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Causes and consequences of telomere lengthening in a wild vertebrate population

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Abstract

Telomeres have been advocated to be important markers of biological age in evolutionary and ecological studies. Telomeres usually shorten with age and shortening is frequently associated with environmental stressors and increased subsequent mortality. Telomere lengthening – an apparent increase in telomere length between repeated samples from the same individual – also occurs. However, the exact circumstances, and consequences, of telomere lengthening are poorly understood. Using longitudinal data from the Seychelles warbler (*Acrocephalus sechellensis*), we tested whether telomere lengthening – which occurs in adults of this species – is associated with specific stressors (reproductive effort, food availability, malarial infection and cooperative breeding) and predicts subsequent survival. In females, telomere shortening was observed under greater stress (i.e., low food availability, malaria infection), while telomere lengthening was observed in females experiencing lower stress (i.e., high food availability, assisted by helpers, without malaria). The telomere dynamics of males were not associated with the key stressors tested. These results indicate that, at least for females, telomere lengthening occurs in circumstances more conducive to self-maintenance. Importantly, both females and males with lengthened telomeres had improved subsequent survival relative to individuals that displayed unchanged, or shortened, telomeres – indicating that telomere lengthening is associated with individual fitness. These results demonstrate that telomere dynamics are bidirectionally responsive to the level of stress that an individual faces, but may poorly reflect the accumulation of stress over an individual's lifetime.

KEYWORDS

ageing, biomarkers, life-history, senescence, stress, telomeres, vertebrates, wild populations

1 | INTRODUCTION

Senescence – the deterioration of health and performance in old age – occurs in nearly all species (Nussey et al., 2013). However, within

species there can be considerable individual variation in the onset and rate of senescence (e.g., Lemaître et al., 2013). Thus, individuals may be biologically older or younger than expected for their chronological age. Measuring “biological age” (Baker & Sprott, 1988)

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is valuable, not only in regards to organismal health but also in terms of understanding fundamental concepts in ecology and evolution; for example, determining trade-offs in life-history strategies and the impact of different environmental stressors (Lemaître et al., 2015; Stearns, 2008).

Telomeres are repetitive nucleotide sequences at the ends of chromosomes, which protect the functional integrity of the genome. Due to the “end replication problem” (Watson, 1972), telomeres shorten with each cell division, until a critical length is reached whereby cells can no longer divide (Campisi, 2003; Olovnikov, 1996). Telomeres also shorten when exposed to sources of cellular damage, such as reactive oxygen species (Reichert & Stier, 2017; Von Zglinicki, 2002). Both the number of cell divisions and cell damage load are cumulative (i.e., age-dependent) but also variable in rate. Telomere length shortens with increasing age in a broad range of taxa (Barrett et al., 2013; Bendix et al., 2014; Stier et al., 2015) but see Fairlie et al. (2016).

There is considerable empirical evidence to support the idea of telomere length, and the rate of shortening, being a marker of biological age. Accelerated telomere shortening occurs as an outcome of life-history events and environmental conditions associated with increased cellular division and reactive oxygen species production, including developmental growth (Monaghan & Ozanne, 2018; Salomons et al., 2009), early-life adversity (Boonekamp et al., 2014; Watson et al., 2015), reproductive effort (Reichert, Stier, et al., 2014; Sudyka et al., 2014) and stress (Chatelain et al., 2020). Shorter telomeres and/or higher attrition rates are associated with increased mortality risk (e.g. Barrett et al., 2013; Fairlie et al., 2016; Haussmann et al., 2005; Vera et al., 2012) and “faster” life histories (Haussmann et al., 2003; Sudyka, Arct, et al., 2019). Therefore, telomere length has been proposed as a valuable biomarker linking past life-history costs to future performance (Young, 2018). Additionally, telomeres can reflect an individual's ability to cope with stresses that would otherwise shorten telomeres. For example, individuals with higher reproductive success often have longer telomeres, despite the stress associated with reproduction (Angelier et al., 2019; Bauch et al., 2013; Sudyka, 2019). Therefore, as well as reflecting past stress and life-history costs, telomere length has been proposed as a marker of intrinsic quality (Angelier et al., 2019; Pauliny et al., 2006).

Over the last decade there has been a rapid expansion in studies investigating the causes and consequences of telomere dynamics across a wide range of taxa and environmental situations. However, our growing awareness of the complexity of telomere dynamics raises important questions on how we interpret telomeres as a biomarker. Importantly, multiple longitudinal studies in humans and some wild vertebrates have shown that within-individual changes in telomere length are highly variable (Fairlie et al., 2016; Hoelzl et al., 2016; van Lieshout et al., 2019; Spurgin et al., 2018; Svenson et al., 2011). Thus, authors have questioned whether single measures of telomere length per individual can accurately reflect biological age and/or individual quality; indeed, several studies have shown that it is the rate of within-individual change in telomere length, rather

than absolute telomere length, which is more informative of past life-history costs and future performance (Boonekamp et al., 2014; Salomons et al., 2009; Wood & Young, 2019). Furthermore, the telomere dynamics observed in longitudinal studies (see above) is frequently bidirectional, that is, an individual's telomeres may lengthen as well as shorten. Until recently, observed telomere lengthening was often attributed to measurement error between samples collected too close in time – relative to the rate of telomere loss – to detect telomere shortening (Chen et al., 2011; Steenstrup et al., 2013). However, it is now recognised that the degree or frequency of observed telomere lengthening is often greater than that expected from measurement error alone (Bateson & Nettle, 2017; van Lieshout et al., 2019; Spurgin et al., 2018).

Telomere lengthening within the same individual may be observed for a variety of reasons. The enzyme telomerase can restore lost telomere length (Blackburn et al., 1989) and, since telomeres shorten during cell division, telomerase is most active in cell lineages requiring greater proliferation potential, such as haematopoietic stem cells (Haussmann et al., 2007; Morrison et al., 1996). Telomeres can also lengthen via alternative mechanisms, independent of telomerase (see Cesare & Reddel, 2010 for a discussion). Importantly, telomere measurements may increase in subsequent assays due to changes in clonal cell composition, that is, an increase in long-telomere cells relative to short-telomere cells. All the mechanisms explained above are relevant to the telomere dynamics of blood, the tissue most often utilised for ecological and evolutionary studies on vertebrates (Nussey et al., 2014). Furthermore, in mammals the proportions of circulating leucocyte cell types (with differing telomere lengths; Weng, 2012) can also change dramatically within an individual, for example in response to infection, resulting in apparent changes in overall telomere length (Beirne et al., 2014). In birds and reptiles, blood-derived assays of telomere length overwhelmingly stem from nucleated erythrocytes (Stier et al., 2015), and telomerase activation or turnover in haematopoietic cell lines could, in theory, create heterogeneity in measured telomere length.

The importance of telomere lengthening in wild populations remains uncertain. Since telomere attrition occurs as a consequence of life-history or environmental stress costs, telomere lengthening may reflect investment in self-maintenance when those costs are alleviated. For example, wild edible dormice (*Glis glis*) that receive supplementary food exhibit lengthened telomeres (Hoelzl et al., 2016). In other wild species, changes in telomere length reflect temporal differences in environmental conditions, with lengthening coinciding with more favourable environments (e.g. Foley et al., 2020; Mizutani et al., 2013). Telomere dynamics can also reflect changes in parasitic pressure. For example, infection with malaria has been associated with telomere attrition in wild and captive birds (Asghar et al., 2016 and 2015), but the clearing of infections in humans is associated with telomere lengthening (Asghar et al., 2018). The ability of telomeres to both shorten and lengthen, rather than being an irreversible one-way ratchet, suggests that we may have to rethink our interpretation of telomere dynamics. Instead of reflecting the accumulation of all

past stressors and growth, telomere length may be more of a short-term marker, reflecting an individual's current condition consequent on the challenges and trade-offs faced by an individual. However, in contrast to telomere shortening, the circumstances under which telomere lengthening occurs in natural populations remain poorly understood.

Given the fitness costs associated with shorter, or more rapidly shortening, telomeres (see above), one might expect improved fitness to be associated with telomere lengthening. Recent reviews argue that telomere dynamics are a noncausal biomarker of accumulated cellular damage – such as that occurring from oxidative stress – that subsequently impacts fitness (Simons, 2015; Young, 2018). However, there is evidence that active restoration of telomere length can impact organismal performance. First, telomere lengthening could reduce the frequency of critically short telomeres – thought to directly contribute to organismal ageing by inducing cellular senescence and apoptosis (Van Deursen, 2014; Vera et al., 2012). Secondly, telomerase has wider restorative effects on cells (Cong & Shay, 2008; Criscuolo et al., 2018). Both telomerase activity and telomere lengthening are associated with tissue regeneration (Anchelin et al., 2011; Reichert, Bize, et al., 2014) and telomerase overexpression in mice is beneficial to a range of health parameters (Bernardes de Jesus et al., 2012; Simons, 2015). Conversely, active telomere lengthening could also have negative effects, such as proliferating cancers (Shay & Wright, 2011) or by diverting energy from competing traits (Young, 2018). Nonetheless, telomere lengthening has the potential to be associated with organismal performance, and this impact is not dependent on telomere length playing a causal role in organismal ageing.

In this study, we aim to determine when and why telomere lengthening occurs, and assess its association with survival, in a wild population of the facultative cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*). Previous studies on this population have shown that telomeres shorten with age, and individuals with shorter telomeres are less likely to survive to the following year (Barrett et al., 2013). Furthermore, telomere shortening is associated with various stresses in this species, including inbreeding (Bebbington et al., 2016), intraspecific antagonistic interactions (Bebbington et al., 2017) and parental care (Hammers et al., 2019). However, telomere lengthening occurs frequently (i.e., 44% of successive samples taken from the same adult individual exhibit an increase in telomere length), and is greater than that expected from measurement error alone (Spurgin et al., 2018). We predict that telomere lengthening occurs in individuals that experience reduced stress. Specifically, we predict that, for adults, telomere lengthening will be associated with reduced reproductive effort (less breeding, higher food availability and the presence of helpers) and an absence of malaria (the only known parasite in the population). We expect this relationship to be sex-specific, given that reproductive investments differ between sexes in this species; females lay the eggs, undertake incubation and have higher nestling provisioning rates than do males (van Boheemen et al., 2019; Hammers et al., 2019).

Furthermore, we tested whether telomere lengthening is associated with increased survival.

2 | MATERIALS AND METHODS

2.1 | The Seychelles warbler model system

The Seychelles warbler is a small insectivorous passerine currently distributed across five islands in the Seychelles. The population on Cousin Island (29 ha; 4°20'S, 55°40'E) – containing c. 320 individuals – has been extensively monitored since 1986 (Hammers et al., 2015; Komdeur, 1992). Since 1997, nearly all individuals (>96%) have been ringed with a unique combination of a British Trust for Ornithology (BTO) metal ring and three colour rings for identification (Raj Pant et al., 2020; Richardson et al., 2001). Individuals were usually first caught as nestlings, or as dependent juveniles (<8 months old) with mist nets (see Kingma et al., 2016 for details). Juveniles were aged as fledglings (1–3 months), old fledglings (3–5 months) or subadults (5–12 months) based on behaviour and eye colour (Komdeur, 1992). Since the resighting probability of individuals during the major breeding season is close to one – 0.98 for individuals ≥ 2 years-old (Brouwer et al., 2006) – and dispersal from the island is virtually absent (Komdeur et al., 2004), individuals that were not observed during the major breeding season were assumed dead. First year survival is 0.61 ± 0.09 SE, increasing to 0.84 ± 0.04 SE annual survival in adults (Brouwer et al., 2006). For individuals reaching fledgling age, the mean life expectancy is 5.5 years (Komdeur, 1991), and the maximum recorded lifespan is 19 years (Hammers & Brouwer, 2017).

The population is structured into c. 115 clearly defined territories (Kingma et al., 2016). The availability of the warbler's invertebrate prey (Komdeur, 1992) varies considerably due to the interacting effects of defoliating salt spray (along coastal territories), tree species abundance, elevation and rainfall (Van de Crommenacker et al., 2011). Territories are defended year-round by a single dominant breeding pair, but c. 40% of territories include an additional 1–5 sexually mature subordinates, often past offspring of the same dominant pair (Richardson et al., 2002).

The majority of breeding activity (94% of territories) occurs from June to August, but a minor breeding season also occurs from January to March (Komdeur & Daan, 2005). Breeding attempts usually consist of one-egg clutches (Komdeur, 1994). Only females incubate while both sexes provision chicks and fledglings for c. three months post-fledging. Around one third of subordinates also provide alloparental care to group offspring, hereafter “helpers” (Hammers et al., 2019; Komdeur, 1994). Around 44% of female helpers are also cobreeders (Raj Pant et al., 2019; Richardson et al., 2001). The offspring of cobreeders are jointly cared for by the subordinate female and dominant pair (Bebbington et al., 2018; Richardson et al., 2001). The frequency of extra-pair paternity in the population is high (c. 41%; Raj Pant et al., 2019) and such paternity is nearly always gained

by dominant males from other territories (Richardson et al., 2001), but males only provide parental care in their own territory.

2.2 | Data collection

Our study uses data collected from 1995 to 2015. Each year (June–September), during the major breeding season, each territory was visited at least every two weeks to determine the identity and status of group individuals. During visits, the dominant female was followed for at least 15 min to assess breeding activity (Richardson et al., 2007). Territories with an active nest were visited every 3–4 days until the nestling(s) have fledged or the breeding attempt failed. Observations of incubating and/or provisioning were used to estimate hatching/fledging dates, and to determine whether any subordinates present in the territory were helpers (Richardson et al., 2002; van Boheemen et al., 2019). For each territory, the availability of food was calculated (following Komdeur, 1992). Briefly, the number of insects (on the undersides of leaves) was multiplied by the percentage cover of broad-leaf vegetation within territories. This number was then divided by the number of adult territory occupants to give food availability per individual (Brouwer et al., 2006).

During each major breeding season, as much of the adult population as possible (normally around 30%) was caught and re-sampled: c. 25 μ l of blood was taken from the brachial vein and stored in 100% ethanol (Richardson et al., 2001). DNA extracted from blood samples (following Richardson et al., 2001) was used to confirm sex and assign parentage using MasterBayes 2.52 based on genotypes derived from 30 microsatellite loci (for details see Sparks et al., 2021). The presence of haemosporidian infection (*Haemoproteus nucleococondensis*; hereafter referred to as malaria) - the only known parasite in the Seychelles warbler (Hutchings, 2009) - was screened for following Hellgren et al. (2004). In the Seychelles warbler, nearly all individuals (c. 85%) become infected with malaria in their first year (Hammers et al., 2016). In adults, the prevalence of malaria is much lower (c. 20% at 4 years of age and older) as individuals clear the initial infection, or enter the latent infection stage, where parasites may be absent in blood - and hence are not detected - but persist at low abundance in internal organs. Thus, in our study (of individuals >1 year of age), individuals in which we detected malaria (hereafter “infected”) are either in the late chronic stage of their initial infection, or in subsequent relapses, or reinfections (Valkiunas, 2005). Infection with malaria does not appear to have an impact on annual survival in the Seychelles warbler (Hammers et al., 2016) but has been linked to telomere attrition in the great reed warbler (*Acrocephalus arundinaceus*; Asghar et al., 2015).

2.3 | Telomere analysis

Relative Telomere Length (RTL; the concentration of amplified telomeric DNA relative to that amplified at *GAPDH* - a single copy

gene) had previously been measured using qPCR as part of another study (Spurgin et al., 2018). Intraplate repeatability of *GAPDH* and Telomere Cq values are 0.74 (CI = 0.74, 0.75) and 0.73 (CI = 0.71, 0.74), respectively. Interplate repeatability of RTL is 0.68 (CI = 0.65, 0.70); based on 422 samples measured at least twice at different time points. The within-individual variance of RTL (i.e., from multiple samples across an individual's lifetime) is greater than the variance among repeated measurements of the same sample (Levene's test: $F = 43.63$; $p < .001$). Importantly, this is true when incidences of within-individual decreases and increases in RTL (i.e., between successive samples from the same individual) are analysed separately, indicating that the magnitude of both telomere shortening and (crucially) lengthening observed in our system is greater than that expected from measurement error alone (Spurgin et al., 2018). Since avian erythrocytes are nucleated and vastly outnumber other blood cell types, blood RTL is effectively a measure of erythrocyte RTL (Stier et al., 2015). Individuals with two or more RTL measurements were used in the current study, with the difference between consecutive pairs of RTL measurements (Δ RTL) as the response variable. We excluded RTL measurements from young individuals (<1 year), as previous work in this population has shown that the within-individual rate of attrition per annum is an order of magnitude greater in the first year compared to adult life (Spurgin et al., 2018). For consistency, we focused on RTL measurements from catches only within the major breeding season, since interseasonal Δ RTL could reflect seasonal effects on RTL. Individuals are caught opportunistically, meaning that the follow-up duration between RTL measurements (hereafter Δ RTL period) ranged from one year (i.e., consecutive seasons) to nine years (Figure S1). Δ RTL is not associated with the duration of the Δ RTL period. The final data set comprised 359 Δ RTL measures from 227 adults.

Reproductive effort was measured as the number of offspring raised by an individual during the Δ RTL period; specifically, offspring that had hatched after time 1 and had reached independence (3 months old) before time 2. Social offspring - those for which a dominant breeder provides parental care - are determined from behavioural observations during nest attempts. Offspring are also genotyped to identify genetic parentage. This is an underestimation of total offspring produced, since we excluded offspring for which parents could not be assigned (c. 15% of offspring) and some offspring are likely to have died before being sampled (Edwards et al., 2017). We used the number of social offspring as our estimate of reproductive output in males (since males do not care for offspring sired in other territories). Females (dominants or cobreeders) always contribute to the care of any offspring in the nest; (Richardson et al., 2002). Thus, female reproductive output was the number of co-bred offspring. For both sexes, the majority of individuals had 0–2 offspring within each Δ RTL period (Figure S1). Offspring number was positively correlated with the Δ RTL period (Pearson's $r = 0.69$, $df = 357$, $p < .001$, Figure 1S), meaning that individuals typically produced one offspring every two years.

During the Δ RTL period, we averaged food availability (insect abundance per individual per field season) across field seasons.

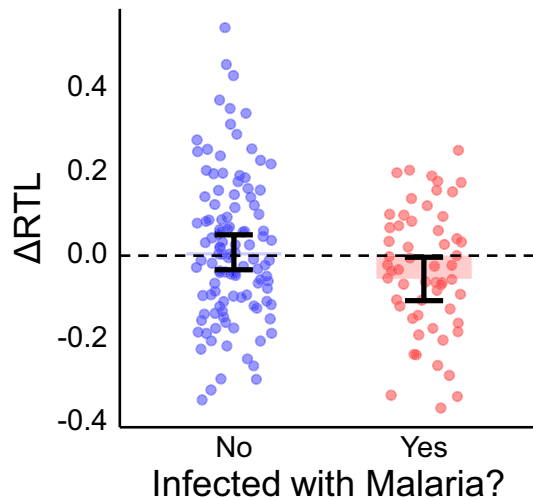


FIGURE 1 The relationship between within-individual change in RTL and malaria status (at initial RTL measurement) for female Seychelles warblers. Negative values of Δ RTL indicate telomere shortening, while positive values indicate telomere lengthening. Bars are model predicted values (Table 1) of Δ RTL with 95% CI for individuals with and without malaria, adjusted for offspring number, food availability and helper status (reference category = no helper). Points are raw data.

Reproductive effort - in terms of time spent incubating and provisioning - of dominant breeders is reduced by the presence of helpers, including cobreeders (van Boheemen et al., 2019; Hammers et al., 2019). Reduced telomere attrition in dominant females has been associated with the presence of helpers in a previous study (Hammers et al., 2019). Therefore, we determined whether nest helpers (including cobreeders) were present in the territories of individuals that produced offspring.

2.4 | Statistical analysis

Using RSTUDIO (version 1.2.5033 and R version 4.0.3, Rstudio Team, 2020) we tested whether food availability, number of offspring, helper presence and malaria status predicted Δ RTL, with the prediction that high food availability, low reproductive output, helper presence and no malaria infection - or a combination of these factors - would result in telomere lengthening. We adjusted Δ RTL following Verhulst et al. (2013); this method subtracts the mean difference between successive samples expected from the regression-to-mean effect, estimated by the correlation between successive samples. In our data set, this correlation was very weak (Pearson's $r = 0.06$, $df = 357$ $p = .22$), as expected given the low within-individual consistency of RTL in this system (Spurgin et al., 2018). This results in an adjusted Δ RTL (hereafter Δ RTL) which is equivalent to RTL at time 2; positive values indicate longer RTL and negative values indicate shorter RTL, relative to the population mean RTL. As expected, Δ RTL was strongly correlated with unadjusted Δ RTL (Pearson's $r = 0.71$, $df = 357$, $p < .001$), meaning that individuals with lengthened or

shortened RTL (relative to their initial RTL) tended to have more positive or more negative Δ RTL, respectively.

The association between factors and Δ RTL was tested using Linear Mixed Models (package LME4 version 1.1-25; Bates et al., 2015). We deliberately focused on a restricted set of fixed effects - chosen a priori based on logic and evidence of influencing telomere dynamics - to avoid data dredging, which could generate false-positive associations. Chosen fixed effects during the RTL period included; mean food availability (continuous), number of offspring (continuous), the duration of the RTL period (continuous) and the presence of helpers (yes or no). Chosen fixed effects at the start of the RTL period included; age (continuous) and malaria status (infected or uninfected). We also included logical two-way interactions; for example, the effect of offspring production on telomere maintenance may depend on food availability and/or helper presence. These effects were likely to differ between the sexes due to differing investments in reproduction (see above). Indeed, initial models (that included both males and females) indicated that associations between Δ RTL and fixed effects depended on two- and three-way interactions with sex (Table S1). To investigate these sex-specific differences in more detail, while also avoiding the need for multiple three-way interactions, separate models were created for males and females. Offspring number, food availability and Δ RTL period were log10 transformed (for normality) and mean centered to remove collinearity between their main effects and interaction (Schielzeth, 2010). All main fixed effects were kept in final models (regardless of significance) but two-way interactions were removed when nonsignificant (see Whittingham et al., 2006). Since most individuals had 0–2 offspring, offspring number was reduced to a categorical variable (zero, one or ≥ 2) for graphical interpretation of interactions.

We included catch year of the first RTL measurement as a random factor, since the subsequent change in RTL may depend on year-to-year-effects. Cohort year was not included as a random factor since Spurgin et al. (2018) previously found no support for cohort-effects influencing Δ RTL. Variation in RTL between qPCR plates (Sparks et al., 2021) could contribute to variation in Δ RTL, since RTL measurements from longitudinal samples were run on separate plates. Therefore, the plate identities of both RTL measurements per Δ RTL were included as random factors. Individuals for which >2 RTL measurements were available had multiple measures of Δ RTL. For example, an individual with three RTL measurements would have two measures of Δ RTL; between measurement 1–2 and 2–3. Δ RTL is previously shown to be highly variable across the same individual's lifetime (i.e., Individuals do not exhibit consistent lengthening or shortening; Spurgin et al., 2018). Thus, in our analysis we used all available measures of Δ RTL per individual and included individual identity as a random factor. Our findings were consistent when only one datum per individual was used.

To test whether Δ RTL influenced subsequent survival, we performed a Cox proportional hazards regression analysis (package SURVIVAL version 3.2-7; Therneau, 2014). The response variable was the number of years an individual lived beyond the sampling date of its last RTL measurement. We included 23 individuals that were

TABLE 1 Linear mixed effects models explaining variation in Δ RTL between consecutive blood samples from the major breeding seasons in female and male Seychelles warblers. For helper presence and malaria terms, the reference categories are no helpers and no malaria, respectively

FEMALES					
Predictor	β	SE	df	t	p-value
(Intercept)	0.036	0.032	92.293	1.119	.266
Food availability	0.017	0.015	82.367	1.127	.263
Number of offspring	-0.033	0.016	154.301	-2.096	.038
Helper presence (Yes)	0.080	0.037	150.072	2.163	.032
Malaria (Yes)	-0.064	0.027	157.627	-2.322	.022
Δ RTL period	-0.002	0.017	138.682	-0.126	.900
Age	-0.007	0.006	155.293	-1.261	.209
Food \times offspring	0.040	0.014	158.938	2.893	.004
Random factors	170 observations	Variance			
Individual identity	108 individuals	<0.001			
Catch year	18 years	0.001			
qPCR plate identity 1	54 plates	0.001			
qPCR plate identity 2	49 plates	0.002			
Residual		0.021			
MALES					
Predictor	β	SE	df	t	p-value
(Intercept)	0.004	0.025	33.224	0.152	.880
Food availability	-0.002	0.015	95.464	-0.113	.910
Number of offspring	0.001	0.018	163.069	0.074	.941
Helper presence (Yes)	0.016	0.039	173.784	0.394	.694
Malaria (Yes)	-0.008	0.030	164.176	-0.286	.775
Δ RTL period	-0.019	0.018	113.981	-1.035	.303
Age	-0.015	0.015	166.929	-1.035	.302
Random factors	189 observations	Variance			
Individual identity	119 individuals	0.006			
Catch year	16 years	0.001			
qPCR plate identity 1	65 plates	0.001			
qPCR plate identity 2	56 plates	0.005			
Residual		0.026			

still alive in 2020 as right-censored data points. 13 individuals translocated to other islands post-sampling were excluded, leaving 214 individuals. Predictor variables were Δ RTL, sex and age at last RTL measurement (since older individuals are expected to have shorter remaining lifespans). Where multiple measures of Δ RTL were available per individual, we used only the last measurement, meaning that each Δ RTL value represents the last known change in telomere length before the individual died. We were interested in whether predicted hazard ratios exhibited a proportional change across the range of Δ RTL values, or whether the association was nonlinear. Therefore, we modelled Δ RTL as both a linear and quadratic function. In this model, positive hazard coefficients would indicate a decreased probability of survival with increasing values of the predictor variable. Hazard ratios represent the effect size of predictors;

for example, a hazard ratio of 2 indicates that the risk of death is twice as high for the corresponding change in a predictor variable.

3 | RESULTS

3.1 | Telomere dynamics

Out of the 359 pairs of consecutive RTL measurements included in our analysis, 166 (46%) showed an increase in length. There was no difference in Δ RTL between males and females (mean \pm SE; males = 0.001 \pm 0.014, females = 0.000 \pm 0.013). Females infected with malaria at their first RTL measurement had more negative Δ RTL than noninfected females (Figure 1). In females, the

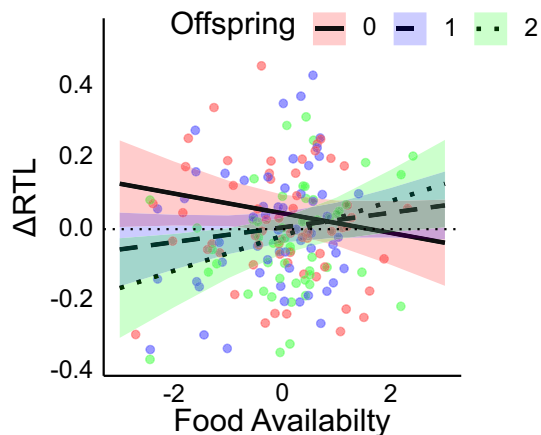


FIGURE 2 The relationship between within-individual change in RTL, mean food availability (mean annual insect-prey availability) and offspring production for female Seychelles warblers. Negative values of Δ RTL indicate telomere shortening, while positive values indicate telomere lengthening. Lines are model predicted slopes (Table 1) with 95% CI for individuals with none, one and two offspring, adjusted for malaria status (reference category = uninfected) and helper presence (reference category = no helper). Points are raw data grouped by number of offspring (zero, one or \geq two).

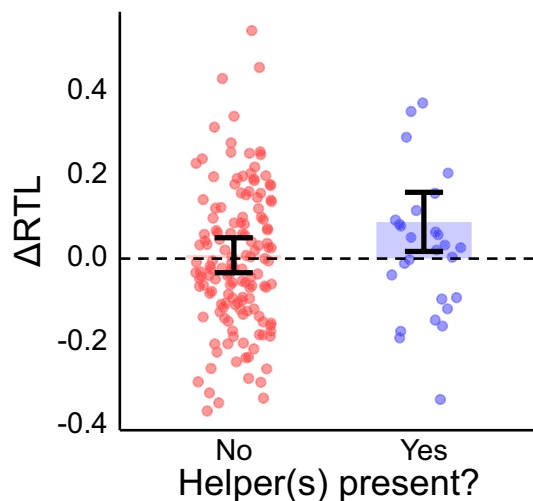


FIGURE 3 The relationship between within-individual change in RTL and helper presence for female Seychelles warblers. The “Yes” group contains females that had one or more helpers (or cobreeders) assisting with the care of at least one offspring during the Δ RTL period (time between samples). Negative values of Δ RTL indicate telomere shortening, while positive values indicate telomere lengthening. Bars are model predicted values (Table 1) with 95% CI for individuals with and without helpers, adjusted for offspring number, food availability and malaria status (reference category = uninfected). Points are raw data grouped by helper presence.

association between offspring number and Δ RTL was dependent on the availability of food within the same period (interaction term in Table 1). Females that produced fewer offspring had Δ RTL close to

zero regardless of food availability (Figure 2; females with zero and one offspring). Females in territories of low mean food availability had a more negative Δ RTL with increasing numbers of offspring, whereas females in territories of high mean food availability had a more positive Δ RTL with increasing numbers of offspring (Figure 2). Females that reared offspring with the assistance of helpers also had more positive Δ RTL change compared to females without helpers (Figure 3). Δ RTL was not associated with Δ RTL period or age (Table 1). None of the chosen explanatory variables predicted Δ RTL in males (Table 1). In all models, results were qualitatively identical when unadjusted Δ RTL was used as the response variable and controlling for initial RTL (Table S2).

3.2 | Telomere dynamics and survival

Individuals with more negative Δ RTL values – indicating greater telomere shortening – had a greater subsequent risk of mortality (relative to individuals with no change in telomere length) while individuals with more positive Δ RTL values – indicating greater telomere lengthening – had a reduced risk of mortality (Figure 4, Table 2). The quadratic function of Δ RTL was nonsignificant; thus, the effect of Δ RTL on mortality risk was constant throughout the range of Δ RTL. The association between mortality risk and Δ RTL was not dependent on the sex or age of these adult individuals (interaction terms reentered into final the model; Table 2). As expected, older individuals had an increased mortality risk. Visual inspection of Schoenfeld residuals showed no violation of the assumption of nonproportional hazards, meaning the effects of predictor variables on mortality risk were constant throughout the remaining lifespan.

4 | DISCUSSION

In our Seychelles warbler population, a change in telomere length (Δ RTL) was associated with life-history factors predicted to influence self-maintenance trade-offs – but only in females. Greater telomere shortening was observed in females with higher reproductive effort when living in areas of poorer food availability, as well as in individuals infected with malaria. Importantly, telomere lengthening was more often observed in females experiencing the reverse circumstance – that is, those not infected with malaria and living in areas of high food availability – and those with helpers at the nest (the presence of which reduces reproductive effort per individual). These opposing changes in telomere length were not due to differences in initial telomere length or regression-to-the-mean effects. Consistent with Δ RTL being negatively correlated with stress, higher subsequent survival probabilities were associated with telomere lengthening, independently of sex and age.

We found that telomeres shortened in individuals that tested positive for malaria, but only in females. This finding is consistent with previous studies demonstrating greater erythrocyte telomere shortening in malaria-infected individuals compared to uninfected

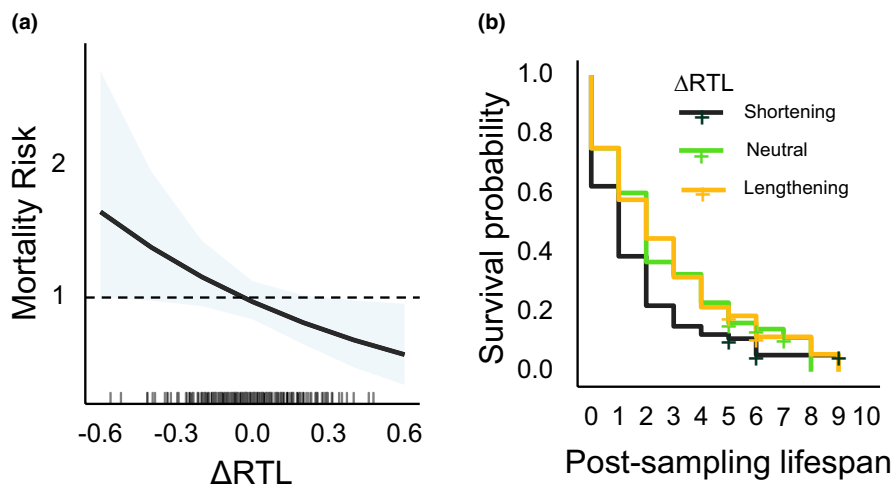


FIGURE 4 (a) The effect of Δ RTL change on mortality risk hazard ratios for Seychelles warblers. The reference hazard ratio (1 – dotted line) is set to a Δ RTL value of zero, with negative values indicating RTL shortening and positive values indicating RTL lengthening. The fit line represents the change in relative hazards – in this case risk of death – with the shaded area being 95% confidence limits. A mortality risk of 2 indicates that the risk of death is twice as high for the corresponding Δ RTL compared to the Δ RTL at 1. The bottom rug represents the distribution of Δ RTL values. (b) Survival curves for adult Seychelles warblers in relation to Δ RTL, which is split into tertiles that can be broadly characterised as RTL shortening, neutral (i.e. no change) and lengthening. Tick marks indicate individuals that were still alive at the end of our study period ($n = 23$). Unit of post-sampling life-span is years.

TABLE 2 Cox proportional hazard model explaining variation in survival after the second of twosamples in relation to the change in telomere length (Δ RTL) between the two samples ($n = 214$). The reference category for sex is female

Predictor	β	HR	z	p -value
Δ RTL	-0.887	0.412	-2.153	.031
Δ RTL ²	-0.505	0.604	-0.356	.722
Sex (male)	0.047	1.048	0.323	.747
Age	0.051	1.052	2.206	.027
Δ RTL \times Sex	-0.061	0.941	-0.072	.943
Δ RTL \times Age	-0.107	0.898	-0.939	.348

individuals (Asghar et al., 2015; Karell et al., 2017). While we expected malaria to affect both sexes equally, sex-specific differences in the impact of malaria on telomere length have also been observed in blue tits (*Cyanistes caeruleus*; Sudyka, Podmokła, et al., 2019b). An emerging view is that telomere shortening is an outcome of immunological responses to infection (Giraudeau et al., 2019). One such response – oxidative stress – is elevated in Seychelles warblers infected with malaria; albeit depending on the breeding stage (van de Crommenacker et al., 2012). In our system, adults that test positive for malaria are most likely in the chronic (i.e., late) or relapse stages of the initial infection (first acquired as juveniles), or have been reinfected after clearing the initial infection (Valkiunas, 2005). Therefore, the telomere shortening we observed seems to reflect a cost of persistent/re-emerging infection, perhaps due to immunological responses – rather than a direct cost of parasitism, which tends to occur during the acute malarial stage (Asghar et al., 2018). However, not knowing when malarial parasites became present or absent in blood, relative to the time of sampling, is a limitation of

our observational study. Furthermore, while the frequency of recurring infection is generally low (c. 20% within two years; Hammers et al., 2016), initially uninfected individuals could have undetected outbreaks within the time period of repeated samples.

We also found that telomere shortening was greater in females that produced more offspring. Moreover, the relationship only occurred when the mean food availability was low during the period of offspring production. Food limitation is expected to increase reproductive effort per unit of reproductive success, and thus increase the costs of reproduction (Harshman & Zera, 2007; Santos & Nakagawa, 2012). For example, individuals on poor-quality territories may have to work harder to meet the food demands of offspring, leading to elevated stress (see Soulsbury & Halsey, 2018). Likewise, Seychelles warblers tend to be in poorer condition (in terms of oxidative stress and body mass) when provisioning chicks, compared to other nest stages, and when occupying poorer quality territories (Van de Crommenacker et al., 2011; Van de Crommenacker et al., 2011). There are now several experimental and observational studies which show that individuals experiencing higher reproductive effort have shorter telomeres and/or experience greater telomere shortening (recently reviewed by Sudyka, 2019). However, few of these studies have explored associations between telomeres and reproduction in the context of food availability. Thus, our finding adds novel insight into the life-history framework of telomere dynamics.

The relationship between telomeres and reproductive effort was only apparent in females. This was expected since parental effort is higher in females; in the Seychelles warbler only females incubate and they also have higher provisioning rates than males (van Boheemen et al., 2019; Hammers et al., 2019). Thus, females benefit more from having nest helpers (Hammers et al., 2019) and may be more responsive to differences in food availability when caring for

offspring (e.g., Low et al., 2012). Alternatively, telomere shortening may correlate with egg production – which is associated with substantial self-maintenance costs (Visser & Lessells, 2001; Williams, 2005) – more than with provisioning effort. Likewise, male telomere shortening may be more correlated with male-specific reproductive behaviours that were not accounted for in this study. For example, Bebbington et al. (2017) showed that Seychelles warbler males, which are more involved in territory defence, have more telomere shortening with increased competition from rival males.

Telomere length increased in females that produced more offspring when experiencing higher food availability, and when the production of offspring was assisted by nest helpers. This finding supports our main prior prediction – that telomere lengthening occurs in individuals experiencing lower levels of life-history stress. The nonbiological explanation – that observed telomere lengthening is a consequence of high measurement error relative to attrition rate (Steenstrup et al., 2013) – seems unlikely for several reasons. Firstly, the degree of within-individual telomere lengthening observed in our system is greater than that expected from measurement error alone (Spurgin et al., 2018). Secondly, high measurement error and a lack of telomere shortening would result in no overall change (i.e., a random scatter of values around zero), whereas we observed an overall increase in telomere length consistent with our predictions. Lastly, our analysis accounted for regression-to-the-mean effects. This suggests that “real” telomere lengthening (i.e., that which is not purely a consequence of measurement error) is more frequent in individuals with less stressful life-histories.

Telomere lengthening may be an outcome of lower reproductive costs associated with high food availability, cooperative breeding and absence of parasite infection. As discussed above, reduced reproductive effort is associated with the maintenance of longer telomeres and/or reduced telomere attrition. Some experimental studies that manipulated offspring number found no change or even slight telomere lengthening in treatment groups with the fewest offspring (Heidinger et al., 2012; Kotrschal et al., 2007; Sudyka et al., 2014); however, these observations tend to be reported as reduced telomere shortening. Furthermore, reduced oxidative damage and telomere lengthening have also been observed in wild rodents receiving food supplements (Fletcher et al., 2013; Hoelzl et al., 2016). Thus, telomere lengthening may occur because plentiful food permits the allocation of energy to mechanisms involved in restoring previously lost telomere length, such as telomerase. This is a possibility in the Seychelles warbler, as high telomerase activity has been observed in the bone marrow (relative to other tissues) in adults of other bird species (Haussmann et al., 2007).

In addition to reflecting the alleviated costs of reproduction in females with helpers and high food availability, telomere lengthening could also be associated with intrinsic quality and/or condition (Bauch et al., 2013; Sudyka, 2019). Numerous studies have shown that telomere length is positively associated with individual quality and reproductive success (e.g., Angelier et al., 2019; Le Vaillant et al., 2015; Parolini et al., 2017; Pauliny et al., 2006). Females which have higher reproductive success, territory quality and nest-helpers are

likely to represent the best quality females in our population, and thus they may be better able to invest in mechanisms that restore/elongate telomere length, despite the potential for reproductive effort to shorten telomeres (Bauch et al., 2013). In contrast, females that produced few or no offspring as a consequence of poor intrinsic quality (rather than an effect of food availability or helper presence) may be unable to invest in such telomere-lengthening mechanisms, resulting in the observed lack of change or shortening of telomere length in these females. However, due to the limitations of observational studies, and the correlative nature of reproductive effort, reproductive success and associated factors (i.e., food availability, cooperative breeding), we are unable to separate the effects of life-history costs and intrinsic quality on telomere dynamics. Nevertheless, our study indicates that the telomere lengthening observed in some wild populations is not necessarily random, or merely an artefact of measurement error, but can instead be associated with important life-history trade-offs and/or traits.

We found that individuals with greater telomere shortening had lower survival prospects. This finding is consistent with short telomeres being negatively associated with survival in the Seychelles warbler (Barrett et al., 2013) and in a range other wild vertebrate species (reviewed in Wilbourn et al., 2018). Telomere shortening can directly impact survival by increasing the frequency of critically short telomeres, which can trigger cellular senescence (Kurz et al., 2004). However, our measure of telomere length is a mean value (i.e., across chromosomes and cells) rather than a measure of the frequency of short telomeres per se (Bendix et al., 2010). The non-causal explanation is that factors which shorten telomeres – such as oxidative stress – also cause wider cellular damage that ultimately increases mortality risk. Interestingly, we show that infection with malaria, for which we have not been able to find a survival impact in this species (Hammers et al., 2016), may increase mortality risk via mechanisms that also shorten telomeres. Importantly, the telomere-survival relationship was not solely driven by negative effects (i.e., cellular damage and/or critically short telomeres), since individuals with lengthened telomeres had better survival prospects relative to individuals with no change in telomere length. This finding is consistent with the positive health and longevity effects of telomerase in mice (Bernardes de Jesus et al., 2012; Simons, 2015) but contrasts with the results of Wood and Young (2019), who found that increased telomere length was not associated with higher nestling survival in white-browed sparrow-weavers (*Plocepasser mahali*). In our study, telomere lengthening was also associated with life-history traits known to benefit survival and longevity in the Seychelles warbler: high food availability (Brouwer et al., 2006) and helpers (Hammers et al., 2019). This suggests that telomere lengthening may be characteristic of a strategy in which individuals make higher reproductive investments in more favourable environments, without incurring survival costs (as suggested by Hoelzl et al., 2016).

Our study adds to the growing body of literature on the bidirectionality of within-individual telomere dynamics in ecological settings. We found that telomere lengthening can reflect good current environmental conditions and subsequently is linked to better

survival prospects. Therefore, our study echoes conclusions from previous studies; that the within-individual variability and lengthening of telomeres means single measures of telomere length may not be a reliable indicator of damage accumulated in an individual's past life, nor their future performance – and hence not a good biological age marker. Future studies should determine the mechanisms behind telomere lengthening observed in wild populations, and whether telomere lengthening is coordinated across multiple tissue types within individuals.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

The study was conceived by Thomas J. Brown and David S. Richardson. Data was collected by David S. Richardson, Hannah L. Dugdale, Lewis G. Spurgin, Terry Burke and Jan Komdeur. Statistical analyses were conducted by Thomas J. Brown with input from David S. Richardson and Hannah L. Dugdale. The manuscript was written by Thomas J. Brown and all authors critiqued the output with important intellectual content. All authors gave their final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study have been made openly available in Dryad Digital Repository at <https://doi.org/10.5061/dryad.xwdbrv1cj>

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SUPPORTING INFORMATION

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