## Survival of African Penguins on Robben and Dassen islands from 2002 to 2006

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I estimated survival of African Penguins on Robben Island and Dassen Island between 2002 and 2006. The basis for the analysis was a data file supplied to me by Barbara Barham on 16 February 2009. It included banding, recapture, and resighting data from throughout the South African range of the penguin. Data on banded birds found dead (recoveries) were also included in this file. I decided to restrict the analysis to adult birds, which was the vast majority of the data. After some trials, I further restricted the analyses to two colonies, Robben and Dassen islands. The reason for this restriction was that I could not obtain reliable estimates for any of the other colonies, whether or not I included dead recoveries, and even with simplifying assumptions imposed (such as constant survival/recapture and linear time trends). It turned out that there were too few dead recoveries to justify the added model complexity, and I also excluded these data.

In the end, I used data on 6694 penguins on Robben Island and 5603 on Dassen Island, observed between 2001 and 2008. I understood that most of these birds were oil-spill victims and had been banded in 2000 after being rehabilitated following the “Treasure” oil spill or being relocated to prevent their becoming oiled. I used the first re-encounter at one of these two colonies as initial encounter rather than the banding occasion because I did not know how many birds were banded and never seen again. So the estimates are based on birds that made it back to one of the islands after having been released. I believe this makes the results more applicable to the wild population because it likely excludes birds that were most negatively affected by the oiling incident. In the data files, the encounters were pooled by calendar year and I took the survival intervals to be from one year to the next.

I used classical capture-mark-recapture (CMR) methods (Lebreton *et al.*, 1992) to estimate survival and recapture probabilities, where recapture refers to the probability of encountering (recapture or resighting) an individual given that it was alive in that particular year. The most general model allowed for differences among colonies and years in survival and recapture rates. In addition, I considered the effects of transients using an age-since-first-encounter model. Assuming that transients only appear once at a colony, birds seen for the first time consist of a mixture of transients and residents. This leads to survival rates that are biased low during the subsequent time step, but after that, survival estimates are unbiased (Pradel *et al.*, 1996). During the first year of the study, the proportion of transients is not known and I therefore cannot present a corrected survival estimate for the year 2001 - 2002. The most general model allowed the proportion of transients to vary among colonies and year. I also considered simpler models with constant proportions of transients, and where survival varied over the years in parallel at both colonies. All models were fitted in program MARK 5.1 (White & Burnham, 1999).

The CMR methods assume equal survival and catchability among individuals. Further assumptions are that the time span during which individuals were recaptured or resighted was short relative to the survival interval. Violation of the latter assumption leads to apparent heterogeneity in survival. The survival estimates are not very sensitive to violation in these assumptions, but if the violations are strong, survival rates may be biased low (Hargrove & Borland, 1994). Heterogeneity in survival and recapture rates leads to overdispersion in the data set, which I estimated using the median- approach in program MARK (White & Burnham, 1999):  was 1.6, which indicates moderate overdispersion. I used this estimate to adjust the confidence interval and based model selection on QAICc, Akaike’s Information Criterion adjusted for overdispersion and sample sizes (Burnham & Anderson, 2002). Further assumptions are that bands are not lost or misread. Misreading of bands would cause heterogeneity in recapture rates and possibly a positive bias in survival estimates. Loss of bands would result in a negative bias in survival estimates. If we want to draw conclusions from this analysis about the whole penguin population, we also need to assume that the banded birds are representative of the population as a whole.

I want to make it clear that I view the results of this analysis as preliminary. Possible issues with heterogeneity especially in recapture rates need to be looked at in more detail.

Table 1: Summary of model selection for capture-mark-recapture analysis. The models consisted of two components describing survival (Phi) and recapture (P) rates. The models included the factors year, colony (col), and effect of transients (trans), either in a fully interactive way (\*), or as additive effects (+). If only a two-way interaction was included, this is indicated by (:) between the two factors involved. The table shows Akaike’s Information Criterion adjusted for overdisperion and sample size (QAICc), and the difference in QAICc between the current model and the best one (delta QAICc). AICc weights give the relative support of a particular model compared to the other models in the set, and QDeviance is the deviance adjusted for overdispersion.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  | Model | QAICc | Delta QAICc | AICc weights | K | QDeviance |
| 1 | Phi(trans:col+year)P(col\*year) | 22111.195 | 0.000 | 0.443 | 24 | 518.736 |
| 2 | Phi(trans:col:year)P(col\*year) | 22111.805 | 0.610 | 0.327 | 30 | 507.309 |
| 3 | Phi(trans+col+year)P(col\*year) | 22113.379 | 2.184 | 0.149 | 23 | 522.926 |
| 4 | Phi(trans\*col\*year)P(col\*year) | 22114.596 | 3.401 | 0.081 | 38 | 494.040 |

Model selection favoured a model with different proportions of transients in the two colonies, but additive effects of colony and year on survival (Model 1, Table 1). The recapture rate depended on interactive effects of year and colony. The second best model (Model 2) was nearly as well supported as the best model and allowed for an interaction between year and colony on survival. With temporal variation in recapture probabilities, the survival estimates for the last year of the study can be unreliable, and I therefore only present survival up to the 2006 - 2007 interval. Both models yielded similar survival rates (Fig. 1 shows the estimates from Model 1). At both colonies, survival declined after 2003. The recapture rates varied from 0.51 to 0.59 on Dassen Island and from 0.16 to 0.48 on Robben Island. The proportion of transients was estimated to be 8.2% on Dassen Island and 27.3% on Robben Island.

While I think these results need to be treated carefully, I believe that the observed trend in survival is real. Extreme heterogeneity in recapture rates can cause apparent time trends in survival (Devineau, Choquet & Lebreton, 2006). However, this seems only to happen if the recapture rates are very low and would not lead to such steep trends as observed here. The estimate of  did not indicate extreme heterogeneity, and the recapture rates were reasonably high to give some degree of confidence in the results. In any case, heterogeneity in recapture rates needs to be further investigated.

survival_model1

Figure 1: Survival estimates for African Penguins on Dassen and Robben islands, obtained from Model 1, Table 1. The x-axis indicates the starting year of the relevant survival interval. For example, the first estimate corresponds to the year 2002 – 2003. The vertical lines represent 95% confidence intervals.

**References**

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**Appendix 1**

Table A1: Survival and recapture estimates from Model 1, Table 1. In addition to the estimates, the table shows standard errors (SE) and lower (LCI) and upper (UCI) bounds of the confidence interval. Recapture estimates for 2008, and thus survival estimates for 2007 – 2008 are unreliable!

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | SE | LCI | UCI |
| Survival, Dassen Island | |  |  |  |
| 2002 – 2003 | 0.697 | 0.017 | 0.662 | 0.729 |
| 2003 – 2004 | 0.682 | 0.021 | 0.640 | 0.721 |
| 2004 – 2005 | 0.561 | 0.025 | 0.511 | 0.610 |
| 2005 – 2006 | 0.535 | 0.032 | 0.473 | 0.597 |
| 2006 – 2007 | 0.462 | 0.033 | 0.399 | 0.526 |
| 2007 – 2008 | 0.307 | 0.028 | 0.255 | 0.363 |
| Survival, Robben Island | |  |  |  |
| 2002 – 2003 | 0.765 | 0.016 | 0.731 | 0.795 |
| 2003 – 2004 | 0.752 | 0.019 | 0.714 | 0.787 |
| 2004 – 2005 | 0.644 | 0.025 | 0.593 | 0.691 |
| 2005 – 2006 | 0.620 | 0.029 | 0.562 | 0.675 |
| 2006 – 2007 | 0.548 | 0.031 | 0.487 | 0.608 |
| 2007 – 2008 | 0.385 | 0.026 | 0.334 | 0.438 |
| Recapture rate, Dassen Island | |  |  |  |
| 2002 | 0.584 | 0.019 | 0.547 | 0.621 |
| 2003 | 0.517 | 0.019 | 0.479 | 0.554 |
| 2004 | 0.532 | 0.022 | 0.489 | 0.574 |
| 2005 | 0.511 | 0.028 | 0.456 | 0.565 |
| 2006 | 0.591 | 0.038 | 0.514 | 0.663 |
| 2007 | 0.521 | 0.051 | 0.422 | 0.619 |
| 2008 | 0.913 | 0.143 | 0.238 | 0.997 |
| Recapture rate, Robben Island | |  |  |  |
| 2002 | 0.179 | 0.031 | 0.126 | 0.247 |
| 2003 | 0.280 | 0.017 | 0.247 | 0.315 |
| 2004 | 0.277 | 0.016 | 0.246 | 0.310 |
| 2005 | 0.165 | 0.013 | 0.141 | 0.193 |
| 2006 | 0.398 | 0.025 | 0.350 | 0.447 |
| 2007 | 0.477 | 0.033 | 0.412 | 0.543 |
| 2008 | 1.000 | 0.013 | 0.000 | 1.000 |

Table A2: Survival and recapture estimates from Model 2, Table 1. For details see Table A1. Recapture estimates for 2008, and thus survival estimates for 2007 – 2008 are unreliable!

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Estimate | SE | LCI | UCI |
| Survival, Dassen Island | |  |  |  |
| 2002 – 2003 | 0.673 | 0.021 | 0.630 | 0.712 |
| 2003 – 2004 | 0.696 | 0.026 | 0.642 | 0.745 |
| 2004 – 2005 | 0.552 | 0.030 | 0.492 | 0.611 |
| 2005 – 2006 | 0.528 | 0.038 | 0.453 | 0.602 |
| 2006 – 2007 | 0.533 | 0.066 | 0.404 | 0.657 |
| 2007 – 2008 | 0.255 | 0.039 | 0.187 | 0.339 |
| Survival, Robben Island | |  |  |  |
| 2002 – 2003 | 0.795 | 0.020 | 0.752 | 0.831 |
| 2003 - 2004 | 0.747 | 0.027 | 0.691 | 0.796 |
| 2004 - 2005 | 0.663 | 0.039 | 0.582 | 0.735 |
| 2005 - 2006 | 0.618 | 0.045 | 0.528 | 0.702 |
| 2006 - 2007 | 0.522 | 0.036 | 0.451 | 0.592 |
| 2007 - 2008 | 0.397 | 0.029 | 0.341 | 0.456 |
| Recapture rate, Dassen Island | |  |  |  |
| 2002 | 0.574 | 0.019 | 0.536 | 0.612 |
| 2003 | 0.527 | 0.020 | 0.488 | 0.566 |
| 2004 | 0.530 | 0.023 | 0.484 | 0.575 |
| 2005 | 0.517 | 0.030 | 0.459 | 0.574 |
| 2006 | 0.606 | 0.041 | 0.523 | 0.684 |
| 2007 | 0.473 | 0.062 | 0.356 | 0.593 |
| 2008 | 1.000 | 0.031 | 0.000 | 1.000 |
| Recapture rate, Robben Island | |  |  |  |
| 2002 | 0.215 | 0.039 | 0.149 | 0.301 |
| 2003 | 0.274 | 0.018 | 0.240 | 0.312 |
| 2004 | 0.278 | 0.018 | 0.244 | 0.314 |
| 2005 | 0.162 | 0.015 | 0.134 | 0.193 |
| 2006 | 0.391 | 0.027 | 0.340 | 0.445 |
| 2007 | 0.493 | 0.035 | 0.425 | 0.560 |
| 2008 | 1.000 | 0.032 | 0.000 | 1.000 |

**Appendix 2**

Figure A1: The year of banding of penguins at Dassen and Robben islands that were used in the study.