

University of Groningen

Early-life seasonal, weather and social effects on telomere length in a wild mammal

van Lieshout, Sil H. J.; Perez Badas, Elisa; Bright Ross, Julius G.; Bretman, Amanda ; Newman, Chris ; Buesching, Christina D.; Burke, Terry; Macdonald, David W.; Dugdale, Hannah L.

Published in:
Molecular Ecology

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Early version, also known as pre-print

Publication date:
2021

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van Lieshout, S. H. J., Perez Badas, E., Bright Ross, J. G., Bretman, A., Newman, C., Buesching, C. D., Burke, T., Macdonald, D. W., & Dugdale, H. L. (2021). Early-life seasonal, weather and social effects on telomere length in a wild mammal. Manuscript submitted for publication.

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

1 **Early-life seasonal, weather and social effects on telomere length in a wild mammal**

2 Sil H.J. van Lieshout^{1,2}, Elisa P. Badás^{1,3}, Julius G. Bright Ross⁴, Amanda Bretman¹, Chris Newman⁴,
3 Christina D. Buesching^{4,5}, Terry Burke^{2,3}, David W. Macdonald⁴ & Hannah L. Dugdale^{1,3}

4 ¹School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK; ²NERC
5 Biomolecular Analysis Facility, Department of Animal and Plant Sciences, University of Sheffield,
6 Sheffield S10 2TN, UK; ³Groningen Institute for Evolutionary Life Sciences, University of Groningen,
7 9747 AG CP Groningen, The Netherlands; ⁴Wildlife Conservation Research Unit, Department of
8 Zoology, University of Oxford, The Recanati-Kaplan Centre, Abingdon, Oxfordshire OX13 5QL, UK;
9 ⁵Department of Biology, The University of British Columbia, Okanagan, Kelowna V1V 1V7, British
10 Columbia, Canada.

11
12 Correspondence author: Sil H.J. van Lieshout

13 E-mail: sil.vanlieshout@gmail.com

14 ORCID: SHJvL, 0000-0003-4136-265X; EPB, 0000-0001-9398-5440; JGB, 0000-0003-2454-1592; AB,
15 0000-0002-4421-3337; CN, 0000-0002-9284-6526; CDB, 0000-0002-4207-5196; TB, 0000-0003-3848-
16 1244; DWM, 0000-0003-0607-9373; HLD, 0000-0001-8769-0099

17
18 **Abstract**

19 Early-life environmental conditions can provide a source of individual variation in life-history
20 strategies and senescence patterns. Conditions experienced in early life can be quantified by
21 measuring telomere length, which can act as a biomarker of survival probability in some species. Here,
22 we investigate whether seasonal changes, weather conditions, and group size are associated with
23 early-life and/or early-adulthood telomere length in a wild population of European badgers (*Meles*
24 *meles*). We found substantial intra-annual changes in telomere length during the first three years of
25 life, where within-individual effects showed shorter telomere lengths in the winter following the first
26 spring and a trend for longer telomere lengths in the second spring compared to the first winter. In

27 terms of weather conditions, cubs born in warmer, wetter springs with low rainfall variability had
28 longer early-life (3–12 months old) telomere lengths. Additionally, cubs born in groups with more cubs
29 had marginally longer early-life telomeres, providing no evidence of resource constraint from cub
30 competition. We also found that the positive association between early-life telomere length and cub
31 survival probability remained when social and weather variables were included. Finally, after sexual
32 maturity, in early adulthood (i.e. 12–36 months) we found no significant association between same-
33 sex adult group size and telomere length (i.e. no effect of intra-sexual competition). Overall, we show
34 that controlling for seasonal effects, which are linked to food availability, is important in telomere
35 length analyses, and that variation in telomere length in badgers reflects early-life conditions and also
36 predicts first year cub survival.

37

38 **Keywords:** telomere length, early-life environment, group size, weather conditions, senescence,
39 season

40

41 **1. Introduction**

42 The early-life environment can affect individual fitness (Lindström, 1999), with consequences for
43 variation in life-history strategies (Metcalfe & Monaghan, 2001) and senescence patterns (Nussey,
44 Kruuk, Morris, & Clutton-Brock, 2007). For example, it has been hypothesised that senescence, the
45 decline in performance in older age, is faster in individuals that experienced adverse early-life
46 environments, due to different energy allocation trade-offs between early- and later-life in response
47 to the environment (Kirkwood & Rose, 1991; Medawar, 1952; Williams, 1957). A more stressful early-
48 life environment, either through a sub-optimal mean or more variable early-life environment, during
49 this sensitive developmental period, could trigger early reproductive investment at the expense of
50 somatic maintenance, leading to faster rates of senescence (Kirkwood & Rose, 1991; Lemaitre et al.,
51 2015). Empirical evidence for such detrimental effects has been found in various wild animal

52 populations (Cooper & Kruuk, 2018; Hammers, Richardson, Burke, & Komdeur, 2013; Reed et al.,
53 2008).

54 Telomere length has been suggested as a non-causal biomarker of senescence in some species
55 (López-Otín, Blasco, Partridge, Serrano, & Kroemer, 2013; Monaghan & Haussmann, 2006), that
56 facilitates quantification of physiological consequences of the conditions experienced (Monaghan,
57 2014). Telomeres are highly conserved nucleoprotein structures at the end of chromosomes
58 consisting of a non-coding sequence (5'-TTAGGG-3') and shelterin proteins (Blackburn, 2000; de
59 Lange, 2005). Telomeres maintain genomic integrity by preventing chromosome degradation and
60 fusion of chromosome ends by forming T-loops (de Lange, 2004). Generally, telomeres shorten with
61 each cell replication due to the end-replication problem (Olovnikov, 1973), but telomere shortening
62 can be accelerated potentially by oxidative damage (Boonekamp, Bauch, Mulder, & Verhulst, 2017;
63 Reichert & Stier, 2017; von Zglinicki, 2002) and through stressors (Epel et al., 2004; Heidinger et al.,
64 2012). Telomeres can, however, elongate via the enzyme telomerase (Blackburn et al., 1989) – which
65 shows a negative correlation with mammalian body mass (Tian et al., 2018) – and other telomere-
66 elongation pathways (Cesare & Reddel, 2010; Mendez-Bermudez et al., 2012). Cells with critically
67 short telomeres ultimately enter replicative senescence, where the accumulation of senescent cells
68 can impair tissue function due to reduced renewal capacity (Campisi, 2005; Campisi & di Fagagna,
69 2007) and potentially lead to organismal senescence (Young, 2018).

70 In some species, variation in early-life telomere length has been linked to season, specifically
71 with winter effects when torpor and hibernation facilitate tolerance of winter food scarcity and
72 reduction of thermoregulatory costs. During hibernation, more frequent arousal – which increases
73 metabolic rate and potentially increases oxidative stress – is associated in arctic ground squirrels
74 (*Urocitellus parryii*) with shorter telomere length (Wilbur, Barnes, Kitaysky, & Williams, 2019) and in
75 edible dormice (*Glis glis*) with increased telomere shortening (Turbill, Ruf, Smith, & Bieber, 2013).
76 Telomere shortening is reduced when the animals' core temperature difference between hibernation
77 and arousal is smaller, in both edible and garden (*Eliomys quercinus*) dormice (Nowack et al., 2019).

78 Conversely, the use of spontaneous daily torpor in non-hibernating Djungarian hamsters (*Phodopus*
79 *sungorus*) is associated with telomere lengthening due to a relatively low energy investment to return
80 to euthermia along with the benefits of reduced metabolic rate in torpor compared to hibernation
81 (Turbill, Smith, Deimel, & Ruf, 2012). In contrast, non-hibernating juvenile garden dormice that more
82 frequently underwent fasting-induced torpor showed higher telomere shortening than individuals
83 undergoing torpor less frequently (Giroud et al., 2014). Species that undergo facultative winter torpor
84 may conserve energy for somatic maintenance that could potentially be invested in telomere
85 restoration/elongation. Additionally, there is evidence in non-hibernating rodents for seasonal effects
86 of food availability on telomere dynamics (Criscuolo, Pillay, Zahn, & Schradin, 2020). However, since
87 telomere length, season and body mass might be intercorrelated (Réale, Festa-Bianchet, & Jorgenson,
88 1999; Tian et al., 2018), body mass needs to be taken into account when studying seasonal effects.

89 In addition to these intra-annual changes in telomere length, extensive evidence links adverse
90 early-life conditions to shorter telomeres (McLennan et al., 2016; Mizutani, Tomita, Niizuma, & Yoda,
91 2013; Watson, Bolton, & Monaghan, 2015), where shorter telomeres are associated with reduced
92 survival probability (Wilbourn et al., 2018). Food availability, often determined by weather conditions
93 (e.g. Campbell, Nouvellet, Newman, Macdonald, & Rosell, 2012), has been positively associated with
94 early-life telomere length (e.g. Foley et al., 2020; Spurgin et al., 2017). Interestingly, early-life food
95 availability may also impact life-history strategies (Bright Ross, Newman, Buesching, & Macdonald,
96 2020). It has been hypothesised that individuals in temporally stochastic environments should
97 modulate their energy trade-offs (Erikstad, Fauchald, Tveraa, & Steen, 1998; Reid, Bignal, Bignal,
98 McCracken, & Monaghan, 2003; Weimerskirch, Zimmermann, & Prince, 2001) and adopt a bet-
99 hedging strategy (Wilbur & Rudolf, 2006). Since weather variability is predicted to increase in the
100 future (IPCC, 2018), it is important to understand the implications of variable early-life conditions for
101 life-history strategies and early-life telomere length. The interplay between the mean of and variability
102 in early-life environmental conditions, such as the availability and variation in food, foraging success
103 and thermal stress for young individuals (Noonan et al., 2015; Nouvellet, Newman, Buesching, &

104 Macdonald, 2013; Webb & King, 1984), can thus impact developmental stress, longevity and may be
105 reflected in early-life telomere length.

106 Social conditions in early-life can also shape life-history strategies and senescence due to
107 increased competition for food and social stress. For example, female red deer (*Cervus elaphus*) that
108 experienced high levels of resource competition in early-life showed faster rates of reproductive
109 senescence (Nussey et al., 2007). Additionally, there is evidence for conspecific resource competition
110 in early-life leading to greater telomere shortening in birds (Boonekamp, Mulder, Salomons, Dijkstra,
111 & Verhulst, 2014; Nettle et al., 2015; Stier, Massemin, Zahn, Tissier, & Criscuolo, 2015), and shorter
112 telomere lengths in wild meerkats (Cram, Monaghan, Gillespie, & Clutton-Brock, 2017). Such patterns
113 can be explained because stressors (including competition) are associated with both shorter telomere
114 lengths and higher telomere shortening (Chatelain, Drobniak, & Szulkin, 2020).

115 The effects of social conditions on senescence may also become apparent after sexual
116 maturity, when individuals compete for mating opportunities (Andersson, 1994; Beirne, Delahay, &
117 Young, 2015). In polygynous species, sex differences in senescence may be attributable to intense
118 intra-sexual competition between males (Clutton-Brock & Isvaran, 2007; Promislow, 1992; Williams,
119 1957). Male investment for mating opportunities may trade off with self-maintenance (Kirkwood &
120 Rose, 1991). Intense male–male competition drives selection for shorter lifespan and faster
121 senescence in males, compared to females (Clutton-Brock & Isvaran, 2007; Williams, 1957). While this
122 prediction has been challenged (Bonduriansky, Maklakov, Zajitschek, & Brooks, 2008; Graves, 2007;
123 Promislow, 2003), and sex-specific senescence may be trait-dependent with respect to the underlying
124 physiological processes (Nussey et al., 2009), higher rates of male-biased actuarial senescence in
125 polygynous and sexual dimorphic species exist (Clutton-Brock & Isvaran, 2007; Promislow, 1992).
126 While social effects may also contribute to senescence in females (Sharp & Clutton-Brock, 2011;
127 Woodroffe & Macdonald, 1995), such sex-specific social effects on senescence are expected to be
128 greater in males (Bonduriansky et al., 2008; Clutton-Brock & Isvaran, 2007; Maklakov & Lummaa,

129 2013). However, whether increased intra-sexual competition (e.g. higher local densities of same-sex
130 individuals) is associated with shorter telomere lengths remains to be tested.

131 To test the effects of early-life social and environmental conditions on telomere length, we
132 use a long-term dataset from a wild population of European badgers (*Meles meles*; henceforth
133 ‘badgers’). Badgers show reproductive senescence with males having a later onset but faster rate of
134 senescence than females (Dugdale, Pope, Newman, Macdonald, & Burke, 2011). Additionally, early-
135 life telomere length (3–12 months old) positively correlates with first-year survival and lifespan in
136 badgers (van Lieshout et al., 2019). In the UK and Ireland, badgers are natally philopatric and can form
137 large social groups (mean group size = 11.3, range = 2–29; da Silva, Macdonald, & Evans, 1994) with
138 latrine-marked borders (Buesching, Newman, Service, Macdonald, & Riordan, 2016; Delahay et al.,
139 2000), although they do transgress these borders when foraging (Ellwood et al., 2017; Noonan et al.,
140 2015) without any sex difference in foraging niche (Robertson, McDonald, Delahay, Kelly, & Bearhop,
141 2014).

142 Regardless of whether badgers undergo facultative winter torpor (Johansson, 1957) or true
143 hibernation (Ruf & Geiser, 2015), badgers do reduce their body temperature by up to 8.9°C (Fowler &
144 Racey, 1988), thus reducing energy expenditure (Newman, Zhou, Buesching, Kaneko, & Macdonald,
145 2011). Badgers in Britain mainly feed on earthworms (*Lumbricus terrestris*; Johnson, Baker, Morecroft,
146 & Macdonald, 2001; Kruuk & Parish, 1981). Earthworms are sensitive to microclimatic conditions
147 (Edwards & Bohlen, 1996; Gerard, 1967; Newman, Buesching, & Macdonald, 2017), making their
148 abundance and distribution highly dependent on weather conditions. High-density badger
149 populations occur in mild areas with damp conditions where earthworms are available (Johnson, Jetz,
150 & Macdonald, 2002; Kruuk, 1978; Macdonald, Newman, & Buesching, 2015; Newman et al., 2017).
151 Foraging efficiency is reduced in adverse weather conditions, due to reduced availability of
152 earthworms, thermal stress when foraging in cold and wet conditions, and/or the choice to remain in
153 thermally-stable underground dens, termed setts (Noonan et al., 2014; Noonan et al., 2018; Nouvellet
154 et al., 2013; Tsunoda, Newman, Buesching, Macdonald, & Kaneko, 2018). Weather conditions can

155 therefore impact survival probability where, for example, higher annual mean daily rainfall is positively
156 associated with adult survival probability in badgers, whereas high annual variability in temperature
157 has detrimental consequences for cub and adult survival (Nouvellet et al., 2013).

158 Badgers have one litter per year, with a mean litter size of 1.5 ± 0.3 (95% CI; range = 1–5;
159 Annavi et al., 2014). Badger cub growth and maturation depends on the number of other cubs and
160 adults present within the social group (Sugianto, Newman, Macdonald, & Buesching, 2019),
161 potentially indicating resource competition within social groups. Adult male badgers invest substantial
162 energy into promiscuity and repeated mounting (Dugdale, Griffiths, & Macdonald, 2011) both within
163 and outside their social group, resulting in high rates (i.e. 48%) of extra-group paternity, of which 85%
164 were in neighbouring groups (Annavi et al., 2014; Dugdale, Macdonald, Pope, & Burke, 2007). Males
165 also exhibit substantial inter-individual variance in reproductive success (Dugdale et al., 2007;
166 Dugdale, Pope, et al., 2011) and evidence of reproductive skew among females within a group
167 (Dugdale, Macdonald, Pope, Johnson, & Burke, 2008; Woodroffe & Macdonald, 1995). With the
168 polygynandrous system (Dugdale, Griffiths, et al., 2011), a slight sexual dimorphism and slight male-
169 biased mortality (Bright Ross et al., 2020; Johnson & Macdonald, 2001; Sugianto, Newman,
170 Macdonald, & Buesching, 2019), and evidence of downstream effects of male–male competition on
171 body mass senescence (Beirne et al., 2015), such intra-sexual competition may be reflected in
172 telomere length in early adulthood.

173 Here, we investigate the relationships between early-life conditions and relative leukocyte
174 telomere length (RLTL), by testing whether: (i) between-individual and within-individual variation in
175 RLTL in early life and early adulthood can be explained by seasonal changes; (ii) adverse early-life
176 weather, as a proxy for food availability and thermal stress, is associated with shorter early-life RLTL
177 and the social conditions that cubs are exposed to (with more cubs potentially leading to resource
178 competition and associated with shorter early-life RLTL, or more cubs reflecting more resources and
179 thus being associated with longer early-life RLTL); (iii) the strength of the association between early-
180 life RLTL and first-year survival probability is dependent on early-life conditions and (iv) adverse social

181 conditions after sexual maturity (i.e. larger same-sex adult group size for females and, for males, more
182 within-group and neighbouring-group adult (>1 year old) males), are associated with shorter RLTL in
183 early post-maturity adulthood.

184

185 **2. Methods**

186 **(a) Study population and trapping**

187 We conducted this study in a high-density population of badgers (mean \pm SE = 36.4 \pm 2.55
188 badgers/km²; Macdonald, Newman, Nouvellet, & Buesching, 2009) in Wytham Woods, Oxfordshire,
189 UK (51°46'24"N, 1°20'04"W); a 424 ha mixed semi-natural woodland surrounded by mixed arable and
190 permanent pasture (Macdonald et al., 2015). The population consisted of 19 \pm 2 (mean \pm 95% CI; range
191 = 14–26; Dugdale et al., 2008) mixed-sex social groups (Johnson, Jetz, et al., 2002; Newman et al.,
192 2011) during the period that we analysed, with a 50% offspring sex ratio (Dugdale, Macdonald, &
193 Newman, 2003). The Wytham badger population is geographically discrete (Macdonald et al., 2009)
194 with only ca. 3% annual immigration/emigration per year (Macdonald & Newman, 2002).

195 We used long-term data (1987 – 2016) from a badger population that was trapped over three
196 two-week periods in May–June, August–September and November, with further trapping in January
197 in focal years (i.e. specific years when ultrasound studies were conducted to calculate implantation
198 dates, see Fig. 1). Badgers were anaesthetised using an intra-muscular injection of 0.2 ml ketamine
199 hydrochloride per kg body weight (McLaren et al., 2005). Upon first capture, badgers were assigned a
200 unique inguinal tattoo for permanent identification. Sex, age class (cub <1 year old; adult \geq 1 year old),
201 capture date and social group were recorded. Age of badgers was defined as the number of days
202 elapsed since the 14th of February, reflecting the average date of synchronised parturition, in the
203 respective birth year (Yamaguchi, Dugdale, & Macdonald, 2006). Age of badgers first caught as adults
204 was inferred from tooth wear, which is commonly used and highly correlated ($r^2 = 0.80$) with known
205 age in this population (Bright Ross et al., 2020; da Silva & Macdonald, 1989; Hancox, 1988; Macdonald
206 et al., 2009). Only badgers that did not have an already-known age and had a tooth wear of 2 (on a 1–

207 5 scale) were included since these typically indicate a 1-year old adult (Bright Ross et al., 2020). We
208 used data on cohorts up to and including 2010, as all cohort members were dead by the end of 2016.
209 Whole blood samples were collected from anaesthetised badgers through jugular venipuncture into
210 vacutainers with an EDTA anticoagulant, and stored immediately at -20°C. Badgers were released after
211 full recovery from anaesthesia. Additionally, bait-marking (Delahay et al., 2000; Macdonald &
212 Newman, 2002) was conducted periodically to delimit group range sizes and deduce social groups.

213

214 **(b) Telomere analyses**

215 Genomic DNA was extracted from whole blood samples ($n = 814$ samples; 533 badgers) using the
216 DNeasy Blood & Tissue kit (Qiagen, Manchester, UK) according to the manufacturer's protocol, with
217 changes by conducting a double elution step (2x 75 μ l AE buffer) and using 125 μ l of anticoagulated
218 blood. DNA integrity was checked by running a random selection of DNA extracts (ca. 20%) on agarose
219 gels to ensure high molecular weight. DNA concentration of all samples was quantified using the
220 Fluostar Optima fluorometer (BMG Labtech, Ortenberg, Germany) and standardized to 20 ng/ μ l, after
221 which samples were stored at -20 °C. We used monochrome multiplex quantitative PCR (MMqPCR)
222 analysis to measure RLTL (Cawthon, 2009). This is a measure that reflects the abundance of telomeric
223 sequence relative to a reference gene, which are both analysed in the same well, and although subject
224 to error represents the mean telomere length across cells in a sample. We used a sub-set of 814
225 samples from the full dataset of 1248 samples detailed in van Lieshout et al. (2019). In the full dataset,
226 Cq-values on the qPCR plates ($n = 34$) declined in a log-linear fashion ($r^2 > 0.99$). Reaction efficiencies
227 were (mean \pm SE) 1.793 ± 0.004 for IRBP and 1.909 ± 0.004 for telomeres. Inter-plate repeatability
228 (intraclass correlation coefficient) calculated with *rptr* 0.9.2 (Stoffel, Nakagawa, & Schielzeth, 2017) –
229 by comparing variance among duplicates of the reference sample within a plate, to variance of the
230 reference sample among plates – was 0.82 for RLTL measurements (95% CI = 0.76–0.87; $n = 142$
231 samples; 34 plates). Intra-plate repeatability calculated with duplicates of the same sample on the
232 same plate, while controlling for plate effects, was 0.90 (95%CI = 0.86–0.93; $n = 1,248$ samples; 34

233 plates) for IRBP, 0.84 (95%CI = 0.79–0.90; $n = 1,248$ samples; 34 plates) for telomere Cq-values and
234 0.87 (95% CI = 0.82–0.91; $n = 1,248$ samples; 34 plates) for RLTL measurements. A detailed description
235 of the MMqPCR analysis can be found in van Lieshout et al. (2019).

236

237 **(c) Weather conditions**

238 Four weather metrics (mean daily temperature, temperature variability, mean daily rainfall, and
239 rainfall variability) were calculated for each season (Spring = end of March to end of June, Summer =
240 end of June to end of September, Autumn = end of September to end of December, Winter = end of
241 December to end of March) from 1987 to 2010 to characterise the developmental stress associated
242 with variation in earthworm food availability and thermoregulatory costs (Macdonald, Newman,
243 Buesching, & Nouvellet, 2010; Noonan et al., 2014; Nouvellet et al., 2013). Wytham Woods had a
244 mean annual temperature of 10.6 °C (± 5.5 SD) and mean annual precipitation of 684 (± 129 SD) mm,
245 1987–2010. Mean daily temperature and rainfall were calculated using mean daily temperature and
246 total daily precipitation values provided by the Radcliffe Meteorological Station, School of Geography,
247 University of Oxford (6 km from the field site). Daily temperatures followed a sinusoidal pattern, and
248 so seasonal temperature variability was calculated as the sum of daily squared residuals from a
249 sinusoidal fit to the corresponding year's temperatures (i.e. cumulative unpredictability). Rainfall did
250 not show annual trends and its seasonal variability was therefore characterised simply as the
251 coefficient of variation (SD/mean) in daily rainfall.

252

253 **(d) Group sizes**

254 Natal group sizes were determined by the number of individuals (cubs and adults) that were present
255 in a social group in the year of an individual's birth. Given high lifetime natal philopatry (35.8%), low
256 permanent dispersal rates (19.1%), and high levels of short-term inter-group movements (Macdonald,
257 Newman, Buesching, & Johnson, 2008), individuals ($n = 1726$) were assigned as a resident of a social
258 group each year, according to published criteria (van Lieshout, Badás, et al., 2020). The number of

259 individuals in a natal social group was then calculated as the sum of individuals present in the social
260 group in that year.

261 Yearly social group size measures were then separated by age class (i.e. cub/adult) and sex
262 (i.e. male/female) to determine sex- and age-specific group sizes per year. To measure intra-sexual
263 competition in females, we calculated female adult group sizes, as females compete with other within-
264 group females (Woodroffe & Macdonald, 1995). However, for males, extra-group paternity is high
265 (48%) and affected by the number of within-group and neighbouring-group candidate fathers (Annavi
266 et al., 2014), so we combined both the number of within-group males and neighbouring-group males.
267 The mean number of cubs in a social group for badgers in our dataset ($n = 533$ badgers) was $3.4 (\pm 2.3$
268 $SD; \text{range } 0\text{--}14)$, the mean number of female adults in a social group was $6.1 (\pm 3.4 SD; \text{range } 0\text{--}19)$
269 and the mean number of male adults in focal plus neighbouring social groups was $25.2 (\pm 11.5 SD;$
270 $\text{range } 1\text{--}59)$.

271

272 **(e) Statistical analyses**

273 Statistical analyses were conducted in R 3.3.1 (R Development Core Team, 2020), using parametric
274 bootstrapping ($n = 5000$) to estimate 95% confidence intervals and determine significance of
275 predictors in *lme4* 1.1-14 (Bates, Machler, Bolker, & Walker, 2015). Model fit was assessed using
276 standard residual plot techniques to ensure approximately normal distribution and constant variance,
277 and fixed effects were ensured not to be collinear ($VIF < 3$). Relative leukocyte telomere length (RLTL)
278 as response variable was first square-root and then Z-transformed (mean = 0, SD = 1) for comparability
279 (Verhulst, 2020). Quadratic fixed effects were included if such relationships were plausible *a priori*,
280 and removed if $p > 0.1$ to test the significance of first-order effects.

281 In this study, we focus on early-life (3–12 months old), but badgers typically reach sexual
282 maturity by 2 years of age (Sugianto et al., 2019), occasionally at age 1 year (Dugdale et al., 2007). Due
283 to delayed implantation resulting in a full year between conception and parturition, badgers thus first

284 produce offspring when they are 2–3 years of age, therefore we define early adulthood as 12–36
285 months old.

286

287 **(i) Seasonal effects on RLTL in early-life and early adulthood**

288 We first tested for an association between season and RLTL (≤ 36 months old) in early-life and early-
289 adulthood in a Gaussian distribution model (identity link function) with RLTL as the response variable
290 ($n = 814$ samples; 533 badgers). Including threshold functions of age at 29 months, such that the slope
291 of the regression of RLTL with age differed for ≤ 29 months and > 29 months of age best explained the
292 relationship between RLTL and age (van Lieshout et al., 2019). Threshold age, age at last capture,
293 season, weight and body length were included as fixed effects, and qPCR plate, row on qPCR plate,
294 social group, cohort (i.e. birth year; 24 levels), year and individual ID as random effects as these may
295 impact RLTL in badgers (van Lieshout, Sparks, et al., 2020).

296 As we found a significant cross-sectional difference in RLTL between spring and winter, we
297 then applied the ‘within-subject centring’ approach described by van de Pol and Wright (2009) to
298 distinguish within- and between-individual effects between spring and winter. Following (Schroeder,
299 Nakagawa, Cleasby, & Burke, 2012), we included two new fixed effects: 1) to estimate the within-
300 individual variation component (β_w) we removed between-individual variation by subtracting the
301 mean season value (coded as: spring = 0, winter = 1) for each individual across all years, from the
302 season value for each RLTL measurement. So, if an individual was measured once in spring and once
303 in winter, it was scored as -0.5 for spring and 0.5 for winter; and, 2) to estimate the between-individual
304 variation between seasons (β_B), we included the mean season value for each individual (van de Pol &
305 Wright, 2009). We then ran a Gaussian distribution model (identity link function) with RLTL as the
306 response variable ($n = 503$ samples; 402 badgers) and threshold age (van Lieshout, 2019), age at last
307 capture, within-individual season effect (β_w), between-individual season effect (β_B), weight and body
308 length as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year and individual ID
309 as random effects. Subsequently, we tested whether the within-individual (β_w) and between-

310 individual (β_B) slopes differed by including season and the between-individual effect (β_B ; i.e. mean
311 season value) in the same model (i.e. season now reflects the within-individual effect).

312 Lastly, to test whether telomere length decreases or increases from spring to winter we used
313 a subset of individuals measured either in their first spring or first winter, plus 11 individuals measured
314 in both their first spring and first winter ($n = 214$ samples; 203 badgers). For the direction of the effect
315 from winter to spring we used a subset of individuals measured either in their first winter or second
316 spring, plus 6 individuals measured in both their first winter and second spring ($n = 84$ samples; 78
317 badgers). In the two models (spring to winter and winter to spring) with a Gaussian distribution and
318 RLTL as the response variable, we included age, age at last capture, season, weight and body length
319 as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year (not in winter to spring
320 model due to singularity) and individual ID as random effects. Subsequently, we used the within-
321 subject centring approach again to separate within- and between-individual effects and test whether
322 these slopes differ (van de Pol & Wright, 2009).

323

324 **(ii) Weather and natal group size effects on early-life RLTL**

325 We tested whether weather and social conditions experienced as a cub (3–12 months old) were
326 associated with early-life RLTL. We first used a GLMM to confirm the previous observation (van
327 Lieshout et al., 2019) that early-life RLTL did not vary with age (in months), controlling for season,
328 weight and body length ($n = 406$, $\beta = 0.154$, 95% CI = -0.158–0.464), and excluded age from subsequent
329 analyses. The effects of first-year conditions on early-life RLTL were then modelled with early-life RLTL
330 as the response variable in a Gaussian-distributed model (identity link function; $n = 406$, samples; 406
331 badgers). First, we determined the season in which the weather conditions (i.e. mean temperature,
332 mean rainfall, temperature variability and rainfall variability) best explained the variation in early-life
333 RLTL (AICc spring = 1133.1 was lowest, versus summer Δ AICc = 11.3, autumn Δ AICc = 10.3, winter
334 Δ AICc = 11.0), with models with Δ AICc <7 from the top model being plausible (Burnham, Anderson, &
335 Huyvaert, 2011). The weather window of spring (end of March to end of June) is the season in which

336 cubs grow the most and thus encounter the strongest developmental stress. This period includes when
337 cubs first emerge above ground from the end of February, are weaned around mid-May, and reach
338 independence at the start of June (Dugdale, Ellwood, & Macdonald, 2010) during which time cubs
339 exhibit high growth rates depending on food availability and social conditions (Sugianto et al., 2019).
340 Secondly, we determined whether the number of cubs, adults or the total number of individuals in
341 the natal group best predicted early-life RLTL using AICc (the lowest AICc = 1133.1 was for number of
342 cubs, versus number of adults Δ AICc = 3.8, total number of individuals Δ AICc = 4.0, number of cubs
343 plus number of adults Δ AICc = 5.8, number of cubs plus total number of individuals Δ AICc = 5.6). Since
344 Δ AICc <7, and VIF>3 for the other combinations in the same model, we ran five separate models with
345 either the number of cubs, number of adults, the total number of individuals, number of cubs plus
346 adults or number of cubs plus total number of individuals in the natal group as a fixed effect along
347 with season, weight, body length, and mean daily temperature, temperature variability, mean daily
348 rainfall and rainfall variability in spring. qPCR plate, row on qPCR plate, social group and cohort were
349 included as random effects.

350

351 **(iii) Covariation between early-life RLTL and weather conditions on cub survival probability**

352 To understand whether the association between early-life RLTL and cub survival probability (van
353 Lieshout et al., 2019) is due to or independent of weather effects, we tested whether the association
354 between early-life RLTL and cub survival probability was still detected when social and weather
355 conditions were included in the model. We first modelled survival to adulthood (≥ 1 year old) as a
356 binary term in a binomially distributed model (logit link function; $n = 406$ samples; 406 badgers), where
357 cubs only caught in their first year of life were coded as 0 and cubs that were caught when older than
358 1 year of age were coded as 1, with early-life RLTL, weight and body length as fixed effects and qPCR
359 plate, row on qPCR plate, social group and cohort were included as random effects. We then also
360 included as fixed effects: number of cubs in the natal group, mean daily temperature, temperature
361 variability, mean daily rainfall and rainfall variability in a given season. We determined the season in

362 which weather conditions best explained the variation in cub survival probability, using AICc (the
363 lowest AICc = 408.9 was in winter, versus spring Δ AICc = 21.6, summer Δ AICc = 16.3 and autumn Δ AICc
364 = 22.5) where models with Δ AICc <7 from the top model are plausible (Burnham et al., 2011). We
365 checked whether the model was overdispersed. While cub survival is negatively impacted by
366 endoparasitic coccidia infection (Newman, Macdonald, & Anwar, 2001), we did not have data to
367 control for coccidia infection. We then applied model selection to test whether including weather and
368 social variables knocked early-life RLTL out of the plausible models. This would indicate that the early-
369 life RLTL and survival probability relationship is driven by covariation between the environment and
370 physiological state (early-life RLTL). As early-life RLTL was retained, we estimated the RLTL model-
371 averaged parameter and 95% confidence interval using the natural averaged method (where the
372 parameter was averaged over models in which it was present; Burnham & Anderson, 2002). This
373 avoids the parameter estimate shrinking towards zero, from inclusion of the relatively less important
374 models where the parameter was not retained (Nakagawa & Freckleton, 2011).

375

376 **(iv) Same-sex group size effects on RLTL in early adulthood**

377 We examined whether same-sex adult group sizes were reflected in RLTL in early adulthood (i.e. 12–
378 36 months old). In a GLMM with RLTL in early adulthood as the response variable with one age
379 threshold separating two periods of 12 to \leq 29 months and >29 and \leq 36 months (see van Lieshout et
380 al., 2019) and season, weight and body length as fixed effects, we determined that RLTL did not vary
381 with age ($n = 376$, 12 to \leq 29 months, $\beta = -0.064$, 95%CI = -0.175–0.050; >29 and \leq 36 months, $\beta = -0.040$,
382 95%CI = -0.184–0.110), and excluded age from the subsequent analysis. The effects of same-sex adult
383 group sizes on RLTL in early adulthood were then modelled with RLTL in early adulthood as the
384 response variable ($n = 376$ samples; 308 badgers). Same-sex adult group size (within-group for females
385 and within- plus neighbouring-group for males), sex and its interaction with group size (to model
386 differential strength in intra-sexual competition among the sexes), age at last capture (to control for

387 selective disappearance), season, weight and body length were included as fixed effects, and qPCR
388 plate, row on qPCR plate, social group, cohort, year and individual ID as random effects.

389

390 **3. Results**

391 **(i) Seasonal effects on RLTL in early-life and early adulthood**

392 When controlling for age, weight and body length, we found a significant effect of season on RLTL with
393 badgers having shorter RLTL in winter compared to spring (Figure 1; Table S1). After partitioning the
394 within- and between-individual effects we found that there was a within-individual effect of shorter
395 RLTL in winter than in spring (Table S2). There was no significant difference between the within- and
396 between- individual slopes (Table S3), and thus, the significant between-individual effect (Table S2)
397 was driven by the within-individual effect. Using a subset of individuals measured only at consecutive
398 seasons, combined with individuals measured once, we found that from spring to winter there was a
399 within-individual decline in RLTL (Table S4 & Figure S1), whereas from winter to the following spring
400 there was a marginally non-significant within-individual increase in RLTL (Table S5 & Figure S1). For
401 both spring to winter and winter to spring the slopes for within- and between-individual effects did
402 not differ (Table S6).

403

404 **(ii) Weather and natal group size effects on early-life RLTL**

405 We found a positive association between spring temperature and early-life RLTL (Figure 2; Table 1 &
406 S7–S10), with cubs experiencing cooler-than-average first springs having shorter early-life RLTL. We
407 also found that cubs experiencing intermediate-to-high mean daily rainfall had longer early-life RLTL
408 (Figure 3; Table 1 & S7–S10) than cubs developing during drier years. Cubs experiencing low rainfall
409 variability also had longer early-life RLTL (Figure 4; Table 1 & S7–S10). We found, while controlling for
410 weather effects, a marginal effect where more cubs in the natal group leads to longer early-life RLTL.
411 In contrast, we found no evidence for an association between the number of adults or total number
412 of individuals in the natal group and early-life RLTL (Table 1 & S7–S10).

413

414 **(iii) Covariation between early-life RLTL and weather conditions on cub survival probability**

415 We first replicated our published finding (van Lieshout et al., 2019) of a positive association between
416 early-life RLTL and survival to adulthood, not controlling for social and weather effects (Table S11).
417 Then we included social and weather conditions in the model: cub survival probability exhibited a
418 negative quadratic relationship with mean daily temperature (Figure S2; Table S12), a negative
419 quadratic association with winter temperature variability (Figure S3; Table S12), a marginal non-
420 significant positive effect of mean daily rainfall (Table S12), a negative association with winter rainfall
421 variability (Figure S4; Table S12) but no significant effect of the number of cubs in a group (Table S12).
422 Using model selection, early-life RLTL was present in the top 39 models and retained in 82/100
423 plausible models (Table S13). The naturally averaged estimate for RLTL in the plausible models was
424 0.366 (95% CI = 0.064 – 0.666; Table S14) and thus the 95% CIs of early-life RLTL overlapped between
425 the models with and without ($\beta = 0.386$, 95% CI = 0.095 to 0.713, Table S11) early-life social and
426 weather variables.

427

428 **(iv) Same-sex group size effects on RLTL in early adulthood**

429 We found no evidence of same-sex adult group size effects on RLTL in early adulthood for females or
430 males (Table S15).

431

432 **4. Discussion**

433 Our results show both between-individual variation and within-individual changes in RLTL across
434 seasons, where a cub's RLTL in their first spring was longer than in the following winter, and an
435 indication that RLTL was longer again in the following spring compared to the preceding winter. Since
436 the between- and within-individual slopes did not differ, the between-individual effect is driven by
437 within-individual change and not selective (dis)appearance. We also found that cubs born in
438 conditions that were warmer and wetter, with little variation in rainfall, had longer early-life RLTL.

439 Sociologically, the number of cubs had a positive effect on early-life RLTL, in contrast to the number
440 of adults or total number of individuals. Our results also suggest that the link between early-life RLTL
441 and cub survival probability is driven by conditions experienced in addition to the early-life social and
442 weather conditions modelled. Additionally, we found no effect of the number of within-group adult
443 females, or both within-group and extra-group adult males (i.e. intra-sexual competition) on RLTL in
444 early adulthood.

445 Our finding that badgers had shorter early-life RLTL (both between and within individuals) in
446 winter, compared to the preceding spring could be linked to the end-replication problem and stressful
447 effects such as disease (Newman et al., 2001), sub-optimal foraging conditions and food availability
448 (Macdonald & Newman, 2002; Newman et al., 2017). The within-individual effect means that between
449 seasons there is an increase or decrease in telomere length for the same individual. Since there is no
450 difference in the slopes for the within-individual and between-individual effect there is no selective
451 disappearance of individuals and the between-individual effect is driven by within-individual changes.
452 We then found a non-significant trend for positive within-individual changes in RLTL from the first
453 winter to the following spring. Body temperatures in badgers fall from November to December (by a
454 maximum of 8.9 °C compared to late-spring) and steadily rise until euthermic levels are reached by
455 late April (Fowler & Racey, 1988; Geiser & Ruf, 1995). During harsh winter conditions, badgers use
456 facultative torpor to reduce their core temperature and metabolic rate, conserving energy (Newman
457 et al., 2011). This reduction of basal metabolic rates (Geiser, 2004) can reduce mitosis (Kruman,
458 Ilyasova, Rudchenko, & Khurkhulu, 1988) and therefore potentially reduce telomere shortening.
459 Similarly, daily torpor cycles in Djungarian hamsters had a positive effect on telomere length (Turbill
460 et al., 2012). However, for species using torpor as a seasonal energy conservation strategy (e.g. edible
461 dormice, garden dormice, and arctic ground squirrels; as do badgers), arousal and return to euthermia
462 has been linked to telomere shortening; although this appears to be in proportion to the extent that
463 body temperature must be re-warmed (Giroud et al., 2014; Hoelzl, Cornils, Smith, Moodley, & Ruf,
464 2016; Turbill et al., 2013; Turbill et al., 2012; Wilbur et al., 2019). We postulate that badgers use torpor

465 and their ability to remain within thermally stable setts (Tsunoda et al., 2018) to try to mitigate RLTL
466 shortening that would otherwise be incurred by the stresses of maintaining activity during winter,
467 when food is scarce and thermal losses are high. More detailed analyses are needed to explore this
468 further, for example, comparing badgers in different regions that experience different degrees of
469 winter severity, with a large longitudinal sample size to disentangle within- and between-individual
470 effects. Importantly, we would need to track which badgers go into torpor, for how long and how
471 often, and then calculate how much energy is conserved. We also do not yet know to what extent
472 torpor-arousal cycles may affect telomere shortening, and where there is likely an optimal balance. In
473 this regard, predicted increases in weather variability (IPCC 2018) that may cause more frequent
474 warm–cold winter episodes, could add to the allostatic load of badgers, causing accelerated RLTL
475 shortening. Since positive within-individual changes in badger telomere length occur, that are greater
476 than measurement error (van Lieshout et al., 2019), such seasonal patterns may explain some of the
477 variability in telomere length patterns across life in badgers. Indeed, there is also evidence of seasonal
478 telomere dynamics in non-hibernating rodents (Criscuolo et al., 2020). Even though we accounted for
479 body weight and length, other factors such as seasonal changes in leukocyte cell composition can also
480 lead to apparent changes in telomere length (Beaulieu, Benoit, Abaga, Kappeler, & Charpentier, 2017),
481 which would require further investigation. For example, there is a greater proportion of neutrophils
482 and lymphocytes that were lymphocytes in spring compared to autumn in badgers (van Lieshout,
483 Badás, et al., 2020), and lymphocytes have shorter telomere lengths than neutrophils in humans and
484 baboons (Baerlocher, Rice, Vulto, & Lansdorp, 2007; Kimura et al., 2010). Nonetheless, our findings
485 also highlight the importance of controlling for seasonal effects when analysing telomere dynamics.

486 Cubs born into more energetically favourable springs (warm, rainy, and low rainfall variability)
487 had longer early-life RLTL. These weather conditions present optimal soil conditions for earthworm
488 surfacing, enhancing food supply (Kruuk, 1978; Newman et al., 2017). Dry conditions in spring have
489 negative consequences for badger foraging success (Macdonald & Newman, 2002). However, while
490 we found no effect of spring temperature variability on early-life RLTL, cubs experiencing lower daily

491 rainfall variability in spring had longer early-life RLTL. Greater rainfall variability can reduce the
492 predictability of food availability and impact foraging activity (Noonan et al., 2014), and may require
493 individuals to modulate their energy trade-offs (Erikstad et al., 1998; Reid et al., 2003; Weimerskirch
494 et al., 2001) and adopt a bet-hedging strategy (Wilbur & Rudolf, 2006). The variability in spring rainfall
495 and thus early-life conditions experienced shape life-history trade-offs, and since variability is likely to
496 increase under current climate change (IPCC, 2018), this can impact ecological and individual resilience
497 (Bright Ross et al., 2020).

498 Our estimate of post-dependence social effects was positive. An explanation for this positive
499 effect may be that in badgers, variation in maternal capacity to lactate may exceed the low variation
500 that is observed in litter size (Dugdale et al., 2007), causing the per-offspring suckling rate to increase
501 with litter size. In contrast, in other species or experimental brood size enlargements in birds, variation
502 in clutch size can exceed variation in parental resource acquisition, causing the per-offspring feeding
503 rate to decrease with litter size (van Noordwijk & de Jong, 1986; Vedder, Verhulst, Bauch, & Bouwhuis,
504 2017; Wilson & Nussey, 2010). An increase in the per-offspring suckling rate with litter size could result
505 in more available resources for cubs and thus longer early-life telomere length. Secondly, groups with
506 more independent cubs may also potentially have more food available per capita which permits faster
507 growth and cell replication without inducing stress, hence facilitating longer early-life telomere length.
508 This result is in contrast with studies reporting that competition for food within litters and juvenile
509 cohorts can cause telomere shortening (Boonekamp et al., 2014; Cram et al., 2017; Nettle et al., 2015).
510 However, these studies were able to measure telomere length within the first month of life. In
511 contrast, we were unable to sample individuals until at least 3 months of age, due to welfare
512 legislation (Protection of Badgers Act, 1992), when the weakest cubs could have already succumbed,
513 reducing group sizes. We therefore do not have a measure of the number of dependent cubs in a
514 group and could only measure RLTL in the first year from 3–12 months of age; thus, we cannot test
515 for social effects during the dependent period, including selective disappearance which may also lead
516 to similar positive associations between the number of cubs and early-life RLTL.

517 We found that the association between early-life RLTL and cub survival probability was
518 retained in the top 39 most plausible models and 82/100 plausible models when including early-life
519 weather and social variables. This indicates that, in badgers, the association between early-life RLTL
520 and survival is not solely driven by covariation between the early-life environment and early-life RLTL
521 (i.e. physiological state). While early-life RLTL in badgers appears to reflect the physiological
522 consequences of conditions experienced, independent of the weather and social variables included in
523 the models, there could still be a genetic component to telomere length or telomere length may
524 genetically covary with survival as seen in other species (Froy et al., 2021; Vedder et al., 2021).
525 Nonetheless, in badgers telomere length can be used as a comprehensive measure of the
526 environmental consequences for physiology and first-year survival probability.

527 There was no significant association between same-sex adult group size and RLTL in early
528 adulthood. While female–female reproductive competition occurs in badgers (Sharp & Clutton-Brock,
529 2011; Woodroffe & Macdonald, 1995), in polygynous species, theory predicts intra-sexual competition
530 for mating opportunities to be stronger among males than females. In Wytham badgers, there is slight
531 sexual dimorphism (Johnson & Macdonald, 2001) and slight male-biased mortality (Bright Ross et al.,
532 2020). Reproductive skew is higher in sexually-mature males than females (Dugdale et al., 2008) and
533 males with a higher body-condition index attain more reproductive success (Dugdale, Griffiths, et al.,
534 2011). High levels of polygynandrous and repeated mounting behaviour may however reduce male–
535 male aggression and infanticide from males (Dugdale, Griffiths, et al., 2011; Wolff & Macdonald,
536 2004). Secondly, cryptic female choice (i.e. delayed implantation, superfecundation and
537 superfetation) may promote sperm competition and mask paternity, and reduce pre-copulatory
538 male–male competition (Birkhead & Pizzari, 2002). Finally, group size and/or density could be a poor
539 metric for competition due to foraging niche variation or variation in sex-ratio; additionally, although
540 the resource dispersion hypothesis predicts that groups approximate territorial carrying capacity,
541 results are mixed (Revilla, 2003). In fact, in our study population results vary with year such that only
542 in some situations larger groups may have proportionally more resources available (Johnson et al.,

543 2001; Johnson, Kays, Blackwell, & Macdonald, 2002). In line with this, we found no evidence that
544 variation in telomere length is due to intra-sexual competition in early adulthood. Badger early-life
545 telomere length may reflect the consequences of the weather conditions experienced, with little
546 impact of early-adulthood social conditions. However, in bad quality years only females in good
547 condition breed, whereas in good quality years breeding success is related to status (Woodroffe &
548 Macdonald, 1995). We can therefore not exclude that there may only be female–female competition
549 in good years. Additionally, early-adulthood male–male competition impacts on body mass
550 senescence in a badger population at the Woodchester Park study population (Beirne et al., 2015).
551 While we detected no significant evidence of direct effects of early-adulthood intra-sexual
552 competition on telomere length, there may be downstream effects on senescence.

553 In conclusion, we demonstrate the importance of accounting for seasonal variation when
554 analysing telomere dynamics because of potential decreases as well as increases in telomere length
555 across seasons. We also evidence that early-life adversity is reflected in shorter early-life telomere
556 lengths in badgers, where the physical (weather) and social environment predict early-life telomere
557 length. When accounting for these environmental effects, the positive association between early-life
558 telomere length and survival probability remains. We conclude that variation in telomere length in
559 badgers reflects early-life conditions, and in addition to this predicts first year cub survival.

560

561 **Ethics**

562 All work was approved by the University of Oxford’s Animal Welfare and Ethical Review Board, ratified
563 by the University of Leeds, and carried out under Natural England Licenses, currently 2017-27589-SCI-
564 SCI and Home Office Licence (Animals, Scientific Procedures, Act, 1986) PPL: 30/3379.

565

566 **Acknowledgements**

567 We thank all members of the Wytham badger team for collecting data. We thank Natalie dos
568 Remedios and Mirre Simons for their help and advice on telomere analyses. We also thank Bill Kunin

569 and Dan Nussey for comments on an earlier draft of this manuscript, and three anonymous reviewers
570 for their comments that greatly improved the manuscript. S.H.J.v.L was funded by a Leeds Anniversary
571 Research Scholarship from the University of Leeds with support from a Heredity Fieldwork Grant from
572 the Genetics Society and a Priestley Centre Climate Bursary from the University of Leeds. Telomere
573 length analyses were funded by a Natural Environment Research Council (NERC) Environmental Omics
574 Visitor Facility - Sheffield, grant to A.B. and H.L.D. (NBAF984) and a Royal Society Research Grant to
575 H.L.D. (RG170425). We declare no conflict of interest.

576

577 **Author contributions**

578 This study was conceived by S.H.J.v.L, A.B., H.L.D; Samples were collected by S.H.J.v.L., C.N., C.D.B.,
579 D.W.M. and H.L.D.; S.H.J.v.L. conducted laboratory work with input from T.B., environmental metrics
580 were calculated by S.H.J.v.L, E.P.B, J.G.B. and statistical analyses were conducted by S.H.J.v.L with
581 input from E.P.B and H.L.D; The paper was written by S.H.J.v.L and H.L.D. with extensive input from all
582 authors. All authors gave final approval for publication.

583

584 **Data accessibility**

585 Data are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.3r2280gf5>) (van
586 Lieshout et al., 2021)

587

588 **References**

- 589 Andersson, M. B. (1994). *Sexual selection*. Princeton, NJ: Princeton University Press.
- 590 Annavi, G., Newman, C., Dugdale, H. L., Buesching, C. D., Sin, Y. W., Burke, T., & Macdonald, D. W.
591 (2014). Neighbouring-group composition and within-group relatedness drive extra-group
592 paternity rate in the European badger (*Meles meles*). *Journal of Evolutionary Biology*, **27**(10),
593 2191-2203. <https://doi.org/10.1111/jeb.12473>
- 594 Baerlocher, G. M., Rice, K., Vulto, I., & Lansdorp, P. M. (2007). Longitudinal data on telomere length in
595 leukocytes from newborn baboons support a marked drop in stem cell turnover around 1 year
596 of age. *Aging Cell*, **6**(1), 121-123. <https://doi.org/10.1111/j.1474-9726.2006.00254.x>
- 597 Bates, D., Machler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects models using
598 lme4. *Journal of Statistical Software*, **67**(1), 1-48. <https://doi.org/10.18637/jss.v067.i01>

599 Beaulieu, M., Benoit, L., Abaga, S., Kappeler, P. M., & Charpentier, M. J. E. (2017). Mind the cell:
600 Seasonal variation in telomere length mirrors changes in leucocyte profile. *Molecular Ecology*,
601 **26**(20), 5603-5613. <https://doi.org/10.1111/mec.14329>

602 Beirne, C., Delahay, R., & Young, A. (2015). Sex differences in senescence: the role of intra-sexual
603 competition in early adulthood. *Proceedings of the Royal Society B: Biological Sciences*,
604 **282**(1811), 20151086. <https://doi.org/10.1098/rspb.2015.1086>

605 Birkhead, T. R., & Pizzari, T. (2002). Postcopulatory sexual selection. *Nature Reviews Genetics*, **3**(4),
606 262-273. <https://doi.org/10.1038/nrg774>

607 Blackburn, E. H. (2000). Telomere states and cell fates. *Nature*, **408**(6808), 53-56.
608 <https://doi.org/10.1038/35040500>

609 Blackburn, E. H., Greider, C. W., Henderson, E., Lee, M. S., Shampay, J., & Shippenlantz, D. (1989).
610 Recognition and elongation of telomeres by telomerase. *Genome*, **31**(2), 553-560.
611 <https://doi.org/10.1139/g89-104>

612 Bonduriansky, R., Maklakov, A., Zajitschek, F., & Brooks, R. (2008). Sexual selection, sexual conflict and
613 the evolution of ageing and life span. *Functional Ecology*, **22**(3), 443-453.
614 <https://doi.org/10.1111/j.1365-2435.2008.01417.x>

615 Boonekamp, J. J., Bauch, C., Mulder, E., & Verhulst, S. (2017). Does oxidative stress shorten telomeres?
616 *Biology Letters*, **13**(5), 20170164. <https://doi.org/10.1098/rsbl.2017.0164>

617 Boonekamp, J. J., Mulder, G. A., Salomons, H. M., Dijkstra, C., & Verhulst, S. (2014). Nestling telomere
618 shortening, but not telomere length, reflects developmental stress and predicts survival in
619 wild birds. *Proceedings of the Royal Society B: Biological Sciences*, **281**(1785), 20133287.
620 <https://doi.org/10.1098/rspb.20133287>

621 Bright Ross, J. G., Newman, C., Buesching, C. D., & Macdonald, D. W. (2020). What lies beneath?
622 Population dynamics conceal pace-of-life and sex ratio variation, with implications for
623 resilience to environmental change. *Global Change Biology*, **26**(6), 3307-3324.
624 <https://doi.org/10.1111/gcb.15106>

625 Buesching, C. D., Newman, C., Service, K., Macdonald, D. W., & Riordan, P. (2016). Latrine marking
626 patterns of badgers (*Meles meles*) with respect to population density and range size.
627 *Ecosphere*, **7**(5), e01328. <https://doi.org/10.1002/ecs2.1328>

628 Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical*
629 *information-theoretic approach* (2nd ed.). NY, USA: Springer-Verlag.

630 Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel
631 inference in behavioral ecology: some background, observations, and comparisons.
632 *Behavioral Ecology and Sociobiology*, **65**(1), 23-35. [https://doi.org/10.1007/s00265-010-](https://doi.org/10.1007/s00265-010-1029-6)
633 [1029-6](https://doi.org/10.1007/s00265-010-1029-6)

634 Campbell, R. D., Nouvellet, P., Newman, C., Macdonald, D. W., & Rosell, F. (2012). The influence of
635 mean climate trends and climate variance on beaver survival and recruitment dynamics.
636 *Global Change Biology*, **18**(9), 2730-2742. <https://doi.org/10.1111/j.1365-2486.2012.02739.x>

637 Campisi, J. (2005). Senescent cells, tumor suppression, and organismal aging: Good citizens, bad
638 neighbors. *Cell*, **120**(4), 513-522. <https://doi.org/10.1016/j.cell.2005.02.003>

639 Campisi, J., & di Fagagna, F. D. (2007). Cellular senescence: when bad things happen to good cells.
640 *Nature Reviews Molecular Cell Biology*, **8**(9), 729-740. <https://doi.org/10.1038/nrm2233>

641 Cawthon, R. M. (2009). Telomere length measurement by a novel monochrome multiplex quantitative
642 PCR method. *Nucleic Acids Research*, **37**(3), e21. <https://doi.org/10.1093/nar/gkn1027>

643 Cesare, A. J., & Reddel, R. R. (2010). Alternative lengthening of telomeres: models, mechanisms and
644 implications. *Nature Reviews Genetics*, **11**(5), 319-330. <https://doi.org/10.1038/nrg2763>

645 Chatelain, M., Drobniak, S. M., & Szulkin, M. (2020). The association between stressors and telomeres
646 in non-human vertebrates: a meta-analysis. *Ecology Letters*, **23**(2), 381-398.
647 <https://doi.org/10.1111/ele.13426>

- 648 Clutton-Brock, T. H., & Isvaran, K. (2007). Sex differences in ageing in natural populations of
649 vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, **274**(1629), 3097-3104.
650 <https://doi.org/10.1098/rspb.2007.1138>
- 651 Cooper, E. B., & Kruuk, L. E. B. (2018). Ageing with a silver-spoon: A meta-analysis of the effect of
652 developmental environment on senescence. *Evolution Letters*, **2**(5), 460-471.
653 <https://doi.org/10.1002/evl3.79>
- 654 Cram, D. L., Monaghan, P., Gillespie, R., & Clutton-Brock, T. (2017). Effects of early-life competition
655 and maternal nutrition on telomere lengths in wild meerkats. *Proceedings of the Royal Society
656 B: Biological Sciences*, **284**(1861), 20171383. <https://doi.org/10.1098/rspb.2017.1383>
- 657 Criscuolo, F., Pillay, N., Zahn, S., & Schradin, C. (2020). Seasonal variation in telomere dynamics in
658 African striped mice. *Oecologia*, **194**(4), 609-620. [https://doi.org/10.1007/s00442-020-04801-
x](https://doi.org/10.1007/s00442-020-04801-
659 x)
- 660 da Silva, J., & Macdonald, D. W. (1989). Limitations of the use of tooth wear as a means of ageing
661 Eurasian badgers, *Meles meles*. *Revue D'Ecologie La Terre et la Vie*, **44**(3), 275-278.
- 662 da Silva, J., Macdonald, D. W., & Evans, P. G. H. (1994). Net costs of group living in a solitary forager,
663 the Eurasian badger (*Meles meles*). *Behavioral Ecology*, **5**(2), 151-158.
664 <https://doi.org/10.1093/beheco/5.2.151>
- 665 de Lange, T. (2004). T-loops and the origin of telomeres. *Nature Reviews Molecular Cell Biology*, **5**(4),
666 323-329. <https://doi.org/10.1038/nrm1359>
- 667 de Lange, T. (2005). Shelterin: the protein complex that shapes and safeguards human telomeres.
668 *Genes & Development*, **19**(18), 2100-2110. <https://doi.org/10.1101/gad.1346005>
- 669 Delahay, R. J., Brown, J. A., Mallinson, P. J., Spyvee, P. D., Handoll, D., Rogers, L. M., & Cheeseman, C.
670 L. (2000). The use of marked bait in studies of the territorial organization of the European
671 badger (*Meles meles*). *Mammal Review*, **30**(2), 73-87. [https://doi.org/10.1046/j.1365-
2907.2000.00058.x](https://doi.org/10.1046/j.1365-
672 2907.2000.00058.x)
- 673 Dugdale, H. L., Ellwood, S. A., & Macdonald, D. W. (2010). Alloparental behaviour and long-term costs
674 of mothers tolerating other members of the group in a plurally breeding mammal. *Animal
675 Behaviour*, **80**(4), 721-735. <https://doi.org/10.1016/j.anbehav.2010.07.011>
- 676 Dugdale, H. L., Griffiths, A., & Macdonald, D. W. (2011). Polygynandrous and repeated mounting
677 behaviour in European badgers, *Meles meles*. *Animal Behaviour*, **82**(6), 1287-1297.
678 <https://doi.org/10.1016/j.anbehav.2011.09.008>
- 679 Dugdale, H. L., Macdonald, D. W., & Newman, C. (2003). Offspring sex ratio variation in the European
680 badger, *Meles meles*. *Ecology*, **84**(1), 40-45. [https://doi.org/10.1890/0012-
9658\(2003\)084\[0040:OSRVIT\]2.0.CO;2](https://doi.org/10.1890/0012-
681 9658(2003)084[0040:OSRVIT]2.0.CO;2)
- 682 Dugdale, H. L., Macdonald, D. W., Pope, L. C., & Burke, T. (2007). Polygynandry, extra-group paternity
683 and multiple-paternity litters in European badger (*Meles meles*) social groups. *Molecular
684 Ecology*, **16**(24), 5294-5306. <https://doi.org/10.1111/j.1365-294X.2007.03571.x>
- 685 Dugdale, H. L., Macdonald, D. W., Pope, L. C., Johnson, P. J., & Burke, T. (2008). Reproductive skew
686 and relatedness in social groups of European badgers, *Meles meles*. *Molecular Ecology*, **17**(7),
687 1815-1827. <https://doi.org/10.1111/j.1365-294X.2008.03708.x>
- 688 Dugdale, H. L., Pope, L. C., Newman, C., Macdonald, D. W., & Burke, T. (2011). Age-specific breeding
689 success in a wild mammalian population: selection, constraint, restraint and senescence.
690 *Molecular Ecology*, **20**(15), 3261-3274. <https://doi.org/10.1111/j.1365-294X.2011.05167.x>
- 691 Edwards, C. A., & Bohlen, P. J. (1996). *Biology and ecology of earthworms*. London: Chapman & Hall.
- 692 Ellwood, S. A., Newman, C., Montgomery, R. A., Nicosia, V., Buesching, C. D., Markham, A., . . .
693 Macdonald, D. W. (2017). An active-radio-frequency-identification system capable of
694 identifying co-locations and social-structure: Validation with a wild free-ranging animal.
695 *Methods in Ecology and Evolution*, **8**(12), 1822-1831. [https://doi.org/10.1111/2041-
210x.12839](https://doi.org/10.1111/2041-
696 210x.12839)
- 697 Epel, E. S., Blackburn, E. H., Lin, J., Dhabhar, F. S., Adler, N. E., Morrow, J. D., & Cawthon, R. M. (2004).
698 Accelerated telomere shortening in response to life stress. *Proceedings of the National*

699 *Academy of Sciences of the United States of America*, **101**(49), 17312-17315.
700 <https://doi.org/10.1073/pnas.0407162101>

701 Erikstad, K. E., Fauchald, P., Tveraa, T., & Steen, H. (1998). On the cost of reproduction in long-lived
702 birds: The influence of environmental variability. *Ecology*, **79**(5), 1781-1788.
703 [https://doi.org/10.1890/0012-9658\(1998\)079\[1781:OTCORI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[1781:OTCORI]2.0.CO;2)

704 Foley, N. M., Petit, E. J., Brazier, T., Finarelli, J. A., Hughes, G. M., Touzalin, F., . . . Teeling, E. C. (2020).
705 Drivers of longitudinal telomere dynamics in a long-lived bat species, *Myotis myotis*. *Molecular*
706 *Ecology*, **29**(16), 2963-2977. <https://doi.org/10.1111/mec.15395>

707 Fowler, P. A., & Racey, P. A. (1988). Overwintering strategies of the badger, *Meles meles*, at 57 °N.
708 *Journal of Zoology*, **214**(4), 635-651. <https://doi.org/10.1111/j.1469-7998.1988.tb03763.x>

709 Froy, H., Underwood, S. L., Dorrens, J., Seeker, L. A., Watt, K., Wilbourn, R. V., . . . Nussey, D. H. (2021).
710 Heritable variation in telomere length predicts mortality in Soay sheep. *Proceedings of the*
711 *National Academy of Sciences of the United States of America*, **118**(15), e2020563118.
712 <https://doi.org/10.1073/pnas.2020563118>

713 Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor.
714 *Annual Review of Physiology*, **66**, 239-274.
715 <https://doi.org/10.1146/annurev.physiol.66.032102.115105>

716 Geiser, F., & Ruf, T. (1995). Hibernation versus daily torpor in mammals and birds - Physiological
717 variables and classification of torpor patterns. *Physiological Zoology*, **68**(6), 935-966.
718 <https://doi.org/10.1086/physzool.68.6.30163788>

719 Gerard, B. M. (1967). Factors affecting earthworms in pastures. *Journal of Animal Ecology*, **36**(1), 235-
720 252. <https://doi.org/10.2307/3024>

721 Giroud, S., Zahn, S., Criscuolo, F. O., Chery, I., Blanc, S., Turbill, C., & Ruf, T. (2014). Late-born
722 intermittently fasted juvenile garden dormice use torpor to grow and fatten prior to
723 hibernation: consequences for ageing processes. *Proceedings of the Royal Society B: Biological*
724 *Sciences*, **281**(1797), 20141131. <https://doi.org/10.1098/rspb.2014.1131>

725 Graves, B. M. (2007). Sexual selection effects on the evolution of senescence. *Evolutionary Ecology*,
726 **21**(5), 663-668. <https://doi.org/10.1007/s10682-006-9144-6>

727 Hammers, M., Richardson, D. S., Burke, T., & Komdeur, J. (2013). The impact of reproductive
728 investment and early-life environmental conditions on senescence: support for the disposable
729 soma hypothesis. *Journal of Evolutionary Biology*, **26**(9), 1999-2007.
730 <https://doi.org/10.1111/jeb.12204>

731 Hancox, M. (1988). Field age determination in the European Badger. *Revue D'Ecologie La Terre et la*
732 *Vie*, **43**(4), 399-404.

733 Heidinger, B. J., Blount, J. D., Boner, W., Griffiths, K., Metcalfe, N. B., & Monaghan, P. (2012). Telomere
734 length in early life predicts lifespan. *Proceedings of the National Academy of Sciences of the*
735 *United States of America*, **109**(5), 1743-1748. <https://doi.org/10.1073/pnas.1113306109>

736 Hoelzl, F., Cornils, J. S., Smith, S., Moodley, Y., & Ruf, T. (2016). Telomere dynamics in free-living edible
737 dormice (*Glis glis*): the impact of hibernation and food supply. *Journal of Experimental Biology*,
738 **219**(16), 2469-2474. <https://doi.org/10.1242/jeb.140871>

739 IPCC. (2018). Global warming of 1.5°C. In V. Masson-Delmotte, P. Zhai, H. O. Pörtner, D. Roberts, J.
740 Skea, P. R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J. B. R.
741 Matthews, Y. Chen, X. Zhou, M. I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, & T. Waterfield
742 (Eds.), *An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial*
743 *levels and related global greenhouse gas emission pathways, in the context of strengthening*
744 *the global response to the threat of climate change*. Geneva, Switzerland: World
745 Meteorological Organization.

746 Johansson, B. (1957). Some biochemical and electro-cardiographical data on badgers. *Acta Zoologica*,
747 **38**(2-3), 205-218. <https://doi.org/10.1111/j.1463-6395.1957.tb00053.x>

748 Johnson, D. D. P., Baker, S., Morecroft, M. D., & Macdonald, D. W. (2001). Long-term resource variation
749 and group size: a large-sample field test of the resource dispersion hypothesis. *BMC Ecology*,
750 **1**(1), 2. <https://doi.org/10.1186/1472-6785-1-2>

751 Johnson, D. D. P., Jetz, W., & Macdonald, D. W. (2002). Environmental correlates of badger social
752 spacing across Europe. *Journal of Biogeography*, **29**(3), 411-425.
753 <https://doi.org/10.1046/j.1365-2699.2002.00680.x>

754 Johnson, D. D. P., Kays, R., Blackwell, P. G., & Macdonald, D. W. (2002). Does the resource dispersion
755 hypothesis explain group living? *Trends in Ecology & Evolution*, **17**(12), 563.

756 Johnson, D. D. P., & Macdonald, D. W. (2001). Why are group-living badgers (*Meles meles*) sexually
757 dimorphic? *Journal of Zoology*, **255**(2), 199-204.
758 <https://doi.org/10.1017/S0952836901001273>

759 Kimura, M., Gazitt, Y., Cao, X. J., Zhao, X. Y., Lansdorp, P. M., & Aviv, A. (2010). Synchrony of telomere
760 length among hematopoietic cells. *Experimental Hematology*, **38**(10), 854-859.
761 <https://doi.org/10.1016/j.exphem.2010.06.010>

762 Kirkwood, T. B. L., & Rose, M. R. (1991). Evolution of senescence: Late survival sacrificed for
763 reproduction. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
764 **332**(1262), 15-24. <https://doi.org/10.1098/rstb.1991.0028>

765 Kruman, I. I., Ilyasova, E. N., Rudchenko, S. A., & Khurkhulu, Z. S. (1988). The intestinal epithelial cells
766 of ground squirrel (*Citellus undulatus*) accumulate at G2 phase of the cell cycle throughout a
767 bout of hibernation. *Comparative Biochemistry and Physiology Part A: Physiology*, **90**(2), 233-
768 236. [https://doi.org/10.1016/0300-9629\(88\)91109-7](https://doi.org/10.1016/0300-9629(88)91109-7)

769 Kruuk, H. (1978). Spatial organization and territorial behaviour of the European badger *Meles meles*.
770 *Journal of Zoology*, **184**(1), 1-19. <https://doi.org/10.1111/j.1469-7998.1978.tb03262.x>

771 Kruuk, H., & Parish, T. (1981). Feeding specialization of the European badger *Meles meles* in Scotland.
772 *Journal of Animal Ecology*, **50**(3), 773-788. <https://doi.org/10.2307/4136>

773 Lemaitre, J. F., Berger, V., Bonenfant, C., Douhard, M., Gamelon, M., Plard, F., & Gaillard, J. M. (2015).
774 Early-late life trade-offs and the evolution of ageing in the wild. *Proceedings of the Royal
775 Society B: Biological Sciences*, **282**(1806), 20150209. <https://doi.org/10.1098/rspb.2015.0209>

776 Lindström, J. (1999). Early development and fitness in birds and mammals. *Trends in Ecology &
777 Evolution*, **14**(9), 343-348. [https://doi.org/10.1016/S0169-5347\(99\)01639-0](https://doi.org/10.1016/S0169-5347(99)01639-0)

778 López-Otín, C., Blasco, M. A., Partridge, L., Serrano, M., & Kroemer, G. (2013). The hallmarks of aging.
779 *Cell*, **153**(6), 1194-1217. <https://doi.org/10.1016/j.cell.2013.05.039>

780 Macdonald, D. W., & Newman, C. (2002). Population dynamics of badgers (*Meles meles*) in
781 Oxfordshire, UK: Numbers, density and cohort life histories, and a possible role of climate
782 change in population growth. *Journal of Zoology*, **256**(1), 121-138.
783 <https://doi.org/10.1017/S0952836902000158>

784 Macdonald, D. W., Newman, C., & Buesching, C. D. (2015). Badgers in the rural landscape -
785 conservation paragon or farmland pariah? Lessons from the Wytham badger project. In D. W.
786 Macdonald & R. E. Feber (Eds.), *Wildlife conservation on farmland volume 2: Conflict in the
787 countryside* (pp. 1-32). Oxford: Oxford University Press.

788 Macdonald, D. W., Newman, C., Buesching, C. D., & Johnson, P. J. (2008). Male-biased movement in a
789 high-density population of the Eurasian badger (*Meles Meles*). *Journal of Mammalogy*, **89**(5),
790 1077-1086. <https://doi.org/10.1644/07-Mamm-a-185.1>

791 Macdonald, D. W., Newman, C., Buesching, C. D., & Nouvellet, P. (2010). Are badgers 'under the
792 weather'? Direct and indirect impacts of climate variation on European badger (*Meles meles*)
793 population dynamics. *Global Change Biology*, **16**(11), 2913-2922.
794 <https://doi.org/10.1111/j.1365-2486.2010.02208.x>

795 Macdonald, D. W., Newman, C., Nouvellet, P. M., & Buesching, C. D. (2009). An analysis of Eurasian
796 badger (*Meles meles*) population dynamics: Implications for regulatory mechanisms. *Journal
797 of Mammalogy*, **90**(6), 1392-1403. <https://doi.org/10.1644/08-MAMM-A-356R1.1>

798 Maklakov, A. A., & Lummaa, V. (2013). Evolution of sex differences in lifespan and aging: Causes and
799 constraints. *Bioessays*, **35**(8), 717-724. <https://doi.org/10.1002/bies.201300021>

800 McLaren, G. W., Thornton, P. D., Newman, C., Buesching, C. D., Baker, S. E., Mathews, F., & Macdonald,
801 D. W. (2005). The use and assessment of ketamine-medetomidine-butorphanol combinations
802 for field anaesthesia in wild European badgers (*Meles meles*). *Veterinary Anaesthesia and*
803 *Analgesia*, **32**(6), 367-372. <https://doi.org/10.1111/j.1467-2995.2005.00206.x>

804 McLennan, D., Armstrong, J. D., Stewart, D. C., Mckelvey, S., Boner, W., Monaghan, P., & Metcalfe, N.
805 B. (2016). Interactions between parental traits, environmental harshness and growth rate in
806 determining telomere length in wild juvenile salmon. *Molecular Ecology*, **25**(21), 5425-5438.
807 <https://doi.org/10.1111/mec.13857>

808 Medawar, P. B. (1952). *An unsolved problem of biology*. London: H.K. Lewis.

809 Mendez-Bermudez, A., Hidalgo-Bravo, A., Cotton, V. E., Gravani, A., Jeyapalan, J. N., & Royle, N. J.
810 (2012). The roles of WRN and BLM RecQ helicases in the alternative lengthening of telomeres.
811 *Nucleic Acids Research*, **40**(21), 10809-10820. <https://doi.org/10.1093/nar/gks862>

812 Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends in*
813 *Ecology & Evolution*, **16**(5), 254-260. [https://doi.org/10.1016/S0169-5347\(01\)02124-3](https://doi.org/10.1016/S0169-5347(01)02124-3)

814 Mizutani, Y., Tomita, N., Niizuma, Y., & Yoda, K. (2013). Environmental perturbations influence
815 telomere dynamics in long-lived birds in their natural habitat. *Biology Letters*, **9**(5), 20130511.
816 <https://doi.org/10.1098/rsbl.2013.0511>

817 Monaghan, P. (2014). Organismal stress, telomeres and life histories. *Journal of Experimental Biology*,
818 **217**(1), 57-66. <https://doi.org/10.1242/jeb.090043>

819 Monaghan, P., & Haussmann, M. F. (2006). Do telomere dynamics link lifestyle and lifespan? *Trends*
820 *in Ecology & Evolution*, **21**(1), 47-53. <https://doi.org/10.1016/j.tree.2005.11.007>

821 Nakagawa, S., & Freckleton, R. P. (2011). Model averaging, missing data and multiple imputation: A
822 case study for behavioural ecology. *Behavioral Ecology and Sociobiology*, **65**(1), 103-116.
823 <https://doi.org/https://doi.org/10.1007/s00265-010-1044-7>

824 Nettle, D., Monaghan, P., Gillespie, R., Brilot, B., Bedford, T., & Bateson, M. (2015). An experimental
825 demonstration that early-life competitive disadvantage accelerates telomere loss.
826 *Proceedings of the Royal Society B: Biological Sciences*, **282**(1798), 20141610.
827 <https://doi.org/10.1098/rspb.2014.1610>

828 Newman, C., Buesching, C. D., & Macdonald, D. W. (2017). Meline mastery of meteorological mayhem:
829 the effects of climate changeability on European badger population dynamics. In D. W.
830 Macdonald, C. Newman, & L. Harrington (Eds.), *Biology and Conservation of Musteloids*.
831 Oxford: Oxford University Press.

832 Newman, C., Macdonald, D. W., & Anwar, M. A. (2001). Coccidiosis in the European badger, *Meles*
833 *meles* in Wytham Woods: infection and consequences for growth and survival. *Parasitology*,
834 **123**(2), 133-142. <https://doi.org/10.1017/S0031182001008265>

835 Newman, C., Zhou, Y. B., Buesching, C. D., Kaneko, Y., & Macdonald, D. W. (2011). Contrasting sociality
836 in two widespread, generalist, mustelid genera, *Meles* and *Martes*. *Mammal Study*, **36**(4),
837 169-188. <https://doi.org/10.3106/041.036.0401>

838 Noonan, M. J., Markham, A., Newman, C., Trigoni, N., Buesching, C. D., Ellwood, S. A., & Macdonald,
839 D. W. (2014). Climate and the individual: Inter-annual variation in the autumnal activity of the
840 European badger (*Meles meles*). *PLoS ONE*, **9**(1), e83156.
841 <https://doi.org/10.1371/journal.pone.0083156>

842 Noonan, M. J., Markham, A., Newman, C., Trigoni, N., Buesching, C. D., Ellwood, S. A., & Macdonald,
843 D. W. (2015). A new magneto-inductive tracking technique to uncover subterranean activity:
844 what do animals do underground? *Methods in Ecology and Evolution*, **6**(5), 510-520.
845 <https://doi.org/10.1111/2041-210X.12348>

846 Noonan, M. J., Newman, C., Markham, A., Bilham, K., Buesching, C. D., & Macdonald, D. W. (2018). In
847 situ behavioral plasticity as compensation for weather variability: implications for future

848 climate change. *Climatic Change*, **149**(3-4), 457-471. [https://doi.org/10.1007/s10584-018-](https://doi.org/10.1007/s10584-018-2248-5)
849 [2248-5](https://doi.org/10.1007/s10584-018-2248-5)

850 Nouvellet, P., Newman, C., Buesching, C. D., & Macdonald, D. W. (2013). A multi-metric approach to
851 investigate the effects of weather conditions on the demographic of a terrestrial mammal, the
852 European badger (*Meles meles*). *PLoS ONE*, **8**(7), 1-7.
853 <https://doi.org/10.1371/journal.pone.0068116>

854 Nowack, J., Tarmann, I., Hoelzl, F., Smith, S., Giroud, S., & Ruf, T. (2019). Always a price to pay:
855 hibernation at low temperatures comes with a trade-off between energy savings and
856 telomere damage. *Biology Letters*, **15**(10), 20190466. <https://doi.org/10.1098/rsbl.2019.0466>

857 Nussey, D. H., Kruuk, L. E. B., Morris, A., Clements, M. N., Pemberton, J. M., & Clutton-Brock, T. H.
858 (2009). Inter- and intrasexual variation in aging patterns across reproductive traits in a wild
859 red deer population. *American Naturalist*, **174**(3), 342-357. <https://doi.org/10.1086/603615>

860 Nussey, D. H., Kruuk, L. E. B., Morris, A., & Clutton-Brock, T. H. (2007). Environmental conditions in
861 early life influence ageing rates in a wild population of red deer. *Current Biology*, **17**(23),
862 R1000-R1001. <https://doi.org/10.1016/j.cub.2007.10.005>

863 Olovnikov, A. M. (1973). Theory of marginotomy - Incomplete copying of template margin in enzymic-
864 synthesis of polynucleotides and biological significance of phenomenon. *Journal of Theoretical*
865 *Biology*, **41**(1), 181-190. [https://doi.org/10.1016/0022-5193\(73\)90198-7](https://doi.org/10.1016/0022-5193(73)90198-7)

866 Promislow, D. (2003). Mate choice, sexual conflict, and evolution of senescence. *Behavior Genetics*,
867 **33**(2), 191-201. <https://doi.org/10.1023/A:1022562103669>

868 Promislow, D. E. L. (1992). Costs of sexual selection in natural populations of mammals. *Proceedings*
869 *of the Royal Society B: Biological Sciences*, **247**(1320), 203-210.
870 <https://doi.org/10.1098/rspb.1992.0030>

871 R Development Core Team. (2020). R: a language and environment for statistical computing. Vienna:
872 R foundation for statistical computing.

873 Réale, D., Festa-Bianchet, M., & Jorgenson, J. T. (1999). Heritability of body mass varies with age and
874 season in wild bighorn sheep. *Heredity*, **83** (5), 526-532.
875 <https://doi.org/10.1038/sj.hdy.6885430>

876 Reed, T. E., Kruuk, L. E. B., Wanless, S., Frederiksen, M., Cunningham, E. J. A., & Harris, M. P. (2008).
877 Reproductive senescence in a long-lived seabird: Rates of decline in late-life performance are
878 associated with varying costs of early reproduction. *American Naturalist*, **171**(2), 89-101.
879 <https://doi.org/10.1086/524957>

880 Reichert, S., & Stier, A. (2017). Does oxidative stress shorten telomeres in vivo? A review. *Biology*
881 *Letters*, **13**(12), 20170463. <https://doi.org/10.1098/rsbl.2017.0463>

882 Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., & Monaghan, P. (2003). Environmental variability,
883 life-history covariation and cohort effects in the red-billed chough *Pyrrhocorax pyrrhocorax*.
884 *Journal of Animal Ecology*, **72**(1), 36-46. <https://doi.org/10.1046/j.1365-2656.2003.00673.x>

885 Revilla, E. (2003). Moving beyond the resource dispersion hypothesis. *Trends in Ecology & Evolution*,
886 **18**(8), 380. [https://doi.org/10.1016/S0169-5347\(03\)00153-8](https://doi.org/10.1016/S0169-5347(03)00153-8)

887 Robertson, A., McDonald, R. A., Delahay, R. J., Kelly, S. D., & Bearhop, S. (2014). Individual foraging
888 specialisation in a social mammal: the European badger (*Meles meles*). *Oecologia*, **176**(2),
889 409-421. <https://doi.org/10.1007/s00442-014-3019-2>

890 Ruf, T., & Geiser, F. (2015). Daily torpor and hibernation in birds and mammals. *Biological Reviews*,
891 **90**(3), 891-926. <https://doi.org/10.1111/brv.12137>

892 Schroeder, J., Nakagawa, S., Cleasby, I. R., & Burke, T. (2012). Passerine birds breeding under chronic
893 noise experience reduced fitness. *PLoS ONE*, **7**(7), e39200.
894 <https://doi.org/10.1371/journal.pone.0039200>

895 Sharp, S. P., & Clutton-Brock, T. H. (2011). Competition, breeding success and ageing rates in female
896 meerkats. *Journal of Evolutionary Biology*, **24**(8), 1756-1762. [https://doi.org/10.1111/j.1420-](https://doi.org/10.1111/j.1420-9101.2011.02304.x)
897 [9101.2011.02304.x](https://doi.org/10.1111/j.1420-9101.2011.02304.x)

898 Spurgin, L. G., Bebbington, K., Fairfield, E. A., Hammers, M., Komdeur, J., Burke, T., . . . Richardson, D.
899 S. (2017). Spatio-temporal variation in lifelong telomere dynamics in a long-term ecological
900 study. *Journal of Animal Ecology*, **87**(1), 187-198. <https://doi.org/10.1111/1365-2656.12741>
901 Stier, A., Massemin, S., Zahn, S., Tissier, M. L., & Criscuolo, F. (2015). Starting with a handicap: effects
902 of asynchronous hatching on growth rate, oxidative stress and telomere dynamics in free-
903 living great tits. *Oecologia*, **179**(4), 999-1010. <https://doi.org/10.1007/s00442-015-3429-9>
904 Stoffel, M. A., Nakagawa, S., & Schielzeth, H. (2017). rptR: repeatability estimation and variance
905 decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*,
906 **8**(11), 1639-1644. <https://doi.org/10.1111/2041-210x.12797>
907 Sugianto, N. A., Newman, C., Macdonald, D. W., & Buesching, C. D. (2019). Extrinsic factors affecting
908 cub development contribute to sexual size dimorphism in the European badgers (*Meles*
909 *meles*). *Zoology*, **135**, 125688. <https://doi.org/10.1016/j.zool.2019.04.005>
910 Sugianto, N. A., Newman, C., Macdonald, D. W., & Buesching, C. D. (2019). Heterochrony of puberty
911 in the European badger (*Meles meles*) can be explained by growth rate and group-size:
912 Evidence for two endocrinological phenotypes. *PLoS ONE*, **14**(3), e0203910.
913 <https://doi.org/10.1371/journal.pone.0203910>
914 Tian, X., Doerig, K., Park, R., Can Ran Qin, A., Hwang, C., Neary, A., . . . Gorbunova, V. (2018). Evolution
915 of telomere maintenance and tumour suppressor mechanisms across mammals. *Philosophical*
916 *Transactions of the Royal Society B: Biological Sciences*, **373**(1741), 20160443.
917 <https://doi.org/10.1098/rstb.2016.0443>
918 Tsunoda, M., Newman, C., Buesching, C. D., Macdonald, D. W., & Kaneko, Y. (2018). Badger setts
919 provide thermal refugia, buffering changeable surface weather conditions. *Journal of Thermal*
920 *Biology*, **74**, 226-233. <https://doi.org/10.1016/j.jtherbio.2018.04.005>
921 Turbill, C., Ruf, T., Smith, S., & Bieber, C. (2013). Seasonal variation in telomere length of a hibernating
922 rodent. *Biology Letters*, **9**(2), 20121095. <https://doi.org/10.1098/rsbl.2012.1095>
923 Turbill, C., Smith, S., Deimel, C., & Ruf, T. (2012). Daily torpor is associated with telomere length change
924 over winter in Djungarian hamsters. *Biology Letters*, **8**(2), 304-307.
925 <https://doi.org/10.1098/rsbl.2011.0758>
926 van de Pol, M., & Wright, J. (2009). A simple method for distinguishing within- versus between-subject
927 effects using mixed models. *Animal Behaviour*, **77**(3), 753-758.
928 <https://doi.org/10.1016/j.anbehav.2008.11.006>
929 van Lieshout, S. H. J., Badas, E. P., Bright Ross, J. G., Bretman, A., Newman, C., Buesching, C. D., . . .
930 Dugdale, H. L. (2021). Data from: Early-life seasonal, weather and social effects on telomere
931 length in a wild mammal. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.3r2280gf5>
932 van Lieshout, S. H. J., Badás, E. P., Mason, M. W. T., Newman, C., Buesching, C. D., Macdonald, D. W.,
933 & Dugdale, H. L. (2020). Social effects on age-related and sex-specific immune cell profiles in
934 a wild mammal. *Biology Letters*, **16**(7), 20200234. <https://doi.org/10.1098/rsbl.2020.0234>
935 van Lieshout, S. H. J., Bretman, A., Newman, C., Buesching, C. D., Macdonald, D. W., & Dugdale, H. L.
936 (2019). Individual variation in early-life telomere length and survival in a wild mammal.
937 *Molecular Ecology*, **28**(18), 4152-4165. <https://doi.org/10.1111/mec.15212>
938 van Lieshout, S. H. J., Sparks, A. M., Bretman, A., Newman, C., Buesching, C. D., Burke, T., . . . Dugdale,
939 H. L. (2020). Estimation of environmental, genetic and parental age at conception effects on
940 telomere length in a wild mammal. *Journal of Evolutionary Biology*, **34**(2).
941 <https://doi.org/10.1111/jeb.13728>
942 van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: their influence on
943 variation in life-history tactics. *American Naturalist*, **128**(1), 137-142.
944 <https://doi.org/10.1086/284547>
945 Vedder, O., Moiron, M., Bichet, C., Bauch, C., Verhulst, S., Becker, P. H., & Bouwhuis, S. (2021).
946 Telomere length is heritable and genetically correlated with lifespan in a wild bird. *Molecular*
947 *Ecology*. <https://doi.org/10.1111/mec.15807>

- 948 Vedder, O., Verhulst, S., Bauch, C., & Bouwhuis, S. (2017). Telomere attrition and growth: a life-history
 949 framework and case study in common terns. *Journal of Evolutionary Biology*, **30**(7), 1409-
 950 1419. <https://doi.org/10.1111/jeb.13119>
- 951 Verhulst, S. (2020). Improving comparability between qPCR-based telomere studies. *Molecular*
 952 *Ecology Resources*, **20**(1), 11-13. <https://doi.org/10.1111/1755-0998.13114>
- 953 von Zglinicki, T. (2002). Oxidative stress shortens telomeres. *Trends in Biochemical Sciences*, **27**(7),
 954 339-344. [https://doi.org/10.1016/S0968-0004\(02\)02110-2](https://doi.org/10.1016/S0968-0004(02)02110-2)
- 955 Watson, H., Bolton, M., & Monaghan, P. (2015). Variation in early-life telomere dynamics in a long-
 956 lived bird: Links to environmental conditions and survival. *Journal of Experimental Biology*,
 957 **218**(5), 668-674. <https://doi.org/10.1242/jeb.104265>
- 958 Webb, D. R., & King, J. R. (1984). Effects of wetting on insulation of bird and mammal coats. *Journal of*
 959 *Thermal Biology*, **9**(3), 189-191. [https://doi.org/10.1016/0306-4565\(84\)90020-2](https://doi.org/10.1016/0306-4565(84)90020-2)
- 960 Weimerskirch, H., Zimmermann, L., & Prince, P. A. (2001). Influence of environmental variability on
 961 breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology*, **12**(1),
 962 22-30. <https://doi.org/10.1093/oxfordjournals.beheco.a000374>
- 963 Wilbourn, R. V., Moatt, J. P., Froy, H., Walling, C. A., Nussey, D. H., & Boonekamp, J. J. (2018). The
 964 relationship between telomere length and mortality risk in non-model vertebrate systems: a
 965 meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*,
 966 **373**(1741), 20160447. <https://doi.org/10.1098/rstb.2016.0447>
- 967 Wilbur, H. M., & Rudolf, V. H. W. (2006). Life-history evolution in uncertain environments: Bet hedging
 968 in time. *American Naturalist*, **168**(3), 398-411. <https://doi.org/10.1086/506258>
- 969 Wilbur, S. M., Barnes, B. M., Kitaysky, A. S., & Williams, C. T. (2019). Tissue-specific telomere dynamics
 970 in hibernating arctic ground squirrels (*Urocitellus parryii*). *Journal of Experimental Biology*,
 971 **222**(18), jeb204925. <https://doi.org/10.1242/jeb.204925>
- 972 Williams, G. C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, **11**(4),
 973 398-411. <https://doi.org/10.2307/2406060>
- 974 Wilson, A. J., & Nussey, D. H. (2010). What is individual quality? An evolutionary perspective. *Trends*
 975 *in Ecology & Evolution*, **25**(4), 207-214. <https://doi.org/10.1016/j.tree.2009.10.002>
- 976 Wolff, J. O., & Macdonald, D. W. (2004). Promiscuous females protect their offspring. *Trends in Ecology*
 977 *& Evolution*, **19**(3), 127-134. <https://doi.org/10.1016/j.tree.2003.12.009>
- 978 Woodroffe, R., & Macdonald, D. W. (1995). Female/female competition in European badgers *Meles*
 979 *meles*: Effects on breeding success. *Journal of Animal Ecology*, **64**(1), 12-20.
 980 <https://doi.org/10.2307/5823>
- 981 Yamaguchi, N., Dugdale, H. L., & Macdonald, D. W. (2006). Female receptivity, embryonic diapause
 982 and superfoetation in the European badger (*Meles meles*): Implications for the reproductive
 983 tactics of males and females. *Quarterly Review of Biology*, **81**(1), 33-48.
 984 <https://doi.org/10.1086/503923>
- 985 Young, A. J. (2018). The role of telomeres in the mechanisms and evolution of life-history trade-offs
 986 and ageing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**(1741),
 987 20160452. <https://doi.org/10.1098/rstb.2016.0452>

988

989

990 **Tables and figures**

991

992

993

994

995

996

997

Table 1: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the number of cubs in the natal group, season and weather effects in spring on early-life (3–12 months old) relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------------|--------------|-------------------------|
| Intercept [†] | -0.009 | 0.118 | -0.228 to 0.218 |
| Number of cubs in natal group | 0.106 | 0.052 | 0.008 to 0.206 |
| Season (Spring) | | | |
| Summer | 0.196 | 0.137 | -0.072 to 0.464 |
| Autumn | 0.131 | 0.277 | -0.409 to 0.656 |
| Winter | -1.001 | 0.383 | -1.741 to -0.232 |
| Mean temperature | -4.036 | 3.767 | -11.38 to 3.367 |
| Mean temperature ² | 4.519 | 3.830 | -3.089 to 11.94 |
| Daily temperature variability | 0.588 | 1.709 | -2.849 to 3.850 |
| Daily temperature variability ² | -0.457 | 1.733 | -3.780 to 3.044 |
| Mean daily rainfall | -1.894 | 0.810 | -3.473 to -0.267 |
| Mean daily rainfall² | 2.074 | 0.836 | 0.368 to 3.692 |
| Daily rainfall variability | -3.911 | 2.019 | -7.818 to 0.014 |
| Daily rainfall variability ² | 3.790 | 2.041 | -0.211 to 7.698 |
| Weight | 0.075 | 0.101 | -0.124 to 0.275 |
| Body length | -0.089 | 0.097 | -0.274 to 0.100 |
| <hr/> | | | |
| Without non-significant 2 nd order effects | | | |
| Intercept ^{††} | 0.009 | 0.110 | -0.197 to 0.216 |
| Number of cubs in natal group | 0.100 | 0.051 | 0.001 to 0.200 |
| Season (Spring) | | | |
| Summer | 0.178 | 0.136 | -0.088 to 0.446 |
| Autumn | 0.097 | 0.274 | -0.447 to 0.614 |
| Winter | -0.995 | 0.380 | -1.726 to -0.237 |
| Mean temperature | 0.403 | 0.087 | 0.227 to 0.577 |
| Daily temperature variability | 0.135 | 0.095 | -0.053 to 0.321 |
| Mean daily rainfall | -1.225 | 0.559 | -2.333 to -0.124 |
| Mean daily rainfall² | 1.356 | 0.555 | 0.255 to 2.467 |
| Daily rainfall variability | -2.843 | 1.414 | -5.563 to -0.112 |
| Daily rainfall variability² | 2.745 | 1.405 | 0.039 to 5.464 |
| Weight | 0.072 | 0.100 | -0.124 to 0.272 |
| Body length | -0.082 | 0.096 | -0.266 to 0.104 |

998

999

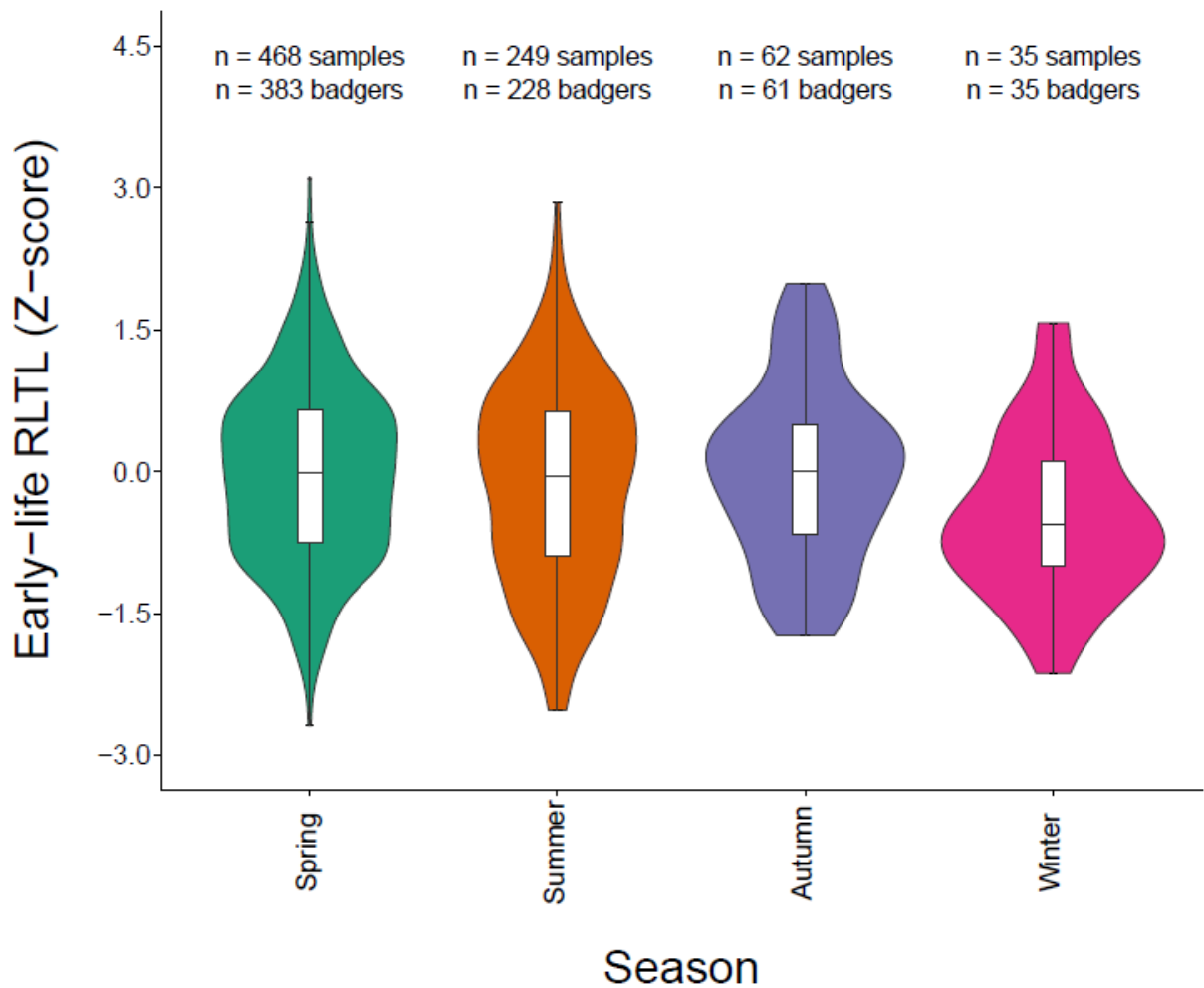
1000

1001

1002

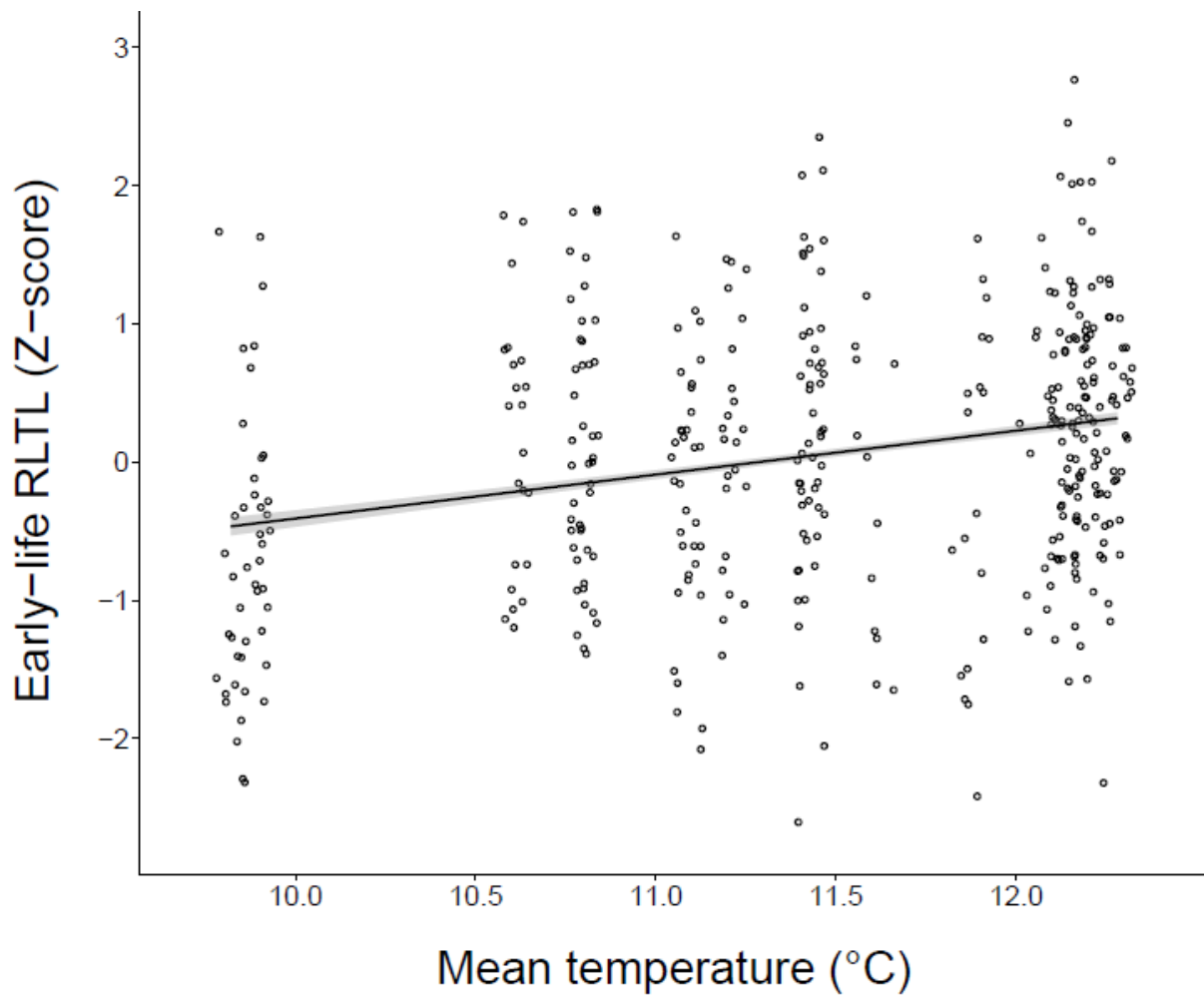
Random effect estimates (variance): [†]qPCR plate ($4.955 \cdot 10^{-2}$), Row on qPCR plate ($1.861 \cdot 10^{-3}$), Social group ($2.798 \cdot 10^{-2}$), Cohort ($7.745 \cdot 10^{-2}$), Residual ($7.537 \cdot 10^{-1}$)

^{††}qPCR plate ($4.911 \cdot 10^{-2}$), Row on qPCR plate ($2.895 \cdot 10^{-3}$), Social group ($2.642 \cdot 10^{-2}$), Cohort ($5.287 \cdot 10^{-2}$), Residual ($7.572 \cdot 10^{-1}$)



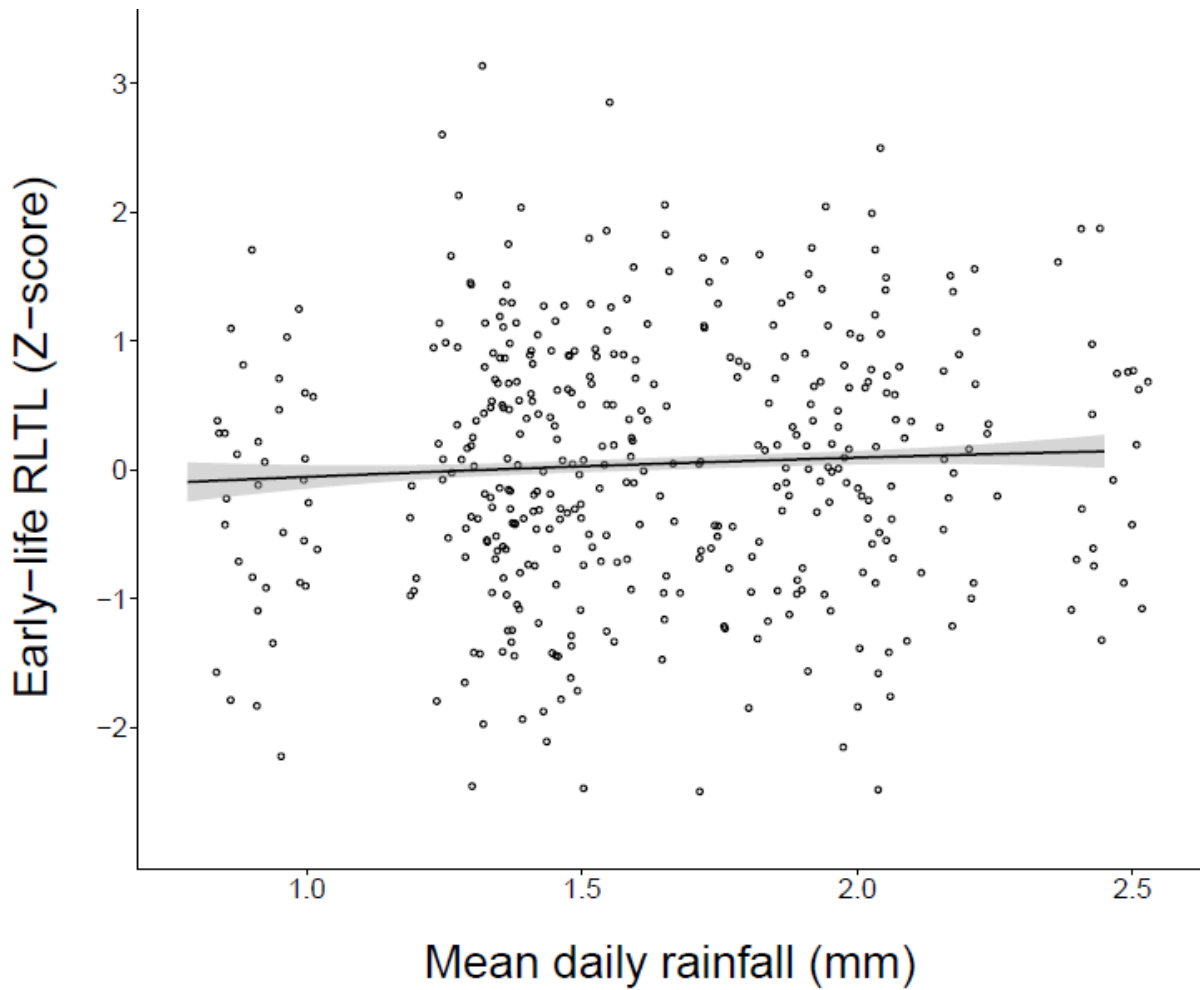
1003
 1004
 1005
 1006
 1007
 1008

Figure 1: Variation in early-life relative leukocyte telomere length (RLTL) among seasons in European badgers. The data distributions and probability densities are shown ($n = 814$ samples; 533 badgers - the sum of badgers in the plot is >533 due to repeated measures). Data were collected in 19 years, across 59 trapping periods. The line in the boxplot represents the median, with first and third quartiles, and whiskers represent 1.57 times the inter-quartile range.



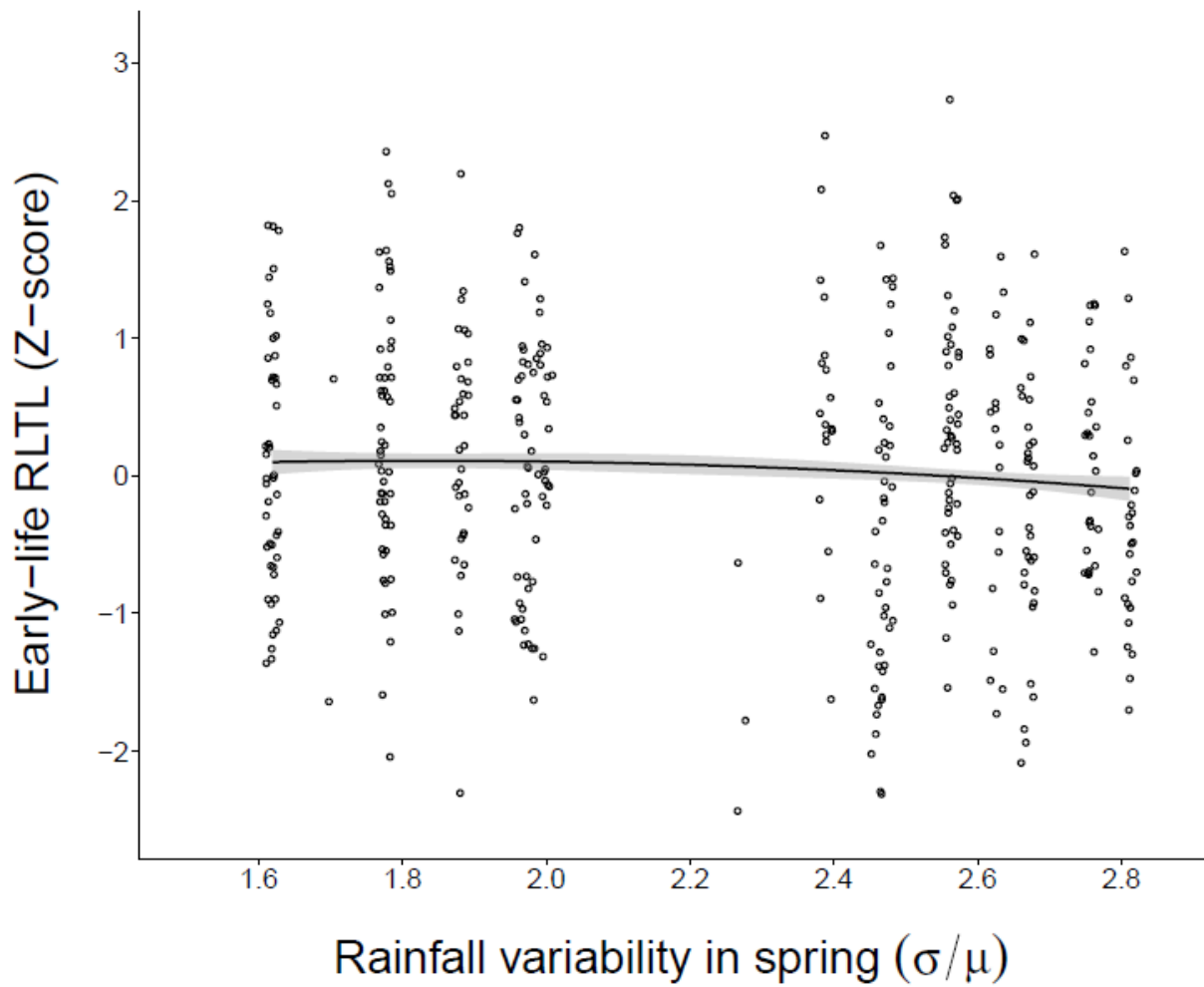
1009
 1010
 1011
 1012
 1013

Figure 2: The association between mean spring temperature and early-life relative leukocyte telomere length (RLTL). Raw data points ($n = 406$ samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the regression from the mixed model, and the 95% confidence intervals as shaded areas.



1014
1015
1016
1017
1018

Figure 3: The association between mean daily rainfall in spring and early-life relative leukocyte telomere length (RLTL). Raw data points ($n = 406$ samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model, and the 95% confidence intervals as shaded areas.



1019
 1020
 1021
 1022
 1023

Figure 4: The association between the rainfall variability in spring and early-life relative leukocyte telomere length (RLTL). Raw data points ($n = 406$ samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model, and the 95% confidence intervals as shaded areas.

Supplemental Information for:

**Early-life seasonal, weather and social effects on
telomere lengths in a wild mammal**

Sil H.J. van Lieshout, Elisa P. Badás, Julius G. Bright Ross, Amanda Bretman, Chris Newman,
Christina D. Buesching, Terry Burke, David W. Macdonald & Hannah L. Dugdale

Table of Contents:

| | |
|------------------------------|---------------|
| Supplementary tables | Pages 2 – 20 |
| Supplementary figures | Pages 21 – 24 |

This supplementary materials document includes supplementary tables and figures.

Table S1: Parameter estimates and 95% confidence intervals (from parametric bootstrapping) of fixed effects from a mixed model of age and seasonal effects on relative leukocyte telomere length (Z-score) in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. A threshold age of 29 months was modelled, such that two parameter estimates are generated for ≤ 29 months and >29 to ≤ 36 months of age. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|--------------------------------|---------------|--------------|-------------------------|
| Intercept | -0.159 | 0.123 | -0.400 to 0.085 |
| Age ≤ 29 months | -0.049 | 0.064 | -0.178 to 0.079 |
| Age >29 and ≤ 36 months | 0.018 | 0.038 | -0.057 to 0.094 |
| Age at last capture | 0.040 | 0.036 | -0.032 to 0.110 |
| Season (Spring) | | | |
| Summer | -0.001 | 0.076 | -0.157 to 0.153 |
| Autumn | 0.057 | 0.135 | -0.198 to 0.315 |
| Winter | -0.518 | 0.183 | -0.875 to -0.172 |
| Weight | 0.042 | 0.035 | -0.027 to 0.113 |
| Body length | 0.058 | 0.058 | -0.058 to 0.170 |

Random effect estimates (variance): qPCR plate ($5.301 \cdot 10^{-2}$), Row on qPCR plate ($4.723 \cdot 10^{-3}$), Social group ($7.617 \cdot 10^{-3}$), Cohort ($6.470 \cdot 10^{-2}$), Year ($1.175 \cdot 10^{-1}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.841 \cdot 10^{-1}$)

Table S2: Parameter estimates and 95% confidence intervals (from parametric bootstrapping) of fixed effects from a mixed model of age effects and both within-individual (β_w ; the mean season value for each individual subtracted from the season value for each RLTL measurement) and between-individual (β_B ; the mean season value for each individual) seasonal effects on relative leukocyte telomere length (Z-score) in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals. A threshold age of 29 months was modelled, such that two parameter estimates are generated for ≤ 29 months and >29 to ≤ 36 months of age. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|--------------------------------------|---------------|--------------|-------------------------|
| Intercept | -0.091 | 0.087 | -0.260 to 0.078 |
| Age ≤ 29 months | 0.045 | 0.084 | -0.112 to 0.210 |
| Age >29 and ≤ 36 months | 0.041 | 0.047 | -0.054 to 0.136 |
| Age at last capture | 0.063 | 0.045 | -0.026 to 0.152 |
| Season (β_w) | -0.109 | 0.042 | -0.192 to -0.026 |
| Season (β_B) | -0.119 | 0.048 | -0.212 to -0.026 |
| Weight | 0.026 | 0.049 | -0.070 to 0.121 |
| Body length | 0.006 | 0.079 | -0.150 to 0.161 |

Random effect estimates (variance): qPCR plate ($2.404 \cdot 10^{-2}$), Row on qPCR plate ($2.684 \cdot 10^{-3}$), Social group ($3.325 \cdot 10^{-4}$), Cohort ($6.338 \cdot 10^{-2}$), Year ($1.480 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.955 \cdot 10^{-1}$)

Table S3: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of age effects and within-individual (β_w ; the mean season value for each individual subtracted from the season value for each RLTL measurement) and the difference in between- and within-individual ($\beta_B - \beta_w$) seasonal effects on relative leukocyte telomere length (Z-score) in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals. A threshold age of 29 months was modelled, such that two parameter estimates are generated for ≤ 29 months and >29 to ≤ 36 months of age. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|--------------------------------------|---------------|--------------|-------------------------|
| Intercept | -0.036 | 0.089 | -0.209 to 0.141 |
| Age ≤ 29 months | 0.045 | 0.084 | -0.112 to 0.210 |
| Age >29 and ≤ 36 months | 0.041 | 0.047 | -0.054 to 0.136 |
| Age at last capture | 0.063 | 0.045 | -0.026 to 0.152 |
| Season (β_w) | -0.786 | 0.307 | -1.384 to -0.187 |
| Season ($\beta_B - \beta_w$) | 0.055 | 0.078 | -0.093 to 0.206 |
| Weight | 0.026 | 0.049 | -0.070 to 0.121 |
| Body length | 0.006 | 0.079 | -0.150 to 0.161 |

Random effect estimates (variance): qPCR plate ($2.404 \cdot 10^{-2}$), Row on qPCR plate ($2.684 \cdot 10^{-3}$), Social group ($3.325 \cdot 10^{-4}$), Cohort ($6.338 \cdot 10^{-2}$), Year ($1.480 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.955 \cdot 10^{-1}$)

Table S4: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the direction of the effect on relative leukocyte telomere length (Z-score) from a cross-sectional model and when separating within- from between-individual effects from spring to winter in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---------------------------------------|---------------|--------------|-------------------------|
| Intercept [†] | -0.001 | 0.123 | -0.236 to 0.249 |
| Age \leq29 months | 0.289 | 0.144 | 0.004 to 0.579 |
| Age at last capture | 0.111 | 0.068 | -0.022 to 0.249 |
| Season (Spring) | | | |
| Winter | -1.431 | 0.488 | -2.392 to -0.461 |
| Weight | 0.176 | 0.172 | -0.181 to 0.519 |
| Body length | -0.156 | 0.127 | -0.400 to 0.092 |

| | | | |
|--------------------------------------|---------------|--------------|-------------------------|
| Intercept ^{††} | -0.165 | 0.112 | -0.380 to 0.062 |
| Age \leq 29 months | 0.290 | 0.149 | -0.007 to 0.586 |
| Age at last capture | 0.102 | 0.068 | -0.030 to 0.238 |
| Season (β_w) | -0.287 | 0.096 | -0.470 to -0.094 |
| Season (β_b) | -0.353 | 0.146 | -0.643 to -0.068 |
| Weight | 0.158 | 0.177 | -0.209 to 0.500 |
| Body length | -0.153 | 0.128 | -0.402 to 0.098 |

Random effect estimates (variance):

[†]qPCR plate ($<1.000 \cdot 10^{-12}$), Row on qPCR plate ($4.175 \cdot 10^{-3}$), Social group ($3.878 \cdot 10^{-2}$), Cohort ($6.284 \cdot 10^{-4}$), Year ($8.181 \cdot 10^{-1}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.569 \cdot 10^{-1}$)

^{††}qPCR plate ($<1.000 \cdot 10^{-12}$), Row on qPCR plate ($3.965 \cdot 10^{-3}$), Social group ($3.830 \cdot 10^{-2}$), Cohort ($5.964 \cdot 10^{-3}$), Year ($7.920 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.566 \cdot 10^{-1}$)

Table S5: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the direction of the effect on relative leukocyte telomere length (Z-score) from a cross-sectional model and when separating within- from between-individual effects from winter to spring in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|------------------------------------|---------------------------|-------------|-----------------|
| Intercept [†] | -0.041 | 0.183 | -0.399 to 0.308 |
| Age \leq 29 months | 0.160 | 0.168 | -0.172 to 0.498 |
| Age at last capture | -0.086 | 0.123 | -0.333 to 0.157 |
| Season (Spring) | | | |
| Winter | -0.356 | 0.416 | -1.173 to 0.486 |
| Weight | 0.055 | 0.185 | -0.309 to 0.423 |
| Body length | 0.014 | 0.186 | -0.356 to 0.369 |
| <hr/> | | | |
| Intercept ^{††} | -0.110 | 0.132 | -0.380 to 0.143 |
| Age \leq 29 months | -0.124 | 0.238 | -0.560 to 0.358 |
| Age at last capture | -0.095 | 0.112 | -0.323 to 0.132 |
| Season (β_w) | -0.408 | 0.217 | -0.807 to 0.034 |
| Season (β_B) | -0.173 | 0.142 | -0.454 to 0.113 |
| Weight | -0.004 | 0.176 | -0.334 to 0.344 |
| Body length | 0.042 | 0.188 | -0.329 to 0.410 |

Random effect estimates (variance):

[†]qPCR plate ($6.170 \cdot 10^{-2}$), Row on qPCR plate ($<1.000 \cdot 10^{-12}$), Social group ($1.599 \cdot 10^{-2}$), Cohort ($7.467 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.587 \cdot 10^{-1}$)

^{††}qPCR plate ($5.188 \cdot 10^{-2}$), Row on qPCR plate ($<1.000 \cdot 10^{-12}$), Social group ($<1.000 \cdot 10^{-12}$), Cohort ($4.522 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.555 \cdot 10^{-1}$)

Table S6: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the direction of the effect on relative leukocyte telomere length (Z-score) to test whether slopes differ between within- and between-individual slopes from spring to winter and winter to spring in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|--------------------------------------|---------------|--------------|-------------------------|
| Intercept [†] | 0.022 | 0.128 | -0.225 to 0.279 |
| Age \leq 29 months | 0.289 | 0.149 | -0.007 to 0.589 |
| Age at last capture | 0.102 | 0.068 | -0.030 to 0.239 |
| Season (β_w) | -1.676 | 0.563 | -2.750 to -0.545 |
| Season ($\beta_B - \beta_w$) | 0.110 | 0.123 | -0.129 to 0.349 |
| Weight | 0.158 | 0.177 | -0.209 to 0.501 |
| Body length | -0.153 | 0.128 | -0.401 to 0.100 |
| Intercept ^{††} | 0.420 | 0.302 | -0.213 to 0.963 |
| Age \leq 29 months | -0.143 | 0.228 | -0.561 to 0.336 |
| Age at last capture | -0.095 | 0.113 | -0.322 to 0.132 |
| Season (β_w) | -2.229 | 1.121 | -4.288 to 0.105 |
| Season ($\beta_B - \beta_w$) | 0.679 | 0.406 | -0.153 to 1.436 |
| Weight | -0.006 | 0.175 | -0.337 to 0.337 |
| Body length | 0.043 | 0.187 | -0.319 to 0.410 |

Random effect estimates (variance):

[†]qPCR plate ($<1.000 \cdot 10^{-12}$), Row on qPCR plate ($3.965 \cdot 10^{-3}$), Social group ($3.830 \cdot 10^{-2}$), Cohort ($5.964 \cdot 10^{-3}$), Year ($7.920 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.566 \cdot 10^{-1}$)

^{††}qPCR plate ($5.188 \cdot 10^{-2}$), Row on qPCR plate ($<1.000 \cdot 10^{-12}$), Social group ($<1.000 \cdot 10^{-12}$), Cohort ($4.522 \cdot 10^{-2}$), Individual ID ($<1.000 \cdot 10^{-12}$), Residual ($7.554 \cdot 10^{-1}$)

Table S7: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the number of adults in the natal group, season and weather effects in spring on early-life (3–12 months old) relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------------|--------------|-------------------------|
| Intercept [†] | -0.037 | 0.117 | -0.254 to 0.194 |
| Number of adults in natal group | -0.028 | 0.053 | -0.130 to 0.080 |
| Season (Spring) | | | |
| Summer | 0.238 | 0.136 | -0.030 to 0.507 |
| Autumn | 0.197 | 0.278 | -0.341 to 0.729 |
| Winter | -1.003 | 0.386 | -1.742 to -0.231 |
| Mean temperature | -3.373 | 3.820 | -10.81 to 4.218 |
| Mean temperature ² | 3.827 | 3.883 | -3.869 to 11.40 |
| Daily temperature variability | 0.044 | 1.714 | -3.413 to 3.382 |
| Daily temperature variability ² | 0.093 | 1.739 | -3.317 to 3.580 |
| Mean daily rainfall | -1.711 | 0.818 | -3.309 to -0.060 |
| Mean daily rainfall² | 1.878 | 0.843 | 0.154 to 3.513 |
| Daily rainfall variability | -3.671 | 2.048 | -7.680 to 0.273 |
| Daily rainfall variability ² | 3.528 | 2.070 | -0.463 to 7.585 |
| Weight | 0.064 | 0.102 | -0.134 to 0.267 |
| Body length | -0.099 | 0.097 | -0.284 to 0.091 |
| Without non-significant 2nd order effects | | | |
| Intercept ^{††} | -0.022 | 0.107 | -0.222 to 0.186 |
| Number of adults in natal group | -0.032 | 0.053 | -0.132 to 0.074 |
| Season (Spring) | | | |
| Summer | 0.220 | 0.135 | -0.046 to 0.485 |
| Autumn | 0.162 | 0.276 | -0.377 to 0.690 |
| Winter | -0.996 | 0.382 | -1.725 to -0.236 |
| Mean temperature | 0.400 | 0.087 | 0.223 to 0.574 |
| Daily temperature variability | 0.133 | 0.094 | -0.054 to 0.321 |
| Mean daily rainfall | -1.141 | 0.560 | -2.250 to -0.046 |
| Mean daily rainfall² | 1.272 | 0.555 | 0.170 to 2.392 |
| Daily rainfall variability | -3.038 | 1.424 | -5.804 to -0.317 |
| Daily rainfall variability² | 2.938 | 1.414 | 0.216 to 5.670 |
| Weight | 0.058 | 0.102 | -0.138 to 0.260 |
| Body length | -0.090 | 0.097 | -0.273 to 0.098 |

Random effect estimates (variance):

[†]qPCR plate ($4.802 \cdot 10^{-2}$), Row on qPCR plate ($2.073 \cdot 10^{-3}$), Social group ($1.727 \cdot 10^{-2}$), Cohort ($8.195 \cdot 10^{-2}$), Residual ($7.687 \cdot 10^{-1}$)

^{††}qPCR plate ($4.721 \cdot 10^{-2}$), Row on qPCR plate ($2.853 \cdot 10^{-3}$), Social group ($1.562 \cdot 10^{-2}$), Cohort ($5.253 \cdot 10^{-2}$), Residual ($7.727 \cdot 10^{-1}$)

Table S8: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the total number of individuals in the natal group, season and weather effects in spring on early-life (3–12 months old) relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------------|--------------|-------------------------|
| Intercept [†] | -0.030 | 0.117 | -0.249 to 0.202 |
| Number of individuals in natal group | 0.016 | 0.054 | -0.086 to 0.122 |
| Season (Spring) | | | |
| Summer | 0.234 | 0.136 | -0.032 to 0.501 |
| Autumn | 0.176 | 0.279 | -0.366 to 0.707 |
| Winter | -1.024 | 0.385 | -1.762 to -0.253 |
| Mean temperature | -3.558 | 3.818 | -11.03 to 4.027 |
| Mean temperature ² | 4.018 | 3.882 | -3.672 to 11.59 |
| Daily temperature variability | 0.064 | 1.713 | -3.419 to 3.379 |
| Daily temperature variability ² | 0.072 | 1.738 | -3.301 to 3.554 |
| Mean daily rainfall | -1.719 | 0.816 | -3.296 to -0.084 |
| Mean daily rainfall² | 1.893 | 0.842 | 0.170 to 3.527 |
| Daily rainfall variability | -3.593 | 2.040 | -7.596 to 0.339 |
| Daily rainfall variability ² | 3.452 | 2.062 | -0.506 to 7.490 |
| Weight | 0.076 | 0.102 | -0.122 to 0.280 |
| Body length | -0.105 | 0.097 | -0.290 to 0.084 |
| Without non-significant 2nd order effects | | | |
| Intercept ^{††} | -0.015 | 0.108 | -0.218 to 0.193 |
| Number of individuals in natal group | 0.011 | 0.054 | -0.091 to 0.115 |
| Season (Spring) | | | |
| Summer | 0.216 | 0.135 | -0.051 to 0.482 |
| Autumn | 0.140 | 0.276 | -0.404 to 0.668 |
| Winter | -1.019 | 0.382 | -1.750 to -0.260 |
| Mean temperature | 0.403 | 0.088 | 0.225 to 0.578 |
| Daily temperature variability | 0.133 | 0.095 | -0.056 to 0.322 |
| Mean daily rainfall | -1.127 | 0.562 | -2.247 to -0.022 |
| Mean daily rainfall² | 1.264 | 0.558 | 0.170 to 2.374 |
| Daily rainfall variability | -2.929 | 1.434 | -5.687 to -0.186 |
| Daily rainfall variability² | 2.830 | 1.425 | 0.094 to 5.582 |
| Weight | 0.071 | 0.101 | -0.124 to 0.272 |
| Body length | -0.096 | 0.097 | -0.277 to 0.093 |

Random effect estimates (variance):

[†]qPCR plate ($4.782 \cdot 10^{-2}$), Row on qPCR plate ($1.108 \cdot 10^{-3}$), Social group ($2.372 \cdot 10^{-2}$), Cohort ($8.127 \cdot 10^{-2}$), Residual ($7.658 \cdot 10^{-1}$)

^{††}qPCR plate ($4.718 \cdot 10^{-2}$), Row on qPCR plate ($1.910 \cdot 10^{-3}$), Social group ($2.200 \cdot 10^{-2}$), Cohort ($5.394 \cdot 10^{-2}$), Residual ($7.695 \cdot 10^{-1}$)

Table S9: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the number of cubs and number of adults in the natal group, season and weather effects in spring on early-life (3–12 months old) relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------------|--------------|-------------------------|
| Intercept [†] | -0.014 | 0.118 | -0.235 to 0.215 |
| Number of cubs in natal group | 0.109 | 0.052 | 0.008 to 0.209 |
| Number of adults in natal group | -0.039 | 0.055 | -0.142 to 0.071 |
| Season (Spring) | | | |
| Summer | 0.195 | 0.137 | -0.073 to 0.463 |
| Autumn | 0.147 | 0.278 | -0.394 to 0.668 |
| Winter | -0.981 | 0.384 | -1.715 to -0.214 |
| Mean temperature | -3.942 | 3.782 | -11.36 to 3.503 |
| Mean temperature ² | 4.421 | 3.845 | -3.180 to 11.96 |
| Daily temperature variability | 0.617 | 1.715 | -2.789 to 3.909 |
| Daily temperature variability ² | -0.486 | 1.740 | -3.815 to 2.970 |
| Mean daily rainfall | -1.908 | 0.814 | -3.493 to -0.282 |
| Mean daily rainfall² | 2.082 | 0.839 | 0.371 to 3.708 |
| Daily rainfall variability | -4.007 | 2.033 | -7.941 to -0.074 |
| Daily rainfall variability ² | 3.887 | 2.055 | -0.107 to 7.875 |
| Weight | 0.064 | 0.101 | -0.133 to 0.267 |
| Body length | -0.082 | 0.097 | -0.267 to 0.106 |
| Without non-significant 2nd order effects | | | |
| Intercept ^{††} | 0.003 | 0.109 | -0.204 to 0.211 |
| Number of cubs in natal group | 0.104 | 0.051 | 0.005 to 0.204 |
| Number of adults in natal group | -0.042 | 0.054 | -0.144 to 0.067 |
| Season (Spring) | | | |
| Summer | 0.178 | 0.136 | -0.088 to 0.445 |
| Autumn | 0.116 | 0.275 | -0.429 to 0.642 |
| Winter | -0.972 | 0.381 | -1.698 to -0.212 |
| Mean temperature | 0.400 | 0.087 | 0.224 to 0.573 |
| Daily temperature variability | 0.136 | 0.094 | -0.051 to 0.322 |
| Mean daily rainfall | -1.248 | 0.559 | -2.358 to -0.144 |
| Mean daily rainfall² | 1.375 | 0.555 | 0.276 to 2.488 |
| Daily rainfall variability | -2.942 | 1.418 | -5.675 to -0.195 |
| Daily rainfall variability² | 2.843 | 1.409 | 0.110 to 5.576 |
| Weight | 0.060 | 0.101 | -0.136 to 0.261 |
| Body length | -0.076 | 0.097 | -0.257 to 0.110 |

Random effect estimates (variance):

[†]qPCR plate ($4.987 \cdot 10^{-2}$), Row on qPCR plate ($2.843 \cdot 10^{-3}$), Social group ($2.409 \cdot 10^{-2}$), Cohort ($7.829 \cdot 10^{-2}$), Residual ($7.561 \cdot 10^{-1}$)

^{††}qPCR plate ($4.929 \cdot 10^{-2}$), Row on qPCR plate ($3.963 \cdot 10^{-3}$), Social group ($2.182 \cdot 10^{-2}$), Cohort ($5.223 \cdot 10^{-2}$), Residual ($7.602 \cdot 10^{-1}$)

Table S10: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the number of cubs and total number of individuals in the natal group, season and weather effects in spring on early-life (3–12 months old) relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence intervals; reference terms in brackets = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------------|--------------|-------------------------|
| Intercept [†] | -0.013 | 0.118 | -0.234 to 0.215 |
| Number of cubs in natal group | 0.122 | 0.058 | 0.012 to 0.233 |
| Number of individuals in natal group | -0.040 | 0.060 | -0.156 to 0.080 |
| Season (Spring) | | | |
| Summer | 0.195 | 0.137 | -0.073 to 0.463 |
| Autumn | 0.146 | 0.278 | -0.395 to 0.669 |
| Winter | -0.982 | 0.384 | -1.714 to -0.215 |
| Mean temperature | -3.920 | 3.779 | -11.33 to 3.492 |
| Mean temperature ² | 4.399 | 3.843 | -3.172 to 11.95 |
| Daily temperature variability | 0.614 | 1.713 | -2.788 to 3.903 |
| Daily temperature variability ² | -0.482 | 1.738 | -3.821 to 2.981 |
| Mean daily rainfall | -1.899 | 0.812 | -3.482 to -0.273 |
| Mean daily rainfall² | 2.072 | 0.838 | 0.363 to 3.694 |
| Daily rainfall variability | -4.000 | 2.031 | -7.929 to -0.078 |
| Daily rainfall variability ² | 3.879 | 2.053 | -0.116 to 7.860 |
| Weight | 0.065 | 0.101 | -0.132 to 0.267 |
| Body length | -0.082 | 0.097 | -0.266 to 0.106 |
| Without non-significant 2nd order effects | | | |
| Intercept ^{††} | 0.003 | 0.109 | -0.203 to 0.211 |
| Number of cubs in natal group | 0.118 | 0.057 | 0.008 to 0.227 |
| Number of individuals in natal group | -0.045 | 0.060 | -0.158 to 0.075 |
| Season (Spring) | | | |
| Summer | 0.178 | 0.136 | -0.088 to 0.445 |
| Autumn | 0.116 | 0.275 | -0.428 to 0.640 |
| Winter | -0.972 | 0.381 | -1.699 to -0.215 |
| Mean temperature | 0.400 | 0.087 | 0.225 to 0.573 |
| Daily temperature variability | 0.136 | 0.094 | -0.051 to 0.321 |
| Mean daily rainfall | -1.242 | 0.558 | -2.346 to -0.142 |
| Mean daily rainfall² | 1.367 | 0.553 | 0.270 to 2.474 |
| Daily rainfall variability | -2.943 | 1.416 | -5.674 to -0.209 |
| Daily rainfall variability² | 2.843 | 1.407 | 0.122 to 5.570 |
| Weight | 0.060 | 0.101 | -0.136 to 0.261 |
| Body length | -0.075 | 0.097 | -0.256 to 0.110 |

Random effect estimates (variance):

[†]qPCR plate (4.980×10^{-2}), Row on qPCR plate (2.772×10^{-3}), Social group (2.460×10^{-2}), Cohort (7.799×10^{-2}), Residual (7.560×10^{-1})

^{††}qPCR plate ($4.921 \cdot 10^{-2}$), Row on qPCR plate ($3.905 \cdot 10^{-3}$), Social group ($2.226 \cdot 10^{-2}$), Cohort ($5.183 \cdot 10^{-2}$), Residual ($7.601 \cdot 10^{-1}$)

Table S11: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the association between relative leukocyte telomere length and survival to adulthood (>1 year old) in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence interval. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|--------------|--------------|-----------------------|
| Intercept | 1.504 | 0.332 | 0.872 to 2.191 |
| Relative leukocyte telomere length | 0.386 | 0.153 | 0.095 to 0.713 |
| Weight | 0.023 | 0.244 | -0.460 to 0.504 |
| Body length | 0.081 | 0.244 | -0.392 to 0.580 |

Random effect estimates (variance): qPCR plate ($<1.000 \cdot 10^{-12}$), Row on qPCR plate ($1.033 \cdot 10^{-1}$), Social group ($3.798 \cdot 10^{-1}$), Cohort ($7.319 \cdot 10^{-1}$)

Table S12: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of the association between relative leukocyte telomere length, winter weather conditions and survival to adulthood (>1 year old) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence interval. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------------|--------------|-------------------------|
| Intercept [†] | 1.781 | 0.301 | 1.239 to 2.399 |
| Relative leukocyte telomere length | 0.441 | 0.172 | 0.113 to 0.792 |
| Number of cubs in natal group | -0.053 | 0.167 | -0.386 to 0.292 |
| Mean temperature | 6.821 | 1.525 | 4.031 to 9.920 |
| Mean temperature² | -6.619 | 1.466 | -9.618 to -3.953 |
| Daily temperature variability | -3.699 | 2.270 | -8.346 to 0.680 |
| Daily temperature variability ² | 4.236 | 2.381 | -0.345 to 9.180 |
| Mean daily rainfall | -0.671 | 1.133 | -2.873 to 1.511 |
| Mean daily rainfall ² | 1.636 | 1.319 | -0.841 to 4.252 |
| Daily rainfall variability | 2.414 | 2.500 | -2.563 to 7.346 |
| Daily rainfall variability ² | -3.365 | 2.407 | -8.107 to 1.409 |
| Weight | -0.090 | 0.297 | -0.656 to 0.528 |
| Body length | 0.177 | 0.281 | -0.369 to 0.736 |
| Without non-significant 2nd order effects | | | |
| Intercept ^{††} | 1.752 | 0.287 | 1.240 to 2.342 |
| Relative leukocyte telomere length | 0.404 | 0.168 | 0.090 to 0.735 |
| Number of cubs in natal group | -0.036 | 0.164 | -0.362 to 0.291 |
| Mean temperature | 6.125 | 1.354 | 3.492 to 8.980 |
| Mean temperature² | -6.106 | 1.355 | -8.978 to -3.470 |
| Daily temperature variability | -3.877 | 2.126 | -8.253 to 0.211 |
| Daily temperature variability² | 4.388 | 2.223 | 0.162 to 8.991 |
| Mean daily rainfall | 0.307 | 0.166 | -0.003 to 0.647 |
| Daily rainfall variability | -1.048 | 0.207 | -1.495 to -0.664 |
| Weight | -0.046 | 0.293 | -0.614 to 0.512 |
| Body length | 0.142 | 0.276 | -0.384 to 0.712 |

Random effect estimates (variance):

[†]qPCR plate ($<1.000 \cdot 10^{-12}$), Row on qPCR plate ($8.172 \cdot 10^{-2}$), Social group ($3.824 \cdot 10^{-1}$), Cohort ($2.789 \cdot 10^{-1}$)

^{††}qPCR plate ($<1.000 \cdot 10^{-12}$), Row on qPCR plate ($1.012 \cdot 10^{-1}$), Social group ($3.952 \cdot 10^{-1}$), Cohort ($6.453 \cdot 10^{-1}$)

MOLECULAR ECOLOGY

Table S13: Comparison of models describing the relationship between early-life relative leukocyte telomere length (RLTL) and cub survival probability with qPCR plate, cohort, social group, and row on qPCR plate as random effects. Models were ordered and numbered by AICc, and the difference from the top model (lowest AICc) is stated in the column termed 'ΔAICc', with only models within ΔAICc <7 (omitting 1196 models). CV_R = Daily rainfall variability, μ_R = mean daily rainfall, μ_T = Mean temperature, σ_T = Daily temperature variability.

| Model | Intercept | μ _T | (μ _T) ² | σ _T | (σ _T) ² | μ _R | (μ _R) ² | CV _R | (CV _R) ² | N cubs in natal group | Body weight | Body length | RLTL | Degrees of freedom | AICc | ΔAICc |
|-------|-----------|----------------|--------------------------------|----------------|--------------------------------|----------------|--------------------------------|-----------------|---------------------------------|-----------------------|-------------|-------------|-------|--------------------|-------|-------|
| 1 | 1.653 | 5.771 | -5.749 | -3.485 | 3.972 | 0.279 | | -0.996 | | | | | 0.368 | 12 | 400.6 | 0.000 |
| 2 | 1.644 | 6.285 | -6.155 | -2.894 | 3.358 | 0.604 | | 0.872 | -1.762 | | | | 0.381 | 13 | 401.8 | 1.193 |
| 3 | 1.661 | 5.565 | -5.562 | -3.894 | 4.406 | -0.514 | 0.802 | -1.031 | | | | | 0.373 | 13 | 401.9 | 1.293 |
| 4 | 1.660 | 6.296 | -6.118 | -3.306 | 3.809 | -0.613 | 1.464 | 2.079 | -2.974 | | | | 0.398 | 14 | 401.9 | 1.333 |
| 5 | 1.662 | 5.812 | -5.792 | -3.503 | 3.978 | 0.285 | | -0.982 | | | 0.093 | | 0.374 | 13 | 402.2 | 1.565 |
| 6 | 1.639 | 5.200 | -5.250 | -3.797 | 4.306 | | | -2.101 | 1.046 | | | | 0.368 | 12 | 402.2 | 1.588 |
| 7 | 1.590 | 4.918 | -4.915 | -3.377 | 3.889 | | | -0.984 | | | | | 0.390 | 11 | 402.3 | 1.650 |
| 8 | 1.657 | 5.797 | -5.780 | -3.472 | 3.951 | 0.282 | | -0.986 | | | | 0.067 | 0.371 | 13 | 402.4 | 1.803 |
| 9 | 1.606 | 6.468 | -6.342 | 0.342 | | 0.803 | | 2.152 | -2.869 | | | | 0.336 | 12 | 402.5 | 1.861 |
| 10 | 1.648 | 5.795 | -5.779 | -3.435 | 3.918 | 0.283 | | -0.996 | | -0.036 | | | 0.373 | 13 | 402.6 | 1.940 |
| 11 | 1.602 | 5.541 | -5.617 | 0.337 | | 0.272 | | -0.850 | | | | | 0.296 | 11 | 402.9 | 2.285 |
| 12 | 1.654 | 6.361 | -6.225 | -2.887 | 3.338 | 0.630 | | 1.006 | -1.875 | | 0.104 | | 0.388 | 14 | 403.3 | 2.660 |
| 13 | 1.613 | 6.448 | -6.293 | 0.360 | | -0.109 | 1.099 | 3.090 | -3.798 | | | | 0.346 | 13 | 403.3 | 2.732 |
| 14 | 1.669 | 6.361 | -6.179 | -3.296 | 3.788 | -0.560 | 1.427 | 2.168 | -3.042 | | 0.094 | | 0.404 | 15 | 403.5 | 2.903 |
| 15 | 1.669 | 5.612 | -5.610 | -3.886 | 4.387 | -0.464 | 0.756 | -1.016 | | | 0.084 | | 0.377 | 14 | 403.6 | 2.942 |
| 16 | 1.649 | 6.332 | -6.202 | -2.868 | 3.324 | 0.617 | | 0.942 | -1.818 | | | 0.074 | 0.384 | 14 | 403.6 | 2.950 |
| 17 | 1.640 | 6.312 | -6.187 | -2.839 | 3.301 | 0.608 | | 0.877 | -1.767 | -0.036 | | | 0.385 | 14 | 403.7 | 3.133 |
| 18 | 1.664 | 5.595 | -5.595 | -3.862 | 4.367 | -0.472 | 0.761 | -1.021 | | | | 0.052 | 0.375 | 14 | 403.8 | 3.177 |
| 19 | 1.656 | 5.590 | -5.593 | -3.841 | 4.349 | -0.522 | 0.814 | -1.031 | | -0.042 | | | 0.378 | 14 | 403.8 | 3.212 |
| 20 | 1.663 | 6.330 | -6.153 | -3.277 | 3.773 | -0.571 | 1.425 | 2.100 | -2.983 | | | 0.053 | 0.400 | 15 | 403.8 | 3.215 |
| 21 | 1.654 | 6.333 | -6.160 | -3.235 | 3.734 | -0.621 | 1.483 | 2.105 | -2.999 | -0.047 | | | 0.404 | 15 | 403.8 | 3.233 |
| 22 | 1.647 | 5.223 | -5.276 | -3.810 | 4.310 | | | -2.100 | 1.057 | | 0.082 | | 0.373 | 13 | 403.9 | 3.246 |
| 23 | 1.616 | 6.531 | -6.401 | 0.330 | | 0.827 | | 2.269 | -2.966 | | 0.104 | | 0.344 | 13 | 403.9 | 3.314 |
| 24 | 1.596 | 4.934 | -4.933 | -3.390 | 3.894 | | | -0.972 | | | 0.077 | | 0.394 | 12 | 403.9 | 3.339 |
| 25 | 1.643 | 5.217 | -5.272 | -3.783 | 4.285 | | | -2.096 | 1.050 | | | 0.059 | 0.370 | 13 | 404.0 | 3.432 |
| 26 | 1.593 | 4.934 | -4.936 | -3.365 | 3.870 | | | -0.975 | | | | 0.056 | 0.392 | 12 | 404.1 | 3.502 |
| 27 | 1.658 | 5.836 | -5.822 | -3.451 | 3.924 | 0.288 | | -0.982 | | -0.036 | 0.093 | | 0.378 | 14 | 404.1 | 3.505 |
| 28 | 1.663 | 5.811 | -5.790 | -3.515 | 3.992 | 0.285 | | -0.984 | | | 0.127 | -0.044 | 0.374 | 14 | 404.1 | 3.537 |
| 29 | 1.636 | 5.215 | -5.270 | -3.763 | 4.270 | | | -2.116 | 1.061 | -0.029 | | | 0.372 | 13 | 404.2 | 3.550 |
| 30 | 1.612 | 6.509 | -6.385 | 0.334 | | 0.814 | | 2.207 | -2.911 | | | 0.080 | 0.340 | 13 | 404.2 | 3.567 |
| 31 | 1.568 | 4.844 | -4.952 | 0.368 | | | | -0.846 | | | | | 0.338 | 10 | 404.2 | 3.569 |
| 32 | 1.590 | 4.920 | -4.918 | -3.369 | 3.881 | | | -0.984 | | -0.006 | | | 0.391 | 12 | 404.3 | 3.649 |
| 33 | 1.600 | 6.516 | -6.398 | 0.339 | | 0.809 | | 2.141 | -2.861 | -0.063 | | | 0.345 | 13 | 404.3 | 3.673 |
| 34 | 1.653 | 5.818 | -5.806 | -3.426 | 3.903 | 0.285 | | -0.986 | | -0.033 | | 0.065 | 0.375 | 14 | 404.4 | 3.755 |
| 35 | 1.611 | 5.571 | -5.650 | 0.328 | | 0.278 | | -0.837 | | | 0.089 | | 0.301 | 12 | 404.5 | 3.877 |
| 36 | 1.607 | 5.563 | -5.644 | 0.331 | | 0.275 | | -0.839 | | | | 0.073 | 0.299 | 12 | 404.7 | 4.044 |
| 37 | 1.596 | 5.594 | -5.677 | 0.335 | | 0.280 | | -0.853 | | -0.068 | | | 0.306 | 12 | 404.7 | 4.066 |

MOLECULAR ECOLOGY

| | | | | | | | | | | | | | | | |
|----|-------|-------|--------|--------|-------|--------|-------|--------|--------|--------|-------|--------|----|-------|-------|
| 38 | 1.602 | 5.463 | -5.548 | 0.340 | | 0.040 | 0.233 | -0.855 | | | | 0.296 | 12 | 404.8 | 4.220 |
| 39 | 1.621 | 6.503 | -6.345 | 0.350 | | -0.054 | 1.056 | 3.161 | -3.850 | | 0.096 | 0.352 | 14 | 404.9 | 4.274 |
| 40 | 1.604 | 5.670 | -5.670 | -2.426 | 2.846 | 0.308 | | -0.932 | | | | | 11 | 404.9 | 4.280 |
| 41 | 1.607 | 6.509 | -6.361 | 0.357 | | -0.138 | 1.144 | 3.121 | -3.831 | -0.076 | | 0.357 | 14 | 405.1 | 4.460 |
| 42 | 1.579 | 4.920 | -5.062 | 0.351 | | | | -1.667 | 0.784 | | | 0.302 | 11 | 405.1 | 4.535 |
| 43 | 1.617 | 6.483 | -6.330 | 0.353 | | -0.062 | 1.053 | 3.099 | -3.796 | | | 0.348 | 14 | 405.2 | 4.544 |
| 44 | 1.650 | 6.387 | -6.256 | -2.830 | 3.279 | 0.635 | | 1.011 | -1.879 | -0.036 | 0.104 | 0.393 | 15 | 405.2 | 4.601 |
| 45 | 1.655 | 6.360 | -6.222 | -2.898 | 3.351 | 0.631 | | 1.009 | -1.879 | | 0.142 | -0.049 | 15 | 405.2 | 4.626 |
| 46 | 1.575 | 5.517 | -5.588 | 0.318 | | 0.302 | | -0.834 | | | | | 10 | 405.3 | 4.690 |
| 47 | 1.669 | 6.354 | -6.168 | -3.328 | 3.824 | -0.588 | 1.460 | 2.193 | -3.071 | | 0.159 | -0.085 | 16 | 405.4 | 4.800 |
| 48 | 1.663 | 6.395 | -6.219 | -3.225 | 3.713 | -0.567 | 1.443 | 2.190 | -3.063 | -0.045 | 0.093 | 0.409 | 16 | 405.4 | 4.810 |
| 49 | 1.664 | 5.636 | -5.640 | -3.832 | 4.330 | -0.471 | 0.767 | -1.017 | | -0.041 | 0.084 | 0.382 | 15 | 405.5 | 4.865 |
| 50 | 1.670 | 5.604 | -5.600 | -3.917 | 4.420 | -0.485 | 0.778 | -1.020 | | | 0.133 | -0.064 | 15 | 405.5 | 4.883 |
| 51 | 1.645 | 6.353 | -6.229 | -2.820 | 3.273 | 0.620 | | 0.944 | -1.820 | -0.032 | | 0.072 | 15 | 405.5 | 4.904 |
| 52 | 1.659 | 5.616 | -5.622 | -3.813 | 4.315 | -0.481 | 0.774 | -1.022 | | -0.039 | | 0.049 | 15 | 405.7 | 5.109 |
| 53 | 1.610 | 6.579 | -6.456 | 0.328 | | 0.832 | | 2.257 | -2.957 | -0.064 | 0.105 | 0.354 | 14 | 405.7 | 5.121 |
| 54 | 1.658 | 6.360 | -6.190 | -3.213 | 3.706 | -0.581 | 1.443 | 2.120 | -3.004 | -0.043 | | 0.049 | 16 | 405.7 | 5.130 |
| 55 | 1.643 | 5.237 | -5.295 | -3.775 | 4.273 | | | -2.115 | 1.071 | -0.029 | 0.082 | 0.376 | 14 | 405.8 | 5.209 |
| 56 | 1.647 | 5.221 | -5.272 | -3.822 | 4.323 | | | -2.104 | 1.059 | | 0.110 | -0.036 | 14 | 405.8 | 5.226 |
| 57 | 1.575 | 6.201 | -6.123 | 0.320 | | 0.695 | | 1.381 | -2.115 | | | | 11 | 405.9 | 5.284 |
| 58 | 1.572 | 4.844 | -4.952 | 0.361 | | | | -0.834 | | | 0.072 | 0.340 | 11 | 405.9 | 5.298 |
| 59 | 1.616 | 6.531 | -6.399 | 0.331 | | 0.828 | | 2.275 | -2.972 | | 0.130 | -0.033 | 14 | 405.9 | 5.298 |
| 60 | 1.596 | 4.931 | -4.928 | -3.399 | 3.903 | | | -0.973 | | | 0.099 | -0.029 | 13 | 405.9 | 5.326 |
| 61 | 1.595 | 4.936 | -4.936 | -3.382 | 3.885 | | | -0.972 | | -0.006 | 0.077 | 0.395 | 13 | 405.9 | 5.337 |
| 62 | 1.570 | 4.850 | -4.961 | 0.363 | | | | -0.837 | | | | 0.060 | 11 | 406.0 | 5.396 |
| 63 | 1.640 | 5.230 | -5.289 | -3.752 | 4.253 | | | -2.110 | 1.063 | -0.026 | | 0.057 | 14 | 406.0 | 5.402 |
| 64 | 1.606 | 6.551 | -6.434 | 0.332 | | 0.819 | | 2.191 | -2.899 | -0.059 | | 0.077 | 14 | 406.0 | 5.404 |
| 65 | 1.658 | 5.837 | -5.820 | -3.461 | 3.935 | 0.289 | | -0.985 | | -0.039 | 0.133 | -0.051 | 15 | 406.1 | 5.468 |
| 66 | 1.593 | 4.935 | -4.937 | -3.361 | 3.866 | | | -0.975 | | -0.003 | | 0.056 | 13 | 406.1 | 5.502 |
| 67 | 1.563 | 4.858 | -4.969 | 0.367 | | | | -0.847 | | -0.035 | | 0.343 | 11 | 406.1 | 5.510 |
| 68 | 1.604 | 5.625 | -5.711 | 0.325 | | 0.285 | | -0.840 | | -0.069 | 0.089 | 0.312 | 13 | 406.3 | 5.651 |
| 69 | 1.613 | 5.482 | -5.497 | -2.810 | 3.255 | -0.409 | 0.725 | -0.964 | | | | | 12 | 406.3 | 5.699 |
| 70 | 1.597 | 6.049 | -5.970 | -1.978 | 2.383 | 0.546 | | 0.431 | -1.285 | | | | 12 | 406.4 | 5.827 |
| 71 | 1.610 | 5.507 | -5.593 | 0.330 | | 0.092 | 0.187 | -0.841 | | | 0.086 | 0.301 | 13 | 406.4 | 5.836 |
| 72 | 1.601 | 5.613 | -5.700 | 0.328 | | 0.282 | | -0.843 | | -0.065 | | 0.069 | 13 | 406.5 | 5.844 |
| 73 | 1.611 | 5.570 | -5.649 | 0.328 | | 0.278 | | -0.838 | | | 0.102 | -0.017 | 13 | 406.5 | 5.873 |
| 74 | 1.593 | 5.060 | -5.142 | -2.815 | 3.260 | | | -2.239 | 1.238 | | | | 11 | 406.5 | 5.874 |
| 75 | 1.595 | 5.507 | -5.601 | 0.338 | | 0.013 | 0.268 | -0.859 | | -0.071 | | 0.306 | 13 | 406.6 | 5.980 |
| 76 | 1.606 | 5.500 | -5.588 | 0.333 | | 0.090 | 0.186 | -0.844 | | | | 0.069 | 13 | 406.6 | 6.003 |
| 77 | 1.612 | 5.701 | -5.703 | -2.429 | 2.842 | 0.312 | | -0.921 | | | 0.074 | | 12 | 406.6 | 6.003 |
| 78 | 1.615 | 6.564 | -6.413 | 0.347 | | -0.081 | 1.098 | 3.187 | -3.879 | -0.075 | 0.095 | 0.363 | 15 | 406.6 | 6.008 |
| 79 | 1.597 | 6.636 | -6.500 | | | 0.838 | | 2.230 | -2.830 | | | 0.309 | 11 | 406.7 | 6.101 |
| 80 | 1.609 | 5.695 | -5.698 | -2.407 | 2.821 | 0.310 | | -0.924 | | | | 0.054 | 12 | 406.8 | 6.152 |
| 81 | 1.619 | 5.734 | -5.823 | | | 0.295 | | -0.732 | | | | 0.299 | 10 | 406.8 | 6.163 |
| 82 | 1.584 | 4.926 | -5.070 | 0.343 | | | | -1.670 | 0.799 | | 0.077 | 0.304 | 12 | 406.8 | 6.221 |
| 83 | 1.622 | 6.501 | -6.340 | 0.351 | | -0.068 | 1.075 | 3.184 | -3.874 | | 0.140 | -0.056 | 15 | 406.8 | 6.229 |
| 84 | 1.606 | 5.664 | -5.662 | -2.444 | 2.866 | 0.307 | | -0.932 | | 0.011 | | | 12 | 406.9 | 6.275 |
| 85 | 1.610 | 6.537 | -6.390 | 0.351 | | -0.093 | 1.098 | 3.123 | -3.823 | -0.072 | | 0.059 | 15 | 406.9 | 6.304 |

MOLECULAR ECOLOGY

| | | | | | | | | | | | | | | | | |
|-----|-------|-------|--------|--------|-------|--------|-------|--------|--------|--------|-------|--------|-------|----|-------|-------|
| 86 | 1.581 | 4.929 | -5.075 | 0.345 | | | | -1.666 | 0.794 | | | 0.065 | 0.303 | 12 | 406.9 | 6.333 |
| 87 | 1.572 | 4.944 | -5.092 | 0.348 | | | | -1.710 | 0.823 | -0.056 | | | 0.307 | 12 | 407.0 | 6.384 |
| 88 | 1.583 | 6.189 | -6.083 | 0.338 | | -0.104 | 0.964 | 2.215 | -2.940 | | | | | 12 | 407.0 | 6.410 |
| 89 | 1.583 | 5.545 | -5.617 | 0.311 | | 0.306 | | -0.823 | | | 0.074 | | | 11 | 407.0 | 6.411 |
| 90 | 1.613 | 6.049 | -5.930 | -2.330 | 2.770 | -0.490 | 1.239 | 1.433 | -2.291 | | | | | 13 | 407.1 | 6.474 |
| 91 | 1.580 | 5.543 | -5.617 | 0.313 | | 0.305 | | -0.825 | | | | 0.062 | | 11 | 407.1 | 6.519 |
| 92 | 1.650 | 6.389 | -6.256 | -2.838 | 3.287 | 0.637 | | 1.016 | -1.886 | -0.039 | 0.148 | -0.056 | 0.394 | 16 | 407.2 | 6.556 |
| 93 | 1.576 | 5.431 | -5.511 | 0.322 | | 0.039 | 0.264 | -0.840 | | | | | | 11 | 407.2 | 6.606 |
| 94 | 1.600 | 5.109 | -5.247 | | | | | -0.719 | | | | | 0.348 | 9 | 407.2 | 6.621 |
| 95 | 1.573 | 5.532 | -5.604 | 0.317 | | 0.305 | | -0.835 | | -0.021 | | | | 11 | 407.3 | 6.669 |
| 96 | 1.663 | 6.393 | -6.213 | -3.252 | 3.743 | -0.598 | 1.483 | 2.224 | -3.101 | -0.052 | 0.166 | -0.095 | 0.411 | 17 | 407.3 | 6.681 |
| 97 | 1.664 | 5.630 | -5.632 | -3.861 | 4.361 | -0.495 | 0.793 | -1.021 | | -0.045 | 0.138 | -0.072 | 0.383 | 16 | 407.4 | 6.791 |
| 98 | 1.532 | 4.734 | -4.755 | -2.297 | 2.747 | | | -0.916 | | | | | | 10 | 407.5 | 6.845 |
| 99 | 1.583 | 6.244 | -6.164 | 0.313 | | 0.707 | | 1.442 | -2.162 | | 0.081 | | | 12 | 407.6 | 6.950 |
| 100 | 1.551 | 4.846 | -4.997 | 0.330 | | | | -1.898 | 1.022 | | | | | 10 | 407.6 | 6.970 |

Table S14: Parameter estimates and 95% confidence intervals of fixed effects from a model averaging approach (natural average) between relative leukocyte telomere length, social and weather variables and survival to adulthood (>1 year old) in European badgers. β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence interval. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|--|---------------|--------------|-------------------------|
| Intercept | 1.631 | 0.252 | 1.134 to 2.124 |
| Relative leukocyte telomere length | 0.366 | 0.153 | 0.064 to 0.666 |
| Number of cubs in natal group | -0.041 | 0.147 | -0.329 to 0.249 |
| Mean temperature | 5.791 | 1.401 | 3.024 to 8.540 |
| Mean temperature² | -5.754 | 1.361 | -8.428 to -3.069 |
| Daily temperature variability | -2.325 | 2.375 | -6.913 to 2.409 |
| Daily temperature variability ² | 3.874 | 2.061 | -0.208 to 7.906 |
| Mean daily rainfall | 0.140 | 0.772 | -1.369 to 1.663 |
| Mean daily rainfall ² | 1.039 | 1.080 | -1.115 to 3.138 |
| Daily rainfall variability | -0.052 | 2.009 | -3.988 to 3.874 |
| Daily rainfall variability ² | -1.840 | 2.436 | -6.590 to 2.972 |

Table S15: Parameter estimates and 95% confidence intervals of fixed effects from a mixed model and parametric bootstrap tests of same-sex group size effects on early-adulthood relative leukocyte telomere length (Z-score) in European badgers (full model and with $p > 0.10$ 2nd order effects removed). β = parameter estimate, S.E. = standard error, 95% CI = 95% confidence interval; reference terms in brackets = reference level for factors; * = interaction. Significant parameter estimates (95% CI does not overlap zero) are in bold.

| Parameter (reference level) | β | S.E. | 95% CI |
|---|---------|-------|-----------------|
| Intercept [†] | -0.127 | 0.283 | -0.670 to 0.436 |
| Number of same-sex adults in group | -0.054 | 0.302 | -0.632 to 0.528 |
| Sex (Female) | 0.109 | 0.292 | -0.465 to 0.676 |
| Season (Spring) | | | |
| Summer | -0.128 | 0.113 | -0.353 to 0.096 |
| Autumn | 0.150 | 0.205 | -0.261 to 0.563 |
| Winter | -0.164 | 0.335 | -0.821 to 0.508 |
| Age at last capture | 0.003 | 0.053 | -0.105 to 0.109 |
| Weight | 0.012 | 0.080 | -0.144 to 0.164 |
| Body length | -0.031 | 0.083 | -0.195 to 0.129 |
| Number of same-sex adults in group * Sex (Female) | 0.072 | 0.311 | -0.540 to 0.675 |
| Without non-significant 2nd order effects | | | |
| Intercept ^{††} | -0.072 | 0.152 | -0.362 to 0.231 |
| Number of same-sex adults in group | 0.013 | 0.093 | -0.169 to 0.201 |
| Sex (Female) | 0.057 | 0.189 | -0.328 to 0.430 |
| Season (Spring) | | | |
| Summer | -0.128 | 0.113 | -0.355 to 0.090 |
| Autumn | 0.149 | 0.205 | -0.260 to 0.549 |
| Winter | -0.164 | 0.334 | -0.814 to 0.458 |
| Age at last capture | 0.002 | 0.053 | -0.102 to 0.106 |
| Weight | 0.014 | 0.079 | -0.139 to 0.169 |
| Body length | -0.029 | 0.083 | -0.189 to 0.133 |

Random effect estimates (variance):

[†]qPCR plate (3.839×10^{-2}), Row on qPCR plate ($<1.000 \times 10^{-12}$), Social group ($<1.000 \times 10^{-12}$), Cohort (5.750×10^{-2}), Year (4.093×10^{-2}), Individual ID (7.779×10^{-8}), Residual (8.358×10^{-1})

^{††}qPCR plate (3.870×10^{-2}), Row on qPCR plate ($<1.000 \times 10^{-12}$), Social group ($<1.000 \times 10^{-12}$), Cohort (5.923×10^{-2}), Year (4.064×10^{-2}), Individual ID (1.280×10^{-7}), Residual (8.329×10^{-1})

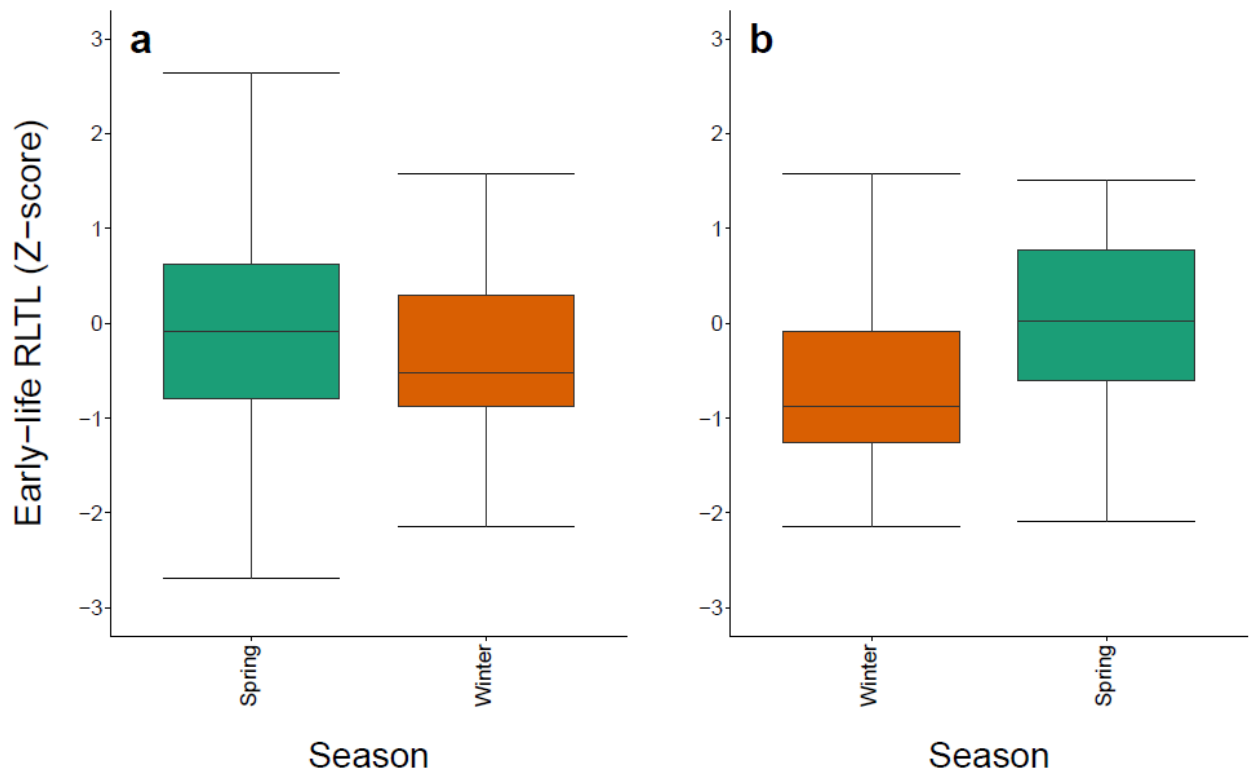


Figure S1: The effect of longitudinal measures from spring to winter (a) and winter to spring (b) on relative leukocyte telomere length (RLTL). Raw data for spring to winter (a; $n = 214$ samples; 203 badgers) and winter to spring (b; $n = 84$ samples; 78 badgers) are shown.

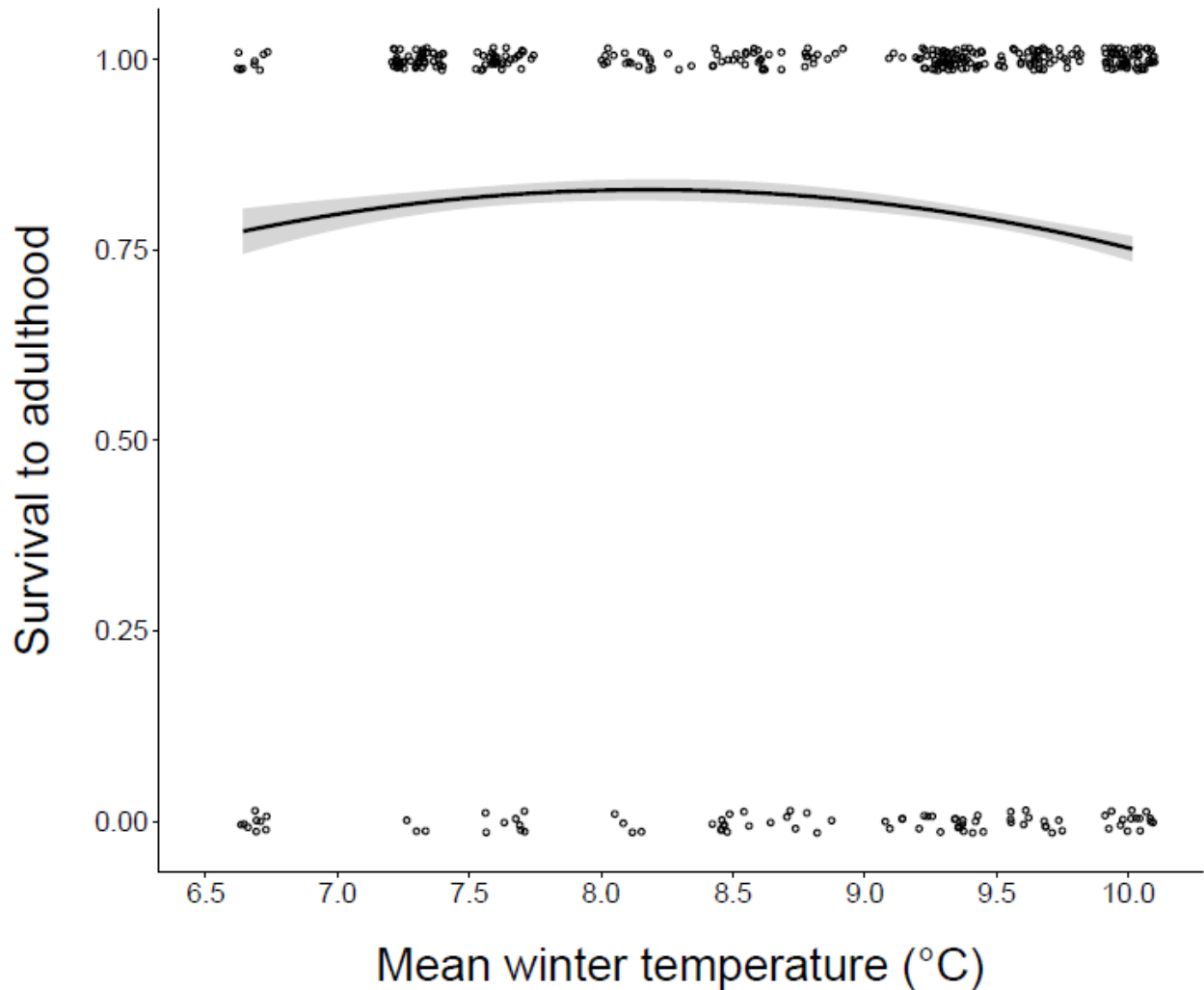


Figure S2: The association between mean winter temperature and survival to adulthood. Raw data points ($n = 406$ samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model, and the 95% confidence intervals as shaded areas.

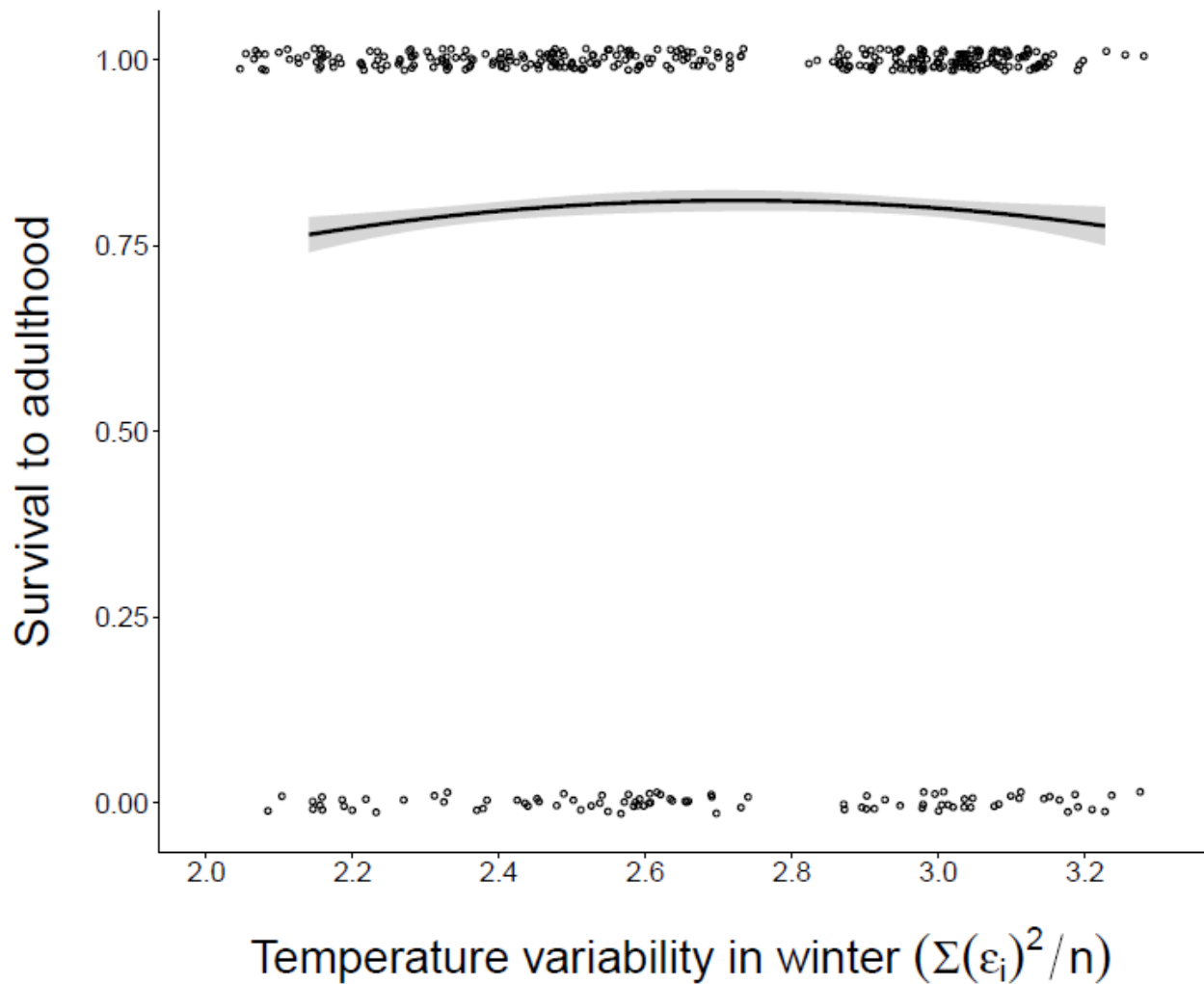


Figure S3: The association between the temperature variability in winter and survival to adulthood. Raw data points ($n = 406$ samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the regression from the mixed model, and the 95% confidence intervals as shaded areas.

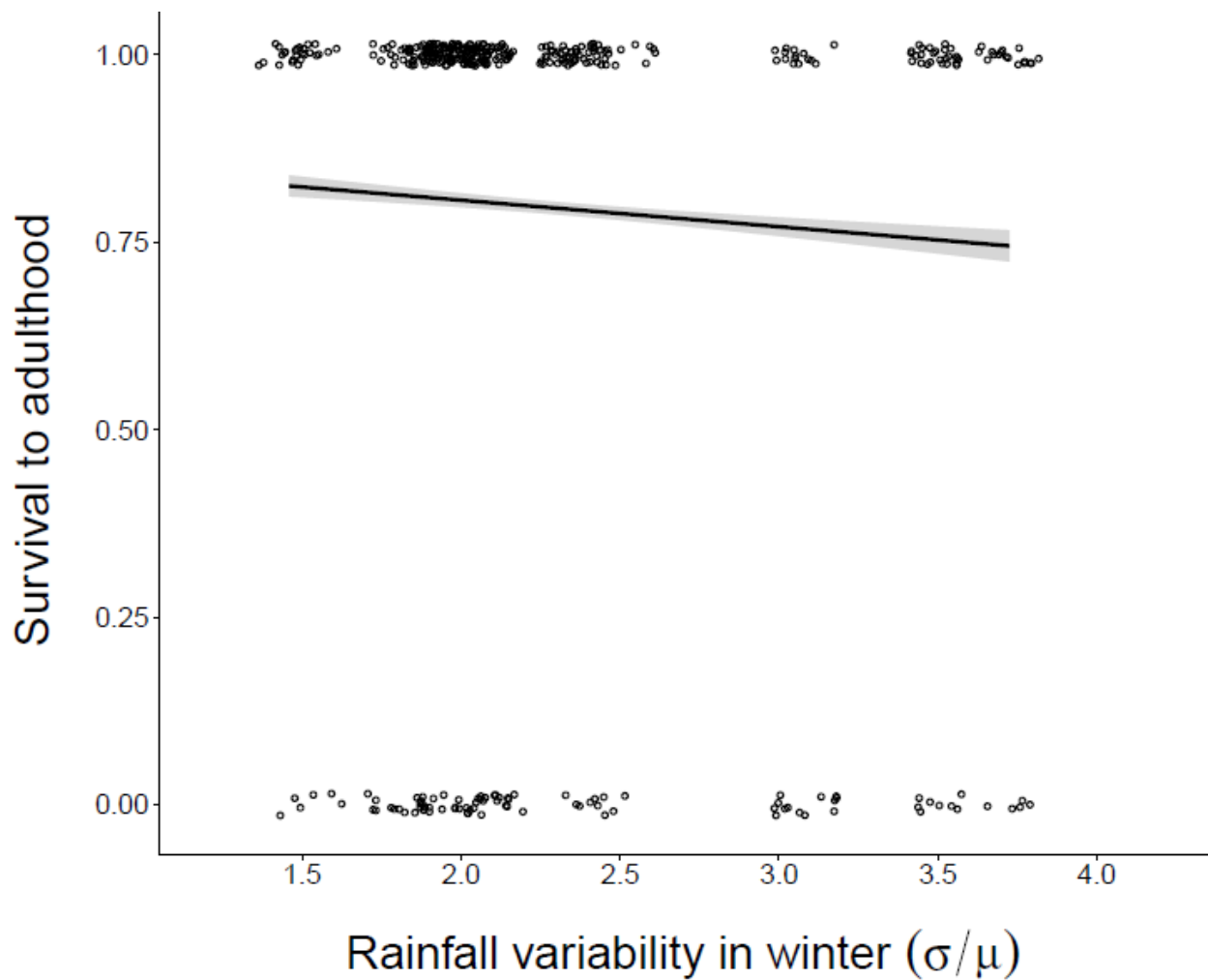


Figure S4: The association between the rainfall variability in winter and survival to adulthood. Raw data points ($n = 406$ samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the regression from the mixed model, and the 95% confidence intervals as shaded areas.