



Re-evaluation of Yellowstone Grizzly Bear Population Dynamics Provides False Insights: Response to Doak & Cutler

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Re-evaluation of Yellowstone Grizzly Bear Population Dynamics Provides False Insights:**Response to Doak & Cutler****Frank T. van Manen***

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For Peer Review

Abstract

Doak & Cutler (2013) critiqued methods used by the Interagency Grizzly Bear Study Team (IGBST) to estimate grizzly bear population size and trend in the Greater Yellowstone Ecosystem. We found major flaws with the premise, implementation, and interpretation of simulations they used to support their arguments. They argued population increases documented by IGBST based on females with cubs-of-the-year were a function of increased search effort. However, their simulations were not reflective of the true observation process nor did results provide statistical support for their conclusion. Doak & Cutler further argued survival and reproductive senescence should be incorporated into population projections but their choice of extreme mortality risk beyond age 20 and incompatible baseline fecundity substantially influenced their simulations, leading to erroneous conclusions. We conclude their critique was unfounded when placed within the context of a thorough understanding of the data, the study system, and previous research findings and publications.

Introduction

Doak & Cutler (2013; hereafter D&C) critiqued methods used to estimate grizzly bear (*Ursus arctos*) population size and trend in the Greater Yellowstone Ecosystem (GYE) by the Interagency Grizzly Bear Study Team (IGBST), a research partnership among federal, state, and tribal agencies formed by the Secretary of the Interior in 1973. Peer review and critique are essential to scientific progress, and the IGBST has a long history of publishing study results, making reports publicly available, presenting background and justification for analysis decisions, and providing careful interpretation of population trend and demographic results. D&C's critique mainly concerns two claims: 1) increase in grizzly bear population estimates from 1983 to 2001 can be attributed to factors other than population size, primarily increased observation effort and sightability of female grizzly bears with cubs-of-the-year (F_{COY}); and 2) estimates of population growth were biased high because survival senescence and reproductive senescence were not properly accounted for in demographic analyses. Here, we discuss both claims and demonstrate the conclusions of D&C are unfounded when placed within the context of a thorough understanding of the data, the study system, and previous research findings and publications.

Population Size and Trend

D&C claim they simulated the “observation process” as a function of number of flight hours and argue, based on simulation results, that increases in bear numbers during the 1983–2001 time period can be explained simply by increases in search effort and sightability.

Search Effort.—We found three major flaws with Doak and Cutler's simulations of the observation process. First, we disagree that D&C's method “explicitly simulates the observation process.” (p. 3). Their approach makes sweeping assumptions about the sampling process and

study system that do not represent reality. They explicitly allow each F_{COY} to be sampled every flight hour, regardless of the spatial location of the flight (see Supporting Information). For this to be realistic, observation flights would have to cover all occupied range in the GYE during each flight hour, which is clearly impossible and why 48 flight observation areas have been established. Even if it were possible, most F_{COY} would be too far away to be seen during most flight hours so their probability of being sighted would be zero for most flight hours. In recent work (Higgs *et al.* 2013), we used a mark-resight estimator based solely on counts of marked (radio collar) and unmarked F_{COY} from the standardized observation flights; this work also addressed the known underestimation bias of the Chao2 estimator (IGBST 2012; see Supplemental Information). For that estimator, we have assumed an individual F_{COY} can only be sighted one time per flight survey and there are only two flights over each observation area per year. This assumption is supported by data on sightings of radio-collared F_{COY} during survey flights without aid of telemetry (Higgs *et al.* 2013). Because D&C assumed that all bears in the entire study area are available to be sighted each flight hour, in their simulations the number of F_{COY} sighted once (f_1) or twice (f_2) quickly stabilize as flight hours increase and are relatively low compared with the number of unique F_{COY} observed (m) because many are sighted more than twice (Fig. 1). The consequence is that the Chao2 estimate for the simulated population of known N is determined essentially by m , rather than the frequency of sightings (f_1 and f_2), which, unsurprisingly, results in a direct correspondence between flight hours and Chao2 estimates (Fig. 1). However, this simplistic relationship to flight hours is the foundation of arguments made by D&C regarding Chao2 estimates and trends.

Second, D&C base their conclusion that the increasing trend in Chao2 was driven by increased search effort on a simple visual comparison of their simulation results with empirical

Chao2 data. IGBST has always carefully compared simulated data characteristics with those of empirical data (e.g., Cherry *et al.* 2007), which D&C did not do. Accordingly, we applied linear regression to each of 1,000 realizations of data produced from D&C's simulation method of the 25-year time series (not 20 years, as D&C described) to obtain a distribution of slope (trend) estimates under their model. We then compared the slope of our empirical estimates of $\ln(\text{Chao2})$ for 1986–2010 ($\hat{\beta} = 0.0404$, $P < 0.001$, $R^2 = 0.61$; Fig. 2A) with the distribution of slopes based on D&C's simulations: 99.9% of D&C's realizations resulted in slopes less than observed from the empirical data (Fig. 2A). Therefore, given the known, constant population of 70 individuals, we found no support for the notion that increase in search effort alone would result in detection of the population trend documented by IGBST based on empirical data, even under the model used by D&C that assumes a much stronger relationship between flight hours and sightings than is realistic for the system.

Finally, D&C's definition of effort as the number of flight hours failed to account for the increase in area surveyed, with their methods assuming each hour is used to survey the same spatial area. IGBST survey efforts have evolved to account for documented range expansion as reported by Blanchard *et al.* (1992), Schwartz *et al.* (2002, 2006c), and Bjornlie *et al.* (2013), who documented a 38% increase in occupied grizzly bear range during 2004–2010 alone. Accordingly, observation areas outside the recovery zone were added in 1989, 1999, and 2007 based on new records of bear presence (e.g., sightings, conflicts). Because dispersal among grizzly bears is substantially male biased (Proctor *et al.* 2004), such expansion initially involved subadult and young adult males. Thus, establishment of F_{COY} occurred subsequent to expansion of observation flight areas. Indeed, only 24 out of 297 initial sightings of F_{COY} were from observation flights outside the recovery zone during 1986–2010, or an average increase of 1

unique F_{COY}/yr . Of course, a larger survey area required additional flight hours (Fig. 3) but we argue that it is search intensity (effort/area surveyed) that matters because the probability of seeing an F_{COY} in these expansion areas was very small, if not zero, prior to expanding the survey area. In other words, it is unrealistic for D&C to assume the population was actually stable or declining but appeared to be increasing because of search effort expanding to new areas. To demonstrate this point, we adjusted annual flight hours based on total area surveyed and repeated the simulations with which D&C generated their Fig. 5. To account for this spatial component of search effort in a way that is tractable under the binomial framework of D&C's simulations, we rescaled the original search hours using the area flown as the adjustment parameter. We used the smallest search area (1988) as the reference category and adjusted flight hours for all other years accordingly (the choice of reference year influences the absolute numbers for flight hours but does not affect relative change in counts across years). Of 1,000 realizations generated by these simulations, all had slopes lower than the Chao2 trend of our empirical data (Fig. 2B).

We conclude that D&C's assertion that estimates of grizzly bear population trend are a direct consequence of search effort is based on substantially flawed simulations of the observation process and is not even consistent with results from their own simulations, particularly after adjusting number of flight hours for increased survey area. Thus, we find no support for their conclusion that "much of the apparent increasing trend in bear numbers during this time period can be parsimoniously explained as a result of increasing search effort." (p. 4). Moreover, we find it remarkable that D&C failed to mention the Chao2 estimator is known to be biased low (Keating *et al.* 2002, Cherry *et al.* 2007) and, as applied to F_{COY} in the GYE, that this bias increases with population size (Schwartz *et al.* 2008).

Sightability.—D&C claim that sightability of F_{COY} has potentially increased over time, which would inflate Chao2 estimates. Indeed, under these assumptions, their simulations show estimates of Chao2 increase with greater mean sightability of individuals. They also show an increase of Chao2 with decreasing coefficient of variation (CV) of sightability (although they incorrectly state that “rising CV in sightabilities results in increased F_{COY} and Chao2 estimates” [D&C Fig. 3 caption]; the relationship is actually opposite because CV *declined* along the horizontal axis). However, details of these relationships were previously reported and published in Keating *et al.* (2002) and Cherry *et al.* (2007). Thus, their argument hinges on the premise that mean sightability of individuals has increased over time, for which D&C provide no quantitative evidence. Instead, they speculate that changes known to be occurring in the ecosystem that affect grizzly bears (e.g., use of army cutworm moth [*Euxoa auxiliaris*] aggregation sites and increased researcher knowledge of those sites; decline of cutthroat trout [*Oncorhynchus clarkii*] and whitebark pine [*Pinus albicaulis*]; reintroduction of wolves [*Canis lupus*]) have led to a progressive increase in mean sightability of grizzly bears. We do not disagree that sightability may increase or decrease due to these factors. However, observations of radio-collared F_{COY} from telemetry flights, which are well distributed throughout the GYE (Schwartz *et al.* 2006d:12), provide no basis for assuming a major shift in sightability (Fig. 4).

Finally, D&C cite Link (2003) and argue that population size is nonidentifiable for estimators using observation frequencies when frequencies are small and variance in sightability is high. Link (2003) was making the point that mark-recapture data cannot identify the true underlying distribution that generated the data. However, Link (2003) did not show that estimators could not approximate true population size. Cherry *et al.* (2007:198) actually

referenced this issue and clearly demonstrated that estimates were close to truth, although still biased low.

Demographic Analyses

Incorporating Survival Senescence in Population Projections.—D&C applied a biologically unrealistic senescence function for independent female survival (see Supporting Information). To examine the influence of survival senescence as modeled by D&C versus empirical data, we used data for 1983–2011 to estimate age-specific survival. Our procedures followed Haroldson *et al.* (2006) but instead of generating a single mean survival rate for the entire period, we estimated age-specific survival of females using age and age² covariates (Fig. 5, solid black line), similar to the analyses of Johnson *et al.* (2004). We used these age-specific, empirical data to repeat the survival senescence population projections of D&C. In contrast to D&C's reduction of 1.1% population growth for both high and low survival scenarios (Tables 1A and 1B), we observed a 0.1% reduction (high survival, Table 1A) and a 0.4% increase of population growth (low survival, Table 1B) compared with projections (Fig. 5, dashed line) using the age-constant survival rates of Harris *et al.* (2006, 2007). These findings suggest little contribution of age-specific survival on population projections and confirm those of Haroldson *et al.* (2006), who found age class did not explain much variation beyond other covariates in the model. We do not dismiss D&C's point that survival senescence may become relevant as this population ages: however, information gained from incorporating age-specific survival should be weighed against increased model complexity and, so far, we found no support for incorporating age-specific survival.

Incorporating Reproductive Senescence in Population Projections.—D&C used an incompatible baseline for fecundity to assess effects of reproductive senescence (see Supporting

Information). To demonstrate the importance of which baseline fecundity is used for comparison, we constrained D&C's combined reproductive and survival senescence simulations to allow for a reproductive senescence-only scenario, which they did not include. A hypothetical population with a compatible baseline of $\bar{m}_{x\ pop*} = 0.2635$ would undergo only a 0.5% (high survival, Table 1A) and 0.5% (low survival, Table 1B) reduction in population growth during 1983–2001 upon inclusion of reproductive senescence, compared with a 2.5% and 2.6% reduction, respectively, using the higher, incompatible baseline of $\bar{m}_{x\ pop} = 0.322$ (Table 1). The lack of a strong reproductive senescence effect confirms findings from our earlier work (see Supporting Information). Clearly, the choice of fecundity baseline changes interpretation regarding impacts of reproductive senescence, which D&C did not acknowledge.

Incorporating Survival and Reproductive Senescence in Population Projections.—

Table 1 shows how D&C's choice of extreme survival senescence and incompatible baseline for reproductive senescence influenced their simulation results. Using the hypothetical fecundity reference data for inference, reductions in population growth due to D&C's combined reproductive and survival senescence are 1.6% (Table 1A) and 1.5% (Table 1B); these reductions are the same as those for survival senescence only (Tables 1A and 1B) because when both senescence functions are combined and an appropriate fecundity reference is used, the extreme survival senescence function of D&C (i.e., almost zero survival past age 20) overrides any reproductive senescence effects. We point this out because D&C implied a strong additive effect from reproductive senescence in their Fig. 6, but this is not possible because their simulations allow no females to survive long enough to reach reproductive senescence age. The additive effect from reproductive senescence was in fact a function of an inappropriate fecundity reference, rather than senescence itself.

Finally, when using the hypothetical reference for fecundity, IGBST estimates of age-specific survival resulted in only a 0.2% reduction (Table 1A) and a 0.2% increase (Table 1B) in population growth with a slightly additive effect when combined with D&C's reproductive senescence (0.4% [Table 1A] and 0% [Table 1B] reduction of population growth, respectively). These changes are not biologically relevant; thus these simulations do not support the importance of incorporating survival and reproductive senescence. We conclude that D&C's choice of an extreme survival senescence function, combined with inappropriate comparison among fecundity schedules to model reproductive senescence, substantially influenced their simulation results, leading to erroneous conclusions.

Discussion

D&C conclude that “we actually know very little about the past trends of this population” and that “with rapidly accelerating impacts, and with Chao2 estimates flattening in the last decade, even as search effort has continued to increase, it is quite likely that the population is now, in fact, declining.” (p. 9). D&C further assert that the comprehensive population studies of IGBST (e.g., Schwartz *et al.* [2006d], Keating *et al.* [2002], Cherry *et al.* [2007], Harris *et al.* [2006, 2007], and IGBST [2006, 2012]) show a “lack of attention to basic issues of wildlife data analysis (accounting for observation effort and realistic treatment of life history patterns)” and “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.” (p. 9). As we demonstrate here, these statements are not supported by their own analyses, are based on selective and incorrect use of existing data, and fail to recognize the broader context provided by available data and other published information.

We recognize that no two investigators are likely to make the exact choices in dealing with complex data. It can be tempting, from afar, to imbue such choices with intent when it merely results from the inevitable differences in choice made by equally qualified and objective investigators. In fact, this is why IGBST has long favored a team approach. Current and past demographic analyses include about a dozen scientists and methods and results are critically evaluated, often involving intensive debates and exhaustive consideration of alternatives. Moreover, IGBST explicitly evaluates stochasticity in the modeling process whenever possible. When faced with the inevitable uncertainty associated with parameter estimation, the study team evaluated such relationships, chose to avoid overestimation of population size and mortality limits (see Supporting Information), and provided complete transparency of the process (e.g., IGBST 2012:20).

Scientific findings produced by IGBST have played an important role in the management of GYE grizzly bears because of its unique role bridging science and policy (Lynch *et al.* 2008:826). Decisions by federal, state, and tribal land managers regarding Yellowstone grizzly bears are not based on any single data source or analysis but rather on the totality of available data, rigorous analyses, and knowledge of the system by a team of experienced scientists. To that regard, we point out that two independent datasets (Chao2 based on unduplicated counts of F_{COY} and population projections based on demographics analyses of intensive known-fate data) have shown very similar population growth trends (Harris *et al.* 2006, 2007; Haroldson *et al.* 2011). Moreover, our interpretation of a positive population trend during 1983–2001 and diminished growth in the last decade (IGBST 2012) is supported by additional indicators, including: (1) standardized observation flights within the Recovery Zone (excluding army cutworm feeding sites where bears are more observable), where search effort has remained

constant or even declined slightly, show observation rates of bears increased from $<1/\text{hr}$ in the mid-1990s to $\sim 3/\text{hr}$ in late 2000s (Fig. 6); (2) proportion of unmarked bears in the capture sample (i.e., first capture) remained constant and high (50–70%) while total individuals captured/yr increased (Fig. 7); and (3) during the 1970s and into the 1980s, grizzly bear range was likely contained within the recovery zone ($23,828 \text{ km}^2$) but expanded to $34,416 \text{ km}^2$ by the end of the 1990s (Schwartz *et al.* 2002) to $50,280 \text{ km}^2$ in 2010 (Bjornlie *et al.* 2013).

We conclude the critique of D&C is unfounded when placed within the context of a thorough understanding of the data, the study system, and previous research findings and publications. The wealth of papers and publicly available reports by the IGBST and collaborating scientists is testimony to their work on keeping decisions and assumptions transparent and open to peer review. Careful reading of those papers and reports addresses most, if not all, of the claims presented by D&C. Furthermore, we would gladly have discussed their questions with them had we been aware of their work prior to publication. The task of IGBST is to use the best available science to ensure that federal and state agencies have objective and reliable data upon which to base their policy and management decisions (e.g., Schwartz *et al.* 2006). Thorough review is critical to the scientific process and can lead to important new insights. However, based on our examination, the simulations and analyses that formed the foundation of D&C's critique led to erroneous conclusions and false insights.

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Table 1. Population size, mean annual population growth (λ), and percent decline in λ for female grizzly bears in the Greater Yellowstone Ecosystem (GYE) based on simulations of Doak & Cutler (2013). We compared influence of survival senescence as implemented by Doak & Cutler with IGBST estimates of age-specific survival. Doak & Cutler used fecundity (m_x) for 1983–2001 from Harris *et al.* (2007) as their reference. We created a second reference model based on Schwartz *et al.* (2003: model D) to demonstrate the effect of having a compatible reference dataset to assess influence of age-specific fecundity; this model is not representative of the GYE (see text and Supporting Information for further explanation). Population projections are based on survival estimates in which bears with unknown fates were censored (A) or assumed dead (B) (Haroldson *et al.* 2006), which Doak & Cutler refer to as “high” and “low” survival scenarios, respectively. We use Doak & Cutler’s terminology of survival and reproductive senescence but see footnotes for corrections.

Population projection scenarios	m_x in reference model based on Harris <i>et al.</i> (2007) ($\bar{m}_{x\ pop} = 0.322$) ^a			m_x in reference model based on Schwartz <i>et al.</i> (2003) ($\bar{m}_{x\ pop} = 0.2635$) ^b		
	N_{2001} ^c	λ 1983–2001 ^d	% reduction of λ	N_{2001} ^c	λ 1983–2001 ^d	% reduction of λ
A. High survival scenario						
Reference model	219	1.074	0	148	1.052	0
Survival senescence ^e	176	1.062	1.1	110	1.035	1.6
Survival senescence (IGBST data) ^f	216	1.073	0.1	143	1.050	0.2
Reproductive senescence ^{g,h}	136	1.047	2.5	136	1.047	0.5
Survival senescence ^e and reproductive senescence ^h	110	1.035	3.6	110	1.035	1.6
Survival senescence (IGBST data) ^f and reproductive senescence ^h	138	1.048	2.4	138	1.048	0.4
B. Low survival scenario						
Reference model	131	1.046	0	88	1.024	0
Survival senescence ^e	108	1.035	1.1	67	1.009	1.5

Survival senescence (IGBST data) ^f	142	1.050	-0.4 ⁱ	93	1.026	-0.2 ^h
Reproductive senescence ^{g,h}	81	1.019	2.6	81	1.019	0.5
Survival senescence ^e and reproductive senescence ^h	66	1.009	3.5	66	1.009	1.5
Survival senescence (IGBST data) ^f and reproductive senescence ^h	90	1.024	2.1	90	1.024	0

^aAs implemented by Doak & Cutler (2013) in their simulations.

^bAs implemented by authors for additional simulations with different m_x for reference model; based on R code in Doak & Cutler (2013) Supporting Information.

^cPopulation size at end of 19-year time series (2001).

^dMean of annual population growth (N_{t+1}/N_t).

^eSenescence as modeled by Doak & Cutler (2013) based on parameter estimates for age and age² from Johnson *et al.* 's (2004) proportional hazards model (Fig. 5, solid gray line).

^fAge-specific survival based on IGBST empirical data (see Fig. 5 [solid black line] for high survival scenario).

^gNot included in simulation models of Doak & Cutler (2013).

^hReproductive senescence modeled as age-specific fecundity based on Schwartz *et al.* (2003: model D).

ⁱNegative value indicates population increase compared with reference data (due to greater survival among ages 6–18 years; Fig. 5).

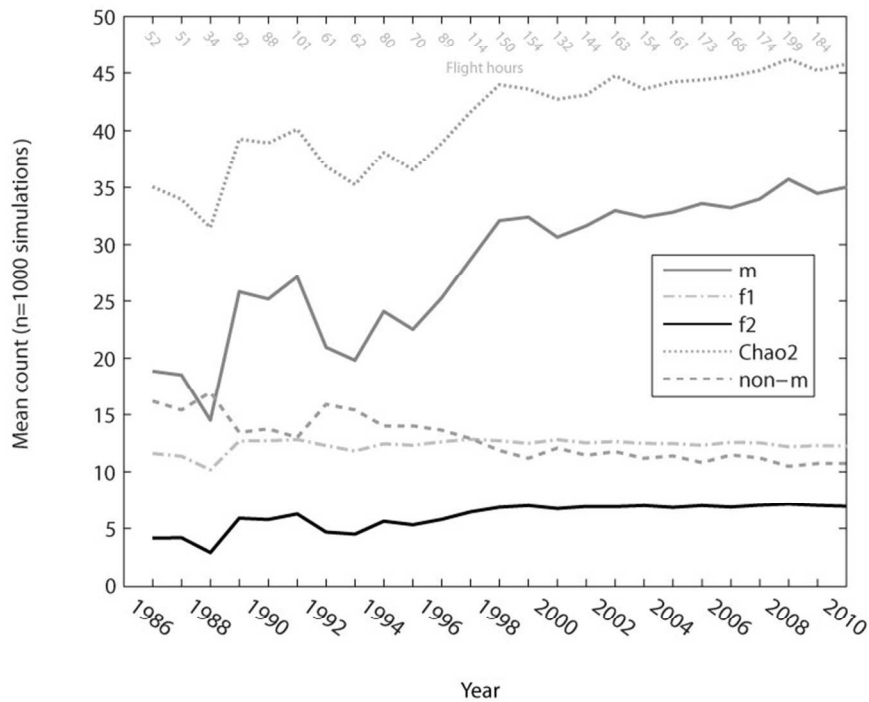


Fig. 1. Mean count of female grizzly bears with cubs-of-the-year (F_{COY}) seen once (f_1), twice (f_2), unique F_{COY} observed (m), Chao2 estimate, and F_{COY} not observed (non- m [Chao2- m]) based on simulations of Doak & Cutler (2013) for a known population of 70 F_{COY} , 1986–2010. Flight hours are shown on top x-axis.

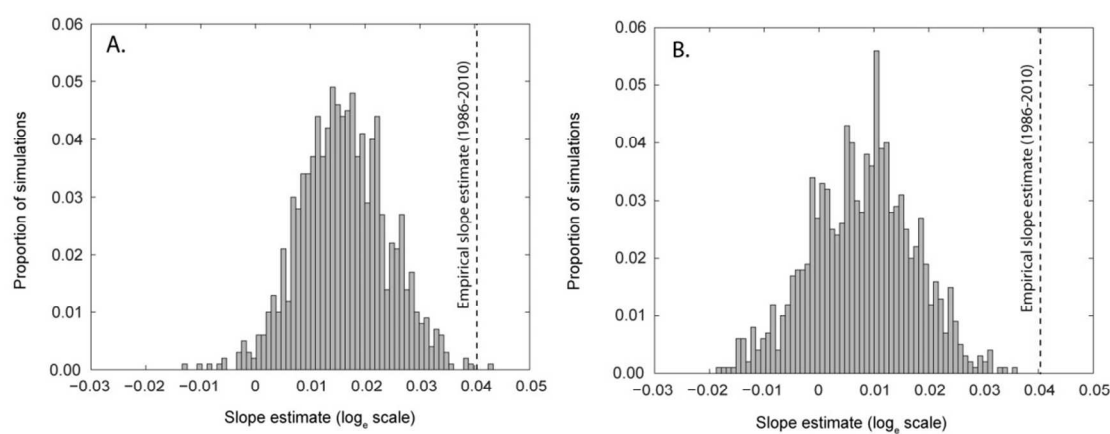


Fig. 2. Distribution of slope estimates obtained from 1,000 simulated realizations of data using linear regression of Chao2 (natural log scale) estimates of female grizzly bears with cubs-of-the-year (F_{COY}) as a function of (A) search effort (number of flight hours; following D&C) and (B) area-adjusted search effort (number of flight hours adjusted for area surveyed, our new analysis) based on 1,000 simulations of 25-year time series. The vertical dashed line shows the analysis value of the actual estimated slope for empirical Chao2 estimates of F_{COY} during 1986–2010 (Haroldson *et al.* 2011).

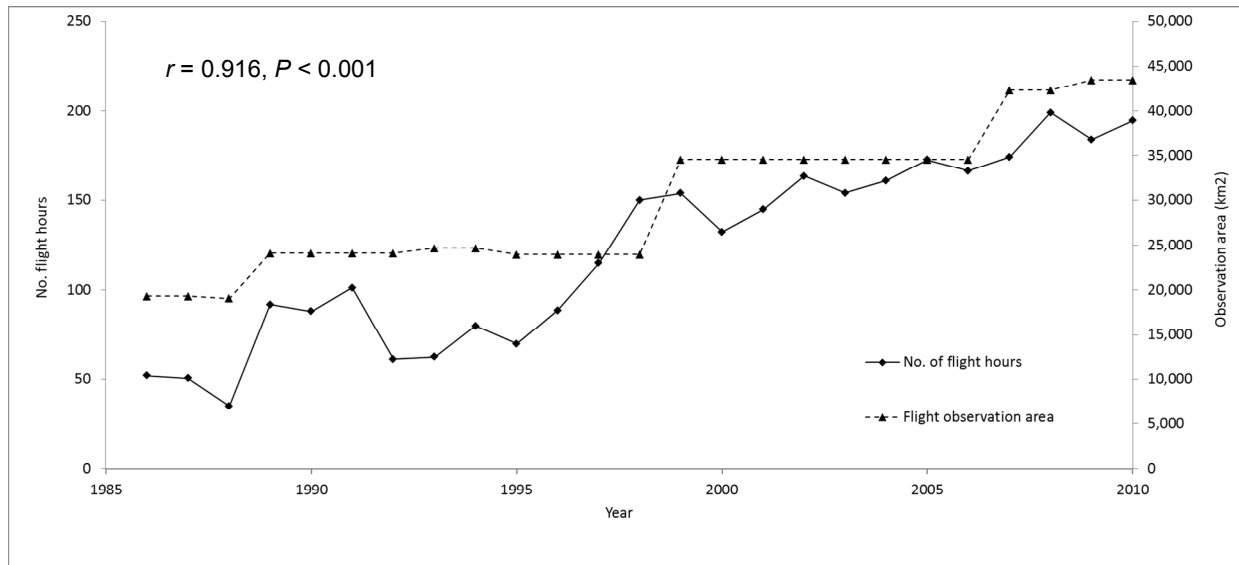


Fig. 3. Number of flight hours increased as flight observation areas for female grizzly bears with cubs-of-the-year were added to accommodate range expansion, Greater Yellowstone Ecosystem, 1986–2010.

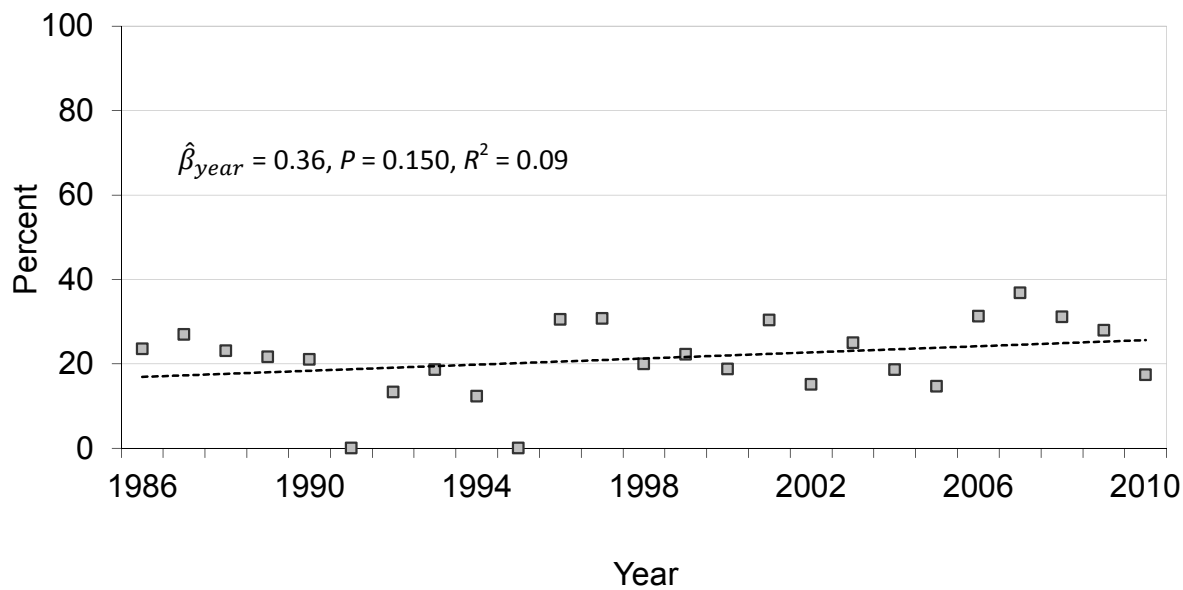


Fig. 4. Percent of locations of radio-marked female grizzly bears with cubs-of-the-year obtained during radio-telemetry flights that resulted in visual observation, Greater Yellowstone Ecosystem, May–August, 1986–2010.

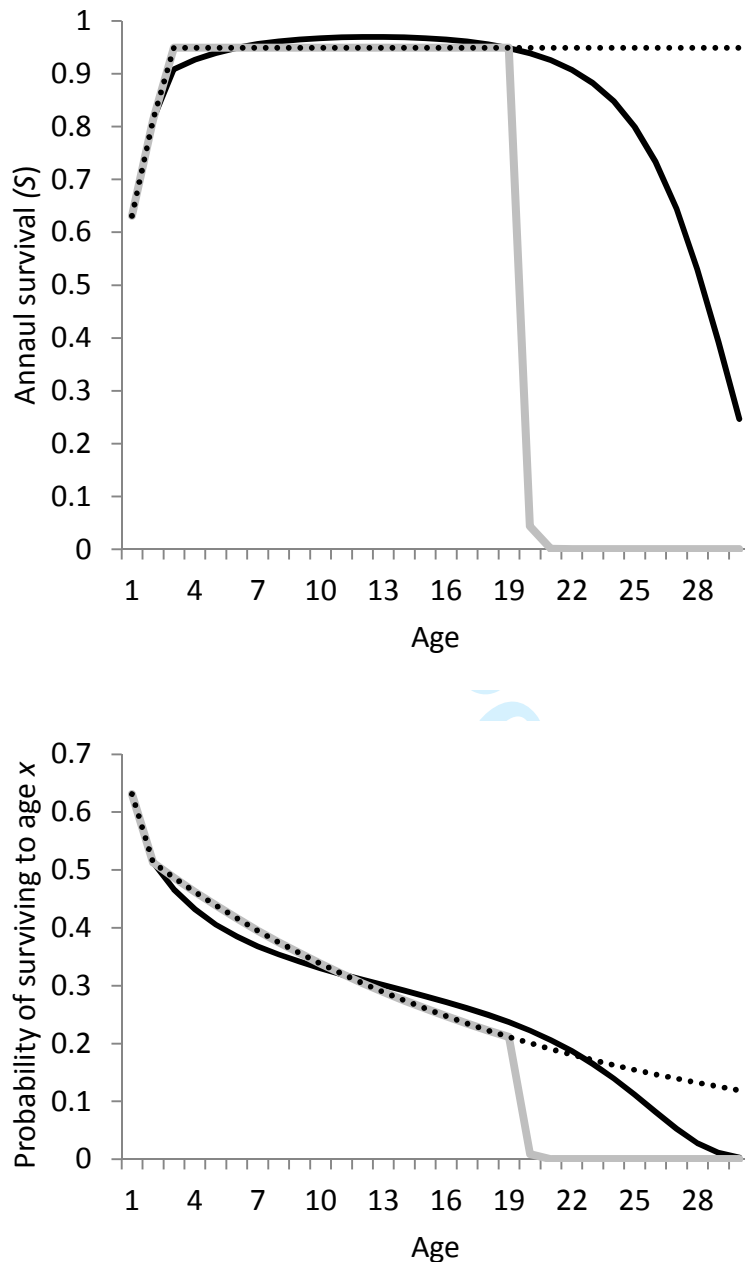


Fig. 5. Age-specific survival (A) and survival probability (B) for female grizzly bears in the Greater Yellowstone Ecosystem, 1986–2010. Dashed line is based on constant independent-aged survival from R code provided by Doak & Cutler (2013) and based on Harris *et al.* (2006, 2007); baseline annual survival ($\bar{S} = 0.949$) was the mean across all years for independent-aged bears (unknown fates censored or high survival scenario) with cub survival of 0.631 and yearling survival of 0.813. Solid gray line incorporates Doak and Cutler’s survival senescence function. Solid black line shows age-specific survival based on empirical data from IGBST for 1983–2011.

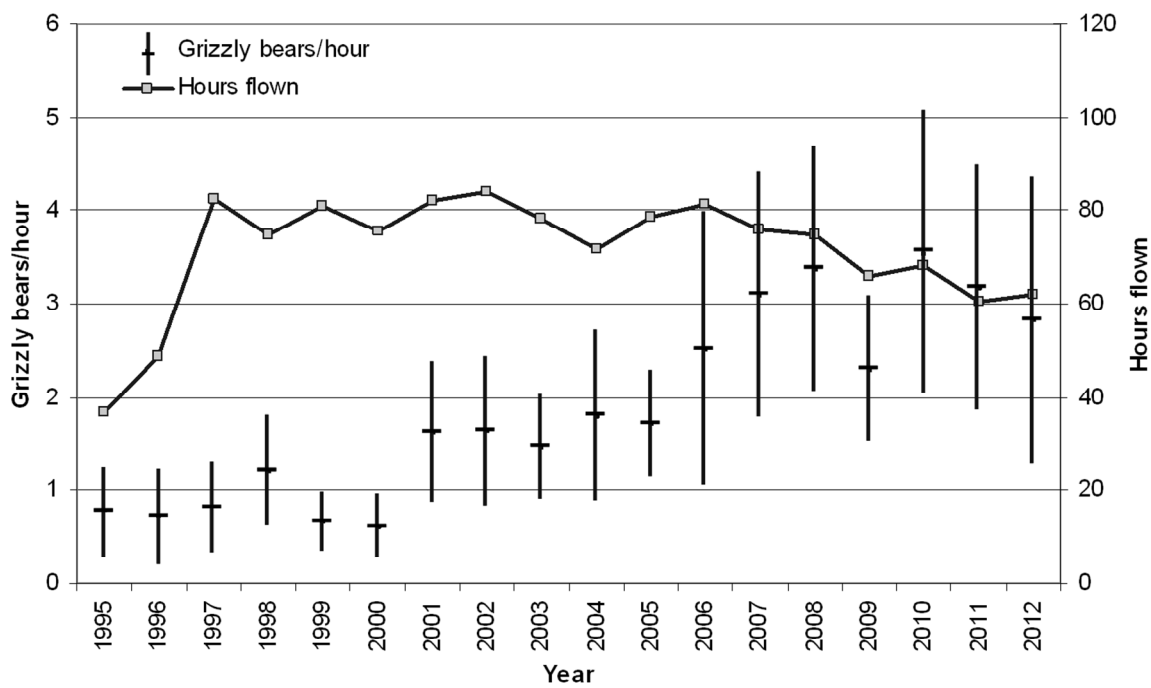


Fig. 6. Mean and 95% confidence intervals for grizzly bears observed per flight hour and total hours flown during 1995–2012 for Recovery Zone Bear Management Units, excluding those that contain army cutworm moth aggregation sites where bears congregate and are more observable.

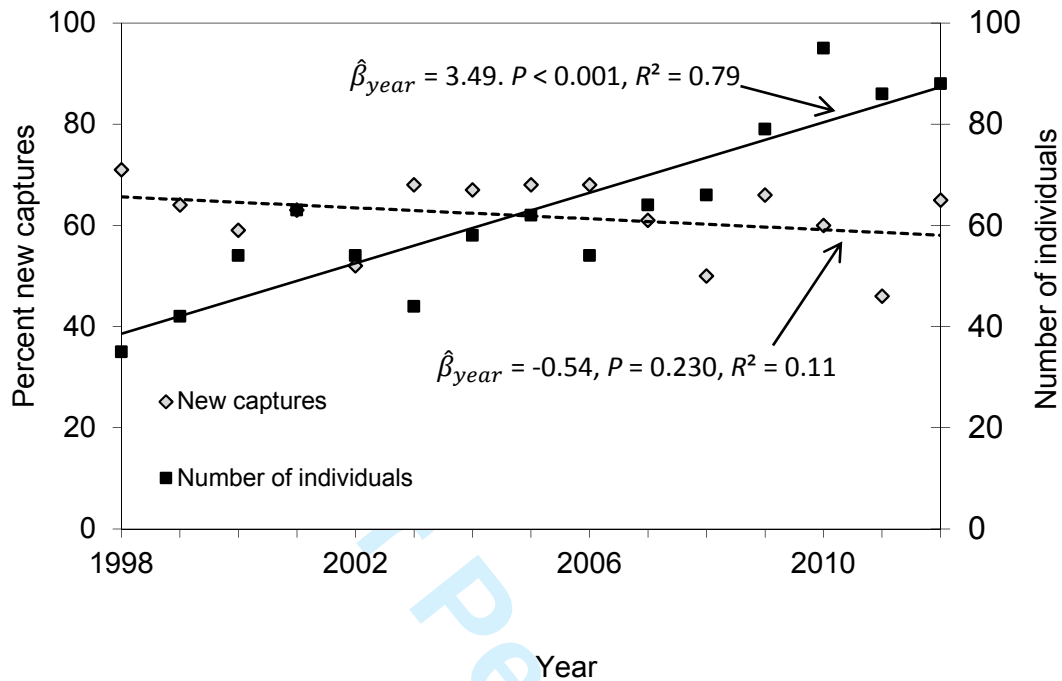


Fig. 7. Number of captures of grizzly bears and proportion of those captures representing new, unmarked individuals, Greater Yellowstone Ecosystem, 1998–2012.