REPORT

AGING

Slow and negligible senescence among testudines challenges evolutionary theories of senescence

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Is senescence inevitable and universal for all living organisms, as evolutionary theories predict? Although evidence generally supports this hypothesis, it has been proposed that certain species, such as turtles and tortoises, may exhibit slow or even negligible senescence—i.e., avoiding the increasing risk of death from gradual deterioration with age. In an extensive comparative study of turtles and tortoises living in zoos and aquariums, we show that ~75% of 52 species exhibit slow or negligible senescence. For ~80% of species, aging rates are lower than those in modern humans. We find that body weight positively relates to adult life expectancy in both sexes, and sexual size dimorphism explains sex differences in longevity. Unlike humans and other species, we show that turtles and tortoises may reduce senescence in response to improvements in environmental conditions.

How much can aging be altered, slowed, or brought to a halt altogether? In the past century, we have witnessed unprecedented increases in human longevity (*1*). Yet, research on humans and nonhuman primates shows that these improvements have resulted from averting early deaths and age-independent sources of mortality, not from reducing the rate of aging (*2*, *3*). The rate of aging is a measure of the speed at which the risk of mortality increases with age. It is the direct result of senescence, a gradual deterioration of bodily functions that manifests as an increase in mortality risk with age after sexual maturity (*4*). Current evolutionary theories of senescence state that, among all organisms with a clear separation between somatic and germline cell lineages, senescence is inevitable (*4*, *5*). Paradoxically, empirical evidence (*6*, *7*) and evolutionary demographic models (*8*, *9*) have proposed that evolution may permit some species to reduce or even avoid the effects of senescence (i.e., negligible senescence).

Species that continue growing after reproductive maturity (e.g., turtles and tortoises) (*8*) are the prime candidates for escaping senescence. These indeterminately growing species may gain survival advantages and larger reproductive potential with age, which allows them to invest more in somatic maintenance and potentially slowing senescence. To date, only a handful of studies have investigated senescence in animal species with indeterminate growth, such as turtles and tortoises (*10*–*13*), where different populations of the same species can show evidence of both senescence and negligible senescence (*12*–*15*). Thus, the question remains: Can some species slow or even avoid growing old? And if so, under what circumstances?

In this work, we carried out an extensive study of age- and sex-specific mortality and growth patterns in turtles and tortoises (order Testudines). Using the Species360 Zoological Information Management System (ZIMS) (*16*), we obtained husbandry records for 52 species spanning a diversity of life-history strategies, body weights, and longevities (table S1). Using Bayesian survival trajectory analysis (*17*, *18*), we estimated for females (47 species) and males (39 species) adult age-specific mortality, remaining adult life expectancy, and aging rates. From the best-fitting models, we calculated 95% credible intervals (CIs) of aging rates at the age when the survival function reached 0.2 (i.e., when 80% of adults are expected to have died) (*19*). We considered this age to be sufficiently advanced to occur after the onset of senescence but not so late as to greatly increase the uncertainty in the estimated aging rates.

CIs of aging rates included zero for 74.5% of species (35 species) for females and 79.5% (31 species) for males (Fig. 1). CIs of some species were either negative [i.e., *Testudo graeca* and *Siebenrockiella crassicollis*, 4.2% (2 species) for females and 2.6% (1 species) for males] or spanned narrowly around zero (e.g., females of *Aldabrachelys gigantea* and males of *Gopherus berlandieri*), which may suggest the existence of negligible senescence among these species. CIs were positive for 21.3% (10 species) for females and 17.9% (7 species) for males, which suggests that these species experience senescence even under protected conditions. CIs were lower than the aging rate of modern humans for 78.7% of species (37 species) for females and 87.2% (34 species) for males (Fig. 1). The distribution of aging rates in testudines was considerably narrower than that for mammals, with minimal overlap between the two distributions (fig. S1). In short, aging rates among testudines fall much below those of most mammals and, for some species, are close to negligible (i.e., are not different from zero; fig. S2, A to D).

Using Bayesian phylogenetic generalized least-squares (PGLS) (*19*), we found that adult life expectancy was positively related to body weight for both sexes, as expected from life-history theory (*20*). Sexual size dimorphism, calculated as the difference in body weight between females and males relative to that of females, related positively to adult male life expectancy (i.e., males are expected to live longer for species where females are the larger sex), possibly owing to a lower risk of male-male aggression among species with female-biased sexual size dimorphism (*21*). With respect to aging rates, we found a marginal positive effect of sexual size dimorphism for both sexes but not of body weight. Because of a lack of accurate reproductive data at older ages, we were unable to test for a potential indirect effect of reproductive output on adult life expectancy and aging rates (*22*).

To further understand how longevity and aging rates vary between sexes, we measured the relative sex difference in adult life expectancy [$\delta_e = (e_{female} - e_{male}) / e_{female}$] and the difference in aging rate ($\delta_a = a_{female} - a_{male}$) for 34 species (Fig. 2) (*19*). Adult male life expectancy exceeded that of females by 20% (±51%) on average, whereas the average sex difference in aging rate was close to zero (−0.002 ± 0.039). CIs of adult life expectancy difference did not include zero for five species with male advantage and two with female advantage. Our finding of a male adult life expectancy advantage is congruent with studies of other reptilian taxa (*23*) but not with results on other tetrapods, such as mammals (*24*). In contrast to previous studies on reptiles (*21*, *25*–*27*), our Bayesian PGLS showed that sex differences in adult life expectancy could not be explained by differences in terrestrial versus aquatic habitats, differences in reproductive effort between sexes, or hibernation (Table 1). However, under human care, differences in habitat are negligible, and individuals may naturally bypass hibernation in response to unlimited access to food,

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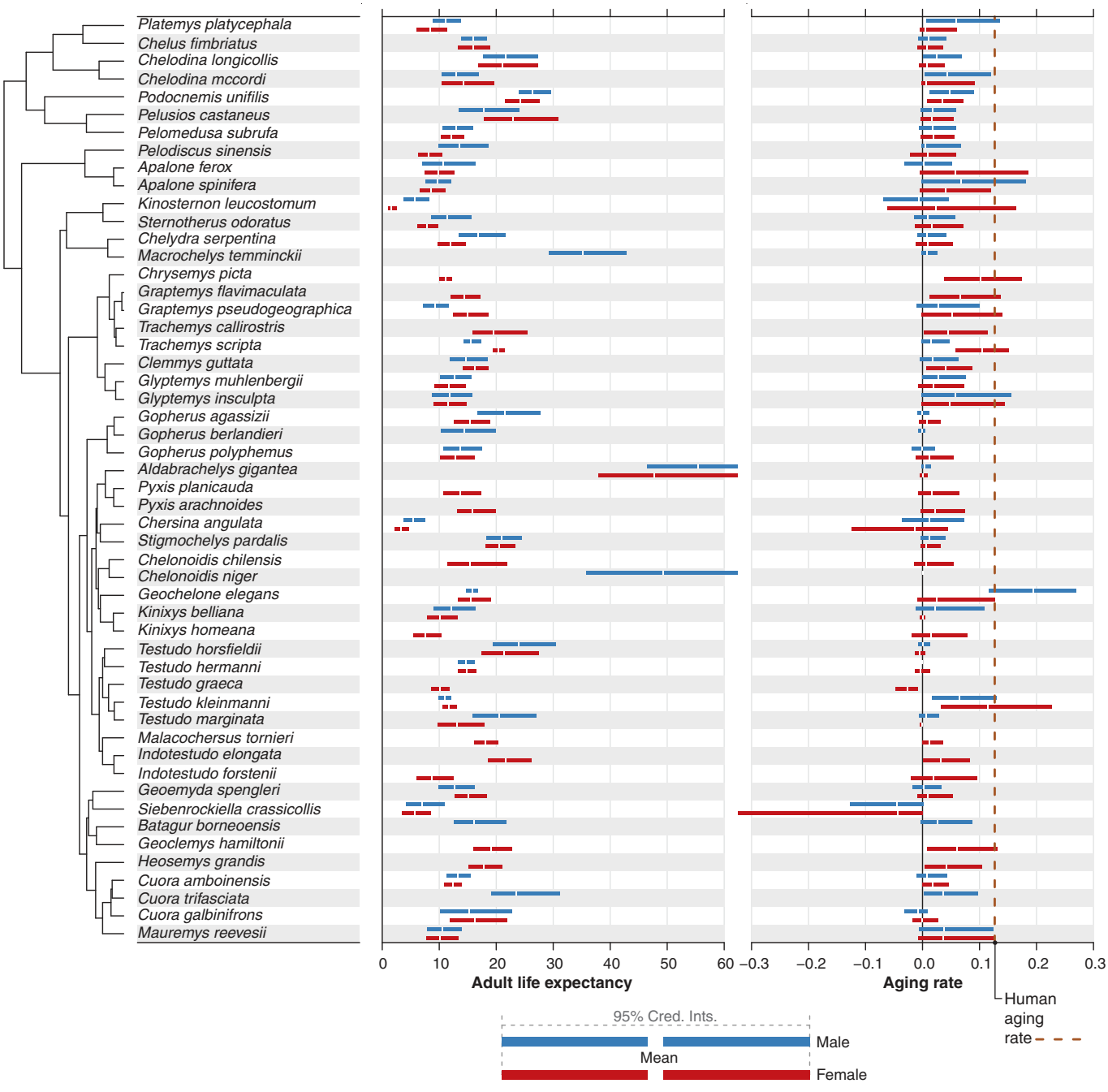

Fig. 1. Adult life expectancy and aging rates for female and male turtles and tortoises. Life expectancies and aging rates and their 95% CIs were calculated using Bayesian survival trajectory analysis (BaSTA). For comparison, we depict modern human aging rates. Cred. Ints., credible intervals.

protection from predation, and thermal stability year-round. Because of the lack of information, we could not test other explanations, such as the costs of sexually selected traits (*28*) or sex determination system (*29*).

Of the variables tested, only sexual size dimorphism strongly related to sex differences in adult life expectancy, whereby our model predicted that females had longer life expectancy when they were larger than males. A similar relationship among anurans has been attributed to sexual bimaturation (*30*). In such cases, females achieve a selective advantage by delaying maturation and attaining larger body sizes, slower growth, and longer life expectancies than males. We were unable to test this hypothesis because of the lack of information on sex-specific ages at maturity. Additionally, being larger than males could benefit females because courtship and mating can be physically harmful, particularly for male-biased sexual size dimorphism (*21*). Accentuated by confinement under human care, we hypothesize that sexual size dimorphism may affect life span in females through its influence on the longevity costs of courtship and mating. To test this hypothesis, future analyses should compare aging rates of populations where sexes are separated against those where they are kept together.

In this work, we have studied populations under protected environments, and thus our

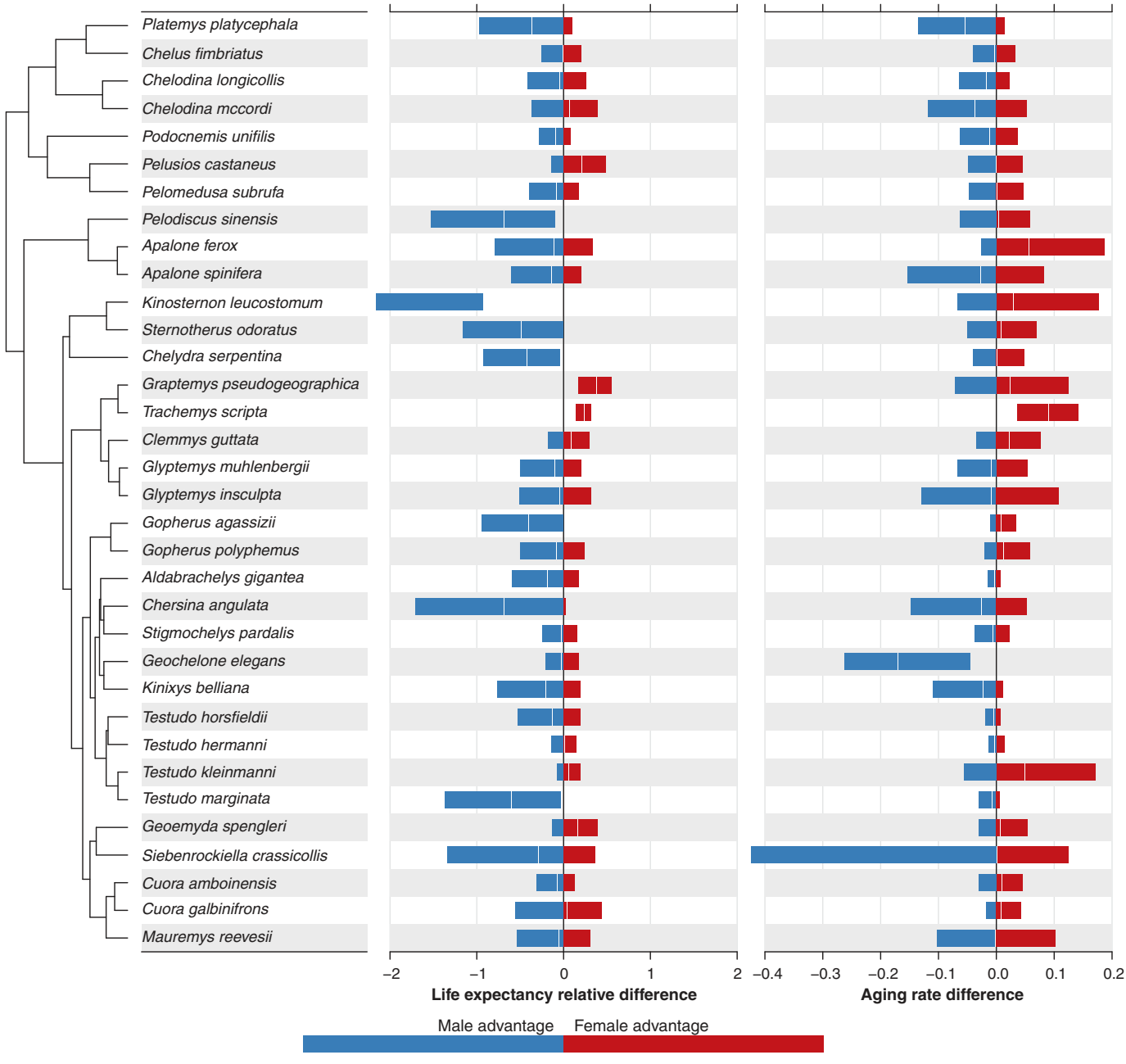

Fig. 2. Sex differences in life expectancy and aging rates. Sex differences in life expectancy were calculated as female minus male life expectancy divided by female life expectancy, whereas sex differences in aging rates were calculated as female minus male aging rates. Bars show the limits of lower and upper 95% CIs of the differences. White lines show the mean difference. Species are grouped according to their phylogenetic classification in (*35*).

results may not be reflective of aging rates and longevities in their natural environments. For instance, studies on vipers and frogs have found that populations can greatly vary their aging rates when exposed to different environmental conditions (*14*, *15*). We compared our results with data from natural environments for three species [*Chrysemys picta* (*13*), *Trachemys scripta* (*31*), and *Kinixys homeana* (*32*)]. We found considerably higher aging rates in natural environments for *T. scripta* (a = 0.04 in nature versus mean a = 0.01 in ZIMS) and *K. homeana* (a = 0.11 in nature versus mean a = 0.02 in ZIMS) (Fig. 3). The aging rates in nature of both species fell on the upper end of the posterior densities of the ZIMS aging rates and outside the 95% CIs (i.e., upper quantile for *T. scripta* of <0.0001 and for *K. homeana* of 0.007) (Fig. 3, B and F). The wild aging rate of *C. picta* was slightly lower (0.05 versus mean a = 0.08 for ZIMS), even though the wild value was contained within the 95% CIs (lower quantile of 0.15), whereas the wild population had a considerably higher baseline mortality level (Fig. 3, C and D). Still, the mechanism(s) underpinning shifts in mortality

Table 1. Bayesian PGLS for female, male, and sex differences in life expectancies and aging rates. Columns show the mean, standard error (SE), and lower and upper 95% CIs from the posterior densities of regression parameters. Zero coverage indicates to which upper or lower quantile of the posterior density zero corresponds to for a parameter: The lower the value, the more different from zero the parameter is. Dashes indicate not applicable. SSD, sexual size dimorphism; Repr. output diff., reproductive output difference.

Sex	Response	Parameters	Mean	SE	Lower	Upper	Zero coverage
Female	Life expectancy	(Intercept)	2.590	0.080	2.428	2.745	–
Female	Life expectancy	log(body weight)	0.139	0.041	0.058	0.221	0.001
Female	Life expectancy	Pagel's λ	0.083	0.063	0.004	0.237	–
Female	Aging rate	(Intercept)	0.020	0.009	0.003	0.037	–
Female	Aging rate	SSD	0.024	0.013	−0.001	0.048	0.056
Female	Aging rate	Pagel's λ	0.088	0.067	0.004	0.249	–
Male	Life expectancy	(Intercept)	2.593	0.079	2.433	2.747	–
Male	Life expectancy	log(body weight)	0.142	0.041	0.062	0.222	0.001
Male	Life expectancy	SSD	0.286	0.121	0.048	0.527	0.018
Male	Life expectancy	Pagel's λ	0.081	0.062	0.003	0.235	–
Male	Aging rate	(Intercept)	0.020	0.009	0.003	0.037	–
Male	Aging rate	SSD	0.024	0.012	−0.001	0.049	0.051
Male	Aging rate	Pagel's λ	0.087	0.064	0.004	0.240	–
Sex differences	Life expectancy	(Intercept)	−0.143	0.058	−0.258	−0.028	–
Sex differences	Life expectancy	SSD	0.231	0.084	0.063	0.400	0.006
Sex differences	Life expectancy	Pagel's λ	0.124	0.092	0.006	0.348	–
Sex differences	Aging rate	(Intercept)	−0.008	0.011	−0.030	0.015	–
Sex differences	Aging rate	Repr. output diff.	0.044	0.026	−0.007	0.095	0.094
Sex differences	Aging rate	Pagel's λ	0.105	0.085	0.004	0.319	–

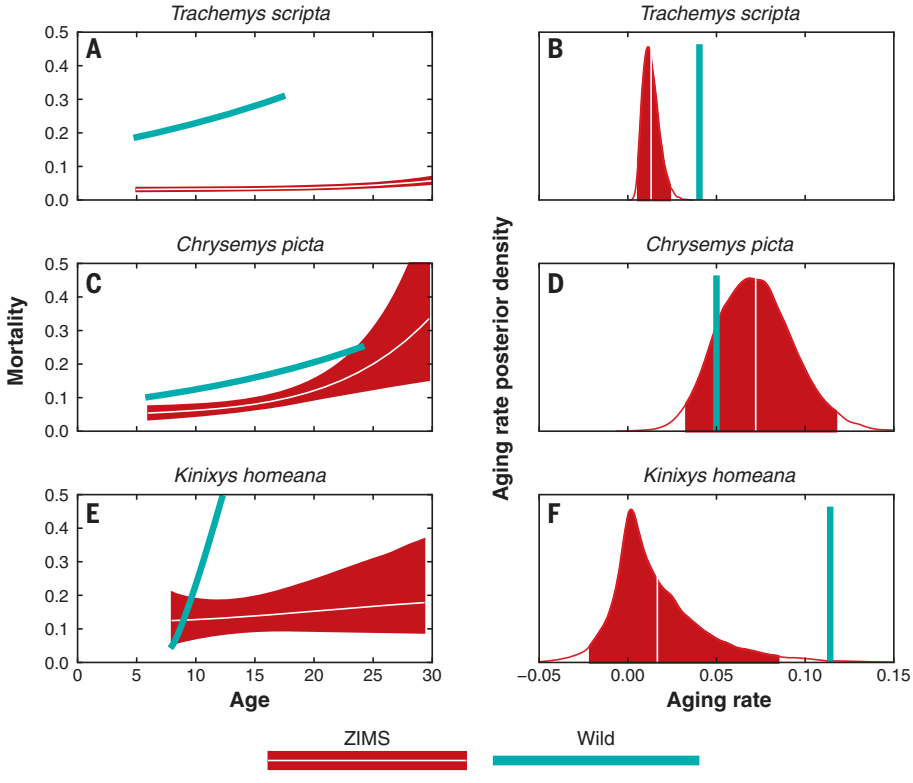

Fig. 3. Comparison of age-specific mortality trajectories and aging rates between wild and zoo and aquarium (ZIMS) female populations of three testudines species. (**A**, **C**, and **E**) Comparison of age-specific mortality trajectories. (**B**, **D**, and **F**) Comparison of aging rates. Green lines show the mortality or aging rate for the wild populations, and the red polygons show the 95% CIs of mortality or of the posterior density of aging rate for the ZIMS populations, as obtained from the BaSTA analysis. White lines depict the posterior means. Wild data for painted turtles (*C. picta*) are from (*13*), data for yellowbelly sliders (*T. scripta*) are from (*31*), and data for home's hingeback tortoise (*K. homeana*) are from (*32*).

trajectories and aging rates between wild populations and those under human care remain unclear. The disposable soma theory (*5*) posits that populations exposed to milder conditions can allocate more energy to survival rather than protection or foraging, thereby prolonging their life spans. However, this theory still predicts that senescence should be inevitable in this group.

Recent studies on humans and nonhuman primates have revealed that, in response to improvements in survival conditions, extensions in longevity emerged from a reduction in infant and juvenile mortality and in the overall level of mortality, but aging rates remained stable (*2*, *3*). Here, we show that under controlled conditions, turtles and tortoises can reduce the effects of senescence and, in some cases, even avoid them.

Current evolutionary theories of senescence have mostly been tested on birds and mammals (*33*, *34*). To fully understand how senescence molds vital rates and how environmental conditions affect senescence, further studies comparing populations under human care and natural environments are needed, particularly for underresearched tetrapods.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abl7811
Materials and Methods
Figs. S1 and S2
Tables S1 to S7
References (*37*–*167*)
MDAR Reproducibility Checklist

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Science

Slow and negligible senescence among testudines challenges evolutionary theories of senescence

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How to cheat senescence?

Compared with birds and mammals, herpetiles, especially turtles and tortoises, are well-known examples of extremely long-lived animals that show little evidence of age-related decline (see the Perspective by Austad and Finch). By comparing aging rates and longevity across 77 species of reptiles and amphibians, Reinke *et al.* found considerable variation in senescence and elucidated some of the drivers of these differences in nature. In another paper, Da Silva *et al.* studied turtles and tortoises in zoos and found clear evidence that negligible senescence occurs under controlled conditions. —SNV

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