



Re-Evaluating Evidence for Past Population Trends and Predicted Dynamics of Yellowstone Grizzly Bears

Daniel F. Doak¹ & Kerry Cutler²

¹ Environmental Studies Program Attn. 215, University of Colorado, Boulder, CO 80309, USA

² Environmental Science, Policy & Management 130 Mulford Hall, UC Berkeley, Berkeley, CA 94720, USA

Keywords

Ursus; Chao estimator; count data; PVA; Yellowstone; senescence; grizzly bear.

Correspondence

Daniel F. Doak, Environmental Studies Program Attn. 215, University of Colorado, Boulder, CO 80309, USA.

Tel: 303-492-3665; fax: 303-492-5207.

E-mail: daniel.doak@colorado.edu

Received

10 March 2013

Accepted

7 June 2013

Editor

Andrew Knight

doi: 10.1111/conl.12048

Abstract

Sampling effort and demographic assumptions may powerfully shape conclusions about the status of endangered species. We re-examined data sets that suggest recent increases, and hence relative safety from future extinction, of the grizzly bear population inhabiting the Greater Yellowstone Ecosystem (GYE), one of the best studied large carnivore populations in the world. We find that inadequate attention to increasing observation effort and also to the life history characteristics of bears is likely to have substantially influenced past analyses of the population's trajectory. We conclude that the GYE grizzly has probably increased far less than generally believed, but also that past analyses have been too inaccurate to allow any firm conclusions about the dynamics or status of this population. The problems we illustrate here apply to many other threatened species and suggest the need for more careful consideration of observation processes that can shape our perceptions of species' history and status.

Introduction

Throughout the world, large predators have been disproportionately impacted by human land-use changes and direct persecution. In addition, many large predators are thought to be of particular importance in structuring their ecological communities (Terborgh & Estes 2010). Together, these patterns have generated a focus on the recovery and maintenance of predator populations. The grizzly bears (*Ursus arctos horribilis*) living in the Greater Yellowstone Ecosystem (GYE) form a small and isolated population of large carnivores, but is widely believed to have rebounded in numbers and to now be relatively safe from extinction. Partly because of its ecological importance, and partly because of the controversy surrounding efforts by the government to remove the population from protection under the U.S. Endangered Species Act (and efforts by other groups to oppose this decision), the Yellowstone grizzly population has been the focus of intense scientific study for over 40 years, with efforts to delist the population dating back to 1999 (Wilkinson 1998; Primm

& Murray 2005), and continuing to the present (in 2011 a federal judge rejected the latest delisting attempt).

Here, we examine the evidence that this population has been increasing in numbers and is relatively safe from extinction. In particular, we re-examine the use of two data sets at the core of the arguments about the population's status, past and present: demographic rate estimates from 1983 to 2001, and relative density estimates from 1973 to the present. The second of these two data sets is one of the most commonly used examples in the literature on count-based population viability analysis (e.g., Dennis *et al.* 1991; Dennis & Taper 1994; Morris & Doak 2002; Lindley 2003; Buonaccorsi & Staudenmayer 2009).

Our results cast doubt on the assertion that this population underwent a sharp increase from 1980 to 1995 and has recently stabilized in numbers, or even continued to increase (Harris *et al.* 2007, Eberhardt & Breiwick 2010). Beyond addressing the status of this population, our results illustrate how shifts in the observation process can alter the perception of population viability and risk. As

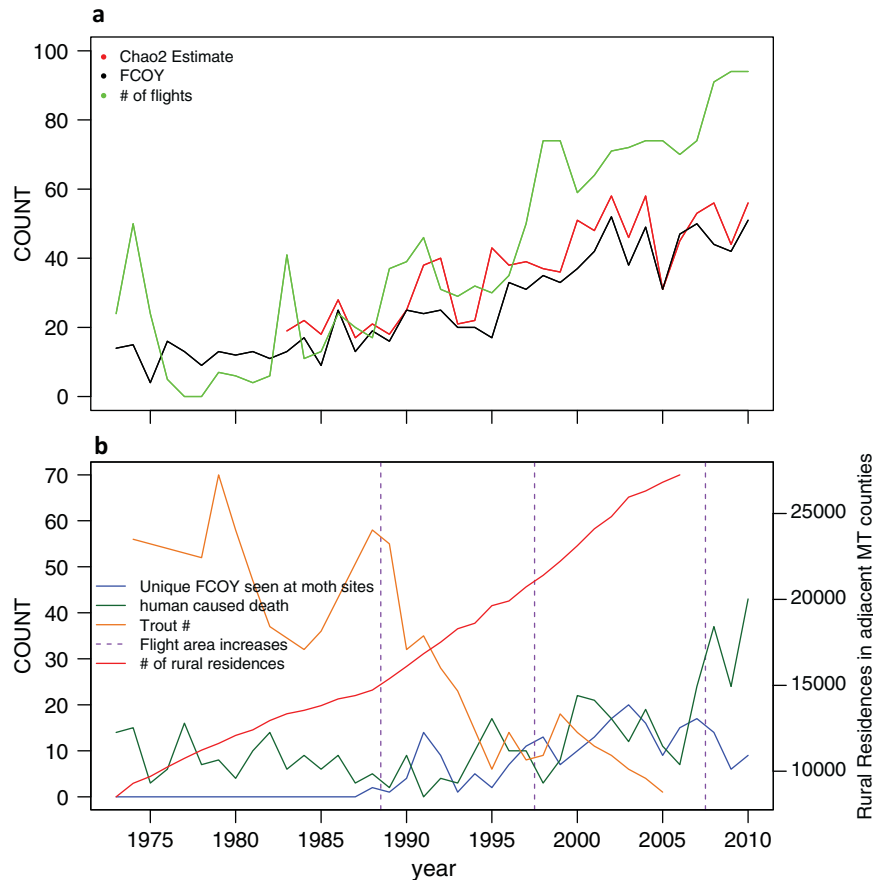


Figure 1 Trends in bear sightings and several important variables influencing observations as well as population dynamics. (A) Numbers of unduplicated females with cubs of the year (Fcoy), Chao2 estimates based on the Fcoy numbers, and the number of observation flights flown to spot bears each year. (B) Trends in the numbers of Fcoy seen at moth sites, known human-caused bear mortalities, the number of rural residences in the GYE (Gude *et al.* 2006), and the number of migrating cutthroat trout at Clear Creek (count $\times 10^3$, Koel *et al.* 2005). Shifts in the flight search areas are also indicated.

species become rare, or are proposed to be recovered, it is common for formal and informal observation effort to change substantially, and our results caution that unless these changes are carefully analyzed (e.g., Boyd 2010; Kery *et al.* 2010; Senyatso *et al.* 2013), they can result in substantial misunderstanding of a population's history and hence safety from future extirpation.

Background

Over the last 50 years, many changes have taken place in the GYE that are likely to influence grizzly populations and multiple shifts in the knowledge and monitoring of grizzlies have also occurred. Some of these changes are illustrated in Figure 1 (also see Appendix S1). The changes most likely to influence our study questions are increasing effort searching for bears each year, increasing bear use of feeding sites where they are easily seen, as

well as human recognition of these sites (in particular, high-elevation moth aggregations, which have been increasingly used by bears since 1981 and were first recognized as feeding sites in 1986; Mattson *et al.* 1991), and three trends almost certain to negatively impact bears: loss of trout runs, ongoing collapse of white-bark pines (both important food sources), and increasing rural development.

Virtually, all data on the dynamics of the GYE population come from the ongoing work of the Interagency Grizzly Bear Study Team (IGBST). The first data set we consider comprises annual estimates of minimum population numbers, used to infer trends in population size. These surveys, which estimate unique (= "unduplicated") females with cubs of the year (Fcoy), were initiated in 1973 and are ongoing. Grizzlies do not reproduce every year and thus on average Fcoy represents $\sim 33\%$ of all adult females and $\sim 27\%$ of the entire bear

population (Eberhardt & Knight 1996). Several factors could complicate interpretation of these population estimates (Mattson 1997; Boyce *et al.* 2001; Keating *et al.* 2002; Cherry *et al.* 2007). Key among these are: increases in standardized sampling effort over time (Figure 1); the use of both standardized and nonstandardized sampling to estimate F_{coy} each year; increasing knowledge of places with high sightability of bears; changing food and habitat use patterns; and the shifting range of bears and also of search effort (see Appendix S1 for more on these issues).

Recognizing that there are multiple problems with F_{coy} as an estimator of relative population size, the IGBST has more recently used the Chao2 estimator (Chao 1989; Wilson & Collins 1992; Keating *et al.* 2002; Cherry *et al.* 2007). Chao2 is one of a widely used family of population size (or species richness) estimators that use the frequencies of observations (how many times each individual is seen within a sampling period) to estimate unobserved individuals. Chao2 uses the relative frequencies of F_{coy} seen once versus twice in a season to estimate the numbers of F_{coy} present but not observed. While Chao2 was adopted in response to concerns that differences in sightability of bears, as well as variation in observation effort, were affecting F_{coy} estimates, it is nonetheless sensitive to heterogeneity in sighting probabilities, as well as the amount of effort that is expended for the observation process each year (Keating *et al.* 2002; Cherry *et al.* 2007). Nonetheless, even the most recent IGBST analyses (IGBST 2012), which suggest moving away from the Chao2 estimator, do not question the history of population growth that is based on the F_{coy} and Chao2 metrics.

The second major data set relevant to our questions are estimates of demographic rates. Since the 1970s, the IGBST has been collaring bears to estimate the vital rates of the population. These include age of first reproduction, litter size, breeding probability, interbirth interval, and survival of different age and sex classes in the population. The IGBST has used these estimates for deterministic calculations of the GYE grizzly bear population growth rate (e.g., Harris *et al.* 2007), arriving at annual population growth rates as high or higher than those indicated by trends in F_{coy} and Chao2.

Methods and results

Relative population size estimates

A key potential failure of the Chao2 estimator as an accurate representation of relative population sizes through time results from the changing intensity of observation effort, and potential changes in the sightability of bears due to dietary shifts and a nonrandom search regimen. Of particular concern, is the confounding of observa-

tion effort and estimated bear numbers (Figure 1). The correlation between observation hours and F_{coy} is high ($r^2 = 0.717$; Figure 2A), suggesting that the apparent rise in bear numbers could be a direct consequence of increased sampling effort (and also, potentially, increasing efficacy of observation, as noted above; see also Boyce *et al.* 2001). At the same time, the ratio of Chao2 to F_{coy} has remained steady over time, suggesting that this estimator may not successfully correct for shifts in observation effort or other changes (Figure 2B).

We conducted several simulations to explore the performance of Chao2 and in particular to determine whether it can provide accurate assessments of population trends with shifting observation and sightability parameters. These simulations are similar to those conducted by Keating *et al.* (2002) and Cherry *et al.* (2007), but we take a more mechanistic approach that explicitly simulates the observation process, based on a distribution of sightabilities of F_{coy} . These P_{obs} values, the probabilities of a bear being seen per hour of observation, can be characterized by a beta distribution. We obtain our baseline estimates of this distribution from the data in Keating *et al.*'s (2002) Table 5, which shows the full frequency distribution of sightings over 16 years, and the number of observation flight hours per year. Using MCMC methods and assuming that the observed frequencies follow a censored beta distribution, we obtained maximum likelihood estimates of the beta parameters a and b (0.4416015 and 50.40902), resulting in a mean hourly sightability of 0.00868429 observations/hour, and a CV in sightability of 1.483754 (code used for this and all other analyses is included in Appendix S1). This mean and CV are similar to those used by simulations by Keating *et al.* (2002) and Cherry *et al.* (2007). While these estimates can only be made for the quantified search effort and cannot be viewed as definitive (Link 2003), they should give a reasonable estimate of the total probability of sighting a bear if quantified search effort is related to total probability of a sighting, as it appears to be (Figure 2).

Next, we simulated different scenarios of changing or constant observation effort, sightability parameters, and actual bear numbers, generating series of F_{coy} and Chao2 estimates to compare with the observed values in these estimators over time. First, with the population held constant at $n = 50$, we varied the CV of sightabilities, while holding mean sightability constant (Figure 3a). The Chao2 estimator is positively related to the CV of sightability, and is actually more sensitive to changing variance in sightability than are F_{coy} values. This sensitivity persists over a range of population sizes (Figure 3b). We conducted similar analyses for mean sightabilities: Chao2 estimates also rise as the mean sightability of bears increases (Figure 4).

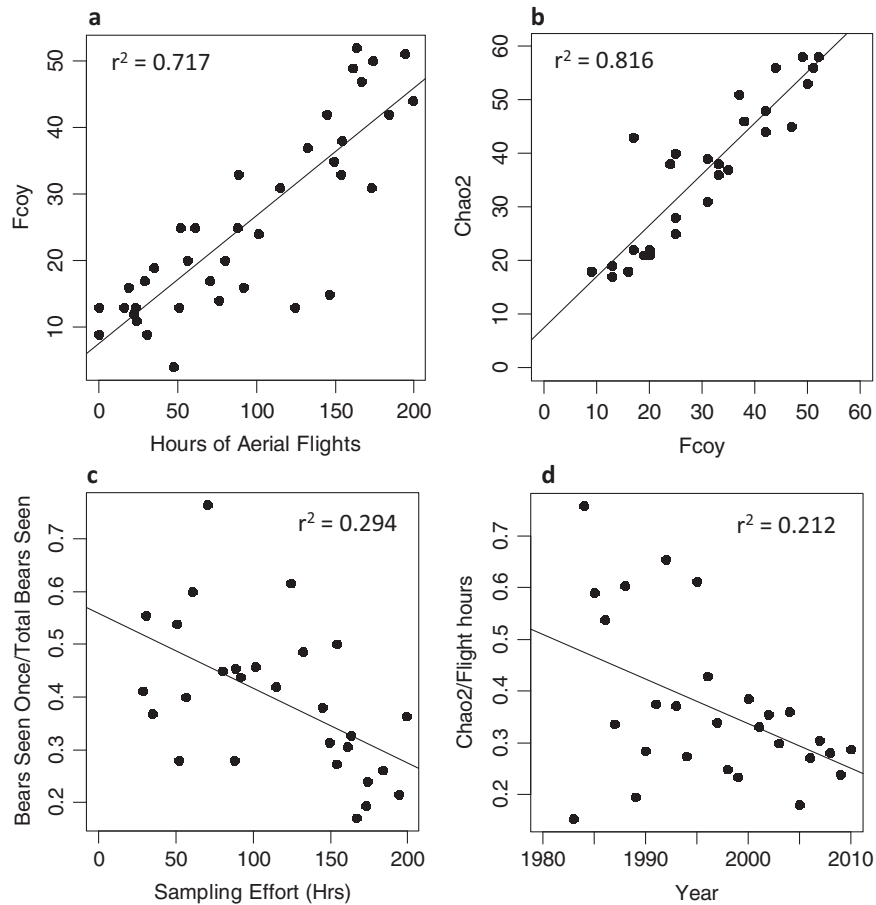


Figure 2 Relationships between two population estimators, (A) Fcoy and Chao2, and search effort. Fcoy counts have risen linearly with hours of formal observation effort. (B) Chao2 population estimates and simple Fcoy estimates show a simple linear relationship. Linear regressions of Chao2 on Fcoy and either year or flight hours show no effects of time or observation effort, suggesting that the Chao2 estimator does not correct for shifting observation effort or sightability of bears. (C) Increased sampling effort over time decreases the number of bears seen only once, suggesting that formal observation effort does affect sighting frequencies and is thus a reasonable proxy for overall observation effort. (D) The ratio of Chao2 to search hours has significantly declined through time, consistent with search efforts having risen far faster than any population growth. High scatter in this ratio in early years, and a much more consistent relationship more recently, also suggest alterations in search efficiency or sightability. Pearson's r^2 correlations are shown for each relationship. Data from 1973 to 2010 on Fcoy and flight hours and from 1983 to 2010 for Chao2.

Changes over time in the mean or variance of bear sightabilities appear likely, but are impossible to quantify with our data. However, the formal search effort for bears has definitely increased. To examine how this rising effort could influence population estimates, we simulated observation of a constant population of $n = 70$ (to giving roughly the observed Chao2 value in 1986) using the observation flight hours reported for each year from 1983 to 2010. Comparison with the actual Chao2 calculated for each year shows how similar this 20-year trend is to one driven solely by changes in observation effort (Figure 5), and that the confidence envelope of simulated values encompasses nearly all observed Chao2 values. Most early Chao2 values are somewhat lower than

the median simulated values, while later observations are often somewhat higher, but residuals from a regression of real Chao2 on simulated medians are not significantly related to year ($P = 0.366$). While the exact number of real Fcoy each year has obviously not remained constant (due to variable number of females reproducing and many other demographic processes), much of the apparent increasing trend in bear numbers during this time period can be parsimoniously explained as a result of increasing search effort.

Other data also support this interpretation. In particular, an objection to our analysis could be that formal observation effort is only part of the observation process used to count Fcoy, and that the increases in both Fcoy

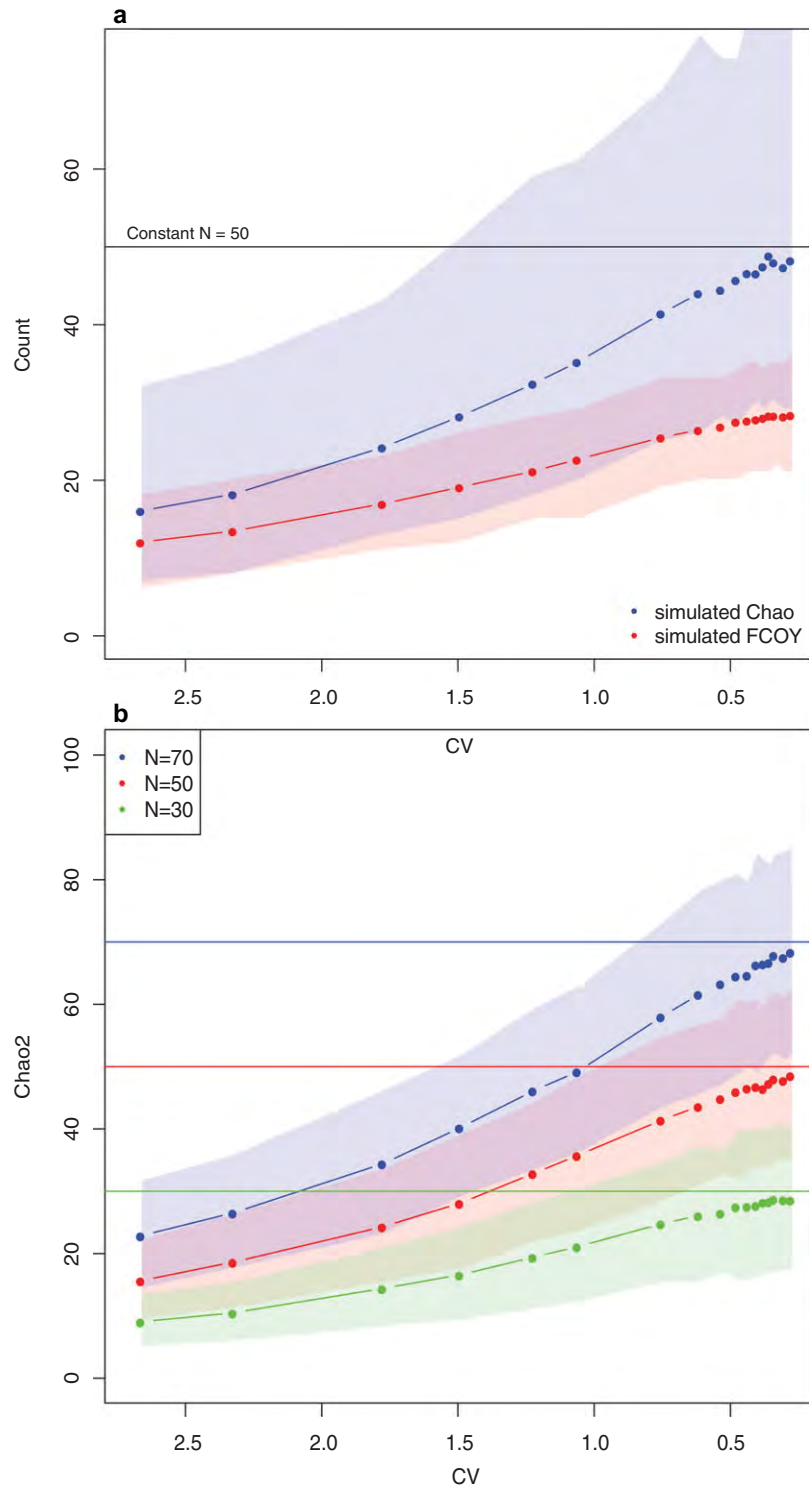


Figure 3 Changes in the heterogeneity of sightability (CV) of bears, such as changes in flight routes or food availability may induce, result in large shifts in Chao2 estimates of bear numbers. We increased the CV by increasing the variance of sightabilities, while keeping both mean sightability of bears and search effort (100 hours) constant. (A) With a constant 50 Fcoy in the population, rising CV in sightabilities results in increased Fcoy and Chao2 estimates, with larger shifts in Chao2 estimates than in simple Fcoy estimates. (B) Effects of CV in sightability on Chao2 estimates are similar in magnitude across a range of real population numbers. All means and shaded 95% confidence limits are based on 1,000 iterations at each parameter value.

and observation hours are simply a coincidence. However, if flight hours did not drive patterns in the mean probability of being observed each year, there should be no relationship between the relative number of bears seen once, twice, or >2 times and formal observation

effort. However, the fraction of bears with single observations has fallen with increasing effort (Figure 2c). This is not a pattern expected if numbers were increasing but observation effort had no effect on the probability of a bear being seen each year. Finally, Fcoy/search

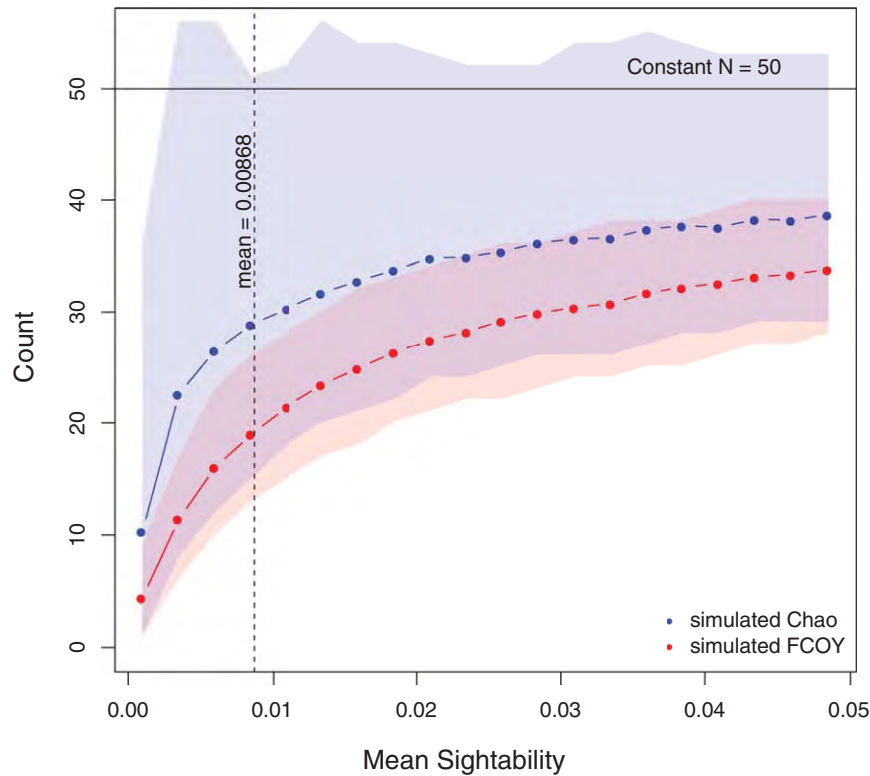


Figure 4 Changes in mean sightability alter both Fcoy and Chao2 estimates of population size. With a constant population number and constant CV in sightability, increasing mean sightability leads to rising estimated population sizes. Chao2 shows essentially identical sensitivity to mean sightability as does Fcoy. All simulations assume 100 search hours. The means and shaded 95% confidence limits are based on 1,000 iterations at each parameter setting. The mean sightability indicated by the dotted line is the value estimated from the data in Keating *et al.* 2002 (see main text for further explanation).

hours and Chao2/search hours both decline over time (Figure 2d; $P = 0.0517$ and $P = 0.0138$, respectively). These ratios (essentially catch-per-unit-effort) should increase with population increases and decrease with increasing search effort. While modest increases in population size, accompanied by larger increases in search effort, could lead to decreasing Chao2/search hours, the significant declines in this ratio are concordant with our simulations of the estimation process, which suggest that little or no population growth is needed to explain the observed trends in Fcoy or Chao2. The declining variability in these ratios over time also suggests temporal shifts in either the observation process or bear sightabilities.

Finding that Chao2 is not a robust estimator of relative or absolute numbers, we also explored the use of two alternative estimators. Simulation tests of the Second-Order Sample Coverage estimator (SC2 in Keating *et al.* 2002) showed that it was not appreciably better than Chao2. Similarly, with the relatively small numbers and high variance in sightability that characterize the GYE grizzly population, the methods described by Mao (2007)

and Mao & You (2009) are not reliable. These results are not surprising, given Link's (2003) findings regarding the nonidentifiability of population sizes from any estimators based on analysis of frequencies, in the absence of other information to ground the analysis.

Demographic analyses

Past use of demographic data for this population have also indicated a rapidly growing population (Harris *et al.* 2007, based on results in Schwartz *et al.* 2006a [Haroldson *et al.* 2006; Schwartz *et al.* 2006b, c]; but see Pease & Mattson 1999). Harris *et al.* calculate best estimates of mean annual population growth rate from 1983 to 2002 of between 1.07 and 1.04. However, these estimates assume that there is no reproductive or survival senescence of bears until they reach age 30, the maximum lifespan. This is a reasonable use of estimated demographic rates if either: (1) there really is no senescence or (2) a random sample of adult bears that represent the true age distribution was used to calculate the mean adult survival and fecundity rates. There is clear evidence for both

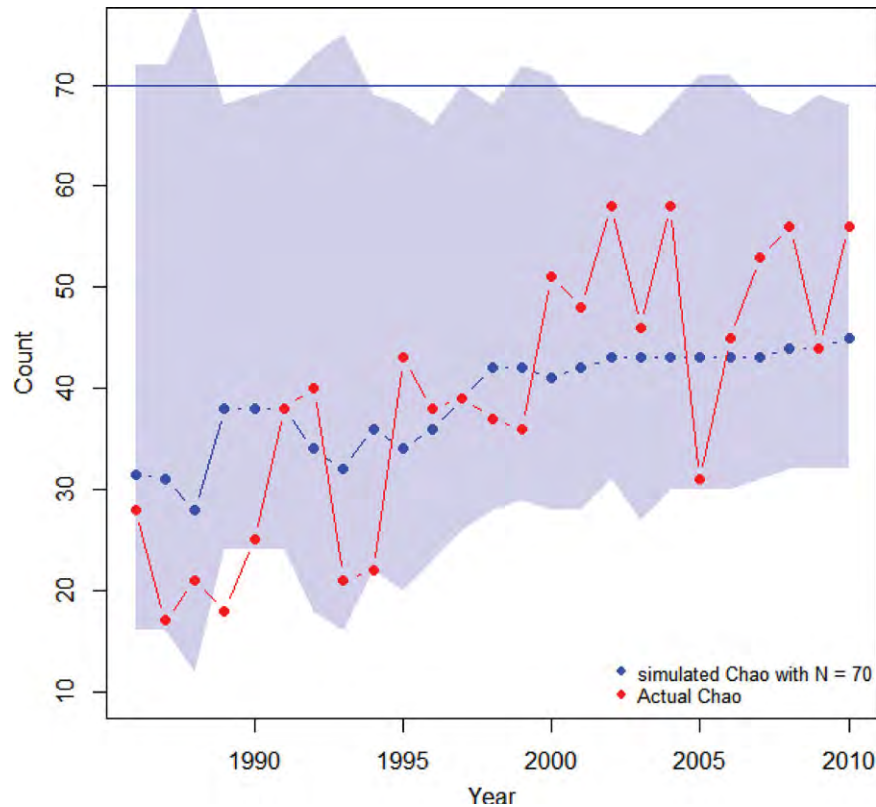


Figure 5 Actual increases in search effort are predicted to result in increasing estimated bear numbers that parallel trends seen in Chao2 estimates for the real population. We calculated simulated Chao2 values by sampling from a constant population with $n = 70$ and using the actual hours of search flights flown in each year. All simulations assume constant mean and CV of sightability as estimated from data in Keating *et al.* 2002 (see text). The medians and shaded 95% confidence limits are based on 1,000 iterations at each parameter value.

reproductive and survival senescence in grizzlies, including the GYE population (Schwartz *et al.* 2003; Johnson *et al.* 2004; see Appendix S1), and the survival rates estimated for collared bears suggest that they do not come from a representative sample of ages. Harris *et al.*'s mean adult female survival estimates of 0.922 and 0.950 would result in 10% or 24% of adult bears surviving to age 30, and between 25% and 42% dying past the age of 20. From 1975 to 1994, the oldest female death observed was at age 24, and only two female deaths of greater than age 20 were observed (Boyce *et al.* 2001). While a similar, simple assessment of the plausibility of the single adult fecundity values used in past analyses is not possible, these too appear to poorly match what is known about age-specific fecundity patterns (see Appendix S1).

To correct for the exclusion of senescence from past demographic models, we constructed models with estimates of annual fecundity and adult, cub and yearly survival from 1983 to 2001 from Haroldson *et al.* (2006), Keating *et al.* (2002), and Harris *et al.* (2007) and including either no senescence, a correction for survival senescence beyond age 20, or corrections for both survival and re-

productive senescence. In these simulations, we either used adult survival rate estimates that assumed missing bears had died, or that censored these individuals (see Appendix S1).

Starting with an adult female population of size 57 and at the first year's stable age distribution, we simulated the size of the bear population through time. With no inclusion of senescence effects, models with high adult survival predict growth rates even greater than those shown by the Chao2 estimates, while models using low adult survival predict roughly the growth seen in Chao2 numbers (Figure 6). However, inclusion of senescence results in considerably lower growth rates. If both reproductive and survival senescence are included in the model, we arrive at predictions of somewhat lower or extremely little growth from 1983 to 2002.

Discussion

Confidence in the recent growth and hence health of the GYE grizzle population has largely rested on Fc0y estimates, and their correction via the Chao2 estimator,

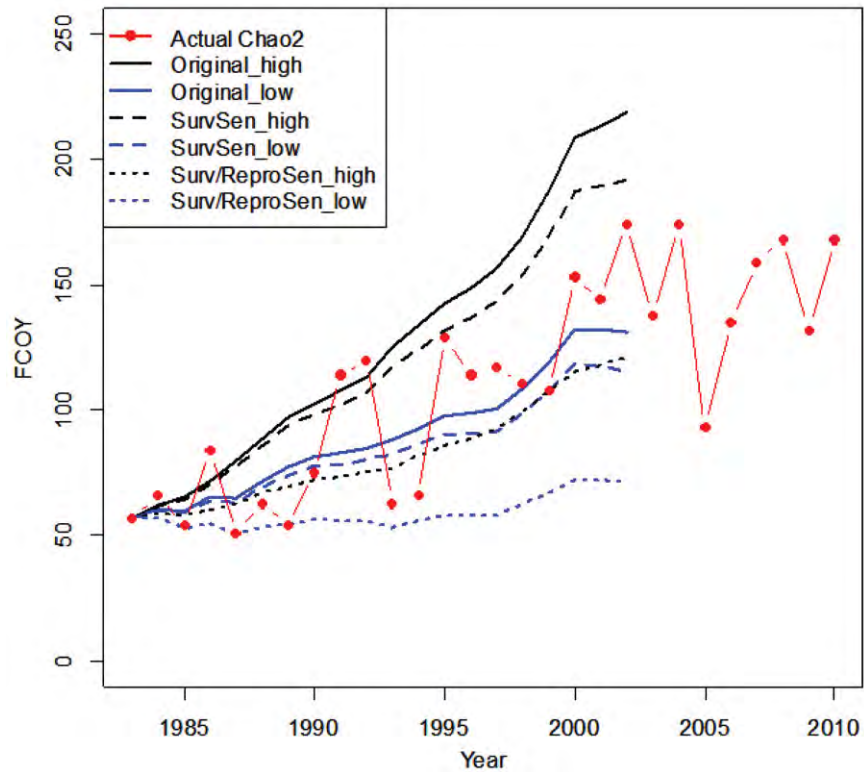


Figure 6 Predicted population trends through time, using different demographic assumptions. Three sets of results are plotted: (A) predicted trends using either high or low adult survival rates, without incorporation of senescence (Original_high and Original_low lines); (B) predicted trends using either high or low adult survival rates, with incorporation of survival senescence (SurvSen_high and SurvSen_low lines); and (C) predicted trends using either high or low adult survival rates, with incorporation of both reproductive and survival senescence (Surv/ReproSen_high and Surv/ReproSen_low lines). For the simulated numbers in each scenario, the mean and variance of the $\log(\lambda)$ values are (respectively): {0.0708, 0.00074}, {0.0439, 0.00135}, {0.0595, 0.00080}, {0.0336, 0.00140}, {0.0345, 0.00044}, and {0.0078, 0.00168}. For the empirical Chao2 estimator over the same period, the mean and variance are {0.0587, 0.10230}. All simulations were started with adult female numbers equal to three times the observed number of Fcoy in 1983 and all age classes at the stable age distribution for this year. Three times the actual Chao2 estimates, plotted in red, are shown for comparison to demographic predictions, for which we plot the predicted number of adult females each year. While Chao2 estimates are plotted up to 2010, we only had survival and reproductive estimates from 1983 to 2001 for demographic predictions.

as well as on the corroborating evidence from demographic rates. In all studies, we found that use the Fcoy or Chao2 grizzly data set authors take published estimates of these numbers at face value, as stable estimators of relative numbers. Even the most recent discussion of population trend data has accepted the basic narrative of long-term growth of this population, even while, in some cases, concluding that new ways to estimate numbers are needed (Eberhardt & Breiwick 2010; IGBST 2012). Our results suggest the need to re-evaluate these apparent trends. We find that a plausible and parsimonious explanation for most or all of the rise in Fcoy estimates is rising search effort, along with possible shifts in the mean and variance in sightability of bears, and that the Chao2 estimator does not meaningfully correct these issues. Similarly, we show that the approach taken in past demographic analyses of ignoring senescence has likely

resulted in overly high population growth estimates, and that incorporation of senescence patterns known for grizzlies results in substantially lower growth estimates for the recent past. These results suggest that a re-evaluation of the acceptable mortality limits for bears is also needed.

Three recommendations follow from our work. First, one of several methods should be used to re-evaluate the last several decades of data on bear numbers, and to do so with explicit treatment of the rapidly changing observation effort. The most reasonable approach would be to analyze only the data collected on standardized observation flights, so that effort could be treated clearly in the estimation of relative numbers. Dealing with the shifting observability of bears is more problematic, but even if this issue cannot be fully resolved, the overwhelming effects of effort could be dealt with in such a reanalysis.

Second, demographic rates should be re-estimated with acknowledgment of senescence effects. Given that senescence is well-known in bears, and that past work has used GYE data for the estimation of both reproductive and survival senescence, it is puzzling that these effects have not been included in past estimates of population growth rates. Verbal arguments that senescence is relatively unimportant (e.g., Schwartz *et al.* 2003) only make sense if age-representative samples of bears are used to estimate all pooled adult rates, which does not seem likely, given that average adult survival estimates suggest large fractions of adults living the maximum age of 30.

Finally, our results suggest that we actually know very little about the past trends of this population, and hence about their likely future fate, especially with rapid declines in multiple food resources and increases in opportunities for human conflicts (Figure 1). While our most basic conclusion is that we cannot confidently assess the past or future trends of this population without further and more careful work, our analyses show that trends in Fcoy and Chao2 are consistent with a population that has grown little, or perhaps not at all, in the recent past, but also that was higher in the past than was realized. In a nonchanging landscape, this might imply considerable safety from future extinction. However, with rapidly accelerating impacts, the flattening Chao2 estimates over the last decade, even as search effort has continued to increase, are consistent with a population that may now be, in fact, declining.

Our basic conclusion is that the perceived dynamics of this population rest on overly simplified uses of the basic data sets available. While the GYE grizzlies have been intensively studied, lack of attention to basic issues of wildlife data analysis (accounting for observation effort and realistic treatment of life history patterns) are likely to have resulted in misunderstandings of the data collected, systematic bias in the inferences about the dynamics of this population, and overconfidence in apparent trends. Given the widespread use of the Chao and related estimators in many other contexts, our work also suggests that caution is needed in interpreting patterns in these statistics in studies of either population numbers or species richness.

More generally, these results highlight the need to carefully consider shifting observation processes for species of conservation concern. Changing knowledge of a species, increasing attention to its plight, or shifts in individual behaviors in the face of habitat changes can all alter the observation process, with nontrivial effects on estimated population viability (e.g., Hernandez-Manrique *et al.* 2013). In different situations, these changes might lead to the perception of greater or less risk than is real, compounding other problems

of implementing necessary management interventions (Martin *et al.* 2012). While a great deal of careful attention has been paid to the observation process in many areas of wildlife and conservation biology (Bellemain *et al.* 2005; Olea & Mateo-Tomas 2011; Chaudhary *et al.* 2012), this is not always the case, especially with very rare species. Our work highlights that in many circumstances more care is needed in making inferences about population trends, especially when these results are being used in a direct policy context (Mace *et al.* 2010).

Acknowledgments

K. Cutler received partial support from the Natural Resources Defense Council to work on this project.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Appendix S1. Re-evaluating evidence for past population trends and predicted dynamics of Yellowstone grizzly bears.

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