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## **Two aspects of longevity are associated with rates of loss of telomeres in birds**

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## **ABSTRACT**

Telomeres, the terminal repetitive DNA sequences at the ends of linear chromosomes, have strong associations with longevity in some major taxa. Longevity has been linked to rate of decline in telomere length in birds and mammals, and absolute telomere length seems to be associated with body mass in mammals. Using a phylogenetic comparative method and 30 species of birds, we examined longevity (reflected by maximum lifespan), absolute telomere length, the rate of change in telomere length (TROC), and body mass (often strongly associated with longevity) to ascertain their degree of association. We divided lifespan into two life-history components, one reflected by body size (measured as body mass), and a component that was statistically independent of body mass. While both lifespan and body mass were strongly associated with a family tree of the species (*viz.*, the phylogeny of the species), telomere measures were not. Telomere length was not significantly associated with longevity or body mass, or our measure of mass-independent lifespan. TROC, however, was strongly associated with mass-independent lifespan, but only to a much lesser degree at best with body mass-predicted lifespan. Our results supported an association of TROC and longevity, in particular longevity that was independent of body size and part of the pace-of-life syndrome of life histories.

## 1 INTRODUCTION

2           Telomeres are repetitive nucleotide sequences at the terminal regions of eukaryote  
3 chromosomes. They serve to protect healthy chromosomes from DNA repair mechanisms that  
4 otherwise act on the terminal ends of chromosomes, and organize the replication of DNA during  
5 cell division (de Lange 2009). During replication, telomere sequences may be lost, thus  
6 shortening the telomere end (Olonikov 1973). Telomerase may replace the lost sequences, thus  
7 lengthening it (Chan and Blackburn 2004). Nonetheless, cells with over-shortened telomeres  
8 become “senescent” or “self-destruct” (termed apoptosis). When apoptosis occurs, the DNA-  
9 encoded information of the cell is removed from the organism (Blackburn 2000). Thus,  
10 telomeres may play a role in both cell senescence (or alternatively in cell immortalization due to  
11 the activity of telomerase; Tian et al. 2018), accumulation of senescent cells in organs (Campisi  
12 2005), and organismal senescence (Blasco 2007; Young 2018). Further, accelerated telomere  
13 loss at a given chronological age may indicate decreasing organismal condition, especially during  
14 early development, and may underline both physiological stress and a shorter life (viz.,  
15 advanced senescence; Haussmann et al. 2003; Bize et al. 2009; Boonekamp et al. 2014; Sudyka  
16 et al. 2016; Pepper et al. 2018; Whittemore et al. 2019; Sheldon et al. 2021).

17           Previous studies have suggested that due to the association of rate of telomere loss from  
18 chromosomes and organismal senescence, telomere dynamics during life are closely and  
19 functionally associated with lifespan among species of different body sizes and pace of life (*e.g.*,  
20 Dantzer and Fletcher 2015; Tricola et al. 2018). These studies primarily focused on birds, and  
21 recognized the possible importance of body size and historical patterns (viz., the influence of  
22 phylogeny) in explaining a general pattern of relatively slowed loss of telomeres during life in

23 larger species with syndromes of slower paces of life. These studies applied phylogenetic  
24 comparisons to 14 and 19 species of birds (TRF data), respectively, relatively small samples for  
25 robust phylogenetic analyses (though Dantzer and Fletcher 2016 presented an analysis that  
26 assumed no significant phylogenetic associations). Tricola et al. (2018) suggested that the rate  
27 of telomere shortening exhibited a strong historical pattern that may have coevolved with  
28 lifespan. Both studies concluded that larger species with relatively slower life histories exhibited  
29 reduced rates of telomere shortening.

30           These key previous studies raised a series of questions that might be examined with a  
31 larger sample of species of birds. First, how flexible are telomere traits over phylogenetic  
32 history? Tricola et al. (2018) found that telomere length was not strongly influenced by the  
33 phylogenetic pattern, but telomere rate of change (TROC) was. Alternatively, Criscuolo et al.  
34 (2021) found that neither adult telomere length nor TROC showed a strong phylogenetic  
35 pattern in a corrected sample size of 52 bird species, a different result that needs to be  
36 explained.

37           Second, how do longevity, body size, and the pace of life interact with telomere  
38 dynamics? Dantzer and Fletcher (2015) found that all three variables covaried strongly with  
39 TROC, and TROC was lower for the longest-lived bird species. The latter result was confirmed by  
40 Tricola et al. (2018) with or without body mass used as a covariate. In a phylogenetic  
41 comparative analysis of 9 species of birds and mammals, Le Pepke and Eisenberg (2020)  
42 reported a low rate of telomere loss in long-lived species, but a trivial effect of body mass.  
43 These studies took a phylogenetic comparative approach where regressions were used to  
44 “control” for the phylogenetic patterns underlying variables. Still, none of them quantified how

45 those phylogenetically-controlled patterns of telomere dynamics change with lifespan at a given  
46 body size; that is, when influences of body size are statistically controlled (Udroiu 2020).

47 Third, does telomere length *per se* change with species lifespan, with or without the  
48 influences of body size taken into account? Gomes et al. (2011) studied 61 species of mammals,  
49 and found that adult telomeres were shorter in the longest-lived species. Both body mass and  
50 longevity showed significant negative associations with telomerase and telomere length,  
51 respectively, independent of the phylogenetic pattern among the species (Gorbunova and  
52 Seluanov 2009). The conclusion of Gomes et al. (2011) was that, for large species to evolve long  
53 lifespans, replicative aging occurred (*i.e.*, short telomeres combined with repressed telomerase  
54 activity). A result confirmed by a re-analysis of the same dataset recently (Pepke and Eisenberg  
55 2021), with emphasis on an inverse association of telomere length with body mass. These  
56 results suggest that short telomeres may have co-evolved in long-lived species as a  
57 consequence of body size, underlying the necessity for large species to control for higher risks of  
58 cell immortalization by a widespread cellular mechanism (Tian et al. 2018). Interestingly, the  
59 phylogeny-adjusted analyses of Tricola et al. (2018) conducted in birds found no significant  
60 association of telomere length and longevity, whether or not influences of body mass were  
61 included. However, longevity and body mass are known to show strong covariance (Dantzer and  
62 Fletcher 2015), and thus may be collinear. The analyses of more bird species by Criscuolo et al.  
63 (2021), however, found no significant association of adult telomere length and either body size  
64 or the pace of life, with or without inclusion of the phylogenetic pattern in the analyses, though  
65 they did not specifically examine longevity and its single-trait association with telomere length.

66 The purpose of our present study was to examine associations of telomere length and

67 TROC on the one hand, and body size and longevity on the other hand in birds. We did this using  
68 a restricted sample size of 30 of the bird species (see below for justification) reviewed in the  
69 comparative analysis of Criscuolo et al. (2021). We first asked whether any of the variables  
70 showed evidence of strong phylogenetic pattern, using the Bayesian meta-analysis approach of  
71 Hadfield and Nakagawa (2010). Longevity and body size are closely associated in birds (*e.g.*,  
72 Bennett and Owens 2002; Dantzer and Fletcher 2015; Criscuolo et al. 2021). Larger species  
73 reflect many aspects of life histories that covary over evolutionary time, in part because it takes  
74 longer to grow and survive to a large body size (Dobson 2007). Further, bird species vary along a  
75 “slow-fast continuum” that reflects alternative paces of life that are independent of body size  
76 (Gaillard et al. 1989). Thus, we examined variation in longevity that was strongly associated with  
77 body size (“mass-predicted lifespan”), and longevity that was statistically independent of body  
78 size (“mass-independent lifespan”). The latter reflects changes in lifespan that can be described  
79 as varying with the pace of life (Dobson and Oli 2007; Criscuolo et al. 2021). Because differences  
80 between phylogenetically-adjusted and unadjusted associations of traits can be biologically  
81 informative (Price 1997), we compared both of the aspects of lifespan to telomere length and  
82 TROC.

83 We also addressed a further issue with respect to how TROC is measured. First, our  
84 sample included estimates of TROC that used mean differences in telomere lengths between  
85 chicks and older birds (after Criscuolo et al. 2021). Such estimates have the advantage of  
86 including the chick period, when the greatest rates of telomere loss occur as birds age (Sidorov  
87 et al. 2009; Monaghan and Ozanne 2018), but they have the disadvantage of including  
88 individuals that do not survive to adulthood (Fletcher and Dantzer 2015). A bias may thus occur

89 between the samples of younger and older birds. Thus, we estimated TROC only from samples  
90 of adult birds. A further problem is that some estimates of telomere length measure only DNA  
91 sequences of the terminal telomere repeats, whereas other methods include DNA sequences  
92 from the body of the chromosome (Remot et al. 2021). We restricted our analyses to those  
93 studies that used the former methods and thus produced the best estimates of telomere  
94 lengths.

95

## 96 **MATERIAL AND METHODS**

97 Our earlier study examined associations between telomere variables and aspects of life  
98 history for bird species (Criscuolo et al. 2021). Our comparative analysis followed the  
99 recommendations of the preferred reporting items for systematics reviews and meta-analysis  
100 (PRISMA) statement (Liberati et al., 2009).

101 In the present study, we focused on 30 species for which adult telomere length, TROC,  
102 and life history variables were all recorded. For these species, telomere lengths were estimated  
103 in kilobases (kb) using electrophoretic separation of telomere restriction fragments or by  
104 quantitative fluorescent in situ hybridization (respectively, TRF and Q-FISH; Remot et al. 2021).  
105 All studies used samples of erythrocytes. TROC was measured as the slope of telomere length  
106 regressed over age (kb/year) for each of the species (Hausmann et al. 2003; Tricola et al. 2018),  
107 but excluding the telomere lengths of hatchling chicks or yearlings (ages of 0-1 year). We  
108 followed Dantzer and Fletcher (2015) and Tricola et al. (2018) in using maximum lifespan in  
109 nature to typify longevity and mean adult female body mass to typify body size, and log-  
110 transformed both variables. Among the 30 species of birds, body-size-independent aspects of



111 longevity (longevity associated with the pace of life) were estimated as the residuals of  
112 maximum lifespan regressed on mean female body mass, and these residuals were checked for  
113 normality using a Q-Q plot and Shapiro-Wilk test. When multiple sources were available, a mean  
114 value of adult telomere length or TROC was used. All sources are reported in the online  
115 supplementary information (ESM1).

116 We divided lifespan into two statistically independent parts, based on the regression of  
117 lifespan onto body size (as estimated by mean adult female body mass for each species). The  
118 first variable represented mass-associated aspects of lifespan, as indicated by the predicted  
119 values of lifespan from the regression, and termed “mass-predicted lifespan.” The residuals  
120 from the analysis were termed “mass-independent lifespan,” and these two measures of  
121 lifespan were statistically uncorrelated. The latter variable estimated lifespan at a given body  
122 size, and may be interpreted as a measure of lifespan on the slow-fast continuum of the pace of  
123 life (Gaillard et al. 1989; Dobson and Oli 2007). Associations of telomere and lifespan variables  
124 were examined by comparison of both correlation and by phylogeny-adjusted correlation (after  
125 Price 1997).

126 A phylogeny was obtained from BirdTree (Figure 1), with 100 phylogenetic trees  
127 downloaded from <http://www.bird.tree.org> (De Magalhaes and Costa 2009; Jetz et al. 2012)  
128 using ape, apTreeshape and caper R packages. Branch lengths were estimated using the  
129 coalescent method, thus reflecting an estimate of relative divergence times for the phylogeny  
130 (Rannala and Yang 2003). Associations of the bird phylogeny with adult telomere length, TROC,  
131 adult female body mass, maximum lifespan, and the residuals of lifespan on body mass were  
132 estimated using Hadfield and Nakagawa’s (2010) Markov chain Monte Carlo generalized linear

133 mixed model (MCMCglmm; Hadfield 2010) package in R (R core team 2020). The MCMCglmm  
134 package was also used to produce phylogeny-adjusted estimate of associations of telomere,  
135 body mass, and longevity variables.

136 MCMCglmm was used to produce two types of results: 1) an estimate of the  
137 phylogenetic pattern in each of the study variables (viz.,  $\rho$  = the proportion of variance that  
138 could be statistically accounted for by a matrix of the phylogenetic pattern); and 2) degree of  
139 correlation of pairs of variables with statistical adjustment to remove the statistical influence of  
140 the phylogenetic pattern. Pearson's correlations, unadjusted for phylogeny, were also  
141 calculated for comparison with phylogeny-adjusted results. Cohen's (1988) criteria for effect  
142 sizes of associations were applied: small  $r = 0.1$ , medium  $r = 0.3$ , and large  $r \geq 0.5$ .

143

## 144 RESULTS

145 The regression of maximum lifespan on adult female body mass was highly significant ( $R^2$   
146 = 0.59,  $F = 40.4$ , d.f. = 1,28,  $P < 0.0001$ ). The residuals of this analysis were fairly close to a  
147 Gaussian distribution (Shapiro-Wilk statistic = 0.98,  $P = 0.84$ ), and were used as an estimate of  
148 mass-independent lifespan. The positive association of maximum lifespan and body mass was  
149 strong and significant ( $r = 0.768$ ,  $t = 6.4$ , d.f. = 28,  $P < 0.0001$ ).

150 Maximum lifespan had a strong associations with the phylogenetic pattern ( $\rho = 0.805$ ,  
151 [credible intervals]  $CI_{0.95} = 0.284 - 0.907$ ,  $N = 30$ ). Body mass (and thus mass-predicted lifespan)  
152 also had a strong association with phylogeny ( $\rho = 0.907$ ,  $CI_{0.95} = 0.414 - 0.994$ ,  $N = 30$ ). Mass-  
153 independent lifespan had at best a small association with phylogeny ( $\rho = 0.073$ ,  $CI_{0.95} = 0.011 -$   
154  $0.495$ ,  $N = 30$ ). Adult telomere length and TROC had trivial to small associations with the

155 phylogeny (respectively;  $\rho = 0.073$  and  $0.062$ ,  $CI_{0.95} = 0.017 - 0.497$  and  $0.018 - 0.568$ ,  $N = 30$ ).

156         Adult telomere length was not significantly correlated with maximum lifespan, mass-  
157 predicted lifespan, or mass-independent lifespan (Figure 2a). Once the phylogenetic pattern was  
158 taken into account statistically, adult telomere length exhibited trivial to moderate correlations  
159 with different estimates of lifespan (adjusted maximum lifespan,  $r = 0.004$ ,  $CI_{0.95} = -0.356 -$   
160  $0.394$ ; adjusted mass-predicted lifespan,  $r = -0.132$ ,  $CI_{0.95} = -0.499 - 0.271$ ; adjusted mass-  
161 independent lifespan,  $r = 0.108$ ,  $CI_{0.95} = -0.232 - 0.768$ ; all d.f. = 27,  $P > 0.20$ ). It is noteworthy  
162 that the adults of large species tended to have shorter telomeres, but at a moderate correlation  
163 at best (unadjusted for phylogeny,  $r = -0.249$ ,  $t = 1.4$ ,  $N = 30$ ,  $P = 0.18$ ).

164         TROC was significantly positively correlated with lifespan ( $r = 0.497$ ,  $t = 3.0$ , d.f. = 28,  $P <$   
165  $0.01$ ), and this pattern was similar but not significant when the phylogenetic pattern was taken  
166 into account (adjusted  $r = 0.366$ ,  $CI_{0.95} = -0.057 - 0.637$ , d.f. = 27,  $P = 0.12$ ) (Figure 2b). TROC  
167 exhibited a small to medium positive association with mass-predicted lifespan that was not  
168 significant ( $r = 0.288$ ,  $t = 1.6$ , d.f. = 28,  $P = 0.12$ ), and with phylogenetic “adjustment” this  
169 association turned slightly negative (adjusted  $r = -0.145$ ,  $CI_{0.95} = -0.522 - 0.225$ , d.f. = 27,  $P >$   
170  $0.20$ ). TROC and mass-independent lifespan exhibited a moderate but significant positive  
171 correlation ( $r = 0.432$ ,  $t = 2.5$ , d.f. = 28,  $P = 0.02$ ), and the effect size of this association was  
172 slightly lower but still significant when the phylogenetic pattern was taken into account  
173 statistically (adjusted  $r = 0.327$ ,  $CI_{0.95} = 0.037 - 0.661$ , d.f. = 27,  $P = 0.04$ ).

174

175 **DISCUSSION**

176 Our first question concerned the association of life history and telomere variables with  
177 the phylogenetic pattern across 30 species of birds. Lifespan and body mass are well known to  
178 covary among bird species and exhibit strong phylogenetic constraint (*e.g.*, Bennett and Owens  
179 2002; Dantzer and Fletcher 2015; Criscuolo et al. 2021). Less is known of phylogenetic  
180 influences on telomere dynamics, but Tricola et al. (2018) suggested little phylogenetic  
181 influence on telomere length and a significant influence on TROC. We found the expected fairly  
182 strong association of phylogenetic pattern and lifespan and mass-predicted lifespan, but a very  
183 weak association of the phylogeny with mass-independent lifespan (long or short life at a given  
184 body size). Telomere length and the rate of decline in telomere length over time exhibited weak  
185 associations with the phylogeny, contrary to the suggestion of Tricola et al. (2018). Given the  
186 fairly strong association of phylogeny with lifespan and body mass, however, it seemed  
187 reasonable to account for the phylogenetic pattern statistically when evaluating associations of  
188 lifespan, body mass, and telomere dynamics.

189 Our second question was whether there was a strong association of lifespan and TROC,  
190 as suggested by Dantzer and Fletcher (2015) and Tricola et al. (2018). For this, we considered  
191 two aspects of longevity. Large animals live longer, as shown by a large number of studies on  
192 life-history traits that scale with body size (*e.g.*, Gaillard et al. 1989; Read and Harvey 1989; Roff  
193 1992; Stearns 1992; Bennett and Owens 2002; Dobson and Jouventin 2007). Larger animals take  
194 longer to grow to adult size and must allocate considerable resources and effort to maintaining  
195 their large number of cells. As such, the first question about longevity is whether it is associated  
196 with the overall size of an organism (Dobson 2007). The second aspect of longevity is associated  
197 with the pace of life, along the so-called “slow-fast continuum” (Gaillard et al. 1989; Dobson and

198 Oli 2007). At a given body size, some species have greater maximum lifespan than others, and  
199 this may be associated with lower reproductive effort, and *vice versa* for short-lived species.  
200 Thus, alternative life-history tactics may be produced among species, at a given body size.

201 For the first aspect of lifespan, that associated with the size of the species, mass-  
202 predicted lifespan had a small association with TROC that was not statistically significant, with  
203 or without statistical adjustment for the phylogenetic pattern (note that with adjustment for  
204 phylogeny, the sign of this correlation turned negative, Figure 2b). However, our lifespan  
205 variable that was independent of body size (*viz.*, mass-independent lifespan) had a moderate  
206 positive association with TROC as judged by its effect size, significant with or without statistical  
207 adjustment for phylogeny. These results suggest that TROC does not vary strongly with body  
208 size *per se*, but rather has at best a poor association with body size, such that longer-lived  
209 species that are somewhat larger exhibited only slightly less telomere loss than somewhat  
210 smaller species. However, at a given body size, birds exhibited a stronger pattern of association  
211 of relative longevity (*i.e.*, a slow pace-of-life) and TROC. Species with the longest lives for their  
212 body mass exhibited the slowest rate of loss of telomeres during life. Thus, the division of  
213 lifespan into two parts associated with different aspects of life histories revealed biologically  
214 meaningful patterns of varying strengths.

215 The analyses of Dantzer and Fletcher (2015), Tricola et al. (2018), Udrouiu (2020), and Le  
216 Pepke and Eisenberg (2020) revealed a general pattern of positive association of longevity and  
217 TROC, but without testing for different underlying aspects of longevity. Our results revealed  
218 nuances to their conclusions: longevity and TROC showed no consistent pattern of change as  
219 body size increased, but rather there was a strong pattern of longevity and TROC increasing

220 together at a given body size. This pattern likely underlies the positive associations of longevity  
221 and TROC found by previous studies. Overall, the general agreement of unadjusted and  
222 phylogeny-adjusted associations (Figure 2) may suggest that correlations in our results were  
223 little influenced by the historical evolutionary pattern reflected by the consensus phylogenetic  
224 tree.

225         Our final question was whether adult telomeres were shorter in the larger and longest-  
226 lived species, as suggested by Gomes et al. (2011) and Pepke and Eisenberg (2021) for  
227 mammals. This latter study suggested that telomere length coevolved with body size, such that  
228 large species have short telomeres, and thus facilitated the evolution of long lifespans, notably  
229 *via* the use of cell replication senescence and the reduction of risks of cell immortalization  
230 (Risques and Promislov 2018; Seluanov et al. 2018). On the other hand, Tricola et al. (2018)  
231 found a slight but non-significant positive association of telomere length and maximum lifespan  
232 among 19 species of birds. While we found that both longevity and body mass followed the  
233 phylogenetic pattern fairly closely, telomere dynamics did not. Nonetheless, we found little  
234 evidence of larger species having shorter telomeres, with or without statistical adjustment for  
235 the influence of the phylogenetic pattern (Figure 2a). In the light of our results, postulating that  
236 large birds use replication senescence, as larger mammals do, as a mechanism favouring long  
237 lifespan is still an unanswered question. This begs the question of whether at least some bird  
238 species have evolved specific anti-ageing or anti-cancer mechanisms that are similar to the  
239 telomere-related control suggested for long-lived mammalian species that weigh less than a  
240 kilogram (Gomes et al. 2011; Tian et al. 2018; but see Seluanov et al. 2018).

241 Comparative studies like the present one help to point out how aging mechanisms at the  
242 cell level may have coevolved with life histories among animal species. So far, as we have seen  
243 above, comparative studies have concluded that large body size and long lifespan have evolved  
244 with short telomeres and reduced loss of telomeres in mammals, or that longevity and reduced  
245 loss of telomeres (but not short telomeres) are matched in birds. This discrepancy might be  
246 attributed to the smaller range of sizes in birds, suggesting that if body size and the number of  
247 cells is the main constraint to the evolution of long telomeres, this may explain why birds show  
248 higher levels of telomere maintenance (*e.g.*, via an enhanced telomerase expression) than  
249 mammals and long up-to Mb telomeres (Delany et al. 2000; Monaghan 2010). Our analysis that  
250 controlled for the effects of body size suggested that enhanced telomere maintenance has  
251 coevolved with longevity in birds independently of body size, and this differently, even in closely  
252 related species. This is, in addition to that of high glycemia and aerobic metabolism, a  
253 paradoxical association with avian longevity (Holmes and Harper 2018), a new aging enigma  
254 that requires continued exploration in relation to species' evolutionary histories.

255

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269 **AUTHORS' CONTRIBUTIONS**

270 FC collected the data, FSD wrote the manuscript and analysed the data, and all three authors  
271 edited/rewrote the manuscript.

272

273 **DATA ACCESSIBILITY**

274 Data file is provided in ESM1.

275



276 **REFERENCES**

277

278 Bennett, P. M., and Owens, I. P. F. (2002). Evolutionary ecology of birds: life histories, mating  
279 systems and extinction. *New York ; U.S.A. : Oxford University Press.*

280 Bize, P., Criscuolo, F., Metcalfe, N. B., Nasir, L., and Monaghan, P. (2009). Telomere dynamics  
281 rather than age predict life expectancy in the wild. *Proceedings of the Royal Society B:*  
282 *Biological Sciences*, 276(1662), 1679-1683. doi:10.1098/rspb.2008.1817

283 Blackburn, E. H. (2000). Telomere states and cell fates. *Nature*, 408, 53-56.

284 Blasco, M. A. (2007). Telomere length, stem cells and aging. *Nature Chemical Biology*, 3(10),  
285 640-649. doi:10.1038/nchembio.2007.38

286 Boonekamp, J. J., Mulder, G. A., Salomons, H. M., Dijkstra, C., and Verhulst, S. (2014). Nestling  
287 telomere shortening, but not telomere length, reflects developmental stress and  
288 predicts survival in wild birds. *Proceedings of the Royal Society B: Biological Sciences*,  
289 281(1785), 20133287-20133287. doi:10.1098/rspb.2013.3287

290 Campisi, J. (2005). Senescent Cells, Tumor Suppression, and Organismal Aging: Good Citizens,  
291 Bad Neighbors. *Cell*, 120(4), 513-522. doi:10.1016/j.cell.2005.02.003

292 Chan, S. R. W. L., and Blackburn, E. H. (2004). Telomeres and telomerase. *Philosophical*  
293 *Transactions of the Royal Society B: Biological Sciences*, 359(1441), 109-122.  
294 doi:10.1098/rstb.2003.1370

295 Cohen, J. (1988). Statistical Power Analysis for the Behavioral Sciences, 2nd edition. *Erlbaum*,  
296 *Hillsdale, NJ.*

297 Criscuolo, F., Dobson, F. S., and Schull, Q. (2021) The influence of phylogeny and life history on  
298 telomere lengths and telomere rate of change among bird species: A meta-analysis.  
299 *Ecology and Evolution*, 11, 12908-11922. doi: 10.1002/ece3.7931

300 Dantzer, B., and Fletcher, Q. E. (2015). Telomeres shorten more slowly in slow-aging wild  
301 animals than in fast-aging ones. *Experimental Gerontology*, 71, 38-47.  
302 doi:10.1016/j.exger.2015.08.012

303 de Lange, T. (2009). How Telomeres Solve the End-Protection Problem. *Science*, 326(5955), 948-  
304 952. doi:10.1126/science.1170633

305 de Magalhaes, J. P., and Costa, J. (2009). A database of vertebrate longevity records and their  
306 relation to other life-history traits. *Journal of Evolutionary Biology*, 22(8), 1770-1774.  
307 doi:10.1111/j.1420-9101.2009.01783.x

308 Delany, M. E., Krupkin, A. B., and Miller, M. M. (2000). Organization of telomere sequences in  
309 birds: evidence for arrays of extreme length and for in vivo shortening. *Cytogenetics and*  
310 *Cell Genetics*, 90, 139-145.

311 Dobson, F. S. (2007). A lifestyle view of life-history evolution. *Proceedings of the National*  
312 *Academy of Sciences USA*, 104, 17565-17566.

313 Dobson, F. S., and Jouventin, P. (2007). How slow breeding can be selected in seabirds: testing  
314 Lack's hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, 274(1607),  
315 275-279. doi:10.1098/rspb.2006.3724

316 Dobson, F. S., and Oli, M. K. (2007). Fast and slow life histories of mammals. *Ecoscience*, 14(3),  
317 292-299.

318 Gaillard, J.-M., Pontier, D., Allainé, D., Lebreton, J. D., Trouvilliez, J., and Clobert, J. (1989). An  
319 analysis of demographic tactics in birds and mammals. *Oikos*, *56*, 59-76.

320 Gomes, N. M. V., Ryder, O. A., Houck, M. L., Charter, S. J., Walker, W., Forsyth, N. R., . . . Wright,  
321 W. E. (2011). Comparative biology of mammalian telomeres: hypotheses on ancestral  
322 states and the roles of telomeres in longevity determination. *Aging Cell*, *10*, 761-768.

323 Gorbunova, V., and Seluanov, A. (2009). Coevolution of telomerase activity and body mass in  
324 mammals: From mice to beavers. *Mechanisms of Ageing and Development*, *130*, 3-9.  
325 doi:10.1016/j.mad.2008.02.008.

326 Hadfield, J. D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models:  
327 The MCMCglmm R Package. *Journal of Statistical Software*, *33*(2), 1-22.

328 Hadfield, J. D., and Nakagawa, S. (2010). General quantitative genetic methods for comparative  
329 biology: phylogenies, taxonomies and multi-trait models for continuous and categorical  
330 characters. *Journal of Evolutionary Biology*, *23*(3), 494-508. doi:10.1111/j.1420-  
331 9101.2009.01915.x

332 Hausmann, M. F., Winkler, D. W., O'Reilly, K. M., Huntington, C. E., Nisbet, I. C. T., and Vleck, C.  
333 M. (2003). Telomeres shorten more slowly in long-lived birds and mammals than in  
334 short-lived ones. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1522),  
335 1387-1392. doi:10.1098/rspb.2003.2385

336 Holmes, D. J., and Harper, J. M. (2018). Birds as Models for the Biology of Aging and Aging-  
337 Related Disease: An Update. In *Conn's Handbook of Models for Human Aging (pp. 301-*  
338 *312)*. Academic Press. doi:10.1016/b978-0-12-811353-0.00022-1

339 Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., and Mooers, A. O. (2012). The global diversity of  
340 birds in space and time. *Nature*, 491, 444-448. doi:10.1038/nature11631

341 Le Pepke, M., and Eisenberg, D. T. A. (2020). Accounting for phylogenetic relatedness in cross-  
342 species analyses of telomere shortening rates. *Experimental Results*, 1.  
343 doi:10.1017/exp.2020.18

344 Liberati, A., Altman, D. G., Tetzlaff, J., Mulrow, C., Gøtzsche, P. C., Loannidis, J. P. A., . . . Moher,  
345 D. (2009). The PRISMA Statement for Reporting Systematic Reviews and Meta-Analyses  
346 of Studies That Evaluate Health Care Interventions: Explanation and Elaboration. *PLoS*  
347 *Medicine*, 6(7), e1000100. doi:doi:10.1371/journal.pmed.1000100. PMC 2707010. PMID  
348 19621070

349 Monaghan, P. (2010). Telomeres and life histories: the long and the short of it. *Annals of the*  
350 *New York Academy of Sciences*, 1206, 130-142. doi:10.1111/j.1749-6632.2010.05705.x

351 Monaghan, P., and Ozanne, S. E. (2018). Somatic growth and telomere dynamics in vertebrates:  
352 relationships, mechanisms and consequences. *Philosophical Transactions of the Royal*  
353 *Society B: Biological Sciences*, 373(1741), 20160446. doi:10.1098/rstb.2016.0446

354 Olonikov, A. M. (1973). A theory of marginotomy -Incomplete copying of template margin in  
355 enzymic-synthesis of polynucleotides and biological significance of phenomenon. *Journal*  
356 *of Theoretical Biology*, 41, 181-190. doi:https://doi.org/10.1016/0022-5193(73)90198-7

357 Pepke, M. L., & Eisenberg, D. T. A. (2021). On the comparative biology of mammalian telomeres:  
358 Telomere length co-evolves with body mass, lifespan and cancer risk. *Molecular Ecology*.  
359 doi:10.1111/mec.15870.

360 Pepper, G. V., Bateson, M., and Nettle, D. (2018). Telomeres as integrative markers of exposure  
361 to stress and adversity: a systematic review and meta-analysis. *Royal Science Open*  
362 *Science*, 5, 180744. doi.org/10.1098/rsos.180744

363 Price, T. (1997). Correlated evolution and independent contrasts. *Philosophical Transactions fo*  
364 *the Royal Society of London B*, 352, 519-529.

365 R core team. (2020). R: A language and environment for statistical computing. *R Foundation for*  
366 *Statistical Computing*.

367 Rannala, B., and Yang, Z. (2003). Bayes estimation of species divergence times and ancestral  
368 population sizes using DNA sequences from multiple loci. *Genetics*, 164, 1645-1656.

369 Read, A. F., and Harvey, P. H. (1989) Life history differences among the eutherian radiations.  
370 *Journal of Zoology*, 219, 329-353.

371 Remot, F., Ronget, V., Froy, H., Rey, B., Gaillard, J.-M., Nussey, D. H., and Lemaitre, J.-F. (2021)  
372 Decline in telomere length with increasing age across nonhuman vertebrates: A meta-  
373 analysis. *Molecular Ecology, early access*, DOI: 10.1111/mec.16145

374 Risques, R. A., and Promislow, D. E. L. (2018). All's well that ends well: why large species have  
375 short telomeres. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
376 373, 20160448. doi:10.1098/rstb.2016.0448 10.6084/m9

377 Roff, D. A. (2002). Life History Evolution. *Sunderland, MA: Sinauer Associates*.

378 Seluanov, A., Gladyshev, V. N., Vijg, J., and Gorbunova, V. (2018). Mechanisms of cancer  
379 resistance in long-lived mammals. *Nature Reviews Cancer*, 18(7), 433-441.  
380 doi:10.1038/s41568-018-0004-9

381 Sheldon, E., Eastwood, J., Teunissen, N., Roast, M., Fan, M., Hall, M., . . . Peters, A. (2021).  
382 Telomere dynamics in the first year of life, but not later in life, predict lifespan in a wild  
383 bird. doi:10.22541/au.162168440.03821228/v1

384 Sidorov, I., Kimura, M., Yashin, A., and Aviv, A. (2009). Leukocyte telomere dynamics and human  
385 hematopoietic stem cell kinetics during somatic growth. *Experimental Hematology*, 37,  
386 514-524. doi:10.1016/j.exphem.2008.11.009

387 Stearns, S. C. (1992). The evolution of life histories. *Oxford University Press*.

388 Sukyka, J., Arct, A., Drobniak, S., Gustafsson, L., and Cichon, J. (2016). Longitudinal studies  
389 confirm faster telomere erosion in short-lived bird species. *Journal of Ornithology*, 157,  
390 373-375. doi:10.1007/s10336-015-1304-4

391 Tian, X., Doerig, K., Park, R., Can Ran Qin, A., Hwang, C., Neary, A., . . . Gorbunova, V. (2018).  
392 Evolution of telomere maintenance and tumour suppressor mechanisms across  
393 mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373,  
394 20160443. doi:10.1098/rstb.2016.0443 10.6084/m9.

395 Tricola, G. M., Simons, M. J. P., Atema, E., Boughton, R. K., Brown, J. L., Dearborn, D. C., . . .  
396 Hausmann, M. F. (2018). The rate of telomere loss is related to maximum lifespan in  
397 birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1741),  
398 20160445. doi:10.1098/rstb.2016.0445

399 Udroi, I. (2020). On the correlation between telomere shortening rate and life span.  
400 *Proceedings of the National Academy of Sciences*, 117, 2248-2249.

401 Whittmore, K., Vera, E., Martinez-Nevaldo, E., Sanpera, C., and Blasco, M. A. (2019). Telomere  
402 shortening rate predicts species life span. *Proceedings of the National Academy of the*  
403 *U.S.A.*, 116(30), 15122-15127.

404 Young, A. J. (2018). The role of telomeres in the mechanisms and evolution of life-history trade-  
405 offs and ageing. *Philosophical Transactions of the Royal Society B: Biological Sciences*,  
406 373(1741), 20160452. doi:10.1098/rstb.2016.0452

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410 **FIGURE LEGENDS**

411 Figure 1. Phylogenetic tree of the 30 bird species for which adult telomere length and telomere  
412 length rate of change (TROC) were collected from published papers on avian telomeres using  
413 the TRF or Q-FISH methodologies. The consensus phylogenetic tree was obtained from  
414 BirdTree.org (100 trees).

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417 Figure 2. a) Correlations of adult telomere length and 3 life-history traits of 30 bird species:  
418 lifespan, mass-predicted lifespan, and mass-independent lifespan. b) Correlations of telomere  
419 length rate of change (TROC) and the 3 aspects of longevity. “Lifespan” shows unadjusted  
420 correlations, “Mass-Pred Lifespan” shows lifespan values predicted from the regression of  
421 lifespan on body size, and “Mass-Ind Lifespan” shows the residuals of the regression of lifespan  
422 on body size. Pearson correlations are shown with horizontal center bars and 95% confidence  
423 intervals with high and low horizontal bars. Triangles show the phylogeny-adjusted correlation  
424 values (none are significantly different from zero at the  $P < 0.05$  level). The horizontal black  
425 dashed lines show zero correlation.

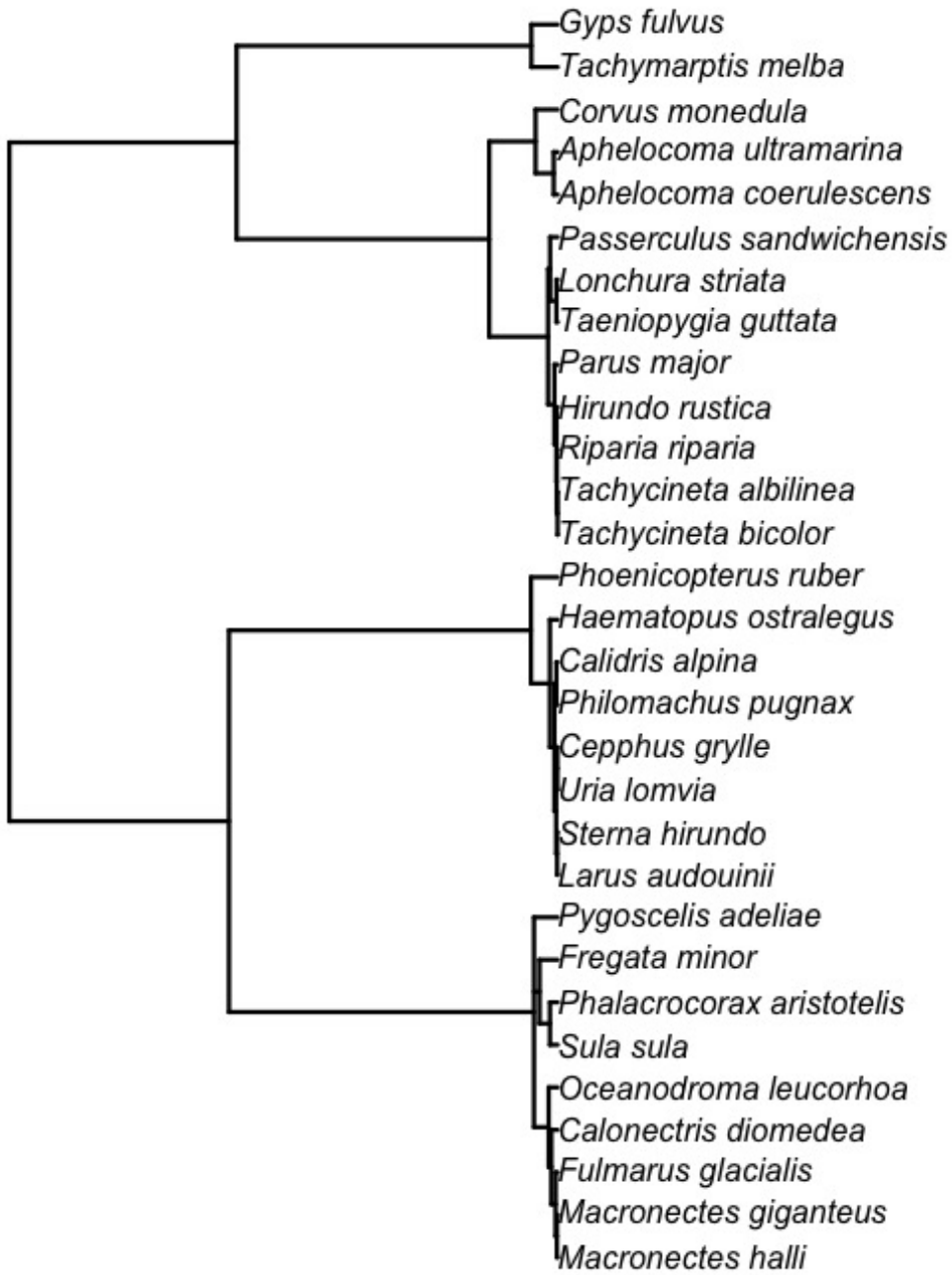
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427 **FIGURES**

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435 Figure 2. a) Correlations of adult telomere length (TL) and 3 life-history traits of 30 bird species:  
436 lifespan, mass-predicted lifespan, and mass-independent lifespan. b) Correlations of telomere  
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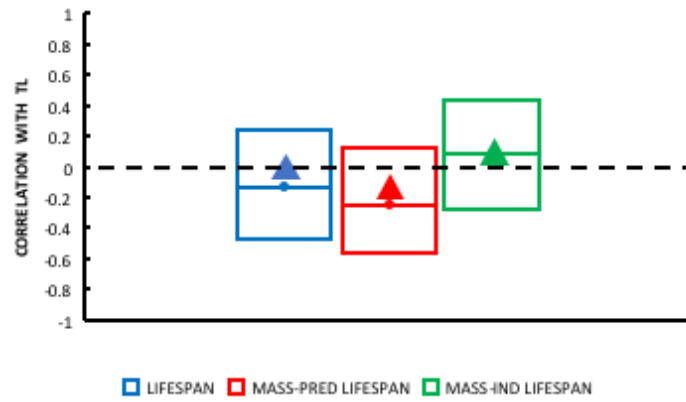
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a)



b)

