Further comments on Robben Island penguin Bayesian analysis

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This paper further addresses concerns raised by Res Altwegg in relation to the penguin population model described in document MCM/2009/SWG-PEL/33 (Robinson and Butterworth, 2009). This model was designed as a simple means to obtain estimates of annual penguin survival taking account of both adult tag-resighting data and moult counts.

Analyses using this model were repeated using Bayesian methods, described in document MCM/2010/SWG-PEL/07 (Robinson and Butterworth, 2010). Res Altwegg provided helpful comments, and these were tabled along with our responses in document MCM/2010/SWG-PEL/09 (Butterworth and Robinson, 2010). It seems still that not all issues were fully dealt with and further clarifications are needed. We attempt to provide these in this document.

In particular, Res Altwegg states in response to Butterworth and Robinson (2010): "The problem is that your models are not reliably separating reproduction and survival. This is a structural problem (i.e. there is structure in the model for which there is inadequate information in the data to be supported." This is a quite understandable reaction to the original result in Robinson and Butterworth (2009), and similar results in the different model of MCM/2008/DEC/SWG-PEL/27, which show some "MLEs" of survival rates on a constraint boundary with a Hessian estimated CV of zero, which could be taken to imply an exact estimate and hence "exact" separation of reproduction and survival rates during a period when direct information on adult survival rates from tagging data was not available.

However, these earlier approaches were initial given time constraints. Hessian estimates of CVs (provided for illustrative purposes in regard to differences in precision with and without tag information) are not reliable for estimates on constraint boundaries. Furthermore, the estimates were not truly MLEs, as with a random effects model for reproduction (breeding success), strictly these random effects should be integrated out to obtain true MLEs. That, however, would be a difficult computational task and the easier, commonly used and appropriate way to deal with such problems is via the Bayesian paradigm.

It is important to appreciate that there is no claim that the approach used completely separates reproduction and survival effects, even over periods for which tagging data are available. In Fig. 1 we reproduce the median and 90% posterior probability interval for annual penguin survival from the Bayesian analysis. In Fig. 2 we show the corresponding plot for annual breeding success. The figures show that the joint posterior reflects uncertainty in both survival rates and breeding success. There

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is, however, a decrease in the width of the probability interval for breeding success in the years when tagging data are available, as might be expected.

Fig. 3 shows a comparison of prior and posterior marginal distributions for a few years for both survival rates and breeding success. (For the results shown, the prior used for survival rates is U[0, 0.98]. For breeding success He^{η}, the prior on H is U[0,2] and the prior on η is N[0,1]. Any realizations for which $He^{\eta} > 2$ are excluded, i.e., no breeding pair can successfully fledge more than two chicks each year.) It is clear from these plots that the priors *are* updated through the process of the analysis. While the information on juvenile and adult abundance from moult counts, the population dynamics equations, and the tag data for some years does *not* allow *exact* estimates of annual breeding success, it *is* able to reduce the uncertainties in the values of these parameters.

A key question, which Res Altwegg asked earlier, is whether these results are sensitive to the specification of the priors used. Robinson and Butterworth (2010) showed that alternative specifications for the survival rate prior made very little difference to results. When sensitivity to alternative specifications of the breeding success prior was tested, in particular rendering this prior even less informative through increasing the standard deviation of η, again the final results are hardly affected.

Future work

The results reported here are not intended as final. In particular, the Poisson-based likelihood used for the tagging data will soon be substituted by the binomial form used in the MARK package.

Res Altwegg has requested that sensitivity to the assumption of equal detectability of juvenile and adult penguins in the moult count be examined. Previous analyses had assumed equal detectability on the basis of comments from Rob Crawford that all birds moult and nearly all would be counted at Robben Island. However, if penguin biologists involved in these counts can provide a prior for this differential detectability, that can readily be incorporated into future calculations.

Finally, it has always been the intention that the analyses of the impact of pelagic catch levels on penguins that were based on results in MCM/2008/DEC/SWG-PEL/27 would be repeated replacing the "MLE" approach of that paper by a fully Bayesian approach to better incorporate uncertainties. Reports of results from that exercise will follow in due course.

References

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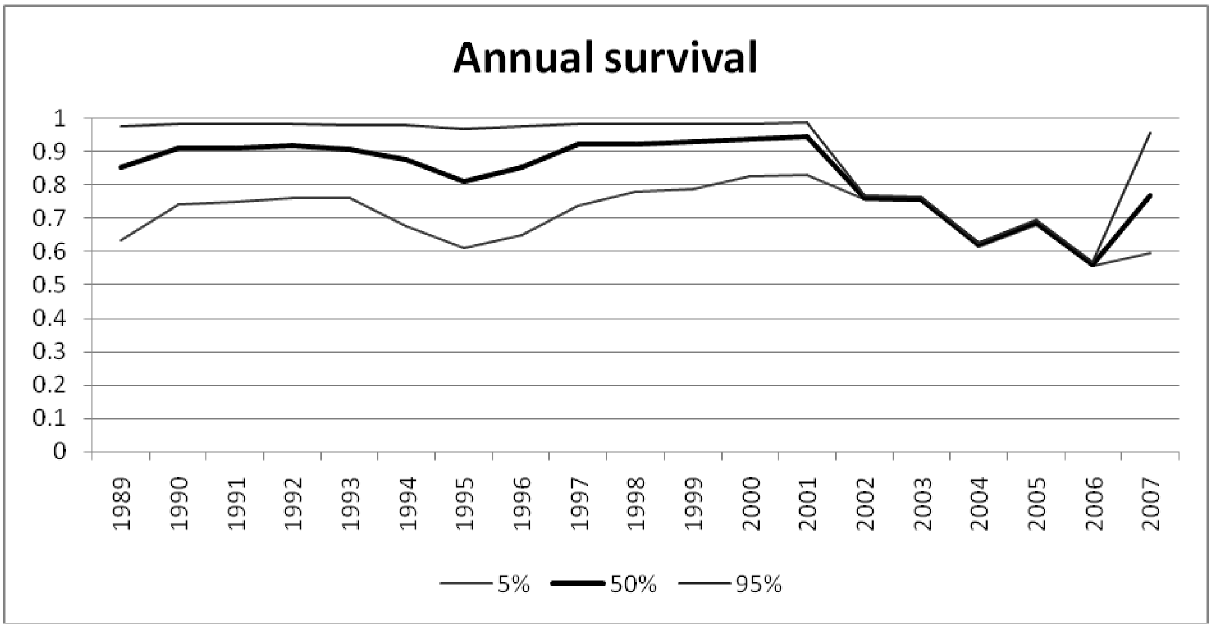


Fig. 1: Annual survival rates calculated when incorporating both moult counts and tagging data (2001 resightings excluded) using the Bayesian analysis. The posterior median is shown along with the 90% probability interval envelope.

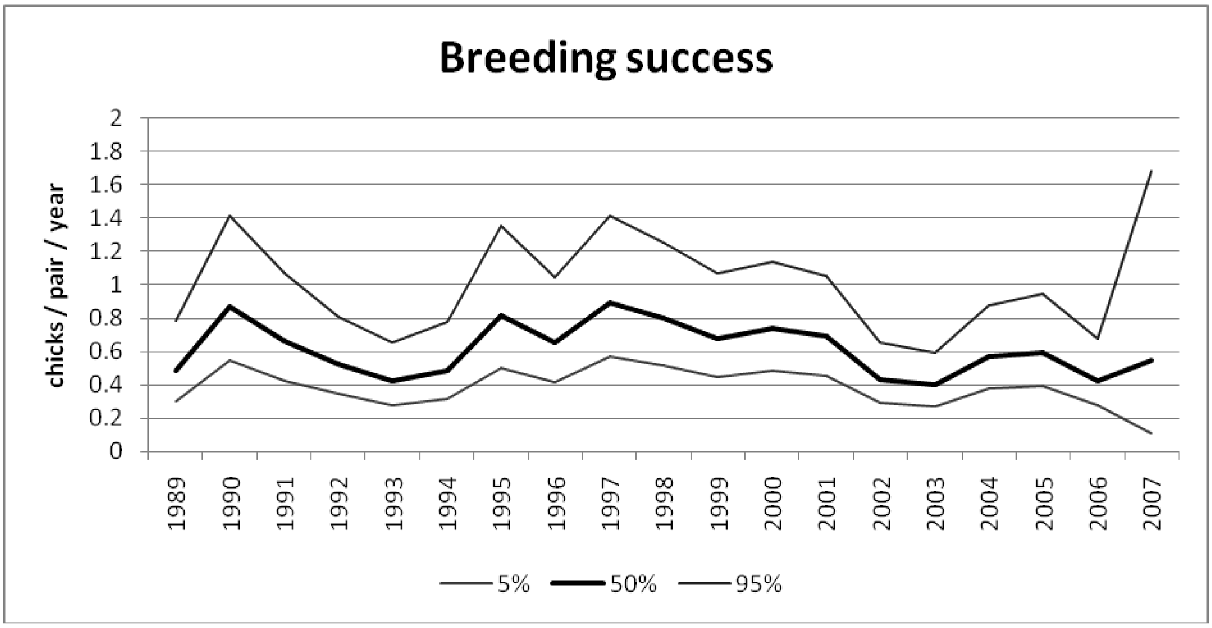
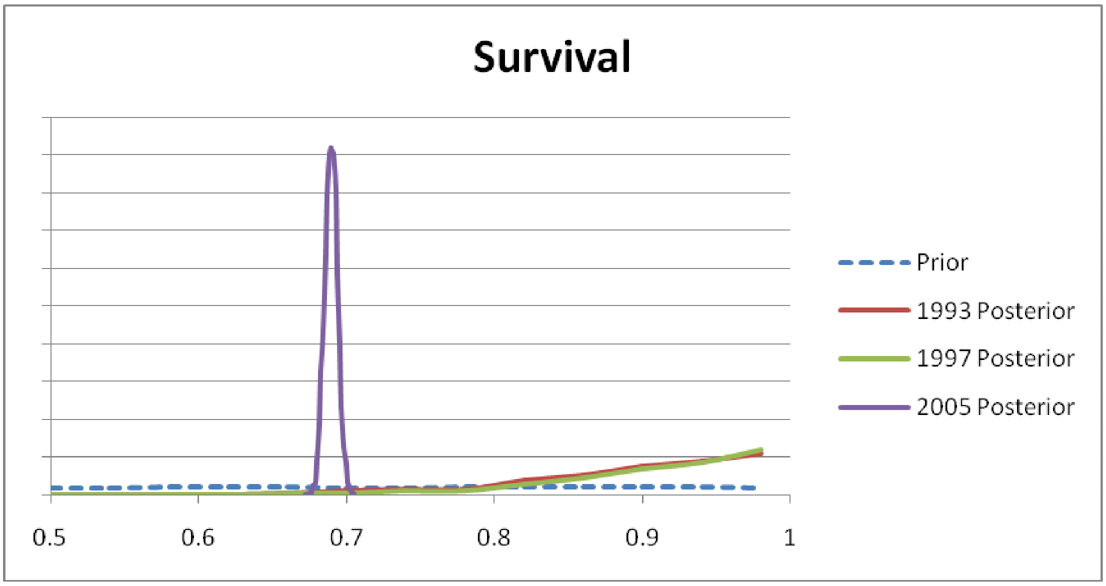


Fig. 2: Annual breeding success rates calculated using the Bayesian analysis. The posterior median is shown along with the 90% probability interval envelope.



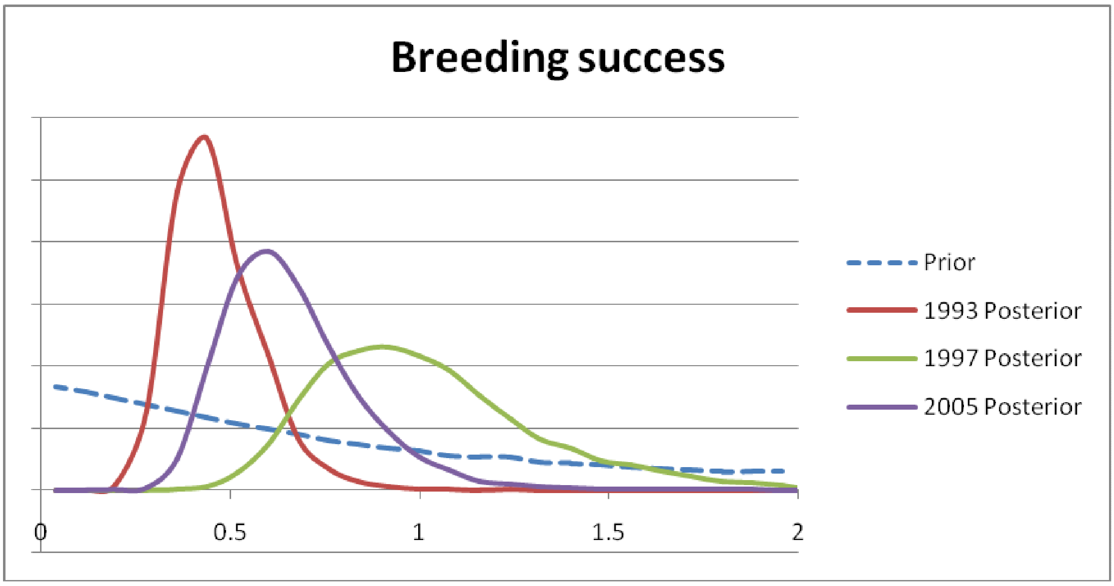


Fig. 3: The prior distributions (dashed lines) for survival rates and breeding success plotted with posterior distributions for the years 1993, 1997 and 2005. The lower level of the prior for higher values of breeding success arises from the $He^{\eta} > 2$ exclusion.