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Actuarial senescence can increase the risk of extinction of mammal populations

ALEXANDRE ROBERT,^{1,4} STÉPHANE CHANTEPIE,¹ SAMUEL PAVARD,² FRANÇOIS SARRAZIN,^{1,3} AND CÉLINE TEPLITSKY¹

¹UMR 7204 MNHN-CNRS-UPMC, Centre d'Ecologie et des Sciences de la Conservation, Muséum National d'Histoire Naturelle, 55, Rue Buffon, 75005 Paris, France

²UMR 7206 CNRS-MNHN-UPD, Muséum National d'Histoire Naturelle, 55, Rue Buffon, 75005 Paris, France

³Université Pierre et Marie Curie, 4 Place Jussieu, 75005 Paris, France

Abstract. Despite recent acknowledgement that senescence can have negative impact on survival and fertility in natural environments across a wide range of animal species, we still do not know if it can reduce the viability of wild endangered populations. Focusing on actuarial senescence (i.e., the decline of survival probabilities at old ages), we use species-specific demographic information to project the extinction risk of wild populations of 58 species of mammals, accounting (or not) for senescence. Our projections reveal potential negative effects of aging on population viability, with an average decrease of 27% of the time to extinction and a potential deterioration of the population-level projected conservation status in 10% of the species. Senescence is associated with particularly strong increases of the extinction risk in species with low mortality rates and long intervals between litters, independently of their place in the phylogeny, indicating that the pace of life history can be used to forecast the detrimental effects of aging on the viability of species. The aim of the various existing systems of classification of threatened species is to set conservation priorities based on assessments of extinction risk. Our results indicate that the quantitative effects of senescence on extinction are highly heterogeneous, which can affect the ranking of species and populations when setting conservation priorities. In mammals, based on life history traits of a few species, generic patterns of senescence can be incorporated into projection population models to minimize these biases in viability assessments.

Key words: conservation biology; extinction; individual-based models; IUCN; long-term field studies; mammals; population dynamics; population viability analysis; senescence.

INTRODUCTION

Over the last decade, a large body of evidence has rapidly accumulated in a wide range of animal species, indicating that declines in vital rates at old ages do occur in wild populations (Bennett and Owens 2002, Ricklefs 2010, Nussey et al. 2013). These findings have led to the conclusions that (1) the demographic manifestations of senescence are substantial and widespread, and (2) there are some remarkable similarities in aging patterns (e.g., shape of survival variation with age) among taxa (Jones et al. 2008, Lynch et al. 2010), but (3) despite these similarities, variation exists among species in terms of both the magnitude of senescence (i.e., the slope of age-related decline in survival rate) and its fitness consequences (e.g., the proportion of aging-related mortalities in a population).

Although it can be characterized by a variety of morphological, immunological, behavioral, or demographic phenomena, senescence is primarily defined as a progressive deterioration in the physiological state of an organism over time (Williams et al. 2006, Rose et al.

2012). From an evolutionary perspective, senescence arises from the decline of the strength of natural selection with age, as the cumulative risk of extrinsic mortality increases (Charlesworth 1994). Based on this hypothesis, two main, not mutually exclusive, genetic processes have been invoked to explain senescence patterns: (1) the accumulation of mutations having deleterious effects on fitness components at old ages (Medawar 1952) and (2) genetic trade-offs between young and old ages due to pleiotropic effects (Williams 1957; see also Kirkwood 1990).

One of the most general evolutionary predictions on senescence patterns is that senescence should occur more rapidly in populations that experience high rates of environmentally imposed mortality, because any deterioration in fitness components at advanced ages will be less selected against if most individuals are likely to have already died from environmental causes at these ages (Williams 1957, Charlesworth 1994; but see Williams et al. 2006). Thus, at an interspecific level, species with high annual young adult survival rates should exhibit lower rates of senescence. However, owing to physiological, behavioral, and energetics trade-offs, high adult survival and longevity are generally associated with low annual fecundities (Promislow and Harvey 1990), which

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Corresponding Editor: T. G. O'Brien.

⁴ E-mail: arobert@mnhn.fr

form two important characteristics of the species categorized as “long-lived” along the life history fast–slow continuum. Slow life histories are generally associated with large body masses (Lindstedt and Calder 1981), although (1) body mass is generally not considered as one of the traits defining the continuum and (2) the relationships between life history traits remain true after the effect of body mass has been removed (see Gaillard et al. 1989, Promislow and Harvey 1990; but see discussion in Bielby et al. 2007, Jeschke and Kokko 2009).

In general agreement with theoretical expectations, recent comparative studies substantiate that the magnitude and consequences of senescence, to a large extent, are determined by the pace of the life history (but see Baudisch 2011). In vertebrates, senescence occurs faster and is stronger in magnitude in short-lived than in long-lived species (Jones et al. [2008]; but see Jones et al. [2014] at a larger taxonomic scale). However, in natural environments, the expected proportion of aging-related mortalities is lower in short-lived vertebrate species (typically a few percentage points in short-lived birds or mammals; see e.g., Bouwhuis et al. 2012) as compared to long-lived ones that experience lower proportions of environment-related mortalities (Ricklefs 1998, 2010, Turbill and Ruf 2010). Comparative demographic analysis indicates that in species with the longest recorded life spans, the majority of all deaths are actually due to senescence (see Ricklefs 2008).

Although these recent developments suggest that senescence should negatively impact the dynamics of wild populations, assessments of its consequences in terms of population dynamics are notably lacking in the ecological literature (Nussey et al. 2008) and these developments have not found any echo in the field of conservation sciences so far. In the current context of escalating biodiversity crisis in which more than one-third of the species so far assessed are threatened with extinction (IUCN 2014), effective prioritization of conservation efforts is to a large extent linked to the ability of ecologists and conservation scientists to evaluate the risk of extinction of species and populations, which in turn requires them to understand and reliably project their dynamics (Brook et al. 2000). Although no quantitative survey of the literature exists on the topic, most published species or population viability assessments do not explicitly consider the effect of declining survival or fertility at old ages on population dynamics, for three main reasons: (1) the lack of specific data on senescence; (2) the (common but never tested) underlying assumption that its impact on the risk of extinction is negligible; (3) the fact that, depending on the approach considered to estimate demographic rates, the effects of senescence can be implicitly included in overall adult survival and fertility estimates (see *Discussion*).

Focusing on the effect of the age-related decline in survival (i.e., actuarial senescence), we used specific

demographic parameters on wild populations of 58 species of mammals and a combination of deterministic and stochastic population models to compare their projected dynamics and extinction risk in the presence or absence of senescence. This allowed us to calculate different metrics of the population dynamics cost of senescence for each species, including an extinction cost. In order to understand how the consequences of senescence are related to extrinsic mortality and life history trade-offs, we examined the relationships between the population dynamics costs of senescence and four species traits: maximum adult survival probability, litter size, number of litters per year, and body mass.

METHODS

Data

Although data from long-term individual-based field studies are becoming increasingly available (Nussey et al. 2013) and constitute the best material for comparative approaches (Gaillard et al. 1994, Nussey et al. 2008), it remains difficult to gather sufficient raw data in the same statistical framework to conduct rigorous comparisons. To date, the study of Jones et al. (2008) on 20 species of birds and mammals provides the most extensive overview of senescence patterns based on individual data. It suggests that research based on life tables provides an accurate picture of the distribution and patterns of actuarial senescence across species. Recently, Lynch and Fagan (2009) compiled a survivorship data set from life table data of wild or free-roaming feral populations of 58 species of mammals. They used a Beta function that provides excellent fit to each of 58 mammalian survivorship schedules to model $l(x)$, the survivorship to age x , as $l(x) = 1 - \text{CDF}[\text{Beta}(x/L; \alpha, \beta)]$, where CDF is the cumulative density function, L is the maximum life span of the species (i.e., the physiological life span recorded for animals in captivity), and α and β are the nonnegative shape parameters of the Beta distribution. We used this function to model survival for each species between ages zero and L . In most species, a peak survival rate is observed at maturity, followed by a more or less important decline in survival with increasing age. All population dynamics models based on these survival data are hereafter referred to as “senescence models.” Values of α , β , and L for all species and methodological details can be found in Lynch and Fagan (2009).

Complementary specific demographic data used in population dynamic models were (1) the age at first reproduction (based on estimates of the age at female maturity) or the proportion of breeders among individuals of different ages; (2) the average number of litters per year; (3) the average litter size; and (4) the species’ mating system. For simplicity, and despite the great diversity of mating systems among the species considered, only two types of systems were considered here: monogamy (for species with monogamous or strictly polyandrous mating systems) and polygyny (for species

with any polygynous, or promiscuous mating system, including female defense, resource defense, lek, or scramble competition). All of this information was obtained from the AnAge Database of Animal Ageing and Longevity (de Magalhães and Costa 2009) and from various other sources from the literature (the AnAge database is *available online*).⁵ Details of species parameters and sources are provided in Appendix A.

We restricted our species sample to the Lynch and Fagan (2009) data set because it provides a unified framework for modeling survival rates. The equilibrium demographic properties of the populations of our data set reflect the diversity of intrinsic species characteristics, as well as the variability of local conditions faced by the various populations sampled, including the qualities of their local environments and the fact that some of these populations can be near their carrying capacity while others can be far below it. This implies that the values of deterministic growth rates do not always reflect the maximum growth rate of a population of the species considered (i.e., the population growth rate without limiting factors and at low density [see Niel and Lebreton 2005]). However, we consider that our large data set is a representative sample of mammal populations with various life history traits facing various environmental conditions.

Models

Deterministic matrix models.—For each species, a one-sex, deterministic senescence model was built using a pre-breeding census Leslie matrix, based on the demographic rates just described. In most cases ($n = 46$), the time step was annual. For some species exhibiting short life histories ($n = 12$), an infra-annual time step was used and demographic rates were adjusted to fit the time step, depending on the age at female maturity (infra-annual time steps varied from 0.111 to 0.5 year). Two examples of life cycles, based on annual and infra-annual time steps, are provided in Appendix B. For each species, the annual deterministic growth rate (λ), the per generation deterministic growth rate (R_0), and the generation time T were calculated. The generation time was calculated as the mean age of the parents of the offspring produced by a population at stable age distribution (thus including all parents producing offspring in a given reproductive season; Caswell 2001).

Stochastic individual-based models.—For the 58 species considered, we developed stochastic two-sex individual-based models based on the same life cycles and demographic rates as for the deterministic matrix models. Individual-based models were used to examine the persistence of populations under various ecological scenarios.

In each time step t (annual or infra-annual), adult males and females paired randomly according to the species' mating system (monogamous or polygynous). Although various regulation processes may maintain populations far under their carrying capacity through e.g., predation, interspecific competition, parasitism, or human actions, here we considered density-dependent regulation at carrying capacity as a first step for addressing the assessment of long-term viability. Population regulation occurred by limiting the number of mating events to a maximum number (ME_{\max}). In the case of monogamy, the number of mating pairs was equal to the minimum of the number of adult males, the number of adult females, and ME_{\max} . In the case of polygyny, the number of mating pairs was equal to the minimum of the number of adult females (provided that there was at least one adult male in the population) and ME_{\max} . The fertility of each female in each time step was taken to be a Poisson process with parameter f , and the sex of each individual was randomly determined according to a 1:1 sex ratio. Each survival event was drawn from a Bernoulli distribution, with age-specific survival probabilities.

In all results presented, the carrying capacities of populations are expressed in terms of the equilibrium number of adult individuals K present in the populations when the maximal number of mating events (ME_{\max}) can occur (e.g., when all available reproduction sites are occupied). Because K was not an input model parameter (the input parameter associated with mechanistic population regulation was ME_{\max}), we determined statistically the relationship between K and ME_{\max} (i.e., the value of ME_{\max} corresponding to the wanted carrying capacity K) for all ecological scenarios investigated (details of the protocol are provided in Appendix C).

We assumed that population dynamics were influenced by catastrophic events (Shaffer 1987). Punctuated catastrophes occur randomly with a probability P_c at each time step (t) to reduce population size by a proportion C (random truncation). The severity of each catastrophic event (C) was drawn from the empirical severity distribution of Reed et al. (2003) and was implemented following the method developed in Robert (2006). The frequency of catastrophic events depended on both the time step considered and the generation time of the species. In the main analysis, we considered a frequency of catastrophes of 14% per generation, based on the results of Reed et al. (2003) obtained in 88 species of vertebrates.

Populations were assumed initially to be at their carrying capacity K (i.e., there were K adults in the population, sex ratio was balanced, and age classes were distributed according to the stable asymptotic distribution). For each of the 58 life cycles, we considered various scenarios for senescence, K and P_c . However, in the main analysis, results are only presented for $K = 250$ mature individuals and $P_c = 14\%$ per generation. For each scenario, median extinction times were recorded

⁵ <http://genomics.senescence.info/species/>

based on 2500 independent population trajectories, and the probabilities of extinction after 10, 20, and 100 years, as well as three and five generations, were recorded to calculate Criterion-E-based IUCN population conservation status (i.e., a qualitative index reflecting the level of threat faced by a population, obtained from quantitative assessment of viability at different time horizons; IUCN 2014).

Null models and comparison indices

Three alternative null models (i.e., models without decline in survival with increasing age) were considered. A first set of two null models was devised to evaluate the impact of including senescence in models classically used in conservation biology. These models assume that all adult mortality is due to extrinsic mortality and are classically used to assess fitness costs of aging (e.g., Bonduriansky and Brassil 2002). In the first, survival probability was held constant from the age of peak survival rate onward (Bouwhuis et al. 2012), without any limitation on the age until which individuals can survive. Such models were implemented in each species by changing the Leslie matrix described previously into an extended Leslie matrix with the last survival transition equal to the peak survival rate. In the second null model, adult survival probability was also held constant and equal to the maximal survival rate, but individuals could not live longer than their species' maximum life span L (i.e., the survival rate between age L and $L + 1$ was set to zero; see *Discussion* and references in Lynch and Fagan 2009, Turbill and Ruf 2010). Finally, in order to separate the effects of senescence per se from the effects of an increase in overall mortality associated with the inclusion of senescence, we considered a third null model with constant adult survival probability computed so that the same fraction of individuals survives to age L under both the senescence and null models. Only results obtained with the first null model are presented in our main results, but all detailed results are provided and discussed in the Appendices.

To quantify demographic and population dynamics changes associated with actuarial senescence, we then calculated four indices based on the comparison between the senescence model and the null model. These indices allowed us to quantify changes in annual deterministic growth rate ($\Delta\lambda$), in generation time (ΔT), in per generation deterministic growth rate (ΔR_0), and in median time to extinction (ΔT_{ext}) associated with aging patterns (details on computations are given in Appendix D).

Statistical analysis

We used univariate and multiple phylogenetic generalized least squares (PGLS) regression models (Freckleton et al. 2002) to examine the relationships between the four indices described previously (dependent variables) and four species traits (independent variables): adult

mass, peak survival probability, litter size, and number of litters per year (data and sources are provided in Appendix A). The peak survival probability was arcsine-square-root-transformed and all other traits were transformed (Napierian logarithm) in all analyses. In all univariate models, quadratic effects were tested and added to multiple regressions when they resulted in improved AIC scores ($\Delta\text{AIC} > 2$). In multiple regressions, all first-order interactions were included. Results are presented for final models resulting from AIC comparisons of models including (or not) interaction terms. All PGLS models used the mammalian phylogenetic supertree (Bininda-Emonds et al. 2007). Pagel's λ was estimated using maximum likelihood to adjust the degree of phylogenetic correction optimally for each data set (Freckleton et al. 2002). All statistical analyses were performed with R 2.14.0 (R Development Core Team 2011) specifically with the *ape*, *geiger*, *caper*, and *motmot* packages (Paradis et al. 2004).

RESULTS

Among the 58 populations investigated, under the first null model (i.e., without actuarial senescence), the median annual growth rate (λ) was 1.11 with 95% CI [0.88–7.5], the median per generation growth rates (R_0) was 1.61 [0.42–5.4], and the median generation time (T) was 3.47 yr [0.25–23.8 yr]. Assuming a carrying capacity of 250 adult individuals, the median time to extinction T_{ext} ranged from 12 to 15 215 yr (median = 219 [24–10 699 yr]).

Incorporating the observed pattern of actuarial senescence (senescence models) led to altogether lower λ (median proportional reduction = 2%), lower R_0 (median = 11%), and lower T (median = 10%). The median values of λ , R_0 , and T with senescence were 1.08 [0.75–7.5], 1.4 [0.37–4.2], and 3.15 [0.25–20.0], respectively. For a carrying capacity of 250 individuals, including senescence led to a reduction of T_{ext} of 27%, on average (median = 21% [–1% to 82.4%]). The median value of T_{ext} with senescence was 196 years [16.1–4570.6]. These changes were associated with a deterioration of the projected IUCN conservation status in 10% of the species (these estimates rely on a population-based application of the IUCN red list E criterion, and do not reflect actual conservation status at the species level; see detailed results in Appendix E).

The reduction in viability (i.e., ΔT_{ext}) associated with senescence was homogenous among orders with the exception of primates, in which reduction was stronger (ANOVA, $F_{9,48} = 4.22$, $P = 0.0005$; see Fig. 1 and details in Appendix F).

Species traits (body mass, peak adult survival rate, litter size, and number of litters per year) were only moderately correlated with the reduction in annual growth rates associated with senescence ($\Delta\lambda$). However, these traits explained a large amount of variance in the change in generation time, ΔT ($R^2 = 47\%$), and in the change in per generation growth rate, ΔR_0 ($R^2 = 71\%$).

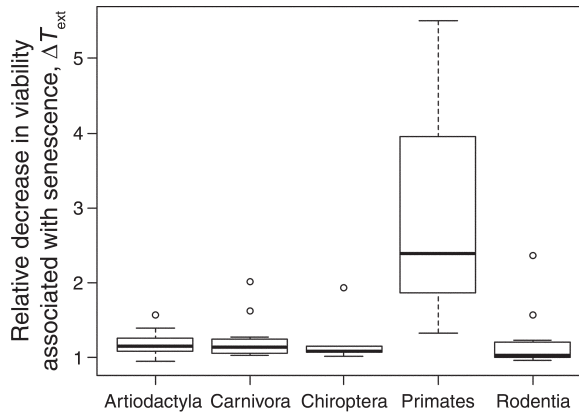


FIG. 1. Proportional changes in median time to extinction associated with actuarial senescence (ΔT_{ext}) in 58 species of mammals as a function of taxonomy (only the five most represented orders are shown). The boundaries of the boxes indicate the 25th (Q1) and 75th (Q3) percentiles, the line in each box indicates the median, and the whiskers indicate the 50% confidence interval range corresponding to $Q_1 - 1.5 \times (Q_3 - Q_1)$ and $Q_3 + 1.5 \times (Q_3 - Q_1)$ for the lower whisker and upper whisker, respectively. The outlying dots show values exceeding this range.

The most important species traits were peak adult survival rate and number of litters per year. Reductions of ΔT and ΔR_0 were stronger in species with high adult survival and/or small number of litters per year (Fig. 2, Table 1; see Appendix G). Body mass and litter size explained considerably less variance than the two other traits, although body mass markedly improved the fit of multiple regression models for ΔT , ΔR_0 , and ΔT_{ext} when included in interaction with life history traits.

The proportional reduction in viability associated with actuarial senescence ΔT_{ext} was highly related to the peak adult survival rate, the number of litters per year, and the interaction between body mass and the number of litters per year (although this apparent interaction was largely related to the correlation between these life history traits, as illustrated in Fig. 3): ΔT_{ext} increased with adult survival but decreased with the number of litters per year.

Overall, we found a weak phylogenetic signal in the cost of senescence among mammals. In all multiple regression models, Pagel's λ was small and not significantly different from zero (see Table 1). In univariate models, only T_{ext} exhibited detectable signal (median maximum likelihood estimate of Pagel's λ was 0.59; see Appendix G).

All qualitative results were robust to changes in population size and frequency of catastrophic events and remained valid when considering the second null model (assuming constant survival probability equal to the maximal survival rate, but maximum life span L). In contrast, under the third null model (assuming that the same fraction of individuals survives to L as in the senescence model) the values of λ , T , R_0 , and T_{ext} were

lower than under the senescence model (see *Discussion*; all additional results are presented in Appendix H).

DISCUSSION

In agreement with theoretical expectations (Williams 1957, Charlesworth 1994, Williams et al. 2006), comparative studies indicate that the rate of senescence declines with increasing longevity or generation time (Jones et al. 2008). However, as noted by Ricklefs (2010), this decline is not fully compensating (i.e., in terms of fitness effects, in long-lived species the lower decline of individual fitness at old ages does not compensate for the fact that more individuals reach these ages, as compared with short-lived species). As a result, the cost of actuarial senescence (i.e., the proportion of aging-related mortality) is generally much higher in long-lived than in short-lived species (Ricklefs 1998, 2008, Turbill and Ruf 2010, Bouwhuis et al. 2012). The processes underlying this variation are still unknown (Ricklefs 2010, Bouwhuis et al. 2012, Nussey et al. 2013). Here, we considered four different metrics of the effects of senescence on population dynamics, to quantify changes in annual deterministic growth rate ($\Delta\lambda$), generation time (ΔT), per generation deterministic growth rate (ΔR_0), and median time to extinction (ΔT_{ext}). Our metrics indicate that actuarial senescence is associated with a significant reduction in both generation time and growth rate of mammal populations. These reductions generally translate into a substantial viability cost, ΔT_{ext} , which is itself strongly related to the speed of the life history.

The viability of a population is affected by the interaction between intrinsic properties and deterministic and stochastic environmental factors (Acker et al. 2014), which makes it difficult to extrapolate the viability of a population from its sole deterministic properties. In the context of estimating the cost of senescence, our results suggest that there is no simple relationship between deterministic costs ($\Delta\lambda$ and ΔR_0) and ΔT_{ext} (see Appendix E). The time to extinction has been proposed by several authors as a reliable measurement of fitness in the presence of environmental perturbations (Tuljapurkar and Orzack 1980, Copper 1984, Robert 2011) and empirical evidence indicates that it scales to the speed of life history (O'Grady et al. 2008). The particularly high correlations that we obtained between some species traits and ΔT_{ext} suggest that the relative change in population viability can be used as an ecologically and evolutionarily meaningful integrative metric of the cost of senescence in comparative work. Specifically, we found that the adult peak survival rate and the number of litters per year, which are two important components of the fast-slow life history continuum (but see discussion in Bielby et al. 2007, Jeschke and Kokko 2009), explain substantial amounts of variance in ΔT_{ext} independently of phylogeny and are primarily responsible for the high viability cost of

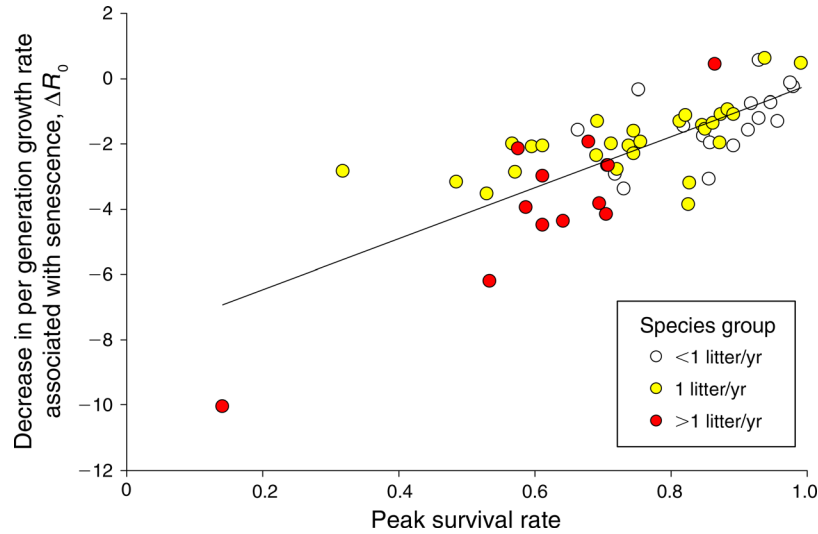


FIG. 2. Positive relationship between the reductions in per generation growth rate associated with actuarial senescence (ΔR_0) and peak adult survival rates in 58 species of mammals, grouped by the number of litters per year. The regression line was obtained from univariate phylogenetic generalized least squares regression.

senescence observed in primates as compared to other mammals (Fig. 3; see Charnov and Berrigan 1993).

Body mass has a special role in the definition of the fast–slow life history continuum (Jeschke and Kokko 2009) and is positively related to longevity (Lindstedt and Calder 1981) and negatively related to the rate of aging (Ricklefs 2007). However, it is often considered that the negative correlation between body mass and the

rate of senescence is mediated by lower extrinsic mortality rates in species with large body size, rather than by physiology (Ricklefs 2010; see also Jones et al. 2008). Our results do not provide any evidence for a strong relationship between the cost of senescence and body mass. For example, bats, which have exceptional longevity relative to their body mass (Wilkinson and South 2002), do not deviate in our estimates of the

TABLE 1. Relationships between changes in population dynamics associated with actuarial senescence ($\Delta\lambda$, ΔT , ΔR_0 , ΔT_{ext}) and four species traits in 58 species of mammals.

Predictor	$\Delta\lambda$		ΔT		ΔR_0		ΔT_{ext}	
	Estimate \pm SE	R^2	Estimate \pm SE	R^2	Estimate \pm SE	R^2	Estimate \pm SE	R^2
a) Univariate regression								
Mass			$0.0057 \pm 0.0023^{**}$	8.7%				
S_{max}			$0.13 \pm 0.039^{***}$	16%	$6.17 \pm 0.89^{***}$	51%	$1.34 \pm 0.41^{***}$	14.5%
LittSize			$-0.047 \pm 0.011^{***}$	27%	$-1.11 \pm 0.38^{***}$	14%	$-0.307 \pm 0.16^*$	4.7%
#Litt			$-0.065 \pm 0.01^{***}$	35%	$-1.3 \pm 0.33^{***}$	20.8%	$-0.68 \pm 0.12^{***}$	35.3%
b) Multiple regression								
Mass		8.5%	$0.04 \pm 0.017^{**}$	47%	$-0.93 \pm 0.3^{**}$	71.3%	$-0.045 \pm 0.014^{**}$	78%
S_{max}	$12.7 \pm 4.4^{**}$						$0.92 \pm 0.33^{**}$	
LittSize								
#Litt			$-0.06 \pm 0.015^{***}$		$-5.53 \pm 0.9^{***}$		$-1.48 \pm 0.27^{***}$	
S_{max}^2	$-5.53 \pm 2.17^*$							
#Litt ²							$0.66 \pm 0.08^{***}$	
Mass \times LittSize			$-0.01 \pm 0.003^*$					
$S_{\text{max}} \times \#Litt$					$4.48 \pm 0.79^{***}$			
Mass $\times S_{\text{max}}$			$-0.04 \pm 0.01^*$		$0.77 \pm 0.25^{**}$			
Mass $\times \#Litt$							$0.13 \pm 0.035^{***}$	

Notes: Significant estimates and coefficient of determination (R^2) from phylogenetic generalized least squares (PGLS) univariate and multiple regression models are presented. All PGLS models use the maximum likelihood estimate of Pagel's λ (for multiple regressions, Pagel's λ is $<10^{-3}$ for $\Delta\lambda$, ΔT , and ΔT_{ext} , and 0.215 for ΔR_0 ; all values of Pagel's λ are significantly lower than 1 and not significantly higher than 0). Dependent variables are the change in deterministic annual growth rate ($\Delta\lambda$) associated with senescence, the change in generation time (ΔT), the change in deterministic per generation growth rate (ΔR_0), and the proportional change in median extinction time (ΔT_{ext} , for a population of 250 mature individuals). Predictors are body mass (Mass), peak adult survival rate (S_{max}), litter size (LittSize), and number of litters per years (#Litt). Only the most significant interaction terms are presented (with $P < 0.01$ for at least one dependent variable). Detailed results are presented in Appendix G.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

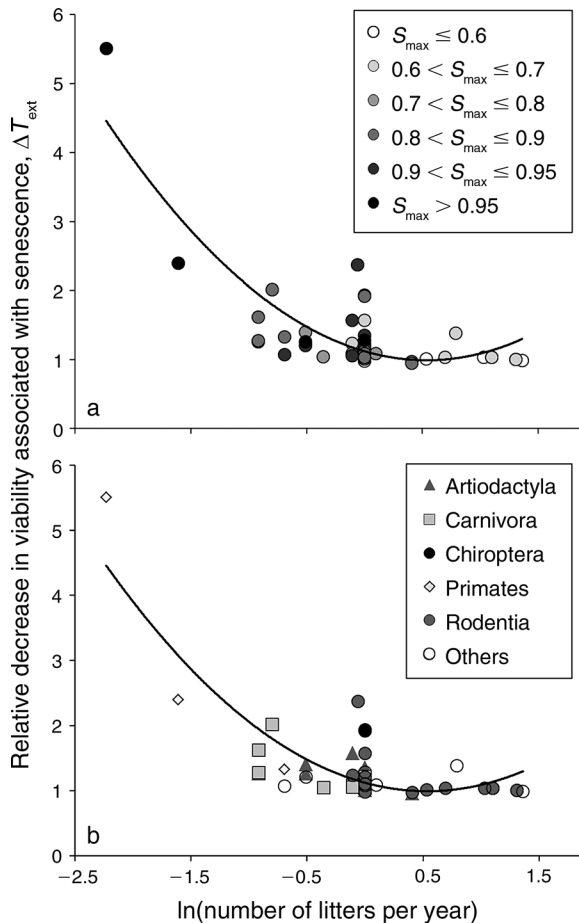


FIG. 3. Negative relationship between proportional reductions in median time to extinction associated with actuarial senescence (ΔT_{ext}) and numbers of litters per year in 58 species of mammals. Differences between symbols are related to (a) the interval of peak adult survival rate (S_{max}) or (b) taxonomical order for each species. The quadratic regression between ΔT_{ext} and \ln -transformed numbers of litters per year obtained from the phylogenetic generalized least squares model is presented by the black lines ($R^2 = 69\%$ in both panels).

demographic cost of actuarial senescence (Figs. 1 and 3b). When considering non-phylogenetically transformed data (not shown) and univariate models, a moderate positive correlation is observed between ΔR_0 and mass ($R^2 = 20\%$), but this correlation disappears when controlling for phylogeny. However, when examining the effects of life history traits on ΔT , ΔR_0 , and ΔT_{ext} , controlling for body mass moderately but significantly improves the fit of models, which is consistent with the view that the relationship between body mass and senescence is mediated by combinations of physiological and ecological mechanisms (Baudisch 2011).

Despite the recent surge of interest in senescence in basic ecology and evolutionary biology (Monaghan et al. 2008) and the abandonment of the idea that it does not occur in wild populations (Nussey et al. 2013),

senescence is generally believed to have minor effects on population dynamics and is still not explicitly considered in the assessment of the viability of endangered species or populations (but see Penteriani et al. 2009). Our results indicate that the effect of actuarial senescence on population dynamics can be substantial and can differ qualitatively according to the reference model considered (i.e., the model without senescence). Our set of null models allowed us to formalize two contrasting scenarios with respect to survival data acquisition.

In the first scenario (which we only considered here to illustrate the limits of our main results), senescence per se (i.e., the pattern of decreasing survival with increasing age) is not explicitly considered in the null model, although it is implicitly included in overall adult mortality. Assuming that estimates of adult survival come from a longitudinal study involving individuals that are marked as adults (of unknown age), senescent effects will indeed implicitly be incorporated and the estimate of overall adult mortality will be slightly negatively biased (Fletcher and Efford 2009). Under this scenario, comparisons between the null and the senescent model indicate that patterns of increasing mortality with age are more favorable to population growth and persistence than constant mortality rates, for a given amount of overall mortality (see the third null model in Appendix H; for theoretical treatment, see Pianka and Parker 1975).

In the second scenario (i.e., first and second null models, on which we focused our main analysis), senescence is not considered at all in the null model and overall adult survival rates are equal to the survival rates of young (non-senescent) adults. In this case, the additional mortality associated with senescence can strongly and negatively affect population dynamics. In a biological conservation context, it is likely that a high proportion of population-specific assessments of survival rates for the purpose of population viability analysis (PVA) tend to underestimate the overall mortality due to the non-detection of senescence patterns. Methods used to compute unbiased survival rates are typically based on longitudinal studies of individuals. In the context of PVA, individuals should preferentially be marked in the year of birth (not as adults), because reliable population dynamics projections necessitate unbiased estimates of both immature and adult survival rates. In most conservation studies, short-term monitoring and small sample sizes lead to low power to detect an increase in mortality with age and underestimate the overall adult mortality rate, due to the absence of senescent adults among the individuals marked as juveniles.

In this context, our projections reveal substantial negative effects of senescence on population viability, with a 27% decrease of the median time to extinction, on average, and a deterioration of the projected conservation status in some species for a fixed carrying capacity, which illustrates that patterns of senescence have the

potential to change substantially the results of PVAs. Undoubtedly, these quantitative estimates of the cost of senescence should be considered with caution, because (1) as previously discussed, the negative effects of senescence on overall adult survival can be considered implicitly if survival is estimated on a random sample of adults (Fletcher and Efford 2009), or if the time scale of the study is long enough (Nussey et al. 2008). (2) Quantitative approaches to modeling senescence would strongly benefit from using long-term individual-based field studies, which, unlike life table data, are free of assumptions regarding population structure and stationarity (see Gaillard et al. 1994, Nussey et al. 2008, 2013). However, gathering large sample sizes (number of species) with such longitudinal data remains difficult. (3) A complete picture of the effect of senescence on population dynamics should include reproductive senescence (Penteriani et al. 2009, Bouwhuis et al. 2012, Froy et al. 2013, Nussey et al. 2013) and its covariation with actuarial senescence.

Importantly, the aim of the various existing systems of classification of threatened species (and associated quantitative methods; Mace et al. 2008) is not only to provide conservationists with a non-biased estimate of the risk of extinction, but also to rank species to set conservation priorities. Our results indicate that the quantitative effects of senescence on extinction are heterogeneous (ranging from almost no effect to a 30-fold reduction in extinction time), which can affect the ranking of species. We did not find evidence for strong phylogenetic signals in our four metrics of the cost of senescence, and taxonomy explains modest levels of variation in ΔT_{ext} . However, the combination of a few life history traits is sufficient to explain high amounts of variance in ΔT_{ext} . For instance, although the time to extinction is reduced by less than 10%, on average, in species with annual peak adult survival rates lower than 60%, the reduction averages 50% in species with adult survival rates higher than 90%. Based on these life history traits, the identification of endangered species that are expected to be impacted by senescence can be straightforward. For such species, even in the absence of specific data on senescence, we advocate that the effect of senescence be routinely considered in species viability assessment by incorporating generic senescence patterns and quantities (Jones et al. 2008, Péron et al. 2010) to projection models, as is already done for inbreeding depression (Noël et al. 2013) and environmental catastrophes (Doxa et al. 2010).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–H are available online: <http://dx.doi.org/10.1890/14-0221.1.sm>