Age at the onset of senescence in birds and mammals is predicted by early-life performance

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Life-history theory predicts that traits involved in maturity, reproduction and survival correlate along a fast–slow continuum of life histories. Evolutionary theories and empirical results indicate that senescence-related traits vary along this continuum, with slow species senescing later and at a slower pace than fast species. Because senescence patterns are typically difficult to estimate from studies in the wild, here we propose to predict the associated trait values in the frame of life-history theory. From a comparative analysis based on 81 free-ranging populations of 72 species of birds and mammals, we find that a nonlinear combination of fecundity, age at first reproduction and survival over the immature stage can account for *ca* two-thirds of the variance in the age at the onset of actuarial senescence. Our life-history model performs better than a model predicting the onset based on generation time, and it only includes life-history traits during early life as explanatory variables, i.e. parameters that are both theoretically expected to shape senescence and are measurable within relatively short studies. We discuss the good-fit of our life-history model to the available data in the light of current evolutionary theories of senescence. We further use it to evaluate whether studies that provided no evidence for senescence lasted long enough to include the onset of senescence.

Keywords: actuarial senescence; comparative analysis; life-history variation; scaling relationship

1. INTRODUCTION

Senescence, the decline in fitness components with age owing to internal physiological deterioration (Medawar 1952), is an evolutionary puzzle generally understood as a consequence of the weaker strength of selection at old ages (Medawar 1952; Williams 1966). Theory and empirical evidence suggest that senescence is widespread in vertebrates (Finch 1990). Yet, the detection of senescence in wild populations is problematic and it is thus uncertain whether senescence is truly ubiquitous (e.g. Miller 2001). This lack of consensus is partly because of the inherent rarity of old individuals, which implies that senescence studies require unusually large longitudinal datasets (Nichols *et al.* 1997). Thus, only a few years ago, Kirkwood (2002, p. 737) still wrote that 'wild animals have the potential to undergo the process of ageing, even though few, if any, of them will ever do so'. Another source of uncertainty is that studies claiming to document an absence of senescence might simply have been too short to encompass the onset of senescence. A sound method predicting the timing of the onset of senescence from life-history traits without necessitating knowledge on whole age-specific patterns would thereby

be useful to evaluate the results of existing studies as well as to design future studies.

Evolutionary theories predict that life-history traits must covary according to the principle of energy allocation to competing biological functions such as survival, growth and reproduction (Williams 1966). One of the best-documented correlations involves future survival or reproduction and current reproductive effort (Stearns 1983, 1992). At the interspecific level, life-history traits measuring biological times covary to shape the fast–slow continuum of life histories that has been used to explain interspecific patterns of variation in life-span: 'fast' species perform better than 'slow' species during early life (earlier start of reproduction, higher fecundity), but die earlier (Charlesworth 1980; Promislow & Harvey 1990).

In evolutionary theories, the baseline rate of mortality plays a key role in shaping senescence (Ricklefs 1998). Briefly, high mortality favours the accumulation of late-acting deleterious mutations (Medawar 1952) and the selection of antagonist mutations (that increase early-life performance at the expense of late-life performance, Williams 1957), because their deleterious effects occur when most individuals have already died or stopped reproducing. Thereby, although mortality rate and life-span cannot be used as an indicator of survival senescence (hereafter called actuarial senescence), a strong correlation between senescence-related traits and

life-history traits associated with the slow–fast continuum of life histories is expected to occur according to the current evolutionary theories. Indeed, a recent analysis of interspecific patterns of ageing across 19 species of birds and mammals (Jones *et al.* 2008) showed that the intensity of senescence varies along the fast–slow continuum of life histories since both the onset of senescence and the rate of decline in fitness with age correlate with the species' generation time (measured as the weighted mean age of females that give birth, *sensu* Leslie 1966).

In this study, we expand on these previous findings by Jones *et al.* (2008) and focus on the onset of actuarial senescence. In most iteroparous species, fitness measures initially increase with age (Forslund & Pärt 1995; Vaupel *et al.* 2004), and then decrease after some species-specific age-threshold (Jones *et al.* 2008). This age-threshold (the onset of senescence) is relatively well documented in the literature but has seldom been the subject of focused studies. Yet, the onset of senescence is a critical life-history parameter because, for given survival and reproductive parameters, it determines the proportion of individuals that actually experience senescence, and thus the strength of selection acting against senescence. We first show that the relationship between early life-history traits and the onset of senescence still holds when we consider a much larger number of vertebrate species than in the previously mentioned studies. We then test whether the age at the onset of actuarial senescence can be predicted more precisely than before using a combination of early life-history traits, namely the average number of emancipated offspring per female and per year (called fecundity thereafter), age at first reproduction and survival rate between emancipation and age at first reproduction (called immature survival thereafter) as predicted by evolutionary theories of senescence, rather than generation time. Finally, we show how obtaining reliable estimates of the age at the onset of senescence could allow evaluating the validity of studies that question the ubiquity of senescence in vertebrate populations.

2. MATERIAL AND METHODS

(a) *A life-history model to predict the onset of senescence across species*

Generation time T is both a reliable measure of species' ranks on the fast–slow continuum of life histories (Gaillard *et al.* 2005) and a good predictor of species-specific rates of senescence (Ricklefs 1998; Jones *et al.* 2008). Our 'reference model' (model 1) was therefore a linear model with $\log T$ as an explanatory variable and, noting Ω the age at the onset of actuarial senescence, $\log \Omega$ as a variable to be explained (as in Jones *et al.* 2008):

model 1 : $\log \Omega = \alpha_1 + \beta_1 \times \log T$,

where α_1 and β_1 are regression parameters to be estimated. Our working hypothesis is that there is a trade-off between Ω and early-life reproductive performance. We have identified three classical measures of such performance that are widely available in various species: survival rate during the immature period s, age at first reproduction a and prime-age fecundity f. The 'data collection' section below provides details on these measures. Based on these traits, three models

(models 2–4) represent the expected trade-offs:

model 2 : $\log \Omega = \alpha_2 + \beta_2 \times \log a$,

model 3 : $\log \Omega = \alpha_3 + \beta_3 \times \log f$,

model 4 : $\log \Omega = \alpha_4 + \beta_4 \times \text{logit} \, s$,

where α_i and β_i are regression parameters to be estimated. We also consider a model where the three trade-offs are acting simultaneously (model 5):

model 5 : $\log \Omega$
$$= \alpha_5 + \beta_5 \times \log a + \gamma_5 \times \log f + \delta_5 \times \text{logit} \, s.$$

Alternatively, early life-history traits might all be correlated to Ω, yet in a nonlinear fashion. In this case, a composite variable of the three measures of early-life reproductive performance can capture more efficiently the expected trade-off. In particular, we can express the total number of recruits produced per year and per female as $f \times s^a$. This is simply the number of offspring multiplied by the probability for them to survive until recruitment, and is therefore a measure of reproductive performance that combines the three early-life traits in a potentially effective manner. Under our working hypothesis, we expect that $\log \Omega$ is inversely proportional to this quantity. Additionally, we expect that senescence should invariably set on after first reproduction as predicted by Hamilton (1966). We thereby propose the following general expression to formalize the relationship between Ω and early-life performance:

model 6 : $\log \Omega = D \times \log a + \dfrac{A}{f^B \times s^{Ca}}$,

where A, B, C and D are constants to be estimated (using capital letters to help distinguish the different model types). We also consider a seventh model, which is a constrained form of model 6, where $B = C$ (model 7). This equality is expected if reproductive performance ($f \times s^a$) is the most parsimonious explanatory variable for the expected trade-off.

(b) *Data collection*

We based our analysis on actuarial senescence because it is the most documented in the literature. We searched for estimates of Ω and of early-life performance a, f and s. The value for a was the average age at first reproduction or, when that measure was not available, the 'common' age at first reproduction, i.e. the first age at which accession to reproduction is widespread in the population. Fecundity f corresponded to the number of emancipated offspring per female and per year ('emancipated' refers to fledged and weaned offspring in birds and mammals, respectively). When age-specific fecundities were available, we selected the prime-age value as f. The choice of f instead of other quantities that are more closely related to reproductive effort *per se* (e.g. total number of eggs produced, offspring weight at birth) was based on the following arguments: (i) this measure is comparable in birds and mammals; (ii) it is widely available for most species; and (iii) it is a measure of the overall result of parental care between conception and emancipation (*sensu* Clutton-Brock 1991). The immature survival rate s corresponded to the average yearly survival probability between emancipation and first reproduction.

We restricted our search to longitudinal studies of marked individuals for which individual age was precisely known (animals had to be marked as young), thus excluding cross-sectional (life table) studies because of the strong hypotheses

Table 1. Comparison of seven models explaining the age at the onset of senescence using early-life performance, first with all the data and second restricting to data from capture–mark–recapture (CMR) studies. All models include a correction for phylogenetic inertia. Best models' Akaike's Information Criterion (AIC) values are in bold. Results were qualitatively the same when not accounting for phylogenetic inertia.

model form	biological meaning	AIC (all data)	AIC (CMR only)
$\log \Omega = \alpha_1 + \beta_1 \times \log T$	linear model where generation time alone explains the variation in the age at the onset of senescence	**626.93**	202.87
$\log \Omega = \alpha_2 + \beta_2 \times \log a$	linear model representing the trade-off between the onset of senescence and age at first reproduction only	662.91	247.06
$\log \Omega = \alpha_3 + \beta_3 \times \log f$	linear model representing the trade-off between the onset of senescence and fecundity only	681.85	240.22
$\log \Omega = \alpha_4 + \beta_4 \times \text{logit } s$	linear model representing the trade-off between the onset of senescence and immature survival only	701.15	270.42
$\log \Omega = \alpha_5 + \beta_5 \times \log a$ $+ \gamma_5 \times \log f + \delta_5 \times \text{logit } s$	linear model representing the trade-off between the onset of senescence and the early life-history traits acting simultaneously but left non-combined as opposed to models 6 and 7	655.62	195.18
$\log \Omega = D \times \log a + \dfrac{A}{f^B \times s^{C \cdot a}}$	nonlinear model representing the trade-off between the onset of senescence and a combination of early life-history traits	**624.75**	**131.27**
$\log \Omega = D \times \log a + \dfrac{A}{f^B \times s^{B \cdot a}}$	nonlinear model similar to model 6 but with a constraint ($B = C$, see main text)	631.52	187.99

underlying the methodology used in these studies (Gaillard *et al.* 1994), and also because the determination of age in such studies is often imprecise for senescent individuals. Only studies of free-ranging populations were included. They provided either the unconstrained relationship between age and survival probabilities (one estimate per age; age-specific survival graphs), or an explicit value of the onset. Where the authors of the original studies explicitly accounted for differences between sexes, we used the female data; otherwise, the sexes were pooled together following the original authors' decision.

We obtained these data for 81 populations of 72 species of vertebrates (34 birds and 38 mammals; electronic supplementary material, appendix S1). Species ranged from the short-lived *Peromyscus leucopus* (weight of 22 g, maximum reported longevity of 2 years, generation time of 1 year) to the long-lived *Diomedea sanfordi* (weight of 7 kg, maximum reported longevity of 58 years, generation time of 24 years) and *Elephas maximus* (weight of 5500 kg, maximum reported longevity of 65.5 years, generation time of 35 years). The original studies used either capture–mark–recapture (CMR) methodology (they statistically accounted for the imperfect detectability of individuals; Lebreton *et al.* 1992; noted 'yes' in the tables) or they assumed capture rate to be one in their study population (noted 'no').

Because the data originated from various sources, many of which did not provide an estimate for the age at the onset of senescence, the estimation of Ω was made visually, by four of the authors who acted as 'judges' (see electronic supplementary material, appendix S2 for details). They were provided with the age-specific survival graphs only but not with species identity, study method or any other information that could have biased their judgement. The judges could estimate that a graph did not support the presence of senescence, in which case we considered the corresponding study as reporting a lack of senescence. We tested the estimates for among-judge agreement (ordered Cohen's $\kappa = 0.88$, between-judges r^2's all >0.90 indicating satisfactory among-judge agreement; Conger 1980). We then computed the median and variance of the visual estimates.

We considered that the more variable the visual estimation by the judges, the less reliable the estimate of Ω. We used the median of the visually estimated onsets of senescence as an empirical measure of Ω.

(c) *Data analyses*

We used a generalized nonlinear least-squares modelling approach (function gnls in R package NLME, Pinheiro *et al.* 2006), using $\log \Omega$ as dependent variable, and $\log T$ and the early-life performance traits a, s, f as explanatory variables to fit our nonlinear models and compute parameter estimates.

We weighed all our regressions by the inverse of the estimated variances of Ω (variance in the visual estimates) following Burnham *et al.*'s (1987) recommendations, thereby giving a greater emphasis to reliable Ω estimates. The method used in the original studies to estimate survival (CMR or not) is known to influence the estimation of senescence patterns (Gimenez *et al.* 2008): CMR studies are considered less biased than non-CMR studies. Hence, we included 'method' as a fixed effect in our models. Phylogenetic inertia is known to induce the statistical non-independence of samples in interspecific comparisons (Felsenstein 1985). Not taking into account phylogenetic dependence among species can therefore artificially inflate the effective sample size for the test of functional relationships between traits. Accordingly, we accounted for the phylogenetic structure of our sample using a correlation structure (Ives & Zhu 2006; function corBrownian in R-package APE: Paradis *et al.* 2004). We used a taxonomy-based phylogeny (birds: Sibley & Monroe 1990; mammals: Wilson & Reeder 2005; electronic supplementary material S3). Because several authors have suggested that the assumptions made by comparative methods are too restrictive (Price 1997; Martins 2000), we also performed the analyses on raw species data and present results from both types of models.

We used an information-theoretic approach to select the best model among the set of seven models using Akaike's Information Criterion (AIC; table 1). The AIC for a given model is the sum of its deviance plus twice its number of

Table 2. Parameter estimates and standard errors (s.e.'s) of the proposed relationship (model 6) in four configurations using capture–mark–recapture (CMR) studies only or all the data, and accounting for phylogenetic inertia or not. p-values are computed using likelihood ratio tests. '*method' refers to the effect of using CMR method or not in the original studies.

(a) all data, phylogeny corrected	estimator	s.e.	p-value	(b) all data, not corrected	estimator	s.e.	p-value
A	1.89	0.10	$<10^{-4}$	A	1.79	0.12	$<10^{-4}$
B	0.33	0.05	$<10^{-4}$	B	0.33	0.09	0.0002
C	0.19	0.04	$<10^{-4}$	C	0.22	0.06	0.0005
D	0.22	0.13	0.10	D	0.15	0.16	0.35
B*method	-0.30	0.07	0.0001	B*method	-0.32	0.13	0.015
C*method	-0.26	0.08	0.0012	C*method	-0.42	0.14	0.0030
D*method	0.33	0.14	0.023	D*method	0.57	0.21	0.0083
(c) CMR only, phylogeny corrected	estimator	s.e.	p-value	(d) CMR only, not corrected	estimator	s.e.	p-value
A	1.78	0.03	$<10^{-4}$	A	1.71	0.03	$<10^{-4}$
B	0.34	0.01	$<10^{-4}$	B	0.32	0.02	$<10^{-4}$
C	0.20	0.01	$<10^{-4}$	C	0.22	0.01	$<10^{-4}$
D	0.22	0.03	$<10^{-4}$	D	0.22	0.04	$<10^{-4}$

parameters. A model is preferred to another competing model if its AIC value is lower by at least two points compared to the other. Our proposed nonlinear models were compared with model 1 and to linear models including one or all of these life-history trade-offs (models 2–5). We performed the same model selection using the data from CMR studies only, to verify that the preferred model was the same when using the best-quality data only.

Some proportion of the observed variation in the age at the onset of senescence was, however, expected to be mechanistically accounted for by the linear part of our models (i.e. parameter D), because Ω invariably occurs after the age at first reproduction, a (Nee *et al.* 2005). To assess the impact of that feature on our results, we generated 100 permutations of the dataset where $\Omega > a$ by random sampling in the existing a, f, s and Ω values and excluding the generated samples, where $\Omega \le a$. For each permuted dataset, we computed the correlation coefficient between Ω and a. Obtaining a high value of r^2 for this correlation would indicate that the mechanistic relationship between Ω and a had an impact on the expected parameter values in our nonlinear model.

The model was then used to predict Ω from early-life performance in other species (including those where no senescence was detected). A bootstrap procedure (1000 random re-samples of the original dataset with replacement; Davison & Hinkley 1997) was employed to compute a standard deviation (s.d.) on predicted onsets.

3. RESULTS AND DISCUSSION

(a) *A life-history model predicting the onset of senescence*

The AIC-based selection procedure favoured the non-linear model 6 over all linear models (models 1–5) including the model based on generation time, T. As expected, the slope of the allometric relationship between Ω and generation time was close to 1 (0.86 ± 0.06 s.e.). Although the difference between this model 1 and model 6 was of 2.2 AIC points only when using the whole dataset, the same analysis restricted to CMR-only data unambiguously selected model 6 (table 1). Thus, our proposed new model was thought to explain some variance in Ω not accounted for by T. It thereby

constituted a more appropriate and more precise predictive model than models 1–5. However, the strong rejection of model 7 (table 1) indicated that, even if the nonlinear structure was favoured as a representation of the life-history trade-off, the reproductive performance $f \times s^a$ was not in itself the key explanatory variable. Finally, we tried a model in which the T-effect was additive to model 6. This model exhibited a lack-of-fit (strongly non-randomly distributed residuals, possibly linked with a high level of correlation between a and T) and is not presented here for that reason.

At the between-species level, we confirmed the positive correlation between age at first breeding a and the onset of senescence Ω (table 2: parameter D). The effect of a was furthermore amplified by a rapid advancement of the onset of senescence with increases in other measures of early-life performance (table 2: parameters A, B and C). The comparison of the three single-trait models (models 2–4) fitted to CMR-only data further indicated that fecundity alone might indeed be a better predictor of Ω than age at first reproduction alone.

In addition, and as illustrated before in comparative studies (e.g. Jones *et al.* 2008), onsets of senescence were overall later than maturity. This suggests a non-negligible phenotypic selection and/or an individual-level increase in performance (e.g. learning, increase of physiological capacity or development of immune system) during the period between a and Ω (Forslund & Pärt 1995).

As introduced in §2, a permutation-based analysis evaluated the effect of the constraint $\Omega > a$ on the model fit. The percentage of variance accounted for by the linear effect of a on Ω in these permuted datasets was 4.4 per cent (s.d.: 4.0; max 17%). Since our life-history model accounted for *ca* 63 per cent of the observed variation in Ω, there was obviously a strong functional relationship among the life-history traits of interest.

On the whole, our results (figure 1) support the idea that high early-life performance comes with early senescence (Williams 1966; Kirkwood & Holiday 1979; see later discussion on evolutionary theories). These results also further suggest, using a larger dataset, that the delayed senescence of birds compared with mammals is
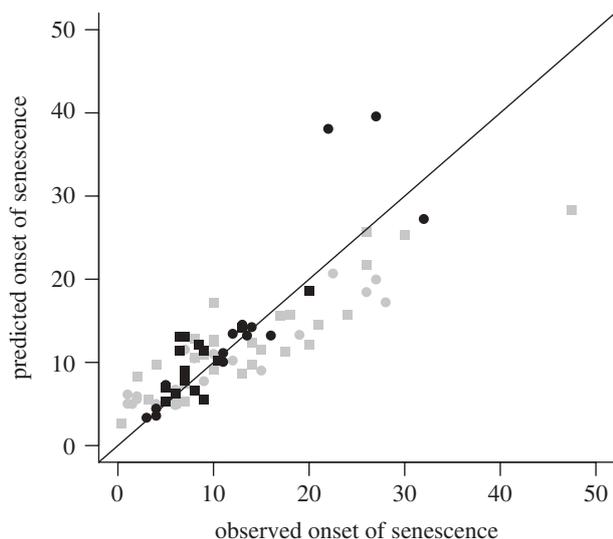
Figure 1. Predicted versus observed ages at the onset of senescence in 81 populations of vertebrates (squares, mammals; circles, birds). Solid line is the first bisector. Black symbols, CMR studies; grey symbols, non-CMR studies. The predicted values were computed accounting for phylogenetic inertia.

related to a slower life history (Jones *et al.* 2008) rather than to phylogenetic inertia or to the sole ability to fly (Holmes & Austad 1995). Indeed, accounting for phylogenetic inertia did not qualitatively affect the relationship between Ω and early-life performance (table 2, parts (a) and (c) versus parts (b) and (d)). Furthermore, it is noticeable that 81 out of 96 selected datasets provided evidence for a late-life decline in survival rate, while the mere detection of senescence was considered challenging until recently (Williams 1992; Kirkwood 2002).

Poikilotherms were not included in our study because of the scarcity of relevant data. Moreover, in poikilotherms, life histories can be very different, especially regarding the production of 'emancipated offspring', which is generally of several orders of magnitude greater than in birds and mammals, and thereby largely out of the range of values used to parameterize the model (see §3*d*). We identified two species that could have been included, the viviparous fish *Poecilia reticulata* (guppies hereafter) and the viviparous reptile *Zootaca vivipara* (lizards), which start senescing at 0.43 and 4-year-old, respectively (guppies: Bryant & Reznick 2004; lizards: Ronce *et al.* 1998). Using our model to predict Ω in guppies and lizards, we found, respectively, $\Omega = 0.66 \pm 0.60$ and $\Omega = 4.55 \pm 1.30$ (bootstrap mean $\pm$ s.d.). These results may suggest that the correlation between life-history traits that we have found is conserved across all vertebrates, cold- and warm-blooded, and is not affected by differences in physiology (see also Ricklefs 1998). Of course, we need much larger sample sizes, and a broader range of life histories to check the validity of this hypothesis. In particular, we want to highlight here than given the relatively narrow range of life-histories that we were able to sample (only three species with an estimated Ω above 30 years), our model can only be safely used in that range. Bootstrap predictions for longer lived species (including humans) were indeed overestimated, an issue that should be dealt with in future developments.

(b) *Studies reporting a lack of senescence*
Our survey of the literature yielded 15 bird and mammal studies for which the judges did not detect the presence of senescence. In order to check whether the apparent absence of senescence was owing to the fact that no individual had reached the age at the onset of senescence, we used the predictive ability of our life-history model to compute an expected value for Ω (table 3). Overall, the results indicated that in all 15 species, the predicted age at the onset of senescence was close to, and in several cases above, the maximum age reached by focal individuals at the end of the study (table 3). We can thus suspect that senescence was not detected in these studies because the individuals were not old enough.

However, in at least three studies, no individual ever reached the predicted Ω, albeit the study duration and sample size seemed largely sufficient at first sight. We suggest that three mechanisms might have led to flawed predictions by our model and/or might have impaired the detection of old individuals in the original studies. First, the number of marked individuals per cohort at the start of a monitoring programme is often lower than that after a few years. In this case, the actual sample size of individuals likely to reach the oldest ages can be much lower than suggested by the total sample size in the dataset. Second, the available measure of *s* corresponded generally to *local* immature survival as opposed to *true* immature survival. This measure could be significantly biased downward in the case of high rates of long-range dispersal out of the study areas (possible explanation for the Common pochard case; table 3). Third, recent changes in the species' patterns of mortality might have caused drops in the actual sample size of individuals surviving until senescence, and also induced lower *s*-values than under the original conditions (possible explanation for the Southern elephant seal case; table 3).

(c) *Link with evolutionary theories of senescence*
The relationship between baseline mortality and senescence rates (Ricklefs 1998) and the correlation between mortality and reproductive performance (Stearns 1992) might be independent. In other words, the rate of baseline mortality would shape patterns of life history as a whole (e.g. Nilsen *et al.* 2009 at the within-species level), and the strength of actuarial senescence in particular (Medawar 1952). However, a true trade-off between life-history traits can also produce the same result that senescence traits correlate with early-life traits along the life-history continuum. The correlation that we report can then be interpreted as the result of the species-specific trade-off between the early-life benefits and late deleterious effects of some genes (Williams 1957; Service & Rose 1985). In short, a first mechanism related to the mutation accumulation theory predicts that the observed correlation between the age at the onset of senescence and early-life performance is a consequence of the speed of life, which itself is driven by the rate of baseline mortality, while a second mechanism related to the antagonistic pleiotropy theory predicts that the observed correlation stems from a true trade-off between early- and late-life performance. Mechanistic studies focusing on the triggers of senescence and of its variation are necessary to decide

Table 3. Predicted onset of senescence (Ω) for published studies showing a lack of actuarial senescence. Given are common and scientific names of the species, location of the study population, class (B, M refers to bird and mammal, respectively), reference (see the following list of references for details), type of methodology used in the reference (capture–mark–recapture (CMR) or not), sample size, duration of the study, maximum age documented in the study (maximum age for which a separate survival probability is provided) and predicted age at the onset of actuarial senescence (Ω and s.d. are the bootstrap mean and standard deviation, respectively).

common name	scientific name	class	reference	CMR	location	sample size	duration	maximum age	Ω	s.d.
Florida scrub jay	*Aphelocoma coerulescens*	B	a	yes	FL (USA)	250	25	10	10.3	1.1
common pochard	*Aythya ferina*	B	b	yes	USA	>10	17	8	13.5	4.0
snow goose	*Chen caerulescens*	B	c	yes	Canada	>10	19	18	46.5	10.2
house martin	*Delichon urbica*	B	d	no	UK	117	>4	4	3.4	0.6
American kestrel	*Falco sparverius*	B	e	no	Patuxent Wildlife Research Center (USA)	884	6	10	16.2	17.4
pied flycatcher	*Ficedula hypoleuca*	B	f	yes	Spain	950	8	4	5.2	1.9
willow ptarmigan	*Lagopus lagopus*	B	g	no	La Pérouse Bay, Manitoba (Canada)	105	4	4	4.4	0.5
Leach's storm-petrel	*Oceanodroma leucorhoa*	B	h	no	Matinicus Rock, Maine (USA)	>3000	20	17	21.2	7.2
indigo bunting	*Passerina cyanea*	B	i	no	E.S. Georges Reserve, S Michigan (USA)	184	10	5	4.0	0.6
greater flamingo	*Phoenicopterus ruber*	B	j	yes	Camargue (France)	>1000	25	24	25.0	4.9
badger	*Meles meles*	M	k	yes	Gloucestershire (UK)	273	9	5	7.2	0.7
southern elephant-seal	*Mirounga leonina*	M	l	yes	Marion Island	1650	14	12	11.6	1.0
mouflon	*Ovis gmelini*	M	m	no	Caroux (France)	169	10	8	10.8	1.6
red squirrel	*Tamiasciurus hudsonicus*	M	n	no	Montana (USA)	193	13	6.7	4.2	0.5
grey fox	*Urocyon cinereoargenteus*	M	o	no	Southern Georgia–Northern Florida (USA)	435	4	3	3.5	0.6

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which one of the above hypotheses is the more influential and widespread.

(d) *General applicability and limits of the approach*

A promising development opened by our interspecific correlative approach is the prediction of Ω in organisms that are currently thought to have negligible senescence (e.g. rockfishes *Sebastes* sp.; Cailliet *et al.* 2001). The applicability of our results to such taxa might, however, be limited by at least two factors. First, data deficiencies currently prevent the use of our model in most species. We strongly encourage research aimed at estimating a, f and s in some of the negligible-senescence taxa. Second, the use of our model should be limited to taxa with comparable life histories to the ones used to parameterize the model. This limit unfortunately excludes most long-lived species to our knowledge, and *a fortiori* taxa with completely different life cycle (hydra and plants). In particular, bootstrap results were clearly overestimated for long-lived homeotherms such as humans and large birds. As a consequence, we feel that our model should be considered valid only in vertebrates whose generation time lies below 20 years, i.e. most species at the exception of the very most long-lived ones.

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