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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⁻¹.h⁻¹.person⁻¹). 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, $\pm 0.0625^{\circ}\text{C}$ 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 (25th June to 21st July), we
290 averaged the minimal daily temperature (Tmin, overnight temperature), the maximal daily
291 temperature (Tmax, afternoon temperature peaks) and the global daily average (Tmean)

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 ± 0.09 ; offspring: concentration: $56.1 \pm 33.2 \text{ ng} \cdot \mu\text{l}^{-1}$,
334 absorbance ratio A260/280: 1.89 ± 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_{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 (σ^2_{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**

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582

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).

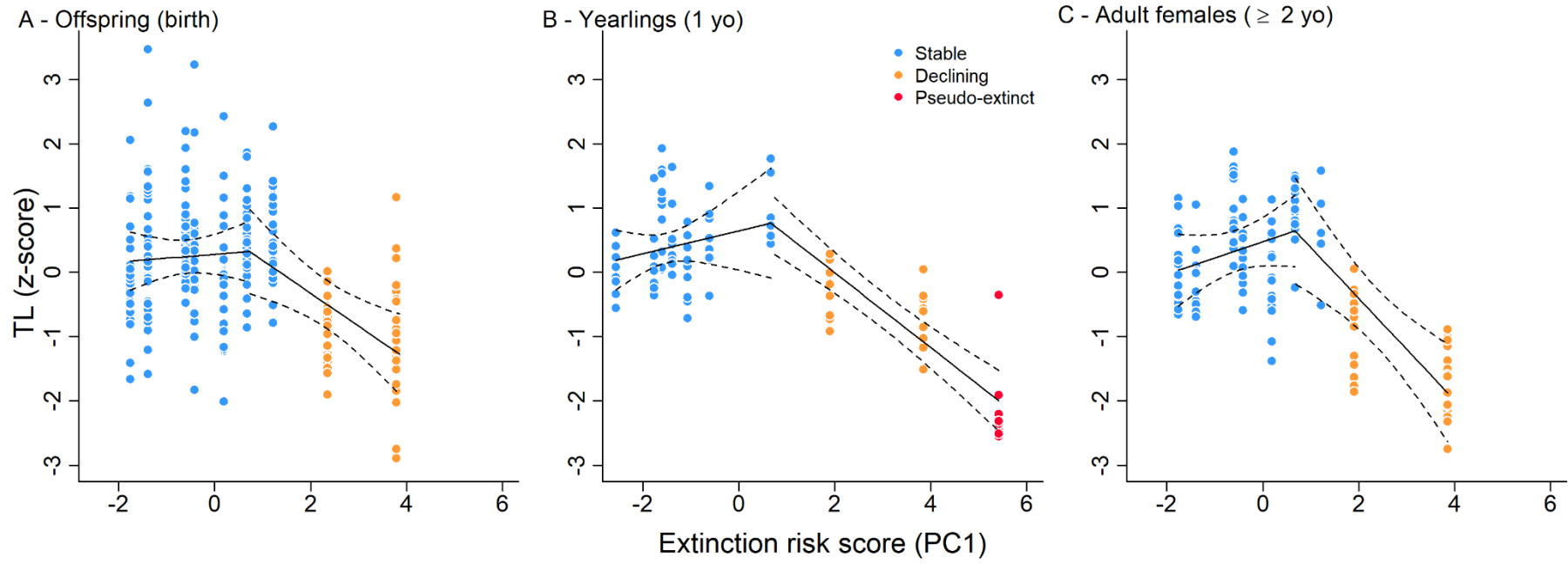
604

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.

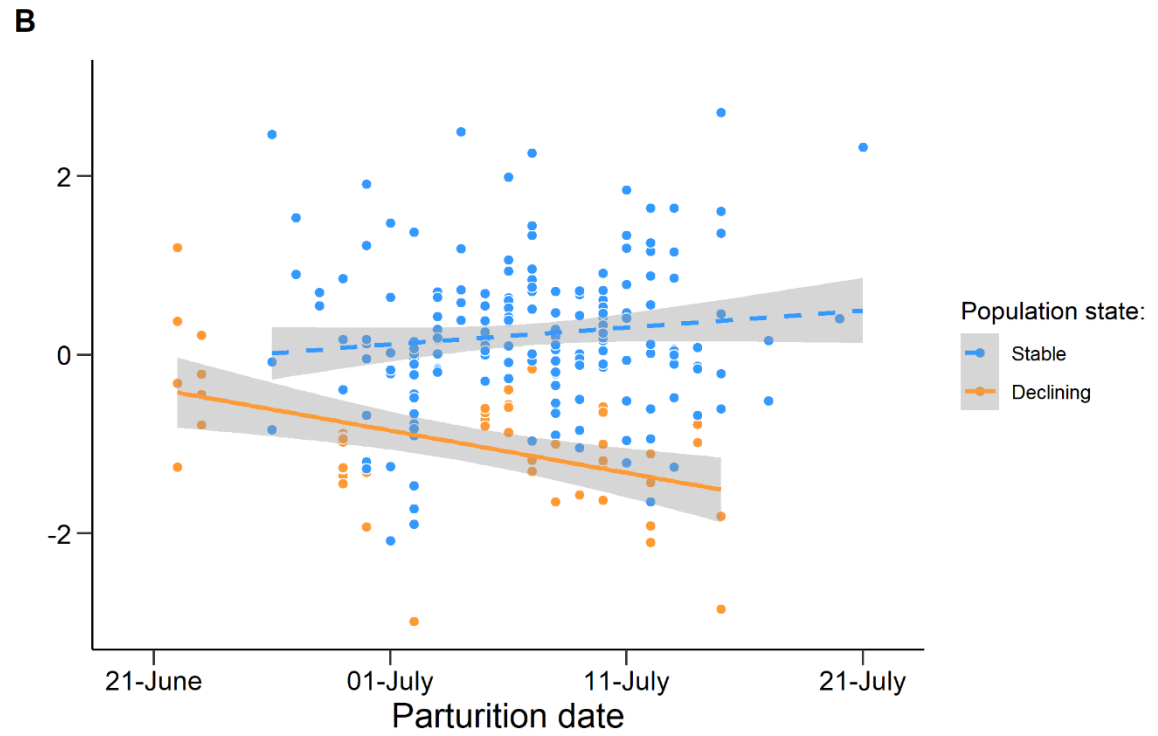
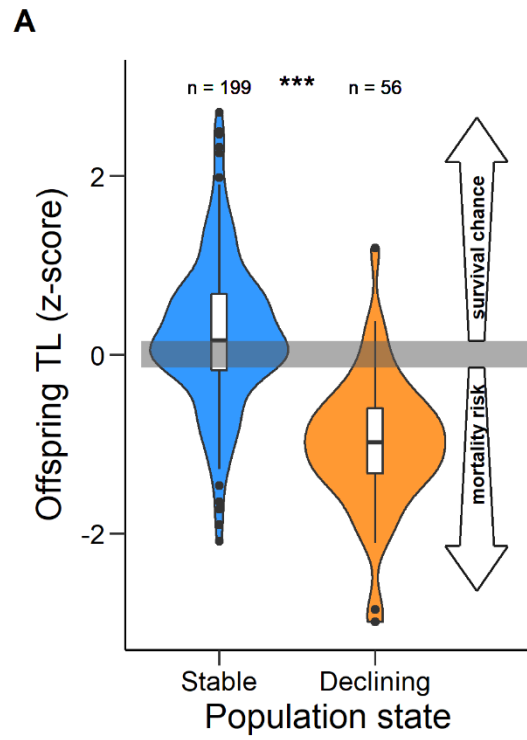
627 Figure 1.



628

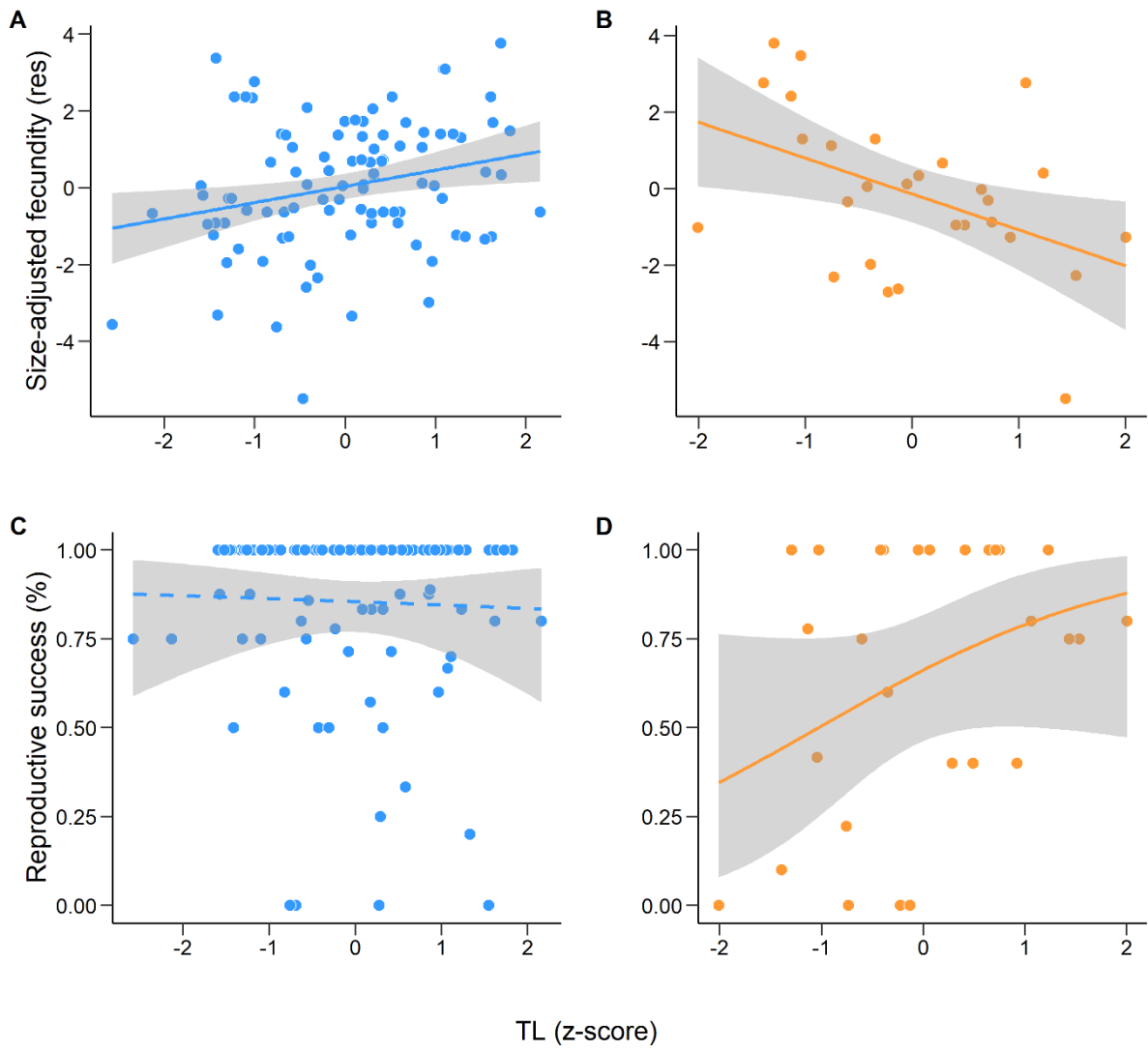
629 Figure 2.

630



631

632 Figure 3.



633

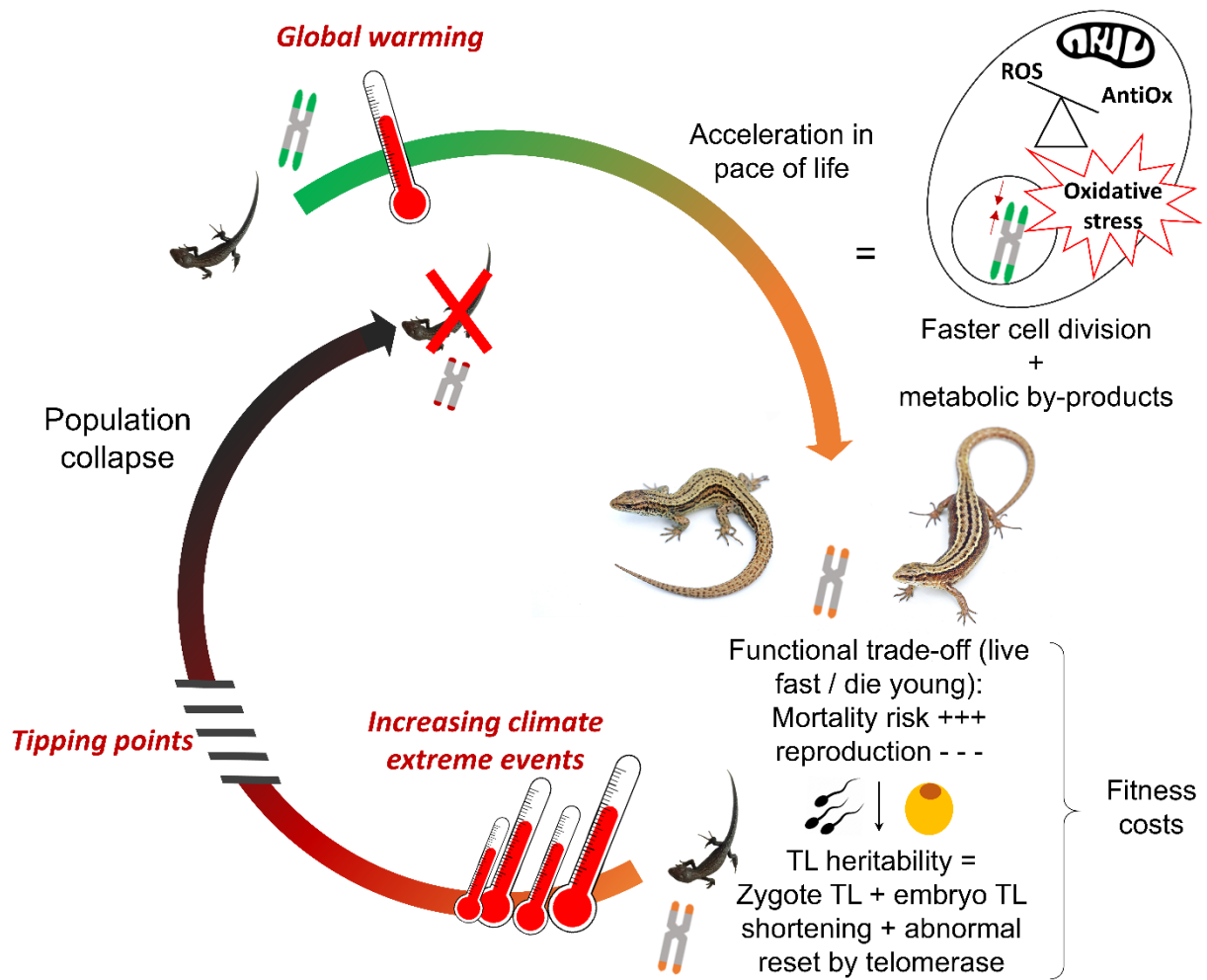


Fig. S1. Localization of the 22 populations along altitudinal gradients (1000-1600m) in the Massif Central Mountain range (France). Each population is identified by its code.

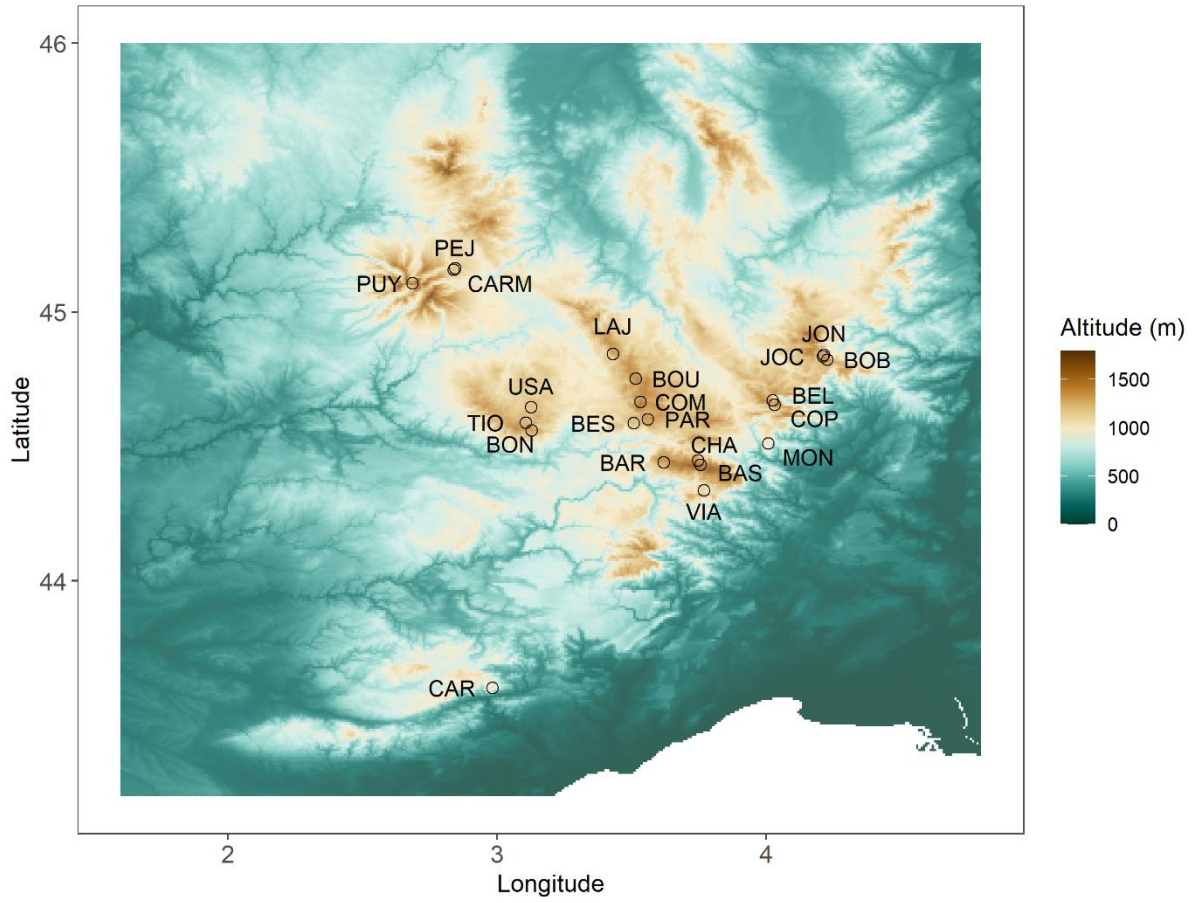


Fig. S2. Principal component analyses to investigate the co-variations in three life-history traits (mean body size = BodySize, recruitment of yearling at 1 yo = Yearling recruitment, and range of ordinal parturition dates = Soonest and Latest parturition), relative changes in lizard abundance over the last decade (Δ abundance), microclimatic temperatures (daily average of minimal temperature, mean temperature and maximal temperature = Tmin, Tmean, and Tmax) and altitude. Circled populations are those used in the present study for telomere assays.

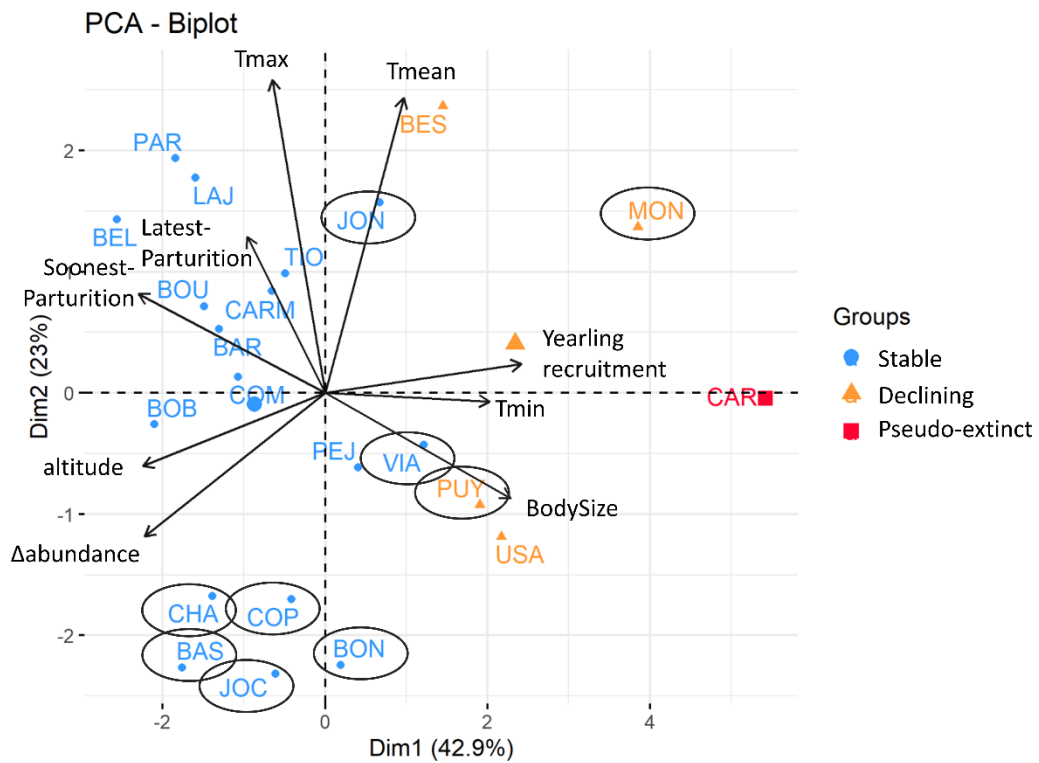


Figure S3. Threshold relationships between TL of common lizards and the relative change in population abundance between 2005 and 2015-2018. Breakpoint occurs for qualitatively similar values of population abundance change in A) offspring (breakpoint: 13.6%, CI95%: -30.7 – 58.0%), B) yearlings (breakpoint: 5.6%, CI95%: -14.6 – 25.8%) and C) adult females (breakpoint: 5.8%, CI95%: -54.5 – 66.1%). Data for yearlings were obtained from an earlier study (1).

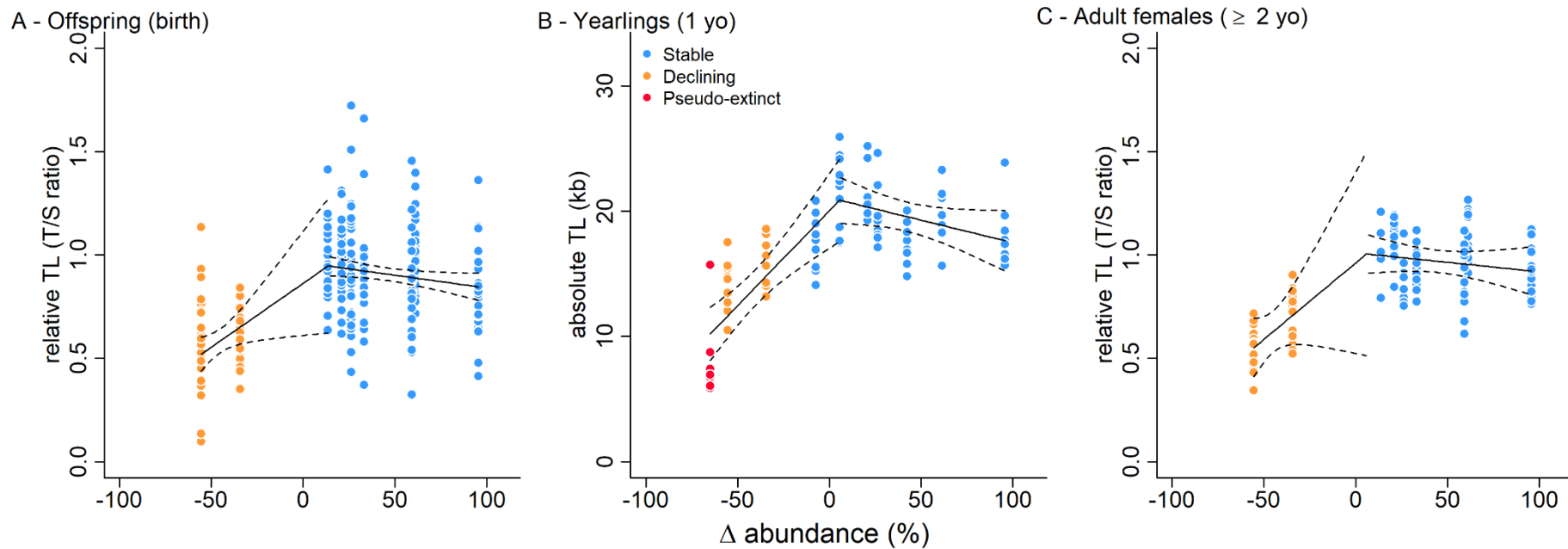


Figure S4. Operative temperatures measured for the two mother basking time treatments in a laboratory where females were maintained at a room temperature shifting according to natural, daily outdoor variability. For each basking time treatment (lights on 3h – blue ribbon, or lights on 9h – red ribbon), we assessed averaged temperature (solid lines) surrounding by thermal ranges (\pm 95% confidence interval) using biophysical models and HOBO sensors (2). For graphical purpose, this plot was restricted to a short 12-day timing but note that treatments lasted until female parturition (between 6 and 32 days). Maximal critical thermal limit (CTmax) ranges from 43.8 to 44.1°C in this species (3), thus highlighting a strong differential between the two basking treatments. See text for details.

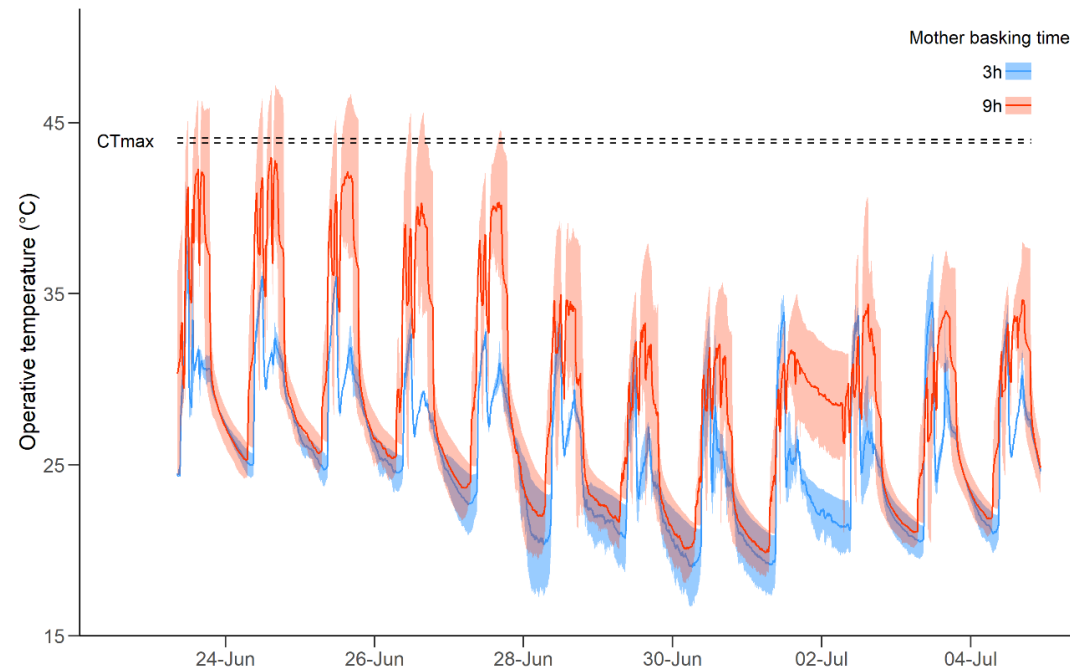


Table S1. Summarized outcomes of final selected models for offspring TL, total fecundity of females and reproductive success of females (see Table S2 & S3). Table provides information on sample size, marginal and condition R2, mean value (intercept), estimates (variance terms and fixed effects $\beta \pm SE$) together with test statistics. See methods section for details on statistical models and analyses.

Lizards	Models	Model summary				Type	Term	Variance				
Offspring	TL ~ Population state + Parturition date + Mother TL + Population state * Parturition date + (1 Population) + (1 Mother)	Number of individuals	R^2_m	R^2_c	Mean TL (T/S ratio)	Random	Population	0.01				
							Mother ID	0.27				
		n = 231	0.33	0.60	0.839	Fixed	Residual	0.40				
								$\beta (\pm SE)$	t-stat	P value		
							Intercept	-0.97 \pm 0.15	-6.4	0.000	***	
							Mother TL	0.16 \pm 0.07	2.4	0.018	*	
							Population state					
							Stable vs Declining	1.24 \pm 0.17	7.2	0.000	***	
							Parturition date	-0.09 \pm 0.03	-3.0	0.003	**	
							Population state * parturition date	0.11 \pm 0.03	3.2	0.002	**	
Females	Fecundity ~ SVL + population state + female TL + population state * female TL + (1 Population)	Number of individuals	r^2_m	r^2_c	Mean litter size	Random	Population	0.03				
							Residual	0.56				
		n = 126	0.40	0.43	6.1	Fixed		$\beta (\pm SE)$	t-stat	P value		
							Intercept	-0.06 \pm 0.19	-0.29	0.769		
							SVL	0.60 \pm 0.07	8.6	0.000	***	
							Population state					
							Stable vs Declining	0.07 \pm 0.22	0.31	0.769		
							Female TL	-0.39 \pm 0.16	-2.5	0.016	*	

Reproductive success ~ SVL + population state + female TL + population state * female TL + (1 Population)	Number of individuals	r^2_m	r^2_c	Mean success (%)	Type	Population state * female TL	0.58 ± 0.18	3.2	0.002	**
						Term	Variance			
	n = 126	0.11	0.19	80.8	Random	Population	0.32			
					Fixed		β (± SE)	z-value	P value	
						Intercept	0.87 ± 0.44	2.0	0.050	*
						SVL	0.20 ± 0.11	1.9	0.053	.
						Population state				
						Stable vs Declining	1.24 ± 0.51	2.4	0.015	*
						Female TL	0.63 ± 0.23	2.7	0.007	**
						Population state * female TL	-0.81 ± 0.28	-2.9	0.004	**

Table S2. Investigation of factors explaining TL variation in offspring at birth. Models are ranked by Akaike Information Criterion (AIC). For offspring, 275 models were generated due to the number of factors examined, so this summary is restricted only to the top-ranked models for AIC < 3 for clarity. Note that including sex did not ameliorate model selection so we discarded this effect for simplicity. All models accounted for population and mother identity as random terms and fixed effects were estimated on maximum likelihood.

Response	Fixed effects												Model summary					
Offspring TL	(Intercept)	Juvenile SVL	Basking treatment	Mother SVL	Mother TL	Parturition date	Population state	Population state * Juvenile SVL	Population state * Basking Treatment	Population state * Mother SVL	Population state * Mother TL	Population state * Parturition Date	rank	df	Log Like	AICc	ΔAIC	weight
	0.26				0.16	0.02	+					+	1	8	-271.7	560.0	0.0	0.1
	0.26				0.21	0.02	+				+	+	2	9	-270.6	560.1	0.1	0.1
	0.26	0.10		-0.11	0.21	0.03	+				+	+	3	11	-268.5	560.2	0.2	0.1
	0.26	0.09		-0.11	0.16	0.03	+					+	4	10	-269.7	560.4	0.4	0.1
	0.26	0.07			0.22	0.03	+				+	+	5	10	-269.7	560.5	0.5	0.1
	0.26			-0.08	0.15	0.02	+					+	6	9	-271.0	560.7	0.7	0.1
	0.26	0.06			0.16	0.02	+					+	7	9	-271.0	560.8	0.8	0.1
	0.26			-0.08	0.20	0.02	+				+	+	8	10	-270.0	561.0	1.0	0.1
	0.26	0.10		-0.13	0.21	0.03	+			+	+	+	9	12	-268.1	561.6	1.6	0.0
	0.26	0.09		-0.13	0.15	0.03	+			+		+	10	11	-269.4	562.0	2.0	0.0
	0.26	0.12		-0.11	0.21	0.03	+	+			+	+	11	12	-268.3	562.0	2.0	0.0
	0.26	0.11		-0.11	0.16	0.03	+	+				+	12	11	-269.5	562.2	2.1	0.0
	0.26		+		0.16	0.02	+					+	13	9	-271.7	562.2	2.2	0.0
	0.26		+		0.21	0.02	+				+	+	14	10	-270.6	562.3	2.3	0.0
	0.26			-0.10	0.15	0.02	+			+		+	15	10	-270.7	562.3	2.3	0.0
	0.26			-0.10	0.20	0.02	+			+	+	+	16	11	-269.6	562.4	2.4	0.0
	0.25	0.10	+	-0.11	0.21	0.03	+				+	+	17	12	-268.5	562.4	2.4	0.0
	0.26	0.09			0.22	0.03	+	+			+	+	18	11	-269.6	562.4	2.4	0.0

0.25	0.09	+	-0.11	0.16	0.03	+		+	19	11	-269.7	562.6	2.6	0.0
0.27					0.02	+		+	20	7	-274.1	562.6	2.6	0.0
0.26	0.08			0.17	0.03	+	+	+	21	10	-270.8	562.6	2.6	0.0
0.26	0.09		-0.12		0.02	+		+	22	9	-271.9	562.7	2.7	0.0
0.26	0.07	+		0.22	0.03	+		+	23	11	-269.7	562.7	2.7	0.0
0.27			-0.09		0.02	+		+	24	8	-273.1	562.9	2.9	0.0
0.26		+	-0.08	0.15	0.02	+		+	25	10	-271.0	562.9	2.9	0.0
0.26	0.06	+		0.17	0.02	+		+	26	10	-271.0	563.0	2.9	0.0

Table S3. Investigation of the relationship between female TL and reproductive performance at adulthood. Models are ranked by Akaike Information Criterion (AIC). All models are presented and accounted for population as random terms and fixed effects were estimated on maximum likelihood. TL and SVL are for individual adult females.

Response	Fixed effects					Model summary					
	(Intercept)	TL	Population state	SVL	Population state * TL	rank	df	logLik	AICc	Δ AICc	weight
Fecundity	-0.06	-0.39	+	0.60	+	1	7	-144.5	304.0	0.0	0.8
	-0.01			0.57		2	4	-149.9	308.0	4.1	0.1
	-0.01	0.07		0.57		3	5	-149.5	309.5	5.5	0.1
	-0.07		+	0.57		4	5	-149.8	310.1	6.1	0.0
	-0.07	0.07	+	0.57		5	6	-149.5	311.6	7.6	0.0
	-0.02					6	3	-176.2	358.7	54.7	0.0
	-0.02	0.06				7	4	-176.0	360.4	56.4	0.0
	-0.12		+			8	4	-176.2	360.6	56.7	0.0
	-0.11	-0.26	+		+	9	6	-174.3	361.2	57.3	0.0
	-0.12	0.06	+			10	5	-175.9	362.4	58.4	0.0
Reproductive success	0.87	0.63	+	0.20	+	1	6	-196.4	405.6	0.0	0.6
	0.91	0.60	+		+	2	5	-198.3	407.1	1.5	0.3
	0.81		+	0.19		3	4	-201.0	410.3	4.8	0.1
	0.86		+			4	3	-202.6	411.4	5.9	0.0
	0.81	0.09	+	0.19		5	5	-200.8	412.0	6.5	0.0
	1.82			0.18		6	3	-203.3	412.7	7.2	0.0
	0.86	0.07	+			7	4	-202.5	413.2	7.7	0.0
	1.84					8	2	-204.7	413.5	8.0	0.0
	1.82	0.08		0.18		9	4	-203.1	414.5	8.9	0.0
	1.84	0.06				10	3	-204.6	415.4	9.8	0.0

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