

1 *Telomeres, pace of life and extinction in warm climates*

2 **Lizards from warm and declining populations are born with extremely**  
3 **short telomeres**

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25

26 **Abstract**

27 Aging is the price to pay for acquiring and processing energy through cellular activity and life  
28 history productivity. Climate warming can exacerbate the inherent pace of aging, as illustrated  
29 by a faster erosion of protective telomere DNA sequences. This biomarker integrates  
30 individual pace-of-life and parental effects through the germline, but whether intra- and inter-  
31 generational telomere dynamics underlies population trends remains an open question. Here,  
32 we investigated the covariation between life history, telomere length (TL) and extinction risk  
33 among three age classes in a cold-adapted ectotherm (*Zootoca vivipara*) facing warming-  
34 induced extirpations in its distribution limits. Telomere length (TL) followed the same  
35 threshold relationships with population extinction risk at birth, maturity, and adulthood,  
36 suggesting inter-generational accumulation of accelerated aging rate in declining populations.  
37 In dwindling populations, most neonates inherited already short telomeres, suggesting they  
38 were born physiologically old and unlikely to reach recruitment. At adulthood, TL further  
39 explained females' reproductive performance, switching from an index of individual quality  
40 in stable populations to a biomarker of reproductive costs in those close to extirpation. We  
41 compiled these results to propose the aging loop hypothesis and conceptualize how climate-  
42 driven telomere shortening in ectotherms may accumulate across generations and generate  
43 tipping points before local extirpation.

44 **Significant statement**

45 This study unraveled the impacts of accelerated aging as a corollary of climate-driven  
46 population decline. We found a transgenerational accumulation of telomere shortening  
47 implying that offspring were already born “old”. We suggest that this process may exacerbate  
48 across generations, leading to an aging loop in the population. This model posits that telomere  
49 dynamics should represent a critical and promising molecular biomarker of population  
50 extirpation as well as a way to test the *in situ* efficiency of conservation decisions.

## 51 **Introduction**

52 Biodiversity is undergoing a global crisis, highlighted by the alarming pace of species loss  
53 worldwide (1, 2). This trend is accelerating, especially due to pervasive effects of climate  
54 warming on extinction risks in range limited or cold-adapted species (3–5). A current issue is  
55 our virtual blindness about the nature and generality of the underlying mechanisms  
56 connecting warmer climates to individual life history, and early warning signals of warming-  
57 induced extinctions (6, 7). All living creatures eventually die but the time separating birth or  
58 first reproduction from death can be altered by climate warming and heat stress because low  
59 body temperatures generally benefit lifespan in both endothermic and ectothermic animals (8–  
60 10). In terrestrial ectotherms, climate warming can also constrain activity patterns (4) and  
61 significantly increase maintenance costs (11, 12) as well as the risks of heat stress (13).  
62 Together, these may eventually alter fundamental life history trade-offs and a switch to a “live  
63 fast, die young” life history strategy along the slow-fast continuum (9, 10, 14).

64         These demographic effects of global warming in terrestrial ectotherms should be  
65 driven by physiological mechanisms whereby higher temperatures cause an acceleration of  
66 growth and reproduction, induce whole-organism oxidative stress, and eventually hasten the  
67 rate of aging (9, 15). Still, how physiological changes in aging rates and longevity will trade  
68 with individual performance in the long run and push populations at the warm edge of the  
69 range distribution on the verge of extinction remain unclear because ectotherms can display a  
70 variety of buffering mechanisms to compensate for these potential changes in lifespan (16).  
71 Telomeres, the protective terminal DNA sequences of linear chromosomes, represent  
72 promising biological markers to investigate these physiological mechanisms of warming-  
73 induced extinctions because they may be internal regulators of life history trajectories (17).  
74 Telomere length (TL) normally shortens at each cell division, and, once a length threshold is  
75 crossed, end-replication problems lead to cell apoptosis or genome instability at cellular and

76 tissue levels (18). The rate of telomere erosion integrates both inherent aging process (i.e.,  
77 standard cells division rates and associated damages accumulation in a given tissue) but also  
78 additional, cumulative effects of stressors, including those due to heat stress (19–21).  
79 Eventually, TL and/or telomere attrition rates in somatic tissue predict lifespan and lifetime  
80 reproductive success among and within species (22–24).

81         Telomere erosion can also be impacted by environmental stressors in the germline,  
82 explaining both immediate fitness costs and transgenerational effects (25). Multiple biotic and  
83 abiotic factors may alter gamete TL (26), which may condition environmental influences on  
84 TL heritability (27). The TL is normally reset by telomerase activity in germ cells, zygotes  
85 and early life (18), but deleterious parental effects such as abnormally high and stressful  
86 developmental temperatures may either directly favor telomere shortening and/or indirectly  
87 affect telomerase repair functions in early life (28, 29). However, impacts of external  
88 temperature on telomere dynamics during embryonic life in juvenile ectotherms are not that  
89 straightforward, as shown by lacking effect of incubation temperature in Atlantic salmon (30)  
90 or thermal effects conditioned by pollutant exposure in American alligators (31).

91         An open question is whether warming-induced acceleration of intra-generational pace-  
92 of-life and population extinction risks further combines with inter-generational patterns of TL  
93 erosion. Testing this demands concurrent measures of TL at different life stages, in parents  
94 and offspring from natural populations chronically exposed to a range of climate conditions  
95 including weather extremes conducive to long-term population decline. We thus used a well-  
96 known geographic gradient of climate-induced extinction risk across the range of the cold-  
97 adapted common lizard (*Zootoca vivipara*), which is now exposed to climate warming and  
98 drying (32) and trapped around mountain ranges in its meridional Western European  
99 distribution (South-France and Northern-Spain). Natural populations experience repeated  
100 summer heat waves and dry spells in lowland habitats that have multiple damaging impacts

101 including a faster pace of life, loss of lifetime reproductive fitness, loss of dispersal, and  
102 higher inbreeding levels that combine to cause extinctions in some populations (4, 14, 33, 34).  
103 We previously established that shorter TL of yearlings in warmer habitats may precede  
104 population extinction but this did not allow us to separate potential intra-generational and  
105 inter-generational mechanisms (35).

106 In this study, we examined whether and how shorter TL could result from maternal  
107 transmission. For more than 10 years, we monitored 22 wild populations of common lizards  
108 in France Massif Central mountain along a geographic and altitudinal gradient ranging from  
109 cold highland to warm lowland margins (Appendix SI, Fig. S1). These populations are spread  
110 along a continuum of extinction risk encompassing recent abundance changes, thermal  
111 conditions, altitude, and life history strategies, as summarized by an extinction risk score  
112 (PC1 score, Appendix SI, Fig. S2). We explored the co-variation between population state and  
113 TL in 126 adult females and their progeny (231 offspring) from 9 representative populations  
114 (7 stable or expanding and 2 declining) to complement TL data collected in yearlings two  
115 years before from the same populations and from a further population potentially extirpated  
116 since then. We further investigated how thermal conditions during pregnancy (i.e., basking  
117 opportunity), maternal traits, and offspring characteristics could explain variation in lizard TL  
118 at birth and further predict female reproductive performance at adulthood.

## 119 **Results**

### 120 *Breakpoints in TL along extinction risk*

121 We found that TL follows the same threshold relationship along PC1 score among newborn,  
122 yearlings and adult females, attaining stunted states concomitant to greater risks of extinction  
123 in the declining populations (Fig. 1). Breaking points before noticeable changes in TL

124 coincided with the demographic threshold of population extinction, and were qualitatively  
125 similar across the three age classes (Appendix SI, Fig. S3).

126

### 127 *Offspring TL are shorter already at birth in collapsing populations*

128 Offspring experienced abnormally short TL in the two natural populations close to  
129 demographic collapse (Appendix SI, Table S1). Based on previous evidence linking juvenile  
130 mortality risk to early life TL in this species (23), we used the range of TL values in yearlings  
131 that did not survive to obtain an estimation of TL thresholds predicting high death risks and  
132 survival chances (Fig. 2a). Below the lower threshold of this TL range, only a very low  
133 proportion of juveniles (7%) in declining populations are expected to survive and reach 1-  
134 year-old and recruitment, corresponding to the lower range seen in inter-annual studies of  
135 multiple birth cohorts marked and monitored in a stable population (36). Inversely, this  
136 calculation predicts way higher survival chance in stable populations (73%), a value getting in  
137 the upper range seen in inter-annual studies of a stable population (36). Offspring TL was also  
138 positively correlated with mother TL (Appendix SI, Table S1) and co-varied interactively  
139 with size-adjusted parturition date and population state (Appendix SI, Table S1). There was  
140 no effect of parturition date in stable populations as opposed to a negative relationship  
141 between TL and parturition date among offspring from declining populations (Fig. 2b). Other  
142 offspring traits (sex or juvenile size) or maternal characteristics (mother size or basking  
143 treatment) had no influence on TL variation at birth (Appendix SI, Table S2).

144 We partitioned variance in a random model on offspring TL among populations  
145 ( $\sigma^2_{\text{population}} = 0.36$ ), among families within the same population ( $\sigma^2_{\text{family}} = 0.31$ ) and within  
146 families ( $\sigma^2_{\text{residuals}} = 0.40$ ). A full-sib analysis among offspring from the same family under the  
147 strong assumption of no maternal effect suggested high levels of TL broad-sense heritability

148 across all populations ( $H^2 = 0.57$ ). Accounting for the variance explained by fixed effects of  
149 the final mixed model (Appendix SI, Table S1 & S2), heritability estimation slightly  
150 decreased to  $H^2 = 0.53$ .

151

### 152 *Adult TL further predicts reproductive performance*

153 In pregnant females, population trajectory and TL interactively explained variation in fitness-  
154 related reproductive traits (SI Appendix, Table S1 & S3), supporting previously observed  
155 reproductive senescence in warming environments for this species (37). Specifically,  
156 reproductive investment (total fecundity corrected for body size) increased with the TL of  
157 pregnant females in stable populations (Fig. 3a) whereas it decreased with TL in declining  
158 populations (Fig. 3b). Instead, no relationship occurs between litter success (the proportion of  
159 viable offspring) and TL of pregnant females in stable populations (Fig. 3c), while litter  
160 success dropped in collapsing populations together with shorter TL of pregnant females (Fig.  
161 3d). These findings shed new light on the classical relationship between TL and fitness (22,  
162 38) by suggesting that fitness costs of shorter TL for reproduction are more likely to occur  
163 under harsh environmental conditions.

### 164 **Discussion**

165 In ectotherms such as the common lizard, climate warming causes an accelerated life history,  
166 which translates into faster body growth, sexual maturation earlier in life, and parturition  
167 sooner in the year in both natural or captive populations (14, 39–41). Despite the short-term  
168 fitness benefits (40), this more productive life history induces demographic costs on the long  
169 run. This is illustrated by a drop in the relative abundance of lizards since 2005 in natural  
170 populations and the loss of lifetime reproductive fitness due to a shorter longevity of lizards in  
171 populations exposed to warmer summer weather (14). Supporting the climate-induced shift to

172 extirpation, we witnessed over the last decade the pseudo-extinction of a wild population in  
173 the warmest location (Mont Caroux, Fig. 1b), in which yearlings were very large but exhibited  
174 completely eroded TL in 2015 (35) and could not be sampled in subsequent years (incl. 2017)  
175 despite our efforts. The causal role of environmental temperatures, potentially together with  
176 drought (23), in triggering these changes in life history strategies and leading to pseudo-  
177 extinctions is now well documented in this cold-adapted lizard and might be a general pattern  
178 in other ectotherms (9).

179

180 *Offspring are being born already “old”*

181 Our results also corroborate previously established impacts of environmental temperatures on  
182 telomere erosion in germline and somatic tissue of non-avian reptiles (29, 42, 43) and more  
183 generally in ectotherms (44). The non-linear relationships between TL and population status,  
184 which combines information on population decline, environmental temperatures and life  
185 history traits, further conforms to the conclusions of a recent review of ageing mechanisms in  
186 ectotherms (9). A steep decline of TL characterized the transition from stable to declining  
187 populations in all age classes, probably because populations at warmer locations are more  
188 regularly exposed to heat waves leading to stress reactions, reactive oxygen species  
189 production and telomere shortening (15). Yet, one of the most striking results from our study  
190 unravels that offspring from declining populations already showed eroded telomeres at birth  
191 with a geographic variability qualitatively matching the one observed in yearlings and adults  
192 (Appendix SI, Fig. S3). Shorter TL could have resulted from inheritance together with  
193 additional attrition or altered resetting by telomerase during embryonic development as  
194 commonly hypothesized (45, 46). Telomerase activity closely explains telomere dynamics in  
195 lizards (47), so its sensitivity to climatic conditions during embryonic life is likely crucial and  
196 deserves specific attention. We cannot draw any firm conclusions regarding the role of early



197 developmental and paternal lineage effects since TL was not sampled in the germline of  
198 adults and in fathers and also because we lack information about TL prior to birth in  
199 offspring. Yet, the lack of effects from the manipulation of maternal basking time on  
200 offspring TL at birth suggests a relatively low influence of daily temperature on embryonic  
201 development (30). In further support of minor pre-natal environmental effects, offspring from  
202 declining populations and born earlier in the year exhibited longer TL than those born two to  
203 three weeks later despite the fact that their mothers spent more time in their natural habitat  
204 than in standard *ad libitum* laboratory conditions. This implies that the proportion of  
205 developmental time spent within the natural habitat did not explain why offspring displayed  
206 shorter TL at birth. Instead, we propose that offspring TL variation falls along a continuum  
207 from early to late phenology indicated by differences in female quality, given the recurrent  
208 finding that reproduction follows a “sooner is better” pattern in lizards living in seasonal  
209 environments (29). These observations coupled with relatively high heritability estimations  
210 from the full-sib analysis and a strong mother-offspring correlation for TL imply that the  
211 shorter telomeres in offspring were more likely inherited at conception through parental  
212 gametes instead of being reset at conception and shortened during early embryonic life.

213

#### 214 *Consequences of shorter TL at adulthood*

215 In general, population variability in TL may reflect either differences in initial TL at  
216 conception and/or birth, differences in TL dynamics with age (e.g., increased telomere erosion  
217 or reduced telomere restoration), selective disappearance of individuals with different TL, or  
218 biases due to the age structure of the population (48). In lizards, TL relates to age following  
219 quadratic or positive relationships (47), so shorter TL in adult females from declining  
220 populations may reflect recent changes in age-distribution biased to a majority of young  
221 adults (2 yo). Importantly, this alteration of telomere dynamics may induce greater annual

222 mortality risks of lizards (49), including in this species (23) and the drop of female  
223 reproductive effort (37), in line with general evidence linking TL with individual quality  
224 across vertebrates (22, 38). Reproductive success is also known to positively correlate with  
225 TL in some species (50) and specifically to the capacity of females to mount antioxidant  
226 shielding among our sampled lizard populations (51). This relationship between TL and  
227 reproduction involves both TL as a biomarker of individual quality to produce offspring  
228 (positive association between TL and reproduction) and TL as a mediator to reproductive  
229 costs (positive association between reproduction and TL shortening) between species (52).  
230 Here, we found context-specific associations between TL of pregnant females measured  
231 during mid-gestation and their fecundity or reproductive success with striking difference  
232 between stable and declining populations. In declining populations, TL variation among  
233 females within the population was positively correlated with reproductive success but  
234 negatively with reproductive effort, whereas it was positively correlated with reproductive  
235 effort in stable populations. This intriguing result suggests a threshold transition from TL as a  
236 biomarker of female quality in stable populations to a cost of reproduction under harsh  
237 conditions. Accordingly, experimental increase of TL with drugs (53) or engineering of  
238 maternal reproductive effort (54) should help investigate if and when TL may switch from an  
239 index to a driver of reproductive costs.

#### 240 *The aging loop hypothesis*

241 We propose a conceptual mechanistic model of an aging loop linking climate warming with  
242 physiological stress and population demography in order to explain how and why population  
243 extirpation may follow a vicious circle dynamic in this species (Fig. 4). Central to this concept  
244 is telomere dynamics, an integrative mediator linking chronic climate stress to pace-of-life  
245 strategies within and between generations, eventually predicting the loss of reproductive  
246 individuals and demographic collapse (Fig. 4). Local extinctions are often preceded by tipping

247 points and early warning signals that precede extinction in deteriorating environments such as  
248 dynamic phenomena related to demographic variance and density dependence, but those are  
249 often difficult to detect without a detailed time series of population dynamics (55). At a lower  
250 organizational level, cell life span and organismal functioning and viability also follow  
251 threshold effects related to telomere shortening (18). As observed here, most individuals from  
252 collapsing populations exhibited TL below the range measured in thriving individuals even at  
253 birth, which implied exacerbated mortality risks in the warmest, low altitude populations.  
254 Associated drops in population resilience capacity to endure any additional and stochastic  
255 events will push it to the edge of extinction before its complete collapse.

## 256 *Conclusion*

257 Applying similar themes from biomedical research in humans, ecological studies have  
258 focused on key aspects of telomere biology regarding age and life history effects, inheritance,  
259 and environmental factors accelerating telomere erosion (19, 56). In line with other recent  
260 studies, we believe the time has come to take into account and model the roles of telomere  
261 dynamics in the conservation biology of wild populations (35, 57–59). Such mechanistic  
262 comprehension might be an essential step to understand the proximate causes of demographic  
263 risks and to promote efficient conservation measures. In particular, TL may represent a  
264 promising tool to outpace tipping points. First, investigating TL dynamics in wild populations  
265 without extensive background demographic data should allow to rapidly identify the  
266 populations most at risk. Second, TL may also constitute a biomarker to test *in situ* the  
267 impacts of restoration programs or reintroduction strategies without relying on detailed, time  
268 consuming demographic studies. Thus, our correlative study of extinction mechanisms in a  
269 single species provides a stepping stone for global analyses of the relationship between  
270 climate warming, pace of life, and accelerated TL erosion along with the development of TL  
271 as a biomarker to anticipate and potentially prevent ongoing population extinctions.

272

## 273 **Materials and Methods**

### 274 *Field Population Survey*

275 Each population was visited during one day to collect ca. 24 pregnant females, 10 adult males  
276 and 20 non-reproductive yearlings in June 2017 and 2018. Males and yearlings were  
277 measured for body mass and body size (snout-to-vent length, SVL) by the same operator and  
278 released at the end of the day. Females were brought back to a field laboratory and released  
279 after parturition (see below). We used the total time spent performing captures in the field, the  
280 number of people involved and the total surface of the population to estimate an index of  
281 lizard abundance (in number of lizards.ha<sup>-1</sup>.h<sup>-1</sup>.person<sup>-1</sup>). The relative change in lizard  
282 abundance since 2005 provides an estimate of demographic trends in recent years (35). Since  
283 2015, populations were also equipped with data-loggers for a month at the peak of annual  
284 activity to characterize thermal conditions. Each year, we recorded temperature every hours  
285 using 3 loggers in each populations (iButtons, Maxim Integrated Products, Sunnyvale, CA,  
286 USA, ± 0.0625°C protected in PVC shelters) placed within vegetation (ensuring no radiative  
287 sunlight) in random locations within each population (60). This sampling allowed us to  
288 measure accurately the microclimate conditions experienced by lizards and classify  
289 population thermal conditions. Each year during almost a month (25<sup>th</sup> June to 21<sup>st</sup> July), we  
290 averaged the minimal daily temperature (T<sub>min</sub>, overnight temperature), the maximal daily  
291 temperature (T<sub>max</sub>, afternoon temperature peaks) and the global daily average (T<sub>mean</sub>)

### 292 *Sampling Design*

293 We analyzed the impacts of life history, environmental conditions, and demographic trends on  
294 adult female and offspring TL in a sub-sample of 9 sites including two declining populations  
295 in June 2017. Pregnant females ( $n = 16$  per population) were measured, weighted and

296 acclimated in individual terrarium following previously published procedures (60). In  
297 particular, they were provided with food (*Tenebrio molitor*) and water *ad libitum* until  
298 parturition. At arrival, we split pregnant females from each population randomly into two  
299 basking treatments to mimic different climate scenarios and associated changes in basking  
300 opportunities. A “cool” group of females had access for 3h in the morning (9:00 to 12:00) to  
301 heat under an incandescent lightbulb (40W) while the “warm” group were exposed for 9h  
302 during the daytime (9:00 to 12:00 and 13:00 to 19:00). Note that a reference group (basking  
303 opportunity for 6h in 8 additional females per populations) was used as control to extract  
304 parturition dates among years. We used HOBO temperature data loggers adapted with copper  
305 cast models to quantify differences in operative temperatures in randomly chosen terraria,  
306 which predicts the equilibrium body temperature of lizards in the absence of behavioral  
307 thermoregulation (61) (Appendix SI, Fig. S4). Females were checked twice a day to record  
308 their parturition date. After parturition, females were weighted and separated from their litter  
309 given the absence of post-birth parental care. We counted and weighted all litter units, which  
310 include both successful (alive) offspring, stillborn or aborted embryos and undeveloped eggs.  
311 Whenever possible, we determined offspring sex from the discriminant function linking the  
312 number of ventral scales and phenotypic sex with a success rate in determination above 96%  
313 (62). Females and litters were released at their capture sites within 2 days following birth.

#### 314 *Sample Collection, DNA Extraction and TL measurement*

315 We sampled two different types of tissues in adult females and in their offspring. In adult  
316 females, we collected red blood cells (RBC) the day of capture using a faintly invasive  
317 protocol for blood sampling (~ 40µl whole blood) from the post-orbital sinus (63). RBCs  
318 were separated from plasma in a centrifuge at 11,000 rpm and immediately stored at -28°C  
319 until DNA extraction and molecular assays. In offspring, we collected tail tip tissues the day  
320 of birth, since their small body size (~ 21mm SVL) make blood samples too invasive and

321 practically impossible in this age class. Tails are composed of a mix of skin, muscles, and  
322 bones and represent global individual TL given that the tail is formed a few days after  
323 ovulation (64). Tail extremities (<2-3 mm) were cut with sterilized scissors and stored in a  
324 mix of pure Ethanol (70%) and TrisEDTA buffer (30%) at -28°C until molecular assays. Note  
325 that this species uses autotomy as a predation avoidance strategy and tail will naturally regrow  
326 following autotomy in juveniles.

327         Molecular assays were performed by operators blinded of the sample origin  
328 (population, basking treatment, etc). DNA was extracted and purified using DNeasy blood  
329 and tissue kits (Qiagen) following manufacturer DNeasy 96 protocols for blood samples  
330 (adult females) or tissues samples (offspring). We assessed DNA concentration, quality and  
331 integrity by optical density spectrophotometry (NanoDrop) and absorbance profile. The great  
332 majority of samples met high quality standards (females: concentration:  $62.8 \pm 23.7 \text{ ng} \cdot \mu\text{l}^{-1}$ ,  
333 absorbance ratio A260/280:  $1.94 \pm 0.09$ ; offspring: concentration:  $56.1 \pm 33.2 \text{ ng} \cdot \mu\text{l}^{-1}$ ,  
334 absorbance ratio A260/280:  $1.89 \pm 0.13$ ). We then determined TL from 7.5 ng DNA using a  
335 real-time quantitative Polymerase Chain Reaction (qPCR) following a protocol previously  
336 developed and validated using tissue samples of this species (65). Briefly, telomeric DNA  
337 repeat sequences (T) were amplified using the Tel1b and Tel2b primers and a reference,  
338 single-copy (S) gene (recombination activating gene 1, RAG-1) was amplified using primers  
339 designed with the *Z. vivipara* reference genome RAG-1 sequence. Samples were randomly  
340 distributed on 9 plates and amplified in qPCR a thermocycler (BioRad CFX96, BioRad,  
341 USA). We calculated TL as the T/S ratio of cycle thresholds following (66). Overall,  
342 amplifications showed high level of efficiencies for both RAG-1 ( $94.4 \pm 2.03\%$ ) and  
343 telomeric sequence ( $89.8 \pm 2.81\%$ ). We further checked that a reference standard was  
344 repeatable between plates (T/S ratio ICC = 0.92) and that individual melting curves ensured  
345 unique amplifications.

346 *Data analyses*

347 We ran all statistical analyses in the R software environment (67). We first built a principal  
348 component analysis (PCA) to characterize how breeding phenology (ordinal parturition date  
349 including latest and earliest dates of each population), probability of being recruited for  
350 yearlings (frequency of breeding yearlings in each population), and the average SVL of  
351 yearlings in each populations co-varied with thermal conditions ( $T_{\min}$ ,  $T_{\max}$ ,  $T_{\text{mean}}$  of the study  
352 year), altitude of the population and demographic trends (abundance changes from 2005 to  
353 2017-2018) among the 22 sampled populations from the two study years. Given that basking  
354 treatments impacted parturition dates, we used females from control conditions (6h) to focus  
355 solely on population differences. This PCA was built using the *ade4* library with centered and  
356 scaled variables (68). This procedure allowed to rank populations along a composite score  
357 (PC1) describing concurrent changes in life history, climate conditions and demographic  
358 changes across populations (see SI Appendix, Fig. S1). Qualitatively similar results were  
359 obtained when we ranked the populations using solely the demographic trends to assess  
360 extinction risks (Appendix SI, Fig. S3). We next performed regression models with  
361 breakpoints using the *segmented* library (69) to update a linear mixed regression model  
362 linking TL data at a given age class with PC1 score of the population. All models included  
363 population identity as a random intercept term to account for non-independence among  
364 observations. TL data were approximatively normally distributed in offspring and adults and  
365 were z-transformed for these analyses. Henceforth, population state was treated as categorical  
366 effect (stable or declining) to optimize model convergence and ease interpretations of results.

367 In offspring, we used linear mixed models of the *nlme* library (70) to check whether  
368 TL variation was further explained by juvenile body size, date of birth, sex, basking  
369 conditions during gestation (hot or cool developmental conditions), population state, mother  
370 TL (scaled by population state), and all first order interactions. All models accounted for

371 additive random intercept of population identity and mother identity (sibling non-  
372 independence). Model performance was averaged using the *dredge* function of the *MuMIn*  
373 library (Appendix SI, Table S2) (71). We also built a random model to obtain variance  
374 between family ( $\sigma^2_{\text{family}}$ ), between population ( $\sigma^2_{\text{population}}$ ) and within family ( $\sigma^2_{\text{residuals}}$ ) to  
375 estimate broad-sense heritability in TL:  $H^2 = 2 * \sigma^2_{\text{family}} / (\sigma^2_{\text{family}} + \sigma^2_{\text{population}} + \sigma^2_{\text{residuals}})$  (72).

376 In pregnant females, we examined the effect of population state, TL (scaled by  
377 population state), and first order interactions on reproductive performance using a generalized  
378 linear mixed model. We considered the total fecundity (the sum of all litter units) to quantify  
379 reproductive investment, and analyzed variation in total fecundity with Gaussian family  
380 models and maximum likelihood. We considered the number of alive offspring against the  
381 number of unsuccessful ones (stillborn aborted, undeveloped) as a marker of reproductive  
382 success, and analyzed this response variable with a logistic regression, logit link, and  
383 binomial error term.

#### 384 **Data availability**

385 Data and codes used in this paper are available in the Supporting Information and at Zenodo  
386 repository (DOI: 10.5281/zenodo.5798028).

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## 408 **Permit**

409 This study was performed in accordance with laws relative to capture, transport and  
410 experiments on *Zootoca vivipara* and under permits from DREAL Languedoc Roussillon  
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583 **Figure caption**

584 **Figure 1.** Threshold relationships between telomere length (TL) of common lizards and a  
585 composite score of the extinction risk of their population (coordinate along the main axis of a  
586 PCA – SI Appendix, Fig. S2; high values of PC1 indicate population collapse, high night-time  
587 temperatures, low altitude and a fast pace-of-life). Breakpoint occurs for qualitatively similar  
588 tipping points of extinction risk scores in A) offspring (breakpoint: 0.73, CI95%: -0.69 –  
589 2.15), B) yearlings (breakpoint: 0.67, CI95%: -0.60 – 1.95) and C) adult females (breakpoint:  
590 0.67, CI95%: -0.28 – 1.63). Data for yearlings were obtained from an earlier study (35) and  
591 included one population presumably extinct between 2015 and 2017-2018 (pers. obs.). All TL  
592 data were centered and standardized by a z-score transformation to ease visualization (raw  
593 distribution available at Appendix SI, Fig. S3). Best regression lines and confidence bands are  
594 displayed with individual data points.

595

596 **Figure 2.** Offspring common lizards are born “old” in declining populations. A) Offspring  
597 telomere length (TL) is already short at birth in offspring from declining populations  
598 compared to those from stable ones. Based on a previously established range of TL values for  
599 thriving young lizards (23), we estimated the threshold TL for early life survival (grey bar)  
600 and predicted that 90% of offspring should not even attain recruitment. B) Offspring TL is  
601 negatively correlated to parturition date (adjusted to mother SVL) in declining populations  
602 (orange symbols, solid line,  $p = 0.003$ ) but not in stable ones (blue symbols, dashed line,  $p =$   
603  $0.251$ ).

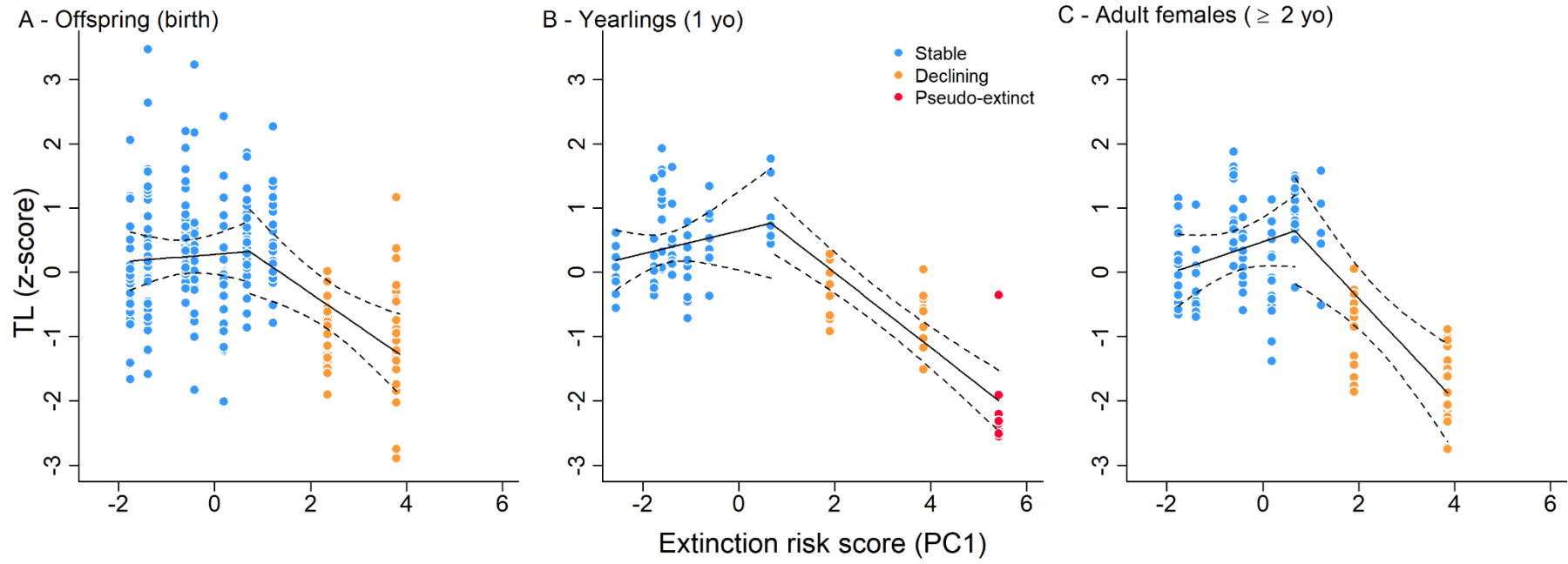
604

605 **Figure 3.** Context-dependent relationships between TL in pregnant female common lizards  
606 and their reproductive output are obvious from a post-hoc comparison of stable and declining  
607 populations. A, B) Total fecundity adjusted for female SVL increases slightly with TL in  
608 stable populations ( $p = 0.020$ ), but decreases with TL in declining populations ( $p = 0.012$ ). C,  
609 D) Litter success correlates positively with TL only in declining populations ( $p = 0.007$ ).  
610 Figures represent raw data points, best regression lines and 95% confidence bands.

611

612 **Figure 4.** The “aging loop hypothesis” for climate-induced population decline in the common  
613 lizard. We propose that climate warming increases the pace of life and rate of physiological  
614 aging, which eventually leads to a vicious circle through accumulation of shorter telomeres in  
615 the population. Telomeres get short sooner because warmer temperatures induce faster cell  
616 division and greater oxidative stress and /or because of an increased frequency of stressful  
617 weather events. Across generations, shorter telomeres may accumulate in the populations if  
618 telomere length is heritable and because of the shortening of telomeres through the germline.  
619 This pattern can either result from direct impacts of elevated physiological rates on telomere  
620 attrition or indirect alteration of normal resetting processes through telomerase activity during  
621 embryonic development. Greater telomere loss may then predict lower reproductive fitness  
622 that amplify across generations. Shorter TL in early life is associated with lower survival rate  
623 in this species (23) implying that offspring are born physiologically too “old” to survive to  
624 adulthood. Eventually, after a given tipping point, climate warming should bring down the  
625 number of recruits together with the resilience of the population. Abbreviations: ROS =  
626 reactive oxygen species, AntiOx= antioxidant defenses.

627 Figure 1.

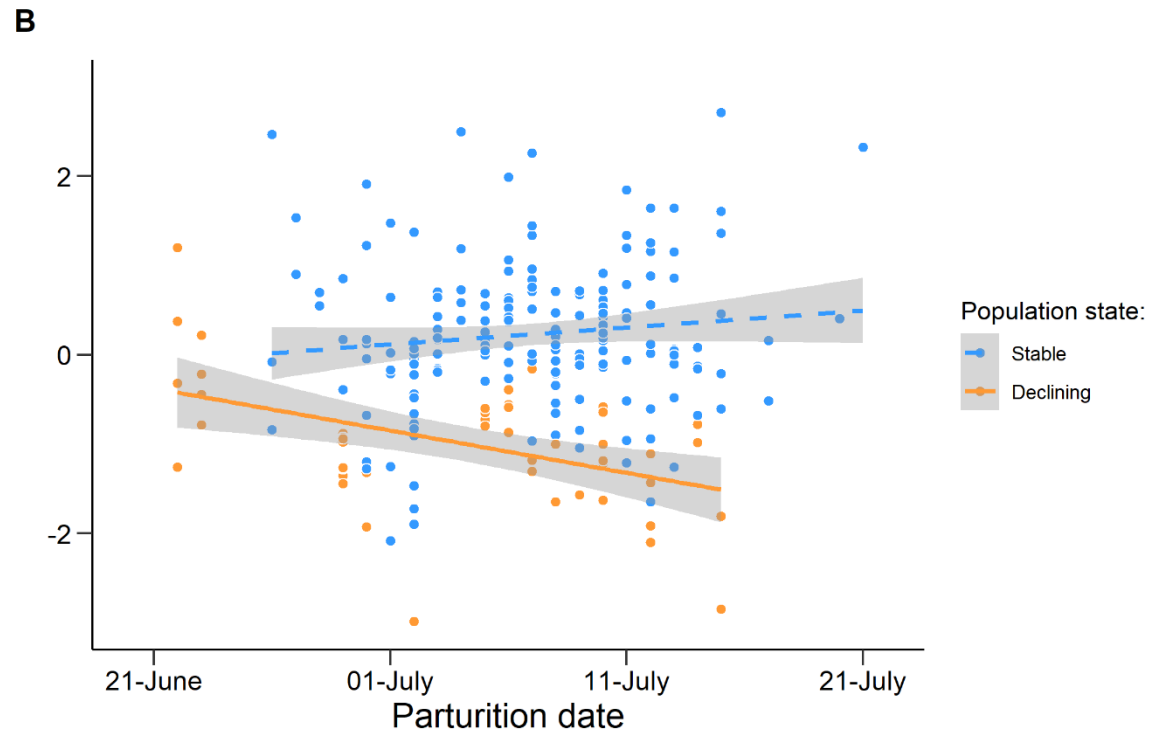
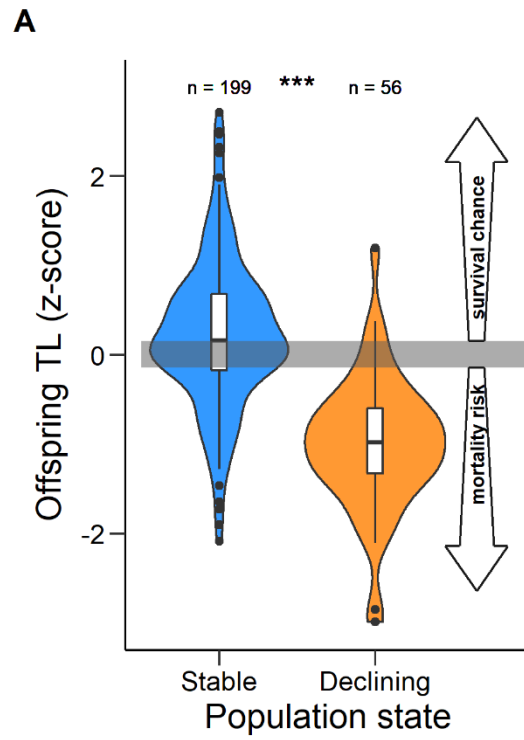


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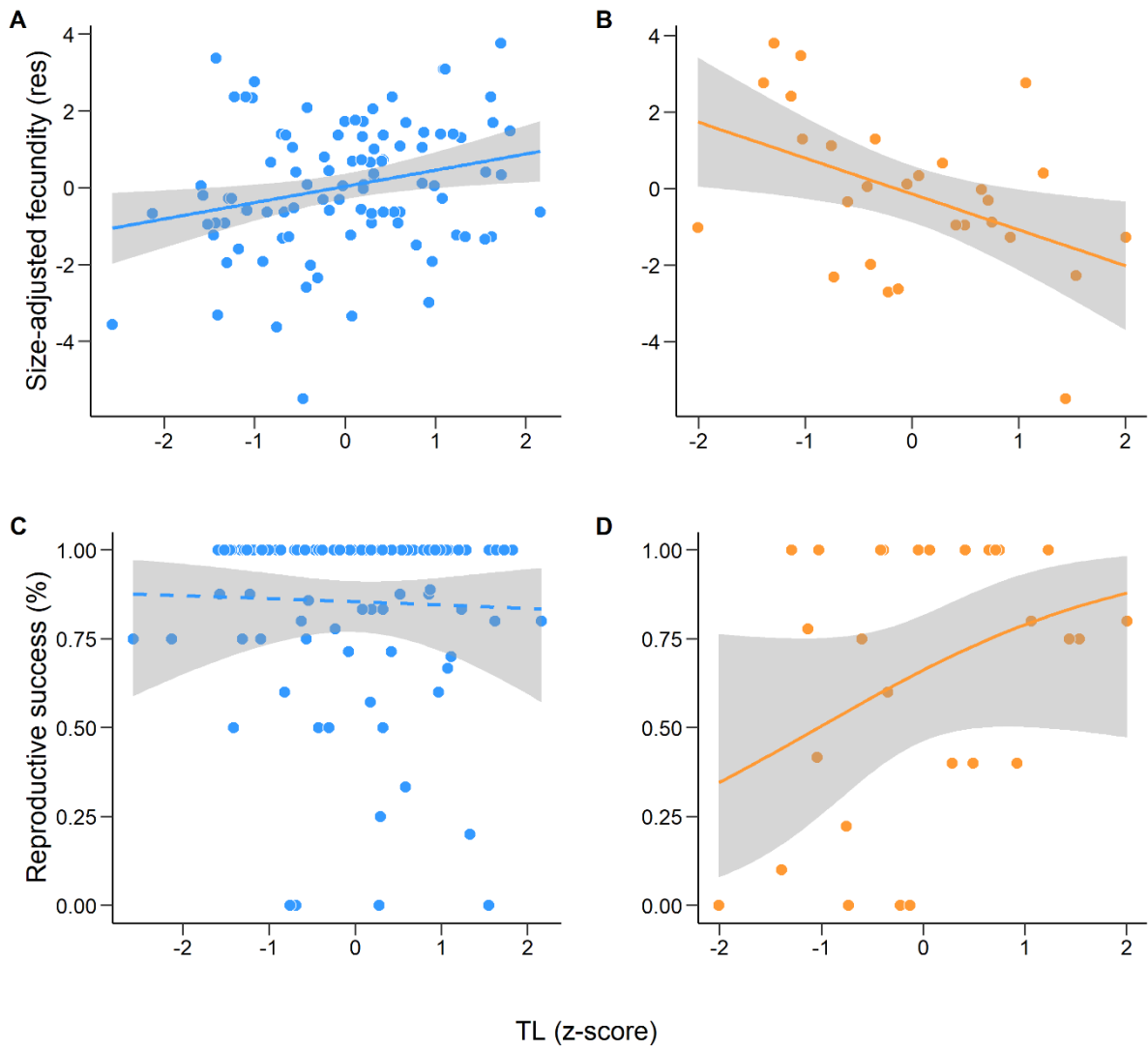
629 Figure 2.

630



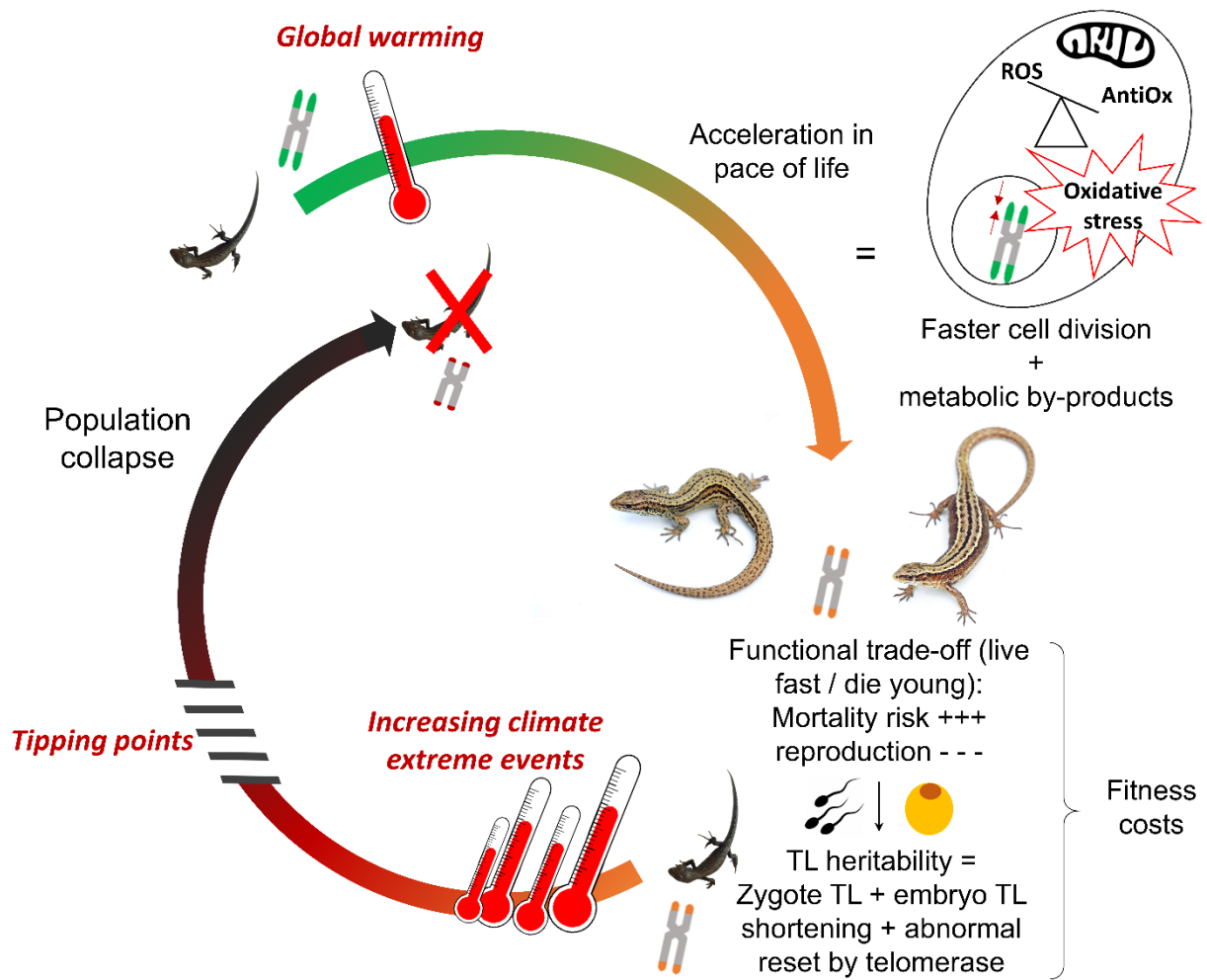
631

632 Figure 3.



633

634 Figure 4.



635