

# Climate change and ageing in ectotherms

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## Abstract

Human activity is changing climatic conditions at an unprecedented rate. The impact of these changes may be especially acute on ectotherms since they have limited capacities to use metabolic heat to maintain their body temperature. An increase in temperature is likely to increase the growth rate of ectothermic animals, and may also induce thermal stress via increased exposure to heat waves. Fast growth and thermal stress are metabolically demanding, and both factors can increase oxidative damage to essential biomolecules, accelerating the rate of ageing. Here, we explore the potential impact of global warming on ectotherm ageing through its effects on reactive oxygen species production, oxidative damage, and telomere shortening, at the individual and intergenerational levels. Most evidence derives primarily from vertebrates, although the concepts are broadly applicable to invertebrates. We also discuss candidate mechanisms that could buffer ectotherms from the potentially negative consequences of climate change on ageing. Finally, we suggest some potential applications of the study of ageing mechanisms for the implementation of conservation actions. We find a clear need for more ecological, biogeographical, and evolutionary studies on the impact of global climate change on patterns of ageing rates in wild populations of ectotherms facing warming conditions. Understanding the impact of warming on animal life histories, and on ageing in particular, needs to be incorporated into the design of measures to preserve biodiversity to improve their effectiveness.

## KEYWORDS

global warming, oxidative stress, senescence, telomere, thermal stress

## 1 | INTRODUCTION

Climatic conditions are currently changing at unprecedented rate (Diffenbaugh & Field, 2013). Climate projections forecast a global temperature increase up to 4°C by the end of the current century, and an increasing likelihood of extreme climatic events such as heat waves and droughts (IPCC, 2014). Climatic changes have already impacted on many organisms and ecosystems (Parmesan, 2006), even though individuals often have the ability to detect such changes and modify their behaviour, physiology or life history to reduce the

impact on fitness (Hoffmann & Sgrò, 2011). Understanding the influence of climate change on wild organisms is crucial if we are to devise appropriate conservation research plans and policies.

The impact of climate change is expected to be particularly severe on ectothermic animals (Kingsolver, Diamond, & Buckley, 2013). The limited abilities of ectotherms to use metabolic heat to maintain their body temperature makes them especially vulnerable to temperature fluctuations (Bickford, Sheridan, & Howard, 2011; Seebacher, White, & Franklin, 2015). Despite most ectotherms exhibit behavioural plasticity that allows them to adjust their body temperature to

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environmental conditions, rising temperatures can put ectotherms outside their physiological optima and closer, or even above, their thermal tolerance limits (Kingsolver et al., 2013; Sunday et al., 2014). A mismatch between the rate of change in environmental conditions and the capacity of ectotherms to cope with these changes may severely affect their physiology and lead to decreases in fitness.

While the effects of global warming on several components of ectothermic physiology are well understood (Abram, Boivin, Moiroux, & Brodeur, 2017; Gunderson, Dillon, & Stillman, 2017; Gunderson & Stillman, 2015), one particular aspect that has hitherto received little attention is its effect on the dynamics of ageing. Ageing can broadly be defined as the time-dependent functional decline that affects most living organisms (López-Otín, Blasco, Partridge, Serrano, & Kroemer, 2013). Here, we highlight three routes by which climate change might alter the rate of ageing in ectotherms: (a) warmer average temperatures causing an acceleration of growth rates; (b) more frequent heat waves inducing thermal stress; and (c) changes in the pace-of-life of parents affecting the ageing rate of their offspring. As we show below, all three scenarios can induce the loss of organismal homeostasis and accelerate senescence in ectotherms. Here, in using the term 'ectotherm', we are primarily referring to vertebrates, since this is where most relevant existing data on ageing mechanisms occur, but the processes are likely to be also relevant to invertebrates. At present, it is unclear whether organisms have the capacity to compensate for these potential changes in lifespan, or the demographic consequences for populations. Further research is clearly needed to fully evaluate the effects of climate change on rates of ageing of wild organisms, and to incorporate these issues into biodiversity conservation actions.

## 2 | GLOBAL WARMING, FAST GROWTH, AND AGEING IN ECTOTHERMS

At the individual level, warmer environments induce thermal plasticity in most ectotherms, resulting in fast growth but often smaller size later in life, a process that can be also mediated through size-dependent feedbacks (Ohlberger, 2013). This is a common pattern in arthropods (Angilletta & Dunham, 2003), fish (Baudron, Needle, Rijnsdorp, & Tara Marshall, 2014), amphibians (Ruthsatz, Peck, Dausmann, Sabatino, & Glos, 2018), and reptiles (Price et al., 2017). Thermally induced alterations in growth can be particularly costly for ectotherms at early ontogenetic stages, since at this point resources are prioritized towards the development of new structures and away from somatic maintenance (Dmitriew, 2011; Metcalfe & Monaghan, 2001). Many ectotherms develop complex life cycles and are especially sensitive to warming impacts on growth if these occur in early life stages, that is, before metamorphosis (Huey et al., 2012).

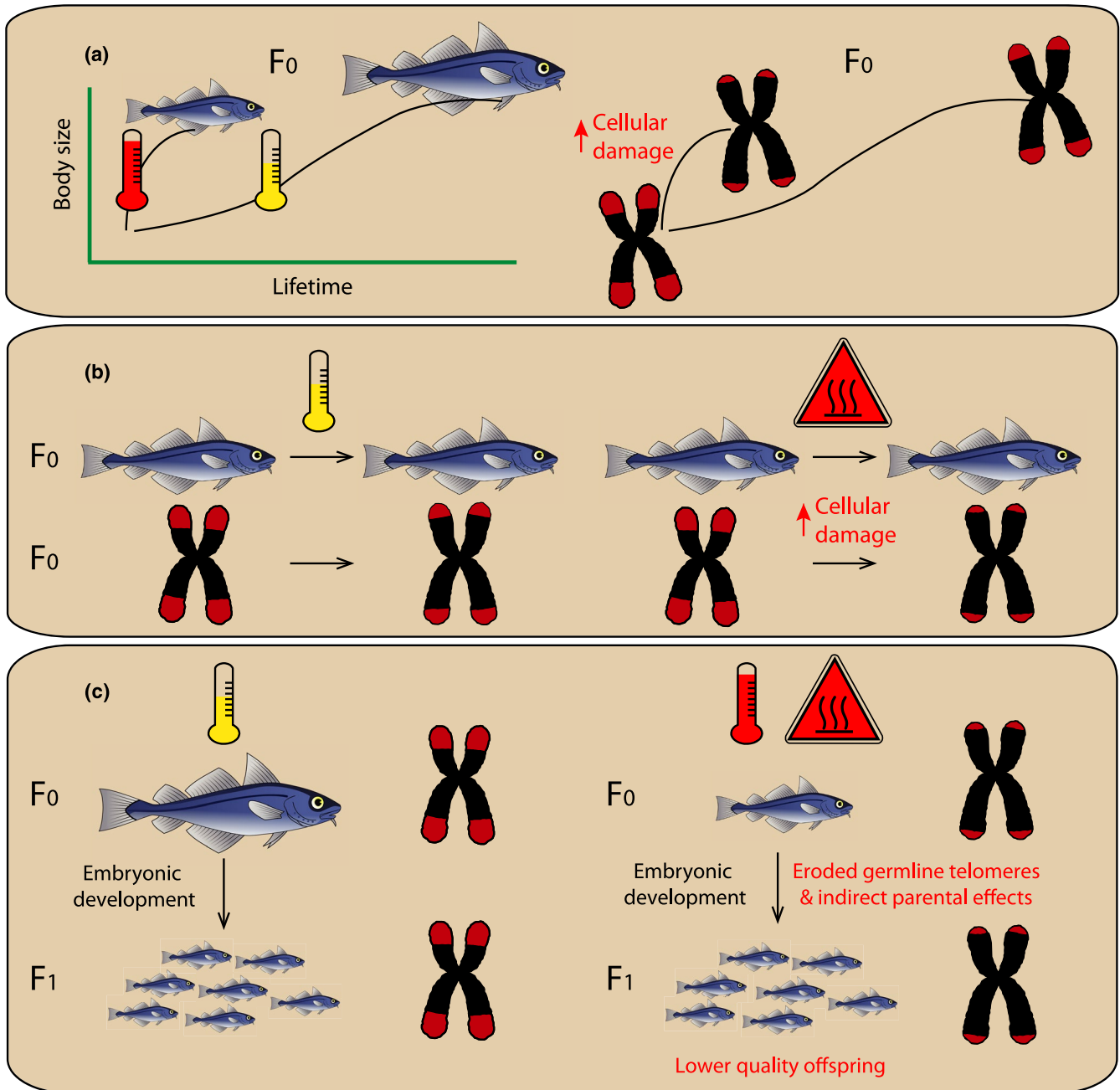
Environmentally induced acceleration of growth is known to impact on lifespan. The costs of rapid growth were first demonstrated in fish showing a negative relationship between growth rate and longevity (Comfort, 1963). A negative relationship between faster growth in early life and later survival has been found in other fish

species, and also in insects (e.g. Lee & Roh, 2010), amphibians (e.g. Altwegg & Reyer, 2003), and reptiles (e.g. Olsson & Shine, 2002). While most of these studies have been correlational, a trade-off between growth rate and lifespan has been demonstrated experimentally in sticklebacks (Lee, Monaghan, & Metcalfe, 2013). In this study, temperature-induced faster growth was associated with reduced longevity, while experimental slowing of growth was associated with increased longevity, confirming the role of thermally induced growth in shaping the pattern and pace of ageing in ectotherms.

Across-species comparisons indicate that larger endotherms live longer than smaller ones ( $r^2 = .46$  and  $.39$  in birds and mammals, respectively; Speakman, 2005). In contrast, body size explains only a small portion of the variance in longevity in vertebrate ectotherms, as observed in amphibians ( $r^2 = .07-.14$ ; Stark & Meiri, 2018) or reptiles ( $r^2 = .04-.23$ ; Stark, Tamar, Itescu, Feldman, & Meiri, 2018). The weaker correlation between body size and maximum lifespan in vertebrate ectotherms than in endotherms probably indicates that the traits have evolved at least partially independently in species with indeterminate growth. Ectotherms can potentially show some degree of thermal independence via a reduced heat exchange rate with the environment. The ability to be thermally independent mainly benefits larger-bodied ectotherms under cold environments rather than warming conditions. However, reductions in body size due to induced fast growth caused by warming may facilitate heat loss in large species. Among-species differences in the rate of growth from birth to maturation, and the variation in this rate caused by rising temperatures, may be even more relevant than differences in body size to understand the impact of warming on ageing in ectotherms. Another unexplored topic is how among-species differences in life expectancy at birth can affect responses to warming. The likelihood of being exposed to warming and thermal stress during a single lifetime is, obviously, higher in long-lived species, but these species have often evolved protective mechanisms to slow the ageing process (Tian, Seluanov, & Gorbunova, 2017). Further comparative research will help to disentangle the relative importance of growth, body size, and lifespan on ectotherms ageing under a global warming scenario.

### 2.1 | Fast growth and oxidative damage

The reduction in lifespan of ectotherms experiencing faster growth could be due to greater mitochondrial activity (Figure 1a). Rapid growth requires the formation in the mitochondria of increased amounts of ATP, and this can lead to the generation of reactive oxygen species (ROS) as a by-product. While ROS have many beneficial physiological functions such as maintenance of homeostasis and cell signalling, they can also cause oxidative damage to essential biomolecules like membrane lipids, proteins, and DNA when their concentration exceeds the antioxidant capacity of cells to detoxify them (Halliwell & Gutteridge, 2015). This damage can lead to accelerated ageing of the cells and ultimately the whole organism (Halliwell & Gutteridge, 2015). A meta-analysis across all animal groups has



**FIGURE 1** Mechanisms whereby environmental warming could increase the rates of ageing in ectotherms. (a) Left side: differences in individual growth trajectories and body size at maturation in response to normal (yellow thermometer) or warm (red thermometer) thermal conditions; right side: fast growth may include cellular damage and a consequent increase in the rate of shortening of the telomeres (the red caps on the ends of the chromosomes). (b) Left side: ectotherms have evolved to cope with normal temperature regimes without incurring in thermal stress; right side: heat waves induce thermal stress, leading to cellular damage and consequent faster erosion of telomeres. Such responses would not necessarily include significant changes in growth since they often take place during a brief period of time. (c) Possible intergenerational effects of climate warming on telomere length. Left side: normal thermal regimes result in normal telomere lengths in offspring; right side: higher mean temperatures and heat waves in parental generation have deleterious effects on offspring. Such effects, evident at very early offspring life stages, could be caused by faster erosion of germline telomeres, by poor parental condition and/or impaired parental care during post-natal stages during post-natal stages

shown that faster growth is associated with greater oxidative damage (Smith, Nager, & Costantini, 2016). In ectotherms, fast growth can alter the redox status in insects (e.g. De Block & Stoks, 2008), fish (e.g. Guerra, Zenteno-Savín, Maeda-Martínez, Philipp, & Abele, 2012), amphibians (e.g. Burraco, Valdés, & Orizaola, 2020),

and reptiles (e.g. Furtado-Filho, Polcheira, Machado, Mourão, & Hermes-Lima, 2007). These effects can persist over long time periods, even across life stages. For instance, juvenile fish growing faster in response to elevated winter temperatures experienced severe oxidative and DNA damage later in life at the time of breeding (Kim,

Noguera, & Velando, 2019). Amphibians can also experience redox imbalances at metamorphosis as a negative consequence of growing at high rates earlier in life, when compensating for delayed hatching (Burraco et al., 2020).

## 2.2 | Warmer temperature and telomeres

Oxidative stress can also induce faster ageing through its impact on telomeres. Telomeres are specialized sections of non-coding DNA that mark and protect the ends of chromosomes. Telomere regions are essential for maintaining genome stability by preventing end-to-end fusion of chromosomes, and also protect the coding sequences from loss at the ends of the lagging DNA strands that occurs during DNA replication (Richter & von Zglinicki, 2007). The length of the telomeres becomes shorter at each cell division. Cells enter a state of replicative senescence once their telomeres reach a critically short length; this is followed by either cell death or a change in cell secretory profile to a more pro-inflammatory state (Aubert & Lansdorp, 2008). Such changes can provide a link between the rate of telomere shortening and tissue (and hence organismal) senescence. The causal relationship between oxidative stress and the rate of telomere shortening has been evidenced via the administration of antioxidants, which slow the rate of telomere erosion (Badás et al., 2015; Pineda-Pampliega et al., 2020), and confirmed through field and laboratory studies (reviewed in Barnes, Fouquerel, & Opresko, 2018; Monaghan & Ozanne, 2018; Reichert & Stier, 2017). A recent meta-analysis (Chatelain, Drobnick, & Szulkin, 2020) supports the idea that oxidative stress mediates telomere shortening, although this relationship is mainly linked to differences in the levels of the antioxidant machinery.

Differences in telomere length or loss rate can predict life expectancy, but the telomere–fitness relationship is highly variable in ectotherms and still need further research (Olsson, Wapstra, & Friesen, 2018a, 2018b). Telomere loss can also indicate the degree of stress exposure of an individual across the life course, although as yet most of the evidence of this comes from endotherms (Bateson & Poirier, 2019; Tricola et al., 2018; Wilbourn et al., 2018). The variation in telomere length among populations of brown trout correlates negatively with the river temperatures they experienced in the previous summer, and thus telomere length has been suggested as a marker of past thermal stress in fish (Debes, Visse, Panda, Ilmonen, & Vasemägi, 2016). In ectotherms, fast growth can lead to accelerated telomere shortening, as found in juvenile fish (McLennan et al., 2016; Pauliny, Devlin, Johnsson, & Blomqvist, 2015) or amphibian larvae (Burraco, Díaz-Paniagua, & Gomez-Mestre, 2017). Since differences in length-at-age and rate of loss of telomeres can be considered as ageing biomarkers, a detailed understanding of telomere dynamics over a species' lifetime, and across taxa, will improve our predictions of the impact of warming on ectotherm ageing. To this end, knowing the age of individuals is helpful in studies in the wild. In temperate vertebrate ectotherms, growth shows seasonal variation and age can be determined through skeletochronology, for example, by

counting lines of arrested growth in reptiles and amphibians, growth rings in fish scales or bands in fish otoliths (Zhao, Klaassen, Lisovski, & Klaassen, 2019).

However, when faster growth is induced by higher temperatures, the relationship with telomere attrition is not always straightforward since adult ectotherms can undergo partial telomere restoration as a result of expressing the enzyme telomerase. Telomerase restores telomere length and is more often active in somatic tissue after birth in ectotherms than in endotherms (Olsson, Wapstra, & Friesen, 2018a). Telomerase expression is predicted to be higher in warmer environments, so potentially compensating for damage to telomeres in those organisms experiencing temperature-induced fast growth (Olsson et al., 2018a). This hypothesis is supported by recent research showing that lizards held in hot basking conditions for 3 months experienced increases in telomere length, unlike those held in cooler conditions (Fitzpatrick et al., 2019). Further empirical studies will clarify the possible interaction between temperature, growth, and telomerase expression.

The study of telomere dynamics in populations inhabiting divergent temperature conditions might allow us to evaluate the effects of human-induced thermal stress on ageing rates. This would be particularly relevant for populations of ectotherms living in regions of rapid thermal change, especially if they have long generation times that slow the potential rate of adaptation to changing environments (Morley, Peck, Sunday, Heiser, & Bates, 2019). Species with shorter generation time and larger populations are predicted to evolve quickly while maintaining genetic variation (Hoffmann & Sgrò, 2011). Artificial selection experiments comparing the genetic responses to warming conditions will help to evaluate the relative importance of generation time, population size, and plasticity, in evolutionary adaptation processes. Unfortunately, there is a lack of studies combining biogeographical and gerontological approaches which would allow us to appropriately predict the impact that global warming will have on the comparative rates of ageing of ectotherms along climatic gradients.

## 3 | HEAT WAVES AND AGEING IN ECTOTHERMS

Forecasts for the next 50 years predict a dramatic increase in the likelihood of heat waves (IPCC, 2014), characterized by sudden rises in air or water temperature that could reach the upper thermal limits for many ectotherms (Gunderson & Stillman, 2015). Heat waves are one of the most powerful environmental forces affecting the welfare and physiology of ectotherms (Kingsolver et al., 2013), and may cause the acceleration of senescence by inducing thermal stress. Similar to the alterations caused by other stressful conditions, thermal stress can disrupt individual's homeostasis and compromise organismal health. In vertebrates, the response to stressful conditions is mainly regulated by neuroendocrine pathways. These pathways mediate biological processes such as growth or reproduction (Crespi, Williams, Jessop, & Delehanty, 2013) but also accelerate the rate of ageing, as determined, for example, by a higher rate of telomere

attrition (Angelier, Costantini, Blevin, & Chastel, 2018; Haussmann & Heidinger, 2015). Stress often leads to a higher secretion of hormones that enhances cellular catabolism and exacerbates the generation of ROS, with putative impacts on antioxidant defences and the rate of telomere shortening (Haussmann & Heidinger, 2015; Haussmann & Marchetto, 2010; Monaghan, 2014). The antioxidant machinery of ectotherms seems to be particularly sensitive to extreme thermal events, as indicated by strong redox responses to high temperatures observed in arthropods (e.g. Yang, Huang, & Wang, 2010) and fish (e.g. Banh, Wiens, Sotiri, & Treberg, 2016). On the other hand, the redox machinery of some reptiles seems relatively insensitive to thermal stress (e.g. Stahlschmidt, French, Ahn, Webb, & Butler, 2017), which may be a consequence of the down-regulation of particular genes in response to warming (Bentley, Haas, Tedeschi, & Berry, 2017).

Exposure to heat waves can result in accelerated erosion of telomeres in ectothermic animals likely as a consequence of enhanced cellular metabolism under thermal fluctuations (Figure 1b). For instance, sturgeons facing thermal stress experience higher rate of telomere shortening (Simide, Angelier, Gaillard, & Stier, 2016) and show increased juvenile mortality (Kappenman, Fraser, Toner, Dean, & Webb, 2009). Desert lizards, which do not show signs of telomere shortening or reductions in survival when exposed to gradual warming, experience telomere shortening and lower overwinter survival after a week of simulated heat wave conditions (Zhang et al., 2018). This is perhaps surprising, given the lack of oxidative stress induced by high temperatures in other reptiles, and highlights the need for more comprehensive studies investigating the impact of temperature on physiological indicators of ageing in ectotherms.

#### 4 | INTERGENERATIONAL EFFECTS OF CLIMATE CHANGE ON AGEING RATES IN ECTOTHERMS

Stress experienced by parents can influence the physiology of their offspring. To establish whether the environmental conditions experienced by parents can influence the rates of ageing of their offspring, we need to understand the mechanisms whereby rates of ageing could be transmitted between generations. In the absence of detailed information on life expectancy (not normally available over multiple generations), the usual approach is to use a biomarker of the rate of ageing, such as telomere length. Telomere length at a given developmental stage is a function of their initial length (i.e. at zygote), minus the accumulated shortening, plus the amount of restoration experienced until that point (Dugdale & Richardson, 2018).

Heritability estimates for telomere length in animals range from 0.18 to >1 (reviewed in Dugdale & Richardson, 2018; Haussmann & Heidinger, 2015; Reichert et al., 2015), tending to be higher when measured earlier in life (Dugdale & Richardson, 2018). However, in ectotherms (in contrast to most endotherms), telomeres show signs of elongation after birth in several species (reptiles: Ujvari et al., 2017; fish: McLennan et al., 2018; amphibians: Burraco et al., 2020). This

makes it far from straightforward to decide the point in ontogeny at which telomere length should be compared between parents and offspring.

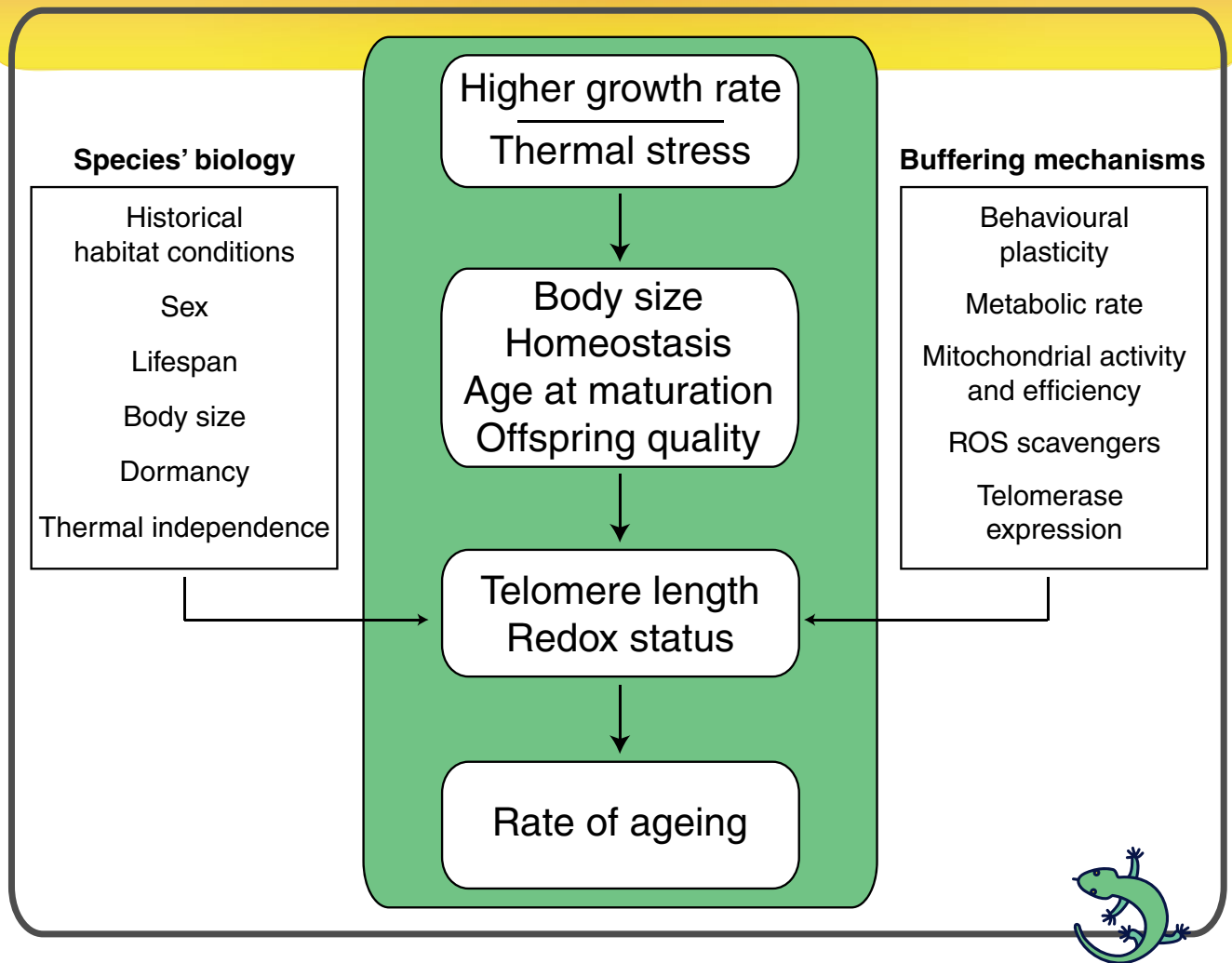
If climate warming causes a reduction in the physiological condition of ectotherms at the time of breeding, this could lead to shorter telomeres in their offspring through two different routes. First, stressors could affect germline telomere lengths, causing offspring to inherit shorter telomeres from parents that were exposed to more stressful environments. Second, indirect parental effects can cause faster ageing in offspring, either during the embryonic stages (e.g. through maternally derived stress hormones or suboptimal temperatures during development), or in the early post-natal stages (e.g. through changes in parental behaviour or care; Haussmann & Heidinger, 2015). Both routes may be particularly important for ectotherms in a warming world because higher temperatures can induce maturation earlier in life and at a smaller size (Angilletta, Steury, & Sears, 2004). Smaller size at breeding is often associated with the production of lower-quality offspring and poor parental care, which can negatively affect offspring performance at embryonic and post-birth stages (Angilletta et al., 2004), and cause accelerated ageing (Haussmann & Heidinger, 2015; Figure 1c). Detrimental thermal conditions experienced by parents can lead to poor offspring condition as a consequence of a reduction in the energy invested by the parents in each offspring. However, although rare, compensatory responses by parents or changes in breeding strategies could mitigate this effect, for example by reducing clutch size to allocate a larger amount of energy to each offspring (Charnov & Ernest, 2006).

There are several other factors that ideally should be considered when studying the intergenerational effects of warming on ageing dynamics in ectotherms. Many ectotherms show sexual dimorphism, with females typically larger than males, and temperature-dependent sex determination during embryogenesis can also occur. The negative consequences on ageing caused by warming may be exacerbated in species producing females at higher incubation temperatures. Embryos developing as females, and hatching at smaller sizes due to warming, could then show compensatory growth responses, which may result in a lifespan penalty (Metcalf and Monaghan, 2003). Sex differences in lifespan and ageing can also be driven by the reproductive strategy of species. For example, in polygynous species, survival declines with age faster in males than in females (Clutton-Brock & Isvaran, 2007); warming could exacerbate such sex differences in lifespan by uncoupling the time at which each sex reaches sexual maturation, a process that may be particularly important in semelparous species.

#### 5 | CANDIDATE MECHANISMS TO BUFFER THE EFFECTS OF WARMING ON AGEING IN ECTOTHERMS

Different mechanisms could allow ectotherms to counteract the negative effects of climate change on their ageing rate (Figure 2). Temperature-induced plasticity is a ubiquitous feature of ectothermic

## Global warming pressures on the ageing of ectotherms



**FIGURE 2** Putative impacts of warming conditions on ageing in ectotherms. Higher temperatures are predicted to cause faster growth or thermal stress in ectotherms, which can involve changes in body size, physiological homeostasis, age at maturation, and/or offspring quality. Both faster growth and thermal stress can cause a detrimental impact on ageing-related mechanisms, as for example inducing telomere attrition or oxidative stress. From an eco-evolutionary point of view, a species' biology and buffering mechanisms will likely define the extent to which warming will impact on ageing both at the individual or intergenerational levels

animals (Gunderson et al., 2017). Adaptive behavioural plasticity can be essential for thermoregulation in mobile ectotherms and may play an important role both under gradual warming and during thermal stress events. At low and medium latitudes, where exposure to the sun can otherwise cause body temperatures to increase above an organism's thermal limits, many ectotherms have developed behavioural strategies to avoid overheating (Abram et al., 2017). This is mainly explained by the fact that metabolic responses do not follow a linear pattern, and at those latitudes small increases in temperature may induce significant changes in metabolism. However, species at higher latitudes, including polar environments, may be as vulnerable to global warming as those in the tropics because they may have very narrow thermal tolerances (Johansson, Orizaola, & Nilsson-Örtman, 2020; Somero, 2010).

The ability to plastically modify the onset of some life strategies can reduce the negative impact of warming on ectotherm ageing. Dormancy, diapause and resting egg stages, processes very common in ectotherms living in highly seasonal environments, involve a significant decrease in development and physical activity. In an endotherm, the edible dormouse, a reduction in telomere attrition has been observed during hibernation (Turbill, Ruf, Smith, & Bieber, 2013), although intermittent arousal also carries costs in terms of increased telomere loss (Hoelzl, Cornils, Smith, Moodley, & Ruf, 2016). Under a global warming scenario, dormant ectotherms will probably experience a reduction in the duration and number of dormancy events. Therefore, individuals may need to adjust their use of dormancy in response to environmental temperatures, to reduce the negative effects on ageing. The possible role of this process



in regulating ageing dynamics has not been tested yet in ectotherms, but a recent study shows that higher winter and summer temperatures impact positively and negatively, respectively, on telomere lengths in a hibernating lizard (Axelsson, Wapstra, Miller, Rollings, & Olsson, 2020).

Adaptive physiological plasticity can also help ectotherms acclimate to warmer conditions (Gunderson et al., 2017; Norin & Metcalfe, 2019; Seebacher et al., 2015). However, both behavioural and physiological plasticity may prove insufficient to fully compensate for the effects of warming (Gunderson et al., 2017; Gunderson & Stillman, 2015). This is exemplified by the fact that physiological (e.g. locomotor, metabolic, heart, enzymatic activity) rates in ectotherms have increased up to 20% over the last 20 years as result of climate change, and chronic exposure to higher temperatures has resulted in reductions in their thermal sensitivity (Norin & Metcalfe, 2019; Seebacher et al., 2015). Metabolic rates of terrestrial, freshwater, and marine ectothermic species are predicted to keep increasing in the coming decades (Seebacher et al., 2015). Plasticity is, on average, higher in aquatic than terrestrial ectotherms (Gunderson & Stillman, 2015; Huey et al., 2012; Morley et al., 2019), and it may buffer the negative impact of warming on ectotherm physiology. However, plasticity alone cannot fully protect aquatic ectotherms from overheating (Gunderson et al., 2017). Among ectotherms, crustacea and fish are expected to have smaller decreases in thermal safety margins when environmental temperatures rise than insects, reptiles, and amphibians (Gunderson & Stillman, 2015). Measured impacts of past and current global warming on ectothermic metabolism would suggest that there will be a global acceleration in the rate of senescence of ectotherms as warming continues.

There are also potential molecular mechanisms that could buffer warming impact on ageing. These mechanisms might either prevent damage in cells by reducing the generation of ROS, or repair the damage already caused. Both metabolic rate, usually measured in terms of whole-body oxygen consumption, and mitochondrial efficiency, defined as the amount of ATP generated per molecule of oxygen consumed, show great within- and among-individual variation, and can change in response to environmental conditions (Salin, Auer, Rey, Selman, & Metcalfe, 2015; Salin et al., 2019). Metabolic plasticity at the organelle and tissue/organ level may allow organisms to adjust ROS production to increase their resilience to climate change (Norin & Metcalfe, 2019; Seebacher et al., 2015). Greater mitochondrial uncoupling, which reduces the rate of ROS production at the expense of ATP production efficiency, has been proposed as a mechanism to reduce the rate of senescence (the 'uncoupling to survive' hypothesis, Mookerjee, Divakaruni, Jastroch, & Brand, 2010). This mitigation measure comes at a cost of reduced ATP availability and also increased body heat, since the uncoupling process involves a thermogenic reaction; there is thus an interesting trade-off between ROS production and body temperature in organisms facing warming. Animals may respond by increasing their production of ROS scavenger molecules so as to prevent excessive oxidative damage caused by responses to warming. As an example, one of the first cellular lines of defence against pro-oxidants is the reduced form of glutathione,

the production of which can increase in response to stress events (Angelier et al., 2018). An increased availability of ROS scavengers can allow greater metabolic activity, as demonstrated in endotherms through enhanced growth (Velando, Noguera, da Silva, & Kim, 2019). However, there is little knowledge about the costs of increased ROS scavenger production—note that ROS are known to play an essential role in signalling pathways (Costantini, 2019).

The enhancement of repair mechanisms might also slow down ageing in ectotherms. The enzyme telomerase restores telomere length and may play a key role in the extensive regenerative capacity in organisms with indeterminate growth (Gomes, Shay, & Wright, 2010). If selection favours higher levels of telomerase expression in response to warming, it may mitigate the potential damage to telomeres caused by growth acceleration or by thermal stress (Olsson et al., 2018a). However, the prolonged action of telomerase can induce 'immortal cells' and tumorigenesis (Blasco, 2007), which may expose adult ectotherms to a higher risk of cancer (Olsson et al., 2018a; Young, 2018), although our knowledge of the prevalence of cancer in wild animals is very limited.

Field and laboratory studies, ideally including cross-fostering and transgenerational approaches, will help us to understand whether the action of buffering mechanisms is driven either by plasticity or local adaptation across populations. A higher degree of complexity can be added by considering the possibility that the dynamics of ageing-related mechanisms may be tissue-specific. Although telomere lengths seem to correlate among tissues (e.g. in reptiles: Rollings et al., 2019, 2020), differences in cell division and turnover rate, together with the possible tissue-specific expression of buffering mechanisms, may imply divergent responses in ageing-related mechanisms at the tissue level. Evidence from mammals suggests that telomere attrition rates are similar across tissues in adults, but not necessarily so in early life (Daniali et al., 2013; Sabharwal et al., 2018), so the life stage at which the temperature effects occur could be important. Conducting longitudinal studies on the variation of ageing mechanisms at the tissue level is challenging, since terminal sampling is often required, but cross-sectional studies should help to disentangle this topic. It is clear that much more research is needed to fully understand the role that behavioural, physiological, and molecular mechanisms can play in buffering the effects of climate change on the ageing of ectotherms.

## 6 | HOW MIGHT THESE CONCEPTS HELP IN THE CONSERVATION OF ECTOTHERMS—AND WHAT DO WE STILL NEED TO FIND OUT?

There are issues that need to be taken into account in the context of ectotherm conservation in the face of environmental warming. It is crucial to know how different environmental conditions affect the ageing rate of ectotherms at the individual level and across developmental stages or lifetimes, as well as to understand how among-species differences in life histories can influence the

impact of environmental change on ageing dynamics. Studies of the ageing machinery in ectotherms inhabiting contrasting environments may provide insights into the current health status of populations that may aid in defining conservation actions. As an example, forest clearing reduces canopy cover and leads to an increase in the duration of sunlight exposure, modifying the thermal regime in nest sites of lizards (e.g. Shine, Barrott, & Elphick, 2002). Comparing the ageing dynamics of populations with different access to forest shade would help to better evaluate the impact that forest management can have in mitigating the adverse effect of rising temperatures on these lizard populations. A similar approach can be applied to aquatic ectotherms. Climate change is increasing the likelihood of droughts and the sudden change of water temperature in small ponds. The evaluation of ageing dynamics across populations may help to identify those populations under risk due to thermal stress and to implement conservation actions such as the installation of microclimate refuges, the restoration of breeding sites, or the manipulation of hydroperiod at breeding ponds (Shoo et al., 2011).

Several research questions are still unresolved regarding the impact of warming on the ageing of ectotherms. We need to know the relative importance of high average temperature versus heat waves in affecting rates of ageing, and which ectothermic taxa are most vulnerable to changes in ageing. This is particularly important for invertebrates, where there is currently virtually no information on ageing mechanisms in wild populations. An understanding of these differences will allow managers to develop effective conservation measures that will protect not only declining populations but also others that are apparently healthy. Furthermore, it will allow more accurate modelling of the impact of future warming scenarios on ageing rates in ectotherms that can feed into population models used to set conservation priorities.

## 7 | CONCLUSIONS

Temperature increases associated with climate change may alter ageing-related processes in ectotherms, as a consequence of changes in their growth trajectories or an increased risk of thermal stress, and both processes may include intergenerational effects (Figure 2). However, there is a need for more ecological, biogeographical, and evolutionary studies on the impact of global climate change on patterns of senescence in wild populations of ectotherms (even more in invertebrates) facing warming conditions. This research should also investigate the possible role of candidate behavioural, cellular, and physiological mechanisms for buffering the predicted negative consequences of warming on the rate of ageing. We also need to understand the putative population consequences of changes in ageing rate, and to link these to location-specific predictions of climate change, to determine which populations and/or species are most vulnerable. Ideally, this information needs to be combined with species-specific knowledge on plasticity or evolutionary adaptability in response to thermal changes (Morley et al., 2019). Understanding

the basic effects of climate warming on the ageing rates of ectothermic species will help in developing global and local scientific-based policies aiming at reducing the negative consequences of climatic change on biodiversity.

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## CONFLICT OF INTEREST

We declare no conflict of interest.

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## REFERENCES

- Abram, P. K., Boivin, G., Moiroux, J., & Brodeur, J. (2017). Behavioural effects of temperature on ectothermic animals: Unifying thermal physiology and behavioural plasticity. *Biological Reviews*, 92, 1859–1876. <https://doi.org/10.1111/brv.12312>
- Altwegg, R., & Reyer, H. U. (2003). Patterns of natural selection on size at metamorphosis in water frogs. *Evolution*, 57, 872–882.
- Angelier, F., Costantini, D., Blevin, P., & Chastel, O. (2018). Do glucocorticoids mediate the link between environmental conditions and telomere dynamics in wild vertebrates? A review. *General and Comparative Endocrinology*, 256, 99–111. <https://doi.org/10.1016/j.ygcn.2017.07.007>
- Angilletta, J. R., & Dunham, A. E. (2003). The temperature-size rule in ectotherms: Simple evolutionary explanations may not be general. *American Naturalist*, 162, 332–342. <https://doi.org/10.1086/377187>
- Angilletta Jr., M. J., Steury, T. D., & Sears, M. W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44, 498–509.
- Aubert, G., & Lansdorp, P. M. (2008). Telomeres and aging. *Physiological Reviews*, 88, 557–579. <https://doi.org/10.1152/physrev.00026.2007>
- Axelsson, J., Wapstra, E., Miller, E., Rollings, N., & Olsson, M. (2020). Contrasting seasonal patterns of telomere dynamics in response to environmental conditions in the ectothermic sand lizard, *Lacerta agilis*. *Scientific Reports*, 10, 1–9. <https://doi.org/10.1038/s41598-019-57084-5>
- Badás, E. P., Martínez, J., de Aguilar, R., Cachafeiro, J., Miranda, F., Figuerola, J., & Merino, S. (2015). Ageing and reproduction: Antioxidant supplementation alleviates telomere loss in wild birds. *Journal of Evolutionary Biology*, 28, 896–905. <https://doi.org/10.1111/jeb.12615>
- Banh, S., Wiens, L., Sotiri, E., & Treberg, J. R. (2016). Mitochondrial reactive oxygen species production by fish muscle mitochondria: Potential role in acute heat-induced oxidative stress. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology*, 191, 99–107. <https://doi.org/10.1016/j.cbpb.2015.10.001>



- Barnes, R. P., Fouquerel, E., & Opresko, P. L. (2018). The impact of oxidative DNA damage and stress on telomere homeostasis. *Mechanisms of Ageing and Development*, 177, 37–45.
- Bateson, M., & Poirier, C. (2019). Can biomarkers of biological age be used to assess cumulative lifetime experience. *Animal Welfare*, 28, 41–56. <https://doi.org/10.7120/09627286.28.1.041>
- Baudron, A. R., Needle, C. L., Rijnsdorp, A. D., & Tara Marshall, C. (2014). Warming temperatures and smaller body sizes: Synchronous changes in growth of North Sea fishes. *Global Change Biology*, 20, 1023–1031. <https://doi.org/10.1111/gcb.12514>
- Bentley, B. P., Haas, B. J., Tedeschi, J. N., & Berry, O. (2017). Loggerhead sea turtle embryos (*Caretta caretta*) regulate expression of stress response and developmental genes when exposed to a biologically realistic heat stress. *Molecular Ecology*, 26, 2978–2992.
- Bickford, D. P., Sheridan, J. A., & Howard, S. D. (2011). Climate change responses: Forgetting frogs, ferns and flies? *Trends in Ecology & Evolution*, 26, 553–554. <https://doi.org/10.1016/j.tree.2011.06.016>
- Blasco, M. A. (2007). Telomere length, stem cells and aging. *Nature Chemical Biology*, 3, 640. <https://doi.org/10.1038/nchembio.2007.38>
- Burraco, P., Díaz-Paniagua, C., & Gomez-Mestre, I. (2017). Different effects of accelerated development and enhanced growth on oxidative stress and telomere shortening in amphibian larvae. *Scientific Reports*, 7, 7494. <https://doi.org/10.1038/s41598-017-07201-z>
- Burraco, P., Valdés, A. E., & Orizaola, G. (2020). Metabolic costs of altered growth trajectories across life transitions in amphibians. *Journal of Animal Ecology*, 89, 855–866. <https://doi.org/10.1111/1365-2656.13138>
- Charnov, E. L., & Ernest, S. M. (2006). The offspring-size/clutch-size trade-off in mammals. *American Naturalist*, 167, 578–582. <https://doi.org/10.1086/501141>
- Chatelain, M., Drobniak, S. M., & Szulkin, M. (2020). The association between stressors and telomeres in non-human vertebrates: A meta-analysis. *Ecology Letters*, 23, 381–398. <https://doi.org/10.1111/ele.13426>
- Clutton-Brock, T. H., & Isvaran, K. (2007). Sex differences in ageing in natural populations of vertebrates. *Proceedings of the Royal Society B: Biological Sciences*, 274, 3097–3104. <https://doi.org/10.1098/rspb.2007.1138>
- Comfort, A. (1963). Effect of delayed and resumed growth on the longevity of a fish (*Lebistes reticulatus*, Peters) in captivity. *Gerontology*, 8, 150–155. <https://doi.org/10.1159/000211216>
- Costantini, D. (2019). Understanding diversity in oxidative status and oxidative stress: The opportunities and challenges ahead. *Journal of Experimental Biology*, 222, jeb194688. <https://doi.org/10.1242/jeb.194688>
- Crespi, E. J., Williams, T. D., Jessop, T. S., & Delehanty, B. (2013). Life history and the ecology of stress: How do glucocorticoid hormones influence life-history variation in animals? *Functional Ecology*, 27, 93–106. <https://doi.org/10.1111/1365-2435.12009>
- Daniali, L., Benetos, A., Susser, E., Kark, J. D., Labat, C., Kimura, M., ... Aviv, A. (2013). Telomeres shorten at equivalent rates in somatic tissues of adults. *Nature Communications*, 4, 1–7. <https://doi.org/10.1038/ncomms2602>
- De Block, M., & Stoks, R. (2008). Compensatory growth and oxidative stress in a damselfly. *Proceedings of the Royal Society B: Biological Sciences*, 275, 781–785. <https://doi.org/10.1098/rspb.2007.1515>
- Debes, P. V., Visse, M., Panda, B., Ilmonen, P., & Vasemägi, A. (2016). Is telomere length a molecular marker of past thermal stress in wild fish? *Molecular Ecology*, 25, 5412–5424. <https://doi.org/10.1111/mec.13856>
- Diffenbaugh, N. S., & Field, C. B. (2013). Changes in ecologically critical terrestrial climate conditions. *Science*, 341, 486–492. <https://doi.org/10.1126/science.1237123>
- Dmitriew, C. M. (2011). The evolution of growth trajectories: What limits growth rate? *Biological Reviews*, 86, 97–116. <https://doi.org/10.1111/j.1469-185X.2010.00136.x>
- Dugdale, H. L., & Richardson, D. S. (2018). Heritability of telomere variation: It is all about the environment! *Philosophical Transactions of the Royal Society B*, 373, 20160450. <https://doi.org/10.1098/rstb.2016.0450>
- Fitzpatrick, L. J., Olsson, M., Parsley, L. M., Pauliny, A., Pinfold, T. L., Pirtle, T., ... Wapstra, E. (2019). Temperature and telomeres: Thermal treatment influences telomere dynamics through a complex interplay of cellular processes in a cold-climate skink. *Oecologia*, 191, 767–776. <https://doi.org/10.1007/s00442-019-04530-w>
- Furtado-Filho, O. V., Polcheira, C., Machado, D. P., Mourão, G., & Hermes-Lima, M. (2007). Selected oxidative stress markers in a South American crocodylian species. *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology*, 146, 241–254. <https://doi.org/10.1016/j.cbpc.2006.11.017>
- Gomes, N. M., Shay, J. W., & Wright, W. E. (2010). Telomere biology in Metazoa. *FEBS Letters*, 584, 3741–3751. <https://doi.org/10.1016/j.febslet.2010.07.031>
- Guerra, C., Zenteno-Savín, T., Maeda-Martínez, A. N., Philipp, E. E. R., & Abele, D. (2012). Changes in oxidative stress parameters in relation to age, growth and reproduction in the short-lived catarina scallop *Argopecten ventricosus* reared in its natural environment. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, 162, 421–430. <https://doi.org/10.1016/j.cbpa.2012.04.018>
- Gunderson, A. R., Dillon, M. E., & Stillman, J. H. (2017). Estimating the benefits of plasticity in ectotherm heat tolerance under natural thermal variability. *Functional Ecology*, 31, 1529–1539. <https://doi.org/10.1111/1365-2435.12874>
- Gunderson, A. R., & Stillman, J. H. (2015). Plasticity in thermal tolerance has limited potential to buffer ectotherms from global warming. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150401. <https://doi.org/10.1098/rspb.2015.0401>
- Halliwel, B., & Gutteridge, J. M. (2015). *Free radicals in biology and medicine*. New York, NY: Oxford University Press.
- Hausmann, M. F., & Heidinger, B. J. (2015). Telomere dynamics may link stress exposure and ageing across generations. *Biology Letters*, 11, 20150396. <https://doi.org/10.1098/rsbl.2015.0396>
- Hausmann, M. F., & Marchetto, N. M. (2010). Telomeres: Linking stress and survival, ecology and evolution. *Current Zoology*, 56, 714–727. <https://doi.org/10.1093/czoolo/56.6.714>
- Hoelzl, F., Cornils, J. S., Smith, S., Moodley, Y., & Ruf, T. (2016). Telomere dynamics in free-living edible dormice (*Glis glis*): The impact of hibernation and food supply. *Journal of Experimental Biology*, 219, 2469–2474.
- Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature*, 470, 479. <https://doi.org/10.1038/nature09670>
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society B*, 367, 1665–1679. <https://doi.org/10.1098/rstb.2012.0005>
- IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Core Writing Team, R. K. Pachauri, & L. A. Meyer (Eds.). Geneva, Switzerland: IPCC, 151 pp.
- Johansson, F., Orizaola, G., & Nilsson-Örtman, V. (2020). Temperate insects with narrow seasonal activity periods can be as vulnerable to climate change as tropical insect species. *Scientific Reports*, 10, 8822.
- Kappenman, K. M., Fraser, W. C., Toner, M., Dean, J., & Webb, M. A. (2009). Effect of temperature on growth, condition, and survival of juvenile shovelnose sturgeon. *Transactions of the American Fisheries Society*, 138, 927–937. <https://doi.org/10.1577/T07-265.1>
- Kim, S. Y., Noguera, J. C., & Velando, A. (2019). Carry-over effects of early thermal conditions on somatic and germline oxidative damages are mediated by compensatory growth in sticklebacks. *Journal of Animal Ecology*, 88, 473–483.

- Kingsolver, J. G., Diamond, S. E., & Buckley, L. B. (2013). Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional Ecology*, *27*, 1415–1423. <https://doi.org/10.1111/1365-2435.12145>
- Lee, K. P., & Roh, C. (2010). Temperature-by-nutrient interactions affecting growth rate in an insect ectotherm. *Entomologia Experimentalis et Applicata*, *136*, 151–163. <https://doi.org/10.1111/j.1570-7458.2010.01018.x>
- Lee, W. S., Monaghan, P., & Metcalfe, N. B. (2013). Experimental demonstration of the growth rate–lifespan trade-off. *Proceedings of the Royal Society B: Biological Sciences*, *280*, 20122370. <https://doi.org/10.1098/rspb.2012.2370>
- López-Otín, C., Blasco, M. A., Partridge, L., Serrano, M., & Kroemer, G. (2013). The hallmarks of aging. *Cell*, *153*, 1194–1217. <https://doi.org/10.1016/j.cell.2013.05.039>
- McLennan, D., Armstrong, J. D., Stewart, D. C., McKelvey, S., Boner, W., Monaghan, P., & Metcalfe, N. B. (2016). Interactions between parental traits, environmental harshness and growth rate in determining telomere length in wild juvenile salmon. *Molecular Ecology*, *25*, 5425–5438. <https://doi.org/10.1111/mec.13857>
- McLennan, D., Armstrong, J. D., Stewart, D. C., McKelvey, S., Boner, W., Monaghan, P., & Metcalfe, N. B. (2018). Telomere elongation during early development is independent of environmental temperatures in Atlantic salmon. *Journal of Experimental Biology*, *221*, jeb-178616. <https://doi.org/10.1242/jeb.178616>
- Metcalfe, N. B., & Monaghan, P. (2001). Compensation for a bad start: Grow now, pay later? *Trends in Ecology & Evolution*, *16*, 254–260. [https://doi.org/10.1016/S0169-5347\(01\)02124-3](https://doi.org/10.1016/S0169-5347(01)02124-3)
- Metcalfe, N. B., & Monaghan, P. (2003). Growth versus lifespan: Perspectives from evolutionary ecology. *Experimental Gerontology*, *38*, 935–940. [https://doi.org/10.1016/S0531-5565\(03\)00159-1](https://doi.org/10.1016/S0531-5565(03)00159-1)
- Monaghan, P. (2014). Organismal stress, telomeres and life histories. *Journal of Experimental Biology*, *217*, 57–66. <https://doi.org/10.1242/jeb.090043>
- Monaghan, P., & Ozanne, S. E. (2018). Somatic growth and telomere dynamics in vertebrates: Relationships, mechanisms and consequences. *Philosophical Transactions of the Royal Society B*, *373*, 20160446. <https://doi.org/10.1098/rstb.2016.0446>
- Mookerjee, S. A., Divakaruni, A. S., Jastroch, M., & Brand, M. D. (2010). Mitochondrial uncoupling and lifespan. *Mechanisms of Ageing and Development*, *131*, 463–472. <https://doi.org/10.1016/j.mad.2010.03.010>
- Morley, S. A., Peck, L. S., Sunday, J. M., Heiser, S., & Bates, A. E. (2019). Physiological acclimation and persistence of ectothermic species under extreme heat events. *Global Ecology and Biogeography*, *28*, 1018–1037. <https://doi.org/10.1111/geb.12911>
- Norin, T., & Metcalfe, N. B. (2019). Ecological and evolutionary consequences of metabolic rate plasticity in response to environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*, 20180180. <https://doi.org/10.1098/rstb.2018.0180>
- Ohlberger, J. (2013). Climate warming and ectotherm body size—From individual physiology to community ecology. *Functional Ecology*, *27*, 991–1001. <https://doi.org/10.1111/1365-2435.12098>
- Olsson, M., & Shine, R. (2002). Growth to death in lizards. *Evolution*, *56*, 1867–1870.
- Olsson, M., Wapstra, E., & Friesen, C. (2018a). Ectothermic telomeres: It's time they came in from the cold. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *373*, 20160449. <https://doi.org/10.1098/rstb.2016.0449>
- Olsson, M., Wapstra, E., & Friesen, C. R. (2018b). Evolutionary ecology of telomeres: A review. *Annals of the New York Academy of Sciences*, *1422*, 5–28.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. <https://doi.org/10.1146/annurev.ecolsys.37.091305.110100>
- Pauliny, A., Devlin, R. H., Johnsson, J. I., & Blomqvist, D. (2015). Rapid growth accelerates telomere attrition in a transgenic fish. *BMC Evolutionary Biology*, *15*, 159. <https://doi.org/10.1186/s12862-015-0436-8>
- Pineda-Pampliega, J., Herrera-Dueñas, A., Mulder, E., Aguirre, J. I., Höfle, U., & Verhulst, S. (2020). Antioxidant supplementation slows telomere shortening in free-living white stork chicks. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20191917. <https://doi.org/10.1098/rspb.2019.1917>
- Price, E. R., Sirsat, T. S., Sirsat, S. K. G., Kang, G., Keereetawee, J., Aziz, M., ... Dzialowski, E. M. (2017). Thermal acclimation in American alligators: Effects of temperature regime on growth rate, mitochondrial function, and membrane composition. *Journal of Thermal Biology*, *68*, 45–54. <https://doi.org/10.1016/j.jtherbio.2016.06.016>
- Reichert, S., Rojas, E. R., Zahn, S., Robin, J. P., Criscuolo, F., & Massemin, S. (2015). Maternal telomere length inheritance in the king penguin. *Heredity*, *114*, 10–16. <https://doi.org/10.1038/hdy.2014.60>
- Reichert, S., & Stier, A. (2017). Does oxidative stress shorten telomeres in vivo? A review. *Biology Letters*, *13*, 20170463.
- Richter, T., & von Zglinicki, T. (2007). A continuous correlation between oxidative stress and telomere shortening in fibroblasts. *Experimental Gerontology*, *42*, 1039–1042. <https://doi.org/10.1016/j.exger.2007.08.005>
- Rollings, N., Friesen, C. R., Whittington, C. M., Johansson, R., Shine, R., & Olsson, M. (2019). Sex- and tissue-specific differences in telomere length in a reptile. *Ecology and Evolution*, *9*, 6211–6219. <https://doi.org/10.1002/ece3.5164>
- Rollings, N., Wayne, H. L., Krohmer, R. W., Uhrig, E. J., Mason, R. T., Olsson, M., ... Friesen, C. R. (2020). Sperm telomere length correlates with blood telomeres and body size in red-sided garter snakes, *Thamnophis sirtalis parietalis*. *Journal of Zoology*, in press. <https://doi.org/10.1111/jzo.12789>
- Ruthsatz, K., Peck, M. A., Dausmann, K. H., Sabatino, N. M., & Gos, J. (2018). Patterns of temperature induced developmental plasticity in anuran larvae. *Journal of Thermal Biology*, *74*, 123–132. <https://doi.org/10.1016/j.jtherbio.2018.03.005>
- Sabharwal, S., Verhulst, S., Guirguis, G., Kark, J. D., Labat, C., Roche, N. E., ... Aviv, A. (2018). Telomere length dynamics in early life: The blood-and-muscle model. *The FASEB Journal*, *32*, 529–534. <https://doi.org/10.1096/fj.201700630r>
- Salin, K., Auer, S. K., Rey, B., Selman, C., & Metcalfe, N. B. (2015). Variation in the link between oxygen consumption and ATP production, and its relevance for animal performance. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20151028. <https://doi.org/10.1098/rspb.2015.1028>
- Salin, K., Villasevil, E. M., Anderson, G. J., Lamarre, S. G., Melanson, C. A., McCarthy, I., ... Metcalfe, N. B. (2019). Differences in mitochondrial efficiency explain individual variation in growth performance. *Proceedings of the Royal Society B: Biological Sciences*, *286*, 20191466. <https://doi.org/10.1098/rspb.2019.1466>
- Seebacher, F., White, C. R., & Franklin, C. E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change*, *5*, 61. <https://doi.org/10.1038/nclimate2457>
- Shine, R., Barrott, E. G., & Elphick, M. J. (2002). Some like it hot: Effects of forest clearing on nest temperatures of montane reptiles. *Ecology*, *83*, 2808–2815. [https://doi.org/10.1890/0012-9658\(2002\)083\[2808:SLIHEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2808:SLIHEO]2.0.CO;2)
- Shoo, L. P., Olson, D. H., McMennamin, S. K., Murray, K. A., Van Sluys, M., Donnelly, M. A., ... Hero, J.-M. (2011). Engineering a future for amphibians under climate change. *Journal of Applied Ecology*, *48*, 487–492. <https://doi.org/10.1111/j.1365-2664.2010.01942.x>
- Simide, R., Angelier, F., Gaillard, S., & Stier, A. (2016). Age and heat stress as determinants of telomere length in a long-lived fish, the Siberian sturgeon. *Physiological and Biochemical Zoology*, *89*, 441–447. <https://doi.org/10.1086/687378>

- Smith, S. M., Nager, R. G., & Costantini, D. (2016). Meta-analysis indicates that oxidative stress is both a constraint on and a cost of growth. *Ecology and Evolution*, 6, 2833–2842. <https://doi.org/10.1002/ece3.2080>
- Somero, G. N. (2010). The physiology of climate change: How potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*, 213, 912–920. <https://doi.org/10.1242/jeb.037473>
- Speakman, J. R. (2005). Body size, energy metabolism and lifespan. *Journal of Experimental Biology*, 208, 1717–1730. <https://doi.org/10.1242/jeb.01556>
- Stahlschmidt, Z. R., French, S. S., Ahn, A., Webb, A., & Butler, M. W. (2017). A simulated heat wave has diverse effects on immune function and oxidative physiology in the corn snake (*Pantherophis guttatus*). *Physiological and Biochemical Zoology*, 90, 434–444.
- Stark, G., & Meiri, S. (2018). Cold and dark captivity: Drivers of amphibian longevity. *Global Ecology and Biogeography*, 27, 1384–1397. <https://doi.org/10.1111/geb.12804>
- Stark, G., Tamar, K., Itescu, Y., Feldman, A., & Meiri, S. (2018). Cold and isolated ectotherms: Drivers of reptilian longevity. *Biological Journal of the Linnean Society*, 125, 730–740. <https://doi.org/10.1093/biolinean/bly153>
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5610–5615. <https://doi.org/10.1073/pnas.1316145111>
- Tian, X., Seluanov, A., & Gorbunova, V. (2017). Molecular mechanisms determining lifespan in short- and long-lived species. *Trends in Endocrinology & Metabolism*, 28, 722–734. <https://doi.org/10.1016/j.tem.2017.07.004>
- Tricola, G. M., Simons, M. J. P., Atema, E., Boughton, R. K., Brown, J. L., Dearborn, D. C., ... Haussmann, M. F. (2018). The rate of telomere loss is related to maximum lifespan in birds. *Philosophical Transactions of the Royal Society B*, 373, 20160445. <https://doi.org/10.1098/rstb.2016.0445>
- Turbill, C., Ruf, T., Smith, S., & Bieber, C. (2013). Seasonal variation in telomere length of a hibernating rodent. *Biology Letters*, 9, 20121095. <https://doi.org/10.1098/rsbl.2012.1095>
- Ujvari, B., Biro, P. A., Charters, J. E., Brown, G., Heasman, K., Beckmann, C., & Madsen, T. (2017). Curvilinear telomere length dynamics in a squamate reptile. *Functional Ecology*, 31, 753–759. <https://doi.org/10.1111/1365-2435.12764>
- Velando, A., Noguera, J. C., da Silva, A., & Kim, S. Y. (2019). Redox-regulation and life-history trade-offs: Scavenging mitochondrial ROS improves growth in a wild bird. *Scientific Reports*, 9, 2203. <https://doi.org/10.1038/s41598-019-38535-5>
- Wilbourn, R. V., Moatt, J. P., Froy, H., Walling, C. A., Nussey, D. H., & Boonekamp, J. J. (2018). The relationship between telomere length and mortality risk in non-model vertebrate systems: A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20160447. <https://doi.org/10.1098/rstb.2016.0447>
- Yang, L. H., Huang, H., & Wang, J. J. (2010). Antioxidant responses of citrus red mite, *Panonychus citri* (McGregor) (Acari: Tetranychidae), exposed to thermal stress. *Journal of Insect Physiology*, 56, 1871–1876. <https://doi.org/10.1016/j.jinsphys.2010.08.006>
- Young, A. J. (2018). The role of telomeres in the mechanisms and evolution of life-history trade-offs and ageing. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373, 20160452.
- Zhang, Q., Han, X., Hao, X., Ma, L., Li, S., Wang, Y., & Du, W. (2018). A simulated heat wave shortens the telomere length and lifespan of a desert lizard. *Journal of Thermal Biology*, 72, 94–100. <https://doi.org/10.1016/j.jtherbio.2018.01.004>
- Zhao, M., Klaassen, C. A., Lisovski, S., & Klaassen, M. (2019). The adequacy of aging techniques in vertebrates for rapid estimation of population mortality rates from age distributions. *Ecology and Evolution*, 9, 1394–1402. <https://doi.org/10.1002/ece3.4854>

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