### Telomeres reveal silver spoon effects in a wild population

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### Abstract

1. Favourable conditions early in life can confer delayed fitness advantages. However, the mechanistic basis of these 'silver spoon effects' remains poorly understood. Telomeres - protective caps on the ends of chromosomes - shorten in response to early life stress, and early life telomere shortening can cause reduced later life survival. It is thus possible that telomeres provide a 'missing link' between early-life environmental variation and later-life fitness.
2. The prevalence and strength of silver spoon effects has consequences for individual fitness and population growth rates. Understanding the physiological and ecological links between early life experiences and later life survival is therefore fundamental to our understanding of life-history evolution and population ecology alike.
3. We studied how telomere length and shortening link spatiotemporal variation in early-life conditions to survival in the Seychelles warbler (*Acrocephalus sechellensis*). The Seychelles warbler system is excellently suited to addressing this question, due to the long-term lonigtudinal data on survival and senescence. We combined this with cross-sectional and longitudinal telomere measurements taken from over 300 birds from multiple cohorts, and analyse how the variation in the early life environment within and across cohorts affects telomere dynamics and survival.
4. We show that early-life telomere length and shortening rates vary markedly across cohorts, and that this variation is related to temporal fluctuations variation in food availability. Individuals born in breeding seasons with high food availability have longer telomeres and reduced telomere shortening compared to individuals born in years with low food availability. Within cohorts, we found telomere length in chicks was related to growth, and to the number of helpers present in the natal territory. However, the number of helpers was not related to telomere shortening rates, nor to telomere length in fledgling or subadult birds.
5. Our results show that telomeres can reveal complex hidden costs at the individual and cohort levels, and suggest that they may provide a link between early-life conditions and late-life survival in wild populations.

**Keywords:** Ageing; Life-history; Seychelles warbler; Telomeres

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### Introduction

Being subject to favourable environmental conditions during development and growth can confer fitness advantages later in life (so called 'silver spoon effects') (Grafen 1988; Monaghan 2008). There is now evidence that adult fitness can be affected by a range of early-life experiences, including variation in habitat quality and resource availability (Madsen & Shine 2000; Van de Pol *et al.* 2006; Hayward, Rickard & Lummaa 2013), population density (Nussey *et al.* 2007; Douhard *et al.* 2013) and natural or anthropogenic environmental disturbance (Reid *et al.* 2003; Cartwright *et al.* 2014). Understanding the causes and consequences of these early-life experiences is key to understanding many ecological and evolutionary processes, including patterns of natural and sexual selection, population growth rates and even local extinction (Coulson *et al.* 2001; Roach & Carey 2014). Understanding silver spoon effects is therefore of central interest to ecologists, evolutionary biologists and conservationists.

While it is clear that silver spoon effects can occur, we have little understanding of how and under what conditions early-life environments will affect adult fitness. Because the phenotypic consequences of an adverse environment can depend on an individual's genetic or epigenetic makeup (Hoffman & Hercus 2000; Richards 2006), the later-life consequences of a good/poor start are expected to vary among individuals, populations and species. Moreover, it is not always possible to fully quantify what constitutes a good or bad environment, and any 'hidden' environmental variation may obscure relationships relationships between the early-life conditions that are measured and adult phenotypes. Indeed, the pervasiveness of silver spoon effects varies between species (Drummond, Rodríguez & Oro 2011), cohorts (Reid *et al.* 2003) and sexes (Wilkin & Sheldon 2009). In order to better understand the later-life consequences of early-life experiences, we therefore need to understand, or at least be able to measure, how the environment differentially affects individuals within a population.

A key process that has been associated with adult survival is the rate at which telomere repeats are lost. Telomeres are protective caps on the ends of chromosomes which shorten with age (Monaghan & Haussmann 2006), and in response to oxidative damage that can occur due to environmental stress (Von Zglinicki 2002). When telomeres reach a critical shortness cells senesce (Campisi 2003), resulting in organismal senescence and death (Wong *et al.* 2003). These links between telomere length and senescence have inspired a great deal of recent research into telomere ecology (Haussmann & Marchetto 2010; reviewed in Horn, Robertson & Gemmell 2010; Monaghan 2014). While there is little evidence the relationship between telomere dynamics and survival is causal (Simons 2015), there is now excellent evidence that telomeres can act as biomarkers of cost in wild populations, retaining signatures of ecological stress that are otherwise difficult to detect (Monaghan 2014; Schultner *et al.* 2014; Asghar *et al.* 2015).

There is evidence from a range of taxa that the greatest rate of telomere loss occurs in early life (e.g. (Frenck, Blackburn & Shannon 1998; Haussmann, Vleck & Nisbet 2003)), and that the extent of this telomere shortening is influenced by the conditions experienced early in life (Price *et al.* 2013; Monaghan 2014; Reichert, Criscuolo & Zahn 2015; Nettle *et al.* 2015). Importantly, early-life telomere dynamics are related to both short-term and late-life survival (Heidinger *et al.* 2012; Boonekamp *et al.* 2014), and to other parameters such as cognition (Nettle, Andrews & Monaghan 2015). However, the extent to which telomeres provide a link between early-life conditions and late-life survival in the wild is very poorly understood. Moreover, how early life telomere dynamics vary over spatial and temporal scales is not known.

The longitudinal study (since 1986) of the Seychelles warbler (*Acrocephalus sechellensis*) population on Cousin Island provides an excellent model system for studying senescence in the wild (Hammers *et al.* 2015). Specifically, it is ideally suited for assessing the relationship between early-life environmental variation, telomere length and late-life fitness. Firstly, due to the isolated nature of the study population and intensive field monitoring, we have excellent survival data and sampling material spanning many years (see methods, below). Secondly, telomere length predicts survival independently of age in adult Seychelles warblers, suggesting that telomeres act as a biomarker of cost in this species (Barrett *et al.* 2013). Finally, ecological conditions on Cousin are variable over space and time due to spatiotemporal variation in foliage cover and food availability (Van de Crommenacker *et al.* 2011).

In Seychelles warblers, oxidative stress is linked to natal territory quality (Van de Crommenacker *et al.* 2011), but neither natal territory quality nor natal local density are linked to early-life or adult survival (Brouwer *et al.* 2006; Hammers *et al.* 2013). In this study we analyse patterns of early-life telomere length and subsequent survival to test the prediction that telomeres fill a missing link between early-life environmental variation and late-life fitness. Specifically we predict that: i) individuals raised in good quality conditions will have longer telomeres, and ii) having longer telomeres in early life is associated with greater short and long-term survival.

### Methods

##### Study species and sampling

The Seychelles warbler is a small (~15 g), insectivorous passerine bird with a mean life expectancy of 5.5 years at fledging (Hammers *et al.* 2013). The population on Cousin Island (04'20'S, 55'40'E) has been intensively studied since 1986 (Richardson, Burke & Komdeur 2003; Barrett *et al.* 2013). Individuals are usually ringed in their first year of life, and so are of known age. They are then followed throughout their lives, and as they are non-migratory endemics and are naturally confined to the island (Komdeur *et al.* 2004), a biannual census of birds on Cousin during the main (June-August) and minor (December-February) breeding seasons gives an accurate measure of levels of local density and individual survival rate (Barrett *et al.* 2013). Full details of catching and census methods can be found in Brouwer *et al.* (Brouwer, Richardson & Komdeur 2012).

All territories are mapped during the main and minor breeding seasons based on detailed observational data of foraging and territorial defence behaviour, and surveyed for territory quality (Richardson *et al.* 2003). Territory quality is calculated based on territory size, foliage cover and insect abundance (Komdeur 1992) and averaged within territories (Hammers *et al.* 2013). Cousin is also subject to intra- and inter-annual variation in rainfall and food availability, and such island-wide temporal variation may override the effects of absolute territory quality. As an estimate of variation in food availability, we calculated an index of the number of insects across the entire island during. This index represents the average number of insects found per unit leaf area over all surveys carried out on the island in a breeding season.

Each time a bird is caught on Cousin body mass and tarsus length are measured, and age is assessed on the basis of eye colour and previous captures (Richardson *et al.* 2003). A blood sample (ca 25 l) is taken from each bird via brachial venipuncture, and stored in 1 m1 absolute ethanol in a 1.5 ml screw-cap microfuge tube at room temperature.

##### Molecular methods

Genomic DNA was extracted from a ~2 mm2 flake of preserved blood using the DNeasy Blood and Tissue Kit (Qiagen), following the manufacturer's protocol, with the modification of overnight lysis at 37oC and a final DNA elution volume of 80 l. DNA concentration and purity were quantified using a NanoDrop 8000 Spectrophotometer (ThermoScientific), and DNA integrity was validated by by visualization with ethidium bromide after electrophoresis on a 1.2% agarose gel. Sex was determined using the molecular method outlined by Griffiths *et al.* (1998).

Telomere lengths were measured from 327 samples taken cross-sectionally from birds aged less than twelve months, between 1995 and 2012. Of these birds, 81 were nestlings less than two months old (chicks), 118 were aged between two and six months (fledglings), and 128 were aged seven to twelve months (subadults). We measured absolute telomere quantity per diploid genome using a quantitative PCR (qPCR) assay (full details in (Barrett *et al.* 2012)).

##### Statistical analyses

We performed all analyses using R version 3.0.1 (R Development Core Team 2011). Our sampling regime covers 17 years, and temporal variation in rainfall and food availability on Cousin over this period is expected to result in variation in a range of social and evironmental variables (Brouwer *et al.* 2012). This makes it difficult to disentangle how spatial and temporal processes differentially affect early-life telomere dynamics. To get around this, we seperately analysed how variation in early life conditions among and within breeding seasons was related to variation in early life telomere length.

First, to analyse whether temporal variation in food availability drives population-level variation in telomere dynamics, we calculated average telomere length among all birds born in a given breeding season (i.e. a cohort). We tested for a difference in telomere length amomg cohorts using a one-way ANOVA, and then used linear regression to test whether variation in mean telomere length among cohorts is explained by temporal variation in insect abundance.

We then tested tested how spatially varying early-life environmental and social conditions influence telomere length within cohorts using linear models. For these analyses, telomere length was standarsised by mean-centering within cohorts, thus controlling for any temporal variation in telomere length. As explanatory variables we included tarsus length, sex, territory quality and the number of helping and non-helping subordinates present in the natal territory (Brouwer *et al.* 2012). We used model averaging to assess how these variables shape telomere length and dynamics in early life. We created a full model containing all of the above terms, and a top model set was then defined, containing all models with AICc 6 compared to the best supported model (Burnham, Anderson & Huyvaert 2011). We report model averaged coefficients, confidence intervals, and 'relative importance', which reflects the relative weights of each predictor variable across the top model set. Model averaging was carried out using the MuMIn package (version 1.10.5) in R (Bartoń 2012).

For a subset of first-year birds (n = 98 individuals) we had longitudinal data (i.e samples from individuals caught both in their first year and as an adult). For these individuals we calculated a rate of telomere loss between the first-year sample and earliest adult sample by subtracting the adult telomere length from the early-life telomere length and dividing this difference by the length of time (in days) between sampling events. To account for regression to the mean effects, we applied a correction based on correlations among samples within individuals following Verhulst *et al.* (2013). Using this dataset we repeated the analyses of among and within cohort telomere dynamics, replacing telomere length with telomere loss as the response variable.

Finally, we analysed the effects of telomere dynamics on survival, again by looking at variation both within and among cohorts. First, we tested the prediction that cohort-level telomere dynamics are associated with survival by comparing the mean telomere length and loss of each cohort with the mean lifespan of all individuals, using linear regression. We then used parametric survival analysis to test whether individual-level telomere length and loss were related to to survival. For this analysis, implemented in the FlexSurv package in R, we mean-centred telomere length within cohorts to eliminate cohort-level variation in telomeres and survival. The survival time distribution was chosen by comparing the fit of a range of distributions (exponential, Weibull, log-normal, gamma, gompertz and generalized F) against the observed survival data, by visually inspecting plots and by comparing AIC values. As explanatory variables of survival we included early-life telomere length/loss (we ran a seperate analysis for each, using the cross-seciotna and longitudinal data, respectively), plus the factors identified as being related to telomere length in the previous analysis. With this approach we aimed to assess the effect of early-life telomere length on survival while controlling for potentially confounding variables that may be correlated with telomere dynamics.

### Results

##### Early-life telomere length and age

Mean ( standard error) telomere length in first-year birds was 5.15 0.20 kb. This is lower than the mean for one year-old birds based on cross-sectional data (5.46 0.15 kb). However, when we considered age classes seperately, we found substantial age-related variation in telomere length within the first year of life (F = 8.84; *P* = < 0.01). This revealed that chicks have longer telomeres than any other age group, but also that there was an apparent increase in average telomere length from the fledgling to subadult stages (Fig. 1A). However, a longitudinal analysis of telomere loss showed that chicks, fleglings and subadults all lost telomeres early in life (intercept of model of telomere loss and age class significantly greater than zero; *P* = 0.29), but that there was no difference in the rate of telomere loss among age classes (F = 0.90; *P* = 0.41; Fig. 1B). This suggests that the apparent increase in telomere length between fledglings and subadults in the cross-sectional data was a result of the sampling, rather than telomere elongation.

##### Temporal variation in early life telomere dynamics

Early-life telomere length varied significantly among breeding seasons (one-way ANOVA, F = 2.22; *P* = < 0.001), and this variation in average telomere length over breeding seasons was positively related to island-wide food aviilability (linear regression, R2 = 0.40; F = 9.39; *P* = 0.008; Fig. 2A). Running the regression of cohort-level telomere length and food availability seperately for each age class revealed a postive and significant relationship in fledglings (R2 = 0.45; F = 8.18; *P* = 0.017) and subadults (R2 = 0.41; F = 7.63; *P* = 0.018), but a marginally non-significant *negative* relationship was found for chicks (R2 = 0.44; F = 5.49; *P* = 0.052).

The rate of telomere shortening in early life did not vary significantly among breeding seasons (F = 1.39; *P* = 0.16); however, what variation there was in rates of telomere shortening could be explained by temporal variation in food availability (R2 = 0.26; F = 4.51; *P* = 0.05). This pattern corresponded with the cross-sectional data: individuals born in seasons with low food availability lost telomeres, on average, at a faster rate than those born in years with high food availability (Fig. 2B). Unforutunately our limited sample size within the longitudinal dataset precluded us from running this analysis seperately for each age class.

##### Spatial variation in early life telomere dynamics

The top model explaining within-season variation in chick telomere length contained tarsus length and the number of helpers present in the natal territory (Table S1), and this model was a much better fit than the null model (AICc = 10.65). Both tarsus length and the number of helpers had high relative importance in the top model set (Fig. 3A), and the model containing these variables explained a reasonable amount of variation in telomere length (R2 = 0.24). Telomere length was positively related to the number of helpers (Fig. 3C), and negatively related to tarus length (Fig. 3D).

For fledglings, the null model was the top model explaining early-life telomere length (Table S1). Moreover, none of the explanatory terms had high importance in the top model set, and confidence intervals of all estimates close to zero (Fig. 4A), suggesting that none of the variables analysed had a significant effect on fledgling telomere length. For sub-adults, the top model contained territory quality (Table S1), which was negatively related to sub-adult telomere length (Fig. 4B). However, territory quality explained a tiny amount of variation in subadult telomere length (R2 = 0.03), and there was only a small difference in AIC between the model containing territory quality and the null model (AICc = 0.81). Moreover, the confidence intervals of the territory quality effect overlapped with zero (Fig. 4B).

For the subset of individuals with longitudinal data, we tested whether the factors previously identified as being related early-life telomere length (i.e. tarsus length, sex and number of helpers) were also associated with differences in rates of early life telomere loss. Due to a limited sample size, we considered all age classes together for this analysis. We found that none of these variables were associated with differences in telomere shortening (all *P* > 0.05).

##### Early life telomere dynamics and survival

At the population-level, we found no evidence that individuals born in breeding seasons with high food avilability had longer lifespans (R2 = 0.09; F = 1.42; *P* = 0.25), nor that individuals born in years where average telomere length was longer had longer lifespans (R2 = 0.007; F = 0.13; *P* = 0.72; Fig. 5A). Interestingly, however, we found a strong, negative relationship between population-level telomere loss and lifespan (R2 = 0.289; F = 6.92; *P* = 0.02; Fig. 5B), which suggests that individuals born in periods where early-life telomere shortening is lowest live, on average, longer overall.

For the individual-based survival analysis, a log-normal survival model best fitted the Seychelles warbler data (AIC = 1115.35, AIC of next best distribution (Weibull) = 1134.82). A survival model including all first year birds, early-life telomere length was not associated with survival (estimate = 0.064, CI = < 0.001-0.189). However, we did find differential survival effects among age classes. Chick telomere length had no effect on survival (estimate = < 0.001, CI = < 0.001-0.127; Fig. 6A). However, telomere length at both the fledgling and subadult stage was significantly related to survival (fledglings: estimate = 0.249, CI = 0.018-0.481; subadults: estimate = 0.205, CI = 0.036-0.374). In both cases this effect was positive, with longer telomeres in early life associated with increased survival later in life (Figs 6B, 6C). Finally, using the longitudinal data, we found no effect of early-life telomere shortening on subsequent survival (estimate = 0.11, CI = < 0.001-0.339).

### Discussion

Here we show that telomeres link early-life conditions to later-life survival in the Seychelles warbler. We first show that telomere length and rates of shortening in early life are subject to strong cohort effects, and that cohort-level telomere dynamics can be explained by island-wide temporal variation in food availability. We then show that within cohorts, the social environemnt (i.e. number of helpers) affects telomere length, but that this effect is age-dependent. Finally, we show that telomere length in early life predicts later-life survival. These findings have important implications for research on life history evolution in wild populations.

Our finding that food availability is related to early-life telomere length adds to a growing body of evidence from humans and wild animals, showing that the natal environment can have pronounced impacts on early-life telomere length (reviewed in Price *et al.* 2013; Monaghan 2014). However, very few studies have shown that temporal variation in environmental conditions affects telomere dynamics in natural populations (Mizutani *et al.* 2013; Watson, Bolton & Monaghan 2015). We suspect this is more due to a lack of available long-term datasets with telomere screening, rather than the Seychelles warbler being unique. Indeed, the environment on Cousin is benign in comparison with many regions outside the tropics, where populations undergo large fluctuations in size (e.g. (Coulson *et al.* 2001)). We therefore expect that as more long-term studies generate telomere datasets, the effects of temporal changes in the environment on telomere dynamics will become increasingly clear.

If temporal variation in early-life telomere dynamics is common in nature, this has a number of ramifications for our understanding of telomere dynamics in natural populations. First, our findings suggest that telomere dynamics

We found that after controlling for among-cohort variation in telomere length, tarsus length and the number of helpers were the most important predictors of telomere length in Seychelles warbler chicks.

In captive zebra finches, juvenile telomere length predicts late-life survival (Heidinger *et al.* 2012), and in wild bird populations early-life telomere length has recently been linked to survival during the nestling-phase (Watson *et al.* 2015), and survival to adulthood (Boonekamp *et al.* 2014). Our results are, to our knowledge, the first to demonstrate that early-life telomere length is associated with late-life survival in a wild population. Previous studies have shown that in juvenile Seychelles warblers, the number of helpers, but not temporal variation in food availability, predicts later-life survival (Brouwer *et al.* 2006, 2012; Hammers *et al.* 2013).

That we found a relationship between telomere length, but not loss, and survival is surprising as other studies have found the opposite (Boonekamp *et al.* 2014).

There are numerous promising avenues for future research into telomere molecular ecology in this system and others. Here we have considered survival, but telomere length and shortening in early life may also be linked to recruitment into the breeding population and/or reproductive senescence.

Together with previous research on the Seychelles warbler, our results confirm that both temporal and spatial variation in the early-life environment is linked to later-life survival, and our results suggest that telomeres go some to way to capturing this complexity. Thus, our results support the idea that telomeres can be used as a 'generic currency' with which we can measure variation in costs among individuals and populations (Asghar *et al.* 2015). The prospect of using telomeres as indicators of population health is a particularly interesting one, as such an approach would be useful to a broad range of conservation and animal health practitioners. Our findings suggest that telomere length at the population level does reflect environmental stress. However, our analyses are confined to a single island, and research across populations with different environments and genetic histories is required in order to provide further insight into the usefulness of telomeres as biomarkers of population health.

### Data accessibility

This manuscript was written in R Markdown (<http://rmarkdown.rstudio.com/>). All data and scripts required to reproduce the manuscript, and all figures and analyses contained within it, will be made available on GitHub.

### Acknowledgements

Nature Seychelles facilitate the long-term Seychelles warbler project, allowing us to stay on Cousin Island, and providing accommodation and facilities during field work. The Seychelles Bureau of Standards and Department of Environment gave permission for sampling and fieldwork. Emma Barrett laid the foundations for this study, generating much of the telomere data. We thank everyone who has helped in the field, and the current Seychelles warbler research group for useful discussions. This work was funded by two Natural Environment Research Council (NERC) grants to DSR (NE/F02083X/1 and NE/K005502/1) on which JK, TB and HLD were project partners. HLD was funded by a NERC fellowship.

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