Independent female mortalities were exceeded in 3 years under current methods.
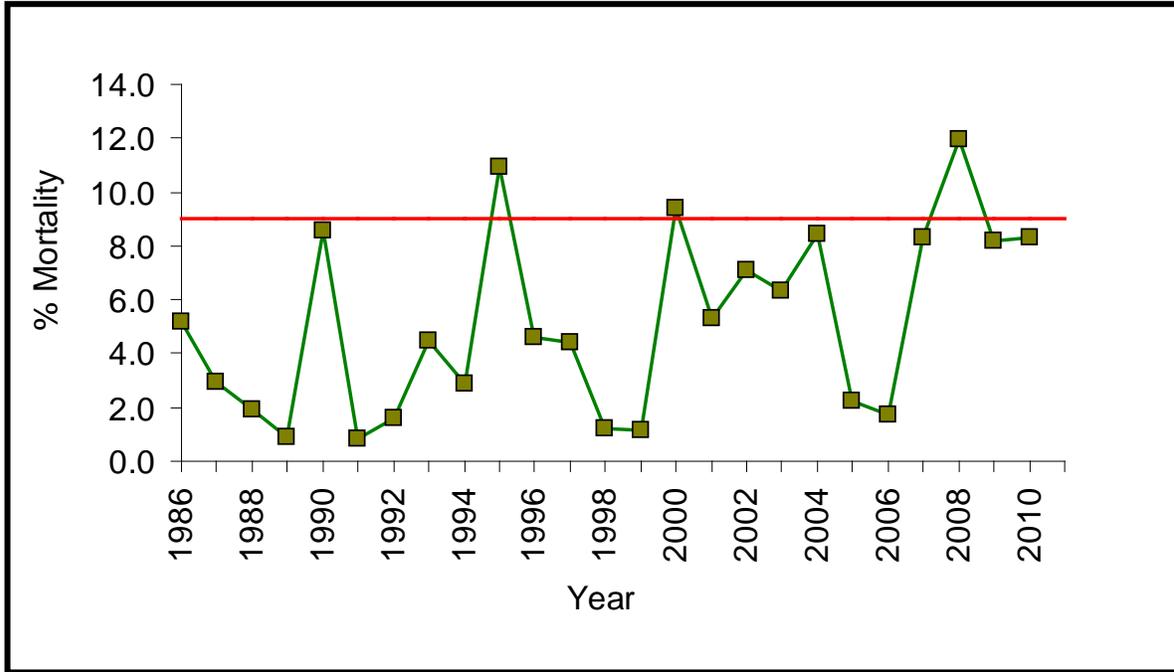
Appendix F

Yearly results for sustainability of independent males under the current 15% mortality limit (red horizontal line), Greater Yellowstone Ecosystem, 1986–2010. Independent male mortalities were exceeded in 6 years under current methods.