### 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 is correlated with reduced later-life survival. As telomeres are able to measure the impact of early life costs, they may provide a 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.
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 availability of long-term longitudinal survival and senescence data unconfounded by dispersal. We combined this with cross-sectional and longitudinal telomere measurements taken from over 300 birds from multiple cohorts, and analysed how 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 in food availability. Individuals born in breeding seasons with high food availability have reduced telomere shortening compared to individuals born in years with low food availability. Within cohorts, we found that telomere length in nestlings was negatively related to tarsus length (which likely represents nestling growth), and positively related to the number of helpers present in the natal territory. However, neither tarsus length nor the number of helpers was related to telomere length in fledged birds. Finally, we found that longer telomeres and reduced telomere shortening rates in early life were associated with increased survival later in life.
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 initial condition, and genetic or epigenetic makeup (Hoffman & Hercus 2000; Richards 2006), the later-life consequences of a good or 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 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 stress levels which can be elevated due to environmental factors (Von Zglinicki 2002). When telomeres reach a critical shortness cells senescence (Campisi 2003), and the accumulation of these cells can result 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 direct evidence the relationship between telomere dynamics and survival is causal (Barrett & Richardson 2011; 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 link between early-life conditions and late-life survival is limited to a few species, and thus 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 (reviewed in Hammers *et al.* 2015). 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). Ecological conditions an population density on Cousin are variable over space and time due to weather-induced changes in foliage cover and food availability (Van de Crommenacker *et al.* 2011). Seychelles warblers remain on their natal territories for at least six months, and variation in natal territory quality has been linked to changes in levels of oxidative stress (Van de Crommenacker *et al.* 2011). However, neither natal territory quality nor natal local density appear to be linked to early-life or adult survival (Brouwer *et al.* 2006; Hammers *et al.* 2013). Facultative cooperative breeding occurs in the Seychelles warbler (Komdeur 1994a; Richardson, Komdeur & Burke 2003), and the presence of helping subordinates (but not non-helping subordinates) in the natal territory has been associated with increased survival later in life (Brouwer, Richardson & Komdeur 2012). Lastly, we have an established protocol for assessing absolute telomere length in this species (Barrett *et al.* 2012), and telomere length predicts survival independently of age in adult Seychelles warblers, suggesting that telomeres act as a biomarker of cost (Barrett *et al.* 2013). Thus, we have an excellent system in which to assess the costs of different social and environmental conditions experienced early in life, and to assess the later life consequences of early-life conditions.

In this study we test the prediction that telomeres link early-life environmental variation to late-life fitness. Because telomere dynamics are expected to reflect individual-level variation in the costs of early-life experiences, they may allow a more sensitive analysis of the effects of early-life environmental variation than would be possible with a direct comparison of the early-life environment and survival. With this in mind, 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 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 of *ca*. 320 birds on Cousin Island (04'20'S, 55'40'E) has been intensively studied since 1986 (Richardson, Burke & Komdeur 2003; Spurgin *et al.* 2014). This species has two breeding seasons, running from June-August (main breeding season) and December-February (minor breeding season), when the breeding females on each of the *ca*. 115 territories lay one or, rarely, two or three eggs (Komdeur, Bullock & Rands 1991). As a result of this low reproductive output, combined with a higher mortality rate among first-year birds (61% survival; Brouwer *et al.* 2006), cohort sizes in the Seychelles warbler are small (<50).

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 naturally confined to the island (Komdeur *et al.* 2004), a biannual census of birds on Cousin during each breeding season gives accurate measures of local density and individual survival (Barrett *et al.* 2013). The isolated nature of the Cousin population is a key advantage of the system for analyses involving survival, which in other systems are often confounded by emigration (see Ergon & Gardner 2014 for a recent discussion). Full details of catching and census methods can be found in Brouwer *et al.* (2012).

Seychelles warblers are highly territorial and all territories are mapped during the breeding seasons using 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 territory quality estimates obtained across years are averaged to obtain a single value for each territory (Hammers *et al.* 2013). Cousin is subject to intra- and inter-annual variation in rainfall and food availability, and such island-wide temporal variation may override the effects of individual territory quality. As an estimate of seasonal variation in food availability, we calculated an index of the number of insects across the entire island during each breeding season. 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 (to the nearest 0.1g and 0.1mm, respectively), and age is confirmed 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 ml of 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 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 a total of 406 samples from 323 birds caught within their first year of life, between 1995 and 2009. Of these birds, 80 were nestlings less than one month old (chicks), while the remaining 243 were fledglings and subadults aged between two and twelve months (hereafter referred to as fledglings). For a subset of first-year birds (n = 83 individuals) we had longitudinal data, with samples from individuals caught both in their first year and then again within two years. We measured absolute telomere quantity per diploid genome for all samples 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 14 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 environmental variables (Brouwer *et al.* 2012). This makes it difficult to disentangle how spatial and temporal processes differentially affect early-life telomere dynamics. To overcome this, we analysed how variation in early life conditions was related to variation in early-life telomere length separately among and within breeding seasons.

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), excluding cohorts where we had samples from 5 birds. We tested for a difference in telomere length among 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 conducted individual-level analyses to test how spatially varying early-life environmental and social conditions influence telomere length within cohorts, using general linear models. For these analyses, both response and explanatory variables were standardised by mean-centering within cohorts, thus controlling for any between-cohort temporal variation in telomere length and the social and ecological environment. As explanatory variables we included age class (nestling or fledgling), tarsus length, sex, territory quality and the number of helping and non-helping subordinate birds present in the natal territory. We also included interactions between age class and all the other variables. 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 individuals with longitudinal data 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 above 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 rate of loss of each cohort with the mean lifespan of all individuals in that cohort, using linear regression. For this analysis we excluded any recent breeding seasons where >10% of individuals in a cohort were still alive. We then used parametric survival analysis to test whether individual-level telomere length and rate of loss were related to to survival. Again, we mean-centred variables within cohorts to eliminate between-season temporal 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 separate analysis for each, using the cross-sectional 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 within the first year of life separately, we found substantial age-related variation in telomere length (F = 7.42; *P* = 0.007). Nestlings had longer telomeres than any other age group, but there was an apparent increase in average telomere length from the fledgling to adult stages (Fig. 1A). A longitudinal analysis of telomere loss showed that nestlings and fledglings both lost telomeres early in life, but that there was no difference in the rate of telomere loss among age classes (F = 0.46; *P* = 0.50; Fig. 1B).

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

Early-life telomere length varied significantly among breeding seasons (one-way ANOVA, F = 2.13; *P* = 0.002), and this variation in average telomere length over breeding seasons was positively related to island-wide food availability (linear regression, R2 = 0.37; F = 6.91; *P* = 0.022; Fig. 2A). Running the regression of cohort-level telomere length and food availability separately for each age class revealed a positive, significant relationship in fledglings (R2 = 0.41; F = 6.82; *P* = 0.026), but no relationship in nestlings (R2 = 0.61; F = 3.09; *P* = 0.221).

The rate of telomere shortening in early life (taken from the smaller subset of birds with longitudinal samples) did not vary significantly among breeding seasons (F = 0.95; *P* = 0.53); however, what variation there was in rates of telomere shortening could be explained by temporal variation in food availability (R2 = 0.30; F = 5.14; *P* = 0.04). 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). Unfortunately we did not have sufficient sample sizes within cohorts to run this analysis separately among age classes.

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

The top model explaining within-season variation in early-life telomere length contained age class, tarsus length and the number of helpers present in the natal territory, as well as interactions between age class and both tarsus length and the number of helpers (Table S1). This model was much better supported than the null model (AICc = 14.72). 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 = 0.11). Telomere length was positively related to the number of helpers in nestlings, but not in fledglings (Fig. 3B). Tarsus length was negatively related to telomere length in nestlings, but not in fledglings (Fig. 3C).

For the subset of individuals with longitudinal data, we tested whether the factors previously identified as being related to early-life telomere length (i.e. tarsus length 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 loss (all *P* > 0.05).

##### Early life telomere dynamics and survival

At the population-level, there was a positive but non-significant relationship between telomere length and lifespan (R2 = 0.079; F = 1.28; *P* = 0.28; Fig. 4A). Testing this relationship separately for each age class revealed that there was no age-specific relationship between cohort-level telomere length and lifespan (both *P* > 0.2). There was a negative relationship between population-level telomere loss and lifespan, although this was marginally non-significant (R2 = 0.202; F = 3.80; *P* = 0.07; Fig. 4B).

For the individual-based survival analysis, a log-normal survival model best fitted the Seychelles warbler data (AIC = 1108.59, AIC of next best distribution (Weibull) = 1127.05). A survival model including all first year birds showed that early-life telomere length had a positive effect on survival, but this relationship was marginally non-significant (estimate = 0.056, CI = -0.072-0.184). Running this analysis among age classes revealed differential survival effects. Nestling telomere length had no effect on survival (estimate = -0.128, CI = -0.344-0.089; Fig. 5A), but telomere length at the fledgling stage was significantly related to survival (estimate = 0.247, CI = 0.105-0.389). This effect was positive, with longer telomeres in early life associated with increased survival later in life (Fig. 6B). Finally, using the longitudinal data, we found no effect of early-life telomere shortening on subsequent survival (estimate = 0.16, CI = -0.088-0.401).

### 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 environment (i.e. number of helpers) affects telomere length specifically at the nestling stage. 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 and rate of shortening 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 dynamics (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, and the studies that have done so are limited to just two seasons (Mizutani *et al.* 2013; Watson, Bolton & Monaghan 2015). The long-term Seychelles warbler dataset has allowed us, using many more cohorts than has been possible in other studies, to show that temporal variation in environmental conditions does indeed affect telomere dynamics, and that this effect can be seen at the population level. Interestingly, in the Seychelles warbler annual variation in food availability is not directly linked to survival (Brouwer *et al.* 2006; Hammers *et al.* 2013). It has been suggested that telomeres act as biomarkers of cost in natural populations, as they are able to capture individual and cohort-level variability in the costs experienced as a result of environmental pressures (Asghar *et al.* 2015). Our results confirm that telomeres can detect hidden costs in natural populations that are not detectable using life-history and environmental data alone

We suspect the novelty of our findings of temporal, environmentally-induced variation in telomere dynamics within a population 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). If our findings are replicated in other systems and population-level variation in early-life telomere dynamics is common in nature, this has a number of ramifications for our understanding of senescence in natural populations. First, our findings suggest that the telomere dynamics of a population at a given point in time represent a snapshot of a temporally varying process. More research is now needed within and across multiple cohorts and populations to better understand the complexity of telomere evolutionary ecology. Secondly, our findings raise the interesting prospect of using telomeres as indicators of population health - an approach that would be useful to a broad range of conservation and animal health practitioners. However, further 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.

We found that within cohorts, tarsus length and the number of helpers were the most important predictors of telomere length in Seychelles warblers, and that these effects occurred specifically at the nestling stage. The tarsus effect most likely reflects the fact that in passerine birds tarsus length is correlated with age during the nestling stage (Ricklefs 1976). Telomere loss is most rapid early in life due to ongoing cell replication (Frenck *et al.* 1998), and a negative correlation between telomere length and body size in early life is therefore expected.

Ours is the first study to show that the presence of helping co-breeders has a beneficial effect on offspring in terms of their telomeres. In the Seychelles warbler the survival benefits to a nestling of their being helpers in the natal territory is well established (Komdeur 1994b; Brouwer *et al.* 2012), and that this effect is detected in terms of differential telomere length, is therefore encouraging. However, we found no evidence that the number of helpers was related to telomere loss - this is perhaps surprising as telomere loss is expected to be a better indicator of stress than telomere length *per se* (Boonekamp *et al.* 2014). Our (lack of) finding here is probably due to the limited nature of our longitudinal dataset, both in terms of sample size and resolution (i.e. time between sampling events). Seychelles warblers are rarely been sampled multiple times within their first year of life, so much of the telomere shortening that occurs in early life will be missed with our sampling regime. It is likely, therefore that the effects of environmental variation on telomere loss will only be detected when they are very strong using this dataset. Thus telomere length constitutes a better indicator of early life stress.

While the relationship between telomeres and mortality in adults has been established for some time (Cawthon *et al.* 2003), only recently has the link between early-life telomere dynamics and later-life survival been studied. In captive zebra finches, juvenile telomere length predicts late-life survival (Heidinger *et al.* 2012), and in wild bird populations early-life telomere dynamics have 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 later-life survival in a wild population. This effect can be seen at the individual level, and (to a lesser extent) at the cohort level, although the nature of the relationship varies according to the age class at which telomeres are measured. At the individual level, we found that telomere length in fledglings, but not nestlings, was related to survival. This is unsurprising, as only by the fledgling stage is telomere length likely to reflect the accumulation of early life stress (see also previous paragraph). The relationships between population-level telomere length and lifespan in the expected direction (Fig. 4), but not significant, which is perhaps not surprising given that even though we have a long-term dataset, we are still restricted in terms of sample size when conducting cohort-level analyses. Nonetheless, our data support the general conclusion that early-life telomere dynamics are important indicators of early-life stress.

There are numerous promising avenues for future research into telomere evolutionary ecology in this system and others. Here we have considered survival, but telomere length and shortening in early life may also be linked to other components of fitness (reviewed in Monaghan 2014). Reproductive senescence occurs in the Seychelles warbler (reviewed in Hammers *et al.* 2015), making this system well suited to examining how telomere length affects lifetime reproductive success. A further avenue for future research will be examining, in a quantitative genetic framework, how genetic and environmental components, and their interactions, affect telomere dynamics and senescence in natural populations (Asghar *et al.* 2014; Becker *et al.* 2015). We expect that by gaining a fuller understanding of telomere dynamics in natural populations, the fields of life-history evolution and evolutionary ecology will be greatly enhanced.

### Data accessibility

This manuscript was written in R Markdown (<http://rmarkdown.rstudio.com/>). All data and scripts required to reproduce the manuscript, figures and analyses 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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