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

Sil H. J. van Lieshout[1,2] | Elisa P. Badás[1,3] | Julius G. Bright Ross[4] |
Amanda Bretman[1] | Chris Newman[4] | Christina D. Buesching[4,5] | Terry Burke[2] |
David W. Macdonald[4] | Hannah L. Dugdale[1,3]

[1]School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK

[2]NERC Environmental Omics Visitor Facility, Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

[3]Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands

[4]Wildlife Conservation Research Unit, Department of Zoology, The Recanati-Kaplan Centre, University of Oxford, Abingdon, UK

[5]Department of Biology, The University of British Columbia, Okanagan, Kelowna, British Columbia, Canada

Correspondence
Sil H. J. van Lieshout, School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, UK
Email: sil.vanlieshout@gmail.com

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Abstract

Early-life environmental conditions can provide a source of individual variation in life-history strategies and senescence patterns. Conditions experienced in early life can be quantified by measuring telomere length, which can act as a biomarker of survival probability in some species. Here, we investigate whether seasonal changes, weather conditions and group size are associated with early-life and/or early-adulthood telomere length in a wild population of European badgers (*Meles meles*). We found substantial intra-annual changes in telomere length during the first 3 years of life, where within-individual effects showed shorter telomere lengths in the winter following the first spring and a trend for longer telomere lengths in the second spring compared to the first winter. In terms of weather conditions, cubs born in warmer, wetter springs with low rainfall variability had longer early-life (3–12 months old) telomeres. Additionally, cubs born in groups with more cubs had marginally longer early-life telomeres, providing no evidence of resource constraint from cub competition. We also found that the positive association between early-life telomere length and cub survival probability remained when social and weather variables were included. Finally, after sexual maturity, in early adulthood (i.e., 12–36 months) we found no significant association between same-sex adult group size and telomere length (i.e., no effect of intrasexual competition). Overall, we show that controlling for seasonal effects, which are linked to food availability, is important in telomere length analyses, and that variation in telomere length in badgers reflects early-life conditions and also predicts first year cub survival.

KEYWORDS
early-life environment, group size, season, senescence, telomere length, weather conditions

1 | INTRODUCTION

The early-life environment can affect individual fitness (Lindström, 1999), with consequences for variation in life-history strategies (Metcalfe & Monaghan, 2001) and senescence patterns (Nussey et al., 2007). For example, it has been hypothesized that senescence, the decline in performance in older age, is faster in individuals that experienced adverse early-life environments, due to different energy allocation trade-offs between early and later life in response to the environment (Kirkwood & Rose, 1991; Medawar, 1952; Williams, 1957). A more stressful early-life environment, either through a suboptimal mean or more variable early-life environment, during this sensitive developmental period could trigger early reproductive investment at the expense of somatic maintenance, leading to faster rates of senescence (Kirkwood & Rose, 1991; Lemaitre et al., 2015). Empirical evidence for such detrimental effects has been found in various wild animal populations (Cooper & Kruuk, 2018; Hammers et al., 2013; Reed et al., 2008).

Telomere length has been suggested as a noncausal biomarker of senescence in some species (López-Otín et al., 2013; Monaghan & Haussmann, 2006), that facilitates quantification of physiological consequences of the conditions experienced (Monaghan, 2014). Telomeres are highly conserved nucleoprotein structures at the end of chromosomes consisting of a noncoding sequence (5′-TTAGGG-3′) and shelterin proteins (Blackburn, 2000; de Lange, 2005). Telomeres maintain genomic integrity by preventing chromosome degradation and fusion of chromosome ends by forming T-loops (de Lange, 2004). Generally, telomeres shorten with each cell replication due to the end-replication problem (Olovnikov, 1973), but telomere shortening can be accelerated potentially by oxidative damage (Boonekamp et al., 2017; Reichert & Stier, 2017; von Zglinicki, 2002) and through stressors (Epel et al., 2004; Heidinger et al., 2012). Telomeres can, however, elongate via the enzyme telomerase (Blackburn et al., 1989)—which shows a negative correlation with mammalian body mass (Tian et al., 2018)—and other telomere-elongation pathways (Cesare & Reddel, 2010; Mendez-Bermudez et al., 2012). Cells with critically short telomeres ultimately enter replicative senescence, where the accumulation of senescent cells can impair tissue function due to reduced renewal capacity (Campisi, 2005; Campisi & di Fagagna, 2007) and can potentially lead to organismal senescence (Young, 2018).

In some species, variation in early-life telomere length has been linked to season, specifically with winter effects when torpor and hibernation facilitate tolerance of winter food scarcity and reduction of thermoregulatory costs. During hibernation, more frequent arousal—which increases metabolic rate and potentially increases oxidative stress—is associated in arctic ground squirrels (*Urocitellus parryii*) with shorter telomere length (Wilbur et al., 2019) and in edible dormice (*Glis glis*) with increased telomere shortening (Turbill et al., 2013). Telomere shortening is reduced when the animals' core temperature difference between hibernation and arousal is smaller, in both edible and garden (*Eliomys quercinus*) dormice (Nowack et al., 2019). Conversely, the use of spontaneous daily torpor in

nonhibernating Djungarian hamsters (*Phodopus sungorus*) is associated with telomere lengthening due to a relatively low energy investment to return to euthermia along with the benefits of reduced metabolic rate in torpor compared to hibernation (Turbill et al., 2012). In contrast, nonhibernating juvenile garden dormice that more frequently underwent fasting-induced torpor showed higher telomere shortening than individuals undergoing torpor less frequently (Giroud et al., 2014). Species that undergo facultative winter torpor may conserve energy for somatic maintenance that could potentially be invested in telomere restoration/elongation. Additionally, there is evidence in nonhibernating rodents for seasonal effects of food availability on telomere dynamics (Criscuolo et al., 2020). However, because telomere length, season and body mass might be intercorrelated (Réale et al., 1999; Tian et al., 2018), body mass needs to be taken into account when studying seasonal effects.

In addition to these intra-annual changes in telomere length, extensive evidence links adverse early-life conditions to shorter telomeres (McLennan et al., 2016; Mizutani et al., 2013; Watson et al., 2015), where shorter telomeres are associated with reduced survival probability (Wilbourn et al., 2018). Food availability, often determined by weather conditions (Campbell et al., 2012), has been positively associated with early-life telomere length (Foley et al., 2020; Spurgin et al., 2017). Interestingly, early-life food availability may also impact life-history strategies (Bright Ross et al., 2020). It has been hypothesized that individuals in temporally stochastic environments should modulate their energy trade-offs (Erikstad et al., 1998; Reid et al., 2003; Weimerskirch et al., 2001) and adopt a bet-hedging strategy (Wilbur & Rudolf, 2006). Because weather variability is predicted to increase in the future (IPCC, 2018), it is important to understand the implications of variable early-life conditions for life-history strategies and early-life telomere length. The interplay between the mean of and variability in early-life environmental conditions, such as the availability and variation in food, foraging success and thermal stress for young individuals (Noonan et al., 2015; Nouvellet et al., 2013; Webb & King, 1984), can thus impact developmental stress and longevity, and may be reflected in early-life telomere length.

Social conditions in early life can also shape life-history strategies and senescence due to increased competition for food and social stress. For example, female red deer (*Cervus elaphus*) that experienced high levels of resource competition in early life showed faster rates of reproductive senescence (Nussey et al., 2007). Additionally, there is evidence for conspecific resource competition in early life leading to greater telomere shortening in birds (Boonekamp et al., 2014; Nettle et al., 2015; Stier et al., 2015), and shorter telomere lengths in wild meerkats (Cram et al., 2017). Such patterns can be explained because stressors (including competition) are associated with both shorter telomere lengths and greater telomere shortening (Chatelain et al., 2020).

The effects of social conditions on senescence may also become apparent after sexual maturity, when individuals compete for mating opportunities (Andersson, 1994; Beirne et al., 2015). In polygynous species, sex differences in senescence may be attributable to intense intrasexual competition between males (Clutton-Brock

& Isvaran, 2007; Promislow, 1992; Williams, 1957). Male invest-ment for mating opportunities may trade off with self-maintenance (Kirkwood & Rose, 1991). Intense male–male competition drives selection for shorter lifespan and faster senescence in males, com-pared to females (Clutton-Brock & Isvaran, 2007; Williams, 1957). While this prediction has been challenged (Bonduriansky et al., 2008; Graves, 2007; Promislow, 2003), and sex-specific senescence may be trait-dependent with respect to the underlying physiolog-ical processes (Nussey et al., 2009), higher rates of male-biased actuarial senescence in polygynous and sexual dimorphic species exist (Clutton-Brock & Isvaran, 2007; Promislow, 1992). While so-cial effects may also contribute to senescence in females (Sharp & Clutton-Brock, 2011; Woodroffe & Macdonald, 1995), such sex-specific social effects on senescence are expected to be greater in males (Bonduriansky et al., 2008; Clutton-Brock & Isvaran, 2007; Maklakov & Lummaa, 2013). However, whether increased intrasex-ual competition (e.g., higher local densities of same-sex individuals) is associated with shorter telomeres remains to be tested.

To test the effects of early-life social and environmental condi-tions on telomere length, we use a long-term data set from a wild population of European badgers (*Meles meles*; hereafter 'badgers'). Badgers show reproductive senescence with males having a later onset but faster rate of senescence than females (Dugdale et al., 2011). Additionally, early-life telomere length (3–12 months old) positively correlates with first-year survival and lifespan in bad-gers (van Lieshout et al., 2019). In the UK and Ireland, badgers are natally philopatric and can form large social groups (mean group size = 11.3, range = 2–29; da Silva et al., 1994) with latrine-marked borders (Buesching et al., 2016; Delahay et al., 2000), although they do transgress these borders when foraging (Ellwood et al., 2017; Noonan et al., 2015) without any sex difference in foraging niche (Robertson et al., 2014).

Regardless of whether badgers undergo facultative winter torpor (Johansson, 1957) or true hibernation (Ruf & Geiser, 2015), badgers do reduce their body temperature by up to 8.9℃ (Fowler & Racey, 1988), thus reducing energy expenditure (Newman et al., 2011). Badgers in Britain mainly feed on earthworms (*Lumbricus terrestris*; Johnson et al., 2001; Kruuk & Parish, 1981). Earthworms are sensi-tive to microclimatic conditions (Edwards & Bohlen, 1996; Gerard, 1967; Newman et al., 2017), making their abundance and distribution highly dependent on weather conditions. High-density badger popu-lations occur in mild areas with damp conditions where earthworms are available (Johnson et al., 2002; Kruuk, 1978; Macdonald et al., 2015; Newman et al., 2017). Foraging efficiency is reduced in ad-verse weather conditions, due to reduced availability of earthworms, thermal stress when foraging in cold and wet conditions, and/or the choice to remain in thermally stable underground dens, termed setts (Noonan et al., 2014, 2018; Nouvellet et al., 2013; Tsunoda et al., 2018). Weather conditions can therefore impact survival probability where, for example, higher annual mean daily rainfall is positively associated with adult survival probability in badgers, whereas high annual variability in temperature has detrimental consequences for cub and adult survival (Nouvellet et al., 2013).

Badgers have one litter per year, with a mean litter size of 1.5 ± 0.3 (95% confidence interval [CI]; range = 1–5; Annavi et al., 2014). Badger cub growth and maturation depends on the number of other cubs and adults present within the social group (Sugianto et al., 2019a), potentially indicating resource competition within social groups. Adult male badgers invest substantial energy into promis-cuity and repeated mounting (Dugdale et al., 2011) both within and outside their social group, resulting in high rates (i.e., 48%) of extra-group paternity, of which 85% is from neighbouring groups (Annavi et al., 2014; Dugdale et al., 2007). Males also exhibit substantial in-terindividual variance in reproductive success (Dugdale et al., 2007; Dugdale, Pope, et al., 2011) and evidence of reproductive skew among females within a group (Dugdale et al., 2008; Woodroffe & Macdonald, 1995). With the polygynandrous system (Dugdale, Griffiths, et al., 2011), a slight sexual dimorphism and slight male-biased mortality (Bright Ross et al., 2020; Johnson & Macdonald, 2001; Sugianto et al., 2019a, 2019b), and evidence of downstream effects of male–male competition on body mass senescence (Beirne et al., 2015), such intrasexual competition may be reflected in telo-mere length in early adulthood.

Here, we investigate the relationships between early-life con-ditions and relative leukocyte telomere length (RLTL), by testing whether: (i) between-individual and within-individual variation in RLTL in early life and early adulthood can be explained by seasonal changes; (ii) adverse early-life weather, as a proxy for food availabil-ity and thermal stress, is associated with shorter early-life RLTL and the social conditions that cubs are exposed to (with more cubs po-tentially leading to resource competition and associated with shorter early-life RLTL, or more cubs reflecting more resources and thus being associated with longer early-life RLTL); (iii) the strength of the association between early-life RLTL and first-year survival probabil-ity is dependent on early-life conditions; and (iv) adverse social con-ditions after sexual maturity (i.e., larger same-sex adult group size for females and, for males, more within-group and neighbouring-group adult [>1 year old] males) are associated with shorter RLTL in early post-maturity adulthood.

2 | METHODS

2.1 | Study population and trapping

We conducted this study in a high-density population of badgers (mean ± *SE* = 36.4 ± 2.55 badgers per km²; Macdonald et al., 2009) in Wytham Woods, Oxfordshire, UK (51°46′24″N, 1°20′04″W); this is a 424-ha mixed seminatural woodland surrounded by mixed arable and permanent pasture (Macdonald et al., 2015). The population consisted of 19 ± 2 (mean ± 95% CI; range = 14–26; Dugdale et al., 2008) mixed-sex social groups (Johnson, Jetz, et al., 2002; Newman et al., 2011) during the period that we analysed, with a 50% offspring sex ratio (Dugdale et al., 2003). The Wytham badger population is geographically discrete (Macdonald et al., 2009) with only ~3% an-nual immigration/emigration per year (Macdonald & Newman, 2002).

We used long-term data (1987–2016) from a badger population that was trapped over three 2-week periods in May–June, August–September and November, with further trapping in January in focal years (i.e., specific years when ultrasound studies were conducted to calculate implantation dates, see Figure 1). Badgers were anaesthetized using an intramuscular injection of 0.2 ml ketamine hydrochloride per kg body weight (McLaren et al., 2005). Upon first capture, badgers were assigned a unique inguinal tattoo for permanent identification. Sex, age class (cub < 1 year old; adult ≥ 1 year old), capture date and social group were recorded. Age of badgers was defined as the number of days elapsed since the 14th of February, reflecting the average date of synchronized parturition, in the respective birth year (Yamaguchi et al., 2006). Age of badgers first caught as adults was inferred from tooth wear, which is commonly used and highly correlated ($r^2 = .80$) with known age in this population (Bright Ross et al., 2020; Hancox, 1988; Macdonald et al., 2009; da Silva & Macdonald, 1989). Only badgers that did not have an already-known age and had a tooth wear of 2 (on a 1–5 scale) were included since these typically indicate a 1-year-old adult (Bright Ross et al., 2020). We used data on cohorts up to and including 2010, as all cohort members were dead by the end of 2016. Whole blood samples were collected from anaesthetized badgers through jugular venipuncture into vacutainers with an EDTA anticoagulant, and stored immediately at −20°C. Badgers were released after full recovery from anaesthesia. Additionally, bait-marking (Delahay et al., 2000; Macdonald & Newman, 2002) was conducted periodically to delimit group range sizes and deduce social groups.
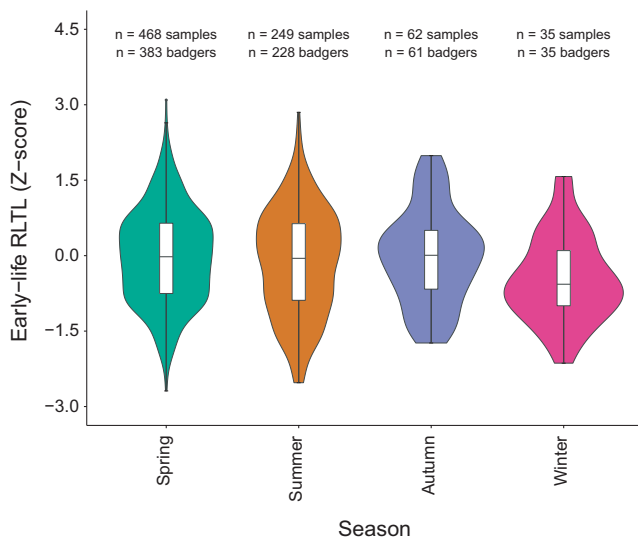

FIGURE 1 Variation in early-life relative leukocyte telomere length (RLTL) among seasons in European badgers. The data distributions and probability densities are shown (n = 814 samples; 533 badgers—the sum of badgers in the plot is >533 due to repeated measures). Data were collected in 19 years, across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

2.2 | Telomere analyses

Genomic DNA was extracted from whole blood samples (n = 814 samples; 533 badgers) using the DNeasy Blood & Tissue kit (Qiagen) according to the manufacturer's protocol, with changes by conducting a double elution step (2× 75 μl AE buffer) and using 125 μl of anticoagulated blood. DNA integrity was checked by running a random selection of DNA extracts (~20%) on agarose gels to ensure high molecular weight. The DNA concentration of all samples was quantified using the Fluostar Optima fluorometer (BMG Labtech) and standardized to 20 ng/μl, after which samples were stored at −20°C. We used monochrome multiplex quantitative polymerase chain reaction (MMqPCR) analysis to measure RLTL (Cawthon, 2009). This is a measure that reflects the abundance of telomeric sequence relative to a reference gene, which are both analysed in the same well, and although subject to error represents the mean telomere length across cells in a sample. We used a subset of 814 samples from the full data set of 1248 samples detailed in van Lieshout et al., (2019). In the full data set, Cq-values on the qPCR plates (n = 34) declined in a log-linear fashion ($r^2 > .99$). Reaction efficiencies were (mean ± SE) 1.793 ± 0.004 for IRBP and 1.909 ± 0.004 for telomeres. Interplate repeatability (intraclass correlation coefficient) calculated with RPTR 0.9.2 (Stoffel et al., 2017)—by comparing variance among duplicates of the reference sample within a plate, to variance of the reference sample among plates—was 0.82 for RLTL measurements (95% CI =0.76–0.87; n = 142 samples; 34 plates). Intraplate repeatability calculated with duplicates of the same sample on the same plate, while controlling for plate effects, was 0.90 (95% CI =0.86–0.93; n = 1248 samples; 34 plates) for IRBP, 0.84 (95% CI =0.79–0.90; n = 1248 samples; 34 plates) for telomere Cq-values and 0.87 (95% CI =0.82–0.91; n = 1248 samples; 34 plates) for RLTL measurements. A detailed description of the MMqPCR analysis can be found in van Lieshout et al. (2019).

2.3 | Weather conditions

Four weather metrics (mean daily temperature, temperature variability, mean daily rainfall and rainfall variability) were calculated for each season (Spring = end of March to end of June, Summer = end of June to end of September, Autumn = end of September to end of December, Winter = end of December to end of March) from 1987 to 2010 to characterize the developmental stress associated with variation in earthworm food availability and thermoregulatory costs (Macdonald et al., 2010; Noonan et al., 2014; Nouvellet et al., 2013). Wytham Woods had a mean annual temperature of 10.6°C (±5.5 SD) and mean annual precipitation of 684 mm (±129 SD), 1987–2010. Mean daily temperature and rainfall were calculated using mean daily temperature and total daily precipitation values provided by the Radcliffe Meteorological Station, School of Geography, University of Oxford (6 km from the field site). Daily temperatures followed a sinusoidal pattern, and so seasonal temperature variability was calculated as the sum of daily squared residuals from a sinusoidal fit to

the corresponding year's temperatures (i.e., cumulative unpredictability). Rainfall did not show annual trends and its seasonal variability was therefore characterized simply as the coefficient of variation (*SD*/mean) in daily rainfall.

2.4 | Group sizes

Natal group sizes were determined by the number of individuals (cubs and adults) that were present in a social group in the year of an individual's birth. Given high lifetime natal philopatry (35.8%), low permanent dispersal rates (19.1%) and high levels of short-term intergroup movements (Macdonald et al., 2008), individuals (*n* = 1726) were assigned as a resident of a social group each year, according to published criteria (van Lieshout, Badás, et al., 2020). The number of individuals in a natal social group was then calculated as the sum of individuals present in the social group in that year.

Yearly social group size measures were then separated by age class (i.e., cub/adult) and sex (i.e., male/female) to determine sex- and age-specific group sizes per year. To measure intrasexual competition in females, we calculated female adult group sizes, as females compete with other within-group females (Woodroffe & Macdonald, 1995). However, for males, extragroup paternity is high (48%) and affected by the number of within-group and neighbouring-group candidate fathers (Annavi et al., 2014), so we combined the number of both within-group males and neighbouring-group males. The mean number of cubs in a social group for badgers in our data set (*n* = 533 badgers) was 3.4 (±2.3 *SD*; range 0–14), the mean number of female adults in a social group was 6.1 (±3.4 *SD*; range 0–19) and the mean number of male adults in focal plus neighbouring social groups was 25.2 (±11.5 *SD*; range 1–59).

2.5 | Statistical analyses

Statistical analyses were conducted in R 3.3.1 (R Development Core Team, 2020), using parametric bootstrapping (*n* = 5000) to estimate 95% confidence intervals and determine significance of predictors in LME4 1.1-14 (Bates et al., 2015). Model fit was assessed using standard residual plot techniques to ensure approximately normal distribution and constant variance, and fixed effects were ensured not to be collinear (variance inflation factor [VIF] < 3). RLTL as a response variable was first square-root and then Z-transformed (mean =0, *SD* =1) for comparability (Verhulst, 2020). Quadratic fixed effects were included if such relationships were plausible a priori, and removed if *p* > .1 to test the significance of first-order effects.

In this study, we focus on early life (3–12 months old), but badgers typically reach sexual maturity by 2 years of age (Sugianto et al., 2019a), occasionally at age 1 year (Dugdale et al., 2007). Due to delayed implantation resulting in a full year between conception and parturition, badgers thus first produce offspring when they are 2–3 years of age, and therefore we define early adulthood as 12–36 months old.

2.5.1 | Seasonal effects on RLTL in early life and early adulthood

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

As we found a significant cross-sectional difference in RLTL between spring and winter, we then applied the "within-subject centring" approach described by van de Pol and Wright (2009) to distinguish within- and between-individual effects between spring and winter. Following Schroeder et al., (2012), we included two new fixed effects: (i) to estimate the within-individual variation component (β_W) we removed between-individual variation by subtracting the mean season value (coded as: spring =0, winter =1) for each individual across all years, from the season value for each RLTL measurement. So, if an individual was measured once in spring and once in winter, it was scored as −0.5 for spring and 0.5 for winter; and (ii) to estimate the between-individual variation between seasons (β_B), we included the mean season value for each individual (van de Pol & Wright, 2009). We then ran a Gaussian distribution model (identity link function) with RLTL as the response variable (*n* = 503 samples; 402 badgers) and threshold age (van Lieshout etal., 2019), age at last capture, within-individual season effect (β_W), between-individual season effect (β_B), weight and body length as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year and individual ID as random effects. Subsequently, we tested whether the within-individual (β_W) and between-individual (β_B) slopes differed by including season and the between-individual effect (β_B; i.e., mean season value) in the same model (i.e., season now reflects the within-individual effect).

Lastly, to test whether telomere length decreases or increases from spring to winter we used a subset of individuals measured either in their first spring or first winter, plus 11 individuals measured in both their first spring and first winter (*n* = 214 samples; 203 badgers). For the direction of the effect from winter to spring we used a subset of individuals measured either in their first winter or second spring, plus six individuals measured in both their first winter and second spring (*n* = 84 samples; 78 badgers). In the two models (spring to winter and winter to spring) with a Gaussian distribution and RLTL as the response variable, we included age, age at last capture, season, weight and body length as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year (not in winter to spring model due to singularity) and individual ID as random effects. Subsequently, we used the within-subject centring approach again

to separate within- and between-individual effects and test whether these slopes differ (van de Pol & Wright, 2009).

2.5.2 | Weather and natal group size effects on early-life RLTL

We tested whether weather and social conditions experienced as a cub (3–12 months old) were associated with early-life RLTL. We first used a generalized linear mixed model (GLMM) to confirm the previous observation (van Lieshout et al., 2019) that early-life RLTL did not vary with age (in months), controlling for season, weight and body length (n = 406, β = 0.154, 95% CI = −0.158 to 0.464), and excluded age from subsequent analyses. The effects of first-year conditions on early-life RLTL were then modelled with early-life RLTL as the response variable in a Gaussian-distributed model (identity link function; n = 406, samples; 406 badgers). First, we determined the season in which the weather conditions (i.e., mean temperature, mean rainfall, temperature variability and rainfall variability) best explained the variation in early-life RLTL (corrected Akaike information criterion [AICc] spring =1,133.1 was lowest, vs. summer ΔAICc =11.3, autumn ΔAICc =10.3, winter ΔAICc =11.0), with models with ΔAICc <7 from the top model being plausible (Burnham et al., 2011). The weather window of spring (end of March to end of June) is the season in which cubs grow the most and thus encounter the strongest developmental stress. This period includes when cubs first emerge above ground from the end of February, are weaned around mid-May and reach independence at the start of June (Dugdale et al., 2010) during which time cubs exhibit high growth rates depending on food availability and social conditions (Sugianto et al., 2019a, 2019b). Second, we determined whether the number of cubs, adults or the total number of individuals in the natal group best predicted early-life RLTL using AICc (the lowest AICc = 1,133.1 was for number of cubs, vs. number of adults ΔAICc = 3.8, total number of individuals ΔAICc = 4.0, number of cubs plus number of adults ΔAICc = 5.8, number of cubs plus total number of individuals ΔAICc = 5.6). Since ΔAICc < 7, and VIF > 3 for the other combinations in the same model, we ran five separate models with either the number of cubs, number of adults, the total number of individuals, number of cubs plus adults or number of cubs plus total number of individuals in the natal group as a fixed effect along with season, weight, body length, mean daily temperature, temperature variability and rainfall variability in spring. qPCR plate, row on qPCR plate, social group and cohort were included as random effects.

2.5.3 | Covariation between early-life RLTL and weather conditions on cub survival probability

To understand whether the association between early-life RLTL and cub survival probability (van Lieshout et al., 2019) is due to or independent of weather effects, we tested whether the association between early-life RLTL and cub survival probability was still

detected when social and weather conditions were included in the model. We first modelled survival to adulthood (≥1 year old) as a binary term in a binomially distributed model (logit link function; n = 406 samples; 406 badgers), where cubs only caught in their first year of life were coded as 0 and cubs that were caught when older than 1 year of age were coded as 1, with early-life RLTL, weight and body length as fixed effects and qPCR plate, row on qPCR plate, social group and cohort included as random effects. We then also included as fixed effects: number of cubs in the natal group, mean daily temperature, temperature variability, mean daily rainfall and rainfall variability in a given season. We determined the season in which weather conditions best explained the variation in cub survival probability, using AICc (the lowest AICc =408.9 was in winter, vs. spring ΔAICc =21.6, summer ΔAICc =16.3 and autumn ΔAICc =22.5) where models with ΔAICc <7 from the top model are plausible (Burnham et al., 2011). The model was not overdispersed. While cub survival is negatively impacted by endoparasitic coccidia infection (Newman et al., 2001), we did not have data to control for coccidia infection. We then applied model selection to test whether including weather and social variables knocked early-life RLTL out of the plausible models. This would indicate that the early-life RLTL and survival probability relationship is driven by covariation between the environment and physiological state (early-life RLTL). As early-life RLTL was retained, we estimated the RLTL model-averaged parameter and 95% CI using the natural averaged method (where the parameter was averaged over models in which it was present; Burnham & Anderson, 2002). This avoids the parameter estimate shrinking towards zero, from inclusion of the relatively less important models where the parameter was not retained (Nakagawa & Freckleton, 2011).

2.5.4 | Same-sex group size effects on RLTL in early adulthood

We examined whether same-sex adult group sizes were reflected in RLTL in early adulthood (i.e., 12–36 months old). In a GLMM with RLTL in early adulthood as the response variable with one age threshold separating two periods of 12 to ≤29 months and >29 and ≤36 months (see van Lieshout et al., 2019) and season, weight and body length as fixed effects, we determined that RLTL did not vary with age (n = 376, 12 to ≤29 months, β = −0.064, 95% CI = −0.175 to 0.050; >29 and ≤36 months, β = −0.040, 95% CI = −0.184 to 0.110), and excluded age from the subsequent analysis. The effects of same-sex adult group sizes on RLTL in early adulthood were then modelled with RLTL in early adulthood as the response variable (n = 376 samples; 308 badgers). Same-sex adult group size (within-group for females and within- plus neighbouring-group for males), sex and its interaction with group size (to model differential strength in intrasexual competition among the sexes), age at last capture (to control for selective disappearance), season, weight and body length were included as fixed effects, and qPCR plate, row on qPCR plate, social group, cohort, year and individual ID as random effects.

3 | RESULTS

3.1 | Seasonal effects on RLTL in early life and early adulthood

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

3.2 | Weather and natal group size effects on early-life RLTL

We found a positive association between spring temperature and early-life RLTL (Figure 2; Table 1; Tables S7–S10), with cubs experiencing cooler-than-average first springs having shorter early-life RLTL. We also found that cubs experiencing intermediate-to-high mean daily rainfall had longer early-life RLTL (Figure 3; Table 1; Tables S7–S10) than cubs developing during drier years. Cubs experiencing
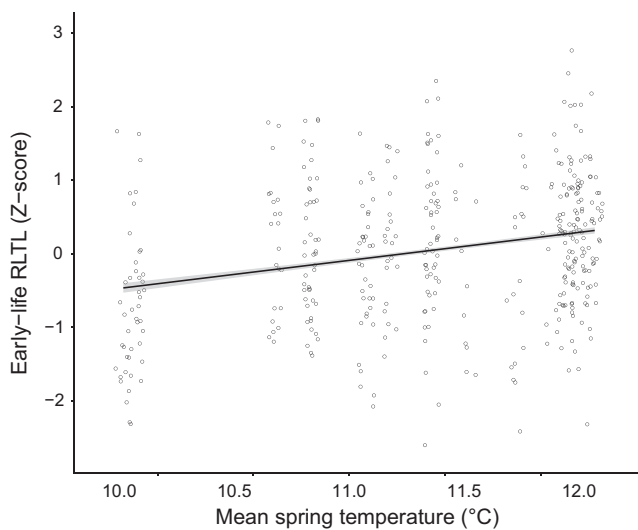

FIGURE 2 The association between mean spring temperature and early-life relative leukocyte telomere length (RLTL). Raw data points (n = 406 samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the regression from the mixed model, and the 95% confidence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

low rainfall variability also had longer early-life RLTL (Figure 4; Table 1; Tables S7–S10). We found, while controlling for weather effects, a marginal effect where more cubs in the natal group was correlated with longer early-life RLTL. In contrast, we found no evidence for an association between the number of adults or total number of individuals in the natal group and early-life RLTL (Table 1; Tables S7–S10).

3.3 | Covariation between early-life RLTL and weather conditions on cub survival probability

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

3.4 | Same-sex group size effects on RLTL in early adulthood

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

4 | DISCUSSION

Our results show both between-individual variation and within-individual changes in RLTL across seasons, where a cub's RLTL in their first spring was longer than in the following winter, and an indication that RLTL was longer again in the following spring compared to the preceding winter. The between- and within-individual slopes did not differ. Although we detect a between-individual effect, it was negative so there was no evidence of selective disappearance, and the between-individual effect may be driven by sampling variance. We also found that cubs born in conditions that were warmer and wetter, with little variation in rainfall, had longer early-life RLTL. Sociologically, the number of cubs had a positive effect on early-life RLTL, but there was no effect of the number of adults or total number of individuals. Our results also suggest that the link between

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 $p > .10$ second-order effects removed)

Parameter (reference level)	β	SE	95% CI
Intercept[a]	−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 rainfall^2	**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
After removing second order effects $p >.10$			
Intercept[b]	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 rainfall^2	**1.356**	**0.555**	**0.255 to 2.467**
Daily rainfall variability	**−2.843**	**1.414**	**−5.563 to −0.112**
Daily rainfall variability^2	**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

Notes: β = parameter estimate, SE = standard error, 95% CI = 95% confidence intervals; reference terms in parentheses = reference level for factors. Significant parameter estimates (95% CI does not overlap zero) are in bold.
Random effect estimates (variance):
[a]qPCR plate (4.955 ××10^{-2}), Row on qPCR plate (1.861 × 10^{-3}), Social group (2.798 × 10^{-2}), Cohort (7.745 × 10^{-2}), Residual (7.537 × 10^{-1});
[b]qPCR plate (4.911 × 10^{-2}), Row on qPCR plate (2.895 × 10^{-3}), Social group (2.642 × 10^{-2}), Cohort (5.287 × 10^{-2}), Residual (7.572 × 10^{-1}).

early-life RLTL and cub survival probability is driven by conditions experienced in addition to the early-life social and weather conditions modelled. Additionally, we found no effect of the number of within-group adult females, or both within-group and extra-group adult males (i.e., intrasexual competition) on RLTL in early adulthood.

Our finding that badgers had shorter early-life RLTL (both between and within individuals) in winter compared to the preceding spring could be linked to the end-replication problem and stressful effects such as disease (Newman et al., 2001), suboptimal foraging conditions and food availability (Macdonald & Newman, 2002; Newman et al., 2017). The within-individual effect means that between seasons there is an increase or decrease in telomere length for the same individual.

We then found a nonsignificant trend for positive within-individual changes in RLTL from the first winter to the following spring. Body temperatures in badgers fall from November to December (by a maximum of 8.9°C compared to late spring) and steadily rise until euthermic levels are reached by late April (Fowler & Racey, 1988; Geiser &
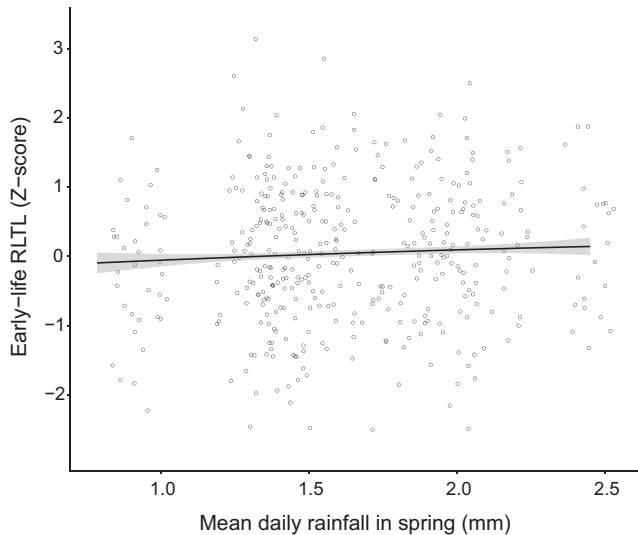
FIGURE 3 The association between mean daily rainfall in spring and early-life relative leukocyte telomere length (RLTL). Raw data points (*n* = 406 samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model, and the 95% confidence intervals as shaded areas
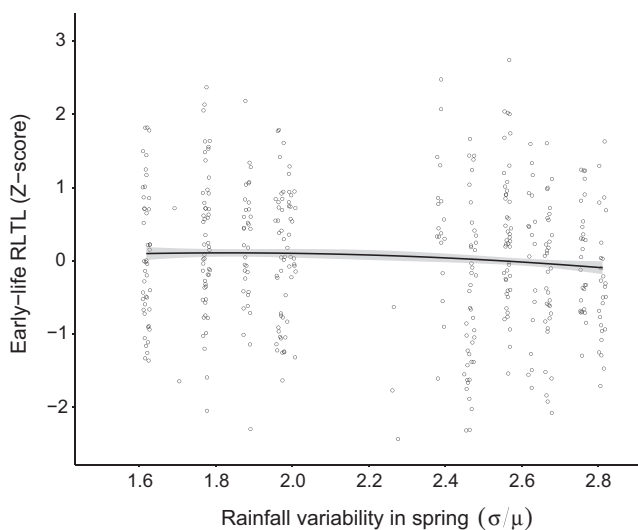

FIGURE 4 The association between rainfall variability in spring and early-life relative leukocyte telomere length (RLTL). Raw data points (*n* = 406 samples; 406 badgers) are shown, and jittered for clarity on the amount of data. The fitted line represents the quadratic regression from the mixed model,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

Ruf, 1995). During harsh winter conditions, badgers use facultative torpor to reduce their core temperature and metabolic rate, conserving energy (Newman et al., 2011). This reduction of basal metabolic rates (Geiser, 2004) can reduce mitosis (Kruman et al., 1988) and therefore potentially reduce telomere shortening. Similarly, daily torpor cycles in Djungarian hamsters had a positive effect on telomere length (Turbill et al., 2012). However, for species using torpor as a seasonal energy conservation strategy (e.g., edible dormice, garden

dormice and arctic ground squirrels; as do badgers), arousal and return to euthermia has been linked to telomere shortening; however, this appears to be in proportion to the extent that body temperature must be rewarmed (Giroud et al., 2014; Hoelzl et al., 2016; Turbill et al., ,2012, 2013; Wilbur et al., 2019). We postulate that badgers use torpor and their ability to remain within thermally stable setts (Tsunoda et al., 2018) to try to mitigate RLTL shortening that would otherwise be incurred by the stresses of maintaining activity during winter, when food is scarce and thermal losses are high. More detailed analyses are needed to explore this further, such as by comparing badgers in different regions that experience different degrees of winter severity, with a large longitudinal sample size to disentangle within- and between-individual effects. Importantly, we would need to track which badgers go into torpor, for how long and how often, and then calculate how much energy is conserved. We also do not yet know to what extent torpor–arousal cycles may affect telomere shortening, and where there is probably an optimal balance. In this regard, predicted increases in weather variability (IPCC, 2018) that may cause more frequent warm–cold winter episodes could add to the allostatic load of badgers, causing accelerated RLTL shortening. Since positive within-individual changes in badger telomere length occur, which are greater than measurement error (van Lieshout et al., 2019), such seasonal patterns may explain some of the variability in telomere length patterns across life in badgers. Indeed, there is also evidence of seasonal telomere dynamics in nonhibernating rodents (Criscuolo et al., 2020). Even though we accounted for body weight and length, other factors such as seasonal changes in leukocyte cell composition can also lead to apparent changes in telomere length (Beaulieu et al., 2017), which would require further investigation. For example, there is a greater proportion of neutrophils and lymphocytes that were lymphocytes in spring compared to autumn in badgers (van Lieshout, Badás, et al., 2020), and lymphocytes have shorter telomere lengths than neutrophils in humans and baboons (Baerlocher et al., 2007; Kimura et al., 2010). Nonetheless, our findings also highlight the importance of controlling for seasonal effects when analysing telomere dynamics.

Cubs born into more energetically favourable springs (warm, rainy and low rainfall variability) had longer early-life RLTL. These weather conditions present optimal soil conditions for earthworm surfacing, enhancing food supply (Kruuk, 1978; Newman et al., 2017). Dry conditions in spring have negative consequences for badger foraging success (Macdonald & Newman, 2002). However, while we found no effect of spring temperature variability on early-life RLTL, cubs experiencing lower daily rainfall variability in spring had longer early-life RLTL. Greater rainfall variability can reduce the predictability of food availability and impact foraging activity (Noonan et al., 2014), and may require individuals to modulate their energy trade-offs (Erikstad et al., 1998; Reid et al., 2003; Weimerskirch et al., 2001) and adopt a bet-hedging strategy (Wilbur & Rudolf, 2006). The variability in spring rainfall and thus early-life conditions experienced shape life-history trade-offs, and since variability is likely to increase under current climate change (IPCC, 2018), this can impact ecological and individual resilience (Bright Ross et al., 2020).

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

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

There was no significant association between same-sex adult group size and RLTL in early adulthood. While female–female reproductive competition occurs in badgers (Sharp & Clutton-Brock, 2011; Woodroffe & Macdonald, 1995), in polygynous species, theory predicts intrasexual competition for mating opportunities to be stronger among males than females. In Wytham badgers, there is slight sexual dimorphism (Johnson & Macdonald, 2001) and slight male-biased mortality (Bright Ross et al., 2020). Reproductive skew is higher in sexually mature males than females (Dugdale et al., 2008) and males with a higher body-condition index attain more reproductive success (Dugdale, Griffiths, et al., 2011). High levels of polygynandrous

and repeated mounting behaviour may, however, reduce male–male aggression and infanticide from males (Dugdale, Griffiths, et al., 2011; Wolff & Macdonald, 2004). Second, cryptic female choice (i.e., delayed implantation, superfecundation and superfetation) may promote sperm competition and mask paternity, and reduce precopulatory male–male competition (Birkhead & Pizzari, 2002). Finally, group size and/or density could be a poor metric for competition due to foraging niche variation or variation in sex-ratio; additionally, although the resource dispersion hypothesis predicts that groups approximate territorial carrying capacity, results are mixed (Revilla, 2003). In fact, in our study population results vary with year such that only in some situations larger groups may have proportionally more resources available (Johnson et al., 2001, 2002). In line with this, we found no evidence that variation in telomere length is due to intrasexual competition in early adulthood. Badger early-life telomere length may reflect the consequences of the weather conditions experienced, with little impact of early-adulthood social conditions. However, in low-quality years only females in good condition breed, whereas in high-quality years breeding success is related to status (Woodroffe & Macdonald, 1995). We can therefore not exclude that there may only be female–female competition in good years. Additionally, early-adulthood male–male competition impacts on body mass senescence in a badger population at the Woodchester Park study population (Gloucestershire, UK) (Beirne et al., 2015). While we detected no significant evidence of direct effects of early-adulthood intrasexual competition on telomere length, there may be downstream effects on senescence.

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

AUTHOR CONTRIBUTIONS

ETHICAL APPROVAL

DATA AVAILABILITY STATEMENT

ORCID

Sil H. J. van Lieshout https://orcid.org/0000-0003-4136-265X
Elisa P. Badás https://orcid.org/0000-0001-9398-5440
Julius G. Bright Ross https://orcid.org/0000-0003-2454-1592
Amanda Bretman https://orcid.org/0000-0002-4421-3337
Chris Newman https://orcid.org/0000-0002-9284-6526
Christina D. Buesching https://orcid.org/0000-0002-4207-5196
Terry Burke https://orcid.org/0000-0003-3848-1244
David W. Macdonald https://orcid.org/0000-0003-0607-9373
Hannah L. Dugdale https://orcid.org/0000-0001-8769-0099

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.