Title: Telomere length in house sparrows increases in early-life and can be paternally inherited

Running title: Paternal inheritance of telomere length

Sophie Bennett[1,2*], Antje Girndt[1,3,4], Alfredo Sánchez-Tójar,[1,3,4] ,Terry Burke[5], Mirre Simons[5], Julia Schroeder[1]

[1] Division of Biology, Imperial College London, Silwood Park, United Kingdom
[2] UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK
[3] Department of Evolutionary Biology, Max Planck Institute for Ornithology, Seewiesen, Germany
[4] Department of Evolutionary Biology, Bielefeld University, Germany
[5] Department of Animal and Plant Sciences, University of Sheffield, Sheffield, United Kingdom

***Corresponding author contact:** bennett.i.sophie@gmail.com

Abstract:

Offspring of older parents in many species display decreased longevity, a faster ageing rate and lower fecundity than offspring born to younger parents. Biomarkers, such as telomeres, that tend to shorten as individual age, may provide insight into the mechanisms of parental age effects. Parental age could determine telomere length either through inheritance of shortened telomeres or through indirect effects, such as variation in parental care with parent ages, which in turn might lead to variation in offspring telomere length. There is no current consensus as to the heritability of telomere length, and the direction and extent of parental age effects however. To address this, here we experimentally investigate how parental age is associated with telomere length at two time points in early life in a captive population of house sparrows (*Passer domesticus*). We experimentally separated parental age from sex effects by allowing the parent birds to only mate with young, or old partners. We found that telomere length of the offspring increased between the age of 0.5 and 3 months at the group and individual level, which has been reported previously predominantly in non-avian taxa. We further show that older fathers produced daughters with a greater early-life increase in telomere length, supporting sex-specific inheritance, and or sex-specific non-genetic effects. Overall, our results highlight the need for more studies testing early-life telomere dynamics and sex-specific heritability of telomere length.

Key words: telomere dynamics, ageing, inter-generational effects, z-linked inheritance, transgenerational effects, Lansing effect

Introduction

Parent age at conception is often associated with their offspring's' life-history, with offspring of older parents commonly having reduced reproductive success and longevity (Heidinger et al., 2016; Priest et al., 2002; Schroeder et al., 2015). Moreover, in some species, offspring of older parents experience higher rates of senescence, cellular ageing, and decreased longevity compared to their older siblings (Bouwhuis et al., 2010; Broer et al., 2013; Torres et al., 2011). While some studies do not find such effects (Froy et al., 2017; Unryn et al., 2005), the associations are reported across a wide range of taxa from rotifers (King, 1983) and insects (Priest et al., 2002) to birds and mammals (Bize et al., 2009; Haussmann et al., 2003b), and is termed the Lansing effect (Lansing, 1947).

The relative length of telomeres, the chromosome capping structures consisting of TTAGGG base pair repeats, is associated with biological age and longevity (Heidinger et al., 2012; Mather et al., 2011; Vedder et al., 2021). Telomeres partly function to prevent DNA damage from reactive oxygen species (Aubert and Lansdorp, 2008). The activity levels of telomerase, the RNA-protein complex responsible for ligating TTAGGG repeats, decline rapidly in early life and are tissue specific (Taylor and Delany, 2000). Together this leads to a gradual telomere shortening over an individual's lifetime (Aubert and Lansdorp, 2008; Finkel and Holbrook, 2000), which is why telomere length is often used as a biomarker for biological age (Mather et al., 2011; Zglinicki and Martin-Ruiz, 2005). However, whether there is a direct causal link between telomere length and an individual's age remains unclear (Boonekamp et al., 2013; Simons, 2015).

In birds, telomere loss is fastest in early-life and an initially longer telomere length is associated with longer subsequent lifespans in captive (Reichert et al., 2013; Wilbourn et al., 2018) and wild (Haussmann et al., 2003a; Heidinger et al., 2016; Reed et al., 2008; Richardson et al., 2001; Salomons et al., 2009; Vedder et al. 2021) bird populations. There is evidence for telomere length being heritable in birds (Vedder et al., 2021), and telomere dynamics have been associated with sex-specific parental age and telomere length (Asghar et al., 2015; Horn et al., 2011; Reichert et al., 2015; Salomons et al., 2009). This suggests that indeed, some Lansing-type effects may be inherited via telomere length. However, the direction of the association between telomere length, and maternal and paternal age varies even within bird species (Dugdale and Richardson, 2018). In birds, the offspring of older mothers may have shorter telomeres and a faster attrition rate, especially in early development (Asghar et al., 2015; Salomons et al., 2009). Conversely, negative associations between paternal age and offspring telomere length have been observed in the absence of maternal correlation (Horn et al., 2011).

Between taxa, studies on the heritability of telomere length are conflicting. The heritability of telomere length can be sex-specific and is often larger in the heterogametic sex; suggesting some degree of maternal inheritance in birds (Asghar et al., 2015; Horn et al., 2011; Reichert et al., 2015) and paternal inheritance in humans (Eisenberg et al., 2017; Njajou et al., 2007; Nordfjäll et al., 2009). However, homogametic inheritance of telomere length has also been found in humans (Broer et al., 2013), in some bird species (Bauch et al., 2019; Bouwhuis et al., 2018), and in lizards (Olsson et al., 2011). A sex-specific lack of heritability has also been found in several bird species (Atema et al., 2015; Heidinger et al., 2012; Kucera, 2018). Overall, parental age effects on offspring telomere length, dynamics and heritability are complex, and vary in extent and direction of impact within and between taxa.

Here, we test for sex-specific, age-related parental effects on offspring telomere dynamics in captive house sparrows *Passer domesticus.* By pairing different age categories of parent birds, we experimentally test the hypothesis that offspring of older parents have shorter telomeres and faster telomere attrition rates than offspring from younger parents.

Methods:

Study species and experimental design:

We used captive house sparrows at the Max Planck Institute for Ornithology, Seewiesen, Germany, during the breeding season of 2014. We used 42 pairs of male and female sparrows, which were assigned to four treatments, each with an equal sex ratio and a uniform distribution of ages across both sexes to control for age-assortative mating. We experimentally bred pairs in one of four age combinations: old-female/ old-male (OO, n=8 pairs), old-female/ young-male (OM, n=11 pairs), young-female/ old-male (YO, n=13 pairs), and young-female/ young-male (YY, n=10 pairs). Young birds hatched the preceding summer. Old (O) was defined as sparrows aged 4 years and older, although most individuals were 7 years or older (Males: 8 years = 2, 9 years = 21; Females: 4 years = 1, 7 years= 10, 8 years= 4, and 9 years= 1). The difference in age distribution between females and males corresponded to that observed in the wild, where females live shorter than males(Schroeder et al., 2012). We did not use the middle aged groups because in wild house sparrows, reproductive senescence may start at 3 years for females (Schroeder et al., 2012), or 5 years in males (Hsu et al. 2017). Each treatment group was replicated twice in two separate breeding groups located in separate aviaries. Each replicate aviary contained 15.3±4.9 (mean±s.d.) males and 14.6±2.4 females of the respective age class. Bird husbandry is described in Girndt et al. (2017).

Each replicate aviary was equipped with one more nest box than breeding pairs to reduce male-male competition for nest boxes. Sparrows were then allowed to naturally display, form pair bonds, choose a mate restricted by the age class present, and raise their young (Girndt et al, 2018). We systematically monitored breeding and identified the parents attending each nest box by observing the individual birds' colour ring combinations.

Blood sample collection:

We took blood samples from chicks 0.5 months after they hatched (n= 75). After fledging, offspring remained in the same aviary as their parents and siblings, and 2.5 months later were blood sampled again (n=59). Blood samples were collected from the brachial vein of offspring using 1mm capillary tubes and stored in 1ml of 96% ethanol. We collected samples of 56 individuals at both 0.5 and 3 months to test for within-individual changes.

DNA extraction and quantification:

Following standard DNA extraction (Richardson et al., 2001), we measured the DNA concentration of the samples using a ThermoScientific NanoDrop8000 Spectrophotometer and standardised the concentration in our samples to 20-30ng/ml to ensure equal amplification of samples during qPCR. Where necessary, samples were diluted with T10E0.1 (10mM Tris-HCl, pH 8.0, 0.1mM EDTA, pH 8.0) or concentrated using a ThermoScientific Savant DNA SpeedVac Concentrator.

Estimation of telomere length:

We used multiplex qPCR to determine relative telomere length. We determined 'T' as the number of telomere repeats and 'S' as the number of control gene repeats. We then used the T/S ratio as a proxy for telomere length. The four DNA primers we used are described in Criscuolo et al. (2009). We used DNA from house sparrows not included in this analysis as standards at five DNA concentrations of 80, 20, 5, 1.25 and 0.31ng/ml, on each plate. We then used these standards to produce a standard curve for all analysed samples. In each well we added 1.5μl of DNA sample, 0.9μl of each primer, 10μl of Sybr®Select Master Mix and 4.9μl ddH_2O. We ran each plate with an equal number of 0.5 and 3 months sample pairs from the same individual to account for any potential sample and plate effects when comparing within-individual changes in telomere length. We ran 42 samples, the five standards and a negative (with all components except a DNA sample) in duplicate on each 96-well plate. We ran the qPCR cycling conditions using QuantStudio 12kFlex Software v1.2.2 following the cycle timings given in Cawthon (2009). We analysed the software output to calculate the T/S ratio in each sample (Appendix 1.1). We altered the thresholds for the standard curve of the telomere and GAPDH primers for each plate to optimise amplification efficiencies to between a standard of 95-110. Efficiencies for each plate were between 99.3-99.7 for

GAPDH and 99.3-105.8 for telc and telg. The standard curve for each plate had an R^2 of 0.99 and the intra- and inter-plate variation coefficients all met adequate levels (Cawthon, 2009). We also ran a melt curve to examine whether the expected two products were generated in the reaction. Additionally, we checked all plate amplification curves to see if DNA was present in the control, as this would indicate contamination. In all plates DNA was absent, or present only in very low levels in negatives, apart from very late amplification due to primer dimerization. We repeated any sample duplicates that had a standard deviation of >0.05 following thresholding and used the mean T/S ratio of duplicates in our analysis. T/S ratios of offspring at 0.5 months old are referred to as $T/S_{0.5}$ and samples at 3 months old T/S_3 in our analyses. We then calculated the difference between the two measurements as ΔT/S. All samples were analysed for telomere length at the same time and had a similar shelf time (Lieshout et al., 2020). All reagents and equipment were produced by Thermo Fisher Scientific, Waltham, Massachusetts, US.

Ethical Note:

The Government of Upper Bavaria, Germany, approved the care, handling and husbandry of all birds in this study and granted a license for animal experiments to JS (Nr311.5–5682.1/1-2014-024).

Statistical Analysis:

Next, we tested for a change in telomere length over the 2.5 months period by running a linear mixed-effects model (LMM) with T/S as response variable, time of sampling (0.5 months or 3 months) as an explanatory fixed factor, and individual chick ID as a random effect on the intercept. Then we tested whether telomere lengths in offspring were more variable at either 0.5, or 3 months using a two-tailed F-test. Next, we ran two further LMMs with the response variable $T/S_{0.5}$ and T/S_3, respectively. For each model we tested the fixed effects of the paternal and maternal age categories (either ‘young’ or ‘old’). To test for sex-specific parental effects, we included offspring sex as a categorical variable (with ‘male’ as the reference level) and an interaction of chick sex with parental age in the $T/S_{0.5}$ model. Because not all chicks were sampled at exactly 3 months after hatching (mean±s.d.= 100.8 days±8.4), we also tested for an effect of the exact age in days of offspring in T/S_3 with a LMM with T/S_3 as the response variable, and ‘sample age’ as an explanatory covariate. We found that ‘sample age’ did not have a statistically significant effect on T/S_3 (posterior mode= -0.001, 95% credible interval= -0.01, 0.001, pMCMC=0.809). Still, to account for any potential bias we retained ‘sample age’ as a fixed effect in the T/S_3 model.

As the 0.5 months samples were a mix of newly-, and already-extracted DNA samples, we also tested whether time of extraction had any effect on the calculated T/S ratio as a result of DNA degradation (Madisen et al., 1987) (n samples newly-extracted= 10 out of 75). We fitted a LMM with $T/S_{0.5}$ as the response and the time of extraction as a fixed factor, either 'newly-' or 'already-extracted'. We found no statistically significant difference between newly-, and already-extracted samples (posterior mode= -0.06, 95% credible interval= -0.20, 0.08, pMCMC=0.389).

We included the nest box ID and aviary ID in which chicks were born as random effects on the intercept in all models to account for variance between broods and aviaries. We also included the random term of qPCR plate ID in all models to account for between-plate variance on the intercept. All models were run using the Markov chain Monte Carlo (MCMC) method in the R package MCMCglmm v.2.29 (Hadfield, 2010).

Model validation:

As we used a Bayesian modelling approach, we deemed fixed terms to be statistically significant if their 95% credible intervals (95CI) did not span zero, and we also report MCMC-p-values (pMCMC) (Hadfield, 2010). All terms were retained in models irrespective of their statistical significance. We directly assessed model autocorrelation for fixed and random effects to ensure the risk of type I errors was not inflated. We also inspected iteration and density plots to ensure that effects showed equal variation around a constant mode and demonstrated convergence (Gelman and Hill, 2006; Hadfield, 2010). We examined collinearity of fixed effects, as collinearity could distort model results, which did not exceed 0.7 (Dormann et al., 2013). We ran all models for 100,000 iterations with a thinning interval of 10 and used default priors. All statistical analyses were carried out in R v.3.6.1 (R Core Team, 2019)

Results:

Unexpectedly, the telomere length for offspring increased within 80% of individuals between 0.5 and 3 months of age (n = 45/56) for those where both measurements were available. On average, the difference between $T/S_{0.5}$ and T/S_3 was statistically significantly positive (Figure 1 and Table 1). Further, as chicks aged, they varied more in their telomere lengths; there was greater variance in T/S_3 than in $T/S_{0.5}$ (coefficient of variance (CV)±s.e.: 0.5 months: 0.22±0.02, n=75, 3 months: 0.27±0.02, n=59; F-test: F=0.43, p<0.01).

Table 1: Results from a Bayesian MCMC linear mixed-effects model testing the difference between telomere length in house sparrow chicks at 0.5 and 3 months of age.

Parameter	*Estimate*	*95% confidence intervals*	p_{MCMC}
Intercept	**0.93**	**0.84 - 0.99**	**<0.001**
Chick age	**0.19**	**0.12 - 0.26**	**<0.001**
Random effects			
Chick ID	0.00	0.00 - 0.01	
Nest box	0.02	0.01 - 0.04	
Aviary	0.00	0.00 - 0.00	
qPCR plate ID	0.00	0.00 - 0.01	
Residual	0.04	0.02 - 0.05	

Chick age was modelled as a binary variable of either 0.5 months or 3 months, with 0.5 months as a reference level. 0.5 months: n=75 chicks, 3 months: n=59. Estimates shown are posterior modes.

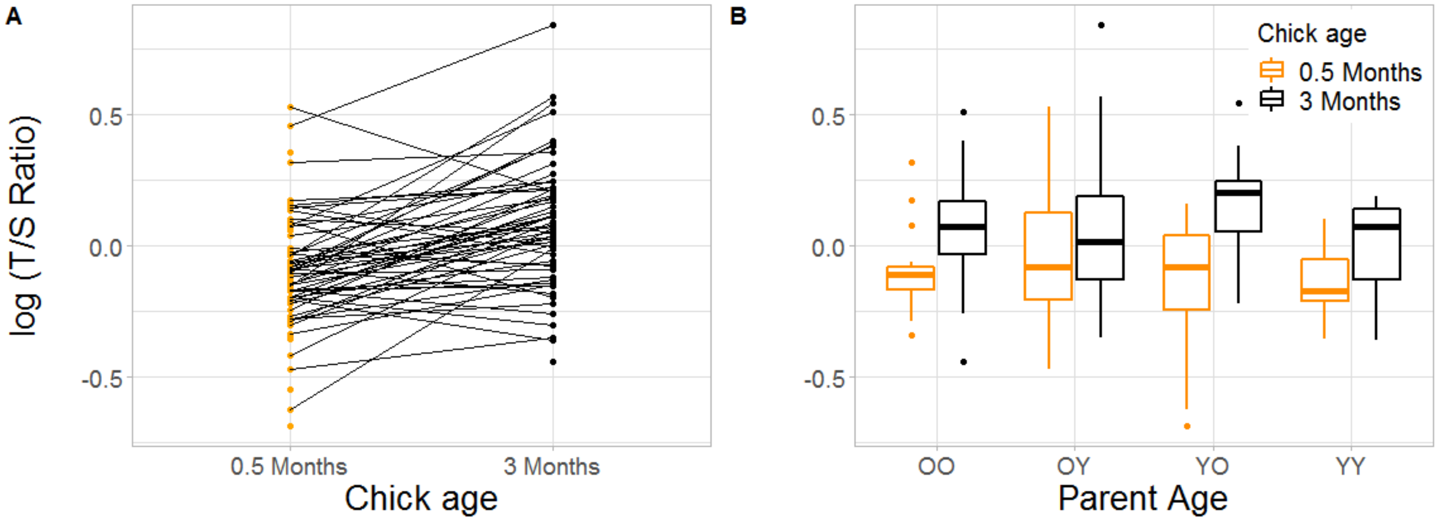

Figure 1: Change in telomere length (log(T/S Ratio)) within house sparrow chicks at 0.5 and 3 months of age. A) Individuals are connected by a line (n offspring with samples at 0.5 months=75, at 3 months=59). B) Boxplots show the mean (central line) and 25th and 75th percentiles (lower and upper box bounds respectively) of the log(T/S Ratio) within age group of the chicks' parents (Y = <2 years old, O > 3 years old for females and >7 years old for males). T/S Ratio is presented on a log scale to aid visualisation. YO = young mothers, old fathers (n=19, 12). OO = both parents old (n=18, 19). OY = old mothers, young fathers (n=17, 18). YY = both parents young (n=15, 10).

We did not find a statistically significant effect of parental age class on $T/S_{0.5}$, which is shortly before sparrows gain independence and fledge from their nest (Table 2). However, the T/S_3 model detected statistically significant effects of paternal age, and the interaction between these two variables. This means that daughters of young fathers had shorter telomeres than daughters of old fathers (Table 2, Fig. 2).

Table 2: Results from two Bayesian MCMC general linear mixed-effects models with telomere length of house sparrow chicks at age 0.5 months and 3 months as response variables, respectively.

	$T/S_{0.5}$			T/S_3		
Parameter	*Estimate*	*95% CI*	p_{MCMC}	*Estimate*	*95% CI*	p_{MCMC}
Intercept	**0.97**	**0.84 - 1.10**	**<0.001**	**1.57**	**0.32 – 2.71**	**0.022**
Chick sex	-0.08	-0.22 - 0.11	0.469	-0.23	-0.41 - 0.61	0.121
Maternal age	-0.07	-0.23 - 0.08	0.346	0.06	-0.32 - 0.21	0.711
Maternal age x Chick sex	0.06	-0.15 - 0.25	0.597	0.09	-0.21 - 0.43	0.573
Paternal age	-0.03	-0.20 - 0.10	0.481	**-0.27**	**-0.52 - 0.00**	**0.047**
Paternal age x Chick sex	0.6	-0.07 - 0.34	0.168	**-0.40**	**0.09 - 0.71**	**0.162**
Sample day				0.00	-0.01 - 0.01	0.694
Random effects						
Nest box	0.01	0.00 - 0.03		0.01	0.00 - 0.02	
Aviary	0.00	0.00 - 0.01		0.01	0.00 - 0.01	
qPCR plate ID	0.00	0.00 - 0.01		0.00	0.00 - 0.01	
Residual	0.08	0.03 - 0.11		0.08	0.03 - 0.11	

Maternal and paternal age were modelled as a binary variable of either young or old; young was <2 years old, and old was determined as >3 years old for females and >7 years for males). 0.5 months: n=69 chicks, 3 months: n=59. The reference level for parental ages was ‘old’, and the ‘female’ was the reference level for chick sex. Estimates shown are posterior modes.

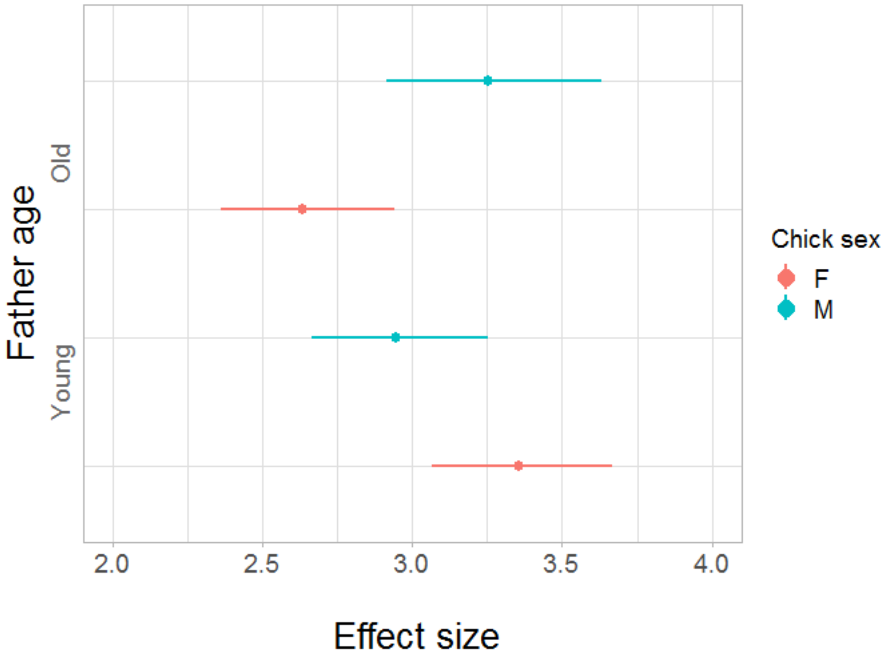

Figure 2: Post-hoc effect size plot from a linear mixed-effects model testing the relationship between T/S_3, father age, and sex of chicks (Table 1). Fathers were assigned an age category of young, ‘Y’, or old, ‘O’. A young father was <2 years old, and an old father was determined as >7 years old. Chick sex is indicated as either female, ‘red’, or male, ‘blue’. The number of offspring in

each category; Y, and female=12, male=16, O, and female=16, male=15. Squares represent the model estimates effect sizes of T/S ratio for each paternal age x chick sex combination and associated lines represent 95% credible intervals (derived using the R package ‘lsmeans’ (Lenth, 2016).

Discussion:

Individual chick telomere length increased between 0.5 and 3 months of age. This increase disagrees with much of the published literature, which generally find a decrease in telomere length in early-life (Boonekamp et al., 2014; Cerchiara et al., 2017; De Meyer et al., 2007; Hoelzl et al., 2016; Salomons et al., 2009). While a population level increase in telomere length has previously been found in some long-lived bird species (Haussmann et al., 2007; Pauliny et al., 2012), other studies have found that telomeres elongation for a proportion of chicks is more common in smaller, shorter-lived species (Brown et al., 2021; Eisenberg, 2019). For example, a study on jackdaws *Corvus monedula* found that between 5 and 30 days post-hatching, telomere lengths increased for 25% of sampled offspring (Grasman et al., 2011). An increase in early-life telomere length has also been observed in non-avian taxa, including water pythons *Liasis fuscus* (Ujvari and Madsen, 2009) and European badgers *Meles meles* (van Lieshout et al., 2019). A lack of comparable published research exploring a change in telomere length using multiple time points in early life may, in part, explain the surprising nature of our observed increase in telomere length in early-life.

An increase in telomere length can have methodological and/or biological explanations. First, it could be due to DNA in samples degrading over time (Madisen et al., 1987; but see Seutin et al., 1991). Since we used pre-extracted DNA for the majority of 0.5 month samples, we investigated whether differential telomere degradation rates between extracted DNA and blood sample types could be a cause for the observed increase. However, we found no statistically significant difference between the telomere lengths of newly- and already-extracted samples and thus, telomere degradation is an unlikely explanation for our results.

Second, qPCR plates contained both 0.5 and 3 months samples, and between-plate variance was negligible in all our models, highlighting that this element of our methodology had little impact on our results. Overall, we monitored procedural efficiency throughout data collection and did not identify any other potential methodological sources of variation, and so, we are convinced that the increase in telomere length observed in our study has a biological explanation. For example, telomerase activity might have been maintained in the offspring after the first sample was taken. Indeed, two studies have shown that telomerase activity can be maintained up to five weeks post-hatching in zebra finches *Taeniopygia guttata* (Haussmann et al., 2007) and chickens *Gallus gallus*

(Taylor and Delany, 2000). Yet, neither of these studies assessed telomerase activity at multiple time points in the same individual's early-life post-hatching, which remains as an interesting future avenue for the field.

While we expected that old parents would produce offspring with shorter telomeres, as found in other short-lived bird species (Bauch et al., 2019; Criscuolo et al., 2017; Sparks et al., 2020), our experimental approach found that old fathers produced daughters with longer telomeres, but only 3 months after hatching, indicating an environmental effect. Similar positive effects of parental age have also previously been found in long and short-lived bird species (Dupont et al., 2018, Asghar et al., 2015; Becker et al., 2015). Positive effects of parental age on offspring telomere length may arise from a potentially improved parental care that older individuals may be able to provide compared to inexperienced, young breeders. Again though, previous studies have found a negative effect of parental age resulting from the poorer condition of these old individuals (Bouwhuis et al., 2018; Criscuolo et al., 2017), or a lack of an effect of parental age on parental care (Nakagawa et al., 2007). Further, in some studies testing parent sex-specific effects, offspring telomere length was found to correlate only with maternal age, and only relatively soon after hatching (ten days: Reichert et al. (2015); nine days: Asghar et al. (2015)). As we found no inflouence of maternal age in our study, an influence of maternal age on offspring telomere length may well have been present, but already diminished below detectable levels 0.5 months after hatching.

While telomere lengths in offspring have been shown to be affected by an offspring's environment (Dugdale and Richardson, 2018; Lieshout et al., 2021), effects of paternal age in birds have been found to be independent of this (Bauch et al., 2019; Boonekamp et al., 2014). As such, overall, there is growing support for at least contributory paternal inheritance of telomere length in some species of birds (Bouwhuis et al., 2018; Olsson et al., 2011; this study). The combined positive effect of having an older father has been theorised to result from an upregulation of telomerase activity in sperm and a subsequent increase in gamete telomere length as males age (De Meyer et al., 2007); as such a positive association of paternal telomere length with age has also been found in humans (Kimura et al., 2008; Unryn et al., 2005). Therefore, a combination of telomerase activity in sperm in fathers, a form of Z-linked inheritance, and potential parental care benefits discussed above may explain the positive effect of increasing father age on offspring telomere lengths, with larger effects seen on daughters compared to sons as observed here.

However, we did not detect an effect of parental age on offspring telomere length at 0.5 months after hatching. Heidinger et al. (2016) similarly found no effect of parental age on offspring telomere length in very early-life at 25 days after hatching in European shags *Phalacrocorax* *aristotelis*. Further, variation in pre-fledging telomere length may in part be explained by brood-specific additive genetic effects (Voillemot et al., 2012). As such, it may be that at later time points effects of parent age and post-fledging environmental factors appear to be more important than brood-specific effects in determining offspring telomere length. Again, there is a need for more studies investigating the relationship between paternal age and telomere dynamics to detect when and how patterns of telomere dynamics are driven.

In sum, our results indicate that paternal age effects are more influential on offspring telomere length than maternal age effects in our population of house sparrows, with the daughters of older fathers having longer telomeres. Future analyses of telomerase activity levels in both the sperm of adult males and the somatic tissues of offspring would yield further insights into the drivers of parental age effects on offspring telomere dynamics in early-life.

Acknowledgements:

The authors would like to thank to Natalie dos Remedios for her help and support with processing samples, and Marta Precioso for helpful discussions on the methodology. We thank Annemarie Grötsch and Natalie Fischer for care of the captive population.

Competing interests' statement:

No competing interests declared.

Author contributions:

Conceptualization: SB, JS; Methodology: SB, JS, MJPS; Validation: SB, MJPS; Formal analysis: SB, JS; Investigation: SB, AG, JS, AST; Resources: JS, MJPS, TB; Data curation: SB, JS, TB; Writing- original draft: SB; Writing- review & editing: SB, JS, AG, AST, MJPS; Visualization: SB, JS, AG, AST; Supervision: JS; Project administration: JS, TB; Funding acquisition: JS, TB.

Funding:

AG was supported by the Bielefeld Young Researcher's Fund; AST was funded by the German Research Foundation (DFG) as part of the SFB 592 TRR 212 (NC^3; project numbers 316099922, 396782608); MJPS is a Wellcome Sir Henry Dale Fellow [MJPS]. This work was funded by the Volkswagen Foundation and a Grant CIG from the European Union [PCIG12-GA-2012-333096 to JS].

Data availability statement:

The data and code are available at the Open Science Foundation through this anonymous link: https://osf.io/6kwzh/?view_only=96b0d8a81ce84ba09b364e514ab0072e. Upon acceptance of this work the data and code will be permanently hosted in a public repository and their DOI provided.

References:

Asghar, M., Bensch, S., Tarka, M., Hansson, B., Hasselquist, D., 2015. Maternal and genetic factors determine early life telomere length. Proc. R. Soc. Lond. B Biol. Sci. 282, 20142263. https://doi.org/10.1098/rspb.2014.2263

Atema, E., Mulder, E., Dugdale, H.L., Briga, M., Noordwijk, A.J. van, Verhulst, S., 2015. Heritability of telomere length in the Zebra Finch. J. Ornithol. 156, 1113–1123. https://doi.org/10.1007/s10336-015-1212-7

Aubert, G., Lansdorp, P.M., 2008. Telomeres and Aging. Physiol. Rev. 88, 557–579. https://doi.org/10.1152/physrev.00026.2007

Bauch, C., Boonekamp, J.J., Korsten, P., Mulder, E., Verhulst, S., 2019. Epigenetic inheritance of telomere length in wild birds. PLOS Genet. 15, e1007827. https://doi.org/10.1371/journal.pgen.1007827

Becker, P.J.J., Reichert, S., Zahn, S., Hegelbach, J., Massemin, S., Keller, L.F., Postma, E., Criscuolo, F., 2015. Mother–offspring and nest-mate resemblance but no heritability in early-life telomere length in white-throated dippers. Proc. R. Soc. B Biol. Sci. 282, 20142924. https://doi.org/10.1098/rspb.2014.2924

Bize, P., Criscuolo, F., Metcalfe, N.B., Nasir, L., Monaghan, P., 2009. Telomere dynamics rather than age predict life expectancy in the wild. Proc. R. Soc. Lond. B Biol. Sci. 276, 1679–1683. https://doi.org/10.1098/rspb.2008.1817

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. Proc. R. Soc. Lond. B Biol. Sci. 281, 20133287. https://doi.org/10.1098/rspb.2013.3287

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, 330–332. https://doi.org/10.1111/acel.12050

Bouwhuis, S., Charmantier, A., Verhulst, S., Sheldon, B.C., 2010. Trans-generational effects on ageing in a wild bird population. J. Evol. Biol. 23, 636–642. https://doi.org/10.1111/j.1420-9101.2009.01929.x

Bouwhuis, S., Verhulst, S., Bauch, C., Vedder, O., 2018. Reduced telomere length in offspring of old fathers in a long-lived seabird. Biol. Lett. 14, 20180213. https://doi.org/10.1098/rsbl.2018.0213

Broer, L., Codd, V., Nyholt, D.R., Deelen, J., Mangino, M., Willemsen, G., Albrecht, E., Amin, N., Beekman, M., de Geus, E.J.C., Henders, A., Nelson, C.P., Steves, C.J., Wright, M.J., de Craen, A.J.M., Isaacs, A., Matthews, M., Moayyeri, A., Montgomery, G.W., Oostra, B.A., Vink, J.M., Spector, T.D., Slagboom, P.E., Martin, N.G., Samani, N.J., van Duijn, C.M., Boomsma, D.I., 2013. Meta-analysis of telomere length in 19 713 subjects reveals high heritability, stronger maternal inheritance and a paternal age effect. Eur. J. Hum. Genet. 21, 1163–1168. https://doi.org/10.1038/ejhg.2012.303

Brown, thomas, Dugdale, H., Spurgin, L., Komdeur, J., Burke, T., Richardson, D., 2021. Causes and Consequences of Telomere Lengthening in a Wild Vertebrate Population (preprint). Authorea. https://doi.org/10.22541/au.161408541.15345829/v1

Cawthon, R.M., 2009. Telomere length measurement by a novel monochrome multiplex quantitative PCR method. Nucleic Acids Res. 37, e21–e21. https://doi.org/10.1093/nar/gkn1027

Cerchiara, J.A., Risques, R.A., Prunkard, D., Smith, J.R., Kane, O.J., Dee Boersma, P., 2017. Telomeres shorten and then lengthen before fledging in Magellanic penguins (Spheniscus magellanicus). Aging 9, 487–493. https://doi.org/10.18632/aging.101172

Criscuolo, F., Bize, P., Nasir, L., Metcalfe, N.B., Foote, C.G., Griffiths, K., Gault, E.A., Monaghan, P., 2009. Real-time quantitative PCR assay for measurement of avian telomeres. J. Avian Biol. 40, 342–347. https://doi.org/10.1111/j.1600-048X.2008.04623.x

Criscuolo, F., Zahn, S., Bize, P., 2017. Offspring telomere length in the long lived Alpine swift is negatively related to the age of their biological father and foster mother. Biol. Lett. 13, 20170188. https://doi.org/10.1098/rsbl.2017.0188

De Meyer, T., Rietzschel, E.R., Buyzere, D., L, M., De Bacquer, D., Van Criekinge, W., Backer, D., G, G., Gillebert, T.C., Van Oostveldt, P., Bekaert, S., 2007. Paternal age at birth is an important determinant of offspring telomere length. Hum. Mol. Genet. 16, 3097–3102. https://doi.org/10.1093/hmg/ddm271

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Dugdale, H.L., Richardson, D.S., 2018. Heritability of telomere variation: it is all about the environment! Philos. Trans. R. Soc. B Biol. Sci. 373, 20160450. https://doi.org/10.1098/rstb.2016.0450

Dupont, S.M., Barbraud, C., Chastel, O., Delord, K., Ruault, S., Weimerskirch, H., Angelier, F., 2018. Young parents produce offspring with short telomeres: A study in a long-lived bird, the Black-browed Albatross (Thalassarche melanophrys). PLOS ONE 13, e0193526. https://doi.org/10.1371/journal.pone.0193526

Eisenberg, D.T.A., 2019. Paternal age at conception effects on offspring telomere length across species—What explains the variability? PLOS Genet. 15, e1007946. https://doi.org/10.1371/journal.pgen.1007946

Eisenberg, D.T.A., Tackney, J., Cawthon, R.M., Cloutier, C.T., Hawkes, K., 2017. Paternal and grandpaternal ages at conception and descendant telomere lengths in chimpanzees and humans. Am. J. Phys. Anthropol. 162, 201–207. https://doi.org/10.1002/ajpa.23109

Finkel, T., Holbrook, N.J., 2000. Oxidants, oxidative stress and the biology of ageing. Nature 408, 239–247. https://doi.org/10.1038/35041687

Froy, H., Bird, E.J., Wilbourn, R.V., Fairlie, J., Underwood, S.L., Salvo-Chirnside, E., Pilkington, J.G., Bérénos, C., Pemberton, J.M., Nussey, D.H., 2017. No evidence for parental age effects on offspring leukocyte telomere length in free-living Soay sheep. Sci. Rep. 7, 9991. https://doi.org/10.1038/s41598-017-09861-3

Gelman, A., Hill, J., 2006. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press.

Girndt, A., Chng, C.W.T., Burke, T., Schroeder, J., 2018. Male age is associated with extra-pair paternity, but not with extra-pair mating behaviour. Sci. Rep. 8, 8378. https://doi.org/10.1038/s41598-018-26649-1

Girndt, A., Cockburn, G., Sánchez-Tójar, A., Løvlie, H., Schroeder, J., 2017. Method matters: Experimental evidence for shorter avian sperm in faecal compared to abdominal massage samples. PLOS ONE 12, e0182853. https://doi.org/10.1371/journal.pone.0182853

Grasman, J., Salomons, H.M., Verhulst, S., 2011. Stochastic modeling of length-dependent telomere shortening in Corvus monedula. J. Theor. Biol. 282, 1–6. https://doi.org/10.1016/j.jtbi.2011.04.026

Hadfield, J., 2010. MCMC methods for Multi-response Generalised Linear Mixed Models: The MCMCglmm R package. J. Stat. Softw. 33, 1–22.

Haussmann, M.F., Vleck, C.M., Nisbet, I.C.T., 2003a. Calibrating the telomere clock in common terns, Sterna hirundo. Exp. Gerontol., Proceedings of the 2nd Symposium on Organisms with Slow Aging (SOSA-2) 38, 787–789. https://doi.org/10.1016/S0531-5565(03)00109-8

Haussmann, 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. Exp. Gerontol. 42, 610–618. https://doi.org/10.1016/j.exger.2007.03.004

Haussmann, M.F., Winkler, D.W., O'Reilly, K.M., Huntington, C.E., Nisbet, I.C.T., Vleck, C.M., 2003b. Telomeres shorten more slowly in long-lived birds and mammals than in short–lived ones. Proc. R. Soc. Lond. B Biol. Sci. 270, 1387–1392. https://doi.org/10.1098/rspb.2003.2385

Heidinger, B.J., Blount, J.D., Boner, W., Griffiths, K., Metcalfe, N.B., Monaghan, P., 2012. Telomere length in early life predicts lifespan. Proc. Natl. Acad. Sci. 109, 1743–1748. https://doi.org/10.1073/pnas.1113306109

Heidinger, B.J., Herborn, K.A., Granroth-Wilding, H.M.V., Boner, W., Burthe, S., Newell, M., Wanless, S., Daunt, F., Monaghan, P., 2016. Parental age influences offspring telomere loss. Funct. Ecol. 30, 1531–1538. https://doi.org/10.1111/1365-2435.12630

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). Sci. Rep. 6, 36856. https://doi.org/10.1038/srep36856

Horn, T., Robertson, B.C., Will, M., Eason, D.K., Elliott, G.P., Gemmell, N.J., 2011. Inheritance of Telomere Length in a Bird. PLOS ONE 6, e17199. https://doi.org/10.1371/journal.pone.0017199

Kimura, M., Cherkas, L.F., Kato, B.S., Demissie, S., Hjelmborg, J.B., Brimacombe, M., Cupples, A., Hunkin, J.L., Gardner, J.P., Lu, X., Cao, X., Sastrasinh, M., Province, M.A., Hunt, S.C., Christensen, K., Levy, D., Spector, T.D., Aviv, A., 2008. Offspring's Leukocyte Telomere Length, Paternal Age, and Telomere Elongation in Sperm. PLOS Genet. 4, e37. https://doi.org/10.1371/journal.pgen.0040037

King, C.E., 1983. A re-examination of the Lansing effect. Hydrobiologia 104, 135–139. https://doi.org/10.1007/BF00045959

Kucera, A., 2018. Sperm Telomere Dynamics: Natural Variation and Sensitivity to Environmental Influences in House Sparrows (Passer domesticus) (PhD). North Dakota State University.

Lansing, A.I., 1947. A Transmissible, Cumulative, and Reversible Factor in Aging. J. Gerontol. 2, 228–239. https://doi.org/10.1093/geronj/2.3.228

Lenth, R., 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software. J. Stat. Softw. 69, 1–33. https://doi.org/10.18637/jss.v069.i01

Lieshout, S.H.J. van, Froy, H., Schroeder, J., Burke, T., Simons, M.J.P., Dugdale, H.L., 2020. Slicing: A sustainable approach to structuring samples for analysis in long-term studies. Methods Ecol. Evol. 11, 418–430. https://doi.org/10.1111/2041-210X.13352

Lieshout, S.H.J. van, Sparks, A.M., Bretman, A., Newman, C., Buesching, C.D., Burke, T., Macdonald, D.W., Dugdale, H.L., 2021. Estimation of environmental, genetic and parental age at conception effects on telomere length in a wild mammal. J. Evol. Biol. 34, 296–308. https://doi.org/10.1111/jeb.13728

Madisen, L., Hoar, D.I., Holroyd, C.D., Crisp, M., Hodes, M.E., Reynolds, J.F., 1987. The effects of storage of blood and isolated DNA on the integrity of DNA. Am. J. Med. Genet. 27, 379–390. https://doi.org/10.1002/ajmg.1320270216

Mather, K.A., Jorm, A.F., Parslow, R.A., Christensen, H., 2011. Is Telomere Length a Biomarker of Aging? A Review. J. Gerontol. Ser. A 66A, 202–213. https://doi.org/10.1093/gerona/glq180

Nakagawa, S., Ockendon, N., Gillespie, D.O.S., Hatchwell, B.J., Burke, T., 2007. Does the badge of status influence parental care and investment in house sparrows? An experimental test. Oecologia 153, 749–760. https://doi.org/10.1007/s00442-007-0765-4

Njajou, O.T., Cawthon, R.M., Damcott, C.M., Wu, S.-H., Ott, S., Garant, M.J., Blackburn, E.H., Mitchell, B.D., Shuldiner, A.R., Hsueh, W.-C., 2007. Telomere length is paternally inherited and is associated with parental lifespan. Proc. Natl. Acad. Sci. 104, 12135–12139. https://doi.org/10.1073/pnas.0702703104

Nordfjäll, K., Svenson, U., Norrback, K.-F., Adolfsson, R., Roos, G., 2009. Large-scale parent–child comparison confirms a strong paternal influence on telomere length. Eur. J. Hum. Genet. 18, 385–389. https://doi.org/10.1038/ejhg.2009.178

Olsson, M., Pauliny, A., Wapstra, E., Uller, T., Schwartz, T., Blomqvist, D., 2011. Sex Differences in Sand Lizard Telomere Inheritance: Paternal Epigenetic Effects Increases Telomere Heritability and Offspring Survival. PLOS ONE 6, e17473. https://doi.org/10.1371/journal.pone.0017473

Pauliny, A., Larsson, K., Blomqvist, D., 2012. Telomere dynamics in a long-lived bird, the barnacle goose. ResearchGate 12, 257. https://doi.org/10.1186/1471-2148-12-257

Priest, N.K., Mackowiak, B., Promislow, D.E.L., 2002. The role of parental age effects on the evolution of aging. Evolution 56, 927–935. https://doi.org/10.1554/0014-3820(2002)056[0927:TROPAE]2.0.CO;2

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Found. Stat. Comput. Vienna Austria Version 3.6.1.

Reed, T.E., Kruuk, L.E.B., Wanless, S., Frederiksen, M., Cunningham, E.J.A., Harris, M.P., 2008. Reproductive senescence in a long-lived seabird: rates of decline in late-life performance are associated with varying costs of early reproduction. Am. Nat. 171, E89–E101. https://doi.org/10.1086/524957

Reichert, S., Criscuolo, F., Verinaud, E., Zahn, S., Massemin, S., 2013. Telomere Length Correlations among Somatic Tissues in Adult Zebra Finches. PLOS ONE 8, e81496. https://doi.org/10.1371/journal.pone.0081496

Reichert, S., Rojas, E.R., Zahn, S., Robin, J.-P., Criscuolo, F., Massemin, S., 2015. Maternal telomere length inheritance in the king penguin. Heredity 114, 10–16. https://doi.org/10.1038/hdy.2014.60

Richardson, D.S., Jury, F.L., Blaakmeer, K., Komdeur, J., Burke, T., 2001. Parentage assignment and extra-group paternity in a cooperative breeder: the Seychelles warbler (Acrocephalus sechellensis). Mol. Ecol. 10, 2263–2273. https://doi.org/10.1046/j.0962-1083.2001.01355.x

Salomons, H.M., Mulder, G.A., Zande, L. van de, Haussmann, M.F., Linskens, M.H.K., Verhulst, S., 2009. Telomere shortening and survival in free-living corvids. Proc. R. Soc. Lond. B Biol. Sci. 276, 3157–3165. https://doi.org/10.1098/rspb.2009.0517

Schroeder, J., Burke, T., Mannarelli, M.-E., Dawson, D.A., Nakagawa, S., 2012. Maternal effects and heritability of annual productivity. J. Evol. Biol. 25, 149–156. https://doi.org/10.1111/j.1420-9101.2011.02412.x

Schroeder, J., Nakagawa, S., Rees, M., Mannarelli, M.-E., Burke, T., 2015. Reduced fitness in progeny from old parents in a natural population. Proc. Natl. Acad. Sci. 112, 4021–4025. https://doi.org/10.1073/pnas.1422715112

Simons, M.J.P., 2015. Questioning causal involvement of telomeres in aging. Ageing Res. Rev. 24, 191–196. https://doi.org/10.1016/j.arr.2015.08.002

Sparks, A.M., Spurgin, L.G., Velde, M. van der, Fairfield, E.A., Komdeur, J., Burke, T., Richardson, D.S., Dugdale, H., 2020. Telomere heritability and parental age at conception effects in a wild avian population. EcoEvoRxiv. https://doi.org/10.32942/osf.io/eq2af

Taylor, H.A., Delany, M.E., 2000. Ontogeny of telomerase in chicken: Impact of downregulation on pre- and postnatal telomere length in vivo. Dev. Growth Differ. 42, 613–621. https://doi.org/10.1046/j.1440-169x.2000.00540.x

Torres, R., Drummond, H., Velando, A., 2011. Parental age and lifespan influence offspring recruitment: a long-term study in a seabird., Parental Age and Lifespan Influence Offspring Recruitment: A Long-Term Study in a Seabird. PloS One PLoS ONE 6, 6, e27245–e27245. https://doi.org/10.1371/journal.pone.0027245, 10.1371/journal.pone.0027245

Ujvari, B., Madsen, T., 2009. Short Telomeres in Hatchling Snakes: Erythrocyte Telomere Dynamics and Longevity in Tropical Pythons. PLOS ONE 4, e7493. https://doi.org/10.1371/journal.pone.0007493

Unryn, B.M., Cook, L.S., Riabowol, K.T., 2005. Paternal age is positively linked to telomere length of children. Aging Cell 4, 97–101. https://doi.org/10.1111/j.1474-9728.2005.00144.x

van Lieshout, S.H.J., Bretman, A., Newman, C., Buesching, C.D., Macdonald, D.W., Dugdale, H.L., 2019. Individual variation in early-life telomere length and survival in a wild mammal. Mol. Ecol. 28, 4152–4165. https://doi.org/10.1111/mec.15212

Vedder, O., Moiron, M., Bichet, C., Bauch, C., Verhulst, S., Becker, P.H., Bouwhuis, S., 2021. Telomere length is heritable and genetically correlated with lifespan in a wild bird. Mol. Ecol. Early-view. https://doi.org/10.1111/mec.15807

Voillemot, M., Hine, K., Zahn, S., Criscuolo, F., Gustafsson, L., Doligez, B., Bize, P., 2012. Effects of brood size manipulation and common origin on phenotype and telomere length in nestling collared flycatchers. BMC Ecol. 12, 17. https://doi.org/10.1186/1472-6785-12-17

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. Philos. Trans. R. Soc. B Biol. Sci. 373, 20160447. https://doi.org/10.1098/rstb.2016.0447

Zglinicki, T. v, Martin-Ruiz, C.M., 2005. Telomeres as Biomarkers for Ageing and Age-Related Diseases. Curr. Mol. Med. 5, 197–203. https://doi.org/info:doi/10.2174/1566524053586545