

1 **Title:** Evidence of paternal effects on telomere length increases in early-life

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3 **Running title:** Paternal influence of telomere length

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5 Sophie Bennett^{1,2*}, Antje Girndt^{1,3,4}, Alfredo Sánchez-Tójar^{1,3,4}, Terry Burke⁵, Mirre Simons⁵, Julia
6 Schroeder¹

7

8 ¹ Division of Biology, Imperial College London, Silwood Park, United Kingdom

9 ² UK Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK

10 ³ Department of Evolutionary Biology, Max Planck Institute for Ornithology, Seewiesen, Germany

11 ⁴ Department of Evolutionary Biology, Bielefeld University, Germany

12 ⁵ School of Biosciences, Ecology and Evolutionary Biology, University of Sheffield, Sheffield,

13 United Kingdom

14

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

16 **Abstract:**

17 Offspring of older parents in many species have decreased longevity, a faster ageing rate and lower
18 fecundity than offspring born to younger parents. Biomarkers of ageing, such as telomeres, that tend
19 to shorten as individuals age, may provide insight into the mechanisms of such parental age effects.
20 Parental age may be associated with offspring telomere length either directly through inheritance of
21 shortened telomeres or indirectly, for example through changes in parental care in older parents
22 affecting offspring telomere length. Across the literature there is considerable variation in estimates
23 of the heritability of telomere length, and in the direction and extent of parental age effects on
24 telomere length. To address this, we experimentally tested how parental age is associated with the
25 early-life telomere dynamics of offspring at two time points in a captive population of house
26 sparrows *Passer domesticus*. Birds are an emerging model of ageing and telomere biology. We
27 experimentally separated parental age from sex effects, and removed effects of age-assortative
28 mating, by allowing the parent birds to only mate with young, or old partners. The effect of parental
29 age was dependent on the sex of the parent and the offspring, and was found in the father-daughter
30 relationship only. Older fathers produced daughters with a greater early-life increase in telomere
31 length. Overall we found that offspring telomere length increased between the age of 0.5 and 3
32 months at the group and individual level. This finding is rare in birds with such increases more
33 commonly associated with non-avian taxa. Our results suggest parental age effects on telomere
34 length are sex-specific either through indirect or direct inheritance. The study of similar patterns in
35 different species and taxa will help us further understand variation in telomere length and its
36 evolution.

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

39 ***Introduction***

40 Parent age at conception is often associated with their offspring's life-history, with offspring of
41 older parents commonly having reduced reproductive success and longevity (Heidinger et al., 2016;
42 Monaghan et al., 2020; Priest et al., 2002a; Schroeder et al., 2015), but see (Travers et al., 2021).
43 Moreover, in some species, offspring of older parents experience higher rates of senescence,
44 cellular ageing, and decreased longevity compared to their older siblings that may be associated
45 with telomere attrition (Bouwhuis et al., 2010; Broer et al., 2013; Torres et al., 2011). While some
46 studies did not find such cross-generational effects of age (Froy et al., 2017; Unryn et al., 2005), the
47 cross-generational effects of age are reported across a wide range of taxa from rotifers (King, 1983)
48 and insects (Priest et al., 2002a) to birds and mammals (Bize et al., 2009; Haussmann et al., 2003),
49 and is termed the Lansing effect (Lansing, 1947).

50 One biomarker associated with biological age and longevity is the relative length of telomeres, the
51 chromosome capping structures consisting of TTAGGG base pair repeats in vertebrates (Heidinger
52 et al., 2012; Mather et al., 2011; Vedder et al., 2021). At each cell division telomeres shorten as the
53 very ends of chromosomes are not replicated, known as the end-replication problem (Levy et al.,
54 1992). Telomeres also partly function to prevent reactive oxygen species from damaging coding
55 DNA and are damaged themselves in the process (Aubert and Lansdorp, 2008). The activity levels
56 and expression of telomerase, the enzyme capable of elongating telomeres, decline rapidly in early
57 life and are tissue specific (Taylor and Delany, 2000). Together these processes lead to a gradual
58 telomere shortening over an individual's lifetime (Aubert and Lansdorp, 2008; Finkel and
59 Holbrook, 2000), which is why telomere length has been investigated as a biomarker for biological
60 age (Mather et al., 2011; Zglinicki and Martin-Ruiz, 2005). However, whether there is a direct
61 causal link between telomere length and ageing remains unclear (Boonekamp et al., 2013; Simons,
62 2015).

63 In birds, telomere loss is fastest in early-life and an initially longer telomere length is associated
64 with longer subsequent lifespans in captive and wild (Heidinger et al., 2016; Salomons et al., 2009;
65 Wilbourn et al., 2018) bird populations. There is evidence for telomere length being heritable in
66 birds (Vedder et al., 2021), and telomere dynamics have been associated with sex-specific parental
67 age and telomere length (Asghar et al., 2015; Reichert et al., 2015). However, the direction of the
68 association between telomere length, and maternal and paternal age varies even within bird species
69 (Dugdale and Richardson, 2018; Heidinger and Young, 2020). In some bird species, the offspring of
70 older mothers may have shorter telomeres and a faster attrition rate, especially in early development
71 (Asghar et al., 2015). Conversely, negative associations between paternal age and offspring

72 telomere length have been observed in the absence of maternal correlation (Horn et al., 2011;
73 Noguera et al., 2018; Sparks et al., 2021).

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

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

88 ***Materials and Methods:***

89 ***Study species and experimental design:***

90 We used captive house sparrows at the Max Planck Institute for Ornithology, Seewiesen, Germany,
91 during the breeding season of 2014. We used 42 pairs of male and female sparrows, which were
92 assigned to four treatments, each with an equal sex ratio and a uniform distribution of ages across
93 both sexes to control for age-assortative mating. We experimentally bred pairs in one of four age
94 combinations: old-female/ old-male (OO, n=8 pairs), old-female/ young-male (OY, n=11 pairs),
95 young-female/ old-male (YO, n=13 pairs), and young-female/ young-male (YY, n=10 pairs). Young
96 birds hatched the preceding summer. Old (O) was defined as sparrows aged 4 years and older,
97 although most individuals were 7 years or older (Males: 8 years = 2, 9 years = 21; Females: 4 years
98 = 1, 7 years= 10, 8 years= 4, and 9 years= 1). The difference in age distribution between females
99 and males corresponded to that observed in the wild, where females live shorter than males
100 (Schroeder et al., 2012). We did not use the middle aged groups because in wild house sparrows,
101 reproductive senescence may start at 3 years for females (Schroeder et al., 2012), or 5 years in
102 males (Hsu et al. 2017). Each treatment group was split in two separate breeding groups located in
103 separate aviaries. Each replicate aviary contained 15.3 (s.d= 4.9) males and 14.6 (s.d=2.4) females
104 of the respective age class. Bird husbandry is described in Girndt et al. (2017).

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

110 ***Blood sample collection:***

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

116 ***DNA extraction and quantification:***

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

122 ***Estimation of telomere length:***

123 We used multiplex qPCR to determine relative telomere length. We determined 'T' as the number
124 of telomere repeats and 'S' as the number of control gene repeats. We then used the T/S ratio as a
125 proxy for telomere length. The four DNA primers we used are described in Criscuolo et al. (2009).
126 We used DNA from house sparrows not included in this analysis as a dilution standard at five DNA
127 concentrations of approximately 80, 20, 5, 1.25 and 0.31ng/ml, on each plate. We then used these
128 standards to produce a standard curve for all analysed samples. In each well we added 1.5µl of
129 DNA sample, 0.9µl of each primer, 10µl of Sybr®Select Master Mix and 4.9µl ddH₂O. We ran
130 each plate with an equal number of 0.5 and 3 months sample pairs from the same individual to
131 account for any potential sample and plate effects when comparing within-individual changes in
132 telomere length. We ran 42 samples, the five standards and a negative (with all components except
133 a DNA sample) in duplicate on each 96-well plate. We ran the qPCR cycling conditions using
134 QuantStudio 12kFlex Software v1.2.2 following the cycle timings given in Cawthon (2009). We
135 analysed the software output to calculate the T/S ratio in each sample using a custom script that
136 performed background subtraction, thresholding and standard curve correction (Appendix 1.1). We
137 altered the thresholds for the standard curve of the telomere and GAPDH primers for each plate

138 based on amplification plots resulting in efficiencies of between 99.3-99.7 for GAPDH and 99.3-
139 105.8 for telc and telg. The standard curve for each plate had an R^2 of 0.99 and the intra- and inter-
140 plate variation coefficients all met adequate levels (Cawthon, 2009). We also ran a melt curve to
141 confirm whether the expected two products were generated in the reaction. Additionally, we
142 checked all plate amplification curves to see if DNA was present in the control, as this would
143 indicate contamination. In all plates DNA was absent, apart from very late amplification due to
144 primer dimerization. We repeated any sample duplicates that had a standard deviation of >0.05
145 following thresholding and used the mean T/S ratio of duplicates in our analysis. To test the
146 reliability of these measurements we also calculated the repeatability of the T/S ratios at both time
147 points using the individually duplicated T/S measurements, using the R package 'rptR' v.0.9.22
148 (Stoffel et al., 2017) with 1000 bootstrap iterations. Based on duplicates of the same sample the
149 sample repeatability of the T/S ratios at 0.5 months was 0.98 (95% confidence interval: 0.97, 0.99),
150 and at 3 months it was 0.99 (95% confidence interval: 0.99, 0.99). In our analyses, T/S ratios of
151 offspring at 0.5 months old are referred to as T/S_{0.5} and samples at 3 months old as T/S₃. We then
152 calculated the difference between the two measurements as $\Delta T/S$. The within-individual
153 repeatability of T/S ratios between the two time points was 0.27 (95% confidence interval: 0.01,
154 0.51). All samples were analysed for telomere length at the same time and had a similar shelf time
155 (Lieshout et al., 2020). All reagents and equipment were produced by Thermo Fisher Scientific,
156 Waltham, Massachusetts, US.

157 ***Ethical Note:***

158 The Government of Upper Bavaria, Germany, approved the care, handling and husbandry of all
159 birds in this study and granted a license for animal experiments to JS (Nr311.5–5682.1/1-2014-
160 024).

161 ***Statistical Analysis:***

162 We tested for a change in telomere length over the 2.5 months period by running a linear mixed
163 effects model (LMM) with T/S as response variable, time of sampling (0.5 or 3 months) as a fixed
164 effect, and individual chick ID as a random effect on the intercept. Next, we ran two further LMMs
165 with the response variable T/S_{0.5} and T/S₃, respectively. For each of these two models we tested the
166 fixed effects of the paternal and maternal age categories (either 'young' or 'old' with 'old' as the
167 reference level). To test for sex-specific parental effects, we included offspring sex as a fixed effect
168 (with 'male' as the reference level) and an interaction of chick sex with parental age in the T/S_{0.5}
169 model. Because not all chicks were sampled at exactly 3 months after hatching (mean= 100.8 days,
170 s.d.= 8.4), we also tested for an effect of the exact offspring age in days in T/S₃ using a LMM with
171 T/S₃ as the response variable. There is a potential effect of the time a blood or DNA sample has

172 been stored until analysis (Sibma, 2021) and therefore we added ‘sample age’ as a fixed factor
173 effect. We found that ‘sample age’ (a two-level categorical variable of either ‘previously-’ or
174 ‘newly-extracted’) did not have a statistically significant effect on T/S_3 (posterior mode= -0.001,
175 95% credible interval, 95%CI= -0.01, 0.001, pMCMC= 0.81). Still, to account for any potential bias
176 we retained ‘sample age’ as a fixed effect in the T/S_3 model. Note that our results however
177 remained qualitatively similar whether or not we retained sample age in the model.

178 As the 0.5 months samples were also a mix of previously-, or newly-extracted DNA samples, we
179 tested whether time of extraction had any effect on the calculated $T/S_{0.5}$ ratio as a result of DNA
180 degradation (Madisen et al., 1987) (n samples newly-extracted= 10/75). We fitted a LMM with
181 $T/S_{0.5}$ as the response and the time of extraction as a fixed effect, either ‘newly-’ or ‘already
182 extracted’. We found no statistically significant difference between newly- and already-extracted
183 samples (posterior mode= -0.06, 95%CI= -0.20, 0.08, pMCMC=0.389). Further, a previous study
184 investigating house sparrow telomere length found that the repeatability between newly- and
185 previously-extracted samples was moderate (0.45, 95%CI= 0.35, 0.63; [Sibma, 2021](#)).

186 We included the nest box ID and aviary ID in which chicks were born as random effects on the
187 intercept in all models to account for variance between broods and aviaries. We also included the
188 random term of qPCR plate ID in all models to account for between-plate variance on the intercept.
189 We examined the collinearity of the fixed effects, as collinearity could distort model results, but it
190 did not exceed 0.7 (Dormann et al., 2013). All models were run using the Markov chain Monte
191 Carlo (MCMC) method in the R package MCMCglmm v.2.29 (Hadfield, 2010).

192 ***Model validation:***

193 As we used a Bayesian modelling approach, we deemed fixed effects to be statistically significant if
194 their 95% credible intervals did not span zero, and we also report MCMC-p-values (pMCMC)
195 (Hadfield, 2010). All terms were retained in models irrespective of their statistical significance. We
196 directly assessed model autocorrelation for fixed and random effects to ensure that the risk of type I
197 errors was not inflated. We also inspected iteration and density plots to ensure that effects showed
198 equal variation around a constant mode and demonstrated convergence (Gelman and Hill, 2006;
199 Hadfield, 2010). We ran all models for 100,000 iterations with a thinning interval of 10 and used
200 minimally-informative flat priors. Gelman-Ruben statistics for all variables was between 1 and 1.05
201 indicating convergence (Brooks and Gelman, 1998). Effective sample sizes were >400 at all times
202 and trace plots indicated good mixing of chains. All statistical analyses were carried out in R v.3.6.1
203 (R Core Team, 2021).

204 **Results:**

205 Unexpectedly, the telomere length of 80% of the offspring for which both measurements were
206 available increased between 0.5 and 3 months of age (n=45/56; Fig. 1, Table 1).

207 We did not find a statistically significant effect of parental age class on T/S at 0.5 months, which is
208 shortly before sparrows gain independence and fledge from their nest (Table 2). However, we
209 detected statistically significant effects of paternal age on T/S at 3 months such that daughters of
210 young fathers had shorter telomeres than daughters of old fathers (Table 2, Fig. 2). In contrast,
211 paternal age had no statistically significant effect on the telomere length of sons at three months
212 (Table 2, Fig. 2).

213 **Discussion:**

214 Individual chick telomere length increased between 0.5 and 3 months of age. This increase
215 disagrees with much of the published literature, which generally finds a decrease in telomere length
216 in early-life (Boonekamp et al., 2014; Cerchiara et al., 2017; De Meyer et al., 2007; Hoelzl et al.,
217 2016; Salomons et al., 2009). While a population level increase in telomere length has previously
218 been found in some long-lived bird species (Hausmann et al., 2007; Pauliny et al., 2012), other
219 studies have found that telomeres elongation for a proportion of chicks is more common in shorter-
220 lived species (A. M. Brown et al., 2021; T. Brown et al., 2021; Eisenberg, 2019) and few longer-
221 lived species (Cerchiara et al., 2017). For example, a study on jackdaws *Corvus monedula* found
222 that between 5 and 30 days post-hatching, telomere lengths increased for 25% of sampled offspring
223 (Grasman et al., 2011). An increase in early-life telomere length has also been observed in non-
224 avian taxa, including water pythons *Liasis fuscus* (Ujvari and Madsen, 2009) and European badgers
225 *Meles meles* (Lieshout et al., 2019). A lack of comparable published research exploring a change in
226 telomere length using multiple time points in early life may, in part, explain the surprising nature of
227 our observed increase in telomere length in early-life.

228 An increase in telomere length can have methodological (Sheldon et al., 2021) and/or biological
229 explanations (Ujvari and Madsen, 2009). First, it could be due to DNA in samples degrading over
230 time (Madsen et al., 1987; but see Seutin et al., 1991). Since we used previously-extracted DNA
231 for the majority of 0.5 month samples, we investigated whether differential telomere degradation
232 rates between DNA and blood sample extraction types could be a cause for the observed increase.
233 We found no statistically significant difference between the telomere lengths of newly- and
234 previously-extracted samples and thus, telomere degradation in extracted samples over time seems
235 like an unlikely explanation for our results.

236 Second, qPCR plates contained both 0.5 and 3 months samples, and between-plate variance was
237 negligible in all our models, highlighting that this element of our methodology had little impact on
238 our results. Overall, we monitored procedural efficiency throughout data collection and did not
239 identify any other potential methodological sources of variation; the repeatability estimates for the
240 T/S ratios estimated from within-individual samples were well within the range of those for similar
241 species in other qPCR studies (Kärkkäinen et al., 2021). Consequently, we believe that the increase
242 in telomere length observed in our study has a biological explanation. For example, telomerase
243 activity might have been maintained in the offspring after the first sample was taken. Indeed, two
244 studies have shown that telomerase activity can be maintained up to five weeks post-hatching in
245 zebra finches *Taeniopygia guttata* (Hausmann et al., 2007) and chickens *Gallus gallus* (Taylor and
246 Delany, 2000). Yet, neither of these studies assessed telomerase activity at multiple time points in
247 the same individual's early-life post-hatching, which remains as an interesting future avenue for the
248 field.

249 While we expected that old parents would produce offspring with shorter telomeres, as found in
250 other short-lived bird species in line with predictions of the Lansing effect (Bauch et al., 2019;
251 Criscuolo et al., 2017), our experimental approach found that old fathers produced daughters with
252 longer telomeres, but only 3 months after hatching, potentially indicating an environmental or an
253 age-dependent epigenetic effect. Positive relationships between parental age and offspring telomere
254 length have previously been found previously in long- and short-lived bird species (Asghar et al.,
255 2015; Becker et al., 2015; A. M. Brown et al., 2021; Dupont et al., 2018). Such effects may arise
256 indirectly for example through improved parental care that older individuals provide compared to
257 inexperienced, young breeders. However the positive effect of improved parental care by older
258 parents also shows senescence in the oldest individuals (Beamonte-Barrientos et al., 2010). It is also
259 possible that these effects arise from a phenomenon whereby parents that confer longer telomere
260 length to their young also survive for longer. These positive effects of parental age on telomere
261 length are in contrast to some previous studies that found a negative effect of parental age resulting
262 from the poorer condition of these old individuals (Bouwhuis et al., 2018; Criscuolo et al., 2017), or
263 a lack of an effect of parental age on parental care (Nakagawa et al., 2007). Further, in some studies
264 testing parent sex-specific effects, offspring telomere length was found to correlate only with
265 maternal age, and only relatively soon after hatching (ten days in king penguins *Aptenodytes*
266 *patagonicus*: Reichert et al. (2015); nine days in great reed warblers *Acrocephalus arundinaceus*:
267 Asghar et al. (2015)). As we found no effect of maternal age in our study, an influence of maternal
268 age on offspring telomere length may well have been present, but already diminished below
269 detectable levels 0.5 months after hatching, when our first sampling took place.

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

281 However, we did not detect an effect of parental age on offspring telomere length at 0.5 months
282 after hatching. This is again in contrast to studies finding evidence to support the Lansing effect
283 where offspring of older parents may have shorter telomeres in early-life with potential implications
284 for longevity (Monaghan et al., 2020; Priest et al., 2002b). Heidinger et al. (2016) similarly found
285 no effect of parental age on offspring telomere length in early-life at 25 days after hatching in
286 European shags *Phalacrocorax aristotelis*. Further, variation in pre-fledging telomere length may in
287 part be explained by brood-specific additive genetic effects (Voillemot et al., 2012). As such, it may
288 be that at later time points effects of parent age and post-fledging environmental factors appear to
289 be more important than brood-specific effects in determining offspring telomere length. Again,
290 there is a need for more studies investigating the relationship between paternal age and telomere
291 dynamics to detect when and how patterns of telomere dynamics are driven.

292 In summary, we find that telomere lengths increased in early-life with a likely biological cause.
293 Furthermore, our results indicate that paternal age effects are more influential on offspring telomere
294 length than maternal age effects in our population of house sparrows, with the daughters of older
295 fathers having longer telomeres. Future analyses of telomerase activity levels in both the sperm of
296 adult males and the somatic tissues of offspring would yield further insights into the drivers of
297 parental age effects on offspring telomere dynamics in early-life.

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302 **Competing interests' statement:**

303 No competing interests declared.

304 **Author contributions:**

305 Conceptualization: SB, JS; Methodology: SB, JS, MJPS; Validation: SB, MJPS; Formal analysis:
306 SB, JS; Investigation: SB, AG, JS, AST; Resources: JS, MJPS, TB; Data curation: SB, JS, TB;
307 Writing- original draft: SB; Writing- review & editing: SB, JS, AG, AST, MJPS; Visualization: SB,
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315 **Data availability statement:**

316 The data and code are available at the Open Science Foundation through this link:

317 https://osf.io/6kwzh/?view_only=96b0d8a81ce84ba09b364e514ab0072e.

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540

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

543

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

549

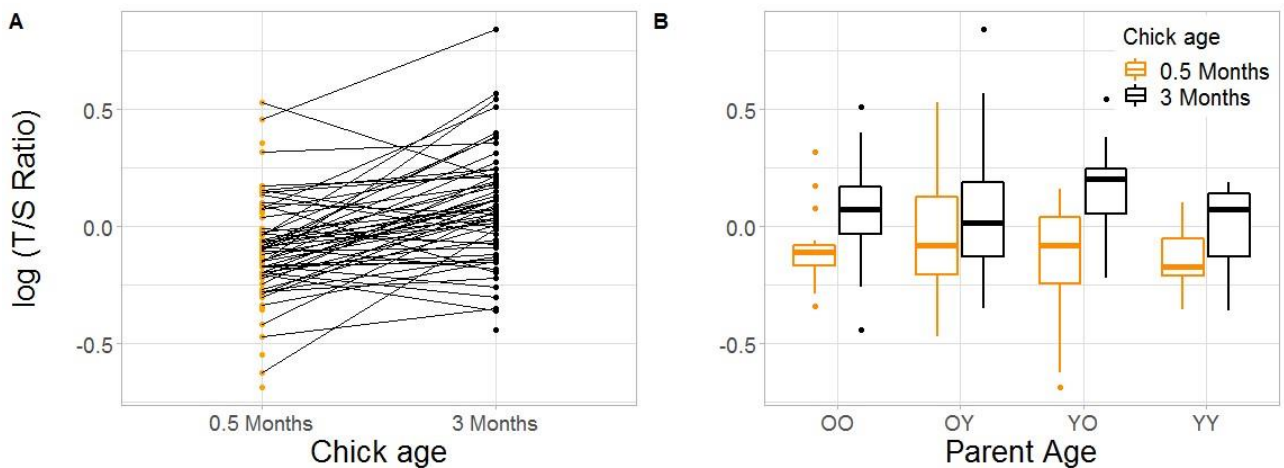
550 Chick age was modelled as either 0.5 months (75 chicks) or 3 months (59 chicks), with 0.5 months as a reference level.
 551 Estimates shown are posterior modes. Statistically significant effects are shown in bold.

552 **Table 2:** Results from two Bayesian MCMC linear mixed-effects models with telomere length of
 553 house sparrow chicks at age 0.5 months ($T/S_{0.5}$) and 3 months (T/S_3) as response variables,
 554 respectively.

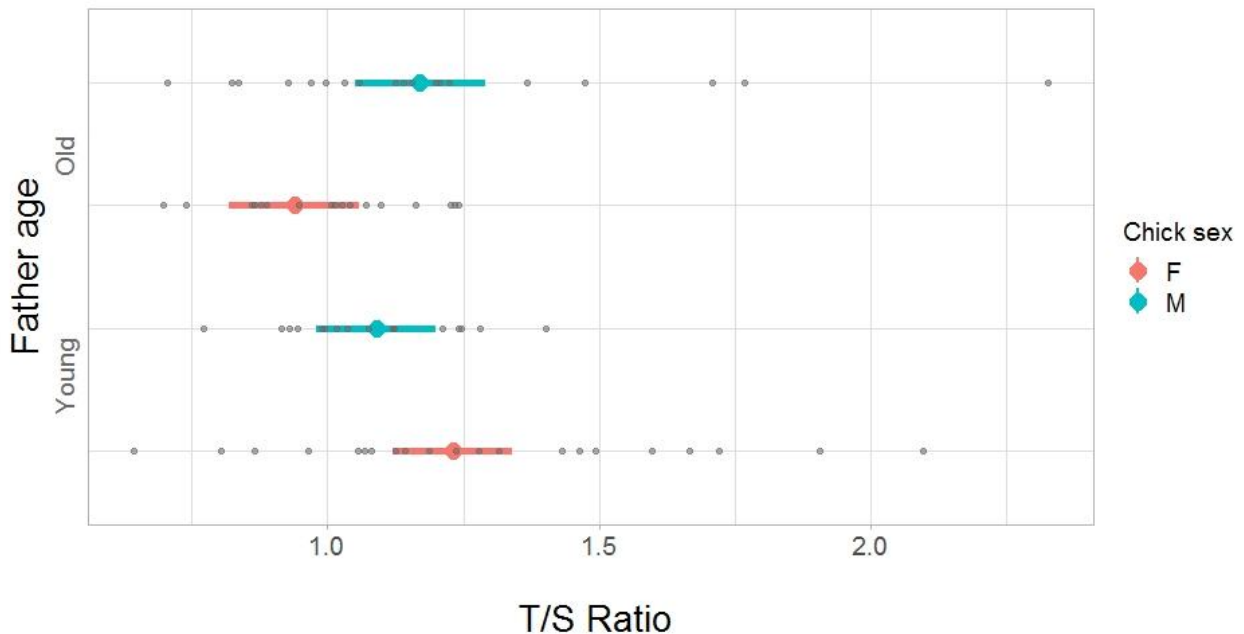
<i>Parameter</i>	<i>T/S_{0.5}</i>			<i>T/S₃</i>		
	<i>Estimate</i>	<i>95%CI</i>	<i>p_{MCMC}</i>	<i>Estimate</i>	<i>95%CI</i>	<i>p_{MCMC}</i>
<i>Intercept</i>	0.97	0.84 - 1.10	<0.001	1.57	0.32 - 2.71	0.022
<i>Chick sex</i>	-0.08	-0.22 - 0.11	0.469	-0.23	-0.41 - 0.61	0.121
<i>Maternal age</i>	-0.07	-0.23 - 0.08	0.346	0.06	-0.32 - 0.21	0.711
<i>Maternal age x Chick sex</i>	0.06	-0.15 - 0.25	0.597	0.09	-0.21 - 0.43	0.573
<i>Paternal age</i>	-0.03	-0.20 - 0.10	0.481	-0.27	-0.52 - 0.00	0.047
<i>Paternal age x Chick sex</i>	0.6	-0.07 - 0.34	0.168	-0.40	0.09 - 0.71	0.016
<i>Sample day</i>				0.00	-0.01 - 0.01	0.694
<i>Random effects</i>						
<i>Nest box ID</i>	0.01	0.00 - 0.03		0.01	0.00 - 0.02	
<i>Aviary ID</i>	0.00	0.00 - 0.01		0.01	0.00 - 0.01	
<i>qPCR plate ID</i>	0.00	0.00 - 0.01		0.00	0.00 - 0.01	
<i>Residual</i>	0.08	0.03 - 0.11		0.08	0.03 - 0.11	

555 Maternal and paternal age were modelled as either young or old; young was <2 years old, and old was determined as >3
 556 years old). 0.5 months: n= 69 chicks, 3 months: n= 59. The reference level for parental ages was 'old', and 'female' was
 557 the reference level for chick sex. Estimates shown are posterior modes. Statistically significant effects are shown in
 558 bold.

559 **Figures:**



560 **Figure 1: Change in telomere length (log(T/S Ratio)) within house sparrow chicks at 0.5 and 3**
561 **months of age.** A) Individuals are connected by a line (n offspring with samples at 0.5 months= 75,
562 at 3 months= 59). B) Boxplots show the mean (central line) and 25th and 75th percentiles (lower
563 and upper box bounds respectively) of the log(T/S Ratio) within age group of the chicks' parents (Y
564 = 3 years old). T/S Ratio is presented on the log scale to aid visualisation. YO = young mothers, old
565 fathers (n= 19, 12). OO = both parents old (n= 18, 19). OY = old mothers, young fathers (n= 17,
566 18). YY = both parents young (n= 15, 10).



567 **Figure 2: Daughters of 'old' fathers had statistically significantly longer telomeres.** Posterior
568 modes (red and blue dots) and corresponding 95% credible intervals (lines) from a linear mixed-
569 effects model testing the relationship between T/S₃, father age, and sex of chicks (Table 1). Fathers
570 were assigned an age category of young, 'Y', or old, 'O'. A young father was <2 years old, and an

571 old father was determined as >7 years old. Chick sex is indicated as either female, 'red', or male,
572 'blue'. The number of offspring in each category; Y, and female= 12, male= 16, O, and female= 16,
573 male= 15. Raw data points are shown as grey dots.