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Older mothers produce offspring with longer telomeres:

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a longitudinal within-parent analysis

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19 **Abstract**

20 As telomere length often predicts survival and lifespan, there is considerable interest in
21 understanding the origins of inter-individual variation in telomere length. Transgenerational effects
22 of parental age on offspring telomere length are thought to be a key source of variation, but the
23 rarity of longitudinal studies that examine the telomeres of successive offspring born throughout the
24 lives of parents leaves such parental age effects poorly understood. Here, we exploit telomere
25 length measures of successive offspring produced throughout the long breeding tenures of parents
26 in wild white-browed sparrow-weaver (*Plocepasser mahali*) societies, to isolate the effects of within-
27 parent changes in age on offspring telomere lengths. Our analyses reveal the first evidence to date
28 of a positive within-parent effect of advancing age on offspring telomere length: as individual
29 mothers age they produce offspring with longer telomeres. We consider the potential for pre- and
30 post-natal mechanisms to explain our findings. As telomere erosion predicts offspring mortality in
31 this species, this positive parental age effect could significantly impact parent and offspring fitness.
32 Our findings support the view that transgenerational effects of parental age can be an appreciable
33 source of inter-individual variation in telomere length.

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36 **1. Introduction**

37 Telomeres are nucleoprotein complexes located at the ends of eukaryotic chromosomes [1]. They
38 consist of a repeating non-coding DNA sequence (TTAGGG_n in vertebrates) and have an important
39 function in maintaining chromosomal integrity [1–3]. Telomeres vary in length both within and
40 among individuals, and average telomere lengths shorten with advancing age in many taxa [2,3].
41 Telomeres may be shortened as a consequence of cell division and exposure to oxidative stress [4,5],
42 and as critically short telomeres can trigger cellular senescence, excessive telomere shortening may
43 have negative effects on performance [1–3,6–8]. Indeed, telomere length (TL) positively predicts
44 survival and lifespan in a range of taxa (e.g. [6–8]) and is often considered a biomarker of somatic
45 integrity [3]. Consequently, there is considerable interest in identifying the origins of the substantial
46 inter-individual variation in TL within populations, given its potential implications for life-history
47 trajectories and fitness. There is mounting evidence to suggest that parental age at offspring
48 conception (hereafter ‘parental age’) predicts offspring TL in both human and non-human animals
49 (e.g. [9–11]). However, the vast majority of studies to date have considered only whether
50 population-level variation in parental age predicts offspring TL (see below). Whether such patterns
51 reflect within-parent effects of advancing age rather than the selective disappearance of certain
52 types of parents with advancing age, remains poorly understood.

53 In humans, population-level studies have consistently demonstrated that paternal (but not
54 maternal) age at conception positively predicts offspring TL (e.g. [9,12]). In non-human animals
55 however there is considerable variation among species in the nature of the population-level
56 relationship between parental age and offspring TL. Studies in mammals, birds, and reptiles have to
57 date found positive [13–15], negative [10,11,16], and no [17,18] relationship, with some finding
58 evidence suggestive of either maternal [13,15] or paternal age effects [11,14,16], or both [10]. In
59 order to understand the mechanistic origins and life-history implications of these relationships,

60 studies now need to establish whether these patterns reflect within-parent effects of advancing age
61 on the phenotypes of their offspring, or arise instead from among-parent processes (e.g. selective
62 disappearance). Just two studies to date have yielded evidence that within-parent changes in age
63 predict offspring TL (and see [19] for an example of no evident effects of within-parent changes in
64 age on offspring TL). First, a study of captive zebra finches (*Taeniopygia guttata*) demonstrated that
65 offspring produced by mothers when they were older (3.5 years of age) had shorter telomeres than
66 those produced by the same mothers when young (6 months of age), while experimentally
67 controlling paternal age [20]. Similarly, a study in a free-living population of jackdaws (*Corvus*
68 *monedula*) found that as individual fathers age they produce offspring with shorter telomeres, while
69 there was no effect of advancing maternal age [21]. These longitudinal studies therefore suggest
70 that advancing parental age can *negatively* impact offspring TL.

71 Here, we investigate parental age effects on offspring TL in a free-living population of white-browed
72 sparrow-weavers (*Plocepasser mahali*) in the Kalahari Desert. We use TL measures from successive
73 offspring produced throughout the long breeding tenures of parents to isolate the effects of within-
74 parent changes in age. White-browed sparrow-weavers live in year-round territorial groups, that
75 comprise a single dominant male and female who completely monopolise within-group
76 reproduction, and 0-12 non-breeding subordinate ‘helpers’ who assist with nestling feeding [22–24].
77 The rate of telomere attrition during development in this species predicts survival to adulthood [25],
78 indicating that parental age effects on offspring TL could have substantial consequences for parent
79 and offspring fitness.

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82 **2. Material and methods**

83 *(a) Study species and field methods*

84 Approximately 40 social groups have been monitored intensively since 2007 in Tswalu Kalahari
85 Reserve (South Africa; 27°16'S, 22°25'E), leaving most individuals of known life-history (see [22–24]).
86 Each group's dominant breeding pair were identified using characteristic behavioural profiles, and
87 were considered the parents of all offspring born in their group during their reproductive tenures
88 (see electronic supplementary material [ESM] for justification and supporting analysis using genetic
89 data). Nests were checked regularly throughout each breeding season (October to April inclusive) to
90 determine egg lay and hatch dates, which allowed estimation of parental age (the parent's age in
91 days on the date that the focal offspring's clutch was laid; see ESM) and offspring age at sampling
92 (days since their hatch date). Blood samples for telomere assessments were routinely taken from
93 nestlings and adult birds (see ESM). As helpers contribute to nestling feeding when present [22,23],
94 we verified that our findings were unaffected by controlling for variation in an offspring's rearing
95 group size (see ESM).

96 *(b) Telomere length measurements*

97 Telomere lengths were estimated from whole blood samples using qPCR analysis of relative
98 telomere length (RTL) (following [26], details are described in ESM and [25]). We analysed 765 blood
99 samples from 356 offspring from 248 clutches, produced by 61 mothers and 60 fathers in 41 social
100 groups between 2010 and 2015 (numbers of mothers and fathers exceed the number of groups due
101 to dominance turnovers during the study).

102 *(c) Statistical analyses*

103 We fitted linear mixed-effects models with the lme4 package [27] in R (v3.6.1) [28] and ranked
104 models by AICc (see ESM). We first investigated the effects of population-level variation in parental

105 age on offspring RTL and, second, the effects of within-parent changes in age. In both cases, the
106 following fixed effect predictors were fitted alongside parental ages: offspring sex and offspring age
107 class (0-10 days [post-hatching], 11-89 days [later dependent period], and ≥ 90 days [independence
108 and adulthood; mean \pm SE age at sampling = 1.40 years \pm 24.3 days; range 3 days – 7.35 years]).
109 These offspring age classes were chosen to identify whether any parental age effects were present
110 in offspring soon after hatching or arose later in offspring development (our work to date has
111 revealed no evidence of changes in mean telomere length with advancing age in this population
112 despite extensive longitudinal sampling; Wood et al. *in review*). Interactions between each parental
113 age variable and offspring age were also included. Offspring ID, clutch ID nested within mother ID,
114 qPCR plate ID, and sampling period (a factor identifying the breeding season and calendar year in
115 which the blood sample was taken) were fitted as random intercepts. We did not fit father ID as it
116 typically estimated zero or near-zero variance when alongside mother ID, due likely to its strong
117 correlation with mother ID (dominant pairs can produce many clutches together; see ESM); our
118 findings do not change if it is included. While global models contained both maternal and paternal
119 age as fixed effects, models containing both were not AICc-ranked because maternal and paternal
120 age were correlated (Pearson's; $r = 0.76$, $t = 31.97$, $df = 763$, $p < 0.001$).

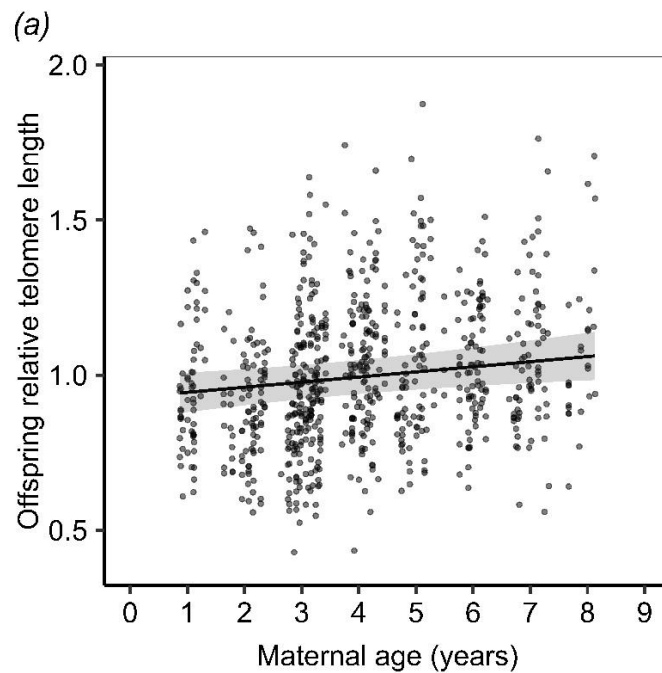
121 After conducting an initial analysis of the effects of population-level variation in maternal and
122 paternal age on offspring RTL, we used within-subject centring [29] to partition the parental age
123 variables into two components and repeated the analysis fitting both components as fixed effects: (i)
124 the parent's "mean age" across all sampled clutches for that parent and, (ii) the parent's " Δ age", the
125 difference between the parental age value for the focal clutch and the parent's mean age. The Δ age
126 variables allow the models to estimate the effect of within-parent changes in age on offspring RTL,
127 while the mean age variables estimate among-parent effects. As parents first encountered as
128 fledglings or adults were assigned a minimum age (see ESM), any parental age relationships
129 detected in the population-level analysis should be interpreted with caution. However, following
130 within-subject centring, the Δ parental age values will be accurate for all parents.

131 **3. Results**

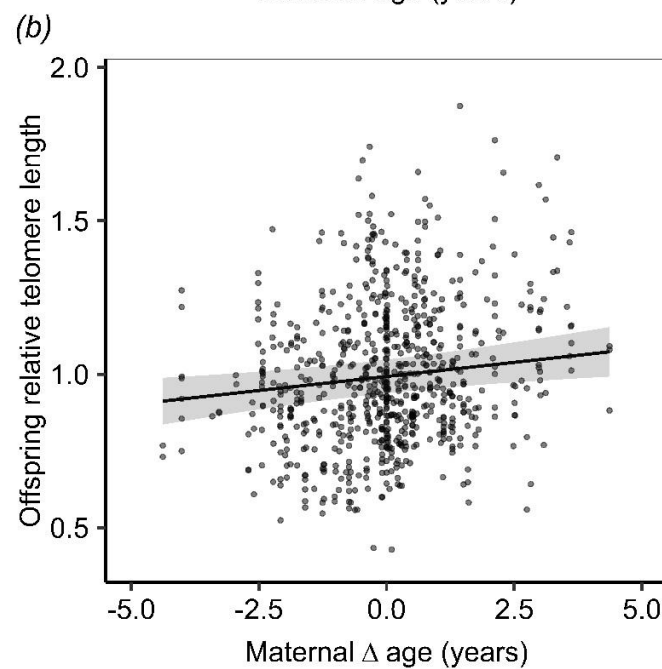
132 Analysis at the population level yielded support for a positive effect of maternal age on offspring RTL
133 (Figure 1a; Table 1). Within-parent centring suggests that this pattern arises from a positive *within-*
134 *mother* effect of advancing maternal age: as individual mothers get older they produce offspring
135 with longer telomeres (Figure 1b; Table 2). The paternal age variables attracted consistently weaker
136 support than maternal age variables (paternal age $\Delta AICc = +2.75$; Table 1; paternal Δ age $\Delta AICc =$
137 $+1.68$; Table 2), suggesting that their positive relationships with offspring RTL could be a by-product
138 of the strong correlation between maternal and paternal age. Our models did not yield clear
139 evidence that the maternal age effect varies in strength with offspring age class (Table 1, 2). We
140 confirmed that these parental age relationships cannot be attributed instead to correlated variation
141 in social group size or uncertainty regarding parental age (see ESM).

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146 **Figure 1.** Relationship between maternal age and offspring RTL. Lines represent model predictions from the
147 top-ranked models from our population-level (a) and within-parent (b) analyses. Shaded area represents upper
148 and lower confidence intervals ($1.96*SE$). Points are unscaled raw data. There is some uncertainty in the
149 maternal (and paternal) age values for some parents, while Δ age values are accurate for all birds (see
150 methods).

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152 **Table 1.** $\Delta 6$ AICc top model after implementation of the nesting rule [30] for the population-level
 153 analysis with scaled predictors of offspring RTL. Estimates are given with standard errors in
 154 parentheses.

Intercept	Offspring age class	Maternal age	Paternal age	Offspring age class: paternal age	df	logLik	AICc	Δ AICc	Adjusted Akaike weight
0.995 (0.028)		0.030 (0.011)			8	253.04	-489.9	0.00	0.634
0.970 (0.033)	+		+	+	12	255.78	-487.1	2.75	0.160
0.989 (0.029)			0.023 (0.013)		8	251.42	-486.7	3.24	0.126
0.988 (0.030)					7	249.95	-485.7	4.14	0.080

155 Predictors absent from top model set: Offspring sex, Offspring age class: maternal age interaction. Paternal
 156 age effect estimates in second-ranked model: for offspring age 0-10 days = -0.017 (0.021); 11-89 days = 0.0003
 157 (0.0178); ≥ 90 days = 0.037 (0.015).

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162 **Table 2.** $\Delta 6$ AICc top model set after implementation of the nesting rule [30] for the *within-parent*
163 analysis with scaled predictors of offspring RTL. Estimates are given with standard errors in
164 parentheses.

Intercept	Maternal Δ age	Paternal Δ age	df	logLik	AICc	Δ AICc	Adjusted Akaike weight
0.993 (0.028)	0.026 (0.009)		8	253.58	-491.0	0.00	0.665
0.990 (0.028)		0.026 (0.011)	8	252.74	-489.3	1.68	0.286
0.988 (0.030)			7	249.95	-485.7	5.22	0.049

165 Predictors absent from top model set: Maternal mean age, paternal mean age, offspring age class, offspring
166 sex, all two-way interactions between parental age terms and offspring age class.

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168 **4. Discussion**

169 Our analyses reveal that maternal age positively predicts offspring TL at the population level and
170 suggest that this relationship reflects positive effects of *within-mother* changes in maternal age
171 rather than confounding effects of variation among mothers. A within-parent effect of parental age
172 on offspring TL has only been reported in two other studies (also in birds), both of which reported a
173 negative effect [20,21]. Our findings therefore constitute the first evidence of a positive within-
174 parent effect of advancing parental age on offspring TL.

175 Parental age effects have the potential to arise via both pre-natal mechanisms (e.g. gamete-
176 mediated epigenetic effects) and post-natal mechanisms (including age-related changes in the
177 provision of post-natal care), as has recently been underscored by evidence of both biological parent
178 and foster parent age effects on offspring TL [10,21]. Our models did not yield clear statistical
179 support for an interactive effect of maternal age and offspring age on offspring TL, despite large
180 samples sizes in each offspring developmental age class (see ESM). This highlights the possibility that

181 this effect arose via *pre-natal* mechanisms, such as maternal modification of egg constituents with
182 advancing age [31]. However, there is a need for caution in discounting a role for post-natal
183 mechanisms, as the maternal age effect size quadruples between early development and the period
184 of independence and adulthood (Figure S1). A number of mechanisms exist by which a relationship
185 could arise post-natally. For example, the quality of post-natal maternal care could conceivably
186 increase as mothers age, leading to slower rates of telomere attrition during the nestling period [32].
187 Such a pattern could reflect beneficial effects on offspring of increasing maternal breeding
188 experience (e.g. [33]). While negative effects of parental age (e.g. [10,21]) might be expected to
189 manifest as parents senesce, the senescent period may not be well represented within our data as
190 sampled mothers were not known to exceed 8 years of age and the species can breed beyond 12
191 years of age [25].

192 Offspring produced by older parents often have reduced fitness and lifespan (the ‘Lansing effect’
193 [34,35]). By contrast, our finding of a positive effect of maternal age on offspring TL highlights the
194 possibility in this species of parental age-related increases in offspring performance, given that
195 offspring TL often positively predicts their downstream performance [25]. Indeed, recent work on
196 another social vertebrate has yielded striking evidence of a positive maternal age effect on offspring
197 performance [36]. These apparent benefits of advanced parental age highlight the wider need for
198 analyses of the fitness implications of reproductive senescence to consider parental age-related
199 changes in offspring quality as well as offspring production, given the potential for the former to
200 partially offset the latter.

201 To conclude, we present the first evidence that within-parent changes in age positively predict
202 offspring TL. Our findings, coupled with those of other recent studies that have demonstrated
203 within-parent effects of advancing age on offspring TL [20,21], suggest parental age at reproduction
204 does partially explain inter-individual variation in TL in animal populations. Indeed, follow-up
205 analyses reveal that this maternal age effect in white-browed sparrow-weaver societies persists into

206 offspring adulthood (see ESM). Work is now needed to elucidate the mechanisms driving these
207 parental age effects and to establish the causes of their variation across taxa.

208 **Ethics**

209 The protocols followed in this study were approved by University of Pretoria Animal Ethics
210 Committee (EC023-07 and EC100-12).

211 **Data accessibility**

212 Data are available on Dryad (doi:10.5061/dryad.2jm63xsng) [37].

213 **Competing interests**

214 We declare no competing interests.

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221 **Authors' contributions**

222 A.M.B., E.M.W. and A.J.Y. designed the study. E.M.W. conducted the fieldwork and performed the
223 telomere length analyses. A.J.Y. led the long-term field study. A.M.B., P.C-L. and X.A.H. conducted
224 the microsatellite genotyping analyses. A.M.B. analysed the data and wrote the manuscript. All
225 authors commented on the manuscript and approved the final version.

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231 **References**

- 232 1. Blackburn EH. 2001 Switching and signaling at the telomere. *Cell* **106**, 661–673.
233 (doi:10.1016/S0092-8674(01)00492-5)
- 234 2. Monaghan P. 2010 Telomeres and life histories: the long and the short of it. *Ann. N. Y.*
235 *Acad. Sci.* **1206**, 130–142. (doi:10.1111/j.1749-6632.2010.05705.x)
- 236 3. Young AJ. 2018 The role of telomeres in the mechanisms and evolution of life-history
237 trade-offs and ageing. *Phil. Trans. R. Soc. B* **373**, 20160452.
238 (doi:10.1098/rstb.2016.0452)
- 239 4. Monaghan P, Ozanne SE. 2018 Somatic growth and telomere dynamics in
240 vertebrates: relationships, mechanisms and consequences. *Phil. Trans. R. Soc. B* **373**,
241 20160446. (doi:10.1098/rstb.2016.0446)
- 242 5. von Zglinicki T. 2002 Oxidative stress shortens telomeres. *Trends Biochem. Sci.* **27**,
243 339–344. (doi:10.1016/S0968-0004(02)02110-2)
- 244 6. Heidinger BJ, Blount JD, Boner W, Griffiths K, Metcalfe NB, Monaghan P. 2012
245 Telomere length in early life predicts lifespan. *Proc. Natl. Acad. Sci. U. S. A.* **109**,
246 1743–1748. (doi:10.1073/pnas.1113306109)
- 247 7. Bize P, Criscuolo F, Metcalfe NB, Nasir L, Monaghan P. 2009 Telomere dynamics
248 rather than age predict life expectancy in the wild. *Proc. R. Soc. B* **276**, 1679–1683.

- 249 (doi:10.1098/rspb.2008.1817)
- 250 8. Wilbourn RV, Moatt JP, Froy H, Walling CA, Nussey DH, Boonekamp JJ. 2018 The
251 relationship between telomere length and mortality risk in non-model vertebrate
252 systems: a meta-analysis. *Phil. Trans. R. Soc. B* **373**, 20160447.
253 (doi:10.1098/rstb.2016.0447)
- 254 9. Eisenberg DTA, Hayes MG, Kuzawa CW. 2012 Delayed paternal age of reproduction in
255 humans is associated with longer telomeres across two generations of descendants.
256 *Proc. Natl. Acad. Sci. U. S. A.* **109**, 10251–10256. (doi:10.1073/pnas.1202092109)
- 257 10. Criscuolo F, Zahn S, Bize P. 2017 Offspring telomere length in the long lived Alpine
258 swift is negatively related to the age of their biological father and foster mother. *Biol.*
259 *Lett.* **13**, 20170188. (doi:10.1098/rsbl.2017.0188)
- 260 11. Olsson M, Pauliny A, Wapstra E, Uller T, Schwartz T, Blomqvist D. 2011 Sex differences
261 in sand lizard telomere inheritance: paternal epigenetic effects increases telomere
262 heritability and offspring survival. *PLoS One* **6**, e17473.
263 (doi:10.1371/journal.pone.0017473)
- 264 12. Unryn BM, Cook LS, Riabowol KT. 2005 Paternal age is positively linked to telomere
265 length of children. *Aging Cell* **4**, 97–101. (doi:10.1111/j.1474-9728.2005.00144.x)
- 266 13. Cram DL, Monaghan P, Gillespie R, Clutton-Brock T. 2017 Effects of early-life
267 competition and maternal nutrition on telomere lengths in wild meerkats. *Proc. R.*
268 *Soc. B* **284**, 20171383. (doi:10.1098/rspb.2017.1383)
- 269 14. Eisenberg DTA, Tackney J, Cawthon RM, Cloutier CT, Hawkes K. 2016 Paternal and
270 grandpaternal ages at conception and descendant telomere lengths in chimpanzees

- 271 and humans. *Am. J. Phys. Anthropol.* **162**, 201–207. (doi:10.1002/ajpa.23109)
- 272 15. Asghar M, Bensch S, Tarka M, Hansson B, Hasselquist D. 2015 Maternal and genetic
273 factors determine early life telomere length. *Proc. R. Soc. B* **282**, 20142263.
274 (doi:10.1098/rspb.2014.2263)
- 275 16. Bouwhuis S, Verhulst S, Bauch C, Vedder O. 2018 Reduced telomere length in
276 offspring of old fathers in a long-lived seabird. *Biol. Lett.* **14**, 20180213.
277 (doi:10.1098/rsbl.2018.0213)
- 278 17. Froy H *et al.* 2017 No evidence for parental age effects on offspring leukocyte
279 telomere length in free-living Soay sheep. *Sci. Rep.* **7**, 9991. (doi:10.1038/s41598-017-
280 09861-3)
- 281 18. Belmaker A, Hallinger KK, Glynn RA, Winkler DW, Hausmann MF. 2019 The
282 environmental and genetic determinants of chick telomere length in Tree Swallows
283 (*Tachycineta bicolor*). *Ecol. Evol.* **9**, 8175–8186. (doi:10.1002/ece3.5386)
- 284 19. van Lieshout SHJ, Sparks AM, Bretman A, Newman C, Buesching CD, Burke T,
285 Macdonald DW, Dugdale HL. 2020 Estimation of environmental, genetic and parental
286 age at conception effects on telomere length in a wild mammal. *J. Evol. Biol.* **00**, 1–13.
287 (doi:10.1111/jeb.13728)
- 288 20. Marasco V, Boner W, Griffiths K, Heidinger B, Monaghan P. 2019 Intergenerational
289 effects on offspring telomere length: interactions among maternal age, stress
290 exposure and offspring sex. *Proc. R. Soc. B* **286**, 20191845.
291 (doi:10.1098/rspb.2019.1845)
- 292 21. Bauch C, Boonekamp JJ, Korsten P, Mulder E, Verhulst S. 2019 Epigenetic inheritance

- 293 of telomere length in wild birds. *PLoS Genet.* **15**, e1007827.
294 (doi:10.1371/journal.pgen.1007827)
- 295 22. Harrison XA, York JE, Cram DL, Young AJ. 2013 Extra-group mating increases
296 inbreeding risk in a cooperatively breeding bird. *Mol. Ecol.* **22**, 5700–5715.
297 (doi:10.1111/mec.12505)
- 298 23. Harrison XA, York JE, Cram DL, Hares MC, Young AJ. 2013 Complete reproductive
299 skew within white-browed sparrow weaver groups despite outbreeding opportunities
300 for subordinates of both sexes. *Behav. Ecol. Sociobiol.* **67**, 1915–1929.
301 (doi:10.1007/s00265-013-1599-1)
- 302 24. Cram DL, Blount JD, Young AJ. 2015 The oxidative costs of reproduction are group-
303 size dependent in a wild cooperative breeder. *Proc. R. Soc. B* **282**, 20152031.
304 (doi:10.1098/rspb.2015.2031)
- 305 25. Wood EM, Young AJ. 2019 Telomere attrition predicts reduced survival in a wild social
306 bird, but short telomeres do not. *Mol. Ecol.* **28**, 3669–3680. (doi:10.1111/mec.15181)
- 307 26. Cawthon RM. 2002 Telomere measurement by quantitative PCR. *Nucleic Acids Res.*
308 **30**, e47. (doi:10.1093/nar/30.10.e47)
- 309 27. Bates D, Maechler M, Bolker BM, Walker SC. 2015 Fitting Linear Mixed-Effects Models
310 Using lme4. *J. Stat. Softw.* **67**, 1–48. (doi:10.18637/jss.v067.i01)
- 311 28. R Core Team. 2019 R: A Language and Environment for Statistical Computing. R
312 Foundation for Statistical Computing. Vienna, Austria. <https://www.R-project.org>
- 313 29. van de Pol M, Wright J. 2009 A simple method for distinguishing within- versus
314 between-subject effects using mixed models. *Anim. Behav.* **77**, 753–758.

- 315 (doi:10.1016/j.anbehav.2008.11.006)
- 316 30. Richards SA, Whittingham MJ, Stephens PA. 2011 Model selection and model
317 averaging in behavioural ecology: the utility of the IT-AIC framework. *Behav. Ecol.*
318 *Sociobiol.* **65**, 77–89. (doi:10.1007/s00265-010-1035-8)
- 319 31. Urvik J, Rattiste K, Giraudeau M, Okuliarova M, Horak P, Sepp T. 2018 Age-specific
320 patterns of maternal investment in common gull egg yolk. *Biol. Lett.* **14**. 20180346.
321 (doi:10.1098/rsbl.2018.0346)
- 322 32. Heidinger BJ, Herborn KA, Granroth-Wilding HMV, Boner W, Burthe S, Newell M,
323 Wanless S, Daunt F, Monaghan P. 2016 Parental age influences offspring telomere
324 loss. *Funct. Ecol.* **30**, 1531–1538. (doi:10.1111/1365-2435.12630)
- 325 33. Lv L, Komdeur J, Li J, Scheiber IBR, Zhang Z. 2016 Breeding experience, but not mate
326 retention, determines the breeding performance in a passerine bird. *Behav. Ecol.* **27**,
327 1255–1262. (doi:10.1093/beheco/arw046)
- 328 34. Schroeder J, Nakagawa S, Rees M, Mannarelli M-E, Burke T. 2015 Reduced fitness in
329 progeny from old parents in a natural population. *Proc. Natl. Acad. Sci. U. S. A.* **112**,
330 4021–4025. (doi:10.1073/pnas.1422715112)
- 331 35. Noguera JC, Metcalfe NB, Monaghan P. 2018 Experimental demonstration that
332 offspring fathered by old males have shorter telomeres and reduced lifespans. *Proc.*
333 *R. Soc. B* **285**, 20180268. (doi:10.1098/rspb.2018.0268)
- 334 36. Kroeger SB, Blumstein DT, Armitage KB, Reid JM, Martin JGA. 2020 Older mothers
335 produce more successful daughters. *Proc. Natl. Acad. Sci. U. S. A.* **117**, 4809–4814.
336 (doi:10.1073/pnas.1908551117)

- 337 37. Brown AM, Wood EM, Capilla-Lasheras P, Harrison XA, Young AJ. 2020 Data from:
338 Older mothers produce offspring with longer telomeres: a longitudinal within-parent
339 analysis. *Dryad Digit. Repository*. (doi:10.5061/dryad.2jm63xsng)

340