

Social dominance and rainfall predict telomere dynamics in a cooperative arid-zone bird

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Abstract

In many vertebrate societies dominant individuals breed at substantially higher rates than subordinates, but whether this hastens ageing remains poorly understood. While frequent reproduction may trade off against somatic maintenance, the extraordinary fecundity and longevity of some social insect queens highlight that breeders need not always suffer more rapid somatic deterioration than their nonbreeding subordinates. Here, we used extensive longitudinal assessments of telomere dynamics to investigate the impact of dominance status on within-individual age-related changes in somatic integrity in a wild social bird, the white-browed sparrow-weaver (*Plocepasser mahali*). Dominant birds, who monopolise reproduction, had neither shorter telomeres nor faster telomere attrition rates over the long-term (1–5 years) than their subordinates. However, over shorter (half-year) time intervals dominants with shorter telomeres showed lower rates of telomere attrition (and evidence suggestive of telomere lengthening), while the same was not true among subordinates. Dominants may therefore invest more heavily in telomere length regulation (and/or somatic maintenance more broadly); a strategy that could mitigate the long-term costs of reproductive effort, leaving their long-term telomere dynamics comparable to those of subordinates. Consistent with the expectation that reproduction entails short-term costs to somatic integrity, telomere attrition rates were most severe for all birds during the breeding seasons of wetter years (rainfall is the key driver of reproductive activity in this arid-zone species). Our findings suggest that, even in vertebrate societies in which dominants monopolise reproduction, dominants may experience long-term somatic integrity trajectories indistinguishable from those of their nonreproductive subordinates.

KEYWORDS

life-history, reproduction, social dominance, somatic maintenance, telomere dynamics

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1 | INTRODUCTION

In many animal societies, socially dominant individuals enjoy higher reproductive success than subordinates (Keller & Reeve, 1994), but the effects of social dominance on ageing trajectories and lifespan remain poorly understood (Cram et al., 2015a, 2018; Creel, 2001; Dammann & Burda, 2006; Jemielity et al., 2005; Schmidt et al., 2014). On the one hand, greater investment by dominants in reproduction or the defence of social rank could accelerate age-related declines in somatic integrity (the extent to which somatic tissues are free from biomolecular errors and damage; Kirkwood, 1977; Kirkwood & Holliday, 1979) by elevating rates of biomolecular damage (e.g., yielding oxidative and/or endocrine stress; Blount et al., 2016; Cram et al., 2015a, 2015b; Creel, 2001; Sanderson et al., 2014; Young, 2009) and/or trading-off against investments in somatic maintenance (Harshman & Zera, 2007; Kirkwood, 1977). On the other hand, dominants in some societies may be free of the socially-induced stress that subordinates can experience (Abbott et al., 2003; Young et al., 2006), and may enjoy differential access to the resources needed for somatic maintenance (Barton & Whiten, 1993; Murray et al., 2006). Indeed, the extraordinary lifespans of queens in some social insects highlight the potential for robust somatic maintenance to persist alongside extreme fecundity (Keller & Genoud, 1997; Jemielity et al., 2005; Seehuus et al., 2006; see also Dammann & Burda, 2006; Schmidt et al., 2014 for potential vertebrate parallels). Advances in our understanding of the impact of social dominance on ageing trajectories in social vertebrates require that we now investigate the effect of dominance status on within-individual age-related changes in somatic integrity, but few such studies have been conducted to date (Cram et al., 2018; Fujishiro et al., 2018).

Recent advances in telomere biology offer promise for studies of this kind, as evidence suggests that within-individual changes in telomere length over time ("telomere dynamics") may serve as a useful biomarker of within-individual changes in somatic integrity (Boonekamp et al., 2013; Monaghan & Hausmann, 2006; Young, 2018). Telomeres are ribonucleoprotein complexes that cap the ends of linear chromosomes and, in the absence of telomere maintenance mechanisms (such as the addition of telomeric repeats by telomerase or alternative lengthening pathways; Cesare & Reddel, 2010), typically shorten with successive rounds of cellular replication (Blackburn et al., 2015; Olovnikov, 1973); a process that may be hastened by oxidative stress (Reichert & Stier, 2017). Accordingly, many species show within-individual declines in mean telomere lengths of focal tissues with advancing organismal age, and comparative studies suggest that telomere attrition rates may generally be slower in longer-lived species (Dantzer & Fletcher, 2015; Tricola et al., 2018). The long-term patterns of age-related change in mean telomere length may shroud more complex patterns over the short-term, however, as growing evidence suggests that transient within-individual increases in mean telomere length (the causes of which are debated; Bateson & Nettle, 2017; Steenstrup et al., 2013; Verhulst et al., 2013; see discussion) may also contribute to observed dynamics (e.g., Fairlie et al., 2016; Hatakeyama et al., 2016; Hoelzl,

Smith, et al., 2016; Spurgin et al., 2018; Ujvari & Madsen, 2009). Longitudinal telomere length dynamics have the potential to act as a useful biomarker of age-related changes in somatic integrity for at least two reasons. First, once telomeres become critically short they can trigger apoptosis or cellular senescence (Blackburn, 2000; Hemann et al., 2001); an irreversible state of cell cycle arrest causally implicated in late-life declines in both tissue and organismal performance (Baar et al., 2017; Baker et al., 2016). Second, processes that accelerate telomere attrition may also accelerate the accumulation of deficits in other somatic structures. For example, oxidative damage can accelerate telomere shortening (Reichert & Stier, 2017) and may inhibit telomere repair (Ahmed et al., 2008), which could thereby leave telomere attrition correlated with the accumulation of oxidative damage to other biomolecules. Evidence at the organismal level also lends strength to the view that telomere dynamics provide a useful biomarker of somatic integrity (reviewed in Young, 2018), including evidence that stressful environments can accelerate telomere attrition (Boonekamp et al., 2014; Monaghan, 2014) and that higher rates of telomere attrition can predict mortality (Barrett et al., 2013; Boonekamp et al., 2014; Salomons et al., 2009; Wood & Young, 2019).

The relationship between social rank and within-individual telomere attrition rates has only been investigated to date in meerkat, *Suricata suricatta*, and human, *Homo sapiens*, societies. Socially dominant meerkats, who breed at higher rates than subordinates, show higher telomere attrition rates than subordinates (Cram et al., 2018). By contrast, low socioeconomic status among humans is associated with higher telomere attrition rates and shorter telomeres (Fujishiro et al., 2018; Robertson et al., 2013), and frequently with poorer health and shorter lifespan (Vathesatogkit et al., 2014). Similarly, in a cross-sectional study of spotted hyenas, *Crocuta crocuta*, lower ranking individuals had shorter age-specific telomere lengths, though whether this reflects rank-related differences in the telomere dynamics of adults is not known (Lewin et al., 2015). There is also relevant cross-sectional evidence from two social insects (the black garden ant, *Lasius niger*, and the honeybee, *Apis mellifera*): while queens live much longer than workers in both species, the two castes have similar telomere lengths in early life (Jemielity et al., 2007; Korandová & Frydrychová, 2016), but whether their telomere lengths diverge later in life is unknown. While the effects of social dominance on telomere dynamics per se have rarely been investigated, there is growing evidence that high reproductive effort is associated with higher telomere attrition rates, at least over the short-term (Reichert et al., 2014; Sudyka et al., 2014; Young, 2018). Whether the higher reproductive rates of dominants relative to subordinates in many vertebrate societies result in more rapid telomere attrition over the longer-term may, therefore, depend upon the extent to which dominants employ strategies to mitigate against such attrition, or enjoy differential access to the resources needed to maintain investment in somatic maintenance despite frequent reproduction.

Here we use extensive longitudinal assessments of within-individual rates of change in telomere length to investigate the impacts of dominance status on telomere dynamics in a wild

cooperatively breeding bird, the white browed sparrow-weaver, *Plocepasser mahali*. These birds live in year-round territorial groups of 2 to 12 individuals, in which a single dominant male and female completely monopolise within-group reproduction and vigorously defend their positions against challengers (Lewis, 1982a; Harrison, York, Cram, Hares, et al., 2013; Harrison, York, Cram, & Young 2013; York et al., 2019). All birds start their lives as subordinates in their natal group, only a fraction of whom secure dominance one to six years later (Harrison et al., 2014). Dominants may retain their position for up to 10 years, until their death or expulsion (maximum lifespan exceeds 12 years in both sexes). Dominant females can lay up to six clutches per breeding season (modal clutch size is two), are the sole incubators, and provision nestlings at higher rates than all other bird classes (Harrison et al., 2013; Walker, 2016). Subordinates cooperatively contribute to feeding nestlings, sentinel behaviour and territory defence, but contribute significantly less to these activities than dominants of one or both sexes (Lewis, 1982a; Walker, 2016; Walker et al., 2016; York et al., 2019). Experimental evidence suggests that reproduction entails oxidative stress and body condition costs in this species (Cram et al., 2015b) and dominant females experience steeper within-individual declines in antioxidant levels over the breeding season than all other classes (Cram et al., 2015a). Telomere dynamics may indeed serve as a biomarker of age-related changes in somatic integrity in this species, as young sparrow-weavers with higher telomere attrition rates are less likely to survive to adulthood (Wood & Young, 2019).

We conducted our investigation in two phases. First, we investigated whether dominants and subordinates differed in age-specific telomere length (sampling spanned 0.5–7.4 years of age; 1.6–7.4 for dominants and 0.5–6.1 for subordinates) and their long-term within-individual telomere dynamics (longitudinal sampling spanned 0.4–3.6 years of each bird's life; 2–8 samples per bird), while allowing for the possibility of sex differences in these effects. If reproduction is a major driver of individual variation in telomere attrition rates, dominants would be predicted to show higher telomere attrition rates than subordinates, given their greater investment in reproductive activities. Whether this occurs, however, will depend upon the extent to which dominants employ strategies to mitigate such attrition and/or enjoy differential access to resources. Second, we used within-individual rates of change in telomere length assessed over shorter time windows (breeding seasons [~7 months] and nonbreeding seasons [~5 months]) to investigate the impacts of dominance and breeding activity on short-term telomere dynamics. Specifically, as breeding activity may entail costs to somatic integrity for all group members (e.g., subordinates help to feed offspring), we predicted higher rates of telomere attrition during the breeding season than the nonbreeding season, particularly in wetter years (as rainfall markedly increases reproductive activity [e.g. the likelihood that dominant females lay], and groups rear more fledglings in wetter breeding seasons; Appendix S3). As dominants invest more in reproduction than subordinates, we also predicted that dominants and subordinates may differ most markedly in their telomere attrition rates during the breeding season and in wetter years. We allowed for

the possibility that individuals with longer telomeres show greater telomere attrition (whether for mechanistic or strategic reasons; Verhulst et al., 2013), and for dominants and subordinates to differ in this relationship (conceivably reflecting dominance-related differences in telomere length regulation).

2 | METHODS

2.1 | Study population and field methods

Data were collected from a population of 40 groups of white-browed sparrow-weavers in the Kalahari desert at Tswalu Kalahari Reserve, South Africa (27°16'S, 22°25'E). All birds were fitted with a unique combination of three colour rings and a numbered metal ring under SAFRING licence 1444. Nest checks were conducted regularly throughout the main breeding season from 2007 onwards (October to April inclusive) and nestlings were fitted with a metal ring whilst in the nest. Thus, for the majority of "known-age" birds in this study (81 of 87), age at sampling was calculated as the number of days elapsed between the date the bird was first seen as a nestling and the sampling date. The six other "known age" birds were first caught as fledglings (which have a yellow gape), so their age was calculated as the days elapsed between their date of first capture (as a fledgling) and the sampling date, plus 30 days. Sex was determined by adult beak colour (Leitner et al., 2009) and this study focuses solely on adults (birds over six months of age). Group composition and dominance status were recorded during weekly monitoring of each group: the dominant pair routinely displace other group members and produce synchronised duet song, the dominant female is the sole incubator and the dominant male consistently produces dawn song (Harrison, York, Cram, Hares, et al., 2013; York et al., 2016). Birds were considered group members if they frequently foraged and performed territorial displays with that group, and roosted in the same trees.

To allow the assessment of telomere attrition rates over breeding and nonbreeding seasons, adult birds were blood sampled during nine "sampling periods" which aligned with either (i) the transition from the nonbreeding season to the ensuing breeding season (between September and November each year from 2011 to 2014 inclusive), or (ii) the transition from the breeding season to the following nonbreeding season (between March and May each year from 2011 to 2015 inclusive). All samples were stored in absolute ethanol at room temperature until extraction (see Appendix S1.1 for capture and blood sampling methods). The resulting data were used to assess both long-term age-specific telomere length and short-term telomere attrition.

2.2 | DNA extraction and measurement of telomere length by qPCR

DNA was extracted from whole blood using Gentra PureGene Genomic DNA Purification Kits (Qiagen). Quantity, quality, and integrity were

assessed and any samples that failed were re-extracted, or discarded if further extractions also failed (Appendix S1.1, Figure S1). To quantify the mean relative telomere length of whole-blood samples (referred to here as “RTL”, but as “telomere length” in the results and discussion) we used quantitative PCR (qPCR) as described in Cawthon (2002) with the modifications described below. Control gene (for which we used glyceraldehyde-3-phosphate dehydrogenase; GAPDH) and telomere reactions were carried out on separate 96-well plates on a Stratagene Mx3000 instrument. GAPDH primers were specific to *P. mahali* (GAPDH-F 5'-AAACCAGCCAAGTATGATGACAT-3'; GAPDH-R 5'-CCATCAGCAGCAGCCTTCA-3'; Wood, 2017), and telomere primers were Tel1b (5'-CGGTTTGGTTGGGTTGGGTTGGGTTGGGTTGGGTT-3') and Tel2b (5'-GGCTTGCCTTACCCTTACCCTTACCCTTACCCTTACCCTTACCCT-3'). Each 20 μ l reaction contained 5 ng DNA, and 10 μ l SybrGreen fluorescent dye with low ROX (Agilent Technologies), with primers at a concentration of 200 nM. Thermal cycles for telomere reactions were 15 min at 95°C, followed by 40 cycles of 95°C for 15 s, 57°C for 30 s, and 73°C for 30 s. Thermal cycles for GAPDH were the same, except the annealing temperature which was 60°C. Baseline fluorescence was corrected in LinRegPCR (Ruijter et al., 2009) and RTL was calculated following Pfaffl (2001).

Samples were run in triplicate, as was a between-plate calibration sample (pooled from three birds) and a no-template control, which were included on every plate. A standard curve was also created from the between-plate calibration sample and run on every plate. Mean standard curve efficiency for GAPDH plates was 97.91% ($SD = 4.05$; range = 90.7%–109.4%), with a mean R^2 of 1.00 ($SD = 0.003$, range = 0.988–1.000). The mean standard curve efficiency for Telomere was 98.65% ($SD = 6.11$, range = 85.80%–112.80%), with a mean R^2 of 1.00 ($SD = 0.003$, range = 0.990–1.000). Pairs of samples from which telomere attrition rates were calculated were always run together on a plate. To avoid having plates with small numbers of birds, samples from multiply-sampled birds were sometimes split across plates (26 birds across two plates, nine birds across three plates, two birds across four plates).

To estimate intra- and interplate repeatability of technical replicates the intra-class correlation coefficient (ICC) was calculated (Verhulst et al., 2015) using the “consistency” *icc* function in R (*irr* package; Gamer et al., 2019). To assess intraplate repeatability, a one-way model and “average” units were specified. The intraplate ICC for GAPDH triplicates (after removal of replicates that were removed due to poor amplification) was 0.985 ($N = 400$, 95% confidence interval [CI]: 0.983, 0.988). For Telomere reactions, the intraplate ICC was 0.976 ($N = 403$, 95% CI: 0.972, 0.980). The ICC for duplicates (where one reaction did not pass the quality assessment described above) for GAPDH was 0.993 ($N = 22$, 95% CI: 0.984, 0.997) and for Telomere, it was 0.979 ($N = 18$, 95% CI: 0.946, 0.982). For interplate repeatability a two-way model and “single” units were specified. The interplate ICC for RTL was 0.576 ($N = 23$ samples, each run across three plates, 95% CI = 0.339, 0.772). For detailed qPCR methods see Appendix S1.2.

Within-individual repeatability of telomere length was calculated using the R package rptR (Stoffel et al., 2017) and the 95% CI

was obtained from 1,000 bootstrap iterations. Within-individual repeatability is computed by dividing the between-individual variance in telomere length by the total variance after accounting for fixed effects. The model was fitted with a normal error distribution and included the effects present in the best performing model: sex as a fixed effect, and qPCR plate, social group, season, cohort (breeding season of birth), and Bird ID as random effects. Within-individual repeatability of telomere length was 0.279 (95% CI = 0.16, 0.404).

2.3 | Statistical analyses

Analyses were carried out using an Information-Theoretic (I-T) framework in R 3.0.2 (R Core Team, 2013). In each modelling exercise a global linear mixed effects model was constructed including all predictor terms of interest (Imer in lme4; Bates et al., 2015). As all our predictor variables have the potential for independent additive effects, the fits of all combinations of the predictor variables included in the global model were compared and ranked based on AICc using the package MUMIN (Barton, 2018). Two-way interactions and quadratic terms were only included in the global models if such relationships were considered plausible a priori, and were accompanied in all relevant models by the corresponding first order terms. We retained all models within $\Delta 6$ AICc of the top model (referred to collectively as the “top model set”), as this allows confidence that the most parsimonious model is included in the top model set, but removes models with only very weak support (Harrison et al., 2018; Richards, 2005). To avoid the retention of overly complex models, we removed models from this top model set that were more complex versions of better performing models (Harrison et al., 2018; Richards et al., 2011); top model sets prior to implementation of this “nesting rule” are presented in Appendix S4. Akaike weights were used to assess the relative support for each model. We plotted our findings using effect size estimates from the top model. All continuous predictors were centred and scaled, but were back-transformed for plotting where necessary. Prior to model comparison, in order to ascertain independence of predictors, correlations between all predictor variables were checked and variance inflation factors (VIF) of each global model were checked to assess multicollinearity: all VIFs were below 3 (Fox & Weisberg, 2011). Model residuals of global models were assessed to confirm compliance with model assumptions. Cook's distances were examined to check for points of high influence (influence.ME; Nieuwenhuis et al., 2012).

2.4 | Does dominance status predict telomere length and long-term telomere dynamics?

Our data set consisted of 299 RTL measures from 87 longitudinally sampled adult birds of known age (2–8 RTL measures per bird; median = 3) from 39 social groups. Fifty-four birds were sampled only while subordinate, 26 were sampled only while dominant, and seven were sampled both while subordinate and while dominant. While

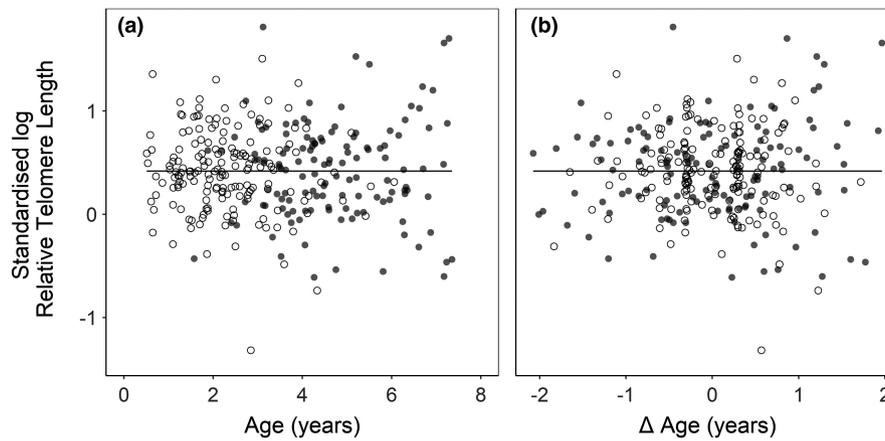


FIGURE 1 (a) Analysis of variation in standardised relative telomere length (z-transformed log RTL) at the population level revealed no evidence that older individuals have shorter mean telomere lengths (see Appendix S2.1 for analysis). (b) Partitioning variation in age in to its within- and among-individual components revealed no evidence of a change in telomere length with within-individual changes in age (Δ Age; Table 1). The points are adjusted to control for random effects and the fixed effect of sex; open points for subordinates, solid points for dominants (partially transparent). Solid line shows the model estimate from the best-supported model for females

TABLE 1 Predictors of standardised relative telomere length (z-transformed log RTL) in adult birds, using age partitioning to isolate the effects of within-individual changes in age (Δ age) from those of among-individual variation in the mean age at sampling (mean age); none of these age terms appeared within the top model set

Intercept	Sex (M)	df	logLik	AICc	Δ AICc	AW
0.420	-0.323	8	-325.137	666.8	0.00	0.904
0.167		7	-328.436	671.3	4.49	0.096

Notes: The table presents the $\Delta 6$ AICc top model set (one line per model) after implementation of the model nesting rule (Richards et al., 2011) (for full output see Table S6). All continuous variables were scaled and centred. Effect size estimates are given for each term; for sex, the estimate is given for males relative to females. Predictors absent from the top model set: Dominance status, Δ age, Δ age: Dominance status, mean age, mean age: Dominance status, Sex: Dominance status, Δ age: mean age, Δ age: Sex, Δ age²

dominant birds naturally tend to be older than subordinates, there was extensive overlap in the ages at sampling of the subordinates (0.5–6.1 years of age) and dominants (1.6–7.4 years of age) in the data set (see Figure 1a), and the VIFs for all predictors in these models were acceptable (highest VIF = 2.69; Fox & Weisberg, 2011). The distribution of RTL was heavily right skewed so log RTL was used as the response. Log RTL was Z-transformed to facilitate comparison to future studies (Verhulst, 2019).

When modelling age-related variation in telomere length, we used age-partitioning (van de Pol & Verhulst, 2006) to isolate the effects of within-individual changes in age from the potentially confounding effects of among-individual variation in age (which could arise, for example, from selective disappearance effects; van Beirne et al., 2016; de Pol & Verhulst, 2006). Age at sampling was partitioned into the mean age of all samples included from that bird (henceforth “mean age”), and the age at which the focal sample was collected minus the bird’s mean age (henceforth “delta age”, which thereby captures within-individual variation in age). In addition to testing for an effect of dominance status on telomere length, we tested whether dominance status affects the rate of change in telomere length with within-individual increases in age, by fitting an interaction between dominance status and delta age. To permit this, for the seven birds with RTL measures taken both while subordinate and while dominant, both mean and delta age were calculated

separately for the samples obtained while subordinate and while dominant. We constructed a global model that included dominance, sex, mean age and delta age and all two-way interactions between these terms as fixed effect predictors. In addition, we included the quadratic effects of delta age and mean age, to allow for the possibility of curvilinear age relationships. The following random effects were also fitted: bird ID, social group ID (to account for variation in RTL due to among-group differences e.g., in territory quality or genetics), qPCR plate, sampling period, and cohort. The “sampling period” term captured which of the nine sampling periods (see above) the focal sample was collected in. A model of age-related variation in telomere length at the population level (i.e., without age partitioning) is presented in Appendix S2.1 (Table S1).

2.5 | Do dominance and rainfall-related reproductive activity predict short-term telomere dynamics?

To investigate the effects of dominance status and reproductive activity (as captured by effects of the breeding season and rainfall; see Introduction and Appendix S3) on the telomere dynamics of adults, we used samples collected at the start and end of four successive breeding seasons (see above) to calculate within-individual changes

in RTL over individual breeding seasons (~7 months in duration) and the intervening nonbreeding seasons (~5 months in duration). Within-individual change in RTL over each season was corrected for regression to the mean using Verhulst's *D* (Verhulst et al., 2013). As the length of time elapsed between successive samples varied (mean \pm SD = 6.6 \pm 1.0 months; range 4.1–8.3 months), we used rate of change in RTL per month as our response variable (calculated as the corrected within-individual change in RTL divided by the time elapsed between samples).

We constructed a global model with dominance status, sex, season (breeding or nonbreeding), adult group size and annual rainfall as fixed effect predictors. As the effect of dominance status could vary with sex, season, rainfall, or group size we also included these two-way interactions. Adult group size was calculated as the average number of adult group members present during the focal breeding or nonbreeding season. Annual rainfall was calculated as the total rainfall over the year preceding the date on which the second RTL sample used in the focal rate calculation was collected (i.e., the sample at the end of the focal interval). As rainfall tends to be much higher in the breeding season, we used annual rainfall to avoid confounding rainfall and season. We allowed for season-dependent effects of annual rainfall (i.e., a season by annual rainfall interaction), as breeding seasons may entail greater costs to somatic maintenance in wetter years (as groups rear more fledglings in wetter breeding seasons; Appendix S3), while nonbreeding seasons may not. In a number of studies the rate of change in RTL over a given period has been found to be higher in individuals with initially longer telomeres (Verhulst et al., 2013). We therefore included RTL at the start of the focal interval, along with its interaction with dominance status (as dominant and subordinate birds could differ in their regulation of telomere length). Finally, to control for potential effects of variation in body condition, we included body mass at the start of focal interval, along with its interaction with within-individual change in mass over the focal period. We controlled for bird ID, social group ID, qPCR plate and sampling year (each "sampling year" being a given breeding season and its ensuing nonbreeding season) as random effects.

We initially conducted our analysis including age as a predictor, using a data set containing only samples from known age birds ($n = 166$ rate estimates). However, as age was not present in the $\Delta 6$ AICc top model set (Appendix S2.2, Table S2) we expanded the data set to include adult birds of unknown age, and removed the age predictor from the model. This approach increased our sample to $n = 187$ rate estimates (87 from dominants, 100 from subordinates) from a total of 101 birds (45 assessed while dominant and 63 assessed while subordinate; seven were assessed in both contexts). The model comparison outcomes using this larger data set are presented in the main paper, and are qualitatively and quantitatively similar to those using the restricted "known-age" data set (Table S2). The removal of six potential outliers did not qualitatively impact the outcomes of the analyses (Table S3).

3 | RESULTS

3.1 | Does dominance status predict telomere length and long-term telomere dynamics in adulthood?

Analysis of the population-level pattern of age-related variation in adult telomere length revealed no evidence of an overall decline in telomere length with increasing age (Table S1, Figure 1a; see Appendix S2.1 for analysis). Following age-partitioning there was also no evidence of an effect of within-individual changes in age (Δ age) on telomere length, despite longitudinal sampling of individuals spanning periods of up to 3.6 years of adult life (Figure 1b; Table 1; nor was there evidence of an effect of mean age). There was no evidence of an effect of dominance status on either age-specific telomere length (Figure 1; Table 1) or the long-term within-individual rate of age-related change in telomere length (i.e., a dominance status: Δ age interaction; Table 1). While there was evidence that males have shorter telomeres than females, there was no evidence of a sex difference in the long-term within-individual rate of age-related change in telomere length (i.e., a sex: Δ age interaction; Table 1).

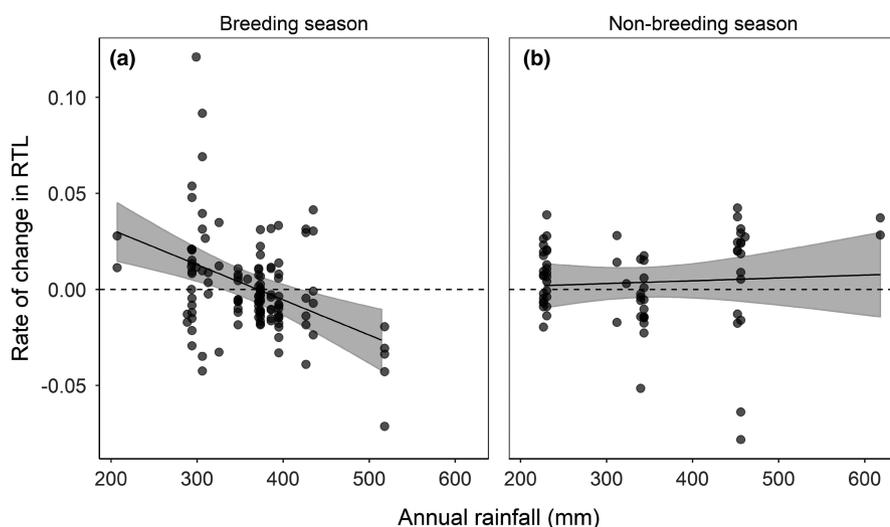


FIGURE 2 Model predicted estimates of the effect of annual rainfall on the rate of change in relative telomere length (RTL) during the (a) breeding season and (b) nonbreeding season. Annual rainfall is the total rainfall in the year preceding the second of the two sampling events used in each 'rate of change in RTL' calculation (see Section 2). Solid lines show the estimates from the top model, plotted for dominant birds and the mean value of initial RTL. Shaded areas show 95% confidence intervals. Points are raw data and are partially transparent

TABLE 2 Predictors of within-individual change in telomere length over individual breeding and nonbreeding seasons

Int	Dominance status (Sub)	Season (N-B)	Start RTL	Annual rain	Season (N-B): annual rain	Status (Sub): annual rain	Status (Sub): start RTL	df	logLik	AICc	Δ AICc	AW
0.006	-0.006	0.000	-0.008	-0.011	0.015	-0.006	0.011	13	451.06	-874.01	0.00	0.606
0.006	-0.006	0.002	-0.008	-0.015	0.017		0.010	12	449.33	-872.86	1.14	0.342
0.003								6	431.80	-851.1	22.87	NA

Notes: The table presents the Δ 6 AICc top model set (one line per model) after implementation of the model nesting rule (Richards et al., 2011), along with the null model (not present in the top model set) (for full output see Table S7). All continuous variables were scaled and centred. Effect size estimates are given for each term. For dominance 'Status' and Season, estimates are given for subordinate birds (Sub) relative to dominants and for the nonbreeding season (N-B) relative to the breeding season. Int, intercept; AW, adjusted Akaike weight. Predictors absent from the top model set: Sex, Group size, Mass, Δ Mass, Status:Sex, Status:Group size

3.2 | Do dominance status and rainfall-related reproductive activity predict the short-term telomere dynamics of adults?

Rainfall is a major driver of reproductive activity in this arid-zone bird: the probability of a dominant female laying a clutch increases with recent rainfall (Table S4, Figure S3), and groups rear more fledglings during higher rainfall breeding seasons (Table S5, Figure S4). Our analyses of short-term telomere dynamics suggest that such rainfall-related reproductive activity during the breeding season may entail short-term costs to somatic integrity: analysis of within-individual rates of change in telomere length over individual breeding and nonbreeding seasons revealed strong support for an interaction between annual rainfall and whether the focal season was a breeding or nonbreeding season (Figure 2; Table 2; present in all models in the Δ AICc < 6 top model set). During the breeding season there was evidence of a negative effect of annual rainfall on the within-individual rate of change in telomere length (Table 2, Figure 2a), while the same was not true for the nonbreeding season (Figure 2b). There was also some evidence of an interaction between annual rainfall and dominance status, in which the effect of annual rainfall on the within-individual rate of change in telomere length was slightly more negative among subordinates (Figure 3b) than dominants (Figure 3a). However, this interaction was only present in the top model (Table 2) and not the second-best-supported model, just 1.20 AICc points below.

We found evidence that an interaction between dominance status and telomere length at the start of the focal season predicts the ensuing telomere dynamics during the season (Figure 4; Table 2; present in all models in the Δ AICc < 6 top model set). This interaction reflected a pattern in which dominant birds with shorter telomeres at the start of the season lost telomere length at a slower rate over the course of the season (Figure 4a), while no such relationship was apparent among subordinates (Figure 4b). Indeed, the data suggest that dominant birds with the shortest telomeres were more likely to experience within-individual *increases* in mean telomere length.

We found no evidence that body mass at the start of the focal season, change in body mass over the focal season, social group size, or sex, predicted within-individual rate of change in telomere length. The removal of six potential outliers (see methods) yielded qualitatively and quantitatively similar results to the analyses presented here, with one exception: it led to the inclusion of one additional term in the top model: a positive effect of the change in body mass over the focal season (Table S3, Figure S2), suggesting that birds that experienced greater reductions in body mass over the course of a focal season may also have lost telomere length at higher rates.

4 | DISCUSSION

As dominant white-browed sparrow-weavers monopolise reproduction (Harrison, York, Cram, Hares, et al., 2013), the classical expectation of a trade-off between investment in reproductive activities

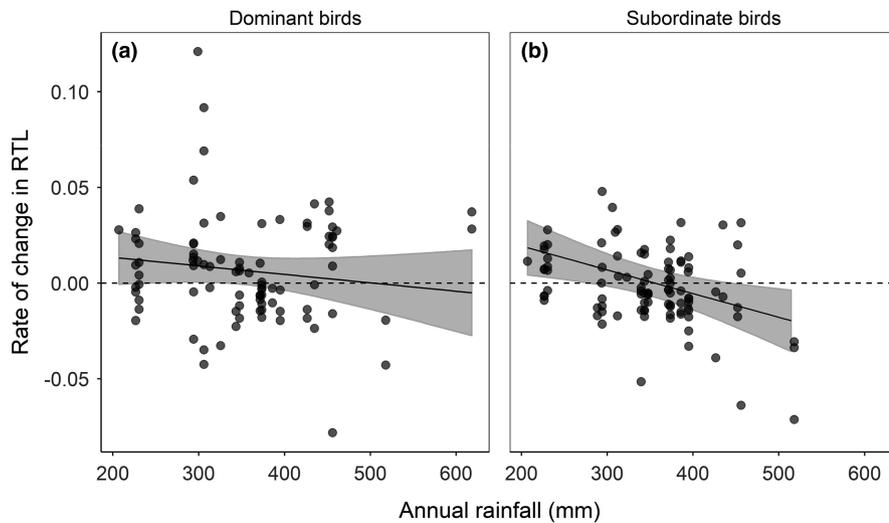


FIGURE 3 Model predicted estimates of the effect of annual rainfall on the rate of change in relative telomere length (RTL) for (a) dominant and (b) subordinate birds. Solid lines show the estimates from the top model, plotted for the breeding season and the mean value of initial RTL. Shaded areas show 95% confidence intervals. Points are raw data and are partially transparent

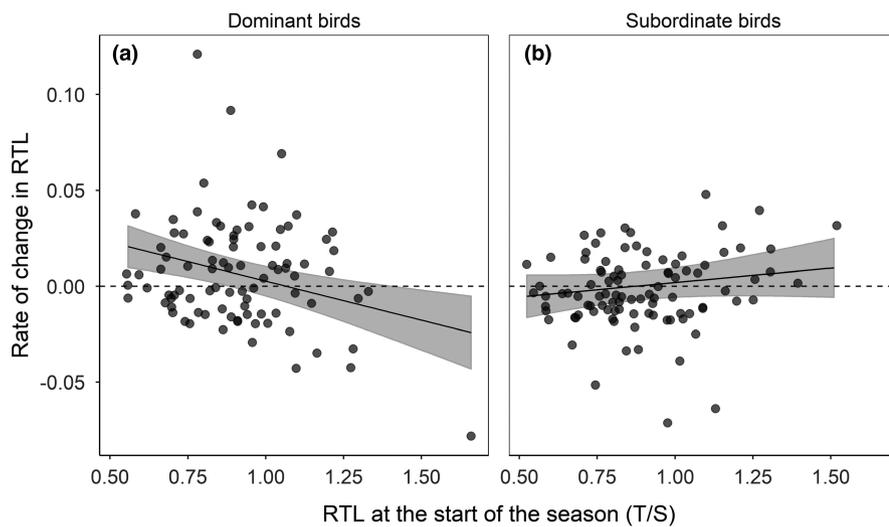


FIGURE 4 Model predicted estimates of the effect of relative telomere length (RTL) at the start of the season on the rate of change in RTL during that season for (a) dominant, and (b) subordinate birds. Solid line shows the estimates from the top model, plotted for the nonbreeding season and for the mean value of annual rainfall. Shaded areas show 95% confidence intervals. Points are raw data and are partially transparent

and the maintenance of somatic integrity would lead to a prediction that, all other things being equal, dominants should show higher telomere attrition rates (a widely recognised biomarker of declines in somatic integrity; Young, 2018) than subordinates. Indeed, just such a pattern has recently been reported in cooperatively breeding meerkats (Cram et al., 2018). Contrary to expectation, we found no evidence of dominance-related differences in either age-specific telomere length or within-individual telomere attrition rates over the longer-term. However, analyses over shorter time intervals (individual breeding and nonbreeding seasons) yielded strong evidence that dominants with shorter telomeres experienced more-positive within-individual changes in telomere length than dominants with longer telomeres, while the same was not true among subordinates. This finding highlights the possibility that dominants invest more heavily than subordinates in telomere length regulation (and/or somatic maintenance more broadly), a strategy that might mitigate the long-term costs of reproductive effort for dominants and explain why their long-term telomere dynamics are comparable to those of subordinates (see discussion below). Consistent with the expectation that reproduction-related activities entail short-term

costs to somatic integrity, telomere attrition rates during the breeding season were found to be most severe for all birds during years of high rainfall (the key driver of reproductive activity in this species; Appendix S3). While net telomere attrition appears more likely during the breeding seasons of wetter years, within-individual increases in telomere length appear more likely during the breeding seasons of drier years (Figure 2a). While there are reasons to interpret evidence of increases in mean telomere length with caution (see below), such context-dependent fluctuations in the direction of short-term changes in telomere length could explain our unusual finding that adults in this species show no evidence of net within-individual telomere shortening over the long term (Figure 1b). Together, our findings suggest that, even in vertebrate societies in which dominants monopolise reproduction, dominants may experience long-term somatic integrity trajectories indistinguishable from those of their nonreproductive subordinates.

It is striking that dominants show age-specific telomere lengths and long-term within-individual telomere dynamics indistinguishable from those of subordinates, despite monopolising reproduction. It seems unlikely that our findings reflect (i) the lack of a

short-term cost of reproduction in this species (as rearing offspring appears to entail both an oxidative stress and body mass cost; Cram et al., 2015a, 2015b), (ii) an insensitivity of telomeres to investment in reproduction-related activities (as telomere attrition appears to be accelerated during wetter breeding seasons [Figure 2a], when groups rear more fledglings [Figure S4]; see below), or (iii) telomere attrition being unrelated to somatic integrity (see Boonekamp et al., [2013] and Young, [2018] for reviews; and telomere attrition in young sparrow-weavers predicts survival to adulthood more strongly than body mass; Wood & Young, 2019). It also seems unlikely that subordinate sparrow-weavers suffer from chronic endocrine stress that might otherwise accelerate telomere attrition (Hausmann & Heidinger, 2015; Monaghan, 2014), as the average circulating glucocorticoid stress hormone levels of subordinates are comparable to those of dominants (Wingfield et al., 1991). One possible explanation is that, while dominants monopolise reproduction and contribute more to territorial defence, sentinelling and offspring care than subordinates (see Introduction), subordinates may invest more than dominants in some other costly activity, leaving the oxidative threats to somatic integrity and the resources available for somatic maintenance more comparable between the two classes than one might otherwise expect. For example, subordinate sparrow-weavers do conduct extra-territorial prospecting forays to facilitate dominance acquisition (Lewis, 1982b) and such forays can entail costs (Kingma et al., 2016; Young & Monfort, 2009). However, it seems unlikely that prospecting behaviour alone can account for our findings, as radio-tracking data reveal that such forays are brief and occur at low frequencies (Capilla-Lasheras, 2019), and because dominant birds evidently conduct extra-territorial forays of their own (as the species shows ~15% extra-group paternity; Harrison, York, Cram, Hares, et al., 2013; Harrison et al., 2013).

Instead, the comparable long-term telomere dynamics of dominants and subordinates may arise because rank-related differences in other aspects of phenotype leave dominants capable of investing more heavily than subordinates in telomere length regulation (and/or somatic maintenance more broadly), despite monopolising reproduction. For example, the superior competitive abilities of dominants may afford them differential access to the resources needed for investment in both traits (Barton & Whiten, 1993; Murray et al., 2006). Indeed, evidence that the short-term telomere attrition rates of dominants depend upon their current telomere length, while those among subordinates do not (Table 2), suggests that dominants may regulate their telomere lengths (and/or somatic maintenance more broadly) in a manner that subordinates do not. Dominant birds with shorter telomeres appear likely to experience increases in mean telomere length, while those with longer telomeres appear more likely to experience telomere attrition or no change in mean telomere length (Figure 4). As shorter telomeres may threaten health, performance and survival (Wilbourn et al., 2018; Young, 2018), investing in the strategic repair of telomeres when short (via mechanisms that may also repair other biomolecules; see below) could certainly yield fitness benefits. Indeed, all else being equal, selection may also favour dominants investing disproportionately

in somatic maintenance, relative to subordinates, given the higher expected future reproductive success of dominants (as few subordinates ever become dominant) and their likely lower mortality risk (as established dominants need not run the mortal risks of dispersal and fighting to win dominance; Cram et al., 2018; Griesser et al., 2006). Indeed, such an argument is frequently made to explain the extraordinary longevity of some eusocial insect queens relative to their workers (Carey, 2001; Keller & Genoud, 1997).

While there are reasons to interpret evidence suggestive of within-individual increases in telomere length with caution (discussed below), such telomere length “regulation” among dominants is mechanistically plausible; it could be achieved, for example, via the upregulation of telomerase expression in the hematopoietic stem cells. Telomerase activity has been detected in bone marrow cells (where the haematopoietic stem cells reside) throughout the lives of some long-lived birds (Hausmann et al., 2004, 2007). And, notably, honeybee queens show higher levels of telomerase activity than their workers at both larval and adult stages, illustrating the potential for rank-related differences in telomerase expression (Korandová & Frydrychová, 2016). Moreover, as telomerase expression can lead to the preferential elongation of short telomeres (Britt-Compton et al., 2009), telomerase upregulation among dominants could also account for the differential increases in telomere length observed here among dominants with shorter telomeres. While telomerase activity in adulthood could conceivably undermine the utility of telomere dynamics as a biomarker of somatic integrity, this need not be the case, as (i) telomerase upregulation could be coupled with upregulation of the wider somatic maintenance machinery (Ahmed et al., 2008; see also Young, 2018), and (ii) telomerase itself appears to have restorative effects independent of its effects on telomeres (Cong & Shay, 2008).

Consistent with the expectation that investment in reproductive activities should entail short-term costs to somatic integrity (Kirkwood, 1977), our analyses revealed that telomere attrition rates were most severe in all birds during years with higher rainfall, and only during the breeding season (Figure 2). This finding suggests that investment in reproduction-related activities by both dominants and subordinates (who help to rear offspring) may indeed have detrimental effects on telomere dynamics, at least over the short-term. Experimental work on this species suggests that cooperative offspring care entails oxidative stress and body mass costs (Cram et al., 2015b), providing a plausible candidate mechanism for the observed association between rainfall and breeding season telomere attrition. Together these findings complement a growing body of evidence that reproductive activity can be associated with higher rates of telomere attrition (e.g., Reichert et al., 2014; Sudyka et al., 2014), consistent with the general expectation that reproductive investment should trade off against lifespan via impacts on somatic integrity (Kirkwood, 1977). Notably though, our findings do not specifically implicate investment in offspring provisioning as a driver of telomere attrition; rainfall-related increases in a range of other reproduction-related activities (e.g., dawn song production, extra-territorial

prospecting, and territorial defence against intruders) could also contribute to the patterns observed. Our analyses also revealed limited evidence of an interaction between dominance status and annual rainfall, in which the relationship between rainfall and telomere attrition (i.e., greater attrition in wetter years) is marginally steeper among subordinates than dominants (Figure 3); a pattern that might again be attributable to dominants investing differentially in telomere regulation or somatic maintenance more broadly (see above). Our findings do not indicate simply that a norm of progressive telomere attrition is accelerated during higher rainfall breeding seasons, but rather suggest that any rain-related acceleration of telomere attrition may occur against a backdrop of increases in telomere length during dry periods (Figure 3; see below), leading to within-individual fluctuations in telomere length over time that do not ultimately manifest as steady age-related declines.

Despite extensive longitudinal sampling we found no evidence of long-term within-individual age-related declines in telomere length. At least two mammalian studies have yielded similar findings (Fairlie et al., 2016; Hoelzl, Smith, et al., 2016). It is of course possible that sparrow-weavers do experience a modest within-individual age-related decline in mean blood cell telomere length that our analyses failed to detect (e.g., due to telomere length measurement error). Modest telomere attrition rates might well be expected in this species, as longer-lived species appear to show slower rates of telomere attrition (Dantzer & Fletcher, 2015; see also Haussmann et al., 2004; Haussmann et al., 2007) and our observations reveal that this species can live for >12 years in the wild. Our analyses do, however, highlight the possibility of compensatory mechanisms that might avert excessive net telomere attrition during adulthood. For example, while net attrition appears more likely during the breeding seasons of wetter years, within-individual increases in mean telomere length appear more likely during the breeding seasons of drier years (Figure 3). These patterns parallel those reported for wild edible dormice (*Glis glis*), in which net telomere attrition was observed during hibernation periods, coupled with apparent telomere elongation during the intervening active season (Hoelzl et al., 2016). Such context-dependence of the direction of change in mean telomere length could readily explain the apparent lack of net telomere attrition over the long-term in our species.

While telomeres in the somatic tissues of vertebrates are generally thought to decrease in mean length with advancing age, there are now many reported cases of apparent within-individual increases in mean telomere length in various life stages (Fairlie et al., 2016; Hatakeyama et al., 2016; Hoelzl, Smith, et al., 2016; Spurgin et al., 2018; Ujvari & Madsen, 2009). While such increases could arise via telomere lengthening mechanisms (including telomerase expression), they should be interpreted with caution given their potential to arise from other mechanisms, including measurement error and associated regression to the mean effects (Bateson & Nettle, 2017; Steenstrup et al., 2013; Verhulst et al., 2013). Our data suggest that, among dominant birds, those with shorter telomeres

were more likely to experience within-individual increases in mean telomere length, even after the implementation of a correction for regression to the mean effects (Verhulst et al., 2013). If measurement error alone was the cause of this pattern, we would expect the same pattern to be apparent among subordinates, but our analyses strongly suggest that this was not the case. Similarly, within-individual increases in telomere length appear to be commonplace in drier breeding seasons but rare in wetter ones (Figure 2); a second pattern that measurement error cannot readily explain. Where increases in mean telomere length are a biological reality, it is nevertheless conceivable that they reflect the selective drop-out of cell lineages with short-telomeres from the cell population under study (e.g., during stem-cell turnover; Ogawa, 1993; Suda et al., 2011), rather than true increases in telomere length within a given cell lineage. Whether stem-cell turnover alone is likely to yield net increases in the mean telomere lengths of daughter cell populations is unclear, however, in part because quiescent stem cells themselves have also been shown to accrue damage over time (Beerman et al., 2014; Wang et al., 2014). Further investigation into the proximate causes of apparent increases in mean telomere length in this and other species (Fairlie et al., 2016; Hatakeyama et al., 2016; Hoelzl, Cornils, et al., 2016; Hoelzl, Smith, et al., 2016; Ujvari & Madsen, 2009), with particular attention to the patterns of telomerase expression in vivo, could therefore be usefully prioritised.

Together, our findings suggest that, even in a vertebrate society in which dominants monopolise reproduction, dominant breeders may have long-term somatic integrity trajectories indistinguishable from those of their nonreproductive subordinates. Our findings echo those of the cross-sectional work to date on eusocial insects (Jemielity et al., 2007; Korandová & Frydrychová, 2016), and contrast with those of the one other longitudinal study of dominance-related differences in telomere dynamics in a wild cooperative vertebrate: dominant meerkats of both sexes breed at higher rates than subordinates and show higher telomere attrition rates (Cram et al., 2018). The contrast with the current findings could reflect additional costs that dominants may suffer in societies, such as those of meerkats, in which subordinates frequently attempt to breed, requiring dominants to invest in active and potentially costly interference in subordinate reproduction (Bell et al., 2012; Young, 2009). For example, dominant female meerkats subject subordinates to prolonged aggression and evictions (Young et al., 2006), a tactic that may entail significant costs to dominants (Bell et al., 2012, 2014). By contrast, we have no evidence that subordinate sparrow-weavers produce offspring within their groups, suggesting that selection has favoured reproductive restraint among subordinates, reducing the need for dominants to invest in their harassment (Cant & Young, 2013; Harrison, York, Cram, Hares, et al., 2013; Young, 2009). Understanding interspecific variation in the dominance-related patterns of somatic deterioration may therefore require attention to rank-related differences in investment in reproductive competition (already a recognised modulator of sex differences in senescence; Beirne et al., 2015) as well as reproduction per se.

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AUTHOR CONTRIBUTIONS

A.J.Y. and E.M.W. designed the study. A.J.Y., E.M.W., P.C.-L., D.L.C., L.A.W. and J.E.Y. led fieldwork and contributed to sample collection. C.R.T., P.B.H. and A.L. provided training and methods development. E.M.W. performed laboratory analysis. E.M.W. performed data analyses with the exception of rainfall analyses which were conducted by P.C.-L. E.M.W. and A.J.Y. wrote the manuscript. All authors edited the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT

Data analysed for this study are available at https://github.com/EmmaMWood/p.mahali_adults (Wood and Young, 2020).

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REFERENCES

- Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T., & Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, *43*(1), 67–82.
- Ahmed, S., Passos, J. F., Birket, M. J., Beckmann, T., Brings, S., Peters, H., Birch-Machin, M. A., von Zglinicki, T., & Saretzki, G. (2008). Telomerase does not counteract telomere shortening but protects mitochondrial function under oxidative stress. *Journal of Cell Science*, *121*, 1046–1053.
- Baar, M. P., Brandt, R. M. C., Putavet, D. A., Klein, J. D. D., Derks, K. W. J., Bourgeois, B. R. M., Stryeck, S., Rijksen, Y., van Willigenburg, H., Feijtel, D. A., van der Pluijm, I., Essers, J., van Cappellen, W. A., van IJcken, W. F., Houtsmuller, A. B., Pothof, J., de Bruin, R. W. F., Madl, T., Hoijmakers, J. H. J., ... de Keizer, P. L. J. (2017). Targeted apoptosis of senescent cells restores tissue homeostasis in response to chemotoxicity and aging. *Cell*, *169*, 132–147.e16.
- Baker, D. J., Childs, B. G., Durik, M., & Al, E. (2016). Naturally occurring p16Ink4a-positive cells shorten healthy lifespan. *Nature*, *530*(7589), 184–189.
- Barrett, E. L. B., Burke, T. A., Hammers, M., Komdeur, J., & Richardson, D. S. (2013). Telomere length and dynamics predict mortality in a wild longitudinal study. *Molecular Ecology*, *22*(1), 249–259.
- Barton, K. (2018). *MuMIn: Multi-model inference*. R Package version 1.40.4. Retrieved from <https://cran.r-project.org/web/packages/MuMIn/index.html>
- Barton, R. A., & Whiten, A. (1993). Feeding competition among female olive baboons, *Papio anubis*. *Animal Behavior*, *46*(4), 777–789.
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.
- Bateson, M., & Nettle, D. (2017). The telomere lengthening conundrum - it could be biology. *Aging Cell*, *16*(2), 312–319.
- Beerman, I., Seita, J., Inlay, M. A., Weissman, I. L., & Rossi, D. J. (2014). Quiescent hematopoietic stem cells accumulate DNA damage during aging that is repaired upon entry into cell cycle. *Cell Stem Cell*, *15*(1), 37–50.
- Beirne, C., Delahay, R., & Young, A. (2015). Sex differences in senescence: the role of intra-sexual competition in early adulthood. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1811), 20151086.
- Beirne, C., Waring, L., McDonald, R. A., Delahay, R., & Young, A. (2016). Age-related declines in immune response in a wild mammal are unrelated to immune cell telomere length. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1825), 20152949.
- Bell, M. B. V., Cant, M. A., Borgeaud, C., Thavarajah, N., Samson, J., & Clutton-Brock, T. H. (2014). Suppressing subordinate reproduction provides benefits to dominants in cooperative societies of meerkats. *Nature Communications*, *5*, 4499.
- Bell, M. B. V., Nichols, H. J., Gilchrist, J. S., Cant, M. A., & Hodge, S. J. (2012). The cost of dominance: suppressing subordinate reproduction affects the reproductive success of dominant female banded mongooses. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 619–624.
- Blackburn, E. H. (2000). Telomere states and cell fates. *Nature*, *408*, 53–56.
- Blackburn, E. H., Epel, E. S., & Lin, J. (2015). Human telomere biology: A contributory and interactive factor in aging, disease risks, and protection. *Science*, *350*(6265), 1193–1198.
- Blount, J. D., Vitikainen, E. I. K., Stott, I., & Cant, M. A. (2016). Oxidative shielding and the cost of reproduction. *Biological Reviews*, *91*(2), 483–497.
- 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*(1785), 20133287.
- Boonekamp, J. J., Simons, M. J. P., Hemerik, L., & Verhulst, S. (2013). Telomere length behaves as biomarker of somatic redundancy rather than biological age. *Aging Cell*, *12*(2), 330–332.
- Britt-Compton, B., Wyllie, F., Rowson, J., Capper, R., Jones, R. E., & Baird, D. M. (2009). Telomere dynamics during replicative senescence are not directly modulated by conditions of oxidative stress in IMR90 fibroblast cells. *Biogerontology*, *10*(6), 683–693.
- Cant, M. A., & Young, A. J. (2013). Resolving social conflict among females without overt aggression. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1631), 20130076.
- Capilla-Lasheras, P. (2019). *The evolution of cooperation in an arid-zone bird: bet-hedging, plasticity and constraints (thesis)*. University of Exeter. Retrieved from <https://gtr.ukri.org/projects?ref=studentship-1622193>
- Carey, J. R. (2001). Demographic mechanisms for the evolution of long life in social insects. *Experimental Gerontology*, *36*(4–6), 713–722.

- Cawthon, R. M. (2002). Telomere measurement by quantitative PCR. *Nucleic Acids Research*, 30(10), e47.
- Cesare, A. J., & Reddel, R. R. (2010). Alternative lengthening of telomeres: Models, mechanisms and implications. *Nature Reviews Genetics*, 11(5), 319–330.
- Cong, Y., & Shay, J. W. (2008). Actions of human telomerase beyond telomeres. *Cell Research*, 18(7), 725–732.
- Cram, D. L., Blount, J. D., & Young, A. J. (2015a). Oxidative status and social dominance in a wild cooperative breeder. *Functional Ecology*, 29(2), 229–238.
- Cram, D. L., Blount, J. D., & Young, A. J. (2015b). The oxidative costs of reproduction are group-size dependent in a wild cooperative breeder. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819), 20152031.
- Cram, D. L., Monaghan, P., Gillespie, R., Dantzer, B., Duncan, C., Spence-Jones, H., & Clutton-Brock, T. (2018). Rank-related contrasts in longevity arise from extra-group excursions not delayed senescence in a cooperative mammal. *Current Biology*, 28(18), 2934–2939.
- Creel, S. (2001). Social dominance and stress hormones. *Trends in Ecology and Evolution*, 16, 491–497.
- Dammann, P., & Burda, H. (2006). Sexual activity and reproduction delay ageing in a mammal. *Current Biology*, 16(4), R117–118.
- Dantzer, B., & Fletcher, Q. E. (2015). Telomeres shorten more slowly in slow-aging wild animals than in fast-aging ones. *Experimental Gerontology*, 71, 38–47.
- Fairlie, J., Holland, R., Pilkington, J. G., Pemberton, J. M., Harrington, L., & Nussey, D. H. (2016). Lifelong leukocyte telomere dynamics and survival in a free-living mammal. *Ageing Cell*, 15(1), 140–148.
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*, 2nd ed. Sage. Retrieved from <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- Fujishiro, K., Needham, B. L., Landsbergis, P. A., Seeman, T., Jenny, N. S., & Roux, A. V. D. (2018). Selected occupational characteristics and change in leukocyte telomere length over 10 years: The Multi-Ethnic Study of Atherosclerosis (MESA). *PLoS One*, 13(9), e0204704
- Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2019). *irr: Variance Coefficients of Interrater Reliability and Agreement*. R package version 0.84.1. Retrieved from <https://CRAN.R-project.org/package=irr>
- Griesser, M., Nystrand, M., & Ekman, J. (2006). Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1881–1886.
- Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E., Robinson, B. S., Hodgson, D. J., & Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, 6, e4794
- Harrison, X. A., York, J. E., Cram, D. L., Hares, M. C., & Young, A. J. (2013). Complete reproductive skew within white-browed sparrow-weaver groups despite outbreeding opportunities for subordinates of both sexes. *Behavioral Ecology and Sociobiology*, 67(12), 1915–1929.
- Harrison, X. A., York, J. E., Cram, D. L., & Young, A. J. (2013). Extra-group mating increases inbreeding risk in a cooperatively breeding bird. *Molecular Ecology*, 22(22), 5700–5715.
- Harrison, X. A., York, J. E., & Young, A. J. (2014). Population genetic structure and direct observations reveal sex-reversed patterns of dispersal in a cooperative bird. *Molecular Ecology*, 23(23), 5740–5755.
- Harshman, L. G., & Zera, A. J. (2007). The cost of reproduction: the devil in the details. *Trends in Ecology and Evolution*, 22(2), 80–86.
- Hatakeyama, H., Yamazaki, H., Nakamura, K.-I., Izumiyama-Shimomura, N., Aida, J., Suzuki, H., Tsuchida, S., Matsuura, M., Takubo, K., & Ishikawa, N. (2016). Telomere attrition and restoration in the normal teleost *Oryzias latipes* are linked to growth rate and telomerase activity at each life stage. *Ageing (Albany NY)*, 8(1), 62–76.
- Hausmann, M. F., & Heidinger, B. J. (2015). Telomere dynamics may link stress exposure and ageing across generations. *Biology Letters*, 11, 20150396.
- Hausmann, M. F., Winkler, D. W., Huntington, C. E., Nisbet, I. C. T., & Vleck, C. M. (2004). Telomerase expression is differentially regulated in birds of differing life span. *Annals of the New York Academy of Sciences*, 1019, 186–190.
- Hausmann, M. F., Winkler, D. W., Huntington, C. E., Nisbet, I. C. T., & Vleck, C. M. (2007). Telomerase activity is maintained throughout the lifespan of long-lived birds. *Experimental Gerontology*, 42(7), 610–618.
- Hemann, M. T., Strong, M. A., Hao, L. Y., & Greider, C. W. (2001). The shortest telomere, not average telomere length, is critical for cell viability and chromosome stability. *Cell*, 107(1), 67–77.
- Hoelzl, F., Cornils, J. S., Smith, S., Moodley, Y., & Ruf, T. (2016). Telomere dynamics in free-living edible dormice (*Glis glis*): the impact of hibernation and food supply. *Journal of Experimental Biology*, 219(16), 2469–2474.
- Hoelzl, F., Smith, S., Cornils, J. S., Aydinonat, D., Bieber, C., & Ruf, T. (2016). Telomeres are elongated in older individuals in a hibernating rodent, the edible dormouse (*Glis glis*). *Scientific Reports*, 6, 36856.
- Jemielity, S., Chapuisat, M., Parker, J. D., & Keller, L. (2005). Long live the queen: Studying aging in social insects. *Age (Omaha)*, 27(3), 241–248.
- Jemielity, S., Kimura, M., Parker, K. M., Parker, J. D., Cao, X., Aviv, A., & Keller, L. (2007). Short telomeres in short-lived males: What are the molecular and evolutionary causes? *Ageing Cell*, 6(2), 225–233.
- Keller, L., & Genoud, M. (1997). Extraordinary lifespans in ants: A test of evolutionary theories of ageing. *Nature*, 389(6654), 958–960.
- Keller, L., & Reeve, H. K. (1994). Partitioning of reproduction in animal societies. *Trends in Ecology and Evolution*, 9(3), 98–102.
- Kingma, S. A., Komdeur, J., Hammers, M., & Richardson, D. S. (2016). The cost of prospecting for dispersal opportunities in a social bird. *Biology Letters*, 12(6), e20160316
- Kirkwood, T. B. L. (1977). Evolution of ageing. *Nature*, 270, 301–304.
- Kirkwood, T. B. L., & Holliday, R. (1979). The evolution of ageing and longevity. *Proceedings of the Royal Society B: Biological Sciences*, 205(1161), 531–546.
- Korandová, M., & Frydrychová, R. Č. (2016). Activity of telomerase and telomeric length in *Apis mellifera*. *Chromosoma*, 125(3), 405–411.
- Leitner, S., Mundy, P., & Voigt, C. (2009). Morphometrics of White-browed Sparrow-Weavers *Plocepasser mahali* in south-western Zimbabwe. *Ostrich*, 80(2), 99–102.
- Lewin, N., Treidel, L. A., Holekamp, K. E., Place, N. J., & Hausmann, M. F. (2015). Socioecological variables predict telomere length in wild spotted hyenas. *Biology Letters*, 11, 20140991.
- Lewis, D. M. (1982a). Cooperative breeding in a population of White-browed Sparrow-weavers *Plocepasser mahali*. *Ibis (Lond 1859)*, 124, 511–522.
- Lewis, D. M. (1982b). Dispersal in a population of White-browed Sparrow-Weavers. *Condor*, 84(3), 306–312.
- Monaghan, P. (2014). Organismal stress, telomeres and life histories. *Journal of Experimental Biology*, 217, 57–66.
- Monaghan, P., & Hausmann, M. F. (2006). Do telomere dynamics link lifestyle and lifespan? *Trends in Ecology and Evolution*, 21(1), 47–53.
- Murray, C. M., Eberly, L. E., & Pusey, A. E. (2006). Foraging strategies as a function of season and rank among wild female chimpanzees (*Pan troglodytes*). *Behavioral Ecology*, 17(6), 1020–1028.
- Nieuwenhuis, R., te Grotenhuis, M., & Pelzer, B. J. (2012). influence. ME: Tools for detecting influential data in mixed effects models. *R Journal*, 4(2), 38–47.
- Ogawa, M. (1993). Differentiation and proliferation of hematopoietic stem cells. *Blood*, 81(11), 2844–2853.
- Olovnikov, A. M. (1973). A theory of marginotomy. The incomplete copying of template margin in enzymatic synthesis of polynucleotides and biological significance of the phenomenon. *Journal of Theoretical Biology*, 41(1), 181–190.

- Pfaffl, M. W. (2001). A new mathematical model for relative quantification in real-time RT – PCR. *Nucleic Acids Research*, 29(9), e45.
- Reichert, S., & Stier, A. (2017). Does oxidative stress shorten telomeres in vivo? A Review. *Biology Letters*, 13(12), 20170463.
- Reichert, S., Stier, A., Zahn, S., Arrivé, M., Bize, P., Massemin, S., & Criscuolo, F. (2014). Increased brood size leads to persistent eroded telomeres. *Frontiers in Ecology and Evolution*, 2, e9.
- Richards, S. A. (2005). Testing ecological theory using the information-theoretic approach: Examples and cautionary results. *Ecology*, 86(10), 2805–2814.
- Richards, S. A., Whittingham, M. J., & Stephens, P. A. (2011). Model selection and model averaging in behavioural ecology: The utility of the IT-AIC framework. *Behavioral Ecology and Sociobiology*, 65(1), 77–89.
- Robertson, T., Batty, G. D., Der, G., Fenton, C., Shiels, P. G., & Benzeval, M. (2013). Is socioeconomic status associated with biological aging as measured by telomere length? *Epidemiology Reviews*, 35(1), 98–111.
- Ruijter, J. M., Ramakers, C., Hoogaars, W. M. H., Karlen, Y., Bakker, O., van den Hoff, M. J. B., & Moorman, A. F. M. (2009). Amplification efficiency: Linking baseline and bias in the analysis of quantitative PCR data. *Nucleic Acids Research*, 37(6), e45.
- Salomons, H. M., Mulder, G. A., van de Zande, L., Haussmann, M. F., Linskens, M. H. K., & Verhulst, S. (2009). Telomere shortening and survival in free-living corvids. *Proceedings of the Royal Society B: Biological Sciences*, 276(1670), 3157–3165.
- Sanderson, J. L., Young, A. J., Hodge, S. J., Kyabulima, S., Walker, S. L., & Cant, M. A. (2014). Hormonal mediation of a carry-over effect in a wild cooperative mammal. *Function Ecology*, 28(6), 1377–1386. <https://doi.org/10.1111/1365-2435.12307>
- Schmidt, C. M., Blount, J. D., & Bennett, N. C. (2014). Reproduction is associated with a tissue-dependent reduction of oxidative stress in eusocial female Damaraland mole-rats (*Fukomys damarensis*). *PLoS One*, 9(7), e103286.
- Seehuus, S.-C., Norberg, K., Gimsa, U., Krekling, T., & Amdam, G. V. (2006). Reproductive protein protects functionally sterile honey bee workers from oxidative stress. *Proceedings of the National Academy of Sciences of the United States of America*, 103(4), 962–967.
- Spurgin, L. G., Bebbington, K., Fairfield, E. A., Hammers, M., Komdeur, J., Burke, T., Dugdale, H. L., & Richardson, D. S. (2018). Spatio-temporal variation in lifelong telomere dynamics in a long-term ecological study. *Journal of Animal Ecology*, 87(1), 187–198.
- Steenstrup, T., Hjelmborg, J. V. B., Kark, J. D., Christensen, K., & Aviv, A. (2013). The telomere lengthening conundrum - Artifact or biology? *Nucleic Acids Research*, 41(13), e131.
- Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11), 1639–1644.
- Suda, T., Takubo, K., & Semenza, G. L. (2011). Metabolic regulation of hematopoietic stem cells in the hypoxic niche. *Cell Stem Cell*, 9(4), 298–310.
- Sudyka, J., Arct, A., Drobnik, S., Dubiec, A., Gustafsson, L., & Cichoń, M. (2014). Experimentally increased reproductive effort alters telomere length in the blue tit (*Cyanistes caeruleus*). *Journal of Evolutionary Biology*, 27(10), 2258–2264.
- Tricola, G. M., Simons, M. J. P., Atema, E., Boughton, R. K., Brown, J. L., Dearborn, D. C., Divoky, G., Eimes, J. A., Huntington, C. E., Kitaysky, A. S., Juola, F. A., Lank, D. B., Litwa, H. P., Mulder, E. G. A., Nisbet, I. C. T., Okanoya, K., Safran, R. J., Schoech, S. J., Schreiber, E. A., ... Haussmann, M. F. (2018). The rate of telomere loss is related to maximum lifespan in birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1741), 20160445.
- Ujvari, B., & Madsen, T. (2009). Short telomeres in hatchling snakes: Erythrocyte telomere dynamics and longevity in tropical pythons. *PLoS One*, 4(10), e7493.
- van de Pol, M., & Verhulst, S. (2006). Age-dependent traits: A new statistical model to separate within- and between-individual effects. *The American Naturalist*, 167(5), 766–773.
- Vathesatogkit, P., Batty, G. D., & Woodward, M. (2014). Socioeconomic disadvantage and disease-specific mortality in Asia: systematic review with meta-analysis of population-based cohort studies. *Journal of Epidemiology and Community Health*, 68, 375–383.
- 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(11), 859–866.
- Verhulst, S., Susser, E., Factor-Litvak, P. R., Simons, M. J. P., Benetos, A., Steenstrup, T., Kark, J. D., & Aviv, A. (2015). Commentary: The reliability of telomere length measurements. *International Journal of Epidemiology*, 44, 1683–1686.
- Walker, L. A. (2016). *The Evolution and Regulation of Cooperation in the Wild* (thesis). University of Exeter. Retrieved from <http://hdl.handle.net/10871/21129>
- Walker, L. A., York, J. E., & Young, A. J. (2016). Sexually selected sentinels? Evidence of a role for intrasexual competition in sentinel behavior. *Behavioral Ecology*, 27(5), 1461–1470.
- Wang, J., Lu, X., Sakk, V., Klein, C. A., & Rudolph, K. L. (2014). Senescence and apoptosis block hematopoietic activation of quiescent hematopoietic stem cells with short telomeres. *Blood*, 124(22), 3237–3240.
- Wilbourn, R. V., Moatt, J. P., Froy, H., Walling, C. A., Nussey, D. H., & Boonekamp, J. J. (2018). The relationship between telomere length and mortality risk in non-model vertebrate systems: a meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1741), 20160447.
- Wingfield, J., Hegner, R., & Lewis, D. M. (1991). Circulating levels of luteinizing hormone and steroid hormones in relation to social status in the cooperatively breeding white-browed sparrow-weaver, *Plocepasser mahali*. *Journal of Zoology*, 225(1), 43–58.
- Wood, E. M. (2017). *Causes and fitness consequences of telomere dynamics in a wild social bird* (thesis). University of Exeter. Retrieved from <https://ore.exeter.ac.uk/repository/handle/10871/29777>
- Wood, E. M., & Young, A. J. (2019). Telomere attrition predicts reduced survival in a wild social bird, but short telomeres do not. *Molecular Ecology*, 28(16), 3669–3680. <https://doi.org/10.1111/mec.15181>
- Wood, E. M., & Young, A. J. (2020). Data for Wood & Young: Social dominance and rainfall predict telomere dynamics in a cooperative arid-zone bird. p.mahali_adults; <https://doi.org/10.5281/zenodo.3668722>
- York, J. E., Radford, A. N., de Vries, B., Groothuis, T. G., & Young, A. J. (2016). Dominance-related seasonal song production is unrelated to circulating testosterone in a subtropical songbird. *General and Comparative Endocrinology*, 233, 43–52.
- York, J. E., Wells, K. J., & Young, A. J. (2019). Dominance-related contributions to collective territory defence are adjusted according to the threat. *Animal Behaviour*, 158, 25–34.
- Young, A. J. (2009). The causes of physiological suppression in vertebrate societies: A synthesis. In R. Hager, & C. B. Jones (Eds.), *Reproductive Skew in Vertebrates: Proximate and Ultimate Causes* (pp. 397–436). Cambridge University Press. <https://doi.org/10.1017/CBO9780511641954.016>
- Young, A. J. (2018). The role of telomeres in the mechanisms and evolution of life-history trade-offs and ageing. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 373(1741), 20160452.
- Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C., & Clutton-Brock, T. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. *Proceedings of the National Academy of Sciences of the United States of America*, 103(32), 12005–12010.

Young, A. J., & Monfort, S. L. (2009). Stress and the costs of extra-territorial movement in a social carnivore. *Biology Letters*, *5*(4), 439–441.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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