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Within-individual repeatability in telomere length: A meta-analysis in nonmammalian vertebrates

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Abstract

Telomere length is increasingly used as a biomarker of long-term somatic state and future survival prospects. While most studies have overlooked this aspect, biological interpretations based on a given telomere length will benefit from considering the level of within-individual repeatability of telomere length through time. Therefore, we conducted a meta-analysis on 74 longitudinal studies in nonmammalian vertebrates, with the aim to establish the current pattern of within-individual repeatability in telomere length and to identify the methodological (e.g., qPCR/TRF) and biological factors (e.g., age class, phylogeny) that may affect it. While the median within-individual repeatability of telomere length was moderate to high ($R = 0.55$; 95% CI: 0.05–0.95; $N = 82$), marked heterogeneity between studies was evident. Measurement method affected the repeatability estimate strongly, with TRF-based studies exhibiting high repeatability ($R = 0.80$; 95% CI: 0.34–0.96; $N = 25$), while repeatability of qPCR-based studies was markedly lower and more variable ($R = 0.46$; 95% CI: 0.04–0.82; $N = 57$). While phylogeny explained some variance in repeatability, phylogenetic signal was not significant ($\lambda = 0.32$; 95% CI: 0.00–0.83). None of the biological factors investigated here significantly explained variation in the repeatability of telomere length, being potentially obscured by methodological differences. Our meta-analysis highlights the high variability in within-individual repeatability estimates between studies and the need to put more effort into separating technical and biological explanations. This is important to better understand to what extent biological factors can affect the repeatability of telomere length and thus the interpretation of telomere length data.

KEYWORDS
ageing, biomarker, lifespan, phylogeny, qPCR, TRF

1 | INTRODUCTION

Telomeres are highly conserved repetitive sequences of non-coding DNA that cap the ends of linear chromosomes of eukaryotic species and contribute to genomic integrity maintenance (Blackburn, 1991). Telomeres shorten with every cell division due to the end replication problem (inability of DNA polymerase to copy terminal DNA) (Levy et al., 1992). Additionally, telomere shortening can be accentuated

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by cellular stressors, such as oxidative stress (Reichert & Stier, 2017; von Zglinicki, 2002). When telomeres reach critically short length, they induce cell senescence, apoptosis, or genomic instability, which in turn contribute to ageing phenotypes (Campisi, 2005). Short telomeres have been associated with increased risks of developing degenerative diseases in humans (e.g., cardiovascular and Alzheimer diseases), while long telomeres could increase the risk of neoplastic diseases (Aviv & Shay, 2018). Yet, short telomeres have been associated with increased mortality risk in both humans and non-model vertebrates (Arbeev et al., 2020; Boonekamp et al., 2013; Wilbourn et al., 2018). While a causal role of telomeres in organismal ageing has been questioned (Simons, 2015; Young, 2018), some recent evidence suggests that experimentally increasing telomere length could extend lifespan in laboratory mice (Muñoz-Lorente et al., 2019). Irrespective of causality controversies, telomere shortening is considered to be a hallmark of ageing (López-Otín et al., 2013) and telomere length has been suggested to act as a biomarker of past stress exposure (Chatelain et al., 2020; Pepper et al., 2018), phenotypic quality (Angelier et al., 2019), future disease risk (Fasching, 2018), survival probability (Wilbourn et al., 2018) as well as fitness prospects (Eastwood et al., 2019).

When making inferences about past stress exposure or predictions about future long-term consequences based on a given telomere length, it is important to consider the associations between successive telomere length measurements. These associations can be quantified as the within-individual repeatability *R* of a trait (Nakagawa & Schielzeth, 2010), which is defined as the between-individual variance divided by the total variance (between-individual variance + within-individual variance; Nakagawa & Schielzeth, 2010). Hence high repeatability can arise due to large between-individual variance, little within-individual variance, or both. The within-individual variance can emerge from biological sources (e.g., individual adjustment to local conditions), in which case the repeatability estimates reflects telomere biology. However, it is also possible that methodological reasons, such as measurement error, increase the within-individual variance. For traits being expected to directionally change with time at the population level, such as telomere length, adjusted repeatability should be calculated by including time or sampling occasion (e.g., capture 1 vs. capture 2) as a fixed factor (Nakagawa & Schielzeth, 2010). Considering the associations between repeated telomere length measurements is important because *R* can vary from high (*R* ~ [0.5–1.0]; Figure 1a) to moderate (*R* ~ [0.25–0.5] Figure 1b) or low (*R* ~ [0.0–0.25] Figure 1c). Low within-individual repeatability would imply that one telomere length measurement is not dependent on the previous measurement, but that telomere length is highly susceptible to environmental variation (or measurement error). Thus, using any given telomere length to infer past or future consequences would be somewhat precarious as telomere length can change sporadically within individuals depending on their individual susceptibilities to environmental factors. However, extremely high within-individual repeatability would imply that environment has little or no impact on telomeres. Thus, in that case telomere length could not be used to assess past experiences or link current conditions to the future fitness and/or survival. However, because telomere lengths of individuals are expected to change at different rates over time, we do not expect telomere length to

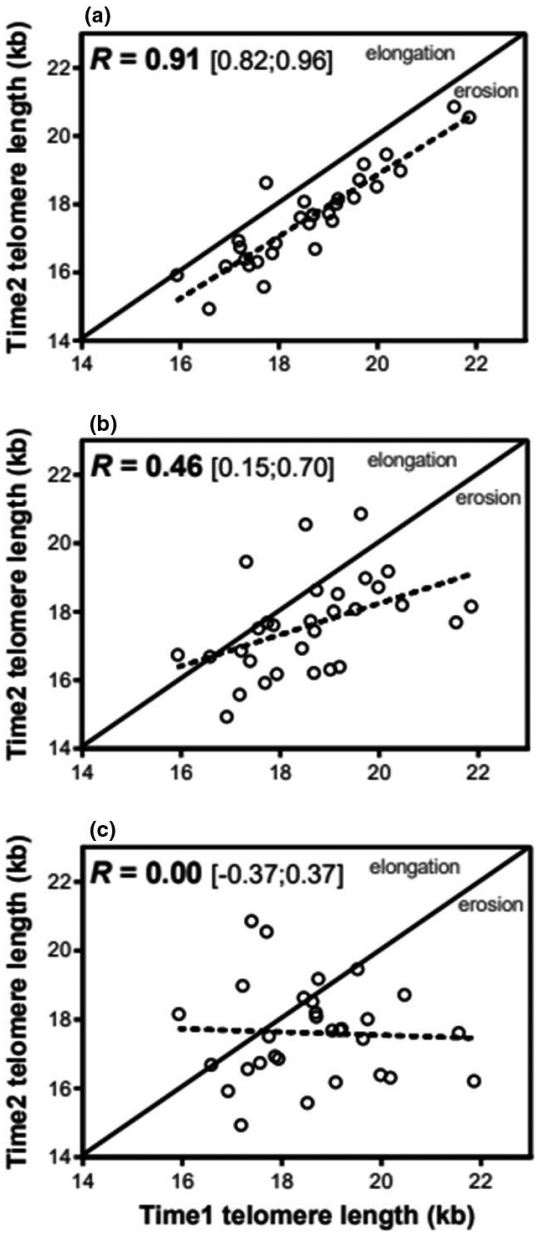

FIGURE 1 Illustrating the variation in within-individual repeatability of telomere length. Simulated data is presented where population-level telomere shortening is constant (i.e., 1 kb loss between time 1 and time 2) but within-individual repeatability is either (a) high (b) moderate or (c) low. Data has been simulated based on collared flycatcher telomere characteristics: mean ±SD =18.6 ± 1.6 kb, 1 kb shortening occurring approximately over 2.5 years of life, *N* = 30, normal distribution (Stier et al., 2020). Repeatability is adjusted for the general shortening with age by including sampling occasion (i.e., t1 or t2) as a fixed effect. Black diagonals show x = y, that is, when the telomere length at first and second measurement are the same, while dotted lines show regression lines for each dataset. Values above the diagonal illustrate telomere elongation (which can for example arise due to measurement error) and below the diagonal telomere shortening

be perfectly repeatable even in the absence of any measurement error. In humans, Benetos et al. (2019) evaluated within-individual repeatability of telomere length to be high (R = [0.85–0.91], but see Martens et al., 2021 for somewhat lower estimates), but the few studies that reported R of telomere length in other species have provided more variable estimates ranging from 0.03 to 0.97 (Bichet et al., 2020; Boonekamp et al., 2017; Fairlie et al., 2016; van Lieshout et al., 2019; Nettle et al., 2016; Pérez-Rodríguez et al., 2019; Spurgin et al., 2018). Nonetheless, longitudinal studies very rarely report within-individual repeatability, while such information appears critical to the interpretation of telomere length data.

Biological within-individual repeatability is important to distinguish from the technical repeatability that is assessed by measuring the same samples more than once on the same and/or on different plates/gels. Technical repeatability quantifies measurement accuracy within an assay. Telomeres are mostly measured with two methods that quantify the telomere length very differently: quantitative PCR (qPCR) and terminal restriction fragment -method (TRF). qPCR is based on PCR and amplification of the target sequences and measures the relative telomere length (T/S) by calculating the amount of telomeric sequence (T) in the DNA sample in relation to the amount of a reference gene that is nonvariable in copy number (S), while TRF measures telomere length by the use of gel electrophoresis. While TRF is considered the gold standard method of telomere measurements for its high reproducibility, it is labor intensive and requires specialized equipment and large amounts of starting DNA. On the contrary, qPCR has high throughput, but is more susceptible to methodological variation. For example, slight differences in the thermal conditions depending on well position during qPCR assay (Eisenberg et al., 2015) or even instability in power supply (Hastings et al., 2020) can lead to differences in relative telomere lengths and therefore lower technical repeatability. Technical repeatability is important because it sets an upper limit to biological repeatability. Therefore, a low within-individual repeatability might not always be biological but might also result from a poor precision in telomere length quantification.

While initial studies of telomeres were mostly cross-sectional and measured telomere length only once per individual, the last decade has been characterized by a marked increase in longitudinal studies measuring telomere length at least twice from each individual. In such longitudinal studies, telomeres are generally expected to shorten with time/age, at least in most endotherm vertebrate species (i.e., mammals and birds; e.g., Stier, Reichert, et al., 2015 for a review in nonmammalian vertebrates). Indeed, while the enzyme telomerase enabling telomere elongation is mainly suppressed in somatic tissues of adult birds and mammals, this is not the case in many ectotherm vertebrate species (i.e., fish, amphibian and reptiles; Gomes et al., 2010), which could explain the diversity of telomere dynamics observed in such taxa (Olsson et al., 2018; Simide et al., 2016). Yet, some longitudinal studies in endotherms have also reported telomere lengthening, which is suggested not to be explained by measurement error alone (van Lieshout et al., 2019; Spurgin et al., 2018). The increasing availability of longitudinal studies now enables us to form a general picture of the within-individual repeatability in telomere length in a variety of species and provides the opportunity to identify the factors that could explain variation in such an important parameter.

Here, we provide, to the best of our knowledge, the first meta-analysis of within-individual repeatability of telomere length and the factors affecting it by focusing on nonmammalian vertebrates. We address several methodological and biological factors that could create variation in the within-individual repeatability of telomere length. The theoretical expectation is that if all individuals shorten telomeres at the same rate and there is little or no measurement error, (1) all individuals will maintain the same relative rank in telomere length throughout life, and (2) the repeatability of telomere length (adjusted for time or sampling occasion) will be close to one. However, a number of factors can affect this repeatability. (i) The two most common methods, TRF and qPCR vary in the reproducibility of results (Lai et al., 2018). The lower reproducibility of qPCR (Aviv et al., 2011) and its greater sensitivity to other methodological factors (e.g., sample storage and DNA extraction method, (Dagnall et al., 2017; Reichert et al., 2017)) are expected to result in a greater increase in the within-individual variance in telomere length compared to TRF studies, consequently resulting in lower within-individual repeatability estimates. Additionally, chromosomes also include nonterminal, interstitial telomeric sequences (ITS) that are included in the telomere length measure obtained by qPCR but also Southern blot TRF and denatured TRF, while in-gel TRF excludes the ITS (Foote et al., 2013). Moreover, all TRF methods include some amount of subtelomeric regions (Baird, 2005). Including ITS or subtelomeric regions in the telomere measurements can possibly artificially inflate R estimates. (ii) Studies measuring telomere length with a long time interval between subsequent sampling occasions are expected to have lower within-individual repeatability than studies using samples taken only a few days from each other, due to both interindividual differences in telomere shortening rate, and potentially due to slight differences in sample handling protocols, such as storage method (Reichert et al., 2017), both increasing within-individual variance. (iii) Most ectotherms can maintain telomerase activity in adulthood, allowing the possibility for telomere restoration (Gomes et al., 2010). We expect the possibility of telomere restoration to vary between individuals, for example, due to individual variation in access to resources (Hoelzl et al., 2016), thereby increasing the within-individual variance and causing more variation in individual ranking over time. Hence, we expect taxa with higher potential telomerase activity (i.e., ectotherms) to have lower repeatability than other taxa that mainly suppress their telomerase activity (i.e., endotherms). Alternatively however, in taxa with telomerase activity, individuals with the highest rate of telomere shortening might have the highest telomerase activity, and if this is the case, we would expect ectotherms to have higher repeatability than endotherms. (iv) Technically, the repeatability of a trait may not be affected by a trait's rate of change, if time or sampling occasion is taken into account in the calculation of R estimate (i.e., adjusted repeatability). For example, if a trait changes at the same rate for all individuals,

this would generate an adjusted repeatability close to one (assuming little measurement error). However, we might expect that with larger rates of change, within-individual variance will tend to increase leading to lower within-individual repeatability. Therefore, our naïve expectation is that a faster rate of telomere shortening might decrease the estimates of within-individual repeatability. Given that telomere shortening is markedly faster in juveniles than in adults (Spurgin et al., 2018; Stier et al., 2020), we can expect juveniles to have lower *R* than adults. (v) Similarly, there is evidence that telomeres shorten faster in short-lived species than in long-lived ones (Dantzer & Fletcher, 2015; Tricola et al., 2018). As the impact of any stressor affecting telomeres would become apparent faster when the rate of shortening is fast, species with short maximum lifespans are expected to have lower within-individual repeatability than species with long maximum lifespans. (vi) Finally, the higher the between-individual variation in telomere shortening rate is, due to, for example, heterogeneity in environmental conditions, the higher the within-individual variance is and the lower the within-individual repeatability will be. Thus, studies on species living in the wild would be expected to have lower *R* than species living in stable captive conditions. Additionally, sample collection and handling might be more variable (e.g., among-sample variation in time to get the sample into a freezer) in the wild than in laboratories, which might increase the variability between telomere length measurements and thus decrease within-individual repeatability by increasing within-individual variance. By testing the importance of these factors, we aim to increase knowledge and awareness about the within-individual repeatability of telomere length and the factors potentially affecting it. This should help to assess the relevance of telomere length as a biomarker for past stress exposure and future long-term costs in particular study systems, as well as to help researchers to make more accurate interpretations of their data. Additionally, it should remind researchers who wish to estimate any past experiences or long-term costs based on given telomere length to design their research aiming at accurate within-individual repeatability via high technical repeatability.

2 | MATERIALS AND METHODS

2.1 | Literature search and data collection

We performed literature searches (last search on 30 September 2019) using Web of Science search engine and the following search terms: "telome* AND bird*", "telome* AND reptile*", "telome* AND ectotherm*", and "telomere dynamics". We identified a total of 1292 records in these searches (Figure S1). In addition, we screened all the studies citing Heidinger et al. (2012), and the reference list of Olsson et al., (2018) to identify additional studies not found in the original searches ($N = 6$). We also included three unpublished data sets, of which one was provided by M. Haussmann (Bucknell University) while others are authors' own unpublished data. After duplicate removal, 1005 records remained, and their titles and abstracts were screened for eligibility based on study species and longitudinal telomere measurements. A total of 124 full text articles were assessed using our inclusion criteria. We included studies that (i) used a nonmammalian (bird or ectotherm) vertebrate study species, ii) measured telomere length at least twice, (iii) had at least one day between the telomere measurements, and (iv) provided the raw data online or upon request. We obtained the raw data sets as the majority of the published articles did not report the within-individual repeatability in telomere length, and this also enabled us to calculate the within-individual repeatabilities in a standardized way. Thus, if the raw data were not available online, we contacted the corresponding authors with a request to provide us with the raw data or to run standardized analyses using an R script that we provided. We chose not to include mammals for two main reasons: (1) human studies are mostly outside of our ecoevolutionary scope, and (2) longitudinal telomere measurements in mammals are almost exclusively measured from white blood cells, and the natural changes in white-blood cell composition (e.g., with season or age) have been previously highlighted to seriously bias the estimation of telomere length (Beaulieu et al., 2017). In nonmammalian vertebrates, longitudinal telomere measurements are almost exclusively measured from nucleated red blood cells, which represent a more homogenous population of blood cells (Stier, Reichert, et al., 2015). We found 71 studies that met our inclusion criteria. Additionally, we were able to include three studies using data that we extracted from scatter plots using the METADIGITIZE package in R (Pick et al., 2019), adding up to 74 eligible studies (Figure S1). We hence excluded 50 (124–74) full text articles for the following reasons: (i) In 27 studies, the data were nonlongitudinal; (ii) in 14 cases all or part of the data was used in more than one publication, in which case we used the first encountered article, or the most complete data set; (iii) in seven cases we were not able to obtain the raw data; and (iv) in two cases the data were not comparable due to major methodological differences (Figure S1).

From each eligible publication we recorded the following biological and methodological factors: taxon, species, sample size, number of telomere samples, study length, telomere measurement method, Age class of individuals, and Environment (Figure 2). Additionally, we obtained maximum lifespan estimates for each species from the AnAge database of animal ageing and longevity (Tacutu et al., 2018) last visited on 7 October 2020. For three species there was no maximum lifespan estimate available and we used the mean maximum lifespan estimate for the genus. We obtained all other predictor data directly from the studies. If present, individuals with only one measurement were excluded from the data sets, to standardize these studies with those that presented only the individuals with two or more measurements. If the number of samples was unequal between individuals, we used an average number of samples per study. Study length was determined as time between successive telomere measurements. If there was variation in time between different sampling points within one study, we used the average time between the samples per study. Some data sets included data for different levels of a categorical variable, for example, some data sets included telomere measurements for both juvenile and adult individuals, or

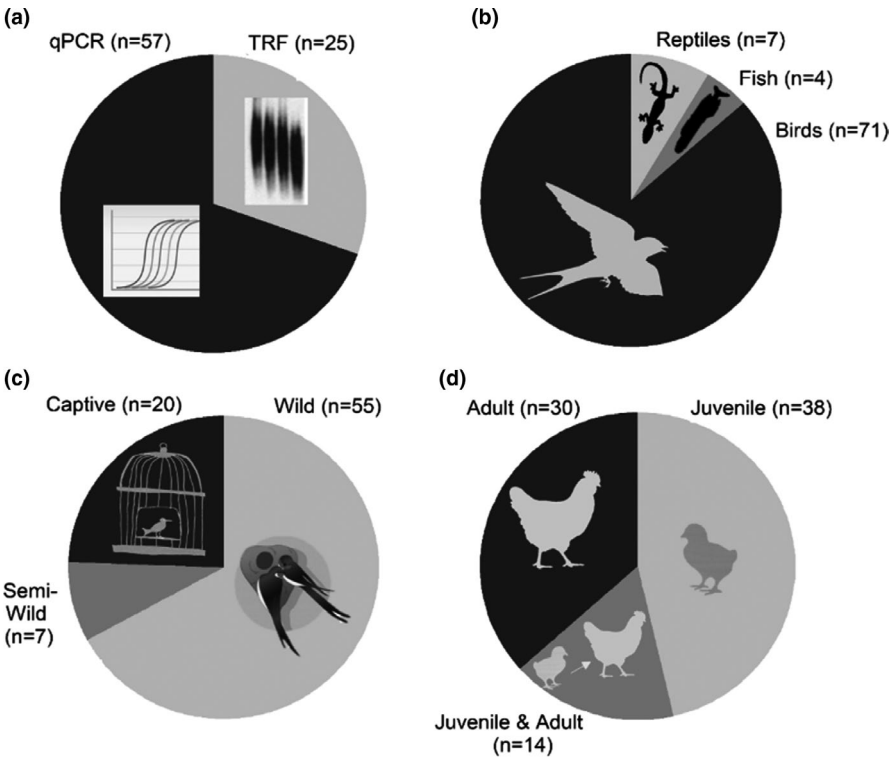

FIGURE 2 Distribution of data for all categorical variables in the study. (a) Measurement method, (b) taxon, (c) environment (semi-wild refers to individuals from wild populations held in captivity during the study), and (d) age classes (juvenile and adults refers to individuals that were measured both as juveniles and after sexual maturation as adults)

for individuals that were sampled only as juveniles and others that were sampled as both juveniles and adults. Because we have reason to believe that within-individual telomere length repeatability might differ between juveniles and adults due to distinct growth patterns (i.e., fast growth vs. essentially no growth at all), in these cases we split the data into two or three according to the age class. In two data sets we did a similar split when the same samples were measured with both qPCR and TRF methods. One data set included data for two different species, and we thus split the data into their respective species. Therefore, we obtained 82 effect size estimates from 74 studies (Table 1).

2.2 | Statistical analyses

We carried out all analyses in R (v. 4.0.1) (R Core Team, 2020). We performed our analyses following Holtmann et al. (2017). First, we checked the distribution of telomere length variable in all 82 data sets, and where needed, we transformed these data using log, square root, or box-cox transformation to fulfill the assumptions of normality (Table S1), but analyses with untransformed values (Table S2, Figure S2) gave conclusions that were consistent with those presented in Table 2. For each of these data sets, we estimated the within-individual repeatability using a linear mixed model LMM approach (Nakagawa & Schielzeth, 2010), that is, repeatability is an intraclass correlation coefficient that captures the between-individual variance (by fitting individual identity as a random intercept) relative to the total variance, with the function rpt of the package RPTR (Stoffel et al., 2017). Since telomeres are expected to shorten with time in most cases, adjusted repeatability was calculated by including sampling occasion (e.g., capture 1 vs. capture 2 vs. capture 3) as a fixed effect. For one study with repeatability <0.005, we estimated the within-individual repeatability using ANOVA approach as the LMM approach biases very low repeatability values upwards (Holtmann et al., 2017; Nakagawa & Schielzeth, 2010). We did not include information on the distribution of the samples across plates or gels, as such information was not available for the vast majority of the studies. Hence, this variance is included in the total variance of the repeatability estimates. Confidence intervals (95% CI) around the repeatability were estimated based on 1,000 bootstraps. These 95% CI are similarly constrained between 0 and 1 thereby underestimating the lower 95% CI of studies with low repeatabilities (upper 95% CI were never close enough to 1 to be biased). To avoid this bias, for studies with a lower 95% CI <0.005, we took the symmetry of the (bootstrapped) upper 95% CI using the standard error and t-value of the t-distribution matching the study's sample size (1.96 when number of individuals >100). Performing this estimation for the whole data range confirmed that the bias emerges when lower 95% CI <0.005 (Figure S3).

We performed mixed-model meta-analyses using general and generalized linear models in R (R Core Team, 2020). In these models the within-individual repeatability of telomere length is the dependent variable, and we performed the analyses using two distributions. First, we followed Holtmann et al. (2017) and standardized all the repeatability estimates and their variance using Fisher's Z-transformation. This transformation renders repeatability estimates close to a normal distribution and after normalizing the heavy tail using the Lambert W × F transformation (Goerg, 2011), we could perform all analyses assuming a normal error distribution. In this approach, we weighed each study according to

TABLE 1 All the studies and effect size groups derived from those studies with associated *R* values included in the meta-analysis

Species	Study	Effect size group	*R*	References
Adélie penguin (*Pygoscelis adeliae*)	Oxidative status and telomere length in a long-lived bird facing a costly reproductive event	Adults	0.528	Beaulieu et al. (2011)
Alpine swift (*Apus melba*)	Telomere dynamics rather than age predict life expectancy in the wild	Adults	0.285	Bize et al. (2009)
Atlantic salmon (*Salmo salar*)	Shorter juvenile telomere length is associated with higher survival to spawning in migratory Atlantic salmon	Juveniles to adults	0.264	McLennan et al. (2017)
Australian painted dragon (*Ctenophorus pictus*)	Telomere dynamics in a lizard with morph-specific reproductive investment and self-maintenance	Adults	0.711	Rollings et al. (2017)
Barn swallow (*Hirundo rustica*)	Early-life telomere dynamics differ between the sexes and predict growth in the barn swallow (*Hirundo rustica*)	Juveniles	0.662	Parolini et al. (2015)
Black-legged kittiwake (*Rissa tridactyla*)	Effects of developmental conditions on growth, stress and telomeres in black-legged kittiwake chicks	Juveniles	0.740	Young et al. (2017)
Black-legged kittiwakes (*Rissa tridactyla*)	Perfluorinated substances and telomeres in an Arctic seabird: cross-sectional and longitudinal approaches	Adults	0.749	Blévin et al. (2017)
Black-legged kittiwake (*Rissa tridactyla*)	Migration and stress during reproduction govern telomere dynamics in a seabird	Adults	0.928	Schultner et al. (2014)
Black-tailed gull (*Larus crassirostris*)	How do growth and sibling competition affect telomere dynamics in the first month of life of long-lived seabird?	Juveniles	0.607	Mizutani et al. (2016)
Black-tailed gull (*Larus crassirostris*)	Environmental perturbations influence telomere dynamics in long-lived birds in their natural habitat	Adults	0.803	Mizutani et al. (2013)
Blue tit (*Cyanistes caeruleus*)	Experimentally increased reproductive effort alters telomere length in the blue tit (*Cyanistes caeruleus*)	Adults	0.479	Sudyka et al. (2014)
Blue tit (*Cyanistes caeruleus*)	Sex-specific effects of parasites on telomere dynamics in a short-lived passerine—a blue tit	Adults	0.398	Sudyka et al. (2019)
Brown trout (*Salmo trutta*)	Telomere dynamics in wild brown trout: effects of compensatory growth and early growth investment	Juveniles	0.455	Näslund et al. (2015)
Coal tit (*Periparus ater*)	Investigating how telomere dynamics, growth and life history covary along an elevation gradient in two passerine species	Coal tit	0.743	Stier et al. (2016)
Coho salmon (*Oncorhynchus kisutch*)	Rapid growth accelerates telomere attrition in a transgenic fish	Juveniles	0.487	Pauliny et al. (2015)
Collared flycatcher (*Ficedula albicollis*)	Effect of prenatal TH on telomere length in Collared flycatcher	qPCR TRF	0.653 0.935	Stier et al. (unpublished data)
Common tern (*Sterna hirundo*)	Telomere attrition and growth: a life-history framework and case study in common terns	Juveniles	0.871	Vedder et al. (2017)
Common tern (*Sterna hirundo*)	Telomere length reflects phenotypic quality and costs of reproduction in a long-lived seabird	Adults	0.787	Bauch et al. (2013)
Common yellowthroat (*Geothlypis trichas*)	Sexual signals reflect telomere dynamics in a wild bird	Adults	0.531	Taff and Freeman-Gallant (2017)

(Continues)

TABLE 1 (Continued)

Species	Study	Effect size group	*R*	References
Dark-eyed junco (*Junco hyemalis*)	Early breeding females experience greater telomere loss	Adults	0.356	Graham et al. (2019)
Eurasian blackbird (*Turdus merula*)	Repeated stressors in adulthood increase the rate of biological ageing	Adults	0.871	Hau et al. (2015)
European shag (*Phalacrocorax aristotelis*)	Parental age influences offspring telomere loss	Juveniles	0.697	Heidinger et al. (2016)
European shag (*Phalacrocorax aristotelis*)	Stress exposure in early post-natal life reduces telomere length: an experimental demonstration in a long-lived seabird	Juveniles	0.550	Herborn et al. (2014)
European shag (*Phalacrocorax aristotelis*)	Telomere loss in relation to age and early environment in long-lived birds	Juveniles to adults	0.586	Hall et al. (2004)
European starling (*Sturnus vulgaris*)	Bottom of the heap: having heavier competitors accelerates early-life telomere loss in the European starling, *Sturnus vulgaris*	Juveniles	0.702	Nettle et al. (2013)
European starling (*Sturnus vulgaris*)	An experimental demonstration that early-life competitive disadvantage accelerates telomere loss	Juveniles	0.917	Nettle et al. (2015)
European starling (*Sturnus vulgaris*)	Brood size moderates associations between relative size, telomere length, and immune development in European starling nestlings	Juveniles	0.730	Nettle et al. (2016)
European starling (*Sturnus vulgaris*)	Early-life adversity accelerates cellular ageing and affects adult inflammation: experimental evidence from the European starling	Juveniles	0.869	Nettle et al. (2017)
European starling (*Sturnus vulgaris*)	Developmental telomere attrition predicts impulsive decision-making in adult starlings	Juveniles to adults	0.520	Bateson et al. (2015)
European starling (*Sturnus vulgaris*)	Telomere length, individual quality and fitness in female European starlings (*Sturnus vulgaris*) during breeding	Adults	0.259	Criscuolo et al. (2018)
European storm petrel (*Hydrobates pelagicus*)	Variation in early-life telomere dynamics in a long-lived bird: links to environmental conditions and survival	Juveniles	0.068	Watson et al. (2015)
Feral pigeon (*Columbia livia*)	Telomere erosion varies with sex and age at immune challenge but not with maternal antibodies in pigeons	Juveniles to adults	0.307	Lardy et al. (2017)
Frillneck lizard (*Chlamydosaurus kingii*)	Curvilinear telomere length dynamics in a squamate reptile	Adults	0.562	Ujvari et al. (2017)
Gouldian finch (*Erythrura gouldiae*)	Morph- and sex-specific effects of challenging conditions on maintenance parameters in the Gouldian finch	Adults	0.818	Fragueira et al. (2019)
Great reed warbler (*Acrocephalus arundinaceus*)	Hidden costs of infection: chronic malaria accelerates telomere degradation and senescence in wild birds	Juveniles to adults	0.723	Asghar et al. (2015)
Great tit (*Parus major*)	Investigating how telomere dynamics, growth and life history covary along an elevation gradient in two passerine species	Great tit	0.738	Stier et al. (2016)
Great tit (*Parus major*)	Ultra-long telomeres shorten with age in nestling great tits but are static in adults and mask attrition of short telomeres	Juveniles	0.491	Atema et al. (2019)

(Continues)

TABLE 1 (Continued)

Species	Study	Effect size group	*R*	References
Great tit (*Parus major*)	Artificial light at night does not affect telomere shortening in a developing free-living songbird: a field experiment	Juveniles	0.131	Grunst et al. (2019)
Great tit (*Parus major*)	Starting with a handicap: effects of asynchronous hatching on growth rate, oxidative stress and telomere dynamics in free-living great tits	Juveniles	0.597	Stier, Massemin, et al. (2015)
Great tit (*Parus major*)	Selective disappearance of great tits with short telomeres in urban areas	Juveniles to adults Adults	0.231 0.398	Salmón et al. (2017)
Jackdaw (*Coloeus monedula*)	Nestling telomere shortening, but not telomere length, reflects developmental stress and predicts survival in wild birds	Juveniles	0.953	Boonekamp et al. (2014)
Jackdaw (*Coloeus monedula*)	Does oxidative stress shorten telomeres in vivo?	Juveniles	0.969	Boonekamp et al. (2017)
Jackdaw (*Coloeus monedula*)	Telomere shortening and survival in free-living corvids	Juveniles	0.929	Salomons et al. (2009)
Japanese quail (*Coturnix japonica*)	Effect of egg size selection on telomere length in Japanese quail	Juveniles	0.645	Haussmann and Tschirren (unpublished data)
Japanese quail (*Coturnix japonica*)	Prenatal temperature and TL in Japanese quail	qPCR	0.662	Stier at al. (unpublished data)
Japanese quail (*Coturnix japonica*)	Pace and stability of embryonic development affect telomere dynamics: an experimental study in a precocial bird model	TRF	0.934	Stier et al. (2020)
King penguin (*Aptenodytes patagonicus*)	Catching-up but telomere loss: half-opening the black box of growth and ageing trade-off in wild king penguin chicks	Juveniles	0.166	Geiger et al. (2012)
King penguin (*Aptenodytes patagonicus*)	Maternal telomere length inheritance in the king penguin	Juveniles	0.283	Reichert, Rojas, et al. (2015)
Lesser black-backed gull (*Larus fuscus*)	Telomere dynamics in relation to early growth conditions in the wild in the lesser black-backed gull	Juveniles	0.542	Foote et al. (2011)
Magellanic penguin (*Spheniscus magellanicus*)	Magellanic penguin telomeres do not shorten with age with increased reproductive effort, investment, and basal corticosterone	Adults	0.109	Cerchiara et al. (2017)
Magnificent frigatebird (*Fregata magnificens*)	Corticosterone, inflammation, immune status and telomere length in frigatebird nestlings facing a severe herpesvirus infection	Juveniles	0.630	Sebastiano et al. (2017)
Painted ground-dragon (*Ctenophorus pictus*)	Long term effects of superoxide and DNA repair on lizard telomeres	Adults	0.523	Olsson, Friesen, et al. (2018)
Pied flycatcher (*Ficedula hypoleuca*)	Interplays between pre- and post-natal environments affect early-life mortality, body mass and telomere dynamics in the wild	Juveniles	0.321	Kärkkäinen et al. (2021)
Pied flycatcher (*Ficedula hypoleuca*)	Vitamin E supplementation—but not induced oxidative stress—influences telomere dynamics during early development in wild passerines	Juveniles	0.603	Pérez-Rodríguez et al. (2019)
Pied flycatcher (*Ficedula hypoleuca*)	Impact of continuous predator threat on telomere dynamics in parent and nestling pied flycatchers	Juveniles Adults	0.196 0.375	Kärkkäinen et al. (2019)

(Continues)

TABLE 1 (Continued)

Species	Study	Effect size group	*R*	References
Pied flycatcher (*Ficedula hypoleuca*)	Sex-specific associations between telomere dynamics and oxidative status in adult and nestling pied flycatchers	Adults	5.44E-18	López-Arrabé et al. (2018)
Sand lizard (*Lacerta agilis*)	Proximate determinants of telomere length in sand lizards (*Lacerta agilis*)	Adults	0.609	Olsson et al. (2010)
Seychelles warbler (*Acrocephalus sechellensis*)	Telomere length and dynamics predict mortality in a wild longitudinal study	Adults	0.191	Barrett et al. (2013)
Siberian sturgeon (*Acipenser baerii*)	Age and heat stress as determinants of telomere length in a long-lived fish, the Siberian sturgeon	Juveniles	0.027	Simide et al. (2016)
Siskin (*Spinus spinus*)	Parallel telomere shortening in multiple body tissues owing to malaria infection	Juveniles	0.288	Asghar et al. (2016)
Spotted snow skink (*Niveoscincus ocellatus*)	Tail loss and telomeres: consequences of large-scale tissue regeneration in a terrestrial ectotherm	Adults	0.190	Fitzpatrick et al. (2019)
Tawny owl (*Strix aluco*)	Pale and dark morphs of tawny owls show different patterns of telomere dynamics in relation to disease status	Adults	0.113	Karell et al. (2017)
Thick-billed murre (*Uria lomvia*)	Age, sex and telomere dynamics in a long-lived seabird with male-biased parental care	Juveniles to adults	0.692	Young et al. (2013)
Water python (*Liasis fuscus*)	Short telomeres in hatchling snakes: erythrocyte telomere dynamics and longevity in tropical pythons	Juveniles Adults	0.104 0.955	Ujvari and Madsen (2009)
White-browed sparrow-weaver (*Plocepasser mahali*)	Telomere attrition predicts reduced survival in a wild social bird but short telomeres do not	Juveniles	0.657	Wood and Young (2019)
Yellow-legged gull (*Larus michahellis*)	Perinatal variation and covariation of oxidative status and telomere length in yellow-legged gull chicks	Juveniles	0.379	Parolini et al. (2019)
Zebra finch (*Taeniopygia guttata*)	Maternal effects underlie ageing costs of growth in the zebra finch (*Taeniopygia guttata*)	Juveniles	0.724	Tissier et al. (2014)
Zebra finch (*Taeniopygia guttata*)	Immediate and delayed effects of growth conditions on ageing parameters in nestling zebra finches	Juveniles Juveniles to adults	0.713 0.320	Reichert, Criscuolo, et al. (2015)
Zebra finch (*Taeniopygia guttata*)	Timing matters: traffic noise accelerates telomere loss rate differently across developmental stages	Juveniles to adults	0.435	Dorado-Correa et al. (2018)
Zebra finch (*Taeniopygia guttata*)	Telomere length in early life predicts lifespan	Juveniles to adults	0.468	Heidinger et al. (2012)
Zebra finch (*Taeniopygia guttata*)	Sex-dependent effects of nutrition on telomere dynamics in zebra finches (*Taeniopygia guttata*)	Juveniles to adults	0.536	Noguera et al. (2015)
Zebra finch (*Taeniopygia guttata*)	Heritability of telomere length in zebra finch	Juveniles to adults Adults	0.814 0.819	Atema et al. (2015) Atema et al. (2015)
Zebra finch (*Taeniopygia guttata*)	Interacting effects of early dietary conditions and reproductive effort on the oxidative costs of reproduction	Adults	0.053	Noguera (2017)
Zebra finch (*Taeniopygia guttata*)	Experimental increase in telomere length leads to faster feather regeneration	Adults	0.418	Reichert, Bize, et al. (2014)
Zebra finch (*Taeniopygia guttata*)	Increased brood size leads to persistent eroded telomeres	Adults	0.518	Reichert, Stier, et al. (2014)
Zebra finch (*Taeniopygia guttata*)	Elevated reproduction does not affect telomere dynamics and oxidative stress	Adults	0.386	Sudyka et al. (2016)

TABLE 2 The results of a phylogenetic model including all tested predictor variables

Random Intercepts	SD	l–95% CI	u–95% CI
Phylogeny	0.28	0.02	0.70
Species	0.29	0.16	0.43
Laboratory identity	0.26	0.15	0.41
Fixed effects	**Estimate**	**l–95% CI**	**u–95% CI**
Intercept (qPCR)	*0.50*	*0.09*	*0.78*
Method (TRF)	*0.58*	*0.43*	*0.70*
Study length (standardized)	*−0.08*	*−0.15*	*−0.01*
Taxon (ectotherms)	−0.04	−0.50	0.53
Environment: Semi wild	−0.17	−0.38	0.06
Environment: Wild	−0.07	−0.26	0.14
Species lifespan (standardized)	−0.06	−0.16	0.05
Ageclass: Juveniles	0.08	−0.05	0.21
Ageclass: Juveniles & Adults	0.10	−0.04	0.23

Notes: Coefficients show *R* values and are the result of back-transformed standardized Z-values. Species accounts for the repeated measures per species, phylogeny for the fact that these species are related, and laboratory identity for the fact that protocols are more similar within a laboratory. Fixed effects in italics show the variables for which the 95% CI did not overlap with zero. Intercept shows qPCR for average study length in a captive adult population of endotherm for a species with an average maximum lifespan. This table shows the model with all terms; a model without phylogeny or that contained only the terms in which 95% CI did not overlap with zero, gave consistent results (Tables S4 A–D). l–95% CI and u-95% CI indicate lower and upper 95% confidence intervals, respectively.

their Fisher-z-transformed variance. Second, we performed all analyses on untransformed repeatability estimates, acknowledging that within-individual repeatability is a continuous distribution of a proportion with two categories (within vs. between individual variance). As such, the repeatability follows a beta distribution (Douma & Weedon, 2019; Ferrari & Cribari-Neto, 2004). Hence, we also performed all analyses using a beta distribution and logit link function and weighing each study according to the inverse of their sample size. For both approaches, model residuals fulfilled all assumptions, followed the quantiles of the used distribution with variance homogeneity and without influential datapoints, as checked with the functions "influence" and testResiduals of the packages influence.ME and DHARMa (Hartig, 2019; Nieuwenhuis et al., 2012). Both approaches gave consistent results and below we present the results of the first approach using Fisher's Z-transformation and a normal error distribution. For the ease of interpretation, we back-transformed Z values to effect size (intraclass correlation coefficient ICC) values and their 95% CI following equation 6 in (Holtmann et al., 2017).

The models contained as fixed effects: (i) measurement method (qPCR or TRF), (ii) study length (continuous variable), (iii) taxon (i.e., ectotherm or endotherm), (iv) environment (captive, semi-wild that is, wild held in captivity, or wild), (v) age class (juveniles, adults or juveniles to adult; the limit between juvenile and adult stage being defined *as* the sexual maturity) and (vi) species maximum lifespan (continuous variable). We standardized continuous fixed effects with a mean of 0 and a variance of 1. We analysed whether there were biases in predictor variables between measurement methods using permutation tests with the function independence_test of the package coin (Hothorn et al., 2008) based on 10,000 permutations. We used χ^2 tests to identify deviations from 50/50. qPCR was used more than twice as often as TRF, accounting for 70% ($N = 57$) of the estimates and 76% ($N = 3757$) of the individuals (Figure 2; $\chi^2 = 5.4$; $p = .02$). There were no TRF measurements in fish, but otherwise there was no taxon-specific or system-specific bias between both methods (Table S3). Indeed, studies from the wild were equally overrepresented in both methods, respectively at 63% ($N = 36$) and 70% ($N = 19$) of the qPCR and TRF estimates ($Z = 1.02$; $p = .40$). Species measured by qPCR had a shorter maximum lifespan than those measured by TRF, respectively with a median maximum lifespan of 15.0 years (95% CI: 7.4–36.8) and 20.3 years (95% CI: 6.0–34.4; Table S3), but this difference was not statistically significant ($Z = -1.29$; $p = .20$). This difference might be driven by researchers working with shorter-lived species resorting to qPCR, as mammals with short lifespans tend to have long telomeres (Risques & Promislow, 2018) and measuring long telomeres with TRF is more difficult than with qPCR. However, we consider this unlikely, as we have TRF data also for small and/or short-lived birds (such as quail, pied flycatcher and zebra finch) as well as for longer-lived ones, and ultimately, telomere length seems not to be associated with maximum lifespan in birds (Tricola et al., 2018), which comprise the largest part of the data in this study. Study length was somewhat shorter in qPCR than TRF studies with respectively 3.3 months (95% CI: 0.6–128) and 10.0 months (95% CI: 0.8–85; Table S3), but this difference was not statistically significant ($Z = -0.38$; $p = .70$). When adjusting study length relative to species maximum lifespan the difference between qPCR and TRF became even smaller at respectively 1.0% (95% CI: 0.13–19) and 3.0% (95% CI: 0.1–15; $Z = 0.05$; $p = .96$). There was also no statistically significant difference between both methods in monitored age classes (juvenile versus adult or both; Table S3; $Z = 1.59$;

$p = .20$). Hence, we did not detect any species-specific bias in the data distribution between TRF and qPCR measurement methods.

To account for the fact that several studies came from the same laboratory ($N = 22$), we included laboratory identity as random intercept. To account for multiple measurements of the same species ($N = 42$), we included species identity as a random intercept. Species are, however, related by phylogeny (Figure 3). We therefore also included phylogeny as a random term in this analysis following Hadfield and Nakagawa (2010) and de Villemereuil and Nakagawa (2014), in which the phylogeny is captured in the variance-covariance matrix between species in the mixed model. This model contains both species and phylogeny as random intercepts because these terms capture different variances, respectively the within-species variance, while the phylogeny accounts for the relatedness between species (de Villemereuil & Nakagawa, 2014). To identify whether there was a role of phylogeny in the within-individual repeatability of telomere length, we estimated the phylogenetic signal lambda (λ), which is the ratio of the variance explained by phylogeny relative to the total variance explained by the model and hence its value ranges from 0 (no signal) to 1 (Freckleton et al., 2002; Hadfield & Nakagawa, 2010). We constructed a phylogeny of the 42 species in this study using the Open Tree of Life (Hinchliff et al., 2015) with the package ROTL (Michonneau et al., 2016). We set the branch lengths following Grafen (1989) with the function compute.brlen from the package APE (Paradis & Schliep, 2019).

We performed the mixed-model meta-analyses without and with phylogeny, which gave consistent results (Table S4). Here we present the analyses with phylogeny performed using a Bayesian approach with the function brm from the package brms (Bürkner, 2017), but note that the conclusions were consistent with those based on a frequentist approach with the functions lmer and gls of the packages lme4 and nlme, respectively (results not shown). For the Bayesian models, we used weakly informative priors and ran four chains each with 1,500,000 iterations, a burnin of 100,000 and a thinning of 250, resulting in a posterior effective sample size of >2,000 and an Rhat of 1, which together with pareto-k-diagnostics ($k < 0.7$), visual inspection of the trace plots and potential scale reduction factor showed that simulations had ran properly (Bürkner, 2017). We evaluated the relative fits of the Bayesian model on the data using the leave-one-out cross-validation (LOO) approach (Vehtari et al., 2017) and compared the models' relative weight with the functions loo and model_weights of the package brms. In brief, a model's weight is an estimate of the probability that the model will make the best predictions on new data, conditional on the alternative models considered with the weights of all models adding up to 1. We determined the statistical significance of the fixed effects and random effects based on their model fit (loo weights for Bayesian models) and the overlap with 0 of the 95% CI of coefficients or variance estimates.

We assessed publication bias based on visual inspection of funnel plots of "meta-analytic" residuals of the model in Table 2 (Figure S4), the Egger's test on the residuals of this model (Egger et al., 1997; Nakagawa & Santos, 2012) and using the trim and fill method (Duval & Tweedie, 2000) with the function trimfill in the package metafor (Viechtbauer, 2010). None of these approaches indicated there was publication bias.

3 | RESULTS

We obtained 82 repeatability estimates from 74 studies on 42 species measured in 22 laboratories based on a total of 4918 individuals. Individuals were measured on average 2.3 times (95% CI: 2.0–3.0)

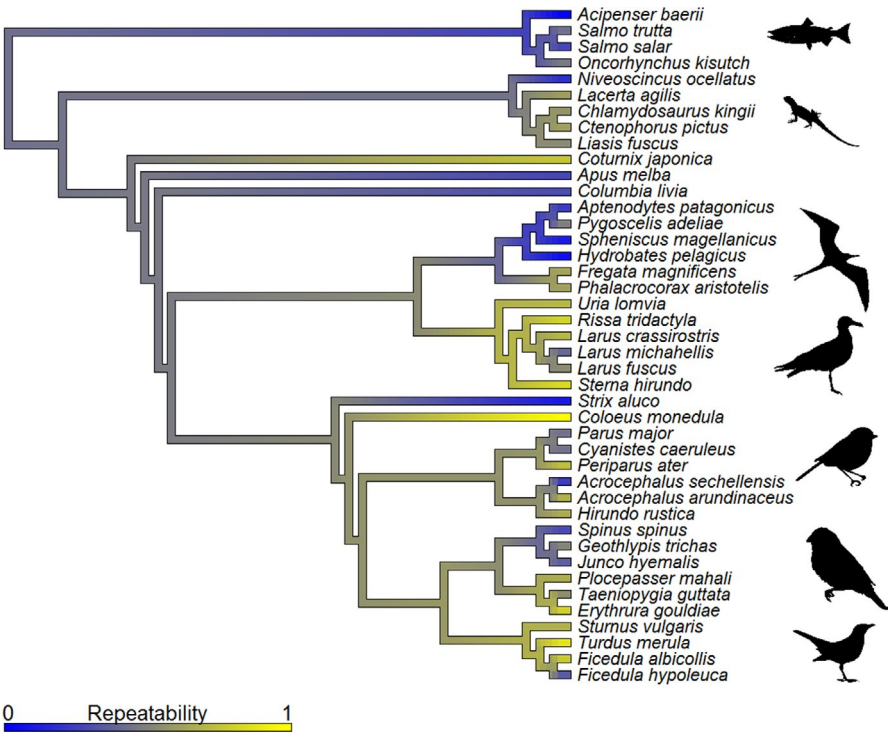

FIGURE 3 Distribution of the within-individual repeatability of telomere length along the phylogeny of the 42 species in this study. Although the phylogenetic signal was not significantly different from 0 (λ: 0.32; 95% CI: 0.00–0.83), phylogeny still captured some variance (Table 2) and a model with phylogeny was favoured over one without phylogeny. The phylogenetic distributions of the other traits in this study are shown in Figure S6

and were monitored for a median of 4.2 months (95% CI: 0.6–121) or 1.4% of the species' maximum lifespan (95% CI: 0.1–19.0). Birds were overrepresented relative to reptiles or fish, accounting for 87% (N = 71, Figure 2) of the estimates and 90% (N = 4439) of the individuals. Studies on wild systems were twice as abundant as studies on semi-wild or captive systems, accounting for 67% (N = 55) of the estimates and 70% (N = 3422) of the individuals (Figure 2).

The within-individual repeatability of telomere length was overall moderate to high, with a median value of R = 0.55. Yet, there was marked variation between studies, as exemplified by the large 95% CI around median R value from 0.05 until 0.95. There was no clear phylogenetic signal for the repeatability of telomere length (λ R = 0.38; 95% CI: 0.00–0.85; Figure S5A; λ model Table 2 = 0.32; 95% CI: 0.00–0.83, Figure S5B), but phylogeny captured some variance (SD: 0.28; 95% CI: 0.02–0.70; Table 2) and a model with phylogeny (Figure 3) was favoured over one without phylogeny, albeit moderately (respective loo-weights 0.57 vs. 0.43). As a control, we checked in the same data set, the phylogenetic signal of maximum lifespan, which was moderate but statistically significant (λ = 0.38; 95% CI: 0.03–0.77; Figure S5C; Figure S6) and a model with phylogeny was strongly favoured over a model without phylogeny (loo-weights of 0.83 vs. 0.17).

There was a statistically significant effect of telomere length measurement method (Table 2): the median within-individual repeatability of TRF-based studies was high at R = 0.80 (N = 25; 95% CI: 0.34–0.96; Figure 4; Figure 5b), while that of qPCR-based studies was almost half of that and more variable at R = 0.46 (N = 57; 95% CI: 0.04–0.82; Figure 4; Figure 5b). Because not all TRF studies used methods that excluded ITS (eight out of 22 effect sizes for which this information was reliably available), we tested whether the R was different for those studies that included ITS than for those that did not, but the difference was not statistically significant (mean $R \pm SD$ = 0.67 ± 0.27 and 0.78 ± 0.15, respectively; t = −0.64, p = .53). Within-individual repeatability of telomere length also decreased with the length of the study (β = −0.08; −0.15 < 95% CI < −0.01; Table 2; Figure 5e). Once these methodological variables were accounted for, none of the biological variables we tested (i.e., taxon, species' maximum lifespan, environment, age class) had a statistically significant effect on the repeatability of telomere length (Table 2; Figure 5a–g). There was a weak negative association between the within-individual repeatability of telomere length and species' maximum lifespan, but the 95% CI of this coefficient overlapped with zero (β = −0.06; −0.16 < 95% CI < 0.05; Table 2; Figure 5f), indicating little statistical support for an association between species' maximum lifespan and the repeatability of telomere length.

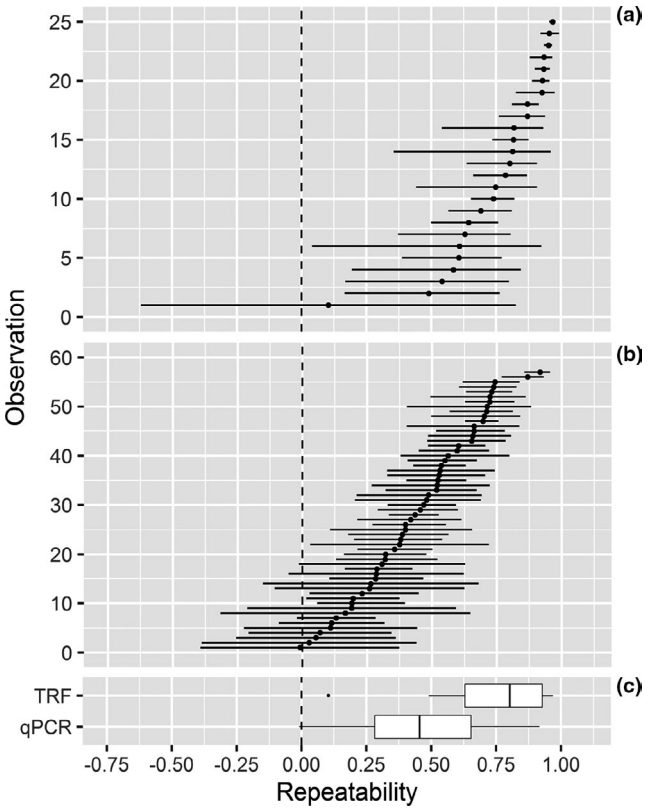

FIGURE 4 Distribution of within-individual repeatability estimates (and 95% CI) of telomere length for studies using (a) TRF and (B) qPCR and (c) their boxplots with median, quartiles and 95% CI. Vertical dashed line denotes a repeatability of 0

4 | DISCUSSION

The within-individual repeatability (R) of measurements over time is a key requirement to identify the dynamics of variables and the factors driving these dynamics. Telomere length changes over time and this change is known to be affected by various factors, for example, pre- and postnatal environmental conditions (Kärkkäinen et al., 2021; Stier et al., 2020), stress exposure (Chatelain et al., 2020), and reproductive effort (Reichert, Stier, et al., 2014). Yet, to link a single telomere measurement to past environmental conditions or future performances (e.g., following reproductive success), telomere length also needs to be repeatable to some extent. Here, we performed a meta-analysis of the within-individual repeatability of telomere length and investigated some biological and methodological variables that might affect this repeatability. Overall, we found telomere length to be relatively repeatable at R = 0.55 but the repeatability was highly variable across studies varying from almost 0 to almost 1. The repeatability was mainly driven by measurement method, with studies using qPCR method showing a repeatability that was almost half and more variable than those using TRF. The within-individual repeatability of telomere length declined with the length of study and tended to decline with species maximum lifespan, although the latter was statistically nonsignificant. Phylogeny explained a minor, but a statistically significant part of the variance in within-individual repeatability. Any other tested biological variable did not have a statistically significant measurable effect on the repeatability estimates. Here, we discuss three major implications of our study.

First, while repeatabilities of physiological traits have been investigated before, to the best of our knowledge this is the first

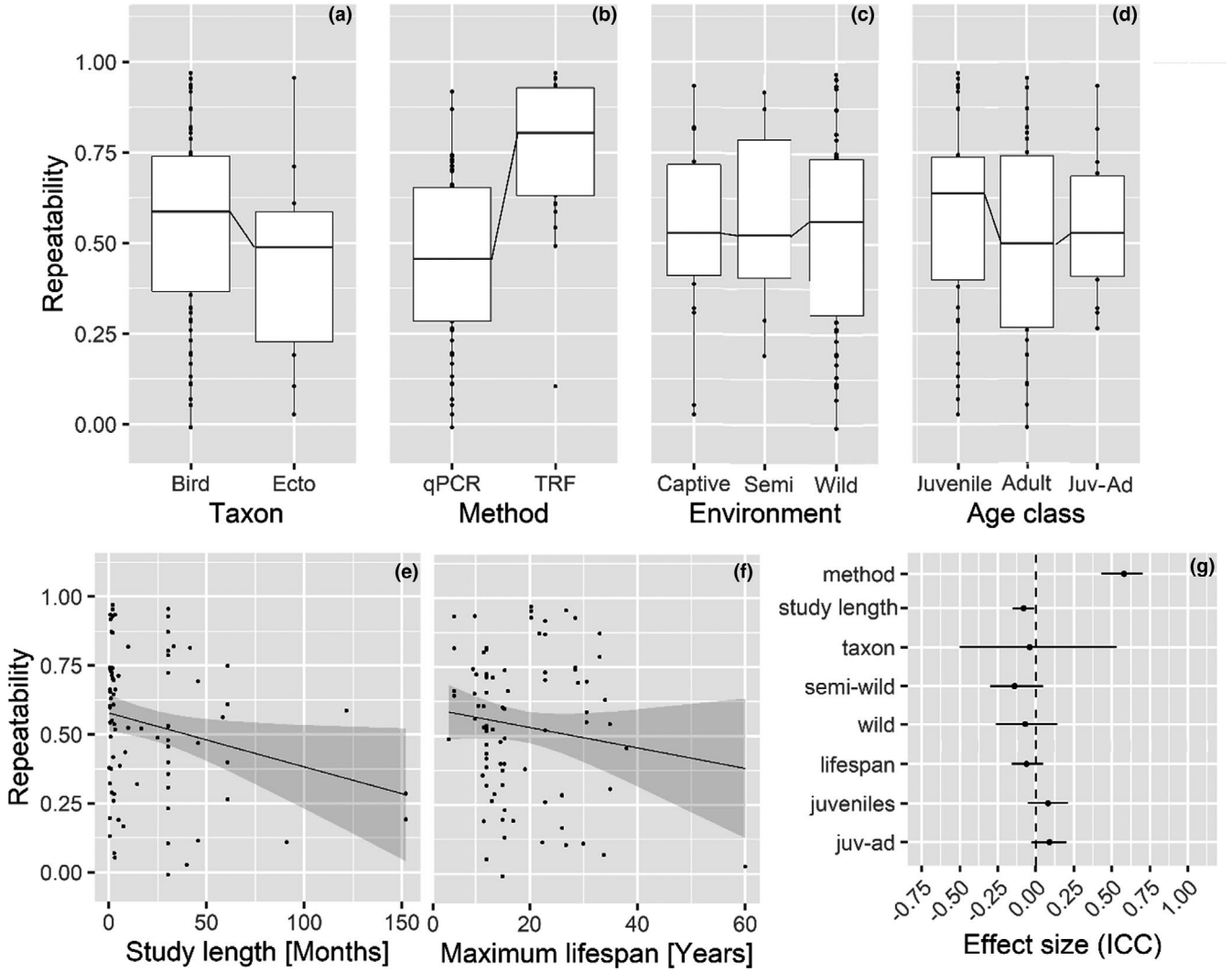

FIGURE 5 Effects of biological and methodological factors on the repeatability of telomere length. Measurement method (b) and study length (e) affected clearly the repeatability of telomere length, while the effect of the biological variables ([a] taxon, [c] environment, [d] age class, and [f] species lifespan) were small and their effect size overlapped with zero (g). For illustration purposes, fits on the continuous predictors are the result of frequentist models on the best fitting model in Table 2, but are consistent with the conclusions of the model in Table 2

meta-analysis on the within-individual repeatability of telomere length. The within-individual repeatability of glucocorticoid levels have been reported to be about half of that of telomere length at $R \approx 0.3$ (Schoenemann & Bonier, 2018; Taff et al., 2018). This is not surprising as repeatability is not expected to be really high for labile traits (Bonier & Martin, 2016), and most arguably within-individual hormone levels are more variable in time than within-individual telomere length. The repeatabilities of metabolic rates (basal, standard and resting) were more similar to our estimates of the repeatability of telomere length: $R \approx 0.60–0.80$ in Nespolo and Franco (2007), $R \approx 0.45–0.55$ in Holtmann et al. (2017), $R \approx 0.42–0.65$ in Auer et al. (2016), $R \approx 0.40–0.50$, but mass-adjusted $R \approx 0.30–0.40$ in Briga and Verhulst (2017). Phylogeny accounted for a large fraction of the variation in the repeatability of metabolic rate between studies (Holtmann et al., 2017). In contrast with metabolic rate, the within-individual repeatability of telomere length was little affected by phylogeny, or the biological factors studied here. Contrary to our prediction, we found a negative association between the within-individual repeatability of telomere length and species maximum lifespan, albeit not statistically significant. There is some evidence that long-lived bird species maintain telomerase activity throughout life (Haussmann et al., 2007), which could explain this negative association if different individuals have different levels of telomere maintenance depending, for example, on resource availability. However, the lack of statistically significant biological factors and the minor role of phylogeny indicate that biological explanations may not be the main drivers of the variation we observed in the within-individual repeatability of telomere length. Yet, we cannot exclude that biological factors might be important in explaining variation in the repeatability of telomere length, but that the currently available data did not enable us to detect such effects.

Second, methodological factors explained most of the variation in the within-individual repeatability of telomere length. Consistent with our expectation, the repeatability of telomere length declined with study length. A similar association was also found for the repeatability of metabolic rate (Auer et al., 2016; Briga & Verhulst, 2017). However, most of the variation in the repeatability was captured by the measurement method. Consistent with our expectation, studies using TRF method to measure telomere length yielded higher repeatability estimates than studies using qPCR. qPCR has greater propensity to measurement error than TRF (Aviv et al., 2011) and any measurement errors in telomere (T) and single copy gene (S) reactions are magnified in the calculated T/S ratio (Nettle et al., 2019). Consequently, it has been shown that measurement error alone can decrease within-individual repeatability in telomere length in longitudinal qPCR studies (Nettle et al., 2019), even if cross-sectional accuracy is confirmed with TRF (Nettle et al., 2020 preprint). Extensive discussions on the measurement reliability between these methods have been published previously elsewhere (Martin-Ruiz et al., 2015a,2015b; Verhulst et al., 2015, 2016). As there is no clear biological explanation for the difference for lower average *R* in qPCR studies than TRF studies, one possible conclusion is that the true biological within-individual repeatability would be close to the average of TRF studies (0.80). This very high repeatability would imply that telomere shortening among individuals would be fairly constant and that environmental effects have little effect on the shortening rates, thus lowering the within-individual variance, especially since we were not able to correct for age differences, which artificially increases between-individual variance (e.g., difference in telomere lengths between young and old adults at first sampling). This would make telomere length a poor biomarker to link environmental conditions to subsequent fitness. However, it is also important to note that the occurrence of ITS in qPCR and some TRF measurements (Foote et al., 2013) and subtelomeric regions in the TRF measurements (Baird, 2005) might affect the within-individual repeatability estimates of telomere length. Amount of ITS can vary between individuals of the same species but is not considered to change with time within an individual (Foote et al., 2013), which could artificially inflate the within-individual repeatability of telomere length by increasing the between-individual variance. While in this study there was no significant difference in the *R* estimates between TRF studies that included or excluded the ITS, we cannot fully rule out that ITS might influence the repeatability estimates, especially since TRF studies including ITS covered only six species. Relatively similarly, the subtelomeric regions captured by TRF can also vary between individuals but are assumed to remain stable within an individual over time. Thus, the occurrence of ITS and of subtelomeric regions might inflate the repeatability of telomere length. This might explain both the importance of measurement method (effect size, Figure 5g), and the large variation observed between qPCR studies. Indeed, while ITS presence and amount is variable between species (Foote et al., 2013), subtelomeric regions are present in basically all organisms (Mefford & Trask, 2002), which might potentially contribute to the high *R* found by TRF studies. Furthermore, in qPCR studies it is assumed that the reference gene used to normalize the amount of telomeric sequence does not vary in copy number between individuals. However, this assumption is rarely tested (Smith et al., 2011). The potential variation in copy number of different reference genes might explain part of the very high variation found in R across qPCR studies.

Third, given the importance of measurement method, there are a number of methodological practices that are known to affect the quality and repeatability of telomere length measurements, especially in qPCR telomere measurements: differences in sample storage (Eastwood et al., 2018; Reichert et al., 2017), DNA extraction method (Dagnall et al., 2017; Seeker et al., 2016), the type of qPCR master mix being used (Morinha et al., 2020a), and even the stability of power supply (Hastings et al., 2020). Furthermore, while DNA integrity is widely known to be important in TRF, it is traditionally thought to be less crucial in qPCR (Aviv et al., 2011). However, recent evidence suggests that DNA degradation can either increase or decrease telomere length measured with qPCR (Ropio et al., 2020; Tolios et al., 2015). Currently, DNA integrity is rarely assessed before performing qPCR analyses, and standard agarose gel electrophoresis might be insufficient to assess DNA integrity for qPCR telomere length measurement (Antoine Stier, personal observation). Practices during the analytical phase can also potentially affect the repeatability of telomere measurements. In longitudinal studies, especially if using long-term data, data are often analysed in batches and/or clusters. Failure to consider the sample structure among the batches and clusters can create variation from which it is impossible to separate the biological variation from the confounding between batch/cluster variation (van Lieshout et al., 2020). When analysing longitudinal samples, the samples from the same individual are often analysed on the same plate/gel to increase statistical power to detect within-individual effects. However, doing so, but not controlling for the plate/gel effect by measuring repeated samples on every plate/gel, can inadvertently increase the within-individual repeatability, while analysing the samples from the same individual on different plates/gels will often decrease the within-individual repeatability. Thus, there are a number of methodological practices that need to be taken into account to improve the repeatability of telomere length in both qPCR and TRF methods. Quantifying the relative importance of these practices is beyond the scope of this meta-analysis but warrants further investigation.

To conclude, telomere length is increasingly used as a biomarker for past stress exposure (Chatelain et al., 2020) and future performance (Eastwood et al., 2019; Heidinger et al., 2012). However, we argue that for a single telomere length to be truly informative about the past or the future, telomere length requires a reasonable within-individual repeatability over time. Some studies suggest associations between early-life telomere length and lifespan, but not between adult telomere length and lifespan (Heidinger et al., 2012; Quque et al., 2021) thereby questioning the importance of within-individual repeatability. Yet, these studies still exhibit moderate within-individual repeatability estimates (e.g., $R = 0.47$ in Heidinger et al., 2012 and $R = 0.34$ in Quque et al., 2021) suggesting the potential importance of within-individual repeatability. Inferring for instance

any long-lasting effects of early-life environmental conditions or predicting future survival probability when the within-individual repeatability is virtually close to 0 (in c. 23% of qPCR studies) might lead to spurious conclusions. Similarly, repeatability often sets an upper limit to heritability (Falconer & Mackay, 1996; Lynch & Walsh, 1997, but see Dohm, 2002) and low repeatability will conceal the heritable component of telomere length. Accordingly, heritability estimates are usually higher for TRF than qPCR studies (Bauch et al., 2020), which is in line with the strong method effect found here for within-individual repeatability. Our study indeed indicates that the within-individual repeatability of telomere length is mainly driven by telomere measurement method, with the repeatability being significantly lower with qPCR than with TRF. Unfortunately, the majority of the longitudinal telomere studies to date have used qPCR, which may partly mask the role of biological variation in telomere length and dynamics. The tendency of decreasing repeatability with increasing sampling interval might ultimately indicate that environment does play a role in shaping individual telomere length trajectories, but differences in sample storage and processing are also more likely to occur with longer sampling interval. It might be worth reassessing whether biological factors drive within-individual repeatability in telomere length when there will be more TRF studies and/or when the repeatability of qPCR has improved. Meanwhile, we encourage scientists to design their research and laboratory practices to aim at accurate repeatability by reducing factors that potentially create technical variation in telomere length measurements. It is noteworthy, that while TRF studies regularly showed higher repeatability estimates than qPCR studies, it is also possible to achieve high repeatability using qPCR. In qPCR studies it is important to pay particular attention to both sample handling and storage and optimizing the qPCR protocol (see Lindrose & Drury, 2020; Morinha et al., 2020b for specific guidelines and Lindrose et al., 2021 for a review of methodological reporting in telomere studies). We particularly encourage scientists to estimate and report the within-individual repeatability *R* of telomere length of their study systems in their manuscripts along with the technical repeatability. Repeatabilities are driven by measurement error and/or biological variables and ideally, we would want to decompose the contribution of both components. To obtain this information, the ideal solution would be to measure the same sample of enough individuals at least twice (with independent DNA extraction and randomized over gels/plates). This way one would be able to partition random variance over samples, gels/plates, individuals, possibly correcting for age as a fixed effect. We are aware that for TRF this could be financially and labor expensive, but for qPCR this should be feasible. With qPCR however, it is important to validate that the used reference gene does not vary in copy number between individuals as it would increase the technical repeatability but lower the within-individual biological repeatability of telomere length. This would thus allow the estimation of the technical and the biology-driven repeatability and hence testing some of the predictions we proposed in this study. Longitudinal studies still rarely report within-individual repeatability of telomere length, while it can be a key statistic for the interpretation of both the reliability of the methodology and the biology driving the dynamics of telomere length and more generally individual traits.

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AUTHOR CONTRIBUTIONS

Antoine Stier and Tiia Kärkkäinen conceived the study and collected data from the literature, Michael Briga and Tiia Kärkkäinen analysed the data. All authors contributed to data interpretation. Tiia Kärkkäinen, Michael Briga and Antoine Stier wrote the manuscript with input from Toni Laaksonen.

OPEN RESEARCH BADGES

This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.6084/m9.figshare.16419063.

DATA AVAILABILITY STATEMENT

Data used in this study are publicly available in Figshare (https://doi.org/10.6084/m9.figshare.16419063).

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