

# **An initial implementation of suggestions by the 2020 Panel to improve estimates of the effect of fishing around islands on penguins by using models with random effects and applied to both aggregated and disaggregated data**

A. Ross-Gillespie and D. S. Butterworth<sup>1</sup>

Contact email: *andrea.ross-gillespie@uct.ac.za*

## **Summary**

Pending availability of data on the month for each observation for further analyses of the island closure experiment to address the suggestions made by the 2020 Panel, some initial analyses are conducted to explore the implications of the Panel's suggestions regarding sample size weighting for data-aggregated approaches, and nesting of random effects for methods using disaggregated data. These are applied to existing data for maximum foraging distance and chick condition. Results indicate that when these Panel suggestions are taken into account, there is little to no real difference in the results which these two approaches provide for the effect of fishing parameter. This is as the Panel anticipated, and in line with an earlier mathematical demonstration that use of the extra data available under the disaggregated approach would not improve the precision of these estimates. Some corresponding earlier results suggesting greater precision for the disaggregated approach were a consequence of applying a random effects approach without appropriate nesting of the data – an approach which is rejected by statistical analyses. Results for estimates of the effect of fishing parameter are more meaningfully expressed in terms of the consequent impact on the penguin population growth rate. For the cases examined initially here, the only meaningful result suggesting a negative impact of fishing in the vicinity of islands is for the maximum foraging distance variable for St Croix island.

*Keywords: Penguin, island closure experiment, random effects, nesting, fishing closure effect estimation, REML*

## **Introduction**

The 2020 Panel (Haddon *et al.* 2020) made a number of suggestions to advance the estimation of the effects of fishing around islands with colonies of penguins, particularly as regards the comparison of approaches applied to either annually aggregated or dis-aggregated (individual) data. These included:

- Use of common data and a common model structure for comparisons
- Inclusion of month as a co-variate
- Consideration of different nesting structures for models using random effects.

Finalised data with information on the month for each observation have been in the process of being compiled. In the meantime, therefore, to provide some initial insight, existing data for two response variables (maximum foraging distance and chick condition) have been used within a simple framework (no co-variates) to explore the implications of the Panel's suggestions. The nature of the individual chick condition data (which include some negative values) precludes use of the customary approach of log-transforming the response variable in that case, but fortunately a relationship of this variable to chick survival is available for a different penguin population. This is used to relate the results from the experiment for this variable directly to their impact on penguin population growth rate.

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<sup>1</sup> Marine Resource Assessment and Management Group, Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch, 7701

## Methods

### **Question 1: How does the precision of the estimated fishing effect differ when models including random effects are applied to aggregated compared to disaggregated data?**

A range of random effects models have been applied to the maximum foraging distance and chick condition data sets, with these data both in aggregated form (aggregated to yield a single value per year and island) and disaggregated form. The basic equation for these mixed models is:

$$f(F_{y,i}) = R + \beta_i + \delta_i^* X_{i,y} + \epsilon_{y,i,s} \quad (1)$$

where

- $F_{y,i}$  is the response variable, possibly log transformed (see below for more details for year  $y$  and island  $i$ ),
- $R$  represents the random effects components (more details below),
- $\beta_i$  is an island effect,
- $\delta_i^*$  is a fishing effect resulting from whether or not the neighbourhood around the island was closed to fishing<sup>2</sup>,
- $X_i$  is a vector with an entry of 1 in years where the neighbourhood of island  $i$  was open to the fishery, and 0 where that neighbourhood was closed, and
- $\epsilon_{y,i}$  is an error term, taken to be normally distributed with constant variance unless otherwise indicated.

#### Data transformation

As has been standard practice, the maximum foraging distance data have been log transformed by taking the negative of the logarithm so that a larger negative number implies a more negative impact on the penguin population, i.e.  $f(F_{y,i}) = -\ln F_{y,i}$ . For chick condition data, however, no transformation has been applied, *inter alia* because of negative values in the disaggregated data set given the manner in which this variable is defined, so that  $f(F_{y,i}) = F_{y,i}$ , and again a negative number implies a negative impact on the penguin population

#### Random effects components

When applied to aggregated data (both maximum distance and chick condition), the random effects component of equation (1) is simply (1|Year), i.e. a random year effect reflecting prevailing feeding conditions (assumed to be the same each year, random variation excepted, for both islands in a pair – because of their close proximity, these conditions at island should each relate closely to the forage fish abundance for that year).

When applied to the disaggregated data, a key question is whether nested or unnested models should be used. It is our understanding that Sherley et al. (2018), albeit unintentionally, used unnested models, while the general preference and particularly that of the review Panel is for nested models (Sherley 2020a&b, Haddon et al. 2020, Bergh 2021).

To illustrate the difference between a nested and an unnested model, consider a mixed model with a Year-Island random effects component. In R notation, an unnested model would have the following form:

$$\text{lmer}(\ln\text{Response} \sim (1|\text{Year}:\text{Island}) + \text{Island} + \text{X}:\text{Island}) \quad (\text{Model I})$$

<sup>2</sup> Note that this equation has been modified for greater generality depending to allow for different transformations ( $f$ ) of the response variable ( $F$ ). Accordingly, the fishing effect parameter has been generalised to  $\delta^*$ . For maximum foraging distance, where the data have been log-transformed,  $\delta^*$  is the standard  $\delta$  parameter for which results have been reported in previous analyses. For chick condition, where the data have not been transformed, the estimated value of what is now termed the  $\delta$  parameter needs to be interpreted differently from what has been done in the past (e.g. with respect to the assumed threshold below which fishing has a biologically meaningful impact on the penguin population) – see the Appendix for more details.

However, a nested model, with island nested within year, has the notation:

$$\text{lmer}(\ln\text{Response} \sim (1|\text{Year}/\text{Island}) + \text{Island} + \text{X}:\text{Island}) \quad (\text{Model IIa})$$

*This Model IIa is exactly the same as:*

$$\text{lmer}(\ln\text{Response} \sim (1|\text{Year}) + (1|\text{Year}:\text{Island}) + \text{Island} + \text{X}:\text{Island}) \quad (\text{Model IIb})$$

Nesting island within year implies that response variables for the two islands are correlated from year to year (i.e. a common (1|Year) component in addition to the island specific (1|Year:Island) component), whereas an unnested model implies that they are not (there is only the island specific (1|Year:Island) random effects component). The rationale underlying the design of the experiment with different treatments of the two islands from year to year was based on the assumption that such correlation exists (because the proximity of the pair of islands would mean that each year the forage fish densities near each island would tend to vary in the same direction about their averages over time), and provides a basis to separate the otherwise confounded effects of year and closure, thereby providing better estimation precision.

*Note that the unnested Model I is essentially a “sub-model” of the nested Model II, so that a likelihood ratio test can be used to compare the fits of the two. Results for such tests are provided in this paper to provide an objective quantitative basis for deciding whether a nested or unnested model is to be preferred.*

A second element is the inclusion in the random effects components of lower level information such as BirdID in the case of maximum foraging distance, and month for chick condition. Models including and excluding these further levels of information have also been explored.

#### Taking sample size into account for the aggregated model

*One criticism of the aggregated approach as applied in the past (Haddon et al. 2020) is that it does not take into account the number of data points used to calculate the annual averages. In order to investigate this (an option not present in R), the equation (1) mixed model (applied to the aggregated data) was recoded in AD Model Builder (ADMB) with the variance for the model residuals redefined as:*

$$\sigma_e^2(i, y) = \frac{\sigma_{i,y}^2}{N_{i,y}} + \tau^2 \quad (1)$$

*where  $\sigma_{i,y}$  is the standard deviation of the data collected for island  $i$  in year  $y$ ,  $N_{i,y}$  is the number of samples collected for island  $i$  in year  $y$ , and  $\tau^2$  is the remaining residual variance and an estimable parameter. On inspection of the annual sd values (see Table 1), it was decided that a sample-size-weighted average over years,  $\sigma^*$ , would be a more robust approach because the precision of year-specific estimates is poor because of instances of low sample size, i.e.:*

$$\text{island-combined: } (\sigma^*)^2 = \sum_{i,y} \sigma_{i,y}^2 (N_{i,y} - 1) / \sum_{i,y} (N_{i,y} - 1)$$

$$\text{island-specific: } (\sigma_i^*)^2 = \sum_y \sigma_{i,y}^2 (N_{i,y} - 1) / \sum_y (N_{i,y} - 1)$$

*Results for  $\sigma^*$  are listed in Table 2.*

#### **Question 2: What is the threshold value for the island closure effect parameter which corresponds a (“biologically meaningful”) 1% change in the annual population growth rate?**

In analyses of penguin data to date, estimates of the fishing effect have been taken to be biologically meaningful if they correspond to a change in the population growth rate of more than 1% pa. If response variables analysed are considered in log space, this has been assumed to correspond to a value of the fishing effect parameter  $\delta$  which is  $< -0.1$  (see Robinson et al. 2014 and the Appendix below) using the relationship between annual survival and the population growth rate. The question is whether this assumption can be replaced by a relationship established from data for at least some of the other response variables. To attempt to answer this question for chick condition, the data available are analysed

here using the following approach: (1) establish a relationship between chick condition and annual survival for another penguin population, and (2) substitute this relationship into the demographic equations of Robinson *et al.* (2014) (which correspond to the corresponding Leslie matrix eigenvalue equation) to establish an appropriate threshold for a change in the value of chick condition corresponding to a 1% change in the annual penguin population growth rate. Further details for this analysis are provided in the Appendix.

## Results

Table 3 gives the details of all the models that have been implemented in an attempt to answer Question 1. Table 4(a) and (b) list the results for these models applied to the West Coast maximum distance foraging trip data. For Table 4(a), the models were run with the Maximum Likelihood Estimation (MLE) method, while Table 4(b) compares a selection of MLE models with models run using the Restricted Maximum Likelihood (REML) method. While REML would be the preferred approach for all models, difficulties were encountered in implementing REML for the ADMB models, and therefore in the interest of comparability all the main models in Table 4(a) were also run with MLE. Table 4(b) serves to illustrate the impact of choice of MLE vs REML. Table 5 to Table 7 list the corresponding results for EC maximum distance, WC chick condition and EC chick condition respectively.

In most cases, the precision for  $\delta^*$  from the aggregated and disaggregated approach were fairly similar<sup>3</sup>. The one notable exception was when an unnested model that included BirdID as a covariate in the random effects component was applied to the maximum distance foraging data. This model yielded a standard error estimate for  $\delta^*$  which was roughly half that estimated by nested models and models applied to aggregated data.

Figure 1 plots the sample-size-weighted residual standard deviations from Equation (1) for Model A1+N, compared to the residual standard deviation for Model A1.

Table 8 lists the results for the likelihood ratio test conducted on a selection of models to investigate whether nested or unnested models are to be preferred. In many cases the nested model is not significantly better than the unnested model, but importantly for maximum distance when BirdID is included in the random effects structure there is strong statistical support for the nested model.

The analyses of the Appendix indicate that a  $\tilde{\delta}$  threshold of -0.09 for chick condition (when these data are not log-transformed) corresponds to a 1% reduction in population growth rate. Figure 2 plots results for the fishing effects ( $\delta^*$ ) from this paper in terms of the change in population growth rate estimated to result from fishing taking place in the vicinity of an island. The plot shows a paired set of results for each response variable and island pair. The left-side pair is for first aggregated then disaggregated data models that reflect results as reported in previous analyses (A1 and DO\_unnest respectively). The right-side pair incorporate the adjustments (respectively of sample size adjustment and random effects' structure selection) suggested by the Panel at their 2020 meeting, as best implemented in this document A2+N and D1+uneqvar respectively).

## Discussion

Question 1: How does the precision of the estimated fishing effect  $\delta$  differ when models including random effects are applied to aggregated compared to disaggregated data?

- In most cases, the precisions (se's) estimated for  $\delta^*$  using the aggregated and disaggregated approaches are in fact fairly similar. The only model with a substantially lower se is DO\_unnested applied to the maximum distance foraging data, i.e. an unnested model including BirdID. The likelihood ratio tests (Table 8) show that when BirdID is included, there is clear statistical preference for the nested model, and therefore there is an objective basis to disregard the unnested models and their smaller estimates of the  $\delta$  standard error (in addition to views expressed to prefer the nested models for other reasons).

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<sup>3</sup>  $\delta^*$  refers to the conventional  $\delta$  for the log-transformed maximum distance data, and to  $\tilde{\delta}$  for the untransformed chick condition data.

- Inclusion of lower level information such as BirdID and month does not make a substantial difference provided the model has an appropriate hierarchical (nested) structure.
- Following implementation of the Panel's suggestions, the models using aggregated and disaggregated data give essentially the same results, with one exception discussed immediately below (see Figure 2). Only for the maximum distance foraging does the adjustment for sample size for the aggregated data approach result in a non-negligible reduction in the se's of the estimates for Dassen and Robben islands; this is not surprising as only in this case are the sample sizes sufficiently low in some years for the observation errors to impact the residual variance (see Figure 1; note that this was also demonstrated earlier in MARAM/IWS/DEC15/PengD/P2). This reduction is not sufficient to completely remove the difference between the aggregated and disaggregated se estimates in this case – this is perhaps a reflection of these se's themselves being imprecisely estimated given a limited number of data.

Question 2: How suitable is the value of -0.1 as the threshold for  $\delta$  for a biologically meaningful impact on the penguin population?

- For the chick condition response variable, negative values preclude simple use of the customary log-transformation approach because of the presence of negative individual values. However, there is a relationship available for another penguin population (Macaroni penguins, see Sherley *et al.* 2018) which allows a change in chick condition to be related to a change in penguin population growth rate.
- For a “biologically meaningful” change of 1% in penguin population growth rate requires a change of  $\delta$  of 0.106 (the critical threshold value, inverse of Equation A9 of the Appendix) for the standard log transformation of the response variable (as for maximum foraging distance), but for the specific case of chick condition with untransformed data the corresponding value of  $\delta$  is 0.091 (inverse of Equation A10 of the Appendix).
- For comparison of results for different response variables, it is preferable to show these in terms of the estimated change in penguin population growth rate (as in Figure 2).

Other points worth noting include:

- In principle, REML estimates of se's would be preferable as they are unbiased. MLE estimates have however been preferred for standard reporting for comparability across the approaches, as REML code options were not available for the method used to introduce a sample size adjustment to the aggregated data approach. For the preferred approach using disaggregated data, a change for MLE to REML increases se estimates of  $\delta^*$  by about 10% - a little more for the maximum foraging distance variable with its smaller number of data.
- Where models have been recoded in ADMB, estimates of precision for the random effects' standard deviation and residuals standard deviations can be obtained. These are shown in parenthesis in Table 4 - Table 7. The variance of the sd parameters are fairly large, indicating that the partitioning of variance to different sources (e.g. random effects vs model residuals) is not able to be achieved very well for these data sets.

## Conclusions and Future work

The key indications from results from this initial work are that:

- When the Panel's suggestions about adjusting for sample size in the aggregated data approach and for random effects' structure selection for the disaggregated approach are taken into account, there is little to no real difference in the results which these two approaches provide. This is as the Panel anticipated, and in line with the mathematical demonstration in FISHERIES/2020/AUG/SWG-PEL/82 that use of the extra data available under the disaggregated approach would not actually improve precision. Some earlier results suggesting greater precision for the disaggregated approach were a consequence of applying a random effects approach without appropriate nesting of the data – likelihood ratio tests show that this approach is not justified.
- Results for estimates of the effect of fishing parameter  $\delta^*$  are more meaningfully expressed in terms of the consequent impact on the penguin population growth rate. For the cases examined initially here, the only meaningful result suggesting a negative impact of fishing in the vicinity of islands is for the maximum foraging distance variable for St Croix island (see Figure 2).

Future work will extend these analyses to these two and other response variables to also take account of the co-variate month (these data having recently become available), as suggested by the Panel.

## References

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**Table 1:** Summary of the data derived from the disaggregated data sets. For max distance, the means and sd's are in log-space, i.e. the data were logged before means and standard deviations were calculated. For chick condition, the means and sd's are in normal space. The column "Open" indicates whether the island in question was open to fishing (1) or closed (0) that year. The number of observations each year is given by *N*. The disaggregated data sets have been provided by J. Coetzee (*pers. comm.*), and the original data providers are DEA/UCT/Cape Nature, Richard Sherley/Lorien Pichegru. Tables of the aggregated data are listed in Coetzee and Merkle (2020).

Maximum foraging distance, WC						Maximum foraging distance, EC					
Island	Year	Mean	SD	Open	N	Island	Year	Mean	SD	Open	N
Dassen	2008	-2.676	0.348	0	10	StCroix	2008	-3.465	0.285	1	20
Dassen	2009	-2.602	0.398	0	3	StCroix	2009	-2.894	0.473	0	15
Dassen	2010	-2.689	0.315	1	28	StCroix	2010	-3.154	0.393	0	22
Dassen	2011	-2.908	0.431	1	45	StCroix	2011	-3.023	0.378	0	21
Dassen	2012	-2.614	0.406	1	47	StCroix	2012	-3.602	0.269	1	23
Dassen	2013	-2.749	0.434	1	38	StCroix	2013	-3.246	0.351	1	71
Dassen	2014	-3.424	0.733	0	8	StCroix	2014	-3.379	0.374	1	19
Dassen	2015	-2.447	0.400	0	15	StCroix	2015	-2.832	0.530	0	12
Dassen	2016	-2.475	0.298	0	19	StCroix	2016	-3.073	0.610	0	6
Dassen	2017	-2.605	0.201	1	14	StCroix	2017	-2.773	0.313	0	18
Dassen	2018	-2.541	0.204	1	2	StCroix	2018	-3.240	0.203	1	19
Robben	2008	-2.517	0.582	1	13	Bird	2008	-2.566	0.479	1	30
Robben	2010	-2.258	0.270	1	11	Bird	2009	-2.479	0.374	1	22
Robben	2011	-2.571	0.513	0	27	Bird	2010	-2.634	0.429	1	36
Robben	2012	-2.091	0.368	0	38	Bird	2011	-2.616	0.553	1	47
Robben	2013	-2.693	0.672	0	13	Bird	2012	-2.719	0.310	0	55
Robben	2014	-2.465	0.594	1	24	Bird	2013	-2.460	0.341	0	110
Robben	2015	-2.296	0.532	1	40	Bird	2014	-2.840	0.271	0	33
Robben	2016	-2.427	0.300	1	40	Bird	2015	-2.640	0.346	1	70
Robben	2017	-2.444	0.377	0	40	Bird	2016	-2.429	0.380	1	70
Robben	2018	-2.355	0.248	0	24	Bird	2017	-2.459	0.451	1	98
						Bird	2018	-2.520	0.751	0	61
Chick condition, WC						Chick condition, EC					
Island	Year	Mean	SD	Open	N	Island	Year	Mean	SD	Open	N
Dassen	2008	0.321	0.459	0	393	StCroix	2008	0.508	0.413	1	179
Dassen	2009	0.285	0.416	0	947	StCroix	2009	0.226	0.353	0	245
Dassen	2010	0.306	0.432	1	583	StCroix	2010	0.228	0.338	0	161
Dassen	2011	0.274	0.390	1	717	StCroix	2011	0.427	0.285	0	48
Dassen	2012	0.302	0.406	1	673	StCroix	2012	0.029	0.346	1	121
Dassen	2013	0.243	0.412	1	430	StCroix	2013	0.319	0.481	1	268
Dassen	2014	0.177	0.396	0	255	StCroix	2014	0.285	0.396	1	147
Dassen	2015	0.350	0.339	0	315	StCroix	2015	0.291	0.318	0	51
Dassen	2016	0.380	0.405	0	453	StCroix	2016	0.037	0.401	0	65
Dassen	2017	0.311	0.351	1	347	StCroix	2017	0.208	0.314	0	92
Dassen	2018	0.270	0.289	1	97	StCroix	2018	0.165	0.377	1	106
Robben	2008	0.270	0.383	1	762	Bird	2008	0.382	0.421	1	195
Robben	2009	0.296	0.400	1	1176	Bird	2009	0.244	0.438	1	272
Robben	2010	0.323	0.424	1	397	Bird	2010	0.280	0.408	1	129
Robben	2011	0.242	0.385	0	464	Bird	2011	0.312	0.355	1	103
Robben	2012	0.503	0.435	0	772	Bird	2012	0.300	0.371	0	167
Robben	2013	0.460	0.427	0	754	Bird	2013	0.314	0.343	0	568
Robben	2014	0.337	0.386	1	475	Bird	2014	0.173	0.291	0	69
Robben	2015	0.353	0.502	1	328	Bird	2015	0.139	0.268	1	123
Robben	2016	0.351	0.405	1	287	Bird	2016	0.158	0.409	1	346
Robben	2017	0.415	0.388	0	284	Bird	2017	0.238	0.341	1	155
Robben	2018	0.399	0.337	0	99	Bird	2018	0.165	0.310	0	145

**Table 2:** Sample-size-weighted averages of the standard deviations in Table 1; note that  $i$  indexes island and  $y$  year. The island-combined averages of the corresponding variances are calculated as:

$$(\sigma^*)^2 = \sum_{i,y} \sigma_{i,y}^2 (N_{i,y} - 1) / \sum_{i,y} (N_{i,y} - 1),$$

while the island-specific averages are calculated as:

$$(\sigma_i^*)^2 = \sum_y \sigma_{i,y}^2 (N_{i,y} - 1) / \sum_y (N_{i,y} - 1).$$

Disaggregated data	West Coast			East Coast		
	Combined	Dassen	Robben	Combined	St Croix	Bird
Maximum foraging distance	0.426	0.400	0.446	0.423	0.362	0.444
Chick condition	0.408	0.404	0.411	0.379	0.388	0.373



**Table 3:** Descriptions of the models for which results have been presented in Table 4 to Table 7, and the R code used to implement them. Note that the “BirdID” co-variate is relevant for the maximum foraging distance data sets; for the chick condition analyses “BirdID” is replaced by “month”. The “lmer” function is from the R lme4 package, and the “lme” function from the R nlme package.

Aggregated data	Description	R Code
A1	The original mixed model (estimates are MLE )	<code>lmer(lnResponse ~ (1 Year) + Island + X:Island,data=Data,REML=FALSE)</code>
A2	A1, but with unequal variance between the islands.	<code>lme(lnResponse ~ Island + X:Island, random=~1 Year, weights=varIdent(form=~1 Island), data=Data,method="ML")</code>
A1+N	A1, with sample-size adjusted variance	Coded in AD Model Builder (ADMB), with $\sigma_{\epsilon}^2(i, y) = \frac{(\sigma_y^*)^2}{N_{i,y}} + \tau^2$
A2+N	A2, with sample-size adjusted variance	Coded in AD Model Builder (ADMB), with $\sigma_{\epsilon}^2(i, y) = \frac{(\sigma_{i,y}^*)^2}{N_{i,y}} + \tau^2$
Disaggregated data	Description	R Code
D0_unnest	the M1 models of Table 2 of FISHERIES/2020/JUL/SWG-PEL/53 (NOT nested)	<code>lmer(lnResponse ~ (1 Island:Year:BirdID) + Island + X:Island,data=Data,REML=FALSE)</code>
D1_unnest	the M4 models of Table 2 of FISHERIES/2020/JUL/SWG-PEL/53 (NOT nested)	<code>lmer(lnResponse ~ (1 Island:Year) + Island + X:Island,data=Data,REML=FALSE)</code>
D0	D0 with nesting included	<code>lmer(lnResponse ~ (1 Year/Island/BirdID) + Island + X:Island,data=Data,REML=FALSE)</code>
D1	D1 with nesting included	<code>lmer(lnResponse ~ (1 Year/Island) + Island + X:Island,data=Data,REML=FALSE)</code>
D0+uneqvar	D0 with unequal variance for the islands	<code>lme(lnResponse ~ Island + X:Island, random=~1 Year/Island/BirdID, weights=varIdent(form=~1 Island), data=Data,method="ML")</code>
D1+uneqvar	D1 with unequal variance for the islands	<code>lme(lnResponse ~ Island + X:Island, random=~1 Year/Island, weights=varIdent(form=~1 Island), data=Data,method="ML")</code>

**Table 4a:** Various models (see Table 3 for descriptions of the models) are applied to the aggregated and disaggregated **West Coast maximum distance foraging** data. Estimates and se's for the closure effect  $\delta$  are listed (including the average se across the two islands), as well as the random effects and residuals standard deviations. Where several values are listed under the random effects' header, these correspond to the different random components of the model. e.g. Year/Island/Bird (D0) shows the sd for Bird:(Island:Year) then Island:Year then Year. The residuals standard deviation has been obtained in two ways. RES\_sd1 is the standard R output as provided by the VarCorr function for the lmer (random effects) application. RES\_sd2 is the standard deviation of the residuals, calculated as  $sd(y-\hat{y})$  where  $y$  is  $-\ln(\text{data})$  and  $\hat{y}=\text{predict}(\text{Fit})$ . For the models with unequal variance, the residual standard deviation RES\_sd1 is given first for Dassen, then for Robben. For A1+N and A2+N (where residual variance has been defined as  $\sigma_{\epsilon}^2(i, y) = \frac{\sigma_{i,y}^2}{N_{i,y}} + \tau^2$ , the RES\_sd1 column reports the  $\tau$  estimates. Where models have been recoded in ADMB, estimates of precision for the random effects' standard deviation and residuals standard deviations can be obtained. Where such information is available, it has been shown in parenthesis.

	Description	Random effects	Dassen delta      se		Robben Delta      se		ave(se)	Random effects sd Year,Island,Bird      Year,Island      Year ( $\sigma_{\alpha}$ )			Residuals sd RES_sd1 ( $\sigma_{RES}$ )      RES_sd2	
Aggregated data												
A1	Original model	Year	0.045	0.162	0.039	0.168	0.165	-	-	0.160 (0.076)	0.221 (0.049)	0.195
A2	Unequal variance for the islands	Year	0.028	0.206	0.038	0.151	0.179	-	-	0.161	0.269 & 0.152	0.200
A1+N	A1, with sample-size adjusted variance	Year	0.008	0.158	0.018	0.152	0.155	-	-	0.152 (0.065)	0.170 (0.054)	0.199
A2+N	A2, with sample-size adjusted variance	Year	0.013	0.158	0.018	0.155	0.157			0.152 (0.067)	0.175 (0.054)	0.199
Disaggregated data												
D0_unnest	Island:Year:Bird	Island:Year:Bird	-0.064	0.072	-0.020	0.056	0.064	0.343	-	-	0.291	0.196
D1_unnest	Island:Year	Island:Year	-0.005	0.127	0.025	0.120	0.124	-	0.167	-	0.426	0.420
D0	Year/Island/Bird	Year/Island/Bird	-0.025	0.116	0.010	0.108	0.112	0.313	0.095	0.119	0.291	0.202
D1	Year/Island	Year/Island	-0.025	0.121	0.025	0.114	0.118	-	0.120	0.110	0.427	0.421
D0+uneqvar	D0 with unequal variance for the islands	Year/Island/Bird	-0.023	0.116	0.011	0.109	0.113	0.289	0.097	0.119	0.289 & 0.299	0.208
D1+uneqvar	D1 with unequal variance for the islands	Year/Island	-0.019	0.122	0.025	0.118	0.120	-	0.111	0.124	0.403 & 0.445	0.420

**Table 4b:** Results for **West Coast maximum distance foraging data** for a selection of models from Table 4a, but with REML estimation instead of MLE. Results from the corresponding models using MLE from Table 4a are duplicated here to ease comparison.

	Description	Dassen		Robben		ave(se)	Random effects sd			Residuals sd	
		delta	se	delta	se		Year,Island,Bird	Year,Island	Year	RES_sd1	RES_sd2
Aggregated data											
A1	Original model	0.045	0.162	0.039	0.168	0.165	-	-	0.160	0.221	0.195
A1_REML	Original model fit with REML instead of MLE	0.047	0.180	0.038	0.187	0.184	-	-	0.174	0.248	0.197
A2	Unequal variance for the islands	0.028	0.206	0.038	0.151	0.179	-	-	0.161	0.269	0.200
A2_REML	Unequal variance for the islands, with REML	0.031	0.205	0.037	0.152	0.179	-	-	0.174	0.298	0.201
Disaggregated data											
D1	Year/Island	-0.025	0.121	0.025	0.114	0.118	-	0.120	0.110	0.427	0.421
D1_REML	Fit D1 with REML	-0.014	0.138	0.030	0.132	0.135	-	0.150	0.120	0.426	0.420
D1+uneqvar	D1 with unequal variance for the islands	-0.019	0.122	0.025	0.118	0.120	-	0.111	0.124	0.403	0.420
D1+uneqvar REML	Fit D2 with REML	-0.009	0.139	0.030	0.136	0.138	-	0.155	0.123	0.402	0.419

**Table 5a:** Repeat of Table 4a for **East Coast maximum distance foraging data**.

	Description	Random effects	St Croix delta    se	Bird delta    se	ave(se)	Random effects sd			Residuals sd	
						Year,Island,Bird	Year,Island	Year	RES_sd1	RES_sd2
Aggregated data										
A1	Original model	Year	-0.367    0.072	0.088    0.075	0.074	-	-	0.072 (0.033)	0.098 (0.021)	0.086
A2	Unequal variance for the islands	Year	-0.366    0.088	0.086    0.072	0.080	-	-	0.072	0.114 & 0.078	0.087
A1+N	A1, with sample-size adjusted variance	Year	-0.393    0.079	0.073    0.066	0.072	-	-	0.083 (0.027)	0.031 (0.047)	0.084
A2+N	A2, with sample-size adjusted variance	Year	-0.388    0.075	0.075    0.069	0.072	-	-	0.081 (0.027)	0.044 (0.036)	0.082
Disaggregated data										
D0_unnest	Island:Year:Bird	Island:Year:Bird	-0.377    0.057	0.040    0.037	0.047	0.209	-	-	0.379	0.337
D1_unnest	Island:Year	Island:Year	-0.419    0.085	0.076    0.073	0.079	-	0.101	-	0.423	0.419
D0	Year/Island/Bird	Year/Island/Bird	-0.440    0.075	0.081    0.063	0.069	0.188	0.000	0.091	0.378	0.340
D1	Year/Island	Year/Island	-0.445    0.077	0.085    0.065	0.071	-	0.000	0.097	0.423	0.421
D0+uneqvar	D0 with unequal variance for the islands	Year/Island/Bird	-0.440    0.070	0.082    0.064	0.067	0.201	0.000	0.092	0.305 & 0.394	0.330
D1+uneqvar	D1 with unequal variance for the islands	Year/Island	-0.446    0.072	0.085    0.065	0.069	-	0.000	0.097	0.364 & 0.443	0.421

**Table 5b:** Results for **East Coast maximum distance foraging data** for a selection of models from Table 5a, but with REML estimation instead of MLE. Results from the corresponding models using MLE from 5a are duplicated here to ease of comparison.

	Description	St Croix		Bird		ave(se)	Random effects sd			Residuals sd	
		delta	se	delta	se		Year,Island,Bird	Year,Island	Year	RES_sd1	RES_sd2
Aggregated data											
A1	Original model	-0.367	0.072	0.088	0.075	0.074	-	-	0.072	0.098	0.086
A1_REML	Original model fit with REML instead of MLE	-0.367	0.080	0.088	0.082	0.081	-	-	0.079	0.109	0.087
A2	Unequal variance for the islands	-0.366	0.088	0.086	0.072	0.080	-	-	0.072	0.114	0.087
A2_REML	Unequal variance for the islands, with REML	-0.366	0.088	0.086	0.072	0.080	-	-	0.078	0.237	0.088
Disaggregated data											
D1	Year/Island	-0.445	0.077	0.085	0.065	0.071	-	0.000	0.097	0.423	0.421
D1_REML	Fit D1 with REML	-0.445	0.082	0.089	0.071	0.077	-	0.027	0.106	0.423	0.420
D1+uneqvar	D1 with unequal variance for the islands	-0.446	0.072	0.085	0.065	0.069	-	0.000	0.097	0.443	0.421
D1+uneqvar_REML	Fit D2 with REML	-0.441	0.080	0.090	0.075	0.078	-	0.048	0.102	0.443	0.420

**Table 6a:** Various models are applied to the aggregated and disaggregated **West Coast chick condition** data. Quantities are as defined in the caption to Table 4a, except that here the data have not been log transformed.

	Description	Random effects	Dassen delta      se		Robben Delta      se		ave(se)	Random effects sd Year,Island,Month    Year,Island    Year ( $\sigma_\alpha$ )			Residuals sd RES_sd1 ( $\sigma_{RES}$ )    RES_sd2	
Aggregated data												
A1	Original model	Year	-0.018	0.035	-0.083	0.035	0.035	-	-	0.016 (0.031)	0.055 (0.012)	0.055
A2	Unequal variance for the islands	Year	-0.018	0.034	-0.083	0.043	0.039	-	-	0.016	0.048 & 0.062	0.055
A1+N	A1, with sample-size adjusted variance	Year	-0.019	0.035	-0.085	0.035	0.035	-	-	0.016 (0.031)	0.052 (0.013)	0.055
A2+N	A2, with sample-size adjusted variance	Year	-0.019	0.035	-0.085	0.036	0.035	-	-	0.016 (0.031)	0.052 (0.013)	0.055
Disaggregated data												
D0_unnest	Island:Year:Month	Island:Year:Month	-0.033	0.032	-0.068	0.038	0.035	0.151	-	-	0.385	0.382
D1_unnest	Island:Year	Island:Year	-0.019	0.035	-0.085	0.035	0.035	-	0.055	-	0.408	0.407
D0	Year/Island/Month	Year/Island/Month	-0.032	0.034	-0.069	0.040	0.037	0.149	0.000	0.023	0.385	0.382
D1	Year/Island	Year/Island	-0.019	0.035	-0.085	0.035	0.035	-	0.052	0.016	0.408	0.407
D0+uneqvar	D0 with unequal variance for the islands	Year/Island/Month	-0.032	0.034	-0.069	0.040	0.037	0.149	0.000	0.023	0.381 & 0.388	0.382
D1+uneqvar	D1 with unequal variance for the islands	Year/Island	-0.019	0.035	-0.085	0.035	0.035	-	0.052	0.016	0.404 & 0.411	0.407

**Table 6b:** Results for **West Coast chick condition** data for a selection of models from Table 6a, but with REML estimation instead of MLE. Results from the corresponding models using MLE from Table 6a are duplicated here to ease of comparison.

	Description	Dassen		Robben		ave(se)	Random effects sd			Residuals sd	
		delta	se	delta	se		Year,Island,Month	Year,Island	Year	RES_sd1	RES_sd2
Aggregated data											
A1	Original model	-0.018	0.035	-0.083	0.035	0.035	-	-	0.016 (0.031)	0.055 (0.012)	0.055
A1_REML	Original model fit with REML instead of MLE	-0.019	0.039	-0.085	0.039	0.039	-	-	0.017	0.061	0.055
A2	Unequal variance for the islands	-0.018	0.034	-0.083	0.043	0.039	-	-	0.016	0.048	0.055
A2_REML	Unequal variance for the islands, with REML	-0.019	0.039	-0.085	0.039	0.039	-	-	0.017	0.053	0.055
Disaggregated data											
D1	Year/Island	-0.019	0.035	-0.085	0.035	0.035	-	0.052	0.016	0.408	0.407
D1_REML	Fit D1 with REML	-0.019	0.039	-0.085	0.039	0.039	-	0.058	0.017	0.408	0.407
D1+uneqvar	D1 with unequal variance for the islands	-0.019	0.035	-0.085	0.035	0.035	-	0.052	0.016	0.404	0.407
D1+uneqvar_REML	Fit D2 with REML	-0.019	0.039	-0.085	0.039	0.039	-	0.058	0.017	0.404	0.407

**Table 7a:** Repeat of Table 6a for **East Coast chick condition data**.

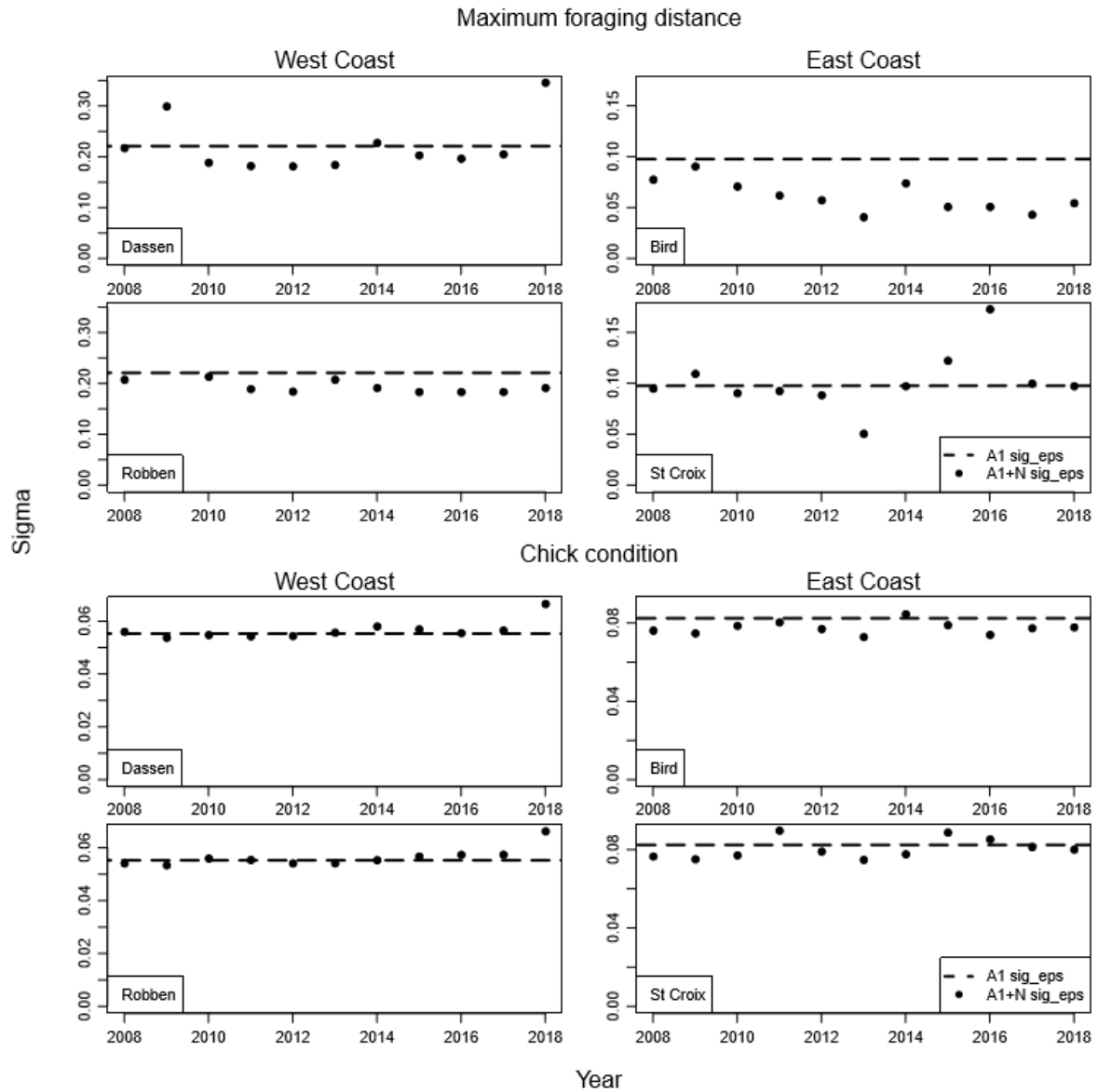
	Description	Random effects	St Croix		Bird		ave(se)	Random effects sd			Residuals sd	
			delta	se	delta	se		Year,Island,Month	Year,Island	Year	RES_sd1	RES_sd2
Aggregated data												
A1	Original model	Year	0.018	0.065	-0.029	0.067	0.066	-	-	0.076 (0.029)	0.082 (0.018)	0.070
A2	Unequal variance for the islands	Year	-0.005	0.088	-0.007	0.050	0.069	-	-	0.074	0.112 & 0.018	0.084
A1+N	A1, with sample-size adjusted variance	Year	0.026	0.064	-0.035	0.070	0.067	-	-	0.076 (0.028)	0.071 (0.020)	0.070
A2+N	A2, with sample-size adjusted variance	Year	0.026	0.064	-0.035	0.069	0.067	-	-	0.075 (0.027)	0.070 (0.020)	0.070
Disaggregated data												
D0_unnest	Island:Year:Month	Island:Year:Month	0.059	0.053	0.068	0.055	0.054	0.148	-	-	0.365	0.361
D1_unnest	Island:Year	Island:Year	0.031	0.066	0.009	0.068	0.067	-	0.103	-	0.379	0.378
D0	Year/Island/Month	Year/Island/Month	0.043	0.061	0.025	0.063	0.062	0.134	0.000	0.064	0.365	0.362
D1	Year/Island	Year/Island	0.026	0.063	-0.035	0.065	0.064	-	0.071	0.075	0.379	0.378
D0+uneqvar	D0 with unequal variance for the islands	Year/Island/Month	0.043	0.061	0.025	0.063	0.062	0.133	0.000	0.064	0.374 & 0.358	0.362
D1+uneqvar	D1 with unequal variance for the islands	Year/Island	0.026	0.063	-0.035	0.064	0.064	-	0.070	0.075	0.388 & 0.373	0.378

**Table 7b:** Results for **East Coast chick condition data** for a selection of models from Table 7a, but with REML estimation instead of MLE. Results from the corresponding models using MLE from Table 7a are duplicated here to ease of comparison.

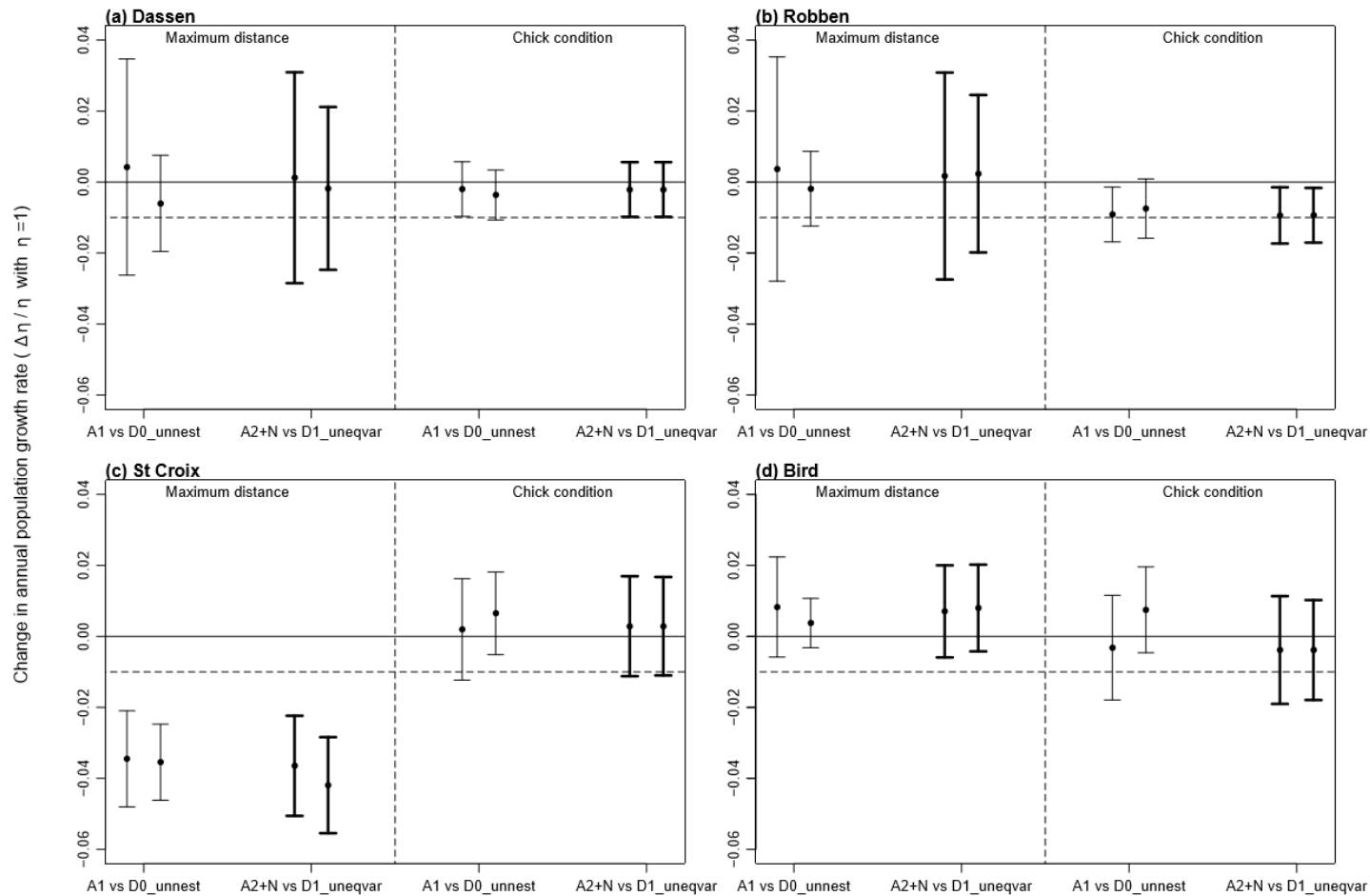
	Description	St Croix		Bird		ave(se)	Random effects sd			Residuals sd	
		delta	se	delta	se		Year,Island,Month	Year,Island	Year	RES_sd1	RES_sd2
Aggregated data											
A1	Original model	0.018	0.065	-0.029	0.067	0.066	-	-	0.076 (0.029)	0.082 (0.018)	0.070
A1_REML	Original model fit with REML instead of MLE	0.018	0.072	-0.027	0.074	0.073	-	-	0.081	0.092	0.071
A2	Unequal variance for the islands	-0.005	0.088	-0.007	0.050	0.069	-	-	0.074	0.112	0.084
A2_REML	Unequal variance for the islands, with REML	-0.005	0.088	-0.007	0.050	0.069	-	-	0.080	0.129	0.083
Disaggregated data											
D1	Year/Island	0.026	0.063	-0.035	0.065	0.064	-	0.071	0.075	0.379	0.378
D1_REML	Fit D1 with REML	0.024	0.070	-0.032	0.072	0.071	-	0.082	0.081	0.379	0.379
D1+uneqvar	D1 with unequal variance for the islands	0.026	0.063	-0.035	0.064	0.064	-	0.070	0.075	0.373	0.378
D1+uneqvar_REML	Fit D2 with REML	0.024	0.070	-0.032	0.072	0.071	-	0.082	0.081	0.373	0.378

**Table 8:** Results for likelihood ratio tests which were conducted to evaluate whether nested or unnested models are to be preferred. For each case, two models (one nested, the other unnested) are compared. The log-likelihood values are listed (note that these are log-likelihood and not negative log-likelihood values, so the less negative value indicates preference), and yields the associated p-value for the comparison. “Neither” in the “Preferred model” column indicates that the nested model is not statistically better than the unnested model.

					InL			
		Model 1	Model 2		Model 1	Model 2	p-value	Preferred model
Max. Dist.	WC	D0_unnest	D0	BirdID included	-300.70	-288.61	5.64E-06	D0 (i.e. nested)
		D1_unnest	D1	BirdID excluded	-297.48	-296.74	0.22	Neither
	EC	D0_unnest	D0	BirdID included	-503.63	-491.65	6.24E-06	D0 (i.e. nested)
		D1_unnest	D1	BirdID excluded	-501.34	-498.65	0.02	D1 (i.e. nested)
Condition	WC	D0_unnest	D0	Month included	-5299.50	-5299.20	0.78	Neither
		D1_unnest	D1	Month excluded	-5762.10	-5762.00	0.80	Neither
	EC	D0_unnest	D0	Month included	-1617.00	-1614.90	0.12	Neither
		D1_unnest	D1	Month excluded	-1710.90	-1709.70	0.11	Neither



**Figure 1:** The sample-size-weighted standard deviation vs year  $\sigma_{\epsilon}(i, y) = \sqrt{\sigma_{i,y}^2 / N_{i,y} + \tau^2}$  implemented in Model “A1+N” are shown by the black points, with the corresponding time-invariant residual standard deviation estimated by Model A1 are shown by the horizontal dashed line. The Model A1 residual standard deviations correspond to the “RES\_sd1” column in Table 4-Table 7. The sample-size-weighted  $\sigma_{\epsilon}(i, y)$  is calculated from the sample-size-weighted averages in Table 2, and the  $\tau$  values correspond to the “RES\_sd1” column in Table 4-Table 7.



**Figure 2:** Zeh plots of the change in annual population growth rate indicated by the  $\delta$  (or  $\tilde{\delta}$  in the case of chick condition) estimates. For maximum foraging distance, these are calculated by multiplying the  $\delta$  point estimates and se values by 0.094 and for chick condition by multiplying the  $\tilde{\delta}$  point estimates and se values by 0.110 (see the Appendix for more information on this calculation which is based on the assumption of a steady population ( $\eta=1$ ), and is relatively insensitive to variations about this assumption). The dashed horizontal lines indicate a “biologically meaningful” (as suggested earlier by the Panel) reduction of a penguin population growth rate of 1% resulting from fishing in the vicinity of an island. The left-side pair of results (reflecting point estimates and 95% confidential intervals approximated by  $\pm 2$  se’s) for first aggregated then disaggregated data models reflect results from models reported in previous analyses, whereas the right-side pair (with bold lines) incorporate the adjustments (respectively of sample size adjustment and random effects’ structure selection) suggested by the Panel at their 2020 meeting.



### Appendix: Exploring the relationship between chick condition and survival rate to evaluate what threshold for the island closure effect parameter $\delta$ corresponds a 1% change in annual penguin population growth rate

In analyses of penguin data to date, estimates of the fishing effect parameter  $\delta$  have been taken (on earlier advice by the Panel) to be biologically meaningful if  $\delta < -0.1$  in cases where the response variable is analysed in log-space. This threshold was based on changes in survival estimates, and corresponds to a value below which (i.e. a  $\delta$  value more negative than -0.1) analysis indicates that the population growth rate will decrease by 1% or more if fishing occurs in the neighbourhood of the island.

Details of the derivation of this threshold are provided in Robinson *et al.* (2014) (MARAM/IWS/DEC14/Peng/B4). The question this Appendix aims to answer is whether the same threshold of -0.1 is appropriate for other penguin response variables as has been assumed to date, specifically for chick condition. Chick condition data are investigated using the following approach: (1) establish a relationship between chick condition and survival, and (2) substitute this relationship in the equations of Robinson *et al.* (2014) to establish how the  $\delta$  estimate for chick condition (where this is evaluated in normal- rather than in log-space, and consequently is now termed  $\tilde{\delta}$ ) relates to a change in penguin population growth rate.

Figure A1 plots the predicted relationship between chick survival and chick condition for the Macaroni penguin population, extracted from Sherley *et al.* (2018). For this extraction, a web-based plot digitiser was used to extract a series of points from the solid black line of Figure S8(C) of Sherley *et al.* (2018) (which shows a predicted relationship between survival and condition) and a linear regression was implemented to retrieve the equation for this straight line. The resulting relationship is:

$$Survival = 0.2321 \cdot Condition + 0.1316 \quad (A1)$$

Figure A2 plots histograms of the South African chick condition data by coast, along with the estimates of survival that are derived from the chick condition data using equation (A1).

In order to calculate a  $\tilde{\delta}$  threshold estimate for chick condition and the penguin population growth rate, essentially the same analysis is followed as in Appendix B of MARAM/IWS/DEC14/Peng/B4. For ease of reference, equations (B.5) and (B.6) from that paper are repeated below:

$$\eta^4 = \eta^3 S + H S^3 \quad (A2)$$

$$\Delta\eta = \frac{S^3}{4\eta^3 - 3\eta^2 S} \Delta H \quad (A3)$$

where  $\eta$  is the population annual proportional growth  $\eta = N_{y+1}/N_y$ ,  $S$  is the mature female annual survival proportion and  $H$  is a measure related to the product of egg production and fledging success (hence encompassing chick survival).

Consider a steady state so that  $\eta = 1$ , then these equations become:

$$1 = S + H S^3 \quad (A4)$$

$$\Delta\eta = \frac{S^3}{4 - 3S} \Delta H \quad (A5)$$

Thus, for a “meaningful” change (decrease) in population growth rate of 1%:

$$\Delta H = \frac{\Delta\eta(4-3S)}{S^3} = (-0.01)(4 - 3S)/S^3 \quad (A6)$$

Table A1 lists the mean chick condition values for the East Coast, West Coast and coast combined. The coast-combined mean chick condition value is  $\overline{Condition} = 0.310$ . From the chick survival-condition relationship (Equation A1),  $\overline{Survival} = 0.204$ , so that  $H = 0.204$ . Solving equation A4 then yields  $S = 0.867$  (note that is very similar to the  $S = 0.88$  evaluated by Robinson *et al.* 2014 from data for the Robben island population). Equation A5 consequently becomes:

$$\Delta\eta = 0.466 \Delta H \quad \text{or} \quad \Delta H = 2.144 \Delta\eta \quad (\text{A7})$$

For the (untransformed) chick condition response variable, the GLM equation used for the analysis is:

$$Condition_{y,i} = \alpha_y + \gamma_i + \tilde{\delta}_i X_{y,i} + \epsilon_{y,i} \quad (\text{A8})$$

where  $X$  is 1 if the island is open and 0 if it is closed. Thus  $\tilde{\delta}$  is the change in chick condition resulting from opening to fishing compared to closing. Differentiating Equation (A8) w.r.t  $X$  gives  $\Delta Condition = \tilde{\delta} \Delta X$ . If  $X$  changes from zero to one (i.e. closed to open, so that the sign of  $\Delta Condition$  is indicative of the impact of fishing, i.e.  $\Delta Condition < 0$  implies a negative impact of fishing), then  $\Delta X = 1$  and  $\Delta Condition = \tilde{\delta}$ .

Hence from the linear regression in Fig A1,  $\Delta H = 0.2321 \tilde{\delta}$ , and for  $\Delta\eta = -0.01$  (i.e. a 1% decrease in the population growth rate resulting from closure, when  $\eta = 1$ ) the critical (threshold) value of  $\tilde{\delta}$  is:

$$\tilde{\delta} = \Delta H / 0.2321 = (2.144 \Delta\eta) / 0.2321 = 9.24 * (-0.01) \sim -0.092$$

The calculations above allow an estimate of  $\delta$  (or  $\tilde{\delta}$ ) to be converted to an estimate of the corresponding change in population growth rate, which is a more biologically intuitive quantity. The specific equations relating  $\Delta\eta$  to  $\delta$  and  $\tilde{\delta}$  (taking  $\eta = 1$  and  $S = 0.867$ ) are:

$$\text{Maximum distance } (\delta^* \text{ in log-space}): \quad \Delta\eta = 0.094\delta \quad (\text{A9})$$

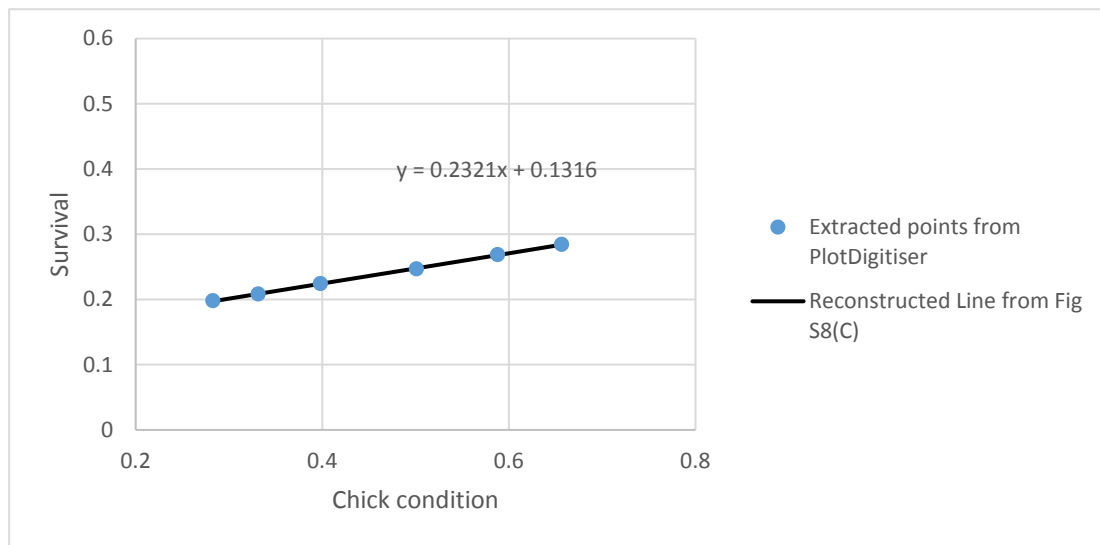
$$\text{Chick condition } (\delta^* \text{ in normal space}): \quad \Delta\eta = 0.108\tilde{\delta} \quad (\text{A10})$$

These equations have been used to provide the results shown in Figure 2.

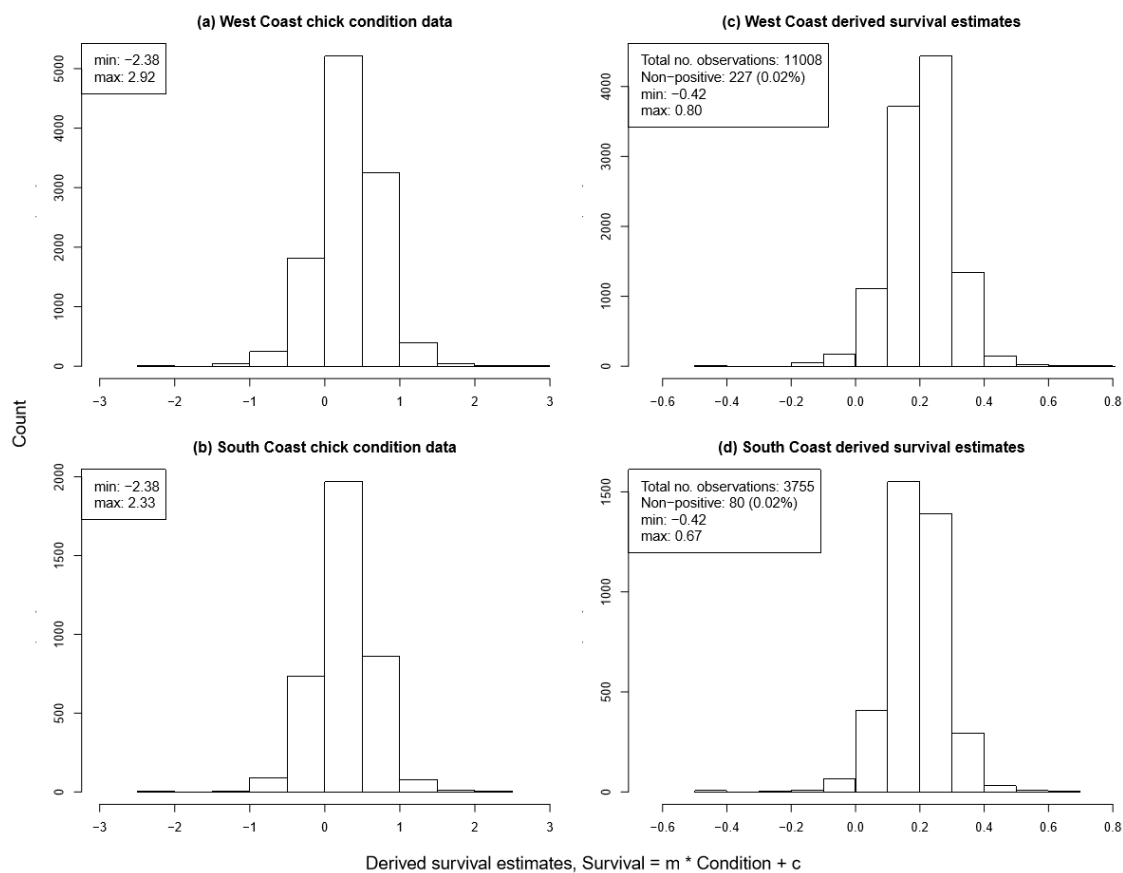
The above calculations are for  $\eta = 1$ . If instead one assumes a decreasing population with  $\eta = 0.95$ , then  $S = 0.819$ , the  $\tilde{\delta}$  threshold changes from -0.092 to -0.094, and equation (A10) changes to  $\Delta\eta = 0.105\tilde{\delta}$ , i.e. these threshold values are relatively insensitive to the value assumed for  $\eta$ .

**Table A1:** The mean chick condition values are reported in the first column, with the mean survival values estimated from Equation (A1) are listed in the second column. The third column lists the estimates of the mature female annual survival proportion  $S$  which follow when  $\eta$  is set to 1 in Equation (A2). Distributions of the chick condition data, as well as the survival rates estimated by the Equation (A1) relationship are shown in Figure A2.

	$\overline{Condition}$	$\overline{Survival} = m * \overline{Condition} + C$	$S$ (from Equation A2 with $\eta = 1$ )
(1) West Coast	0.327	0.208	0.865
(2) East Coast	0.259	0.192	0.872
(3) Coasts combined	0.310	0.204	0.867



**Figure A1:** Extraction of the predicted relationship between chick survival and condition from Figure S8(C) of Sherley *et al.* (2018) for the Macaroni penguin population. The blue dots show the points extracted from the pdf, and the black line shows the regression line through these points, which is essentially a reconstruction of the solid black line of Figure S8(C) of Sherley *et al.* (2018).



**Figure A2:** Histograms of the WC and EC chick condition data (left column) and the corresponding survival estimates obtained using the relationship in Figure A1.