Faculty of Biosciences, Fisheries and Economics
Department of Arctic and Marine Biology

Breeding success in relation to telomere length in a long-lived seabird, the Antarctic petrel (*Thalassoica antarctica*)

Iñigo López-Sarasa

BIO-3950 Master thesis in Biology
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Supervisors

Sébastien Descamps, Norwegian Polar Institute
Nigel Gilles Yoccoz, The Arctic University of Norway

Til mine foreldre, som jeg skylder alt.

Dena zor diedan nere guraso maiteei.

To my parents, to whom I owe everything.

A mis padres, a quienes debo todo.

Just as this island belongs to the gulls

Just as this island belongs to the gulls,
and the gulls to their cry
and their cry to the wind
and the wind to no one,
so is this island the gulls,
and the gulls are their cry
and their cry is the wind
and the wind no one's.

By Herman de Coninck (1944-1997).
Translated from Flemish by Laure-Anne Bosselaar and Kurt Brown

ACKNOWLEDGEMENTS: ON THE SHOULDERS OF GIANTS

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The data for this thesis were collected by a bunch of strong adventurers. Thanks may go to all of them.

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depreciating my workload and forcing me out of the office and into the mountains. Thanks to all you three.

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Table of contents

ABSTRACT

Integrating information about the physiology of individuals and their reproductive performance can be a key aspect in determining the relationships between environmental conditions and demographic parameters, and of the individual variability in these relationships. Telomeres are the protective caps of chromosomes found in eukaryotic cells. They generally shorten in relation to the stressors an individual encounters during its life. Telomere length and telomere dynamics can provide ecologists with an overview of the physiological state of an individual. In order to understand the relationship between telomere length and breeding success, and to explore the change of telomere length with time, we measured telomere length in erythrocytes of wild Antarctic petrels (*Thalassoica Antarctica*) in a longitudinal study covering three field seasons. Our models do not support any relationship between telomere length and breeding success. Telomere loss was small (2.7% of the total range of variation of the telomere variable of the birds in this study). Additionally, we found a potential negative selection of long telomere birds during a breeding season with extreme weather events. We provide suggestions that could help tease apart the effect of environmental vs. individual factors on breeding success.

Keywords: Antarctic petrel, telomere length, breeding success, physiological state, *Thalassoica antarctica*

INTRODUCTION

To unveil the relationships between environmental conditions, demographic parameters and population dynamics of a species, it is necessary to understand the mechanisms by which fluctuations in environmental parameters affect the physiology of individuals (Odum 1941; Ricklefs and Wikelski 2002). Yet, in such an approach, one has to take into account individual heterogeneity, i.e. the "differences among individuals in vital parameters that are not completely random" (sensu Vindenes, Engen et al. 2008) as this can generate individual specific, responses to the environment (Kruuk 2004; Arlt and Pärt 2007; Byholm, et al. 2007; Vindenes, et al. 2008). Physiology has been found to have important effects on demography (Reed, et al. 2006) and by studying physiology, ecologists can understand how organisms are related to and function in their environment (Odum 1941; Ricklefs and Wikelski 2002). This can provide more accurate information about an individual´s response to a stressor than by behavioral studies alone (Walker, et al. 2005). Overall, integrating physiological and ecological data can generate a better understanding of seabird ecology (Le Maho 2002) and their use as bioindicators of the environment (Cairns 1988).

It has been suggested that telomere length and their dynamics can be used as a proxy of the overall physiological performance of an individual (Monaghan and Haussmann 2006). This may thus offer a tool to examine the physiological mechanisms that link environmental conditions to demographic performance. Telomeres are protective caps of eukaryotic chromosomes, composed by non-codifying double-stranded DNA. Shortening of these structures, also referred to as telomere loss, naturally occurs as a consequence of cell replication and oxidative stress (Monaghan and Haussmann 2006). It is directly involved in processes such as cellular ageing and senescence, growth, and changes in the organisms´ performance (Haussmann and Marchetto 2010). Shorter telomeres lead to higher degradation rates of DNA (Monaghan and Haussmann 2006). Since chromosomes without telomeres cannot be distinguished from double stranded breaks, they activate the DNA damage machinery of the cell (Monaghan and Haussmann 2006). Telomere length may be tightly associated with life expectancy (Bize, et al. 2009) reproductive success (Bauch, et al. 2013) and individual fitness (Pauliny, et al. 2006).

The physiological status of an individual may drive the trade-off between self-maintenance and chick feeding (Kitaysky, et al. 1999). Reproduction may have fitness-associated costs (Hamel, et al. 2010), and in long-lived species like seabirds, physiologically old individuals (i.e. short telomeres) may prioritize their own maintenance and thus survival over the survival of their offspring (but when a critical age is reached, in the case of terminal investment (Clutton-Brock 1984), very old birds may allocate more resources during their last breeding attempt (Froy, et al. 2013)). Old senescent birds may also be constrained by limited physiological abilities to breed and raise successfully their young. Therefore, whether old senescent birds restrain their reproduction or reproduction by old birds is constrained by limited physiological abilities (Curio 1983), one may predict a positive association between telomere length and reproductive effort, and, consequently, with reproductive success (Prediction 1). On the other hand, breeding experience can have a positive effect on breeding success in long-lived seabirds (Wooller, et al. 1990). Young, inexperienced birds are generally characterized by long telomeres (Hall, et al. 2004a). Consequently, if breeding experience is a key driver of breeding success, we would expect a negative association between telomere length (inversely correlated with breeding experience) and breeding success (Prediction 2). Finally, in case both experience and senescence affect the relation between telomere length and breeding success simultaneously, a lower breeding success in both young inexperienced and old senescent individuals is expected (Prediction 3) (Rockwell, et al. 1993; Angelier, et al. 2006).

There are few longitudinal studies in seabirds addressing the effect of telomere length on breeding success (Hall, et al. 2004b; Bauch, et al. 2013; Young, et al. 2013). Here, we investigated the relationship between telomere length and breeding success using data from a three-year, cross-sectional and longitudinal study of a long-lived seabird, the Antarctic petrel *Thalassoica antarctica*, testing the four afore mentioned predictions.

Telomere dynamics can also inform about the physiological status of an individual, (Bize, et al. 2009). For this, we also examined the telomere evolution of the individuals with repeated telomere length measurements across two or three seasons. We tested whether telomere length changed as a result of time (season), and if so, whether this effect was similar within individuals.

MATERIALS AND METHODS

Study system and data collection

The Antarctic petrel is a pelagic surface-feeding seabird that only breeds on the Antarctic continent. Antarctic petrels are monogamous, and females lay one egg per breeding attempt, and both mates have a similar parental investment (Lorentsen and Røv 1995). They are medium-sized birds that weigh ca. 600 g. They breed on the ground in scree slopes (Lorentsen and Røv 1995). The study was carried out at the Svarthamaren breeding colony (71°53’ S, 5°10’ E) in Dronning Maud Land, Antarctica. Svarthamaren is the largest known Antarctic petrel colony (Mehlum, et al. 1988; Van Franeker, et al. 1999) and about 200,000 pairs of Antarctic petrels breed at this colony which is located *ca.* 200 km from the coast. Density of nests is high (0.8 breeding pairs per m2 (Mehlum, et al. 1988)), and they are often placed close to rocks, which offer varying amounts of shelter (Varpe and Tveraa 2005). Reproduction starts at the end of November/early December and both parents incubate and feed the chick. For the first 7–15 days following hatching, the male guards the chick at the nest, while the female is at sea (Lorentsen and Røv 1995). Hatching occurs around mid-January and fledging in late February/early March. Potential causes of death of Antarctic petrels are predation by South Polar Skuas (*Catharacta maccormicki*) and weather (i.e. snowmelts and consecutive freezing events) (pers. obs).

Data were collected during three consecutive austral summers: 2011-2012 to 2013-2014 seasons (hereafter seasons 1112 to 1314).

All birds in this study were individually marked with a metal ring. Nests were visited every other day (weather permitting), allowing determination of hatching date (+/- 1 day), hatching success and chick survival. Monitored nests belonged to one of three different study plots (listed as plot 2, 3 and 5). Nests included in this study (and therefore adults breeding on those nests) were randomly chosen among all nests present in the study plots. As over the course of the breeding seasons some nests failed, and a certain sample size was needed, some nests were included in the study later on in the season, creating a potential bias towards birds/nests with a higher likelihood of having a positive breeding success. This will be taken into account when analyzing the relationship between telomere length and breeding success.

One milliliter blood samples were collected from the brachial vein in all adult birds included in this study (n=34 in 2011/12, 39 in 2012/13 and 67 in 2013/14). Since blood is a highly mitotic tissue, and RBCs are nucleated in birds, small blood samples can be collected without negative effects. Blood samples were blotted and dried on a filter paper, which was then stored at cold temperatures. DNA was extracted from dried blood spots using a commercial kit (NucleoSpin® Tissue, Macherey Nagel, Germany).

Telomere analyses

Telomere measurements were conducted following the procedure described by Criscuolo, Bize et al 2009. Briefly, DNA was extracted from two dried blood spots using a commercial kit "NucleoSpin® Tissue, Macherey Nagel, Germany "and according to manufacturer's protocol. See more details in Appendix 1.

Telomere length measurement is based on the determination of a number of amplification cycles necessary to detect a lower threshold of fluorescent signal, the cycle number being proportional to the telomere length (T), or to the number of copies of a control gene (S). A ratio T/S of telomere repeated copy number (T) to single control gene copy number (S) was then calculated for each sample that will reflect relative inter and intra-individual differences in telomere length. Telomere and control gene amplifications were carried out in duplicate on each plate and the mean values of the four measurements of telomere and control gene were used to calculate the final T⁄S ratio for each sample. For each qPCR run, we confirmed that the amplification efficiency was between 95% and 105%, using the dilution curve calculation method (Larionov, et al. 2005), 99.3 to 100.7% for telomere and 99.9 to 100.3% for non-VCN and inter-plate standardization was achieved with a reference bird sample in each qPCR (Criscuolo, et al. 2009).

Intra-plate coefficients of variation (based on CT values) were 1.21% +/- 0.04 for the non-VCN gene assay and 2.17% +/- 0.07 for the telomere assay. Intra-plate coefficients of variation based on the T/S ratio was 15.70% +/- 0.90. Interplate coefficients of variation (based on CT values) were 1.65% +/- 0.07 for the non-VCN gene assay and 2.94% +/- 0.16 for the telomere assay. Inter-plate coefficients of variation based on the T/S ratio was 9.76% +/- 1.27.

The melting curves showed a single peak of amplification for samples and no peak for negative control (water).

Data analyses

All analyses were conducted in R version 3.0.2 (2013-09-25) (R Core Team 2013) using the lme4 (Bates, et al. 2014) and the MCMCglmm (Hadfield 2010) R libraries. We used generalized mixed-effects models (function glmer) to test for the effect of telomere length on three response variables: hatching date (discrete variable), hatching success (binary variable) and survival of the chick at 15 days (binary variable). The survival of the chick at 15 days is an overestimation of the fledging success, but due to field constraints (we were not able to monitor the whole breeding season) we used it as a proxy of the fledging success of the chicks. For the hatching data analyses, we used a Bayesian approach as implemented in MCMCglmm because we had convergence problems in glmer. We checked that the MCMC chains obtained in MCMCglmm converged by using the Gelman-Rubin statistic (Gelman and Rubin 1992). In all models, two random effects were included, the individual bird ("birdID) and the nest ("nestID"), to account for repeated measures on individuals (birds sampled during, at least, two seasons) and on nests (nests for which both mates have been sampled). The T/S ratio variable was transformed into a categorical variable (4 categories, 1 to 4 ranging from shorter to longer telomeres, corresponding to the 4 quartiles) with approximately the same number of individuals in each category. Sex was not included as a covariate because there were no telomere length differences between males and females (Figure 1), a similar investment into reproduction from both sexes and no a priori reason to expect sex differences in the telomere length-breeding success relationships. Size was included as an explanatory variable because there could be a potential relationship between size and telomere length (Seluanov, et al. 2007). As body size could also be associated with breeding success (Michel, et al. 2003), any association between telomere length and breeding success could thus be due to a confounding effect of body size. Gonys height (bill height) was used as a proxy of body size.

There were no body size differences among the different telomere groups. Since body weight is very dependent on the period of weighing during the incubation and chick rearing periods, and to avoid additional noise in our data (see the problems with the study design concerning the date of the first visit to the nest), we did not include it in our models.

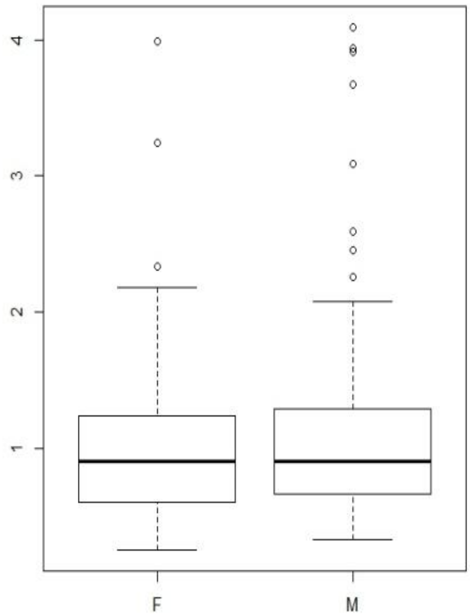

Figure 1 Average *T/S ratio and CI for male and female Antarctic petrels.*

The three years of our study were characterized by very different environmental conditions (Descamps, et al. 2015). Birds with different telomere lengths may respond differently to environmental conditions (Brown and Brown 1998). Hence, interactions between season and telomere length were included in the models. There were important inter-season differences in the average T/S ratio (Figure 2; Results section). As mentioned before, and to avoid a potential bias in breeding success, we included the first visit date (date of initial nest monitoring as number of days after the 1st of December)., we introduced the sampling date as a discrete variable in our models to correct potential biases. We selected birds that were monitored between day 1 and 30 since the beginning of the study There were important hatching success differences between study plots (Figure 4), so in order to remove the plot effect we introduced the categorical variable plot in our models.

The predictor variables are summarized in Table 1:

Table 1 *Predictors and biological meaning of their potential effect on breeding success*

Variables	Proxy of	Biological meaning	Type of variable
Gonys height	Body size	Potential effect of size on breeding success	CONTINUOUS
First visit	-	Accounts for bias of selecting succesful nests later in the season	DISCRETE
Sampling date	-	Accounts for bias of selecting a certain telomere length class due to selection effects	DISCRETE
Plot	-	Inter-plot differences in behaviour and breeding success observed in the field	CATEGORICAL
Season	-	Different environmental conditions between	CATEGORICAL
Telomere group	Physiological status	Potential relation between T/S ratio and breeding performance	CATEGORICAL

For each response variable and predictor variable (except for the season variable), ten different models were ran (Table 2). Then, for each response variable we performed a model selection based on the Akaike information criterion, or AIC and the AIC weights (Burnham and Anderson 2002). We also assessed final models on the basis of parameter uncertainties (i.e. 95% CI).

Table 2 *Models considered to test for the relationship between telomere length (telogroup) and a given response variable (Hatching dates, hatching success and chick survival until 15 days).*

Model
Response variable~ 1 +(1|birdID) + (1|nestID)
Response variable~ firstvisit + plot + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)
Response variable~ season + sampling date +(1|birdID) + (1|nestID)
Response variable~ firstvisit + plot + GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)
Response variable~ telogroup + sampling date +(1|birdID) + (1|nestID)
Response variable~ telogroup + firstvisit + plot + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)
Response variable~ telogroup + season + sampling date +(1|birdID) + (1|nestID)
Response variable~ telogroup + season + firstvisit + plot + GonysHeightscale + sampling date + (1|birdID) + (1|nestID)
Response variable~ telogroup * season + sampling date +(1|birdID) + (1|nestID)
Response variable~ telogroup * season + firstvisit*season + plot*season + GonysHeightscale*season + sampling date * season +(1|birdID) + (1|nestID)

For each analysis, we included a figure obtained from the raw data, with the average and 95 % confidence intervals of each response variable, for each telomere group and season. Although standard errors assume independency of replicates, we included the parameter estimates in the model output.

We also ran three models to understand the telomere dynamics (Table 6; Results section). We computed the average T/S ratio loss per year for all individuals that had repeated T/S ratio measurements across the three different seasons (n=56). Comparing the AIC values between the null model and the season model with the bird as a random effect provides information about the change in telomere length with time. Comparing the season model with bird as a random effect and the season model with the interaction of bird and season as random effects would help us understand if this increase or decline in telomere length is the same or not among individuals (Nussey, et al. 2007).

RESULTS

T/S ratio inter-annual differences

We found great inter-annual differences in the T/S ratio average (Figure 2). The lowest T/S ratio average was obtained during the 1213 season, and the greatest during the 1314 season.

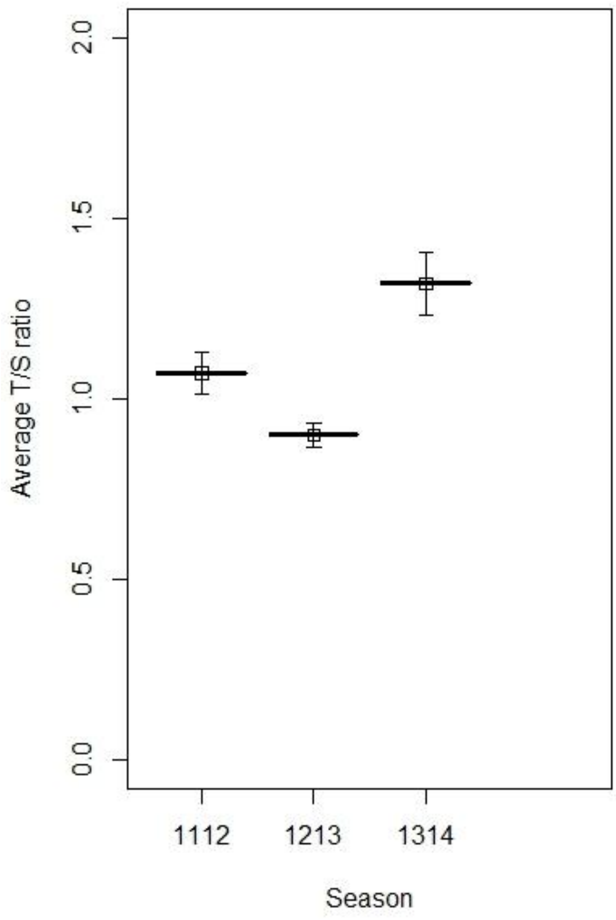

Figure 2 Average *T/S ratio and SE for the three seasons.*

Body size and telomere groups

Body size was more or less constant across telomere groups and seasons, with the exception of long telomeres (group 4) in the 1112 season (Figure 3). As can be seen in Appendix 3, males were larger than females, and since the proportion of males in the long telomere group in the 1112 was far greater than the female proportion (Appendix 4), this explains the variation in body size.

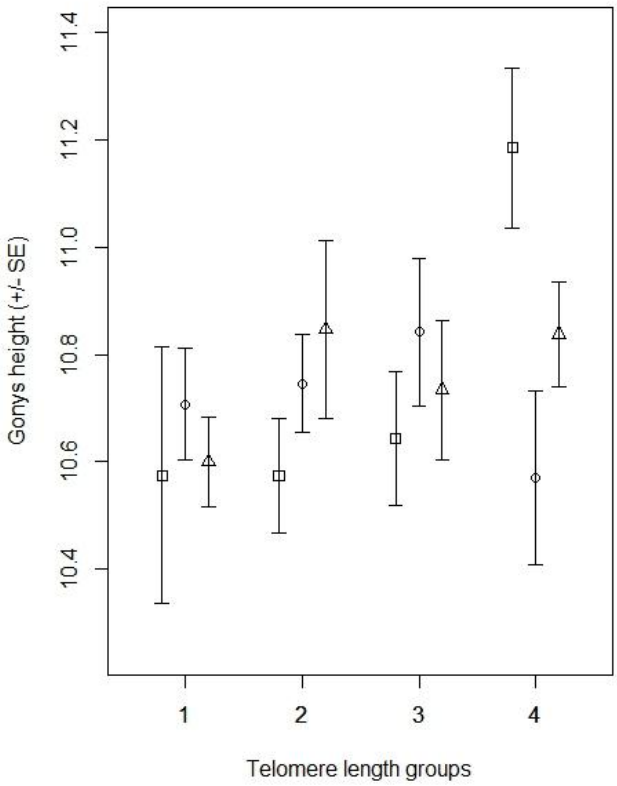

Figure 3 Average *size (gonys height in millimeters) and SE for the three seasons across telomere groups.*

Sampling date and telomere groups

The average sampling date for each telomere group differed strongly between seasons (Figure 4). In particular, in season 1112, long telomere birds were sampled earlier. Birds sampled later had, on average, longer telomeres.

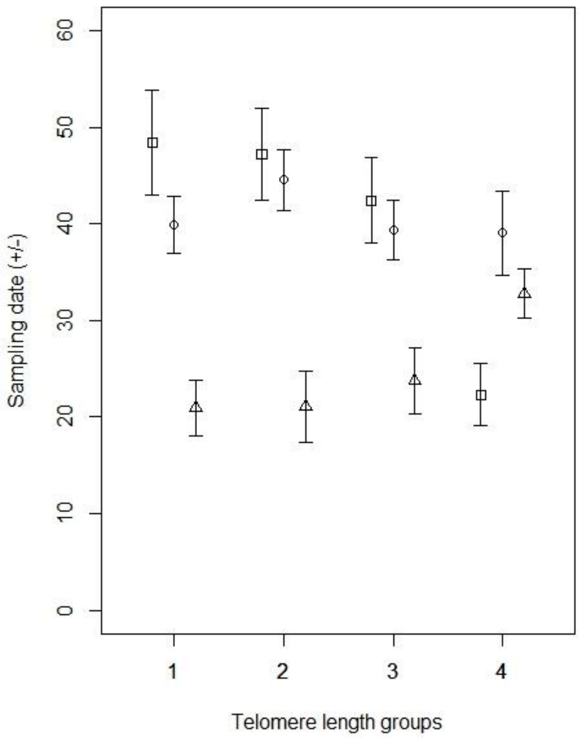

Figure 4 *Sampling dates (Mean ±SE) for each telomere group and for each season: square symbols represent 1112 season, circles represent the 1213 season and triangles the 1314 season.*

Hatching date

The model selected, containing only size and sampling date, shows that there was no evidence for a relationship between telomere length and hatching date (Table 3; Figure 5). The model selection indicates that hatching date was best explained as a function of body size and sampling date. When the telomere group variable was included in the model, the AIC increased from 203.71 in the AIC selected model to 208.4 (Table 3).

Table 3 Results from selected g*eneralized linear mixed effect model fitted using a bayesian approach, with the lowest AIC for the Hatching date analyses (size + sampling date), and model including the telogroup variable. Estimates and standard errors are shown for all fixed effects.*

Covariates + sex	Model	AIC	AIC weights	Δ AIC	Fixed effects	post.mean	l-95% CI	u-95% CI
GonysHeight + sampling date	Hatching date~GonysHeightscale + sampling date +(1|birdID) + (1|nestID)	203.71	0.9893491	0	Intercept	6.18	5.2	7.13
					GonysHeightscale	1.1	0.33	1.92
					sampling date	-0.01	-0.08	0.06
telomere groups + GonysHeight + sampling date	Hatching date~telomere groups + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)	208.04	0.0102321	4.33	Intercept	6.46	5.27	7.61
					telogroup2	-0.62	-1.76	0.49
					telogroup3	0.13	-0.88	1.19
					telogroup4	-0.58	-1.76	0.59
					GonysHeightscale	1.15	0.32	1.97
					sampling date	-0.01	-0.08	0.06

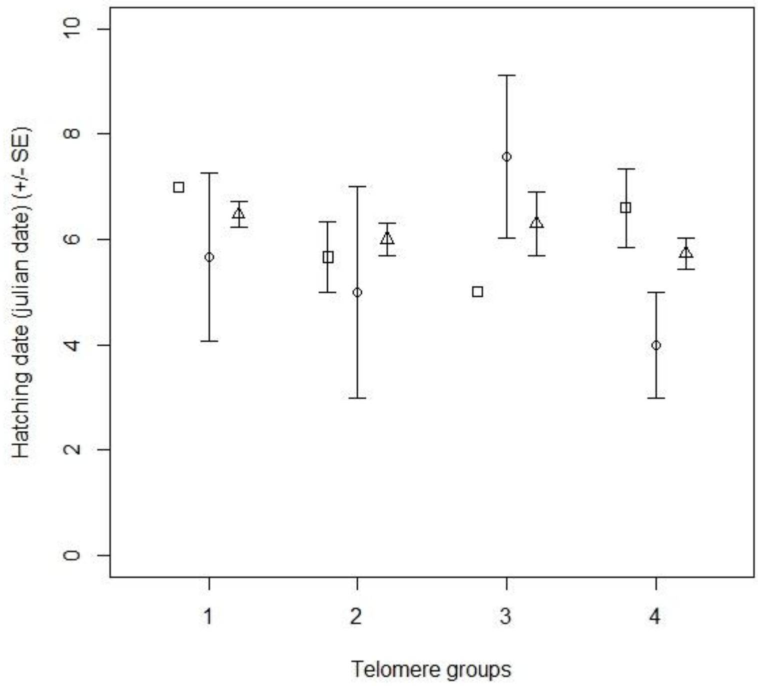

Figure 5 *Average hatching date and SE for each telomere group and season. Square symbols correspond to the 2011/12 breeding season, circles to the 2012/13 breeding season and triangles to the 2013/14 breeding season.*

Hatching success

For each response variable model selection, we included a figure obtained from the raw data, with the average value and its standard errors of each response variable, for each telomere group and season. Although standard errors assume independency of replicates, we included the parameter estimates in the model output.

Our results indicate that hatching success was best explained as a function of the study plot and sampling date (Table 3), with birds in plot 2 and birds sampled early in the season having the lowest hatching success probability (Figure 7). The model with the lowest AIC (Table 4) had no telomere-related variables suggesting that telomere length was not a primary driver of hatching success (Fig. 2).

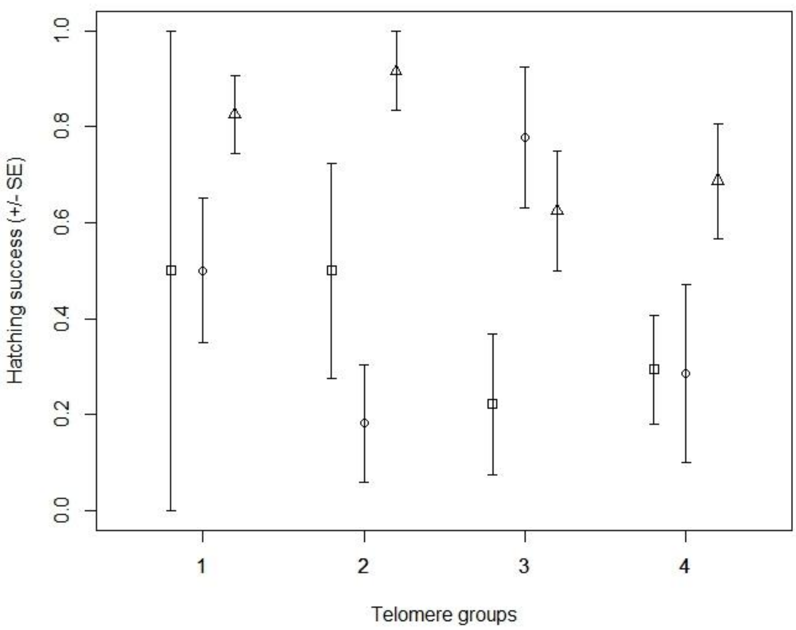

Figure 6 *Mean hatching success and SE for each telomere group and season. Square symbols correspond to the 2011/12 breeding season, circles to the 2012/13 breeding season and triangles to the 2013/14 breeding season. Hatching success for telomere group one has a very low sample size (n=2), hence the large SE bars.*

Table 4 *Results from selected generalized linear mixed-effects models for the hatching success analyses (plot + sampling date), and the best model that included the telomere group variable. Note that for all the levels of the telomere group variable, the 95% confidence intervals overlap zero. Estimates and 95% CI are shown for all fixed effects.*

<table>
<tr><th>Covariates</th><th>Model</th><th>AIC</th><th>AIC weights</th><th>Δ AIC</th><th>Fixed effects</th><th>Estimates</th><th>l-95% CI</th><th>u-95% CI</th></tr>
<tr><td rowspan="4">Plot + sampling date</td><td rowspan="4">Hatchingsuccess~ plot + sampling date +(1|birdID) + (1|nestID)</td><td rowspan="4">148.84</td><td rowspan="4">0.49</td><td rowspan="4">0</td><td>Intercept</td><td>-3.15</td><td>-4.7376</td><td>-1.5624</td></tr>
<tr><td>plot3</td><td>1.23</td><td>0.0148</td><td>2.4452</td></tr>
<tr><td>plot5</td><td>1.72</td><td>0.4068</td><td>3.0332</td></tr>
<tr><td>sampling date</td><td>0.05</td><td>-0.0284</td><td>0.1284</td></tr>
<tr><td rowspan="7">Plot + sampling date + telogroup</td><td rowspan="7">Hatchingsuccess~telogroup + plot + sampling date +(1|birdID) + (1|nestID)</td><td rowspan="7">151.2704</td><td rowspan="7">0.14</td><td rowspan="7">2.43</td><td>Intercept</td><td>-8.46</td><td>-51.8544</td><td>34.9344</td></tr>
<tr><td>telogroup2</td><td>0.49</td><td>-38.416</td><td>39.396</td></tr>
<tr><td>telogroup3</td><td>-0.76</td><td>-33.4724</td><td>31.9524</td></tr>
<tr><td>telogroup4</td><td>-1.83</td><td>-32.2296</td><td>28.5696</td></tr>
<tr><td>plot3</td><td>21.32</td><td>-28.0328</td><td>70.6728</td></tr>
<tr><td>plot5</td><td>23.01</td><td>-29.6944</td><td>75.7144</td></tr>
<tr><td>sampling date</td><td>-0.13</td><td>-2.678</td><td>2.418</td></tr>
</table>

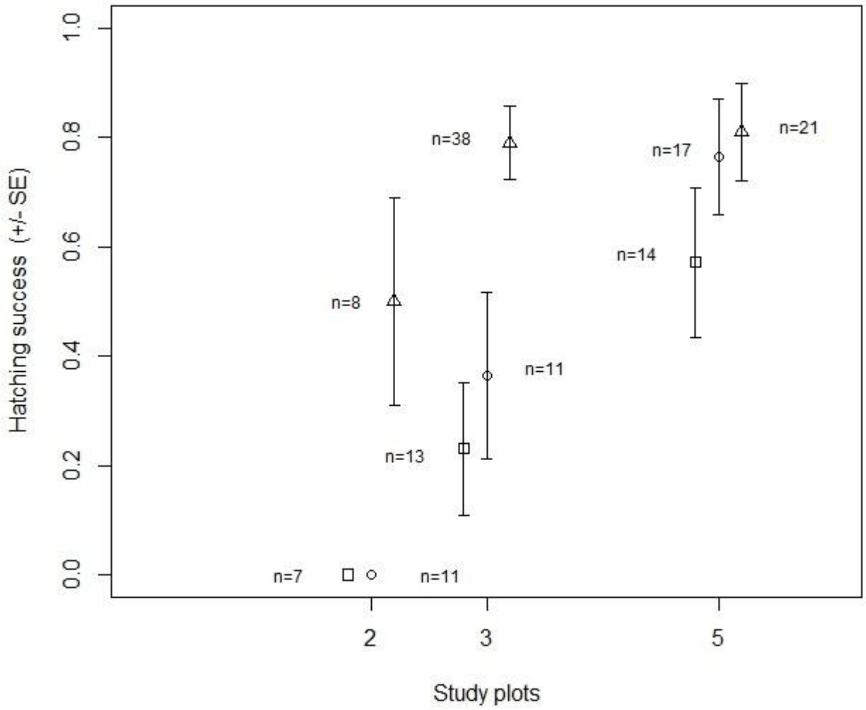

Figure 7 *Average hatching success and SE for each plot and season. Square symbols correspond to the 2011/12 breeding season, circles to the 2012/13 breeding season and triangles to the 2013/14 breeding season. The numbers beside each point represent the sample size for that precise plot and season.*

Survival until 15 days

Survival of the chick until 15 days after hatching was not related to telomere length (Figure 8; Table 5). Indeed, our model selection indicates that it was best explained as a function of the first visit date, plot, body size, season and sampling date. When the telomere group variable was included in the model, the AIC increased from 140.96 in the AIC selected model to 148.6 (Table 4).

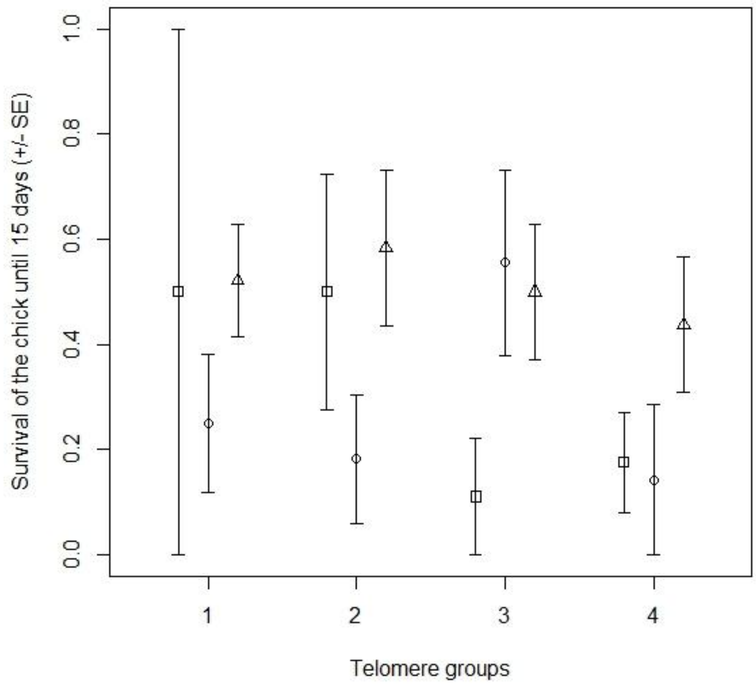

Figure 8 *Average survival until 15 days after hatching and SE for each telomere group and season. Square symbols correspond to the 2011/12 breeding season, circles to the 2012/13 breeding season and triangles to the 2013/14 breeding season. Survival of the chick until the 15th day for telomere group one has a very low sample size (n=2), hence the large SE bars.*

Table 5 *Results from selected generalized linear mixed models for the survival until 15 days analyses (first visit + plot + size + season + sampling date), and model including the telomere group variable. Estimates, standard errors and 95% CI are shown for all fixed effects.*

Covariates+sex	Model	AIC	AIC weights	Δ AIC	Fixed effects	Estimates	l-95% CI	u-95% CI
firstvisit + plot + GonysHeight + season + sampling date	Survival15days~ firstvisit + plot + GonysHeight + season + sampling date +(1|birdID) + (1|nestID)	143.7	0.79	0	Intercept	-55.72	-133.8456	22.4056
					firstvisit	0.6	-0.38	1.58
					plot3	24.28	-37.7148	86.2748
					plot5	19.78	-44.6256	84.1856
					GonysHeight	-7.21	-23.5172	9.0972
					season1213	3.83	-28.51	36.17
					season1314	19.44	-7.8236	46.7036
					sampling date	0.09	-1.3996	1.5796
telogroup + firstvisit + plot + GonysHeight + season + sampling date	Survival15days~ telogroup + firstvisit + plot + GonysHeight + season + sampling date +(1|birdID) + (1|nestID)	148.6	0.07	4.9	Intercept	-62.98	-157.0012	31.0412
					telogroup2	-1.57	-32.7144	29.5744
					telogroup3	-8.17	-38.9224	22.5824
					telogroup4	-18.08	-51.3412	15.1812
					firstvisit	0.49	-0.6076	1.5876
					plot3	48.46	-26.7256	123.6456
					plot5	49.89	-28.1768	127.9568
					GonysHeight	-9.02	-29.9528	11.9128
					season1213	-0.8	-39.3532	37.7532
					season1314	16.44	-17.1544	50.0344
					sampling date	-0.4	-2.164	1.364

Telomere dynamics

33 birds experienced telomere attrition, and 23 birds experience an increase in telomere length (average telomere loss = -0.099; SE=+/-0.086) (Figure 9). However, there was no significant change in T/S ratio during the 3 year period.

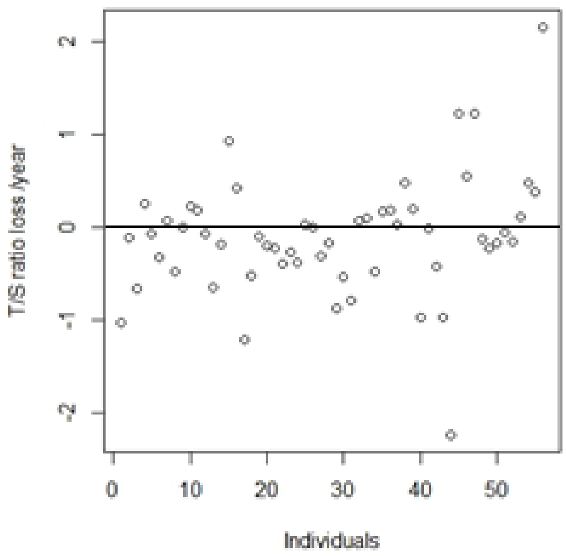

Figure 9 *Relative telomere length (T/S ratio) loss per year for each individual with replicated measurements (white dots). The black horizontal line represents no change. Average relative telomere length loss was = -0.099 (+/- SE=0.086). Sample size n=57.*

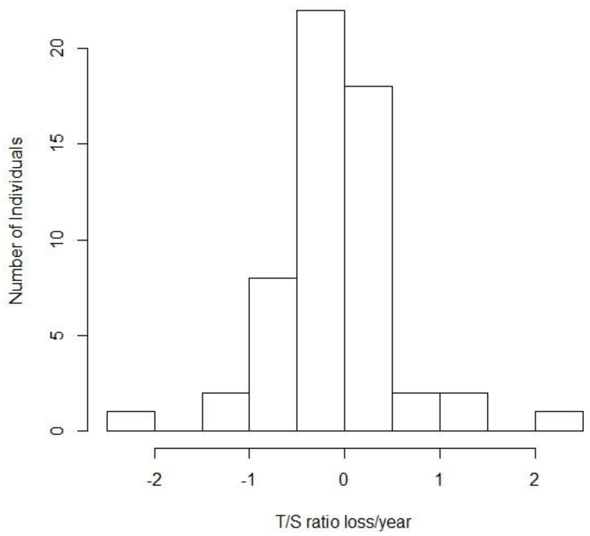

Figure 10 *Relative telomere loss per year frequency distribution. Sample size n=56.*

Our model selection suggests that there is important inter-individual variation in the telomere length dynamics (Table 6). However, this effect is driven by only two individuals, one that showed a great increase in telomere length, and another a great decrease (Figure 10). Without those 2 individuals, our results indicate no change in telomere length during the three years of our study and no variation among individuals in the telomere dynamics (Table 8)

Table 6 *Glmm model selection for the telomere dynamics analyses (dataset with the two extreme values).*

Model	AIC	Δ AIC	AIC *wi*
tsratio ~ 1 + (1|birdID)	241.724	9.628	0.008
tsratio ~ + season + (1|birdID)	247.103	15.007	0.001
tsratio ~ + season + (season|birdID)	232.096	0	0.991

Table 7 *Estimates, standard errors and t-values for the model selected (dataset with the two extreme values).*

Model	Fixed effects	Estimate	SE	t value
tsratio ~ + season + (season|birdID)	season	-0.01105	0.07994	-0.138

Table 8 *Glmm model selection for the telomere dynamics analyses (dataset without the two extreme values).*

Model	AIC	Δ AIC	AIC *wi*
tsratio ~ 1 + (1|birdID)	148.7327	0	0.946441
tsratio ~ + season + (1|birdID)	154.9063	6.1736	0.043202
tsratio ~ + season + (season|birdID)	157.7627	9.03	0.010357

DISCUSSION

There were great inter-annual differences in T/S ratio. Furthermore, according to our model results, telomere length played no important role in the hatching date, hatching success or in the survival of the chick until 15 days.

We did not find a significant inter-annual change in the T/S ratio. The inter-individual variation detected in the models was driven by two birds with extreme values. Once removed, the inter-individual variation disappeared.

None of our model results support any of our initial predictions and Antarctic petrel reproduction seemed independent of individuals' telomere length. Environmental factors (such as extreme climatic events) and small-scale breeding site conditions (i.e. plot) as well as phenotypic traits (such as body size) might play a larger role in determining the breeding outcome of long-lived Antarctic seabirds.

Size had a small, non-biologically relevant, positive effect on survival of the chick until 15 days (0.05 % increase in the probability of the chick surviving until 15 days). However, an increase of 11 millimeter in the gonys height delays hatching date by 4.6 days, which might be an important biological effect.

Breeding plot affected hatching success and survival of the chick until 15 days. The relationship between breeding success and breeding location is complex and requires further research (Descamps, et al. 2009).

During the 2011-2012 breeding season, long telomere birds were sampled earlier than the rest. Antarctic petrels´ breeding success is greatly affected by weather conditions occurring at the colony, explaining 30% of the daily nest survival during the 2011-2012 season, and accounting for up to 30% of the inter-annual variation in colony productivity in the years 1985-2014 (Descamps, et al. 2014). These extreme events experienced by Antarctic petrels at Svarthammaren during the 2011-2012 season translated into many nesting failures. Hence, additional nests were included in the study to increase the sample size. Interestingly, those birds sampled later in the season in 2011-2012 had on average longer telomere than birds sampled earlier. This relation between sampling date and telomere length was only apparent in the first year (the snow storm year) but not in the subsequent years. This suggests that long telomere birds were not present in the study plots after a certain date but only in the snow storm year. Any interpretation remains highly speculative but it could be that long telomere birds corresponded to young inexperienced birds (Hall, et al. 2004b) that were not able to cope with the snow storms. The role of experience in breeding success has been shown in many studies to be a factor of extreme importance in seabirds (Wooller, et al. 1990), especially during the first years of breeding attempts (Ollason and Dunnet 1978). The telomere loss rate is greater in biologically young individuals, suggesting that inexperienced birds have to increase their breeding effort (Beaulieu, et al. 2011), due to their inexperience. For this, we propose that during season 1112 the disappearance of long telomere birds could be partially related to the inexperience of this potentially younger individuals. The hypothesis that birds with short or long telomeres would cope differently with extreme climatic events clearly deserves further investigation.

Telomere loss varies between long-lived and short lived species (Haussmann, et al. 2003). Long-lived species suffer little or no telomere attrition following a costly reproductive event (Beaulieu, et al. 2011), and individual heterogeneity can mitigate these attrition effects if present (Bauch, et al. 2013). On the other hand, short-lived birds experience a decrease in antioxidant capacity (which directly affects telomere length) when encountering costly reproductive events (Alonso-Alvarez, et al. 2004; Wiersma, et al. 2004). It is typical of long-lived birds to suffer little telomere attrition from year to year (Juola, et al. 2006). In our study, most of the birds experienced a small but non-significant decrease on the telomere length (average telomere loss of 2.7 %; +/-2.43%) that fits with previous studies of relative telomere loss (Bize, et al. 2009). However, some individuals experienced an increase in T/S ratio, something that has already been reported in long-lived birds (Bize, et al. 2009). In particular, two individuals experienced a great change in telomere length (one a decrease and the other an increase). There were no methodological reasons to think that these two individual measurements were outliers. In future studies, it would be interesting to confirm the biological consequences for those individuals with extremely divergent telomere evolutions.

Future long-term studies are needed to unveil the relationships between weather conditions during the breeding seasons at the breeding sites and the response from individuals with a different physiological state. If possible, a greater sample size of nests should be monitored to prevent a posterior reduction in sample size. Gathering more longitudinal data would allow us to explore the possible relationship between the telomere-length related disappearance effect and extreme weather events observed in this study, as well as the interaction between telomere dynamics and extreme weather events. Information about wintering grounds and conditions experienced in their wintering areas are much needed in order to correctly estimate the effects of the variables that play a role in the breeding success of Antarctic petrels and in understanding the role of physiology-driven processes.

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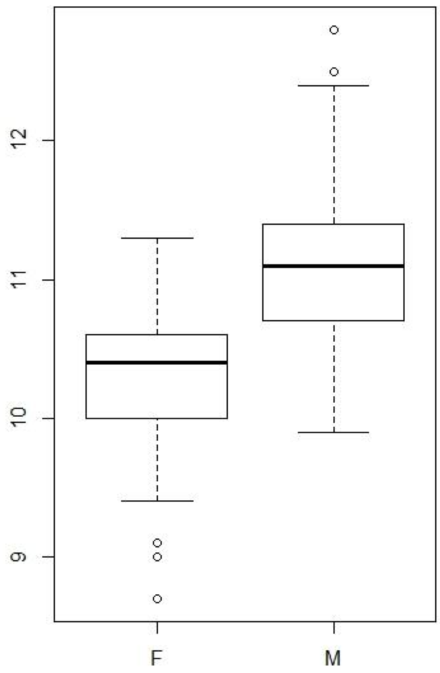
APPENDIXES

Appendix 1

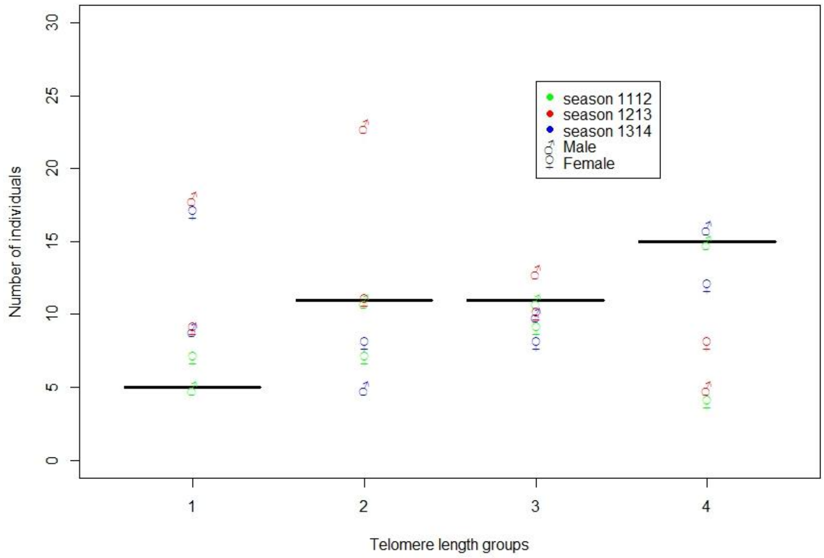
Telomere gene conditions were 2 minutes at 95°C followed by 30 cycles of 30 seconds at 56°C, 1 minute at 72°C and 15 seconds at 95°C. A 20 min final melt step was included on each run with the temperature ramping from 56°C to 95°C. Control gene (or non-variable copy number gene, non-VCN) PCR conditions were 2 minutes at 95°C followed by 40 cycles of 1 minute at 60°C and 1 minute at 95°C. A 20 min final melt step was included on each run with the temperature ramping from 60°C to 95°C. Predicted qPCR amplicon sizes were checked after electrophoresis on a 1.5% agarose gel run in standard TBE (Tris/Borate/EDTA) buffer (90 V for 10 minutes and 130 V thereafter for 30 minutes) and using ethidium bromide staining.

Appendix 2



Appendix 2 *Size (Gonys height in millimeters; y-axis) average and SE for male and female Antarctic petrels*

Appendix 3



Appendix 3 *Number of male and female birds in each season and telomere group. In the telomere group 4 (for the 1112 season) 15 birds were males and 4 were females.*

Appendix 4

Appendix 4 *Model selection for the generalized linear mixed models for the hatching success analyses. Models highlighted in green were the best models for each category of analyses.*

<table>
<tr><th>Covariates</th><th>Model</th><th>AIC</th><th>AIC weights</th><th>Δ AIC</th></tr>
<tr><td rowspan="5">season</td><td>Hatchingsuccess~ 1 +(1|birdID) + (1|nestID)</td><td>151.4742</td><td>0.59</td><td>0</td></tr>
<tr><td>Hatchingsuccess~ season + sampling date +(1|birdID) + (1|nestID)</td><td>153.8253</td><td>0.19</td><td>2.36</td></tr>
<tr><td>Hatchingsuccess~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>154.3549</td><td>0.14</td><td>2.89</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.293</td><td>0.09</td><td>3.82</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + sampling date * season +(1|birdID) + (1|nestID)</td><td>161.0291</td><td>0.01</td><td>9.56</td></tr>
<tr><td rowspan="10">Size/ Size + season</td><td>Hatchingsuccess~ 1 +(1|birdID) + (1|nestID)</td><td>151.4742</td><td>0.43</td><td>0</td></tr>
<tr><td>Hatchingsuccess~ GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>153.9752</td><td>0.13</td><td>2.51</td></tr>
<tr><td>Hatchingsuccess~ season + sampling date +(1|birdID) + (1|nestID)</td><td>153.8253</td><td>0.14</td><td>2.36</td></tr>
<tr><td>Hatchingsuccess~ GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.4846</td><td>0.06</td><td>4.02</td></tr>
<tr><td>Hatchingsuccess~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>154.3549</td><td>0.11</td><td>2.89</td></tr>
<tr><td>Hatchingsuccess~ telogroup + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>155.7757</td><td>0.05</td><td>4.31</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.293</td><td>0.07</td><td>3.82</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>157.1849</td><td>0.03</td><td>5.72</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>157.335</td><td>0.03</td><td>5.87</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + GonysHeightscale*season + sampling date +(1|birdID) + (1|nestID)</td><td>166.2093</td><td>0.01</td><td>14.74</td></tr>
<tr><td rowspan="10">Plot/Plot + season</td><td>Hatchingsuccess~ 1 +(1|birdID) + (1|nestID)</td><td>151.4742</td><td>0.13</td><td>2.63</td></tr>
<tr><td>Hatchingsuccess~ plot + sampling date +(1|birdID) + (1|nestID)</td><td>148.8445</td><td>0.49</td><td>0</td></tr>
<tr><td>Hatchingsuccess~ season + sampling date +(1|birdID) + (1|nestID)</td><td>153.8253</td><td>0.04</td><td>4.99</td></tr>
<tr><td>Hatchingsuccess~ plot + season + sampling date +(1|birdID) + (1|nestID)</td><td>151.8533</td><td>0.11</td><td>3.01</td></tr>
<tr><td>Hatchingsuccess~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>154.3549</td><td>0.04</td><td>5.52</td></tr>
<tr><td>Hatchingsuccess~ telogroup + plot + sampling date +(1|birdID) + (1|nestID)</td><td>151.2704</td><td>0.15</td><td>2.43</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.293</td><td>0.02</td><td>6.45</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + plot + sampling date +(1|birdID) + (1|nestID)</td><td>153.7545</td><td>0.05</td><td>4.91</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>157.335</td><td>0.01</td><td>8.5</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + plot*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>164.9001</td><td>0.01</td><td>16.06</td></tr>
<tr><td rowspan="10">Firstvisit/Firstvisit + season</td><td>Hatchingsuccess~ 1 +(1|birdID) + (1|nestID)</td><td>151.4742</td><td>0.44</td><td>0</td></tr>
<tr><td>Hatchingsuccess~ firstvisit + sampling date +(1|birdID) + (1|nestID)</td><td>154.2731</td><td>0.11</td><td>2.8</td></tr>
<tr><td>Hatchingsuccess~ season + sampling date +(1|birdID) + (1|nestID)</td><td>153.8253</td><td>0.14</td><td>2.36</td></tr>
<tr><td>Hatchingsuccess~ firstvisit + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.6246</td><td>0.06</td><td>4.16</td></tr>
<tr><td>Hatchingsuccess~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>154.3549</td><td>0.11</td><td>2.89</td></tr>
<tr><td>Hatchingsuccess~ telogroup + firstvisit + sampling date +(1|birdID) + (1|nestID)</td><td>155.7482</td><td>0.06</td><td>4.28</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.293</td><td>0.07</td><td>3.82</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + firstvisit + sampling date +(1|birdID) + (1|nestID)</td><td>157.1484</td><td>0.03</td><td>5.68</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>157.335</td><td>0.03</td><td>5.87</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + firstvisit*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>163.6255</td><td>0.01</td><td>12.16</td></tr>
<tr><td rowspan="10">Full models</td><td>Hatchingsuccess~ 1 +(1|birdID) + (1|nestID)</td><td>151.4742</td><td>0.39</td><td>0</td></tr>
<tr><td>Hatchingsuccess~ firstvisit + plot + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>152.7954</td><td>0.2</td><td>1.33</td></tr>
<tr><td>Hatchingsuccess~ season + sampling date +(1|birdID) + (1|nestID)</td><td>153.8253</td><td>0.12</td><td>2.36</td></tr>
<tr><td>Hatchingsuccess~ firstvisit + plot + GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.8005</td><td>0.05</td><td>4.33</td></tr>
<tr><td>Hatchingsuccess~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>154.3549</td><td>0.1</td><td>2.89</td></tr>
<tr><td>Hatchingsuccess~ telogroup + firstvisit + plot + GonysHeightscale + sampling date + season + (1|birdID) + (1|nestID)</td><td>155.192</td><td>0.07</td><td>3.72</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>155.293</td><td>0.06</td><td>3.82</td></tr>
<tr><td>Hatchingsuccess~ telogroup + season + firstvisit + plot + GonysHeightscale (1|birdID) + (1|nestID)</td><td>157.5797</td><td>0.02</td><td>6.11</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>157.335</td><td>0.03</td><td>5.87</td></tr>
<tr><td>Hatchingsuccess~ telogroup * season + firstvisit*season + plot*season + GonysHeightscale*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>163.6255</td><td>0.01</td><td>12.16</td></tr>
</table>

Appendix 5

Appendix 5 *Model selection for the generalized linear mixed models for the survival until 15 days analyses. Models highlighted in green were the best models for each category of analyses.*

Covariates	Model	AIC	AIC weights	Δ AIC
season	Survival15days~ 1 +(1|birdID) + (1|nestID)	153.55	1	0
	Survival15days~ season + sampling date +(1|birdID) + (1|nestID)	168.11	0.01	14.56
	Survival15days~ telogroup + sampling date +(1|birdID) + (1|nestID)	175.65	0.01	22.1
	Survival15days~ telogroup + season + sampling date +(1|birdID) + (1|nestID)	171.82	0.01	18.27
	Survival15days~ telogroup * season + sampling date * season +(1|birdID) + (1|nestID)	193.34	0.01	39.79
Size/ Size + season	Survival15days~ 1 +(1|birdID) + (1|nestID)	153.55	1	0
	Survival15days~ GonysHeightscale + sampling date +(1|birdID) + (1|nestID)	168.43	0.01	14.88
	Survival15days~ season + sampling date +(1|birdID) + (1|nestID)	168.11	0.01	14.56
	Survival15days~ GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)	169.34	0.01	15.79
	Survival15days~ telogroup + sampling date +(1|birdID) + (1|nestID)	175.65	0.01	22.1
	Survival15days~ telogroup + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)	176.89	0.01	23.34
	Survival15days~ telogroup + season + sampling date +(1|birdID) + (1|nestID)	171.82	0.01	18.27
	Survival15days~ telogroup + season + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)	169.75	0.01	16.2
	Survival15days~ telogroup * season + sampling date +(1|birdID) + (1|nestID)	193.34	0.01	39.79
	Survival15days~ telogroup * season + GonysHeightscale*season + sampling date +(1|birdID) + (1|nestID)	193.9	0.01	40.35
Plot/Plot + season	Survival15days~ 1 +(1|birdID) + (1|nestID)	153.55	0.05	6.1
	Survival15days~ plot + sampling date +(1|birdID) + (1|nestID)	162.47	0.01	15.02
	Survival15days~ season + sampling date +(1|birdID) + (1|nestID)	168.11	0.01	20.66
	Survival15days~ plot + season + sampling date +(1|birdID) + (1|nestID)	147.45	0.96	0
	Survival15days~ telogroup + sampling date +(1|birdID) + (1|nestID)	175.65	0.01	7.54
	Survival15days~ telogroup + plot + sampling date +(1|birdID) + (1|nestID)	161.12	0.01	-6.99
	Survival15days~ telogroup + season + sampling date +(1|birdID) + (1|nestID)	171.82	0.01	3.71
	Survival15days~ telogroup + season + plot + sampling date +(1|birdID) + (1|nestID)	170.86	0.01	2.75
	Survival15days~ telogroup * season + sampling date +(1|birdID) + (1|nestID)	193.34	0.01	25.23
	Survival15days~ telogroup * season + plot*season + sampling date * season +(1|birdID) + (1|nestID)	184	0.01	15.89
Firstvisit/Firstvisit + season	Survival15days~ 1 +(1|birdID) + (1|nestID)	153.55	0.1	3.57
	Survival15days~ firstvisit + sampling date +(1|birdID) + (1|nestID)	149.98	0.6	0
	Survival15days~ season + sampling date +(1|birdID) + (1|nestID)	168.11	0.01	18.13
	Survival15days~ firstvisit + season + sampling date +(1|birdID) + (1|nestID)	155.25	0.05	5.27
	Survival15days~ telogroup + sampling date +(1|birdID) + (1|nestID)	175.65	0.01	25.67
	Survival15days~ telogroup + firstvisit + sampling date +(1|birdID) + (1|nestID)	151.85	0.24	1.87
	Survival15days~ telogroup + season + sampling date +(1|birdID) + (1|nestID)	171.82	0.01	21.84
	Survival15days~ telogroup + season + firstvisit + sampling date +(1|birdID) + (1|nestID)	156.15	0.03	6.17
	Survival15days~ telogroup * season + sampling date +(1|birdID) + (1|nestID)	193.34	0.01	43.36
	Survival15days~ telogroup * season + firstvisit*season + sampling date * season +(1|birdID) + (1|nestID)	181.48	0.01	31.5
Full models	Survival15days~ 1 +(1|birdID) + (1|nestID)	153.55	0.01	9.85
	Survival15days~ firstvisit + plot + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)	152.25	0.01	8.55
	Survival15days~ season + sampling date +(1|birdID) + (1|nestID)	168.11	0.01	24.41
	Survival15days~ firstvisit + plot + GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)	143.7	0.79	0
	Survival15days~ telogroup + sampling date +(1|birdID) + (1|nestID)	175.65	0.01	31.95
	Survival15days~ telogroup + firstvisit + plot + GonysHeightscale + sampling date +season+ (1|birdID) + (1|nestID)	148.6	0.01	4.9
	Survival15days~ telogroup + season + sampling date +(1|birdID) + (1|nestID)	171.82	0.01	28.12
	Survival15days~ telogroup + season + firstvisit + plot + GonysHeightscale (1|birdID) + (1|nestID)	166.61	0.01	22.91
	Survival15days~ telogroup * season + sampling date +(1|birdID) + (1|nestID)	193.34	0.01	49.64
	Survival15days~ telogroup * season + firstvisit*season + plot*season + GonysHeightscale*season + sampling date * season +(1|birdID) + (1|nestI	184.48	0.01	40.78

Appendix 6

Appendix 6 *Model selection for the generalized linear mixed models for the hatching date analyses. Models highlighted in green were the best models for each category of analyses*

<table>
<tr><th>Covariates</th><th>Model</th><th>AIC</th><th>AIC weights</th><th>Δ AIC</th></tr>
<tr><td rowspan="5">season</td><td>Hatching date~ 1 +(1|birdID) + (1|nestID)</td><td>258.7488</td><td>6.76793E-06</td><td>23.8049</td></tr>
<tr><td>Hatching date~ season + sampling date +(1|birdID) + (1|nestID)</td><td>249.1412</td><td>0.000825542</td><td>14.1973</td></tr>
<tr><td>Hatching date~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>261.402</td><td>1.79611E-06</td><td>26.4581</td></tr>
<tr><td>Hatching date~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>276.5931</td><td>9.02875E-10</td><td>41.6492</td></tr>
<tr><td>Hatching date~ telogroup * season + sampling date * season +(1|birdID) + (1|nestID)</td><td>234.9439</td><td>0.9991659</td><td>0</td></tr>
<tr><td rowspan="10">Size/ Size + season</td><td>Hatching date~ 1 +(1|birdID) + (1|nestID)</td><td>257.6532</td><td>3.63428E-12</td><td>53.9432</td></tr>
<tr><td>Hatching date~ GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>203.71</td><td>0.9893491</td><td>0</td></tr>
<tr><td>Hatching date~ season + sampling date +(1|birdID) + (1|nestID)</td><td>250.8756</td><td>1.0769E-10</td><td>47.1656</td></tr>
<tr><td>Hatching date~ GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)</td><td>220.5307</td><td>0.000418288</td><td>16.8207</td></tr>
<tr><td>Hatching date~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>262.3495</td><td>3.47251E-13</td><td>58.6395</td></tr>
<tr><td>Hatching date~ telogroup + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>208.04</td><td>0.0102321</td><td>4.33</td></tr>
<tr><td>Hatching date~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>272.2027</td><td>2.51796E-15</td><td>68.4927</td></tr>
<tr><td>Hatching date~ telogroup + season + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>245.3652</td><td>1.69326E-09</td><td>41.6552</td></tr>
<tr><td>Hatching date~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>234.5626</td><td>3.75402E-07</td><td>30.8526</td></tr>
<tr><td>Hatching date~ telogroup * season + GonysHeightscale*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>236.0789</td><td>1.75884E-07</td><td>32.3689</td></tr>
<tr><td rowspan="10">Plot/Plot + season</td><td>Hatching date~ 1 +(1|birdID) + (1|nestID)</td><td>258.9314</td><td>4.88508E-06</td><td>24.4448</td></tr>
<tr><td>Hatching date~ plot + sampling date +(1|birdID) + (1|nestID)</td><td>290.8436</td><td>5.74424E-13</td><td>56.357</td></tr>
<tr><td>Hatching date~ season + sampling date +(1|birdID) + (1|nestID)</td><td>248.5906</td><td>0.000859705</td><td>14.104</td></tr>
<tr><td>Hatching date~ plot + season + sampling date +(1|birdID) + (1|nestID)</td><td>291.4988</td><td>4.13967E-13</td><td>57.0122</td></tr>
<tr><td>Hatching date~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>259.5434</td><td>3.59737E-06</td><td>25.0568</td></tr>
<tr><td>Hatching date~ telogroup + plot + sampling date +(1|birdID) + (1|nestID)</td><td>300.22</td><td>5.28653E-15</td><td>65.7334</td></tr>
<tr><td>Hatching date~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>273.3031</td><td>3.69917E-09</td><td>38.8165</td></tr>
<tr><td>Hatching date~ telogroup + season + plot + sampling date +(1|birdID) + (1|nestID)</td><td>306.2557</td><td>2.58547E-16</td><td>71.7691</td></tr>
<tr><td>Hatching date~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>234.4866</td><td>0.9930925</td><td>0</td></tr>
<tr><td>Hatching date~ telogroup * season + plot*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>244.6917</td><td>0.006039339</td><td>10.2051</td></tr>
<tr><td rowspan="10">Firstvisit/Firstvisit + season</td><td>Hatching date~ 1 +(1|birdID) + (1|nestID)</td><td>257.7609</td><td>1.29E-05</td><td>21.1529</td></tr>
<tr><td>Hatching date~ firstvisit + sampling date +(1|birdID) + (1|nestID)</td><td>239.9134</td><td>9.68E-02</td><td>3.3054</td></tr>
<tr><td>Hatching date~ season + sampling date +(1|birdID) + (1|nestID)</td><td>250.9933</td><td>3.80E-04</td><td>14.3853</td></tr>
<tr><td>Hatching date~ firstvisit + season + sampling date +(1|birdID) + (1|nestID)</td><td>240.1787</td><td>8.48E-02</td><td>3.5707</td></tr>
<tr><td>Hatching date~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>262.8316</td><td>1.02E-06</td><td>26.2236</td></tr>
<tr><td>Hatching date~ telogroup + firstvisit + sampling date +(1|birdID) + (1|nestID)</td><td>249.0278</td><td>1.02E-03</td><td>12.4198</td></tr>
<tr><td>Hatching date~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>274.8322</td><td>2.53E-09</td><td>38.2242</td></tr>
<tr><td>Hatching date~ telogroup + season + firstvisit + sampling date +(1|birdID) + (1|nestID)</td><td>260.49</td><td>3.29E-06</td><td>23.882</td></tr>
<tr><td>Hatching date~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>236.608</td><td>5.05E-01</td><td>0</td></tr>
<tr><td>Hatching date~ telogroup * season + firstvisit*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>237.5752</td><td>3.12E-01</td><td>0.9672</td></tr>
<tr><td rowspan="10">Full models</td><td>Hatching date~ 1 +(1|birdID) + (1|nestID)</td><td>257.164</td><td>9.14E-08</td><td>32.3805</td></tr>
<tr><td>Hatching date~ firstvisit + plot + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>256.7292</td><td>1.14E-07</td><td>31.9457</td></tr>
<tr><td>Hatching date~ season + sampling date +(1|birdID) + (1|nestID)</td><td>248.6866</td><td>6.33E-06</td><td>23.9031</td></tr>
<tr><td>Hatching date~ firstvisit + plot + GonysHeightscale + season + sampling date +(1|birdID) + (1|nestID)</td><td>234.9056</td><td>6.22E-03</td><td>10.1221</td></tr>
<tr><td>Hatching date~ telogroup + sampling date +(1|birdID) + (1|nestID)</td><td>261.3256</td><td>1.14E-08</td><td>36.5421</td></tr>
<tr><td>Hatching date~ telogroup + firstvisit + plot + GonysHeightscale + sampling date +(1|birdID) + (1|nestID)</td><td>258.6068</td><td>4.44E-08</td><td>33.8233</td></tr>
<tr><td>Hatching date~ telogroup + season + sampling date +(1|birdID) + (1|nestID)</td><td>274.5072</td><td>1.57E-11</td><td>49.7237</td></tr>
<tr><td>Hatching date~ telogroup + season + firstvisit + plot + GonysHeightscale (1|birdID) + (1|nestID)</td><td>257.5438</td><td>7.56E-08</td><td>32.7603</td></tr>
<tr><td>Hatching date~ telogroup * season + sampling date +(1|birdID) + (1|nestID)</td><td>233.6188</td><td>1.18E-02</td><td>8.8353</td></tr>
<tr><td>Hatching date~ telogroup * season + firstvisit*season + plot*season + GonysHeightscale*season + sampling date * season +(1|birdID) + (1|nestID)</td><td>224.7835</td><td>9.82E-01</td><td>0</td></tr>
</table>