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

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13 **Abstract:**

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

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

32 ***Introduction***

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

41 The relative length of telomeres, the chromosome capping structures consisting of TTAGGG base
42 pair repeats, is associated with biological age and longevity (Heidinger et al., 2012; Mather et al.,
43 2011; Vedder et al., 2021). Telomeres partly function to prevent DNA damage from reactive
44 oxygen species (Aubert and Lansdorp, 2008). The activity levels of telomerase, the RNA-protein
45 complex responsible for ligating TTAGGG repeats, decline rapidly in early life and are tissue
46 specific (Taylor and Delany, 2000). Together this leads to a gradual telomere shortening over an
47 individual's lifetime (Aubert and Lansdorp, 2008; Finkel and Holbrook, 2000), which is why
48 telomere length is often used as a biomarker for biological age (Mather et al., 2011; Zglinicki and
49 Martin-Ruiz, 2005). However, whether there is a direct causal link between telomere length and an
50 individual's age remains unclear (Boonekamp et al., 2013; Simons, 2015).

51 In birds, telomere loss is fastest in early-life and an initially longer telomere length is associated
52 with longer subsequent lifespans in captive (Reichert et al., 2013; Wilbourn et al., 2018) and wild
53 (Haussmann et al., 2003a; Heidinger et al., 2016; Reed et al., 2008; Richardson et al., 2001;
54 Salomons et al., 2009; Vedder et al. 2021) bird populations. There is evidence for telomere length
55 being heritable in birds (Vedder et al., 2021), and telomere dynamics have been associated with sex-
56 specific parental age and telomere length (Asghar et al., 2015; Horn et al., 2011; Reichert et al.,
57 2015; Salomons et al., 2009). This suggests that indeed, some Lansing-type effects may be inherited
58 via telomere length. However, the direction of the association between telomere length, and
59 maternal and paternal age varies even within bird species (Dugdale and Richardson, 2018). In birds,
60 the offspring of older mothers may have shorter telomeres and a faster attrition rate, especially in
61 early development (Asghar et al., 2015; Salomons et al., 2009). Conversely, negative associations
62 between paternal age and offspring telomere length have been observed in the absence of maternal
63 correlation (Horn et al., 2011).

64 Between taxa, studies on the heritability of telomere length are conflicting. The heritability of
65 telomere length can be sex-specific and is often larger in the heterogametic sex; suggesting some
66 degree of maternal inheritance in birds (Asghar et al., 2015; Horn et al., 2011; Reichert et al., 2015)
67 and paternal inheritance in humans (Eisenberg et al., 2017; Njajou et al., 2007; Nordfjäll et al.,
68 2009). However, homogametic inheritance of telomere length has also been found in humans (Broer
69 et al., 2013), in some bird species (Bauch et al., 2019; Bouwhuis et al., 2018), and in lizards (Olsson
70 et al., 2011). A sex-specific lack of heritability has also been found in several bird species (Atema et
71 al., 2015; Heidinger et al., 2012; Kucera, 2018). Overall, parental age effects on offspring telomere
72 length, dynamics and heritability are complex, and vary in extent and direction of impact within and
73 between taxa.

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

78 ***Methods:***

79 ***Study species and experimental design:***
80 We used captive house sparrows at the Max Planck Institute for Ornithology, Seewiesen, Germany,
81 during the breeding season of 2014. We used 42 pairs of male and female sparrows, which were
82 assigned to four treatments, each with an equal sex ratio and a uniform distribution of ages across
83 both sexes to control for age-assortative mating. We experimentally bred pairs in one of four age
84 combinations: old-female/ old-male (OO, n=8 pairs), old-female/ young-male (OM, n=11 pairs),
85 young-female/ old-male (YO, n=13 pairs), and young-female/ young-male (YY, n=10 pairs). Young
86 birds hatched the preceding summer. Old (O) was defined as sparrows aged 4 years and older,
87 although most individuals were 7 years or older (Males: 8 years = 2, 9 years = 21; Females: 4 years
88 = 1, 7 years= 10, 8 years= 4, and 9 years= 1). The difference in age distribution between females
89 and males corresponded to that observed in the wild, where females live shorter than
90 males(Schroeder et al., 2012). We did not use the middle aged groups because in wild house
91 sparrows, reproductive senescence may start at 3 years for females (Schroeder et al., 2012), or 5
92 years in males (Hsu et al. 2017). Each treatment group was replicated twice in two separate
93 breeding groups located in separate aviaries. Each replicate aviary contained 15.3±4.9 (mean±s.d.)
94 males and 14.6±2.4 females of the respective age class. Bird husbandry is described in Girndt et al.
95 (2017).

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

101 ***Blood sample collection:***
102 We took blood samples from chicks 0.5 months after they hatched (n= 75). After fledging, offspring
103 remained in the same aviary as their parents and siblings, and 2.5 months later were blood sampled
104 again (n=59). Blood samples were collected from the brachial vein of offspring using 1mm
105 capillary tubes and stored in 1ml of 96% ethanol. We collected samples of 56 individuals at both
106 0.5 and 3 months to test for within-individual changes.

107 ***DNA extraction and quantification:***
108 Following standard DNA extraction (Richardson et al., 2001), we measured the DNA concentration
109 of the samples using a ThermoScientific NanoDrop8000 Spectrophotometer and standardised the
110 concentration in our samples to 20-30ng/ml to ensure equal amplification of samples during qPCR.
111 Where necessary, samples were diluted with T10E0.1 (10mM Tris-HCl, pH 8.0, 0.1mM EDTA, pH
112 8.0) or concentrated using a ThermoScientific Savant DNA SpeedVac Concentrator.

113 ***Estimation of telomere length:***
114 We used multiplex qPCR to determine relative telomere length. We determined 'T' as the number
115 of telomere repeats and 'S' as the number of control gene repeats. We then used the T/S ratio as a
116 proxy for telomere length. The four DNA primers we used are described in Criscuolo et al. (2009).
117 We used DNA from house sparrows not included in this analysis as standards at five DNA
118 concentrations of 80, 20, 5, 1.25 and 0.31ng/ml, on each plate. We then used these standards to
119 produce a standard curve for all analysed samples. In each well we added 1.5µl of DNA sample,
120 0.9µl of each primer, 10µl of Sybr®Select Master Mix and 4.9µl ddH_2O. We ran each plate with an
121 equal number of 0.5 and 3 months sample pairs from the same individual to account for any
122 potential sample and plate effects when comparing within-individual changes in telomere length.
123 We ran 42 samples, the five standards and a negative (with all components except a DNA sample)
124 in duplicate on each 96-well plate. We ran the qPCR cycling conditions using QuantStudio 12kFlex
125 Software v1.2.2 following the cycle timings given in Cawthon (2009). We analysed the software
126 output to calculate the T/S ratio in each sample (Appendix 1.1). We altered the thresholds for the
127 standard curve of the telomere and GAPDH primers for each plate to optimise amplification
128 efficiencies to between a standard of 95-110. Efficiencies for each plate were between 99.3-99.7 for

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

141 ***Ethical Note:***

142 The Government of Upper Bavaria, Germany, approved the care, handling and husbandry of all
143 birds in this study and granted a license for animal experiments to JS (Nr311.5–5682.1/1-2014-
144 024).

145 ***Statistical Analysis:***

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

160 As the 0.5 months samples were a mix of newly-, and already-extracted DNA samples, we also
161 tested whether time of extraction had any effect on the calculated T/S ratio as a result of DNA

162 degradation (Madisen et al., 1987) (n samples newly-extracted= 10 out of 75). We fitted a LMM
163 with $T/S_{0.5}$ as the response and the time of extraction as a fixed factor, either 'newly-' or 'already-
164 extracted'. We found no statistically significant difference between newly-, and already-extracted
165 samples (posterior mode= -0.06, 95% credible interval= -0.20, 0.08, pMCMC=0.389).

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

171 ***Model validation:***

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

182 ***Results:***

183 Unexpectedly, the telomere length for offspring increased within 80% of individuals between 0.5
184 and 3 months of age (n = 45/56) for those where both measurements were available. On average,
185 the difference between $T/S_{0.5}$ and T/S_3 was statistically significantly positive (Figure 1 and Table 1).
186 Further, as chicks aged, they varied more in their telomere lengths; there was greater variance in
187 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:
188 0.27±0.02, n=59; F-test: $F=0.43$, $p<0.01$).

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

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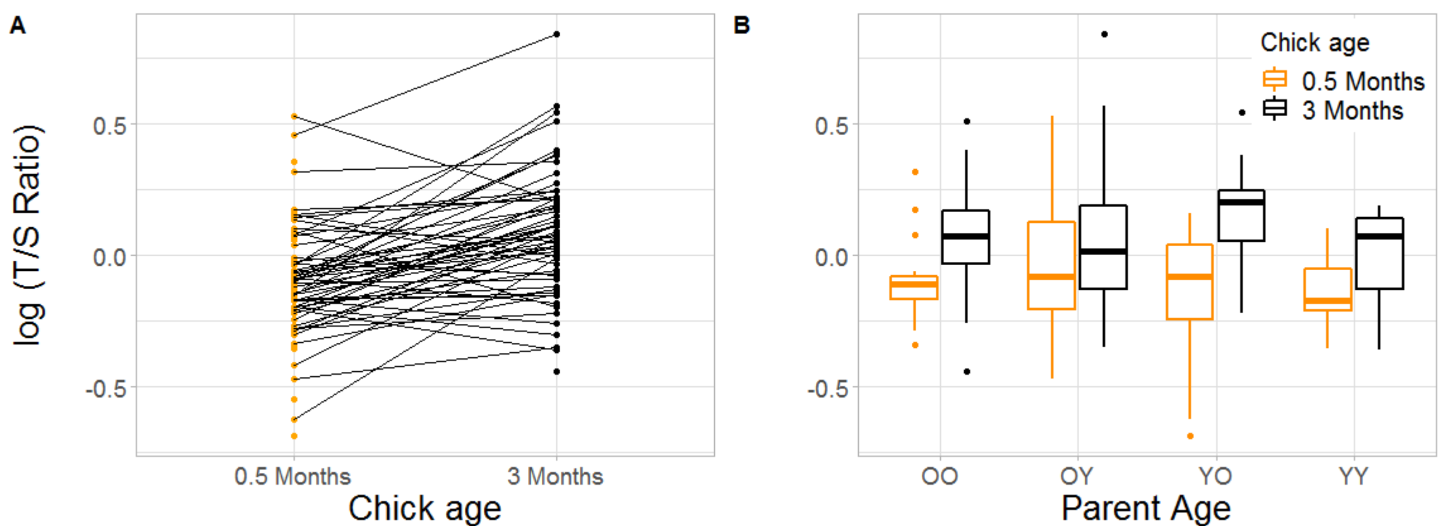
Parameter	*Estimate*	*95% confidence intervals*	p_{MCMC}
Intercept	**0.93**	**0.84 - 0.99**	**<0.001**
Chick age	**0.19**	**0.12 - 0.26**	**<0.001**
Random effects			
Chick ID	0.00	0.00 - 0.01	
Nest box	0.02	0.01 - 0.04	
Aviary	0.00	0.00 - 0.00	
qPCR plate ID	0.00	0.00 - 0.01	
Residual	0.04	0.02 - 0.05	

198 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
199 months: n=75 chicks, 3 months: n=59. Estimates shown are posterior modes.



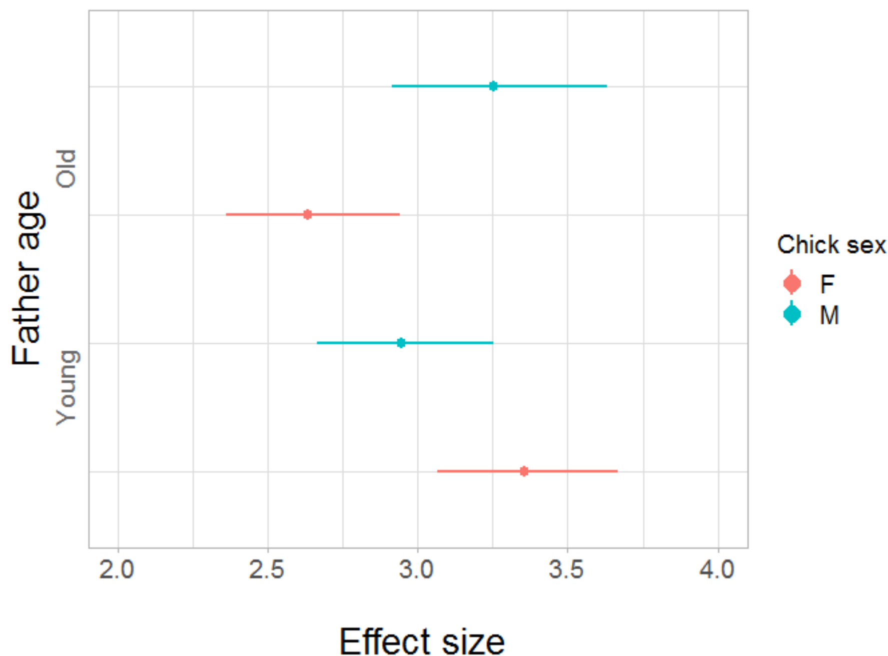
200 **Figure 1**: Change in telomere length (log(T/S Ratio)) within house sparrow chicks at 0.5 and 3
201 months of age. A) Individuals are connected by a line (n offspring with samples at 0.5 months=75,
202 at 3 months=59). B) Boxplots show the mean (central line) and 25th and 75th percentiles (lower and
203 upper box bounds respectively) of the log(T/S Ratio) within age group of the chicks' parents (Y =
204 <2 years old, O > 3 years old for females and >7 years old for males). T/S Ratio is presented on a
205 log scale to aid visualisation. YO = young mothers, old fathers (n=19, 12). OO = both parents old
206 (n=18, 19). OY = old mothers, young fathers (n=17, 18). YY = both parents young (n=15, 10).

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

212 **Table 2:** Results from two Bayesian MCMC general linear mixed-effects models with telomere
213 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	

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



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

223 each category; Y, and female=12, male=16, O, and female=16, male=15. Squares represent the
224 model estimates effect sizes of T/S ratio for each paternal age x chick sex combination and
225 associated lines represent 95% credible intervals (derived using the R package 'lsmeans' (Lenth,
226 2016).

227 ***Discussion:***

228 Individual chick telomere length increased between 0.5 and 3 months of age. This increase
229 disagrees with much of the published literature, which generally find a decrease in telomere length
230 in early-life (Boonekamp et al., 2014; Cerchiara et al., 2017; De Meyer et al., 2007; Hoelzl et al.,
231 2016; Salomons et al., 2009). While a population level increase in telomere length has previously
232 been found in some long-lived bird species (Haussmann et al., 2007; Pauliny et al., 2012), other
233 studies have found that telomeres elongation for a proportion of chicks is more common in smaller,
234 shorter-lived species (Brown et al., 2021; Eisenberg, 2019). For example, a study on jackdaws
235 *Corvus monedula* found that between 5 and 30 days post-hatching, telomere lengths increased for
236 25% of sampled offspring (Grasman et al., 2011). An increase in early-life telomere length has also
237 been observed in non-avian taxa, including water pythons *Liasis fuscus* (Ujvari and Madsen, 2009)
238 and European badgers *Meles meles* (van Lieshout et al., 2019). A lack of comparable published
239 research exploring a change in telomere length using multiple time points in early life may, in part,
240 explain the surprising nature of our observed increase in telomere length in early-life.

241 An increase in telomere length can have methodological and/or biological explanations. First, it
242 could be due to DNA in samples degrading over time (Madisen et al., 1987; but see Seutin et al.,
243 1991). Since we used pre-extracted DNA for the majority of 0.5 month samples, we investigated
244 whether differential telomere degradation rates between extracted DNA and blood sample types
245 could be a cause for the observed increase. However, we found no statistically significant difference
246 between the telomere lengths of newly- and already-extracted samples and thus, telomere
247 degradation is an unlikely explanation for our results.

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

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

259 While we expected that old parents would produce offspring with shorter telomeres, as found in
260 other short-lived bird species (Bauch et al., 2019; Criscuolo et al., 2017; Sparks et al., 2020), our
261 experimental approach found that old fathers produced daughters with longer telomeres, but only 3
262 months after hatching, indicating an environmental effect. Similar positive effects of parental age
263 have also previously been found in long and short-lived bird species (Dupont et al., 2018, Asghar et
264 al., 2015; Becker et al., 2015). Positive effects of parental age on offspring telomere length may
265 arise from a potentially improved parental care that older individuals may be able to provide
266 compared to inexperienced, young breeders. Again though, previous studies have found a negative
267 effect of parental age resulting from the poorer condition of these old individuals (Bouwhuis et al.,
268 2018; Criscuolo et al., 2017), or a lack of an effect of parental age on parental care (Nakagawa et
269 al., 2007). Further, in some studies testing parent sex-specific effects, offspring telomere length was
270 found to correlate only with maternal age, and only relatively soon after hatching (ten days:
271 Reichert et al. (2015); nine days: Asghar et al. (2015)). As we found no inflouence of maternal age
272 in our study, an influence of maternal age on offspring telomere length may well have been present,
273 but already diminished below detectable levels 0.5 months after hatching.

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

286 However, we did not detect an effect of parental age on offspring telomere length at 0.5 months
287 after hatching. Heidinger et al. (2016) similarly found no effect of parental age on offspring
288 telomere length in very early-life at 25 days after hatching in European shags *Phalacrocorax*

289 *aristotelis*. Further, variation in pre-fledging telomere length may in part be explained by brood-
290 specific additive genetic effects (Voillemot et al., 2012). As such, it may be that at later time points
291 effects of parent age and post-fledging environmental factors appear to be more important than
292 brood-specific effects in determining offspring telomere length. Again, there is a need for more
293 studies investigating the relationship between paternal age and telomere dynamics to detect when
294 and how patterns of telomere dynamics are driven.

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

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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.

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