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

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### Abstract

Favourable conditions early in life can confer delayed survival advantages. These 'silver spoon effects' are most likely common in nature and are central to our understanding of life history evolution and population ecology. However, how silver spoon effects vary among individuals, populations and species remains poorly understood. Telomeres can act as biomarkers of cost in wild populations, and may provide insight into how silver spoon effects occur. Using a dataset spanning over a decade, we studied how telomere length links spatiotemporal variation in early-life conditions to survival to in the Seychelles warbler (*Acrocephalus sechellensis*). We show that early-life telomere length varies markedly across birth years, and that this variation is positively related to annual variation in food availability. We then show that having short telomeres as a juvenile is associated with reduced late life survival, but that this relationship was subject to strong cohort effects. Having short telomeres was associated with reduced late-life survival among individuals born in years where food was limited, but not among individuals born in years with high food availability. Our results suggest that telomeres can reveal hidden costs and complex silver spoon effects in wild populations.

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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 resource availability (Hayward, Rickard & Lummaa 2013), population density (Nussey *et al.* 2007) and natural or anthropogenic environmental disturbance (Reid *et al.* 2003). 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 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 (Monaghan 2014). An emerging consensus from this research is that telomeres can act as biomarkers of cost in wild populations, retaining signatures of ecological stress that are otherwise difficult to detect (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 early-life telomere shortening is influenced by the environment (Boonekamp *et al.* 2014). Moreover, a recent laboratory study showed that early-life telomere dynamics are related to late-life survival (Heidinger *et al.* 2012). However, whether telomeres provide a link between early-life conditions and late-life survival in the wild is not known.

The longitudinal study (since 1986) of the Seychelles warbler (*Acrocephalus sechellensis*) population on Cousin Island provides an excellent opportunity to assess 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) passerine bird with a mean life expectancy of 5.5 years at fledging (Hammers *et al.* 2013). The population of *ca.* 320 adults 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 the island 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 biannually 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 yearly effects 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 the main breeding season of each sampling year based on the insect abundance data (see above).

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, 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). We tested whether telomere length varied within the first year of life using one-way ANOVA, with telomere length as the response variable and age class (chick, fledgling or subadult) as a fixed factor. As telomere length varied substantially among age classes (see results) we carried out all subsequent analyses seperately for each age class.

We tested tested whether early-life environmental variation influences telomere length using linear mixed models, with telomere length as the response variable. As explanatory variables we included body condition (calculated as deviation from a regression line of mass on tarsus length; (Van de Crommenacker *et al.* 2011)), sex, territory quality, yearly food availability, and the number of helping and non-helping subordinates present in the natal territory ((Brouwer *et al.* 2012)). Lay Year was included as a random factor, in order to account for any annual variation in telomere length not explained by yearly food availability. 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).

We then used parametric survival analysis to examine variation in early-life telomere length in relation to survival, implemented using the 'flexsurv' package in R. 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, 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 length.

For a subset of first-year birds (n = 112 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).

### Results

##### Early-life telomere length varies with age and among breeding seasons

Mean ( standard error) telomere length in first-year birds was 5.17 0.19 kb. This is lower than the mean for one year-old birds based on cross-sectional data (5.46 0.15 kb; Figure S1). 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 cross-sectional data revealed that chicks have longer telomeres than any other age group, but that subsadults and adults had longer telomeres than fledglings (Fig. 1A). A longitudinal analysis of telomere loss showed that chicks, fleglings and subadults all lost telomeres early in life, with highest and lowest rates of loss in chicks and subaldults, respectively, although the difference among age classes was not significant (F = 0.27; *P* = 0.76; 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.

Early-life telomere length varied significantly among breeding seasons (one-way ANOVA, F = 2.22; *P* = < 0.01; Fig. 2A), and this variation in average telomere length over breeding seasons was positively related to island-wide food aviilability (linear regression, R2 = 0.39; F = 9.47; *P* = < 0.01; Fig. 2B). Similarly, the amount of telomeres lost in early life varied among breeding seasons (F = 2.86; *P* = < 0.01; Fig. 2C), and 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 (linear regression, R2 = 0.29; F = 5.27; *P* = 0.04; Fig. 2D).

##### Factors affecting early-life telomere dynamics within breeding seasons

The top explaining within-season variation in chick telomere length contained tarsus length, sex and the number of helpers present in the natal territory (Fig. 3A; Table S1). All three variables had high relative importance int he top model set (Fig. 3A), and the model containing these variables explained a reasonable amount of variation in telomere length (R2 = 0.17). Female chicks had longer telomeres than males (Fig. 3B), while telomere length was positively related to the number of helpers (Fig. 3C), and negatively related to tarus to length (Fig. 3D). However, it should be noted that model-averaged confidence intervals for sex and the number of helpers (but not tarsus length) marginally overlapped zero. For both juveniles and sub-adults the null model (intercept only) was the top model (Table S1), and no explanatory terms had high relative importance in the top model set, with all estimates close to zero (Fig. 4).

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 loss (all *P* > 0.05).

##### Early life telomere dynamics and survival

A log-normal survival model best fitted the Seychelles warbler data (AIC = 1115.35, AIC of next best distribution = 1134.82). A survival model including juvenile telomere length, body condition and early-life food availability showed that only juvenile telomere length had an effect on survival (estimate = 0.06, CI = < 0.01-0.11; Fig. 2A). This survival effect was most pronounced in individuals between five and ten years of age (Fig. 2B). Because telomere length and annual food availability are highly correlated (*R* = 0.30), we ran an analysis of early-life telomere length on survival excluding early-life food availability, and the telomere effect beacme marginally non-significant (estimate = 0.05, CI = < 0.01-0.10).

### Discussion

Previous studies have shown that in juvenile Seychelles warblers, neither territory quality nor annual variation in food availability predict survival to adulthood or late-life survival (Brouwer *et al.* 2006, 2012; Hammers *et al.* 2013). Here we show that telomeres link early-life conditions to later-life survival in the Seychelles warbler. These findings have a number of 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 correlative and experimental evidence showing that the natal environment can have pronounced impacts on early-life telomere length (Monaghan 2014). However, very few studies have shown that temporal variation in environmental conditions affects telomere length (Mizutani *et al.* 2013). 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.

We found no evidence that telomere length predicts survival to adulthood in Seychelles warblers. This is surprising, as we previously found that telomere length in adult Seychelles warblers predicts survival to the next year (Barrett *et al.* 2013). Moreover, our cross-sectional data show that telomere length is longer, on average, in one year-old birds compared to juveniles (Figure S1), while there was no evidence of telomere lengthening from the longitudinal data. A pattern like this is expected when there is selective disappearance - a known phenomenon in studies of telomere dynamics whereby individuals with short telomeres die, resulting in an apparent increase in telomere length in cross-sectional data (Haussmann & Mauck 2008). Thus, the raw data suggest that a survival effect may occur in early life, but this was not supported by our logistic regression analyses. This contradiction in results may be due to lack of power if a survival effect is present but weak and/or cohort specific. Increased sampling within years will help better elucidate the short-term survival impacts of early-life telomere length in this system.

In captive zebra finches, juvenile telomere length predicts late-life survival (Heidinger *et al.* 2012). Our results are the first to replicate this relationship in the wild. However, the effect varied among cohorts, suggesting that the relationship between early-life telomere length and late-life survival may not be a straightforward one in natural systems. Indeed, it appears that the interplay between the environment, telomeres and late-life survival at a given point in time is a snapshot of a fluid and dynamic evolutionary process. We therefore recommend that relationships involving telomeres from single cohorts should be interpreted with caution until we gain a better understanding of what drives spatiotemporal variation in telomere dynamics and survival.

Together, our results confirm that there is cohort-level variation in the relationship between the early-life environment and later-life survival, and 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.

Despite the promise of telomeres as biomarkers of cost, ecologists interested in understanding variation within populations are still left with the problem of identifying what explains individual-level variation in telomere length. Telomere length in juveniles will be the product of a range of factors, including inherited telomere length at birth (Horn *et al.* 2011), age at sampling (Heidinger *et al.* 2012), the early-life environment (Boonekamp *et al.* 2014), and, potentially, individual quality. In the Seychelles warbler we do not yet know how these different factors contribute to within-cohort variation in telomere length. However, a previous study on the Seychelles warbler showed that maternal heterozygosity influences offspring survival in bad years, but not good years (Brouwer, Komdeur & Richardson 2007). This raises the possibility that in the Seychelles warbler there is variation in individual quality, and high quality individuals are better able to cope with early-life stress (Brouwer *et al.* 2007). Thus in the near future it will become possible to use telomeres to link genetic variation, inheritance, environmental variation and senescence in the Seychelles warbler and other long-term systems.

### Ethics

All research activities were approved by the ethics committee at the University of East Anglia, the Seychelles Department of Environment and the Seychelles Bureau of Standards (approval reference A0347).

### Data accessibility

All data and scripts required to reproduce the analyses within this manuscript are available on GitHub (<https://github.com/lewisspurgin/SW_Early_life_telomeres>)

### Competing interests

There are no competing interests

### Authors' contributions

DSR developed the idea and obtained funding for the overall telomere project; DSR, JK, HLD and TB supervised the overall running of the overall Seychelles warbler project and contributed resources; HLD managed the longitudinal fitness database. EAF, KLB and LGS generated and processed the telomere data; LGS performed the analyses and wrote the manuscript, in discussion with DSR. All authors read and contributed to the manuscript.

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### References

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

Barrett, E.L.B., Boner, W., Mulder, E., Monaghan, P., Verhulst, S. & Richardson, D.S. (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., Burke, T., Hammers, M., Komdeur, J. & Richardson, D.S. (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. *R foundation for statistical computing*.

Boonekamp, J.J., Mulder, G.A., Salomons, H.M., Dijkstra, C. & Verhulst, S. (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., Komdeur, J. & Richardson, D.S. (2007) Heterozygosity-fitness correlations in a bottlenecked island species: A case study on the Seychelles warbler. *Molecular Ecology*, **16**, 3134–3144.

Brouwer, L., Richardson, D. & Komdeur, J. (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.

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

Burnham, K., Anderson, D. & Huyvaert, K. (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.

Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science (New York, N.Y.)*, **292**, 1528–31.

Drummond, H., Rodríguez, C. & Oro, D. (2011) Natural ’poor start’ does not increase mortality over the lifetime. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3421–7.

Frenck, R.W., Blackburn, E.H. & Shannon, K.M. (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. *Reproductive success* (ed T. Clutton-Brock).

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

Hammers, M., Richardson, D.S., Burke, T. & Komdeur, J. (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. & Mauck, R.A. (2008) Telomeres and longevity: Testing an evolutionary hypothesis. *Molecular Biology and Evolution*, **25**, 220–228.

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

Hayward, A.D., Rickard, I.J. & Lummaa, V. (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., Blount, J.D., Boner, W., Griffiths, K., Metcalfe, N.B. & Monaghan, P. (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. & Hercus, M.J. (2000) Environmental Stress as an Evolutionary Force. *BioScience*, **50**, 217–226.

Horn, T., Robertson, B.C., Will, M., Eason, D.K., Elliott, G.P. & Gemmell, N.J. (2011) Inheritance of telomere length in a bird. *PLoS ONE*, **6**.

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., Piersma, T., Kraaijeveld, K., Kraaijeveld-Smit, F. & Richardson, D.S. (2004) Why Seychelles Warblers fail to recolonize nearby islands: Unwilling or unable to fly there? *Ibis*, **146**, 298–302.

Mizutani, Y., Tomita, N., Niizuma, Y. & Yoda, K. (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. & Haussmann, M.F. (2006) Do telomere dynamics link lifestyle and lifespan? *Trends in Ecology and Evolution*, **21**, 47–53.

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

R Development Core Team. (2011) R: A Language and Environment for Statistical Computing (ed RDC Team). *R foundation for statistical computing*, **1**, 409.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (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., Burke, T. & Komdeur, J. (2003) Sex-specific associative learning cues and inclusive fitness benefits in the Seychelles warbler. *Journal of Evolutionary Biology*, **16**, 854–861.

Roach, D.A. & Carey, J.R. (2014) Population Biology of Aging in the Wild. *Annual Review of Ecology, Evolution, and Systematics*, **45**, 421–443.

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

Van de Crommenacker, J., Komdeur, J., Burke, T. & Richardson, D.S. (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.

Verhulst, S., Aviv, A., Benetos, A., Berenson, G.S. & Kark, J.D. (2013) Do leukocyte telomere length dynamics depend on baseline telomere length? An analysis that corrects for ’regression to the mean’. *European Journal of Epidemiology*, **28**, 859–66.

Von Zglinicki, T. (2002) Oxidative stress shortens telomeres. *Trends in biochemical sciences*, **27**, 339–344.

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

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