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Investigating how telomere dynamics, growth and life history covary along an elevation gradient in two passerine species

Antoine Stier, Anne Delestrade, Pierre Bize, Sandrine Zahn, François Criscuolo[#] and Sylvie Massemin[#]

A. Stier (antoine.stier@gmail.com), Univ. of Angers, GECCO (groupe écologie et conservation des vertébrés), 2 Boulevard Lavoisier, Angers FR-49045, France. – A. Delestrade, Centre de Recherche sur les Ecosystèmes d'Altitude (CREA), Observatoire du Mont-Blanc, 67 lacets du Belvédère, FR-74400 Chamonix, France, and Laboratoire d'Ecologie Alpine, Univ. de Savoie (UMR 5553), FR-73376 Le Bourget du Lac, France. – P. Bize, Inst. of Biological and Environmental Sciences, Univ. of Aberdeen, Aberdeen, AB24 2TZ, UK. – S. Zahn, F. Criscuolo and S. Massemin, Univ. of Strasbourg, Inst. Pluridisciplinaire Hubert Curien, Strasbourg, France, and Dépt d'Ecologie, Physiologie et Ethologie (DEPE), CNRS UMR7178, 23 rue Becquerel, FR-67087 Strasbourg Cedex 2, France.

Telomeres are specialized non-coding DNA sequences that cap the end of chromosomes and protect genome integrity. Because telomeres shorten during development and their length at maturity is often associated with survival, one hypothesis is that telomere erosion during early growth is closely associated with life history trajectories of individuals and species. Elevation gradients lead to systematic changes in environmental factors, and thus they provide unique opportunities to explore how life history trajectories and telomere dynamics can covary under various environmental conditions. Here, we address this question in chicks of two tit species distributed foremost at low elevation (the great tit *Parus major*) or at high elevation (the coal tit *Periparus ater*). With increasing elevation, great tits showed delayed breeding, and their chicks a slower development, higher telomere erosion and shorter telomere length at day 16. Although coal tit parents delayed also their breeding with increasing elevation, their chicks had a faster development, higher telomere erosion but no reduced telomere length at day 16. This last result is explained by coal tit chicks having longer telomeres at day 7 at high than low elevation, thus mitigating effects of fast telomere erosion before fledging. Our findings on life histories support the idea that great tits and coal tits are best adapted to low and high elevation, respectively. Our data on telomere provide however no support for a direct link between early growth rate and telomere dynamics, but underline complex interplays between telomere dynamics and environmental conditions experienced early in life, thereby urging for studies identifying how early life conditions actually determine fledgling's telomere length.

Telomeres are non-coding DNA sequences located at the end of eukaryotic chromosomes, informing the cell about the health and integrity of its gene pool (De Lange et al. 2006). Telomeres shorten at each cell division and over organisms' life course in somatic tissues, but they can also shorten in response to various environmental stressors (Monaghan and Haussmann 2006, Herborn et al. 2014, Asghar et al. 2015a). Interestingly, telomere length and/or dynamics has been pointed out as a relevant proxy of survival in birds when measured at adulthood (Bize et al. 2009, Salomons et al. 2009, Barrett et al. 2013) or even at the nestling stage (Heidinger et al. 2012, Stier et al. 2014c, Asghar et al. 2015a). Because telomere length at adulthood is highly correlated to telomere length at the fledging stage (Boonekamp et al. 2014), and because most of telomere loss occurs during early growth, one hypothesis is that changes in telomere length during early growth are closely associated with changes in growth rate and life history trajectories, providing ultimately a causal link between growth rate and lifespan (Monaghan and Haussmann 2006). Early-life telomere length is likely to be determined both by genetic and environmental factors, even if the magnitude of genetic and environmental contributions remains debated so far in birds (Asghar et al. 2015b, Atema et al. 2015, Becker et al. 2015, Reichert et al. 2015). Interestingly, recent studies showed that growing under harsher environmental conditions might be related to increased telomere erosion. Experimental manipulation of brood size or sibling competitive environment have been associated with increased telomere erosion (Boonekamp et al. 2014, Reichert et al. 2014, Nettle et al. 2015), but also to long-term life history consequences (Boonekamp et al. 2014). Data showing that natural conditions experienced early in life are accounting for changes and covariations between telomere lengths, growth and life histories remain however scarce (Geiger et al. 2012, Stier et al. 2014a).

Elevation gradients lead to systematic changes in environmental factors, and can ultimately promote variation in

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[#] These authors share the seniorship of this paper.

life history trajectories (Badyaev and Ghalambor 2001, Bears et al. 2009). Hence, elevation gradients provide unique opportunities to explore changes and covariations between telomere lengths, growth and life history trajectories in free-living bird populations. Here, we followed telomere dynamics and concurrent growth patterns of great tit *Parus major* and coal tit *Periparus ater* chicks from different populations at low, intermediate or high elevations, and therefore facing contrasted environmental conditions. Growing at a higher elevation might be considered as harsher since temperature, oxygen availability and even insect availability is likely to decrease with increasing elevation (Hodkinson 2005, Stier et al. 2014b). For each species, we tested covariations between environmental conditions (i.e. elevation), individual growth characteristics (i.e. initial body mass, growth rate and asymptotic body mass) and telomere dynamics. We predicted that, under harsher environmental conditions (i.e. high elevation), chicks should show reduced growth rate (Bordjan 2013) and/or increased telomere erosion. In addition, we expected that effects of elevation on growth rates and/or telomere lengths might differ between the two tit species. Indeed, great tits and coal tits differ in their elevation preferences (Zang 1980), and we expected coal tits typically breeding in habitats of higher elevation to be less sensitive to changes associated with an increase in elevation (Zang 1980). Finally, because increased telomere erosion has been suggested to be a cost of fast growth (Geiger et al. 2012), we predicted that fast growth should be associated with increased telomere erosion.

Material and methods

Study sites and animals

Great and coal tits were studied using artificial nest boxes located at three different sites (France) from April to June 2011: in the French Alps (34 nest boxes at 1300 and 1900 m of elevation, Vallorcine), in the Vosges (20 nest boxes at 700 m, Grendelbruch), and near Strasbourg (52 nest boxes at 100 m). We successfully monitored 33 nests of great tits (21 nests at 100 m, 8 nests at 700 m, 4 nests at 1300 m) and 14 nests of coal tits (8 nests at 1300 m, 6 nests at 1900 m). Nests were visited every second day throughout the season to determine incubation duration, hatching date and whole clutch mass, clutch/brood size and number of fledglings. Starting from hatching, only 3 to 5 of the first hatching chicks (i.e. selected randomly among the first-day hatched chicks based on body mass/size) per clutch were followed to avoid indirect effects of hatching asynchrony due to late-hatched chicks, previously known to differ from other chicks in terms of physiological quality (e.g. oxidative stress and telomere dynamics, Stier et al. unpubl.). We had data for 95 great (100 m, n = 53; 700 m, n = 22; 1300 m, n = 20) and 69 coal tit chicks (1300 m, n = 39; 1900 m, n = 30).

Growth measurements

We recorded the body mass (± 0.1 g) from hatching every second day until day 16 post-hatching. Fledging occurred at day 17–20 (unpubl.) for both great and coal tits. Individual body mass growth was fitted as: $Y(x) = \dfrac{A}{\left[1 + \exp\left(-K^{*}x - B\right)\right]}$, where $Y(x)$ was the body mass of a chick at age x (g), A is the asymptotic-final mass, K is the growth rate constant (an increase in K value implies an increase in the rate at which mass increases from initial value to asymptotic value) and B is a constant linked to the initial mass (nonlinear regression procedure in SPSS (SPSS 20.0 © 1989–2011 SPSS, USA)). Initial body mass (day 1) was estimated using the parameters obtained for each chick.

Telomere length assay

Chick blood samples (30 µl) were taken from the brachial vein, at day 7 and day 16. Telomere length was measured using extracted DNA from blood cells (Macherey–Nagel Nucleospin® Blood QuickPure extraction kit) following the qPCR protocol previously used in birds (Criscuolo et al. 2009). Runs of qPCR measurements were conducted separately for each species and normalised by a different 'golden sample standard'. Therefore, relative telomere length should not be directly compared between species. Relative telomere lengths were obtained using the ratio of the quantity of 1) telomere repeated sequences relative to 2) the quantity of DNA of a reference gene non variable in copy number among individuals (T/ non-VCN or thereafter T/S ratio). Details are provided in Supplementary material Appendix 1.

Statistical procedures

Breeding parameters were tested using non-parametric Kruskal–Wallis tests and associated post-hoc tests. The effects of elevation on growth parameters (initial body mass, A, K) were tested using linear mixed models, with nest as random effect, elevation as fixed effect, and sex as a fixed cofactor.

The effect of elevation on telomere length per se was assessed using repeated linear mixed models, with time (7 or 16 d) as a repeated effect, nest as a random effect, elevation and the interaction between elevation and time as fixed effects. Sex was included as a cofactor in our analyses, and growth characteristics were included as covariates. When a significant 'elevation × time' interaction occurred, we analysed each time point (day 7 and day 16) independently using linear mixed models.

Telomere dynamics might sometimes be more informative than telomere length per se (Boonekamp et al. 2014). Consequently, we also investigated the effect of elevation on change in telomere length between day 7 and 16 using linear mixed models. We included initial telomere length as a covariate (Verhulst et al. 2014) and growth parameters, and we tested if telomere change was significantly different from 0 within each population using one-tail *t*-tests.

We choose to present the most parsimonious models (including only significant parameters and interactions), but we also reported p-values for non-significant factors (i.e. extracted from the initial full model) in the tables. Means are quoted ± SE.

Results

Breeding parameters

In both species, hatching date was delayed with increasing elevation (great tit, *K–W* $\chi^2 = 17.46$, $p < 0.001$; coal tit, *K–W* $\chi^2 = 6.36$, $p = 0.012$, Fig. 1) and duration of incubation was longer at high elevation (great tit, *K–W* $\chi^2 = 18.06$, $p < 0.001$; coal tit, *K–W* $\chi^2 = 5.44$, $p = 0.020$, Fig. 1). However, clutch size, clutch mass, brood size and number of fledged chicks were non-significantly different across elevations in both great and coal tit pairs (all $p > 0.13$, Fig. 1).

Growth parameters

Initial body mass was not significantly affected by elevation or sex in both species (Table 1a). Growth rates differed among elevations but in opposite directions (Table 1b, Fig. 2a). In great tit chicks, the growth rate *K* decreased with increasing elevation (Fig. 2a, left panel). In contrast, coal tit chicks grew faster at higher elevation (Fig. 2a, right panel). Body mass at fledging (asymptotic mass) did not differ significantly between elevations in any species (Table 1c). Sex affected asymptotic body mass, with males being heavier than females at fledging, both in great (males 17.94 ± 0.21 g vs females 17.47 ± 0.17 g) and coal tits (males 10.17 ± 0.13 g vs females 9.87 ± 0.09 g).

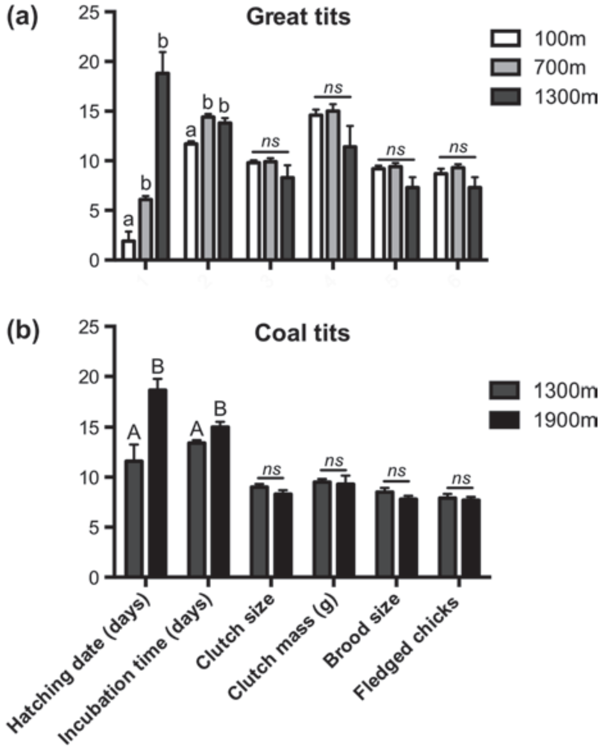

Figure 1. Changes in breeding parameters in great (a) and coal tits (b) along an elevational gradient (mean ± SE). Letters indicate significant differences between groups. Hatching date is expressed as the number of days from the 25 April.

Table 1. Summary of the most parsimonious linear mixed models explaining the variability in body mass growth parameters, i.e. (a) initial body mass, (b) *K* growth rate constant, and (c) asymptotic body mass *A*; for great and coal tit chicks. Significant factors are presented in bold, and the p-values reported for non-significant factors are the p-values of the initial full model (i.e. not the final model).

	Random (nest) effects	Estimates ± SE	F	p
(a) Initial body mass				
Great tits	0.056 ± 0.019			
Intercept		1.67 ± 0.26	42.5	**< 0.001**
Elevation				0.104
Sex				0.241
Coal tits	0.041 ± 0.018			
Intercept		1.03 ± 0.22	20.7	**0.001**
Elevation				0.218
Sex				0.899
(b) Growth rate constant *K*				
Great tits	0.0011 ± 0.0003			
Intercept		0.40 ± 0.04	140.2	**< 0.001**
Elevation		–0.06 ± 0.02	4.5	**0.020**
Sex				0.054
Coal tits	0.0013 ± 0.0006			
Intercept		0.46 ± 0.04	135.9	**0.002**
Elevation		0.05 ± 0.02	4.7	**0.050**
Sex				0.907
(c) Asymptotic mass *A*				
Great tits	1.25 ± 0.33			
Intercept		17.98 ± 1.14	239.9	**< 0.001**
Elevation		–0.68 ± 0.13	14.0	0.382
Sex				**< 0.001**
Coal tits	0.18 ± 0.09			
Intercept		10.16 ± 0.46	497.6	**< 0.001**
Elevation		–0.28 ± 0.13	4.7	0.275
Sex				**0.034**

Estimates are also reported for random (nest) effects.

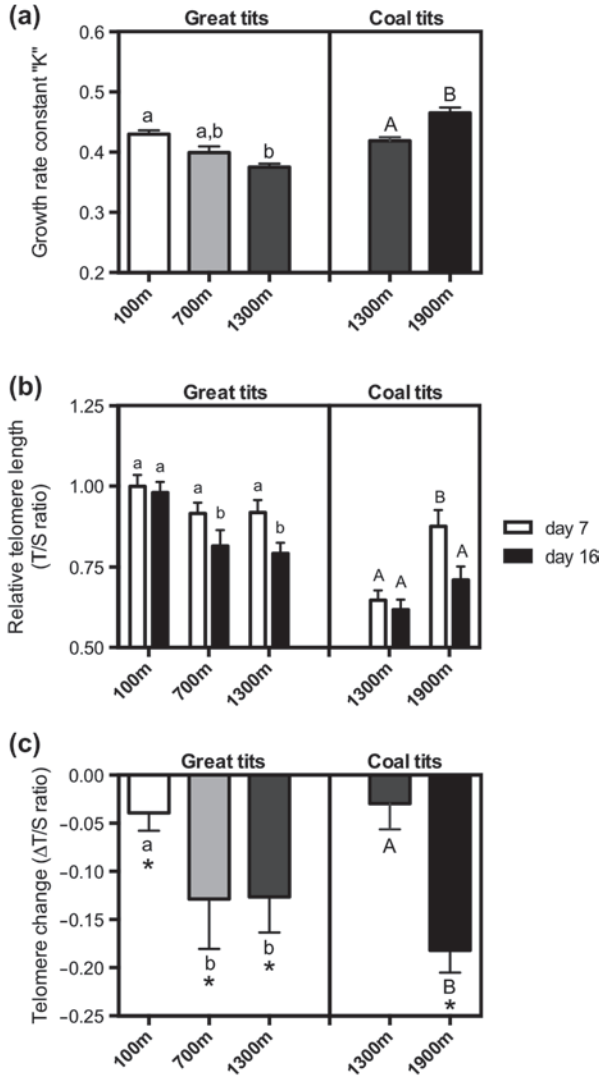

Figure 2. Differences in (a) body mass growth rate *K*, (b) telomere length, and (c) telomere change between day 7 and 16 among great (left panels) and coal tit chicks (right panels) reared at different elevations (mean ± SE). Letters indicate significant differences between groups (see results for details), and * in (c) indicate that telomere change is significantly different from 0 (one-tail *t*-tests; great tits = 100 m: p = 0.040, 700 m: p = 0.025, 1300 m: p = 0.003; coal tits = 1300 m: p = 0.274, 1900 m: p < 0.001). Note that that relative telomere length per se should not be compared between species (see methods for details).

Telomere length

In great tit chicks, telomere length per se was significantly affected by the elevation × time interaction (Table 2a, Fig. 2b left panel). Thus, we analysed separately the differences in telomere length at day 7 and day 16 among elevations. Telomere length was not significantly different among elevations at day 7 (F = 1.57, p = 0.215) whereas this difference became significant at day 16 (F = 7.62, p = 0.001), with great tit chicks having significantly shorter telomeres at 700 and 1300 m than at 100 m (Fig. 2b left panel). We found no significant effect of sex or growth parameters (Table 2a).

In coal tit chicks, the elevation × time interaction was also significant (Table 2b, Fig. 2b right panel). Separating the analyses by time revealed that telomeres at day 7 were significantly longer at higher elevation (F = 16.32, p < 0.001), while no significant difference was found at day 16 (F = 3.25, p = 0.08, Fig. 2b right panel). Interestingly we found a positive relationship between initial body mass and telomere length suggesting that heavier chicks at hatching also showed longer telomeres over the growth period (Table 2b). We found no significant effect of sex or other growth parameters (*A* and *K*; Table 2b).

Telomere dynamics

We found a significant shortening of telomeres in all populations, except in coal tits at 1300 m (Fig. 2c). Telomere shortening was more pronounced at the higher altitudes for both species, and initially long telomeres were more susceptible to erosion than short ones (Table 3, Fig. 2c). Growth parameters were not significantly correlated with telomere dynamics (Table 3). The effect of sex was significant only for coal tits, with females presenting a more pronounced shortening than males (Table 3; males –0.06 ± 0.03 vs females –0.13 ± 0.02).

Discussion

This study shows that great tit and coal tit chicks presented a modification of their growth rates with elevation, but in opposite directions, with slower growth rates with increasing elevation in great tit chicks and faster growth rates with increasing elevation in coal tit chicks. Because growth rate/body mass at fledging is an important proxy of survival in wild birds (Naef-Daenzer et al. 2001), our results support our prediction that great tit chicks are probably better adapted to lower elevation and coal tit chicks to higher elevation. Numerous ecological factors are known to change with increasing elevation, including food availability (e.g. limited abundance of insects, Hodkinson 2005) and exposure to cooler ambient temperatures. Hence, one likely explanation for the slower growth of great tit chicks at higher elevations was poor nutritional conditions (see Bordjan 2013 for similar results). In contrast, the faster growth of coal tit chicks with increasing elevation indicates potentially the occurrence of adaptive developmental plasticity in response to a shorter favourable season, explained for instance by the reallocation of resources towards growth at the expense of self-maintenance processes (see also Stier et al. 2014b). For instance, coal tit chicks might have reallocated resource from costly maintenance processes such as antioxidant defences or telomere repair/protection (e.g. telomerase activity, shelterin proteins) toward building new cells to support fast growth. In addition, coal tit chicks at the higher elevation had a higher resting metabolic rate, and interestingly growth rate was positively correlated with metabolic rate in coal tits (Stier et al. 2014b).

Our study also supports our prediction that growing at higher elevation is costly and leads to increased telomere erosion. Indeed, in both species we detected greater telomere

Table 2. Summary of the most parsimonious repeated linear mixed models explaining the variability in telomere length for (a) great and (b) coal tit chicks. Significant factors are presented in bold, and the p-values reported for non-significant factors are the p-values of the initial full model (i.e. not the final model).

Telomere length	Random (nest) effects	Repeated (time) effects	Estimates ± SE	F	p
(a) Great tits	0.024 ± 0.009	0.026 ± 0.005			
Intercept			0.94 ± 0.17	31.7	**<0.001**
Elevation			0.05 ± 0.08	1.36	0.273
Time			–0.12 ± 0.04	25.5	**<0.001**
Elevation × time			0.09 ± 0.04	3.5	**0.034**
Sex					0.373
Initial body mass					0.743
Growth rate constant *K*					0.715
Asymptotic mass *A*					0.498
(b) Coal tits	0.014 ± 0.008	0.027 ± 0.005			
Intercept			0.48 ± 0.18	4.02	0.065
Elevation			–0.16 ± 0.08	1.15	0.330
Time			–0.18 ± 0.03	31.0	**<0.001**
Elevation × time			0.15 ± 0.03	15.7	**<0.001**
Sex			0.37 ± 0.12	8.9	0.373
Initial body mass					**0.005**
Growth rate constant *K*					0.570
Asymptotic mass *A*					0.754

Estimates are also reported for random (nest) and repeated (time) effects.

erosion between day 7 and 16 at the higher-elevation sites. In great tit chicks, poor nutritional conditions during early growth may have affected telomere maintenance through a less favourable resource trade-off between cell division/organ development and protective mechanisms (Metcalfe and Monaghan 2001). Living at a higher elevation may also increase thermoregulatory and metabolic demands (e.g. temperature was on average 2.33 ± 0.26°C warmer at 1300 m compared to 1900 m, Stier et al. 2014b), thereby potentially increasing oxidative stress associated with higher metabolic rate (but see Stier et al. 2014c for a comprehensive discussion on thermogenesis and oxidative stress), and consequently disrupting telomere maintenance (Ludlow et al. 2014). In coal tit chicks, trade-offs between growth and telomere maintenance are also likely to be involved, and one explanation is the reallocation of resources towards growth at the expense of telomere maintenance. Accordingly, experimental manipulations of growth rate were found to increase telomere erosion in laboratory rats (Tarry-Adkins et al. 2008), and growth rate at high elevation was found to correlate positively with DNA damage level in a previous study on the same coal tit population (Stier et al. 2014b). Yet, in the present study we found no significant correlation between growth rate and telomere erosion. Furthermore, when comparing low and high elevation sites, the higher erosion rate of telomeres in coal tit chicks growing at the higher-elevation site did not result in shorter telomeres at fledging. Coal tit chicks at the high elevation site had longer initial telomere lengths (at day 7), and this buffered the effect of fast erosion on telomere length at day 16. The reason(s) for

Table 3. Summary of the most parsimonious linear mixed models explaining the variability in telomere dynamics during the growth period (i.e. difference between 7 and 16 d) for (a) great and (b) coal tit chicks. Significant factors are presented in bold, and the p-values reported for non-significant factors are the p-values of the initial full model (i.e. not the final model).

Telomere change	Random (nest) effects	Estimates ± SE	F	p
(a) Great tits	0.0004 ± 0.0030			
Intercept		0.13 ± 0.08	5.5	0.075
Elevation		0.12 ± 0.04	6.3	**0.011**
Sex				0.75
Telomere length at 7 days		–0.28 ± 0.07	14.9	**<0.001**
Initial body mass				0.34
Growth rate constant *K*				0.93
Asymptotic mass *A*				0.96
(b) Coal tits	0.00009 ± 0.00206			
Intercept		0.12 ± 0.07	4.7	0.12
Elevation		0.09 ± 0.04	6.0	**0.033**
Sex		–0.07 ± 0.03	4.9	**0.031**
Telomere length at 7 days		–0.30 ± 0.07	17.0	**<0.001**
Initial body mass				0.94
Growth rate constant *K*				0.43
Asymptotic mass *A*				0.41

Estimates are also reported for random (nest) effects.

such difference in telomere length at day 7 (and in telomere dynamics) between elevation sites remains to be studied through cross-fostering and common garden experiments. One hypothesis is that differences between elevation sites in telomere length and growth rate are driven by genetic differences between populations rather than environmental factors. Still, telomere length at 7 days is undoubtedly also influenced by early environmental factors, and unfortunately we were not able to obtain a blood sample at hatching to determine the real 'initial' telomere length given the size of our study species at that time (0.8 to 1.7 g).

The lack of significant relationship between growth rate or body mass at fledging and telomere erosion in our two study species raises nonetheless questions about the occurrence of a simple causal relationship between post-hatching growth rate per se and telomeres erosion in the wild (Geiger et al. 2012). A recent study in wild jackdaws *Corvus monedula* demonstrated that telomere erosion during the growth period was even lower for chicks being heavier at fledging, but only when the brood size was experimentally increased (Boonekamp et al. 2014). Here, we found that coal tit chicks that were heavier just after hatching preserved longer telomeres over growth. Altogether, these findings praise for a more careful examination of the link between early growth conditions and telomere lengths (see also Nettle et al. 2015), and they suggest that prenatal conditions (e.g. egg or incubation quality), post-natal environmental conditions (e.g. elevation) and/or parental genetic quality might play a more important role than post-hatching growth rate per se in determining telomere length and erosion early in life.

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Supplementary material (Appendix JAV-00714 at <www.avianbiology.org/appendix/jav-00714>). Appendix 1.