**Early-life conditions, telomere dynamics and survival: insights from a long-term island bird study**

Lewis G. Spurgin1,2, Kat Bebbington1, Eleanor A. Fairfield1, Martijn Hammers3, Jan Komdeur3, Terry Burke4, Hannah, L. Dugdale3,4, and David S. Richardson1,5,.

1. School of Biological Sciences, University of East Anglia, Norwich Research Park, NR4 7TJ, United Kingdom
2. Department of Zoology, Edward Grey Institute, University of Oxford, Oxford, UK
3. Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands
4. Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK
5. Nature Seychelles, Roche Caiman, Mahé, Republic of Seychelles

**Correspondence:** Lewis Spurgin: [lewisspurgin@gmail.com](mailto:lewisspurgin@gmail.com); David Richardson: [david.richardson@uea.ac.uk](mailto:david.richardson@uea.ac.uk)

**Running head:** Early-life telomeres

### Abstract

1. Understanding the short and long term costs of individual early-life experiences is fundamental to understanding life-history evolution. Telomeres, the protective caps at the ends of chromosomes, shorten in response to oxidative stress, and telomere shortening is correlated with reduced survival. Thus, it is possible that telomere dynamics may help us quantify individual variation in early-life costs, and enhance our understanding of how poor conditions in early life are related to later-life survival.
2. We tested how telomere dynamics are related to spatio-temporal variation in early-life conditions and later-life survival in the Seychelles warbler (*Acrocephalus sechellensis*), using a large dataset of 829 juveniles from multiple cohorts spanning 16 years.
3. We found that at the population level, telomere length decreases with cross-sectional and longitudinal measures of age, and that telomere length decreases most rapidly early in life. However, at the individual level we found no relationship between juvenile and adult telomere length, and that significant reductions in telomere length can only be detected within the first few months of life - after this, longitudinal changes in telomere length were not significantly different from zero.
4. Juvenile telomere length varied markedly among cohorts, and birds born in years with higher population density had longer telomeres. Within cohorts, we found no evidence that the early-life social environment or ecological conditions were related to telomere length or rates of shortening. We also found no relationship between early-life telomere dynamics and survival later in life.
5. Our data suggest that telomeres are subject to strong population-level variation, and that telomeres at a point in time represent a snapshot of a fluid eco-evolutionary process. At the individual-level, however, our data suggest that the resolution of telomeres as biomarkers of cost is likely to be age-dependent, and in some cases limited.

**Keywords:** Life-history; Telomere; Seychelles warbler; Senescence

**Data archival location:** 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.

PAGEBREAK

### Introduction

Exposure to favourable environmental conditions during development and growth can confer fitness advantages later in life (so called 'silver spoon effects'; Grafen 1988; Monaghan 2008). Adult fitness can be affected by a range of early-life experiences, including the quality of the habitat and available resources (Madsen and Shine 2000; Van de Pol et al. 2006; Hayward et al. 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 and 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. We expect the later-life consequences of a good or poor start to vary among individuals, populations and species because the phenotypic consequences of an adverse environment can depend on an individual's initial condition, and genetic or epigenetic makeup (Hoffman and Hercus 2000; Richards 2006). 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 the resulting adult phenotypes. Indeed, the pervasiveness of silver spoon effects varies between species (Drummond et al. 2011), cohorts (Reid et al. 2003) and sexes (Wilkin and Sheldon 2009). We therefore need to understand, or at least be able to measure, how the environment affects individuals differentially within a population in order to elucidate the later-life consequences of early-life experience.

Telomeres - the protective caps on the ends of chromosomes - may provide a solution to this problem. Telomeres shorten with age (Monaghan and Haussmann 2006), and in response to oxidative stress, which can be elevated due to environmental factors (Von Zglinicki 2002). When telomeres become critically short cells senesce (Campisi 2003), and the accumulation of these cells can result in organismal senescence and death (Wong et al. 2003). This association between senescence and telomere length has inspired a great deal of recent research into telomere evolutionary ecology (reviewed in Horn et al. 2010; Haussmann and Marchetto 2010; Monaghan 2014). While there is little direct evidence that the relationship between telomere dynamics and survival is causal (Simons 2015), there is mounting evidence that telomeres can act as biomarkers of cost in wild populations, providing a signature of the ecological stress that has been experienced and is 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 shortening occurs in early life (e.g. Frenck et al. 1998; Haussmann et al. 2003), and that the extent of this shortening is influenced by the conditions experienced during that period (Price et al. 2013; Monaghan 2014; Nettle et al. 2015b; Reichert et al. 2015). Early-life telomere dynamics have been associated with both short-term and late-life survival (Heidinger et al. 2012; Boonekamp et al. 2014), and with other parameters such as cognition (Nettle et al. 2015a). However, few studies have simultaneously analysed how telomere dynamics, early-life conditions and late-life survival are all related in a natural setting. Moreover, how early-life telomere dynamics vary over spatial and temporal scales is poorly understood.

The longitudinal study (since 1986) of the Seychelles warbler (*Acrocephalus sechellensis*) population on Cousin Island provides an excellent 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 unusually comprehensive survival data and tissue samples spanning many years (see Methods, below). Ecological conditions and warbler population density on Cousin vary across 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 the oxidative stress experienced by individuals is associated with natal territory quality (Van de Crommenacker et al. 2011). However, neither early-life nor adult survival appear to be associated with natal territory quality or natal local density (Brouwer et al. 2006; Hammers et al. 2013). Facultative cooperative breeding occurs in the Seychelles warbler (Komdeur 1994; Richardson et al. 2003b), and the presence of helping subordinates (but not non-helping subordinates) in the natal territory is associated with increased survival later in life (Brouwer et al. 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 examine how telomeres are related to early-life environmental variation and short and long-term survival in the Seychelles warbler. 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 how survival is affected by the early-life environment. With this in mind, we first conduct an exploratory analysis of how the environmental and social factors experienced in early life affect telomere dynamics. We then test the hypothesis that longer telomeres and lower rates of telomere shortening in early life are 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 et al. 2003a; 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 et al. 1991). As a result of this low reproductive output, combined with higher mortality in first-year birds (39%; 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, social status (e.g. breeding male/female, helping subordinate, non-helping subordinate) and individual survival (Crommenacker et al. 2011; 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 and Gardner 2014 for a recent discussion). Full details of catching and monitoring 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. 2003a). 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 is calculated as the mean 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). Using information on eye colour (Komdeur 1991) and previous captures (Richardson et al. 2003a), we grouped birds into three age categories: one month old (birds still in the nest), 6 months old (fledglings with light grey eyes) and 10 months old (subadults with light brown eyes). A blood sample (*ca* 25 l) is taken from each bird captured via brachial venipuncture, and stored at room temperature in 1 ml of absolute ethanol in a 1.5 ml screw-cap microfuge tube.

##### Molecular methods

For each sample, 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. Sex was determined using the PCR-based method outlined by Griffiths *et al.* (1998). Prior to telomere analysis, DNA concentration and purity were quantified using a NanoDrop 8000 Spectrophotometer (ThermoScientific), and the following thresholds were applied before samples were included for further analysis: i) DNA concentration must be at least 15 ng l-1 (based on a mean of three measurements), ii) the 260/280 ratio has to be between 1.8 and 2 and, iii) the 260/230 ratio should be higher than 1.8. DNA integrity was further validated by visualization with ethidium bromide after electrophoresis on a 1.2% agarose gel, and all samples with evidence of DNA degradation were re-extracted or excluded. All DNA extractions that passed the above criteria were diluted to 3.3 ng l-1 before telomere measurement. We measured relative telomere length (RTL) for all samples using a quantitative PCR (qPCR) assay of telomeres and a GAPDH control gene, using the molecular methods outlined by Bebbington *et al.* (In Press).

For a subset of first-year birds for which we had longitudinal data, with an additional sample taken as an adult. For these individuals we calculated the within-individual change in RTL by subtracting early-life RTL from adult RTL (hereafter RTL). Negative values of RTL reflect telomere shortening, while positive values reflect telomere lengthening.

##### Statistical analyses

We performed all analyses using R version 3.0.1 (R Development Core Team 2011). Because we are using a different measure of telomere length to the previous study of adult telomere dynamics in this species (Barrett et al. 2013), as well as including many additional samples, we first re-tested, using all available samples, whether telomere length decreases with age and age (a longitudinal measure based on within-subject centring; Pol and Wright 2009) in the Seychelles warbler, using linear mixed models with individual ID as a random effect. For the analysis of age we we only included birds who had been sampled at least twice. We then explored how telomere length varied within the first year of life (telomere length vs age in months) and among cohorts (telomere length vs cohort ID), again using linear mixed models with individual ID as a random effect. We tested how temporal variation in telomere length varied between birds born in main and minor breeding seasons, and with temporal variation in population density (measured as the number of adult birds on the island at the end of each breeding season) and food availability, using linear mixed models with cohort ID as a random effect.

We used general linear mixed models with model averaging to explore how spatial variation in early-life environmental and social conditions influenced telomere length within cohorts. Model averaging was carried out using the MuMIn package (version 1.10.5) in R (Bartoń 2012). We first created a full model containing the following explanatory variables: age (in months), tarsus length, sex, territory quality, season (main or minor) and the number of helping and non-helping subordinate birds present in the natal territory. We also included interaction terms between age and all the other variables as telomere dynamics are expected to vary within the first year of life (Heidinger et al. 2012). As random effects we included cohort, territory ID and qPCR plate ID. Model selection was then performed and a top model set defined, containing all models with AICc 6 compared to the best supported model (Burnham et al. 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. For individuals with longitudinal data (*n* = 243) we repeated the above analyses of telomere dynamics, replacing telomere length with telomere loss as the response variable, and excluding the plate ID random effect (as each measurement of telomere loss was based on two or more measurements, and so run on multiple plates).

We used generalised linear mixed models to test whether telomere length/loss were related to survival to adulthood. Models were set up with a binomial error structure, and included RTL/RTL and juvenile age as explanatory variable, along with the same random effects as for the model averaging (see above). We then used Cox regression, implemented in the survival package in R (Therneau and Lumley 2011), to test whether long-term survival was related to individual-level telomere dynamics. For the cross-sectional data we used lifespan (in years) as survival time, while for the longitudinal data we used remaining lifespan from the second sampling event. We ran these models with cohort as a frailty term to exclude cohort effects, and only included cohorts in which at least 70 percent of individuals had died (all years up to and including 2007).

### Results

We measured telomere lengths using a total of 1748 unique samples from juvenile and adult Seychelles warblers. Of these, 829 samples were taken cross-sectionally from birds caught within their first year of life, and of these juvenile birds, we had additional longitudinal samples for 243. Efficiencies (mean s.d.) for our telomere and GAPDH reactions were (1.79 0.04) and (1.92 0.06) respectively. Inter-plate repeatability of RTL, based on 392 samples measured at least twice, was 0.78 (CI = 0.73-0.82).

##### Early-life RTL

Considering the entire Seychelles warbler lifespan, RTL decreased with age (LMM: t = -5.37; P < 0.001), although there were clear increases in cross-sectional telomere length after one year of age and at several points later in life (Fig. 1A). RTL also decreased with age within individuals (i.e. with age; t = -4.45; P < 0.001; Fig. 1B), and with age within the first year of life (i.e. excluding adult samples; t = -6.33; P < 0.001).

Early-life RTL varied significantly among cohorts (Likelihood ratio test: F = 3.08; P < 0.001). Cohort-level variation in juvenile RTL was positively related to adult population density (LMM controlling for age and cohort: t = 0.76; P 0.457; Figs 2B,2C). Variation in cohort-level RTL was not related temporal variation in food availability (t = -0.31; P 0.765).

Within cohorts, the top model explaining variation in early-life RTL contained age, sex, tarsus length, and the interaction between age and tarsus length (Table S1). The top model was much better supported than a null model (AICc = 38.86), and with the exception of the sex and tarsus effects, model-averaged confidence intervals did not overlap zero (Fig. 3A). Tarsus length was negatively related to RTL in nestlings, unrelated to RTL in fledglings, and positively related to RTL in subadults (Fig. 3B). Males had slightly longer telomeres than females, particularly at the fledgling and subadult stages, although this effect was weak (Fig. 3C).

##### Early-life telomere shortening

Longitudinal data showed that early-life RTL was not related to adult RTL (R2 = 0.031; t = 1.30; P = 0.193; Fig. 4A). RTL was significantly lower than zero in nestlings (t = -4.96; P < 0.001), but not in fledglings (t = 0.80; P = 0.43) or subadults (t = 1.69; P = 0.09). In line with this, RTL increased with age in early life (R2 = 0.08; t = 4.42; P < 0.001; Fig. 4B), suggesting that telomere shortening was highest shortly after the nestling phase.

RTL did not differ significantly among cohorts of nestlings (F = 0.97; P 0.484), although power for this analysis was limited as longitudinal sample sizes within cohorts were low. Model selection revealed that the top model explaining RTL within cohorts of nestlings contained sex and tarsus length (Table S2). This model was a better fit than the null model (AICc = -0.53), although confidence limits for both the sex and tarsus effects overlapped zero (Fig. 5A). RTL was negatively related to tarsus length, and higher in females, indicating greater telomere shortening in smaller nestlings, and in males (Fig. 5B).

##### Early-life telomere dynamics and survival

Early-life RTL was not related to survival to adulthood (estimate = -0.43; P = 0.08), with no interaction effect between RTL and juvenile age (estimate = 0.07; P = 0.32). To test whether cohort-level effects on RTL influenced survival we calculated cohort-level RTL (i.e. the median RTL for each cohort) and added this term to a GLMM, and found that cohort-level RTL was not related to survival to adulthood (estimate = -1.21; P = 0.23). Using the longitudinal data, we found that RTL had no effect on survival to the year after the second sampling event (estimate = 0.44; P = 0.16).

Cox regression showed no effect of individual-level or cohort-level RTL on survival later in life (individual-level: estimate = 0.12, P = 0.43; cohort-level: estimate = -0.47, P = 0.75), and no interaction between RTL and age on survival (individual-level: estimate = -0.07, P = 0.08). RTL was not related to longer-term survival (estimate 0.032, P = 0.926).

### Discussion

Here we use one of the largest datasets to date to assess the relationships between early-life conditions, telomere length and survival in a closed population of Seychelles warblers. We found that, as in other studies, telomeres are lost at the greatest rate early in life. We found that telomere dynamics are subject to strong cohort effects, and that temporal variation in RTL is population density and season. Within cohorts, we found no evidence that the ecological or social environment influenced telomere dynamics, and we found no evidence that early-life telomere length is related to juvenile or later-life survival.

Our study adds the the now substantial body of literature showing that telomere length decreases with age, and that this decrease is most rapid in early life (e.g. Frenck et al. 1998; Haussmann et al. 2003; Heidinger et al. 2012; Fairlie et al. 2016). Our finding that tarsus length was related to juvenile RTL in an age-dependent manner (Fig. 3) most likely represents an additional age effect - in passerine birds tarsus length is correlated with age during the nestling stage, but not after fledging (Ricklefs 1976). Telomere loss is most rapid early in life due to ongoing growth (Frenck et al. 1998), and a negative correlation between RTL and body size in early life is therefore expected (see also Ringsby et al. 2015). We also found weak evidence for sex-specific telomere dynamics in Seychelles warblers, with males having longer-telomeres and higher loss of telomeres (Fig. 3C, Fig. 5B). We do not wish to speculate too much on this effect as confidence intervals for both sex effects overlapped zero. However, it is worth noting while we found no evidence that juvenile RTL has a sex-specific effect on survival, in adults the effect of telomere length on survival is strongest for males (Barrett et al. 2013). Together, these results suggest that sex effects should at least be considered when studying any aspect of telomere dynamics (see also Barrett and Richardson 2011).

Despite our clear finding that RTL decreases with age throughout the Seychelles warbler lifespan (Fig. 1), we found that at the individual-level, juvenile and adult telomere were not correlated, and that telomere shortening can only be detected very early in life (Fig. 4). This is in contrast to other avian studies where birds were reared in laboratory (Heidinger et al. 2012) or nest-box (Boonekamp et al. 2014) conditions, in which juvenile and adult telomere length were highly correlated, and individual-level telomere shortening clearly occurs throughout the juvenile period, and into adulthood. However, in accordance with our study, a recent study on Soay sheep (*Ovis aries*) found only a very weak correlation between juvenile and adult RTL, and a highly complex pattern of telomere dynamics across the lifespan (Fairlie et al. 2016). It is too soon to speculate as to what may be generating this variation among species, but one possibility is that environmental variability itself affects the resolution with which we can observe telomere shortening in natural populations (see also Fairlie et al. 2016). Regardless, our data suggest the efficacy of telomeres as individual biomarkers of cost in wild populations will depend on the age structure of the study population, as well as the sampling resolution.

Perhaps the clearest result from our study is that RTL varies among cohorts. A few studies have now shown that temporal variation in telomere dynamics occurs in natural populations, although these have been limited in the number of seasons (Mizutani et al. 2013; Watson et al. 2015; Fairlie et al. 2016). The long-term Seychelles warbler dataset has allowed us to show that temporal variation in telomere dynamics can occur over substantial time periods. Moreover, because of the large number of cohorts we have been able to show statistically that that temporal variation in RTL is related to variation in the environment (Fig. 1C). In some systems a negative relationship between population density and RTL may be expected, as increased competition for resources is known to effect juvenile telomere length. However, in the Seychelles warbler it is likely that population density acts as an indicator of overall island 'quality' for Seychelles warblers. This can clearly be seen from data from the 1980s and 1990s, when adult population size on Cousin increased as habitat quality improved (Komdeur and Pels 2005). Population size has fluctuated around 300 since the late 1990s (Fig. 2B), and we suggest that this variation captures this island-wide conditions more accurately than measures of insect abundance or territory quality. If cohort-level variation in telomere dynamics continues to be found in other systems, this has potential consequences for our understanding of telomere dynamics in natural populations. In particular, 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 how how and why population-level telomere dynamics vary over space and time.

Despite substantial cohort-level variation in juvenile RTL, within cohorts we found no evidence that any of the social or environmental variables we measured affect juvenile RTL. This is surprising, as a poor social and ecological environment is known to be detrimental to juvenile Seychelles warblers, both in terms of oxidative stress and later life survival (Van de Crommenacker et al. 2011; Brouwer et al. 2012). A possible explanation for this could be that temporal variation in RTL in our data masks our ability to detect spatial trends. However, this is unlikely we controlled for cohort ID, and within-cohort variation in RTL greatly exceeds among-cohort variation (Fig. 1C). A second possibility is that effects are generally weak and levels of noise in our telomere measurements and/or ecological data preclude detection of significant effects. While noise in telomere measurements and problems with power are a problem in any study using qPCR to measure telomere length (Nussey et al. 2014), our sample sizes and levels of repeatability compare favourably with other studies of natural populations that have found significant effects of the early-life environment on telomere length (e.g. **???**). More likely is that early-life RTL in the Seychelles warbler is explained by a set of variables that we have not measured. A key question to be addressed is the extent to which early-life RTL reflects inheritance (Asghar et al. 2014; e.g. Becker et al. 2015). This is important, as inheritance may capture a large amount of unexplained variation in early-life RTL within our dataset. Future research on the Seychelles warbler will examine, in a quantitative genetic framework, how genetic and environmental components, and their interactions, affect telomere dynamics and senescence.

While the relationship between mortality and telomeres in adults has been established for some time (Cawthon et al. 2003), only recently has the link between later-life survival and early-life telomere dynamics been studied. In captive zebra finches, juvenile telomere length predicts late-life survival (Heidinger et al. 2012), and in wild bird populations survival to the nestling phase (Watson et al. 2015), and survival to adulthood (Boonekamp et al. 2014), have been linked with early-life telomere dynamics. It is worth noting that 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 predicts lifetime reproductive success. 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.

### Acknowledgements

We thank Nature Seychelles for facilitating the long-term Seychelles warbler project. The Seychelles Bureau of Standards and Department of Environment gave permission for sampling and fieldwork. Emma Barrett laid the foundations for this study, generating the original telomere qPCR protocol. We thank everyone who has helped in the field, and the Seychelles warbler research group for discussions. This work was funded by two Natural Environment Research Council (NERC) grants to DSR (NE/F02083X/1 and NE/K005502/1). LGS was also funded by an EGI Fellowship from the University of Oxford, and HLD by a NERC fellowship.

### References

Asghar, M., S. Bensch, M. Tarka, B. Hansson, and D. Hasselquist. 2014. Maternal and genetic factors determine early life telomere length. Proceedings of the Royal Society B: Biological Sciences 282:20142263–20142263.

Asghar, M., D. Hasselquist, B. Hansson, P. Zehtindjiev, H. Westerdahl, and S. Bensch. 2015. Hidden costs of infection: Chronic malaria accelerates telomere degradation and senescence in wild birds. Science 347:436–438.

Barrett, E. L. B., and D. S. Richardson. 2011. Sex differences in telomeres and lifespan. Aging Cell 10:913–21.

Barrett, E. L. B., W. Boner, E. Mulder, P. Monaghan, S. Verhulst, and D. S. Richardson. 2012. Absolute standards as a useful addition to the avian quantitative PCR telomere assay. Journal of Avian Biology 43:571–576.

Barrett, E. L. B., T. Burke, M. Hammers, J. Komdeur, and D. S. Richardson. 2013. Telomere length and dynamics predict mortality in a wild longitudinal study. Molecular Ecology 22:249–259.

Bartoń, K. 2012. Package ‘MuMIn’. Model selection and model averaging base on information criteria. R package version 1.7.11.

Becker, P. J. J., S. Reichert, S. Zahn, J. Hegelbach, S. Massemin, L. F. Keller, E. Postma, and F. Criscuolo. 2015. Mother-offspring and nest-mate resemblance but no heritability in early-life telomere length in white-throated dippers. Proceedings of the Royal Society B: Biological Sciences 282:20142924.

Boonekamp, J. J., G. A. Mulder, H. M. Salomons, C. Dijkstra, and S. Verhulst. 2014. Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds. Proceedings of the Royal Society B: Biological Sciences 281:20133287.

Brouwer, L., D. S. Richardson, C. Eikenaar, and J. Komdeur. 2006. The role of group size and environmental factors on survival in a cooperatively breeding tropical passerine. Journal of Animal Ecology 75:1321–1329.

Brouwer, L., D. Richardson, and J. Komdeur. 2012. Helpers at the nest improve late-life offspring performance: evidence from a long-term study and a cross-foster experiment. PLoS ONE 7:e33167.

Burnham, K., D. Anderson, and K. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–25.

Campisi, J. 2003. Cellular senescence and apoptosis: How cellular responses might influence aging phenotypes. Experimental Gerontology 38:5–11.

Cartwright, S. J., M. A. C. Nicoll, C. G. Jones, V. Tatayah, and K. Norris. 2014. Anthropogenic natal environmental effects on life histories in a wild bird population. Current Biology 24:536–40.

Cawthon, R. M., K. R. Smith, E. O’Brien, A. Sivatchenko, and R. A. Kerber. 2003. Association between telomere length in blood and mortality in people aged 60 years or older. Lancet 361:393–395.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Crommenacker, J. van de, J. Komdeur, and D. S. Richardson. 2011. Assessing the cost of helping: the roles of body condition and oxidative balance in the Seychelles warbler (Acrocephalus sechellensis).

Douhard, M., J.-M. Gaillard, D. Delorme, G. Capron, P. Duncan, F. Klein, and C. Bonenfant. 2013. Variation in adult body mass of roe deer: early environmental conditions influence early and late body growth of females. Ecology 94:1805–1814.

Drummond, H., C. Rodríguez, and D. Oro. 2011. Natural ’poor start’ does not increase mortality over the lifetime. Proceedings of the Royal Society B: Biological Sciences 278:3421–3427.

Ergon, T., and B. Gardner. 2014. Separating mortality and emigration: modelling space use, dispersal and survival with robust-design spatial capture-recapture data. Methods in Ecology and Evolution 5:1327–1336.

Fairlie, J., R. Holland, J. G. Pilkington, J. M. Pemberton, L. Harrington, and D. H. Nussey. 2016. Lifelong leukocyte telomere dynamics and survival in a free-living mammal. Aging Cell 15:140–148.

Frenck, R. W., E. H. Blackburn, and K. M. Shannon. 1998. The rate of telomere sequence loss in human leukocytes varies with age. Proceedings of the National Academy of Sciences of the United States of America 95:5607–5610.

Grafen, A. 1988. On the uses of data on lifetime reproductive success. *in* T. Clutton-Brock, ed. Reproductive success. University of Chicago Press, Chicago.

Griffiths, R., M. C. Double, K. Orr, and R. J. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071–5.

Hammers, M., S. A. Kingma, K. Bebbington, J. Van de Crommenacker, L. G. Spurgin, D. S. Richardson, T. Burke, H. L. Dugdale, and J. Komdeur. 2015. Senescence in the wild: Insights from a long-term study on Seychelles warblers. Experimental Gerontology, doi: [10.1016/j.exger.2015.08.019](http://dx.doi.org/10.1016/j.exger.2015.08.019).

Hammers, M., D. S. Richardson, T. Burke, and J. Komdeur. 2013. The impact of reproductive investment and early-life environmental conditions on senescence: support for the disposable soma hypothesis. Journal of Evolutionary Biology 26:1999–2007.

Haussmann, M. F., and N. M. Marchetto. 2010. Telomeres: Linking stress and survival, ecology and evolution. Current Zoology 56:714–727.

Haussmann, M. F., C. M. Vleck, and I. C. T. Nisbet. 2003. Calibrating the telomere clock in common terns, Sterna hirundo. Experimental Gerontology 38:787–789.

Hayward, A. D., I. J. Rickard, and V. Lummaa. 2013. Influence of early-life nutrition on mortality and reproductive success during a subsequent famine in a preindustrial population. Proceedings of the National Academy of Sciences of the United States of America 110:13886–91.

Heidinger, B. J., J. D. Blount, W. Boner, K. Griffiths, N. B. Metcalfe, and P. Monaghan. 2012. Telomere length in early life predicts lifespan. Proceedings of the National Academy of Sciences of the United States of America 109:1743–8.

Hoffman, A. A., and M. J. Hercus. 2000. Environmental Stress as an Evolutionary Force. BioScience 50:217–226. Oxford University Press.

Horn, T., B. C. Robertson, and N. J. Gemmell. 2010. The use of telomere length in ecology and evolutionary biology. Heredity 105:497–506.

Komdeur, J. 1991. Cooperative breeding in the Seychelles warbler. PhD Thesis, Cambridge University.

Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495.

Komdeur, J. 1994. The effect of kinship on helping in the cooperative breeding Seychelles warbler (Acrocephalus sechellensis).

Komdeur, J., and M. D. Pels. 2005. Rescue of the Seychelles warbler on Cousin Island, Seychelles: The role of habitat restoration. Biological Conservation 124:15–26.

Komdeur, J., I. D. Bullock, and M. R. W. Rands. 1991. Conserving the Seychelles Warbler Acrocephalus sechellensis by translocation: a transfer from Cousin Island to Aride Island.

Komdeur, J., T. Piersma, K. Kraaijeveld, F. Kraaijeveld-Smit, and D. S. Richardson. 2004. Why Seychelles warblers fail to recolonize nearby islands: unwilling or unable to fly there? Ibis 146:298–302.

Madsen, T., and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long‐term growth rates of free‐ranging pythons. Journal of Animal Ecology 69:952–958.

Mizutani, Y., N. Tomita, Y. Niizuma, and K. Yoda. 2013. Environmental perturbations influence telomere dynamics in long-lived birds in their natural habitat. Biology Letters 9:20130511.

Monaghan, P. 2008. Early growth conditions, phenotypic development and environmental change. Philosophical Transactions of the Royal Society B: Biological sciences 363:1365.

Monaghan, P. 2014. Organismal stress, telomeres and life histories. Journal of Experimental Biology 217:57–66.

Monaghan, P., and M. F. Haussmann. 2006. Do telomere dynamics link lifestyle and lifespan? Trends in Ecology and Evolution 21:47–53.

Nettle, D., C. Andrews, and P. Monaghan. 2015a. Developmental and familial predictors of adult cognitive traits in the European starling. Animal Behaviour 107:239–248.

Nettle, D., P. Monaghan, R. Gillespie, B. Brilot, T. Bedford, and M. Bateson. 2015b. An experimental demonstration that early-life competitive disadvantage accelerates telomere loss. Proceedings of the Royal Society B: Biological Sciences 282:20141610. The Royal Society.

Nussey, D. H., D. M. Baird, E. L. B. Barrett, W. Boner, J. Fairlie, N. J. Gemmell, N. Hartmann, T. Horn, M. F. Haussmann, M. Olsson, C. Turbill, S. Verhulst, S. Zahn, and P. Monaghan. 2014. Measuring telomere length and telomere dynamics in evolutionary biology and ecology. Methods in Ecology and Evolution 5:299–310.

Nussey, D., L. Kruuk, A. Morris, and T. Clutton-Brock. 2007. Environmental conditions in early life influence ageing rates in a wild population of red deer. Current Biology 17:R1000–R1001.

Pol, M. van de, and J. Wright. 2009. A simple method for distinguishing within-versus between-subject effects using mixed models. Animal Behaviour 77:753–758.

Price, L. H., H. T. Kao, D. E. Burgers, L. L. Carpenter, and A. R. Tyrka. 2013. Telomeres and early-life stress: An overview. Biological Psychiatry 73:15–23.

R Development Core Team. 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing; R Foundation for Statistical Computing.

Reichert, S., F. Criscuolo, and S. Zahn. 2015. Immediate and delayed effects of growth conditions on ageing parameters in nestling zebra finches. The Journal of Experimental Biology 218:491–499.

Reid, J. M., E. M. Bignal, S. Bignal, D. I. McCracken, and P. Monaghan. 2003. Environmental variability, life-history covariation and cohort effects in the red-billed chough Pyrrhocorax pyrrhocorax. Journal of Animal Ecology 72:36–46.

Richards, E. J. 2006. Inherited epigenetic variation–revisiting soft inheritance. Nature Reviews Genetics 7:395–401.

Richardson, D. S., T. Burke, and J. Komdeur. 2003a. Sex-specific associative learning cues and inclusive fitness benefits in the Seychelles warbler. Journal of Evolutionary Biology 16:854–861.

Richardson, D. S., J. Komdeur, and T. Burke. 2003b. Avian behaviour: Altruism and infidelity among warblers. Nature 422:580.

Ricklefs, R. E. 1976. Growth rates of birds in the humid new world tropics. Ibis 118:179–207.

Ringsby, T. H., H. Jensen, H. Pärn, T. Kvalnes, W. Boner, R. Gillespie, H. Holand, I. J. Hagen, B. Rønning, B.-E. Sæther, and P. Monaghan. 2015. On being the right size: increased body size is associated with reduced telomere length under natural conditions. Proceedings of the Royal Society B: Biological Sciences 282:20152331.

Roach, D. A., and J. R. Carey. 2014. Population biology of aging in the wild. Annual Review of Ecology, Evolution, and Systematics 45:421–443.

Schultner, J., B. Moe, O. Chastel, C. Bech, and A. S. Kitaysky. 2014. Migration and stress during reproduction govern telomere dynamics in a seabird. Biology Letters 10:20130889.

Simons, M. J. 2015. Questioning causal involvement of telomeres in aging. Ageing Research Reviews, doi: [10.1016/j.arr.2015.08.002](http://dx.doi.org/10.1016/j.arr.2015.08.002).

Spurgin, L. G., D. J. Wright, M. van der Velde, N. J. Collar, J. Komdeur, T. Burke, and D. S. Richardson. 2014. Museum DNA reveals the demographic history of the endangered Seychelles warbler. Evolutionary Applications 7:1134–1143.

Therneau, T., and T. original S.->. port Lumley. 2011. survival: Survival analysis including penalised likelihood.

Van de Crommenacker, J., J. Komdeur, T. Burke, and D. S. Richardson. 2011. Spatio-temporal variation in territory quality and oxidative status: A natural experiment in the Seychelles warbler (Acrocephalus sechellensis). Journal of Animal Ecology 80:668–680.

Van de Pol, M., L. W. Bruinzeel, D. Heg, H. P. Van der Jeugd, and S. Verhulst. 2006. A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (Haematopus ostralegus). Journal of Animal Ecology 75:616–626.

Von Zglinicki, T. 2002. Oxidative stress shortens telomeres. Trends in Biochemical Sciences 27:339–344.

Watson, H., M. Bolton, and P. Monaghan. 2015. Variation in early-life telomere dynamics in a long-lived bird: links to environmental conditions and survival. The Journal of Experimental Biology 218:668–674.

Wilkin, T. A., and B. C. Sheldon. 2009. Sex differences in the persistence of natal environmental effects on life histories. Current Biology 19:1998–2002.

Wong, K. K., R. S. Maser, R. M. Bachoo, J. Menon, D. R. Carrasco, Y. Gu, F. W. Alt, and R. A. DePinho. 2003. Telomere dysfunction and Atm deficiency compromises organ homeostasis and accelerates ageing. Nature 421:643–648.