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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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 chicks at two time points in a captive population of house sparrows
26 *Passer domesticus*. We experimentally separated parental age from sex effects, and removed effects
27 of age-assortative mating, by allowing the parent birds to only mate with young, or old partners.
28 The effect of parental age was dependent on the sex of the parent and the chicks, and was found in
29 the father-daughter relationship only; older fathers produced daughters with longer telomere lengths
30 post-fledging. Overall we found that chick telomere length increased between the age of 0.5 and 3
31 months at the population and individual level. This finding is unusual in birds with such increases
32 more commonly associated with non-avian taxa. Our results suggest parental age effects on
33 telomere length are sex-specific either through indirect or direct inheritance. The study of similar
34 patterns in different species and taxa will help us further understand variation in telomere length
35 and its evolution.

36 **Keywords:** telomere dynamics, ageing, inter-generational effects, z-linked inheritance,
37 transgenerational effects, Lansing effect

38 ***Introduction***

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

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

62 In birds, telomere loss is fastest in early life and an initially longer telomere length is associated
63 with longer subsequent lifespans in captive and wild bird populations (Heidinger et al., 2016;
64 Salomons et al., 2009; Wilbourn et al., 2018). There is evidence for telomere length being heritable
65 in birds (Vedder et al., 2021), and telomere dynamics have been associated with sex-specific
66 parental age and telomere length (Asghar et al., 2015; Reichert et al., 2015). However, the direction
67 of the association between telomere length, and maternal and paternal age varies even within bird
68 species (Dugdale and Richardson, 2018; Heidinger and Young, 2020). In some bird species, the
69 offspring of older parents may have shorter telomeres and a faster attrition rate, especially in early
70 development (Heidinger et al., 2016). Other studies find this effect only in relation to older mothers
71 (Asghar et al., 2015), or fathers (Horn et al., 2011; Noguera et al., 2018; Sparks et al., 2021).

72 Another body of studies find a positive relationship between parental age and early life telomere
73 lengths in offspring (fathers: Heidinger et al., 2021; mothers: Sparks et al., 2021). Consequently
74 there is a great need for additional studies investigating the complexities of the relationship between
75 parental ages and offspring telomere lengths.

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

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

90 ***Materials and Methods:***

91 ***Study species and experimental design:***

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

105 separate breeding groups located in separate semi-outdoors aviaries. Aviaries had a dimension of
106 1.2m x 4.0m x 2.2m (length x width x height). Each aviary contained between 24-31 individuals. As
107 the outside of aviaries was a semi-permeable mesh the birds experienced essentially natural
108 environmental conditions. Aviaries also received some additional artificial lighting around dawn
109 and dusk to compensate for slightly reduced light levels inside the aviaries at this time of day
110 compared to the local natural conditions. Each aviary contained 15.3 (s.d= 4.9) males and 14.6 (s.d=
111 2.4) females of the respective age class. Bird husbandry is described in more detail in Girndt et al.
112 (2017).

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

118 ***Blood sample collection:***

119 We took blood samples from all chicks before they fledged, 0.5 months after they hatched (samples
120 taken at 12 days post-hatching, n= 75). Blood samples were collected from the brachial vein of
121 chicks using 1mm capillary tubes and stored in 1ml of 96% ethanol. After fledging, chicks
122 remained in the same aviary as their parents and siblings, and were blood sampled again 2.5- 3
123 months later (n= 59, samples taken at 83-115 days post-hatching). We obtained second samples for
124 an additional 15 chicks however, these samples were taken at significantly different time points (24-
125 74 days of age) due to logistical constraints and so were unsuitable for inclusion in this study. We
126 collected samples of 56 individuals at both time points to test for within-individual changes. After
127 collection blood samples were stored at room temperature in ethanol until DNA extraction.

128 ***DNA extraction and quantification:***

129 DNA for all 0.5 month samples and a minority of 3 month samples were extracted just prior to
130 qPCR processing. However, the majority of 0.5 month samples had DNA extracted concurrent with
131 their sampling (up to 18 months previously) and were then frozen at -20°C until being thawed for
132 this study. Following standard DNA extraction (Richardson et al., 2001), the DNA concentration of
133 all samples was measured using a ThermoScientific NanoDrop8000 Spectrophotometer and sample
134 concentration was to 20-30ng/ml to ensure similar amplification of samples during qPCR. Where
135 necessary, samples were diluted with T10E0.1 (10mM Tris-HCl, pH 8.0, 0.1mM EDTA, pH 8.0) or
136 concentrated using a ThermoScientific Savant DNA SpeedVac Concentrator. Purity of samples was

137 checked through measurement of 260/280 absorbance ratios; ratios were between 1.7-2.0 for all
138 samples.

139 ***Estimation of telomere length:***

140 We used multiplex qPCR to determine relative telomere length. We determined 'T' as the number
141 of telomere repeats and 'S' as the number of control gene repeats using GAPDH as a reference
142 gene. We then used the T/S ratio as a proxy for telomere length. The four DNA primers we used are
143 described in Criscuolo et al. (2009). We used DNA from house sparrows not included in this
144 analysis as a golden sample dilution standard at five DNA concentrations of approximately 80, 20,
145 5, 1.25 and 0.31ng/ml, on each plate. We then used these standards to produce a standard curve for
146 all analysed samples. In each well we added 1.5µl of DNA sample, 0.9µl of each primer, 10µl of
147 Sybr®Select Master Mix and 4.9µl ddH_2O. We ran each plate with an equal number of 0.5 and 3
148 months sample pairs from the same individual to account for any potential sample and plate effects
149 when comparing within-individual changes in telomere length. We ran 42 samples, the five
150 standards and a negative (with all components except a DNA sample) in duplicate on each 96-well
151 plate. We ran the qPCR cycling conditions using QuantStudio 12kFlex Software v1.2.2 following
152 the cycle timings given in Cawthon (2009). We analysed the software output to calculate the T/S
153 ratio in each sample using a custom script that performed background subtraction, thresholding and
154 standard curve correction (code provided). We altered the thresholds for the standard curve of the
155 telomere and GAPDH primers for each plate based on amplification plots resulting in efficiencies of
156 between 99.3-99.7 for GAPDH and 99.3-105.8 for telc and telg. The standard curve for each plate
157 had an R^2 of 0.99 and the intra- and inter-plate variation coefficients all met adequate levels
158 (Cawthon, 2009). We also ran a melt curve to confirm whether the expected two products were
159 generated in the reaction. Additionally, we checked all plate amplification curves to see if DNA was
160 present in the control, as this would indicate contamination. In all plates DNA was absent, apart
161 from very late amplification due to primer dimerization. We repeated any sample duplicates that
162 had a standard deviation of >0.05 following thresholding and used the mean T/S ratio of duplicates
163 in our analysis. To test the reliability of these measurements we also calculated the repeatability of
164 the T/S ratios at both time points using the individually duplicated T/S measurements, using the R
165 package 'rptR' v.0.9.22 (Stoffel et al., 2017) with 1000 bootstrap iterations. Based on duplicates of
166 the same sample the sample repeatability of the T/S ratios at 0.5 months was 0.98 (95% confidence
167 interval: 0.97, 0.99), and at 3 months it was 0.99 (95% confidence interval: 0.99, 0.99). The
168 individual repeatability of T/S ratios between the two time points was 0.27 (95% confidence
169 interval: 0.01, 0.51), a similar value to the early life telomere length repeatability estimated by
170 Hiedinger et al. (2021) (r= 0.28, range 0.18-0.5). All samples were analysed for telomere length at

171 the same time and had a similar shelf time (Lieshout et al., 2020). All reagents and equipment were
172 produced by Thermo Fisher Scientific, Waltham, Massachusetts, US.

173 ***Ethical Note:***

174 The Government of Upper Bavaria, Germany, approved the care, handling and husbandry of all
175 birds in this study and granted a license for animal experiments to JS (Nr311.5–5682.1/1-2014-
176 024).

177 ***Statistical Analysis:***

178 In our analyses, T/S ratios of chicks at 0.5 months old are referred to as $T/S_{0.5}$ and samples at 2.5-3
179 months old as T/S_3. We tested for a change in telomere length over the 2.5 months period by
180 running a linear mixed effects model (LMM) with T/S as response variable, time of sampling (0.5
181 or 3 months) as a fixed effect, and individual chick ID as a random effect on the intercept. Next, we
182 ran two further LMMs with the response variable $T/S_{0.5}$ and T/S_3, respectively to test the effect of
183 parental ages on chick telomere lengths at either time point, and whether these effects differed with
184 chick sex. For each of these two models we tested the fixed effects of the paternal and maternal age
185 categories (either 'young' or 'old', with 'old' as the reference level). To test for sex-specific
186 parental effects, we included chick sex as a fixed effect (with 'male' as the reference level) and an
187 interaction of chick sex with parental age in both the $T/S_{0.5}$ and T/S_3 models. As all chicks were
188 sampled at 12 days post-hatching to collect $T/S_{0.5}$ samples, but chicks were of a variable age when
189 T/S_3 samples were taken (mean= 100.8 days, s.d.= 8.4), we also included a fixed effect of the exact
190 chick age in days,'sample day', in the model with T/S_3 as the response. We found no statistically
191 significant effect of 'sample day' on T/S_3 (posterior mode= 0.004, 95%CI= -0.02, 0.007, pMCMC=
192 0.46). Still, to account for any potential bias we retained 'sample day' as a fixed effect in the T/S_3
193 model. Note that our results, however, remained qualitatively similar whether or not we retained
194 sample age in the model.

195 There is also a potential effect of the time a blood or DNA sample has been stored until analysis on
196 quantified telomere lengths (Sibma, 2021). As the $T/S_{0.5}$ samples were a mix of previously-, or
197 newly-extracted DNA samples, we tested whether time of extraction had any effect on the
198 calculated $T/S_{0.5}$ ratio as a result of DNA degradation (Madisen et al., 1987) (n samples newly-
199 extracted= 10/75). We fitted a LMM with $T/S_{0.5}$ as the response and the time of extraction, 'sample
200 age', as a fixed effect two-level categorical variable of, either 'newly-' or 'previously extracted'.
201 Newly-extracted samples were extracted at the same time as the three months samples, previously-
202 extracted samples were extracted 18 months prior. We found no statistically significant difference
203 between newly- and previously-extracted samples (posterior mode= -0.06, 95%CI= -0.20, 0.08,

204 pMCMC=0.389). Further, a previous study investigating house sparrow telomere length found that
205 the repeatability between newly- and previously-extracted samples was moderate (0.45, 95%CI=
206 0.35, 0.63; Sibma, 2021).

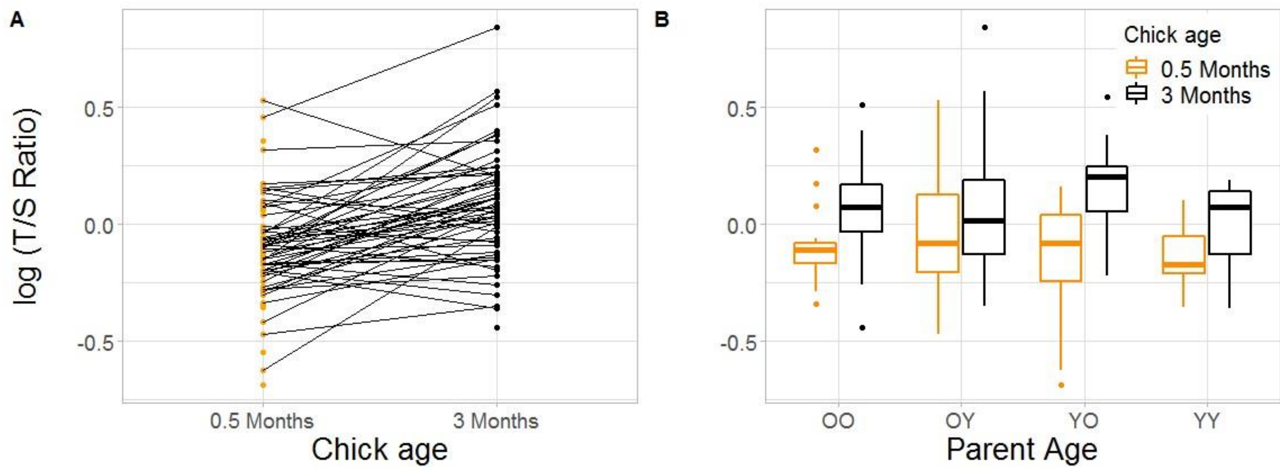
207 We included the nest box ID and aviary ID in which chicks were born as random effects on the
208 intercept in all models to account for variance between broods and aviaries. We also included the
209 random term of qPCR plate ID in all models to account for between-plate variance on the intercept.
210 We include a random effect of chick ID in the first model testing for a change in chick telomere
211 length between the two time periods as we had multiple measurements from individuals. We
212 examined the collinearity of the fixed effects, as collinearity could distort model results, in no cases
213 did this exceed 0.7 (Dormann et al., 2013). All models were run using the Markov chain Monte
214 Carlo (MCMC) method in the R package MCMCglmm v.2.29 (Hadfield, 2010).

215 ***Model validation:***

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

227 ***Results:***

228 Unexpectedly, the telomere length of 80.4% of the chicks for which both measurements were
229 available increased between 0.5 and 3 months of age (n=45/56; Fig. 1, Table 1).



230 **Figure 1: Change in telomere length (log(T/S Ratio)) within house sparrow chicks at 0.5 and 3**
231 **months of age.** A) Individuals are connected by a line (n offspring with samples at 0.5 months= 75,
232 at 3 months= 59). B) Boxplots show the mean (central line) and 25th and 75th percentiles (lower
233 and upper box bounds respectively) of the log(T/S Ratio) within age group of the chicks' parents
234 (young birds, Y, were a parents that hatched the preceding summer, old birds, O, were parents that
235 were ≥4 years old). T/S Ratio is presented on the log scale to aid visualisation. YO = young
236 mothers, old fathers (n= 19 offspring with 0.5 month samples, 12 offspring with 3 month samples).
237 OO = both parents old (n= 18, 19). OY = old mothers, young fathers (n= 17, 18). YY = both parents
238 young (n= 15, 10).

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

241

242

Parameter	*Estimate*	*95% credible 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 ID	0.02	0.01 - 0.04	
Aviary ID	0.00	0.00 - 0.00	
qPCR plate ID	0.00	0.00 - 0.01	
Residual	0.04	0.02 - 0.05	

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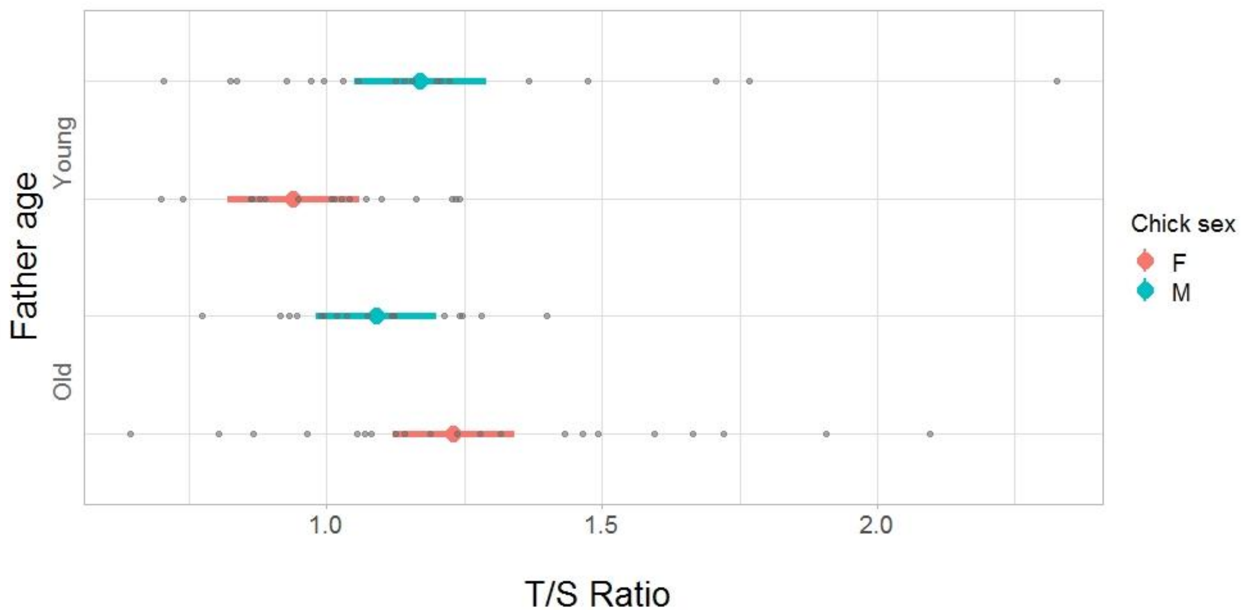
248 Chick age was modelled as either 0.5 months (75 chicks) or 3 months (59 chicks), with 0.5 months as a reference level.
249 Estimates shown are posterior modes. Statistically significant effects are shown in bold.

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



256 **Figure 2: Daughters of 'old' fathers had statistically significantly longer telomeres.** Forest plot
257 of the posterior modes (red and blue dots) and corresponding 95% credible intervals (lines) from a
258 linear mixed-effects model testing the relationship between T/S_3, father age, and sex of chicks
259 (Table 2). Fathers were assigned an age category of young, 'Y', or old, 'O'. A young father hatched
260 in the preceding summer, and an old father was $\geq$4 years old. Chick sex is indicated as either
261 female, 'red', or male, 'blue'. The number of offspring in each category; Y, and female= 12, male=
262 16, O, and female= 16, male= 15. Raw data points are shown as grey dots.

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

	$T/S_{0.5}$			T/S_3		
Parameter	*Estimate*	*95%CI*	p_{MCMC}	*Estimate*	*95%CI*	p_{MCMC}
Intercept	**0.87**	**0.66 - 1.09**	**<0.001**	**1.57**	**0.32 – 2.71**	**0.022**
Chick sex	-0.13	-0.05 - 0.32	0.165	-0.23	-0.41 - 0.61	0.121
Maternal age	-0.08	-0.07 - 0.23	0.346	0.06	-0.32 - 0.21	0.711

Maternal age x Chick sex	0.06	-0.26 - 0.14	0.557	0.09	-0.21 - 0.43	0.573
Paternal age	-0.05	-0.26 - 0.14	0.557	**-0.27**	**-0.52 - -0.03**	**0.047**
Paternal age x Chick sex	-0.14	-0.34 - 0.07	0.177	**-0.40**	**-0.71 - -0.10**	**0.016**
Sample age	-0.01	-0.18 - 0.13	0.801	-	-	-
Sample day	-	-	-	0.00	-0.01 - 0.01	0.694
Random effects						
Nest box ID	0.01	0.00 - 0.03		0.01	0.00 - 0.02	
Aviary ID	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	

266 Maternal and paternal age were modelled as either young or old; young birds hatched the preceding summer, and old
267 birds were 4 years old). 0.5 months: n= 69 chicks, 3 months: n= 59. The reference level for parental ages was ‘old’,
268 ‘female’ for chick sex, and ‘old’ for sample age. Estimates shown are posterior modes. Statistically significant effects
269 are shown in bold.

270 ***Discussion:***

271 Individual chick telomere length increased between 0.5 and 3 months of age. This increase
272 disagrees with much of the published literature, which generally finds a decrease in telomere length
273 in early life (Boonekamp et al., 2014; Cerchiara et al., 2017; De Meyer et al., 2007; Hoelzl et al.,
274 2016; Salomons et al., 2009). While a population level increase in telomere length has previously
275 been found in some long-lived bird species (Haussmann et al., 2007; Pauliny et al., 2012), other
276 studies have found that telomere elongation for a proportion of chicks is more common in shorter-
277 lived species (A. M. Brown et al., 2021; T. Brown et al., 2021; Eisenberg, 2019) and few longer-
278 lived species (Cerchiara et al., 2017). For example, a study on jackdaws *Corvus monedula* found
279 that between 5 and 30 days post-hatching, telomere lengths increased for 25% of sampled offspring
280 (Grasman et al., 2011). An increase in early life telomere length has also been observed in non-
281 avian taxa, including water pythons *Liasis fuscus* (Ujvari and Madsen, 2009) and European badgers
282 *Meles meles* (Lieshout et al., 2019). Indeed, a recent paper by Heidinger et al (2021) also found an
283 increase in telomere lengths in some individuals in a population of house sparrows over time points
284 years apart. A lack of comparable published research exploring a change in telomere length using
285 multiple time points in early life may, in part, explain the surprising nature of our observed increase
286 in telomere length in early life.

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

295 Second, qPCR plates contained both 0.5 and 3 months samples, and between-plate variance was
296 negligible in all our models, highlighting that this element of our methodology had little impact on
297 our results. Overall, we monitored procedural efficiency throughout data collection and did not
298 identify any other potential methodological sources of variation; the repeatability estimates for the
299 T/S ratios estimated from within-individual samples were well within the range of those for similar
300 species in other qPCR studies (Kärkkäinen et al., 2021). Consequently, we believe that the increase
301 in telomere length observed in our study has a biological explanation. For example, telomerase
302 activity might have been maintained in the chicks after the first sample was taken. Indeed, two
303 studies have shown that telomerase activity can be maintained up to five weeks post-hatching in

304 zebra finches *Taeniopygia guttata* (Haussmann et al., 2007) and chickens *Gallus gallus* (Taylor and
305 Delany, 2000). Yet, neither of these studies assessed telomerase activity at multiple time points in
306 the same individual's early life post-hatching, which remains an interesting future avenue for the
307 field.

308 While we expected that old parents would produce chicks with shorter telomeres, as found in other
309 short-lived bird species in line with predictions of the Lansing effect (Bauch et al., 2019; Criscuolo
310 et al., 2017), our experimental approach found that old fathers produced daughters with longer
311 telomeres, but only 3 months after hatching, potentially indicating an environmental or an age-
312 dependent epigenetic effect (Matsushima et al., 2019). Positive relationships between parental age
313 and offspring telomere length have previously been foundin long- and short-lived bird species
314 (Asghar et al., 2015; A. M. Brown et al., 2021; Dupont et al., 2018). Such effects may arise
315 indirectly for example through improved parental care that older individuals provide compared to
316 inexperienced, younger breeders. However, the positive effect of improved parental care by older
317 parents also declines in the oldest individuals as they senesce (Beamonte-Barrientos et al., 2010;
318 Becker et al., 2015). One potential cause for the lack of identifying an effect of maternal age on
319 chick telomere lengths may result from a relative difference in the strength of maternal vs. paternal
320 effects; if maternal effects are weaker, maternal effects may only be detectable with a larger sample
321 size and as such may be present but undetectable in our study. Further, positive effects of parental
322 age on telomere length are in constrast to some previous studies that instead found a negative effect
323 of parental age resulting from the poorer condition of the oldest individuals (Bouwhuis et al., 2018;
324 Criscuolo et al., 2017), or a lack of an effect of parental age on parental care (Nakagawa et al.,
325 2007). In contrast, a recent study in house sparrows found no evidence for parental care effects and
326 instead, stronger evidence for genetic effects of parental age on traits associated with telomere
327 dynamics (Schroeder et al., 2015). It may be possible that the effects observed in our study arise
328 from a phenomenon whereby parents that survive for longer are of an inherent higher genetic
329 quality, and so produce higher quality offspring with longer telomere lengths relative to the average
330 telomere lengths from offspring from younger parents which will include a wider range of adults of
331 varying quality. Complicating this further is a study by Le Pepke et al. (2021) which found that
332 environmental effects were the strongest predictors of telomere length in house sparrows. In
333 addition, few studies investigating parental effects on telomere length continue to sample offspring
334 telomere lengths into the post-fledging period, as in this study, and so will not be accounting for
335 post-fledging parental care and how this may vary with parental age. Little is known about post-
336 fledging parental care in house sparrows, however during this period juveniles tend to form flocks
337 with their parents so it is likely that parental care will continue to be of some importance for chicks

338 after they leave the nest, through e.g. continuing to provide food for young up to 14 days after they
339 fledge (Summers-Smith, 1963). Positive effects of the ages of social parents have also been
340 identified in house sparrows, which may indicate that the quality of individuals in an offspring's
341 social group post-fledging may also influence telomere lengths (Sibma, 2021). Evidently, future
342 studies are required to further investigate post-fledging parental care for this species and others, and
343 the potential effects of parental care in early life on offspring telomere dynamics.

344 While telomere lengths in offspring can be affected by an offspring's environment (Dugdale and
345 Richardson, 2018; Lieshout et al., 2021), effects of paternal age in birds have also been found to be
346 independent of this (Bauch et al., 2019; Boonekamp et al., 2014). As such, there is overall growing
347 support for at least contributory paternal, or z-linked, inheritance of telomere length in some species
348 with a ZW sex-determination system (Bouwhuis et al., 2018; Olsson et al., 2011). These studies
349 support our finding of positive effects of father age on daughters only. In further support of our
350 findings is Schroeder et al. (2015) which identified a sex-specific heritable parental age effect on
351 offspring fitness in house sparrows with daughters of older fathers having higher lifetime
352 reproductive success than sons of older fathers. There is also increasing evidence demonstrating the
353 potential positive effect of father age on offspring telomere lengths (sons and daughters: A. M.
354 Brown et al., 2021, daughters only: Dupont et al., 2018). A combined effect of z-linked inheritance
355 and improved parental care or father quality for offspring of older fathers in our study may then
356 explain why we find a positive effect of father age on daughter telomere lengths. Our results are
357 then in contrast to studies finding that offspring telomere lengths correlate with mother age
358 (Reichert et al. 2015; Asghar et al. 2015). However, effects of maternal age in these studies were
359 identified at earlier time points than the ones used in this study (ten days in king penguins
360 *Aptenodytes patagonicus*: Reichert et al. 2015; nine days in great reed warblers *Acrocephalus*
361 *arundinaceus*: Asghar et al. 2015). It may then be that while we found no effect of maternal age in
362 our study, an influence of maternal age on chick telomere length may well have been present, but
363 already diminished below detectable levels 0.5 months after hatching, when our first sampling took
364 place.

365 We did not detect an effect of either maternal or paternal age on chick telomere length at 0.5
366 months after hatching. This is again in contrast to studies finding evidence to support the Lansing
367 effect where offspring of older parents may have shorter telomeres in early life with potential
368 implications for longevity (Monaghan et al., 2020; Priest et al., 2002b). Heidinger et al. (2016)
369 similarly found no effect of parental age on offspring telomere length in early life at 25 days after
370 hatching in European shags *Phalacrocorax aristotelis*. Further, variation in pre-fledging telomere
371 length may in part be explained by brood-specific additive genetic effects (Voillemot et al., 2012).

372 As such, it may be that at later time points effects of parent age and post-fledging environmental
373 factors appear to be more important than brood-specific effects in determining offspring telomere
374 length. Again, there is a need for more studies investigating the relationship between paternal age
375 and telomere dynamics to detect when and how patterns of telomere dynamics are driven.

376 In summary, we find that telomere lengths increased in early life with a likely biological cause.
377 Furthermore, our results indicate that paternal age effects are more influential on offspring telomere
378 length than maternal age effects in our population of house sparrows, with the daughters of older
379 fathers having longer telomeres. Future analyses of telomerase activity levels in both the sperm of
380 adult males would yield further insights into the drivers of parental age effects on offspring
381 telomere dynamics in early life.

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388 No competing interests declared.

389 **Author contributions:**

390 Conceptualization: SB, JS; Methodology: SB, JS, MJPS; Validation: SB, MJPS; Formal analysis:
391 SB, JS; Investigation: SB, AG, JS, AST; Resources: JS, MJPS, TB; Data curation: SB, JS, TB;
392 Writing- original draft: SB; Writing- review & editing: SB, JS, AG, AST, MJPS; Visualization: SB,
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400 **Data availability statement:**

401 The data and code are available at the Open Science Foundation through this link:
402 https://osf.io/6kwzh/?view_only=96b0d8a81ce84ba09b364e514ab0072e.

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