Van Manen *et al.*, *Doth Protest too Much: New Analyses of the Yellowstone Grizzly Population Confirm the Need to Reevaluate Past Population Trends*

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Grizzly bears are an essential part of healthy, fully functioning ecosystems in western North America. Understanding how grizzlies have responded through time to management and habitat changes is therefore key to understanding and protecting not only this one species, but also entire ecosystems. Our purpose in examining Yellowstone grizzly population growth (Doak and Cutler 2013; henceforth D&C) was to evaluate the potential for problems with analyses that underlie the perceived rate of increase of this population. By doing so, we hoped to prompt members of the IGBST, who control the data sets on this population, to test for and deal with these potential issues. It is therefore disappointing that, in our view, van Manen *et al.* (2014; henceforth VMEA) focus mostly on refuting details in our specific methods—criticisms that we find largely without merit and respond to in detail in Appendix S1—rather than on the larger substance of these concerns.

Two aspects of VMEA's article are particularly puzzling. First, they concentrate on refuting many of the particular simulations that we explicitly presented as examples of general issues. VMAE show, for example, that one particular simulation of observation effort effects does not *completely* explain the full rise in Chao2 estimates of population size (i.e., it explains only up to 77% of estimated annual growth: Appendix S1). VMAE's analysis does not invalidate that observer bias can be a significant effect and is a distraction from the general problem being addressed.

More importantly, there is a perplexing inconsistency between VMEA's blanket rejection of our concerns and the largely confirming results presented on senescence effects in VMEA's manuscript, and on estimation of population growth from survey data by three of these same authors in Higgs *et al.* 2013. VMEA suggest that their models show that senescence has trivial impacts on population growth estimates; in fact, their results show that incorporating senescence sharply reduces previously estimated population growth from 1983 to 2001 (see Appendix S1). Higgs *et al.* (2013), an excellent effort to improve analysis of this population, is exactly the type of approach we support, and is predicated on dealing with many of the observation issues that also motivated our

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work. This study shows that there is so much uncertainty in population estimates that inferences about population trends are extremely weak. This is precisely our basic conclusion. The only serious difference between our view and theirs is that they only look forward in time, but their results reinforce our view that past population changes inferred from less sophisticated analyses must also be reexamined.

We stand by our concerns over what the Yellowstone grizzly data really can and do tell us about this population. As with many conservation controversies, the most productive way forward would be collaborative examination of alternative interpretations of the data by all parties. Alternative, a National Academy of Sciences review, or reanalysis of the various contended issues by some other independent team with access to all of the data, would go a long way towards promoting the best conservation assessment of this population.

Supporting Information

Additional Supporting Information, including extensive text responding to VMEA's arguments, as well as the following tables and figures, may be found in the online version of this article at the publisher's web site:

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.

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

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.

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 (Figure 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 Figure 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.

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