

**Van Manen et al. doth protest too much: new analyses of the Yellowstone grizzly
population confirm the need to re-evaluate past population trends**

SUPPORTING INFORMATION

As we note in the main text of our response, van Manen et al. 2014 (henceforth VMEA) make criticisms of our work that range from trivial to apparently quite serious. Few appear to us to be valid critiques of the work that we performed, especially given the amount of data exclusively available to the IGBST, and that we therefore had and have no way to use. Many of VMEA's characterizations of our work and objections to our methods are also seriously inaccurate or even misleading. Below, we respond to VMEA's arguments, dividing these responses into those about analyses of population trend data and those about demographic analyses.

Chao2 and Fcoy Analyses

VMEA's main criticism is that we use standardized search effort as a surrogate for all observation effort used to generate Fcoy (adult females with cubs of the year) observations, and hence Chao2 estimates of numbers. Much of their discussion is about the possible pitfalls of blindly using standardized search effort alone, and how the ways in which we model the observation process could result in artifactual results, based on the standard search effort protocols. It would be easy to read their article and forget that in Doak and Cutler 2013 (henceforth D&C) we explicitly discuss a key assumption we make: that standardized effort is proportional to, and thus a surrogate for, total effort, and that we provide evidence (D&C Fig. 2 and related text) that this is a reasonable assumption to make. In fact, VMEA provide another piece of evidence that supports this assumption: they show that the fraction of bears sighted during standard observation flights hasn't significantly changed over time, implying that other search effort has remained roughly proportional to formal effort, as formal effort has increased.

VMEA also argue that because search area has changed, the formal search effort concentrated on the core areas that female bears mostly occupy is misrepresented in our work. Since the study team has never published these search area numbers, it would have been difficult to make this correction in our original work (they have published maps of these search regions, but these do not allow the formal incorporation of a correction factor such as VMEA argue for). Moreover, this argument obfuscates the main issue: in virtually any observation process, search effort will have effects on estimated population sizes. In a case such as this one, where standardized search effort has increased substantially (even accounting for search area: see below), and in which estimates are also based on data coming from unquantified search effort, careful acknowledgement of, and correction for, the shifting observation process are necessary. This is

hardly a radical suggestion in wildlife ecology, or even a novel one for this study system (Mattson 1997). The framework that Higgs et al. 2013 take to account for the observation process is one approach to addressing these issues, so the IGBST members do seem to understand this issue, though they seek to dismiss it when brought up in our paper.

VMEA also make much of the significantly higher growth rate predicted by their regression of Chao2 numbers from 1983-2011 versus those predicted by a particular simulation that we present as exemplifying the problem of changing observation effort. A peculiar aspect of VMEA's presentation of these results is the implicit assumption that if our observation process simulation doesn't explain *all* growth in Chao2 numbers, then there is no valid concern with changing observation processes. Also, as we note in the main text, this one particular result was shown to illustrate the problem, which is why we didn't do an exact comparison with models fit to the real data. However, if VMEA want to make this comparison they should do so carefully. If we back-transform the results to mean annual growth rates, the 95% confidence limits around the simulation-based growth rates range up to 1.03178, explaining 77% of the estimated annual growth in the real data (a lambda of 1.041, or annual growth of 4.1%). This is hardly a trivial effect.

We also applied these approaches to simulations that use the area-corrected search effort that VMEA suggest is a better measure of search effort. These annual search areas have not been published, and we thank Dr. van Manen for making them available to us. Even with this correction, search effort increased 66% from 1986 to 2010, and 171% between the lowest and highest years of search (1988 and 2005, respectively). Models based on these area-adjusted search hours (see VMEA Figure 2) show that the 95% confidence limits of estimated growth range up to a lambda of 1.025, explaining 60% of the estimated annual growth rate predicted from the real Chao2 estimates. See below for more discussion of the appropriateness of the area-correction advocated by VMEA and used here, and what we believe are better alternative corrections.

At the heart of most of VMEA's critiques is the idea that their model of increasing bear numbers, not changing sightability or changing search effort, are required to explain changes in Chao2 estimates. One way to assess the likelihood of these two viewpoints is to test the power of different models to explain annual Chao2 estimates. The high correlations between year, army cutworm moth site use, and search effort (including estimates of effort corrected for changing search area) (Table S1) make it difficult to assess significance when more than one factor is included in a regression, so we ran single one-way regressions on logged Chao2 estimates from 1986-2010. In addition to using formal search hours, we also used the area-adjusted search effort suggested by VMEA as well as what we argue below is a better adjustment for effort, based on bear observation areas (BOAs: see explanation in bulleted points below), that we refer to as BOA-corrected effort. We also fit a regression with a linear and squared year effect to match

methods of Haroldson et al. 2011. In all one-way regressions, the regression slopes were significant; for the quadratic year model, the squared year effect did not have a significant slope. Most models also had very similar explanatory power, with the lowest r^2 for the area-adjusted hours model (Table S2). Of the single factor models, number of moth sites used had the highest predictive power. We also asked if year had a significant effect after controlling for the influence of other factors that would influence sightability and effort. Year had no significant effect on the residuals of regressions of $\log(\text{Chao2})$ on moth site use, search hours, or BOA-corrected search effort, and had a marginally significant ($p = 0.048$) effect on residuals from the regression on area-adjusted hours. In this last case, the slope of the regression was 0.0159, or less than half the predicted rate of increase from a regression of $\log(\text{Chao2})$ on hours not correcting for search effort. As these results show, both search effort and variables capturing aspects of changing sightability dramatically reduce or erase the significance of year in explaining rising Chao2 numbers. Moreover, the simplest and most important lesson is that time is too confounded with other aspects of search and sightability factors to easily untangle changing numbers through time with the effects of these other factors.

Other issues directly related to these analyses, that VMEA bring up as serious problems, are:

- **The dominance of m over f1/f2.** VMEA suggest that the way we model search effect will result in an overwhelming effect of number of bears observed, with little effect of the ratio of f1 and f2 (numbers of bears seen once or twice in a season) on the resulting Chao2 estimates. This would be a valid critique if we were trying to model only the effects of formal search effort (as we discuss above, we are assuming exactly the opposite), or if the data used by the IGBST showed that frequency ratio included in the Chao2 estimator actually had large effects on these estimates. Using data from Haroldson 2011, we ran a simple linear regression of Chao2 on m, to number of unique bears seen: the adjusted r^2 for this regression is 0.8323. In other words, m drives the vast majority of variation in the Chao2 estimators in the real data set.
- **Changing Search area.** VMEA argue that flight hours should be corrected to reflect only the effort put into searching the original search area, since the several-times expanded area has far lower densities of adult females. While we agree that some correction is reasonable to make, as we noted above, it requires data that were not available to us, and our analyses show that it has little effect on most of the results we reported (as do the results shown in VMEA Fig 2). We thank Dr. van Manen for providing the data of search areas needed for these analyses. In addition, the correction advocated by VMEA is the most extreme possible, since it entirely discounts the presence of females in the expanded area, and also appears to significantly over-estimate how much search effort is expended in the expanded areas. This is because search effort is allotted by Bear Observation Areas (BOAs). While these BOAs have been added to peripheral areas through time, in 1998 eight of the original BOAs were each split in two. The result is that while total area searched is now 2.3 times higher than in 1988, the total number of BOAs, relative to

those in the core, have only increased 1.8 fold and greater than 50% of all the BOAs searched each year are still in the core. In sum, while changes in the search area are of importance, VMEA's argument for how to correct for this is too extreme, and seems to ignore some of the very arguments they emphasize about how the formal search effort is organized.

- **Changing or stable sightabilities of bears.** VMEA suggest that there is little data to support the idea of shifting sightabilities through time. However, at least one important driver of increasing sightability, the use of moth sites, is deemed so important by Higgs et al. that they eliminated data on bears seen on moth sites from their analyses. There is also no doubt about the increasing use of these sites (Mattson et al. 1991, Bjornlie 2012), and our results shown above make clear the power of moth site use to explain rising Chao2 numbers (Tables S1 and S2). An objection could be made that accounting for bears using moth sites doesn't change the fundamental pattern of Chao2 numbers (see arguments made by Bjornlie 2012). However, these corrections only account for bears directly seen at or very close to moths sites, while movement to or from these high elevation areas, and correlated probabilities of being in easy-to-see high elevation areas (including foraging on other high elevation resources: Mattson et al. 2004), may well magnify the effects of moth site use. We don't have the spatial data to evaluate this supposition, but the very strong effects of moth site use on Chao2 estimates makes this a likely complication to the simple correction of moth site effects by the removal of bears seen on or immediately adjacent to moth sites from analyses (e.g., Figure 6 of VMEA).
- **Observation flights are arranged in such a way as to be poorly approximated by a Poisson spatial process.** At its heart, our model of how searching works is a Poisson process, that assumes that increasing search effort over the entire area leads to increasing probability of seeing any one bear, including seeing it multiple times. While this the same implicit assumption used by study team members in their own simulations (Keating et al. 2002, Cherry et al. 2007), VMEA object that it is unrealistic, given the blocking of this effort into bear search areas and into two time blocks per year. The representation of complex searching processes by a Poisson process is very widely used in many fields, because it is often an excellent approximation in the face of the types of complexities that VMEA note. Is it a reasonable way to represent searching for Yellowstone grizzly bears? We first note that even the formal searching process is very capable of yielding more than 2 sightings of a single bear in a year; the 'search periods' are not instantaneous; the first period often spans 2 months of time and the second round spans 2-4 weeks (West 2012, Table 10 footnote), leaving plenty of opportunity for bears to move between areas. As noted above, our analyses are also on the same data that are used to generate Fcoy and Chao2 estimates, which is to say the entire data set of observations made in any manner. In the only full frequency data published by the study team, from 1986 to 2001 (Keating et al. 2002, Table 4), observation frequencies ranged up to 15 sightings per year and 27% of all Fcoy were seen 3 or more times within a year. As this shows, the ideal sampling

regime described by VMEA does not even vaguely approximate the actual data collection used to generate Chao2 estimates. If the concerns that VMEA detail were serious and applied to the actual data used to estimate Chao2, the observation frequencies of individual bears should be truncated, so that fewer than expected bears would have high numbers of observations in any one year, resulting in a lower than Poisson variance to mean ratio (variance and mean should be equal for a Poisson process). Using Keating et al.'s table of full frequency data taken from 1986 to 2001, and estimating the number of zero observations via the Chao2 estimator, we find that the variance in observation numbers is higher than the mean in 13 or 16 years, and the mean ratio across years is 1.59. This higher than Poisson variance corresponds to a mixed process with bears of very different observabilities, the assumption that we, and also Keating et al., make. If VMEA's point applied, even approximately, then variance in sighting frequencies should be less than their mean, a pattern the data simply do not support.

- **Relative vs. absolute search effort.** We add one last point about search effort, as VMEA's discussion might make this simple fact seem muddled: if observation flight hours are proportional to total observation effort, simulations based on the 'observation hours' will not yield artifactual results. In other words, changing the units of observation effort does change the results.
- VMEA are correct in pointing out that we mis-wrote that the relationship between the CV in sightabilities and Chao2 estimates is positive, when, as is correctly shown in D&C Figure 3B, the relationship is negative. However, the fundamental point – that the mean and variance in sightabilities strongly influence Chao2 estimates – remains.
- **Not properly citing Keating et al 2002 and Cherry et al. 2007.** This is one of the stranger charges of VMEA, as we directly cite these authors for exactly the results that VMEA say we don't credit to them. Apparently, VMEA feel that because we did not use the term 'bias' we slighted these authors and their work. In fact, it is the shifting bias with changing model parameters (which is what we cite them for) that is most important for our and their analyses, and exploring this sensitivity is exactly what we give them credit for.
- **Misunderstanding and mis-representing Link 2003.** VMEA claim that we mis-stated Link's conclusion about population sizes estimation in the face of heterogeneity in sightability. First, while Link for the most part applies the term 'non-identifiability' to the distribution of sightabilities, the title of his paper makes his main point clear: "Nonidentifiability of population size from capture-recapture data with heterogeneous detection probabilities." VMEA go on to say, "However, Link (2003) did not show that estimators could not approximate true population size." This directly contradicts the main point of Link's paper, which he states as: "The problem is this: that while it may be possible to discern heterogeneity in detection probability, it is likely that an analyst will be unable to distinguish between reasonable descriptions of the heterogeneity, *even when these alternative descriptions lead to vastly different inferences about population sizes.*"

[italics added]” VMEA further claim that “Cherry et al. (2007:198) actually referenced this issue and clearly demonstrated that estimates were close to truth, although still biased low.” In fact, Cherry et al. do reference this issue, and then go on to show that two different underlying models for sightability variance can lead to dramatically different patterns of bias with varying effort, confirming Link’s point and ours as well.

As we note above and in the main text, the analyses by Higgs et al. 2013 are an example of how to overcome many of the problems of the inferences made to date using Chao2. VMEA seem to see the Higgs results as a refutation of our analyses, but we view them as confirmation of our concerns. First, there would be no reason to even take the approach of Higgs et al. if the VMEA authors truly believed that observation effort and changing environmental factors didn’t result in shifting observation parameters through time. Second, the main result of Higgs et al. is exactly the same one we arrived at: that the inherent difficulties in estimating annual numbers make accurate trend detection extremely difficult. And finally, the relatively low correlation between the median population estimates of Higgs et al. and Chao2 for the years 1997 to 2012 (Pearson $r^2=0.375$; data from Higgs et al. Fig 4) should give pause concerning inferences made about past population trends from Chao2. We thank Drs. Higgs and van Manen for providing the data from Higgs et al. to make this comparison.

DEMOGRAPHIC ANALYSES

As with their dissection of our Chao2 analyses, VMEA have numerous criticisms of our exploration of whether the incorporation of senescence effects could substantially change previous demographically-based estimates of population growth for the Yellowstone population. Before discussing these in detail, we concentrate on the fundamental result of their own analyses (which use current data on demographic patterns, which are not published and therefore we could not use), which confirm, rather than refute, our concerns.

VMEA used their own, new estimates of age-specific survival and reproductive functions to re-estimate population growth rates from 1983-2001, and compare these to the results of our modeling and of their previous estimates. They find substantial reductions in estimated mean annual growth rates that, compounded over these 18 years, result in even more substantial declines in population growth over the entire time period (Table S3). For example, under the ‘high’ survival estimate scenario, their estimate of mean stochastic lambda with both senescence effects is 1.0503, compared to our estimate of 1.0427, and their previous estimate, not trying to model senescence, of 1.0776. Assuming a starting population of 57 adult females, the former IGBST estimate would predict a 3.8 fold increase in numbers over 18 years; D&C’s model would predict a 2.1 fold increase, and VMEA’s new model including senescence effects would predict a 2.4 fold increase. For the ‘low’ survival scenario, there is a similar drop in predicted

increases when incorporating both senescence effects (Table S1). Overall, VMEA's new models predict increases in numbers considerably closer to those of our models than the estimates based on previous IGBST demographic results.

VMEA's way of reporting of the substantial changes in growth they find makes these changes seem small: they report a percentage reduction in the mean lambda values, rather than the change in the increase rate (e.g., 2% per year), or of $\log(\lambda)$, that would better reveal the significance of these effects. They also do not discuss the compounding effects of these differences across time, which are what make their new estimates of population growth quite close to our own, and distant from estimates based on the IGBST's previous work.

Beyond the fundamental point that their analyses confirm, rather than refute, our models, there are numerous smaller points to address:

- First, we point out a mistake we made in the example demography program we posted in the Supporting Information for D&C. This program uses parameter values for survival senescence that are not the final ones used in generating our Figure 6. We correctly described the parameters used in our actual simulations (from Table 9 of Boyce et al. 2001), but provided a cleaned-up a version of the program that used other parameter values. While this was our mistake, we are surprised that VMEA, who used and modified this program, didn't notice that it generates predictions different from those shown in D&C Figure 6. This difference also accounts for different results shown for D&C models in our Table S1 and VMEA's Table 1. It also relates to our next point.
- VMEA say that we used an "extreme" function for survival senescence, but, as we stated in D&C, all published survival models for the Yellowstone grizzly are in close agreement (Figure S1). The high survival curve presented in VMEA Figure 5 shows far greater survival into later life than do previous estimates of relative survival rates. While no parameters or exact methods (e.g., whether other covariates were included in the analysis) are given to explain how this fit was obtained, it does not correspond well to the age distribution of adult females monitored for demographic data (Figure S2) and shows a surprisingly high survival rate of bears into the late 20s. As VMEA do not present any numerical or graphical explanation of their low survival curve we can't evaluate how well it matches those in the previous literature, or the distribution of monitored bears.
- Another claim of VMEA is that we "ignored all other covariates in the model (i.e., sex, in Yellowstone National Park, number of management actions, distance to development, road density, trail density)" and that this has important effects on our results. This statement is simply wrong, and reflects lack of understanding either of the way we combined annual estimates of overall adult survival for each year with the senescence function (an approach we clearly explained), of the way proportional hazard functions are used and interpreted, or both.

- VMEA take issue with our analysis of the proportion of adult bears that would survive to very old age, based on previous analyses of average adult survival. Their claim is that our presentation is misleading, as many young bears die before reaching the adult class. However our point pertains to representation of the adult class and survival rates for this class and their plausibility. The mortality rates of young classes is not relevant to this point, and in fact obscure the issue.
- VMEA are correct that Harris et al. 2006 did conduct limited simulations of reproductive senescence, and we were mistaken in not mentioning this. However, we note that in this article Harris et al. show extremely limited results from these simulations, making it hard to evaluate these models. We also note that Harris et al. conclude that reproductive senescence is not important because they only ran models that counter-balanced this effect with the influence of mother age on litter size and cub survival, effects that is not well-supported by the IGBST's own analyses (Schwartz et al. 2006a and b).
- The second column of VMEA's Table 1, and considerable discussion in their paper, is centered on the idea of an appropriate reference value for mean fecundity. What VMEA are arguing for here is exactly a point we make in our paper (see first paragraph of the Demographic Analysis section of D&C): there are correct ways to get stage-averaged vital rate values that will implicitly incorporate senescence effects. We have no quarrel with their reasoning, it is just irrelevant to the issues at hand.
- Finally, VMEA argue that there is no reason to suggest that age bias in bears used for demographic rate analyses could have skewed estimates of vital rates. However, the data they present themselves suggest otherwise (Figure S2). Adult females monitored for demographic information over-represent younger and prime-age animals, and markedly under-represent older bears, at least if the high survival curve VMEA have fit is actually accurate. As we note above, since they did not show any information about their low survival curve, we cannot compare its distribution to that of the monitored females.

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Table S1. Correlations between different explanatory variables that could be used to explain changes in Chao2 estimates through time. These results are for data from 1986 through 2010, the years for which we have search area data with which to conduct the search effort corrections that VMEA make. Area-adjusted search hours indicate the corrected search effort advocated by VMEA, while BOA-corrected search hours uses the correction we describe in the SI text.

	Year	Moth sites used	search hours	Area-adjusted search hours
Year				
Moth sites used	0.88			
search hours	0.93	0.91		
Area-adjusted search hours	0.74	0.86	0.83	
BOA-corrected search hours	0.79	0.89	0.90	0.95

Table S2. Explanatory power from regressions of log(Chao2) values on different independent factors. In all cases, the slope of the regression was significant.

Model	adjusted r ²
Year	0.5896
Year + Year ²	0.6091
Moth sites used	0.6062
search hours	0.5219
Area-adjusted search hours	0.3774
BOA-corrected search hours	0.4534

Table S3. Comparing results of different demographic models that do and do not include senescence. This table is based on the comparisons shown in van Manen et al. 2014, but corrects errors and emphasizes the correspondence of the different models in predicted population growth rates.

Survival rates	Model structure	Source	Ending Number	Mean stochastic lambda	Proportional increase over 18 years
High	Original IGBST		219	1.0776	3.8
	survival senescence	DC	192	1.0698	3.4
	survival senescence	IGBST	216	1.0768	3.8
	Reproductive Senescence	IGBST	136	1.0495	2.4
	Both	DC	121	1.0427	2.1
	Both	IGBST	138	1.0503	2.4
Low	Original IGBST		131	1.0473	2.3
	survival senescence	DC	115	1.0398	2.0
	survival senescence	IGBST	142	1.0520	2.5
	Reproductive senescence	IGBST	81	1.0197	1.4
	Both	DC	71	1.0123	1.2
	Both	IGBST	90	1.0257	1.6

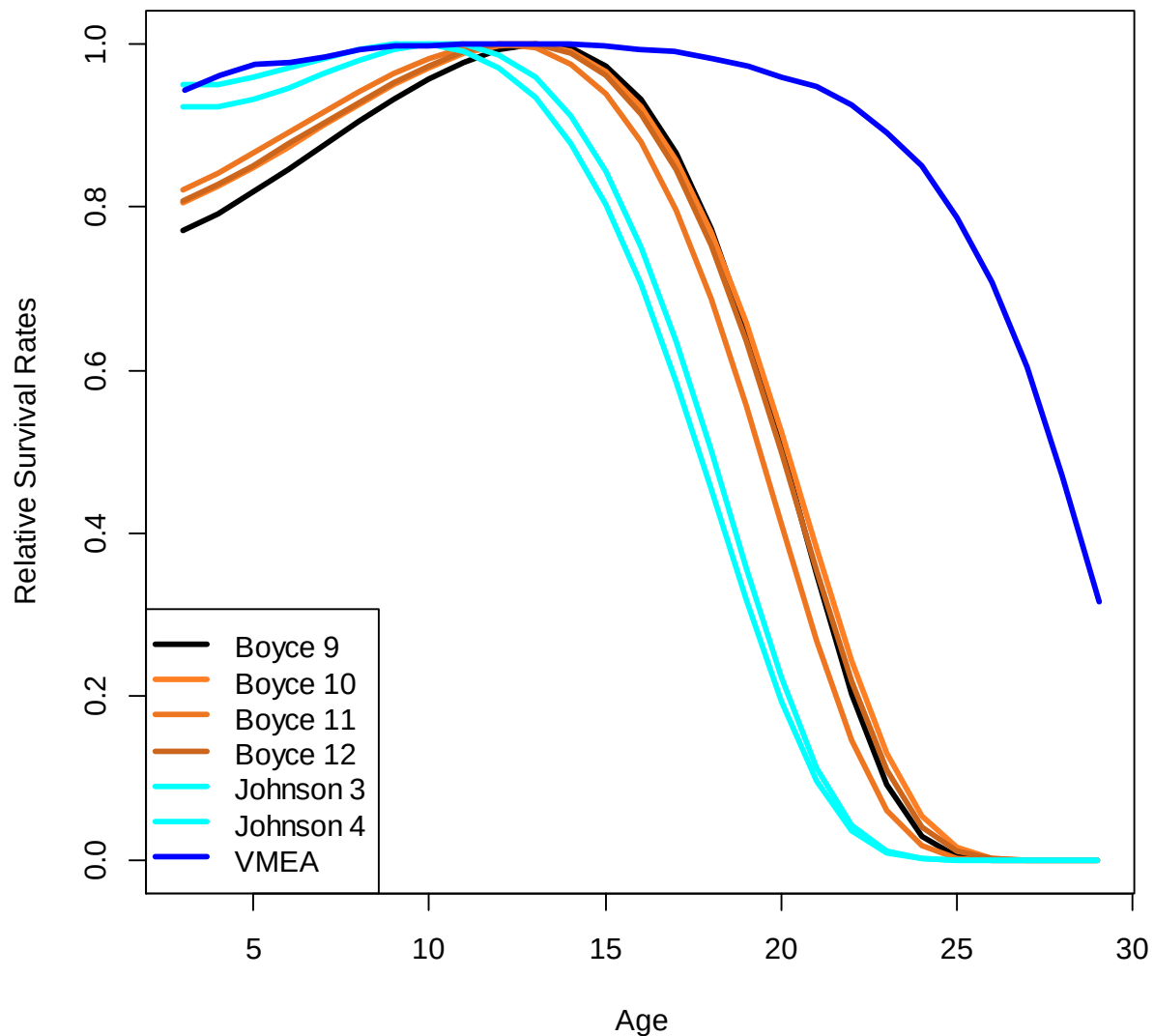


Figure S1. Comparison of different relative survival curves from different sources. All curves show survival relative to the highest age-specific annual survival rate. Boyce et al. (2001) give parameters for 4 models of age dependent survival (numbers refer to the table of Boyce et al. giving parameters for each survival curve), while Johnson et al. (2004) give two models. Finally, we plot the high survival curve of VMEA. All previous survival curves are in close agreement, and the one D&C used (Boyce 9) is one of the most optimistic regarding low senescence. VMEA's survival curve is quite different from any preceding estimate, and also does not match the observed age distribution of monitored bears (Fig. S2)

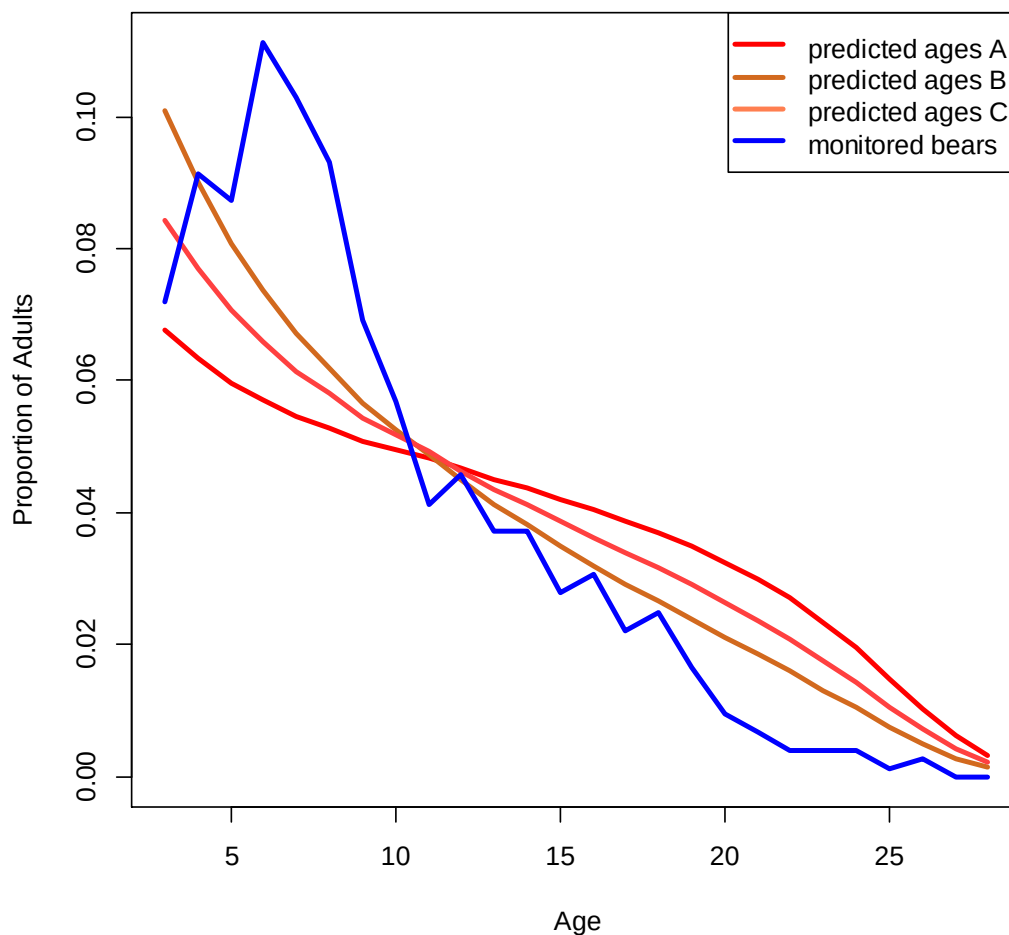


Figure S2. Comparison of the expected distribution of ages of adult female bears, from VMEA's 'high survival' survival curve (VMEA Figure 5) and the age distribution of monitored bears (VMEA Fig. S2). The age distribution given by VMEA in their Figure S2 are for bears sampled over 28 years, making it difficult to adjust expected age distributions to account for population growth. We therefore present three expected age distributions, all based on VMEA's 'high survival' survival curve: A assumes no population growth, B assumes a lambda of 1.05, and C assumes a lambda of 1.027. The latter two assumptions correspond to VMEA's predicted growth rates with high and low survival rates (see Table S3). While VMEA claim that there is no sign of biased sampling of different ages of bears, comparison of the any of the distributions predicted by their survival curve and the ages sampled indicates that there is, in fact, a significant bias towards sampling younger bears. Older bears are either under-sampled, or this survival curve over-estimates survival into older age groups. We do not compare the monitored bear ages to the low survival curve because VMEA do not give any numerical or graphical information on this survival curve in their article.