# LETTER

# Senescence rates are determined by ranking on the fast–slow life-history continuum

Owen R. Jones,[1]* Jean-Michel Gaillard,[2] Shripad Tuljapurkar,[3] Jussi S. Alho,[4] Kenneth B. Armitage,[5] Peter H. Becker,[6] Pierre Bize,[7] Jon Brommer,[8] Anne Charmantier,[9,10] Marie Charpentier,[10,11] Tim Clutton-Brock,[12] F. Stephen Dobson,[13] Marco Festa-Bianchet,[14] Lars Gustafsson,[15] Henrik Jensen,[16] Carl G. Jones,[17] Bo-Göran Lillandt,[4] Robin McCleery,[9,†] Juha Merilä,[4] Peter Neuhaus,[18] Malcolm A. C. Nicoll,[19] Ken Norris,[19] Madan K. Oli,[20] Josephine Pemberton,[21] Hannu Pietiäinen,[8] Thor Harald Ringsby,[16] Alexandre Roulin,[22] Bernt-Erik Saether,[16] Joanna M. Setchell,[11,23] Ben C. Sheldon,[9] Paul M. Thompson,[24] Henri Weimerskirch,[25] E. Jean Wickings[11] and Tim Coulson[1]

## Abstract

Comparative analyses of survival senescence by using life tables have identified generalizations including the observation that mammals senesce faster than similar-sized birds. These generalizations have been challenged because of limitations of life-table approaches and the growing appreciation that senescence is more than an increasing probability of death. Without using life tables, we examine senescence rates in annual individual fitness using 20 individual-based data sets of terrestrial vertebrates with contrasting life histories and body size. We find that senescence is widespread in the wild and equally likely to occur in survival and reproduction. Additionally, mammals senesce faster than birds because they have a faster life history for a given body size. By allowing us to disentangle the effects of two major fitness components our methods allow an assessment of the robustness of the prevalent life-table approach. Focusing on one aspect of life history – survival or recruitment – can provide reliable information on overall senescence.

[1]Division of Biology and Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berks SL5 7PY, UK
[2]Laboratoire de Biométrie et Biologie Evolutive, Unité Mixte de Recherche 5558, Université Claude Bernard Lyon 1, 43 Boulevard du 11 Novembre 1918, Villeurbanne Cedex, F 69622 France
[3]Biological Sciences, Stanford University, Stanford, CA 94305, USA
[4]Ecological Genetics Research Unit, Department of Biological and Environmental Sciences, PO Box 65 (Viikinkaari 1), FIN-00014, University of Helsinki, Finland
[5]Department of Ecology and Evolutionary Biology, The University of Kansas, Lawrence, KS 66045-7534, USA
[6]Institut fuer Vogelforschung, ''Vogelwarte Helgoland'', An der Vogelwarte 21, D-26386 Wilhelmshaven, Germany
[7]Division of Environmental and Evolutionary Biology, Graham Kerr Building, Glasgow University, Glasgow G12 8QQ, UK
[8]Bird Ecology Unit, Department of Biological and Environmental Sciences, PO Box 65 (Viikinkaari 1), FIN-00014, University of Helsinki, Helsinki, Finland
[9]Department of Zoology, Edward Grey Institute, University of Oxford, Oxford OX1 3PS, UK
[10]Centre d'Ecologie Fonctionnelle et Evolutive UMR 5175, CNRS, 1919 Route de Mende, 34293 Montpellier Cedex 5, France
[11]Unité de Génétique des Ecosystèmes Tropicaux, Centre International de Recherches Médicales de Franceville, BP 769, Franceville, Gabon
[12]Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
[13]Department of Zoology, Auburn University, Auburn, AL 36849-5414, USA
[14]Département de biologie, Université de Sherbrooke, Sherbrooke, QC J1K 2R1, Canada

[15]Division of Animal Ecology, Department of Ecology and Evolution, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18d, SE-75236, Sweden
[16]Department of Biology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
[17]Durrell Wildlife Conservation Trust, Les Augres Manor, Trinity, Jersey, UK
[18]Institute of Zoology, University of Neuchâtel, Eco-Ethology, Rue Emile-Argand 11, case postale 158, CH-2009 Neuchâtel, Switzerland
[19]Centre for Agri-Environment Research (CAER), School of Agriculture, Policy and Development, University of Reading, Earley Gate, PO Box 237, Reading RG6 6AR, UK
[20]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611-0430, USA
[21]Institute of Evolutionary Biology, University of Edinburgh, Ashworth Laboratories, King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK
[22]Department of Ecology and Evolution, Biophore, University of Lausanne, CH-1015 Lausanne, Switzerland
[23]Department of Biological Anthropology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK
[24]School of Biological Sciences, University of Aberdeen, Lighthouse Field Station, George Street, Cromarty, Ross-shire IV11 8YJ, UK
[25]Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique, 79360 Villiers en Bois, France
*Correspondence: E-mail: owen.jones@imperial.ac.uk.
†Deceased

## INTRODUCTION

The study of senescence (a decline in fitness with age caused by physiological degradation) in wild populations of vertebrates has been contentious. Although capture–mark–recapture studies on some systems have been revealing (e.g. Loison *et al.* 1999; Gaillard *et al.* 2003; Reznick & Bryant 2007), claims that it is widespread based on analyses of life tables (Nesse 1988; Promislow 1991) have been challenged because of data quality and assumptions about equilibrium dynamics (Caughley 1977; Gaillard *et al.* 1994). Claims that specific species or groups do not exhibit senescence (Finch 1998; Finch & Austad 2001), typically based on anecdote and observation of the occasional very long-lived individual (Cailliet *et al.* 2001; Miller 2001), have been discredited in fish (Reznick *et al.* 2002, 2006) and birds (e.g. Calder 1984; Bennett & Owens 2002). Now that the focus of detecting senescence has moved on from the analysis of life tables to the analysis of detailed individual life history records (e.g. Loison *et al.* 1999; Ericsson *et al.* 2001; Bronikowski *et al.* 2002; Mysterud *et al.* 2002, 2005) it is timely to revisit the frequency of senescence in birds and mammals.

Most research on senescence focuses on actuarial senescence (a decline in survival rate with age; Loison *et al.* 1999; Ericsson & Wallin 2001; Cameron & Siniff 2004). However, biologists now appreciate that senescence is complex and can also occur in fecundity (Ericsson *et al.* 2001; Reid *et al.* 2003), morphological traits (Carranza *et al.* 2004; Reimers *et al.* 2005), behaviour (Chen *et al.* 2005; Angelier *et al.* 2007) and physiology (Angelier *et al.* 2007). Because of this, analyses of senescence using individual life history data should look at senescence across the whole life history and not just one component of it. However, research to date has failed to achieve this.

Comparative senescence research has identified some intriguing patterns. One specific and frequently repeated claim is that birds senesce more slowly than mammals of an equivalent size (Finch 1994; Holmes & Austad 1995). Various hypotheses have been proposed to explain this including flight (Pomeroy 1990), brain size (Sacher 1978) and physiology (Holmes *et al.* 2001). Within birds and mammals rates of senescence have been proposed to fall along the 'speed of living' continuum (Ricklefs 1998), but whether this can explain between-group differences has never been explored. If biologists are to make any generalizations concerning mechanisms and processes associated with senescence it will be necessary for them to understand how it operates within and between groups of individuals.

In this study, we address these issues using data from 20 populations of vertebrates with a contrasting range of body sizes and life history (see Material and methods). First, we use detailed individual-based data from a range of species and do not rely on life tables. Second, we use these data to examine whether rates of senescence vary between mammals and birds, and attempt to explain previous findings. Third, we look at senescence in average individual fitness, rather than a single component of fitness. This approach yields fresh insight into the patterns of senescence in birds and mammals. By allowing us to disentangle the effects of the two major components of fitness, it allows us to assess the robustness of the more commonly used life-table approach where estimates of mortality are made with some strong assumptions (Caughley 1977). No previous comparisons have accounted for the slower life history of birds compared with mammals of a similar size. Here we use generation time as a measure of 'speed of living' to rectify this.

## MATERIAL AND METHODS

### Data sets

We used 20 detailed data sets on 19 species to investigate senescence in a range of terrestrial vertebrates with a range of contrasting life histories. Body size ranged from *c.* 10 g (collared flycatcher) to *c.* 85 kg (red deer), generation time [weighted mean age of reproducing females (Leslie 1966)] ranged from 1.7 years (great tits) to 18.8 years (fulmars; see Table S1). Our only criterion for selection was availability of data on annual survival and reproductive performance of individuals of known age. We did not filter data sets on length of study or sample size, although retrospectively it is apparent that such a criterion would have yet further strengthened our conclusions. Species included were Soay sheep *(Ovis aries),* bighorn sheep *(O. canadensis),* common tern *(Sterna hirundo),* roe deer *(Capreolus capreolus),* red deer *(Cervus elaphus),* Mauritius kestrel *(Falco punctatus),* Ural owl *(Strix uralensis),* barn owl *(Tyto alba),* collared flycatcher *(Ficedula albicollis),* mute swan *(Cygnus olor),* great tit *(Parus major),* northern fulmar *(Fulmarus glacialis),* southern fulmar *(Fulmarus glacialoides),* Siberian jay *(Perisoreus infaustus),* yellow bellied marmot *(Marmota flaviventris),* Alpine swift *(Apus melba),* Columbian ground squirrel *(Spermophilus columbianus),* house sparrow *(Passer domesticus)* and mandrill *(Mandrillus sphinx).* The mean length of the studies was 24.4 ± 2.6 years and the mean number of individuals in each study was 957 ± 376 individuals. Each study had data on annual survival and reproductive performance of individuals of known age from the female component of the population. These data were used to calculate each female's annual individual fitness contribution (IFC) for each year they were in the population (Coulson *et al.* 2006). IFC has two components – survival and recruitment. Thus, IFC of individual *i* for a year, *t*, is defined as the sum of recruitment and survival. The way recruitment was estimated varied

among populations. Where possible it was defined as the number of offspring produced between the census at time *t* and the census at time *t + 1* that were still alive at the census at time *t + 1*. Where this information (number alive at time *t + 1*) was not available, we used the number of weaned (mammals), or fledged (birds), offspring. The survival score was defined as 1 for the individual's survival, and 0 for the individual's death, between time *t* and *t + 1*.

Where individuals were not observed in year *t*, but were known to survive (because they were observed in the following year), a survival score of one was assigned for year *t*. However, this event did not often occur because the annual detection probability in the case studies we included here was especially high (typically > 0.85) so that accounting for possible variation in detection probability over time was not required (Catchpole *et al.* 2004). Because IFC is composed of survival and recruitment components, it is possible for individuals to achieve the same IFC score by different means. Thus, an individual could, for example, have a score of 1 by surviving, but leaving no recruits, or by not surviving but having 1 recruit.

## Modelling IFC as a function of age

We first modelled IFC as a function of age within each study using generalized additive models (GAM; Hastie & Tibshirani 1990). GAM are an extension of generalized linear models that allow nonparametric smoothers in addition to parametric terms. They are fitted using a local scoring algorithm which iteratively fits weighted additive models by backfitting, achieved by the iterative smoothing of partial residuals. The GAM approach was favoured over a logistic generalized linear modelling (GLM) approach because GAM do not make strong assumptions about the data distribution and are more sensitive to the distributional subtlety of the data. The GAM models were fitted using the 'gam' procedure from the 'gam' package (Hastie 2006). A Gaussian error distribution and spline smoothers, with default settings, were used throughout. Survival and recruitment were modelled in an analogous way. These GAM models enabled us to estimate the age at onset of senescence, which was assumed to be at the point where the fitness measure was predicted to be at its peak by the GAM.

## Estimating rates of senescence

Rates of senescence in the fitness measures (IFC, survival probability and recruitment) were estimated using least-squares linear regression models to describe the decline in the age-specific mean of the measure from the age at onset of senescence (as modelled by the GAM) to the maximum age for the population. The regression models were fitted through the mean values for each fitness measure (IFC, survival and recruitment) and the points were weighted by 1/variance (unless there was no variation, in which case an arbitrary, small weight of one-tenth of the smallest weight was used). The use of these weights ensures that the small number of individuals in the oldest age classes do not have an undue influence on the estimate of the slope. Thus, the senescence rate is defined as the decline in the age-specific mean, per unit time (year). We took the absolute value of the estimated slope of the regression line so that we could normalize the values using a logit-transformation (this transformation is not possible if the values are negative). Henceforth, we will refer to the logit-transformed absolute senescence rate simply as the senescence rate.

## Correlating senescence with life-history measures

Given a knowledge of the life history of the taxa included in the analyses, we were able to correlate, using robust linear regression (Salibian-Barrera 2006), the logit transformed absolute senescence rate with life-history indicators including: adult female body mass, class (Aves/Mammalia), generation time, age at primiparity, maximum fecundity (per year), and basal metabolic rates. Generation time was defined as the weighted mean age of reproducing females (sensu Leslie 1966). Body mass and basal metabolic rate data were obtained from the literature while the other parameters were calculated from the data sets directly. We searched for BMR estimates of the different species included in our comparative analysis of senescence in the literature (see Appendix S1). When the species-specific data were not available, we retained the BMR values reported for congeneric species with similar body mass because both phylogeny and body mass have been identified as the main sources of inter-specific variation in BMR (Cruz-Neto *et al.* 2001; White & Seymour 2003). We failed to find data for two species (*Apus melba* and *Mandrillus sphynx*, the BMR data for both genera were available only for species of very different body mass). Body mass data for females were again derived from various sources (see Appendix S1), where more than one measurement was available we took the average.

Senescence rate was logit transformed to normalize it and the other continuous variables were log-transformed for the same reason. Diagnostic plots of the models were checked to verify that these transformations improved the fit relative to untransformed data.

Recapture rates are known to be high in the studies used here (typically > 0.80). In addition, there is little evidence that, for adults, recapture rates vary with age for any vertebrate species (Catchpole *et al.* 2004). Nevertheless, we checked the impact that including individuals that did not have a known death age had on our estimates: we found that

the correlation between estimates using all available individuals and only those individuals with known age of death did not depart from unity (Fig. S1). We therefore conclude that varying capture probability is not a problem in this study.

All calculations and statistical modelling were carried out using R for Mac OSX Version 2.3.1 (R Development Core Team 2006). The regressions between senescence and life-history measures were conducted using the 'roblm' procedure (Salibian-Barrera 2006).

## RESULTS

### General patterns

Mean IFC was initially modelled as a function of age using generalized additive models (Hastie & Tibshirani 1990; Fig. 1a–c). Patterns of variation in IFC with age varied amongst species. However, the analyses revealed some striking qualitative similarities. For most species, IFC varied in a characteristically modal way with IFC initially increasing to a peak and then declining with age (Fig. 1a–c and supporting material Fig. S2). The similarity in shape of most of these curves suggests that senescence is widespread in wild vertebrates.

The species which showed a different (i.e. non-modal) pattern for the age-IFC relationship were the collared flycatcher, Ural owl and the northern fulmar. The first two of these showed markedly different demographies, with IFC declining steadily from the youngest age-classes rather than being modal. The collared flycatcher is a migratory passerine and females do not always return to the same breeding sites in each year, which may explain the decrease in IFC with age. We do not currently understand the observed pattern in Ural owls. The northern fulmar data set is a special case because it lacked data for the first 8 years of life due to the dispersal of individuals between fledging and recruitment to the population: we suspect it would be modal if data existed and data from the southern fulmar supports this.
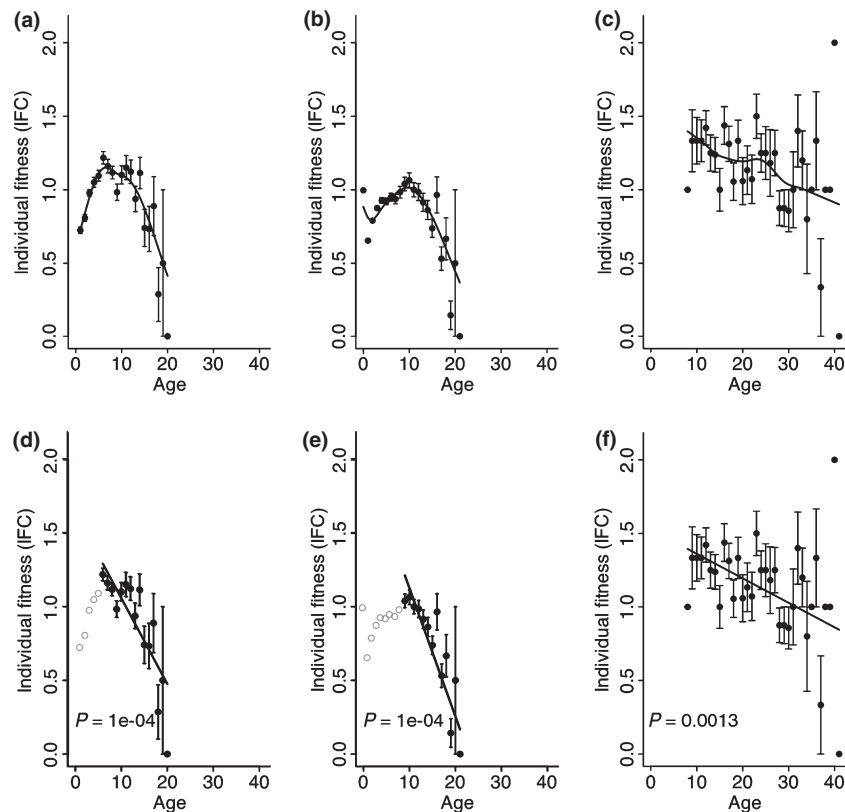


**Figure 1** Relationship between individual fitness contribution and age for three of the vertebrate species. The points represent the mean, and error bars represent the standard errors of the mean, at a particular age. The curved line in the top row (a–c) represents the fit from a generalized additive model (GAM) while the straight line in the bottom row (d–f) represents the fit from the linear model where black points are those included in the regression and white points were omitted because they occur before the peak in IFC. Species are: (a and d) bighorn sheep (Ram Mountain); (b and e) mute swan; (c and f) northern fulmar. See supporting material for equivalent graphs for all species (Figs. S2 and S3).

We next looked at the rate of senescence. We defined the senescence rate as the slope of the linear regression between mean IFC and age for all ages beyond the onset of senescence, which was defined as the peak of mean IFC (Fig. 1(d-f), and Fig. S3). The senescence rate was negative for 17 data sets and statistically significant (i.e. the slope of the IFC-age relationship for ages older than peak IFC was < 0 with a *P*-value of < 0.05) in 13 of the 20 data sets analysed (Table 1; one-tailed *t*-test: $t_{17} = 5.553$, $P < 0.001$). This is a relatively stringent statistical criterion as many species senesce rapidly (see below) which means the regressions are based on few points thus making the attainment of statistical significance at $P < 0.05$ challenging. Senescence was no more readily detected in mammal data sets than in bird data sets (binomial GLM: $z$-value = 0.711, $P = 0.477$). None of the life-history traits considered explained a significant amount of the variation in the probability of detection of senescence.

**Table 1** The rates of IFC-, survival-, and recruitment-senescence for the data sets used in this study

| Common name | Rate of IFC senescence | Rate of survival senescence | Rate of recruitment senescence |
| --- | --- | --- | --- |
| Alpine swift | 0.09* | 0.01* | 0.11* |
| Barn owl | 0.04 | 0.00 | – |
| Collared flycatcher | 0.13* | 0.07* | – |
| Great tit | 0.17* | 0.07* | 0.09* |
| Mauritius kestrel | 0.19* | 0.04* | 0.17* |
| Mute swan | 0.09* | 0.02* | 0.02* |
| Northern fulmar | 0.01* | 0.00 | 0.01* |
| Southern fulmar | 0.03* | 0.01* | 0.01 |
| Siberian jay | 0.02 | 0.10 | – |
| House sparrow | 0.07* | 0.03 | 0.09 |
| Common tern | 0.01 | 0.00 | – |
| Ural owl | 0.00 | 0.00 | – |
| Bighorn sheep (ram mountain) | 0.06* | 0.03* | 0.03* |
| Bighorn sheep (sheep river) | 0.02* | 0.01 | 0.09* |
| Mandrill | 0.01 | 0.00 | – |
| Yellow bellied marmot | – | 0.10* | 0.01 |
| Red deer | 0.07* | 0.04* | 0.02* |
| Roe deer | 0.13* | 0.04* | 0.11* |
| Soay sheep | 0.16* | 0.07* | 0.08* |
| Columbian ground squirrel | 0.10 | 0.03 | – |

Rates of senescence that are significantly different from 0 are indicated by asterisks. Statistically significant rates of senescence were detected in 13/20 data sets using IFC method, 11/20 data sets using survival data only, and 10/20 data sets using recruitment data only. –, cases when no evidence of senescence was detectable because the association with age and IFC, survival or recruitment was not unimodal.

For some species, it was not possible to estimate a senescence rate: for example, in the case of the yellow bellied marmot, the small sample sizes in older age classes resulted in a high variance in IFC, hampering the power of our test – we were unable to detect an age at onset of senescence. We were also unable to detect an age at onset of senescence in the common terns and this may be because they are long-lived in comparison to the length of the study (Nisbet *et al.* 2002). PIT-tag marking was begun in 1992 yet 20-year-old birds are known to successfully reproduce. Significant senescence was not detected in the mandrills because no individuals had reached sufficiently old age –the study has been running for 20 years, yet female mandrills can live significantly longer than this (Setchell *et al.* 2005).

Most previous research on the detection of senescence has focussed on actuarial senescence (Loison *et al.* 1999; Ericsson & Wallin 2001; Cameron & Siniff 2004). Our next analyses were devised to address whether analyses of IFC and its components – survival and recruitment – generated comparable results. We partitioned senescence into its fecundity and survival components by first fitting GAM through the mean age-specific survival and recruitment rates and second, fitting linear models between the mean age-specific survival and recruitment for ages beyond the onset of senescence (Table 1). Patterns varied across species. With the exception of the house sparrow all species showed survival senescence (Table 1; Fig. S4) although this was only statistically significant at $P < 0.05$ in 11 of the species, while 10 species showed significant recruitment senescence (Table 1; Fig. S5). Senescence was detected in IFC in the house sparrow but not in either component of fitness. The fact that survival senescence was not detected in the Sheep River bighorn sheep population conflicts with a previous report of survival senescence in this population (Jorgenson *et al.* 1997) because we did not correct for the effect of high cougar predation (Festa-Bianchet *et al.* 2006) and a pneumonia outbreak that occurred in the population in 1986.

## Life-history predictors and class

Our next set of analyses addressed whether life-history traits and class (birds or mammals) influenced rates of senescence. There were several associations between the senescence rate and life-history predictors (Table 2). In univariate analyses, faster senescence rates were significantly associated with earlier first reproduction, shorter generation lengths and high maximum fecundity. We tested for an effect of phylogenetic inertia using independent contrasts (Purvis & Rambaut 1995) and found that the effect sizes we estimated from non-phylogenetically corrected models were not influenced by phylogenetic effects (see Table S2). We therefore present the results of the non-phylogenetically

**Table 2** Robust linear regression models for logit senescence rate and Ln age at onset of senescence

| Response | Trait (logged) | Slope ± SEM | $R^2$ | d.f. | $t$-value | $P$-value |
|---|---|---|---|---|---|---|
| Logit rate | Age at primiparity | −1.273 ± 0.167 | 0.541 | 15 | −7.628 | < 0.001 |
| Logit rate | Generation time | −0.896 ± 0.212 | 0.394 | 15 | −4.223 | < 0.001 |
| Logit rate | Maximum fecundity | 0.852 ± 0.275 | 0.322 | 15 | 3.105 | 0.007 |
| Logit rate | Basal metabolic rate | −0.104 ± 0.083 | 0.066 | 13 | −1.255 | 0.232 |
| Age at onset | Age at primiparity | 0.598 ± 0.234 | 0.332 | 15 | 2.555 | 0.022 |
| Age at onset | Generation time | 0.760 ± 0.201 | 0.683 | 15 | 3.792 | 0.002 |
| Age at onset | Maximum fecundity | −0.490 ± 0.221 | 0.301 | 15 | −2.212 | 0.043 |
| Age at onset | Basal metabolic rate | 0.120 ± 0.057 | 0.303 | 13 | 2.100 | 0.056 |

Yellow bellied marmot, Ural owl and common tern were omitted from the analysis because it was not possible to determine either a rate or a start-point (see Figs S2 and S3). $R^2$-values are not calculable for the robust regression models. Therefore, we have used the $R^2$ from a standard regression model as an approximation.

**Table 3** Multivariate modelling of senescence

| Model | (a) Survival senescence | | (b) Recruitment senescence | | (c) Fitness senescence | | (d) Age at onset | |
|---|---|---|---|---|---|---|---|---|
| | AIC | Order | AIC | Order | AIC | Order | AIC | Order |
| GT + CLA + MET | 61.785 | 7 | 40.007 | 5 | 40.007 | 4 | 23.530 | 4 |
| CLA + MET | 59.583 | 3 | 43.362 | 2 | 43.362 | 5 | 26.736 | 5 |
| CLA + GT | 59.096 | 2 | 38.468 | 4 | 38.468 | 3 | 21.781 | 2 |
| MET + GT | 60.083 | 4 | 38.042 | 3 | 38.042 | 2 | 21.956 | 3 |
| MET | 60.481 | 5 | 44.474 | 6 | 44.474 | 6 | 30.205 | 6 |
| GT | 58.200 | 1 | 37.997 | 1 | 37.997 | 1 | 19.401 | 1 |
| CLA | 60.702 | 6 | 45.138 | 7 | 45.138 | 7 | 35.401 | 7 |

Summary information on the Akaike information criterion (AIC) values, and ordering of the models [from best (1) to worst (7)] that were fitted to explain (a) recruitment senescence, (b) survival senescence, (c) fitness senescence and (d) the age at onset of senescence. GT, generation time; CLA, class, MET, metabolic rate.

corrected models. The life-history parameters, we investigated are all correlated (Table S3), so which life-history predictor should we use? Generation time is the most appropriate single-number metric for describing a species' life history (Gaillard *et al.* 2005) because it encompasses all demographic rates. We therefore focus on generation time as our primary measure of life-history strategy on the fast–slow continuum in our analyses.

Having reported univariate correlations between rates of senescence and life-history descriptors, we next examined how generation time, metabolic rate and body size interact to influence senescence (Table 3). We analysed the relationship between basal metabolic rate (BMR), body mass and the senescence rate in a multiple regression framework. As expected, log-transformed body mass and log-transformed BMR were strongly correlated ($R^2 = 0.917$; $F_{1,16} = 178.7$; $P < 0.001$). It is, therefore, not surprising that they give qualitatively similar results when analysed in relation to senescence rates alongside other life-history covariates.

Mammals had a higher senescence rate than birds when BMR was used as a covariate (the logit senescence rate of

birds was −2.81 ± 0.34, while the rate for mammals was −1.55 ± 0.71). However, the significant effect of class disappeared with the addition of generation time: the coefficient for class was reduced from 1.26 to 0.27 (and the t-value from 1.77 to 0.33). In addition, the Akaike Information Criterion (AIC) values (Akaike 1973) showed that the best model was the one with generation time (GT) fitted as a main effect. Thus, although the other life-history variables may play a role in determining the rate of senescence, it is generation time that is most important.

The results using individual components of fitness (survival and recruitment) were qualitatively similar with the ordering of the models in terms of AIC being well correlated (Table 3). The analysis of the age at onset of senescence (the age where the GAM-modelled IFC peaked) was also revealing (Table 3). Again, we found that there were good correlations between the age at onset of senescence and the life-history related traits (Table 3) and that, again, generation time was the best predictor (robust linear model; slope = 0.760 ± 0.201; $t_{1,15} = 3.792$; $P = 0.002$). There was a positive correlation between the age at onset of senescence and the age at

primiparity (robust linear model: slope = 0.598 ± 0.234; $t_{1,15}$ = 2.555; $P$ = 0.022).

Multicollinearity has been cited as a potential concern in the analysis of ecological data (Graham 2003). One of the diagnostic features of problematic multicollinearity is grossly inflated variances surrounding the estimates of effect size. Comparisons of estimates ± standard error for the terms in the multiple regression model with those of the single variable models indicates that multicollinearity is not a problem here (Fig. S6).

## DISCUSSION

### General patterns

It has previously been suggested that detecting senescence would be difficult in wild animals because high levels of mortality would remove individuals from the population before they start to senesce (Kirkwood & Austad 2000). It is therefore striking that we detected senescence in such a wide range of species. Contrary to what one might expect given the reported lower adult mortality rates of birds compared with mammals of a similar size (Lack 1954; Holmes & Austad 1995) senescence was no more detectable in mammal data sets than in bird data sets. It was interesting that survival was the component of fitness where senescence was most likely to be detected – recruitment senescence was detected in all large mammal species examined but in none of the small mammals. The pattern was less clear in birds, with both the smallest bird in the analysis (the great tit) and the largest (the mute swan) showing recruitment senescence. Nevertheless, our results, which do not make assumptions about stable age structure and constant environments [in contrast to life tables (Gaillard *et al.* 1994)], suggest that previous research focussing on actuarial senescence (e.g. Nesse 1988; Promislow 1991) has provided an accurate picture of how widespread senescence is. However, in some cases, the choice of fitness component can influence the probability of detecting senescence, and the probability of detecting senescence in a quantitative character may depend on the association of the character with different components of fitness.

### Life-history and class

The results of the regression analysis of life-history predictors and Class suggest that the reason birds have a lower senescence rate than mammals (Lack 1954; Holmes & Austad 1995) is that they have a slower life history (i.e. generation time) than mammals for a given BMR. The results from body mass gave qualitatively similar results, which is not surprising given the strong correlation between

them (see above). These results suggest that birds have a relatively slower life history than mammals for a given metabolic rate or body size [see also (Finch 1994; Holmes & Austad 1995)]. For the first time, we show that the magnitude of senescence is to a large extent determined by the speed of the life history.

The fact that senescence was generally found in survival and recruitment suggests that, contrary to trade-off hypotheses, birds and mammals partition resources into both components of fitness, although in a different way. It also suggests that there may be constraints to the life history – we find no evidence that either birds or mammals consistently protect survival to the detriment of reproduction or visa versa – that could occur via a choice in resource allocation (Cichon & Kozlowski 2000). This implies that life-history variation, at least in these groups, is constrained such that survival and recruitment must both senesce.

Natal dispersal would cause an underestimate of senescence rate for recruitment and IFC. However, we are not aware of evidence for any associations between life history, or taxonomy, and natal dispersal rates. We therefore conclude that errors due to natal dispersal are unlikely to qualitatively affect the life-history correlations here.

### Age at onset of senescence

The positive correlation between the age at onset of senescence and age at primiparity lends support to Hamilton's prediction (Hamilton 1966) that senescence should begin at the age at primiparity. However, the slope was significantly lower than the expected allometric slope of 1, suggesting that the advantage of reproducing late (in terms of a delay in senescence) is relatively small for late breeding species. The suggestion that fitness should steadily decrease after sexual maturity (Williams 1957; Hamilton 1966) is not borne out by this study because, as Gaillard *et al.* (1994) found with survival probability, all three of the fitness measures we used continue to increase past the age of sexual maturity, before stabilizing and eventually declining. The qualitative similarity between the results for the analysis of the onset of senescence and the results for the senescence rates, and especially the strong correlation with generation time (Fig. 2) found for both measures, is striking. Together these results suggest that examining senescence through average individual fitness components provides a powerful approach to identifying generalities that may support or refute existing theory.

## CONCLUSIONS

Our main conclusion suggests that the onset and rate of senescence in reproduction and survival are tightly associated with generation time, so that senescence is embodied in
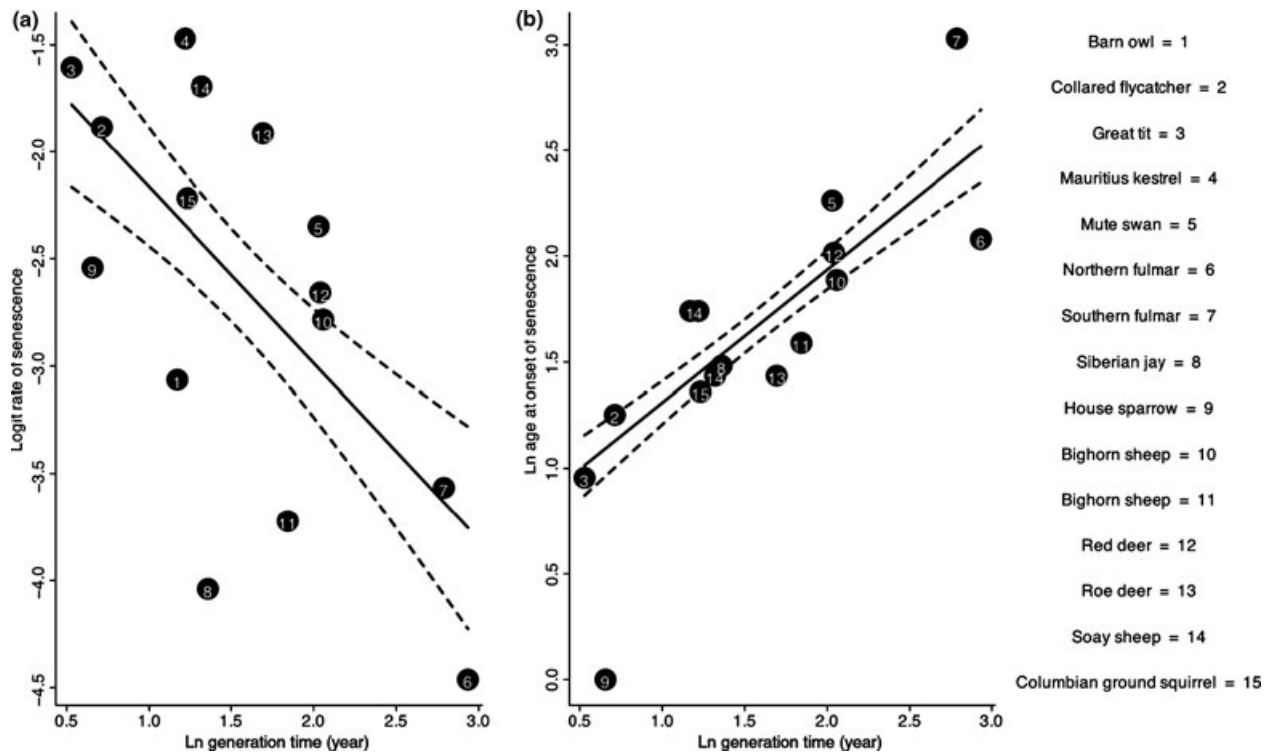
**Figure 2** Relationship between Ln generation time and (a) the logit senescence rate and (b) Ln age-at-onset of senescence. The solid lines represent the predictions from a robust linear model while the dashed lines represent the standard errors of the mean for the predictions. See Table 2 for a summary of the regression models.

the life history strategy of a given species, either bird or mammal. So, for a given pace of life, birds and mammals senesce at similar rates. As we did not report any opposite response to ageing between reproduction and survival, we suggest that focusing on one aspect of the life history – either survival or recruitment – can provide reliable evidence of overall senescence. However, because there is more to ageing than an increase in the probability of death, we suggest that a clearer picture of senescence can be obtained using IFC. We expect that further analyses of long-term individual-based time series of vertebrates, including mammalian taxonomic groups not included here such as carnivorous mammals and small rodents, will allow future studies to test the generality of the association between generation time and senescence rates we reported here, and will help identify processes associated with rates of senescence and factors that lead to variation in rates of senescence between life histories and individuals.

## REFERENCES

Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In: *Second International Symposium on Information Theory* (eds Petrov, B.N. & Csaki, F.). Akademiai Kiado, Budapest, Hungary, pp. 267–281.

Angelier, F., Weimerskirch, H., Dano, S. & Chastel, O. (2007). Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behav. Ecol. Sociobiol.*, 61, 611–621.

Bennett, P. & Owens, I. (2002). *Evolutionary Ecology of Birds – Life Histories, Mating Systems and Extinction*. OUP, Oxford.

Bronikowski, A.M., Alberts, S.C., Altmann, J., Packer, C., Carey, K.D. & Tatar, M. (2002). The aging baboon: comparative demography in a non-human primate. *Proc. Natl Acad. Sci. USA*, 99, 9591–9595.

Cailliet, G.M., Andrews, A.H., Burton, E.J., Watters, D.L., Kline, D.E. & Ferry-Graham, L.A. (2001). Age determination and validation studies of marine fishes: do deep-dwellers live longer? *Exp. Gerontol.*, 36, 739–764.

Calder, W.A. (1984). How long is a long-term study. *Auk*, 101, 893–894.

Cameron, M.F. & Siniff, D.B. (2004). Age-specific survival, abundance, and immigration rates of a Weddell seal (Leptonychotes weddellii) population in McMurdo Sound, Antarctica. *Can. J. Zool. Rev. Can. Zool.*, 82, 601–615.

Carranza, J., Alarcos, S., Sanchez-Prieto, C.B., Valencia, J. & Mateos, C. (2004). Disposable-soma senescence mediated by sexual selection in an ungulate. *Nature*, 432, 2215–2218.

Catchpole, E.A., Morgan, B.J.T. & Coulson, T. (2004). Conditional methodology for individual case history data. *J. R Stat. Soc. Ser. C Appl. Stat.*, 53, 123–131.

Caughley, G. (1977). *Analysis of Vertebrate Populations*. Wiley, New York.

Chen, G.H., Wang, Y.J., Wang, X.M., Zhou, J.N. & Liu, R.Y. (2005). Effect of aging on species-typical behaviors in senescence-accelerated mouse. *Physiol. Behav.*, 85, 536–545.

Cichon, M. & Kozlowski, J. (2000). Ageing and typical survivorship curves result from optimal resource allocation. *Evol. Ecol. Res.*, 2, 857–870.

Coulson, T., Benton, T.G., Lundberg, P., Dall, S.R.X., Kendall, B.E. & Gaillard, J.M. (2006). Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc. R. Soc. B Biol. Sci.*, 273, 547–555.

Cruz-Neto, A.P., Garland, T. & Abe, A.S. (2001). Diet, phylogeny, and basal metabolic rate in phyllostomid bats. *Zool. Anal. Complex Syst.*, 104, 49–58.

Ericsson, G. & Wallin, K. (2001). Age-specific moose (Alces alces) mortality in a predator-free environment: evidence for senescence in females. *Ecoscience*, 8, 157–163.

Ericsson, G., Wallin, K., Ball, J.P. & Broberg, M. (2001). Age-related reproductive effort and senescence in free-ranging moose, *Alces alces. Ecology*, 82, 1613–1620.

Festa-Bianchet, M., Coulson, T., Gaillard, J.M., Hogg, J.T. & Pelletier, F. (2006). Stochastic predation events and population persistence in bighorn sheep. *Proc. R Soc. B Biol. Sci.*, 273, 1537–1543.

Finch, C.E. (1994). *Longevity, Senescence, and the Genome*. University of Chicago Press, Chicago.

Finch, C.E. (1998). Variations in senescence and longevity include the possibility of negligible senescence. *J. Gerontol. A Biol. Sci. Med. Sci.*, 53, B235–B239.

Finch, C.E. & Austad, S.N. (2001). History and prospects: symposium on organisms with slow aging. *Exp. Gerontol.*, 36, 593–597.

Gaillard, J.M., Allaine, D., Pontier, D., Yoccoz, N.G. & Promislow, D.E.L. (1994). Senescence in natural-populations of mammals – a reanalysis. *Evolution*, 48, 509–516.

Gaillard, J.M., Loison, A., Festa-Bianchet, M., Yoccoz, N.G. & Solberg, E. (2003). Ecological correlates of life span in populations of large herbivorous mammals. *Popul. Dev. Rev.*, 29, 39–56.

Gaillard, J.M., Yoccoz, N.G., Lebreton, J.D., Bonenfant, C., Devillard, S., Loison, A. *et al.* (2005). Generation time: a reliable metric to measure life-history variation among mammalian populations. *Am. Nat.*, 166, 119–123.

Graham, M.H. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology*, 84, 2809–2815.

Hamilton, W. (1966). The moulding of senescence by natural selection. *J. Theor. Biol.*, 12, 12–45.

Hastie, T.J. (2006). *GAM: Generalized Additive Models*. R package version 0.97. Available at http://www.r-project.org.

Hastie, T.J. & Tibshirani, R.J. (1990). *Generalized Additive Models*. Chapman & Hall, London.

Holmes, D.J. & Austad, S.N. (1995). The evolution of avian senescence patterns – implications for understanding primary aging processes. *Am. Zool.*, 35, 307–317.

Holmes, D.J., Fluckiger, R. & Austad, S.N. (2001). Comparative biology of aging in birds: an update. *Exp. Gerontol.*, 36, 869–883.

Jorgenson, J.T., FestaBianchet, M., Gaillard, J.M. & Wishart, W.D. (1997). Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology*, 78, 1019–1032.

Kirkwood, T.B.L. & Austad, S.N. (2000). Why do we age? *Nature*, 408, 233–238.

Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.

Leslie, P.H. (1966). The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.),. *J. Anim. Ecol.*, 35, 291–301.

Loison, A., Festa-Bianchet, M., Gaillard, J.M., Jorgenson, J.T. & Jullien, J.M. (1999). Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology*, 80, 2539–2554.

Miller, J.K. (2001). Escaping senescence: demographic data from the three-toed box turtle (*Terrapene carolina triunguis*). *Exp. Gerontol.*, 36, 829–832.

Mysterud, A., Steinheim, G., Yoccoz, N.G., Holand, O. & Stenseth, N.C. (2002). Early onset of reproductive senescence in domestic sheep, *Ovis aries. Oikos*, 97, 177–183.

Mysterud, A., Solberg, E.J. & Yoccoz, N.G. (2005). Ageing and reproductive effort in male moose under variable levels of intrasexual competition. *J. Anim. Ecol.*, 74, 742–754.

Nesse, R.M. (1988). Life table tests of evolutionary – theories of senescence. *Exp. Gerontol.*, 23, 445–453.

Nisbet, I.C.T., Apanius, V. & Friar, M.S. (2002). Breeding performance of very old common terns. *J. Field Ornithol.*, 73, 117–124.

Pomeroy, D. (1990). Why fly – the possible benefits for lower mortality. *Biol. J. Linn. Soc.*, 40, 53–65.

Promislow, D.E.L. (1991). Senescence in natural-populations of mammals – a comparative-study. *Evolution*, 45, 1869–1887.

Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *CABIOS*, 11, 247–251.

R Development Core Team (2006) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reid, J.M., Bignal, E.M., Bignal, S., McCracken, D.I. & Monaghan, P. (2003). Age-specific reproductive performance in red-billed choughs Pyrrhocorax pyrrhocorax: patterns and processes in a natural population. *J. Anim. Ecol.*, 72, 765–776.

Reimers, E., Holmengen, N. & Mysterud, A. (2005). Life-history variation of wild reindeer (Rangifer tarandus) in the highly productive North Ottadalen region, Norway. *J. Zool.*, 265, 53–62.

Reznick, D. & Bryant, M. (2007). Comparative long-term mark-recapture studies of guppies (*Poecilia reticulata*): differences among high and low predation localities in growth and survival. *Ann. Zool. Fenn.*, 44, 152–160.

Reznick, D., Ghalambor, C. & Nunney, L. (2002). The evolution of senescence in fish. *Mech. Ageing Dev.*, 123, 773–789.

Reznick, D., Bryant, M. & Holmes, D. (2006). The evolution of senescence and post-reproductive lifespan in guppies (*Poecilia reticulata*). *PLoS Biol.*, 4, 136–143.

Ricklefs, R.E. (1998). Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *Am. Nat.*, 152, 24–44.

Sacher, G.A. (1978). Longevity and aging in vertebrate evolution. *Bioscience*, 28, 497–501.

Salibian-Barrera. (2006). *Roblm: MM-Regression Estimators*. R package version 0.6. Available at http://www.r-project.org.

Setchell, J., Charpentier, M. & Wickings, E. (2005). Sexual selection and reproductive careers in mandrills (*Mandrillus sphinx*). *Behav. Ecol. Sociobiol.*, 58, 474–485.

White, C.R. & Seymour, R.S. (2003). Mammalian basal metabolic rate is proportional to body mass (2/3). *Proc. Natl Acad. Sci. USA*, 100, 4046–4049.

Williams, G.C. (1957). Pleiotropy, natural selection, and the evolution of senescence. *Evolution*, 11, 398–411.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

**Appendix S1** Further details of sources for metabolic rate and body mass information.
**Table S1** Details of the data sets used in this study.
**Table S2** Comparison of slopes with and without phylogenetic correction.

**Table S3** Pearson correlation matrix for the life-history variables used in this study.
**Figure S1** Comparison of estimates made with and without excluding individuals lacking a known age at death.
**Figure S2** Senescence GAMs for all studies.
**Figure S3** Linear models of IFC for all studies.
**Figure S4** Linear models of survival senescence.
**Figure S5** Linear models of recruitment senescence.
**Figure S6** Comparisons of estimates from the multiple regression model with those of single variable models.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01187.x

Please note: Blackwell publishing is not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.