

Asynchrony of ageing among traits in a wild bird population

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Abstract

Ageing i.e. age-related changes in a trait, is a highly variable process. Studies have investigated variation in ageing among species and individuals, but little is yet understood about variation between traits. Evolutionary hypotheses argued that traits should age synchronously as selection should improve the trait that first senesces, therefore leading to trait synchrony. However, some past studies have demonstrated that traits do not senesce synchronously. We tested for the (a)synchrony of ageing across 13 reproductive, behavioural, physiological and morphological traits in a population of wild Seychelles warblers (*Acrocephalus sechellensis*). We modelled ageing trajectories for each trait and quantified synchrony between traits with similar ageing trajectory shapes by comparing the onset and rate of ageing and running bivariate models to quantify covariation between traits. We found that 7 traits exhibited ageing while 6 did not. Upon visual comparison of ageing trajectories, there were 3 groups of traits that shared ageing trajectories of the same shape. There was no support for synchronous ageing among any traits. Our study adds to growing evidence that ageing is asynchronous, and that the theory of synchronous ageing was erroneous. Our finding of senescence in direct fitness indices such as survival and reproductive but not in tarsus length gives weak support to newer evolutionary theories of asynchrony of ageing that traits more strongly associated with fitness age faster.

Keywords: Ageing, Senescence, Selection pressure, Seychelles Warbler

39 Introduction

40 Ageing is the age-related change of traits, while senescence is the deterioration of function
41 and fitness associated with advancing age due to the accumulation of cellular damage
42 (Monaghan et al., 2008; Kirkwood & Austad, 2000). Ageing is widespread and highly variable
43 across taxa, among populations and among individuals (Jones et al., 2014; Nussey et al.,
44 2013). Even within individuals, traits can differ in their ageing trajectories – the age of onset
45 and rate of senescence (Hayward et al., 2015). Differing within-individual ageing trajectories
46 between traits is known as asynchronous or mosaic ageing (Walker & Herndon, 2010). The
47 most notable example of asynchronous ageing is menopause (Ricklefs & Finch, 1995; Walker
48 & Herndon, 2010). To date, there is still limited knowledge explaining the evolution of
49 asynchrony of ageing. Further knowledge of patterns of differential ageing across traits is
50 needed to fully understand factors contributing to variation and mechanistic processes
51 underlying senescence. Through studying asynchronous ageing, we can better understand
52 how variation in ageing affects age structures in a population. This is, in turn, important as a
53 population's age structure hugely influences a population's demography, which drives
54 evolution (Charlesworth, 1994; Jones et al., 2014).

55 It was previously proposed that traits within an individual should senesce synchronously i.e.,
56 with the same age of senescence onset (Maynard Smith, 1962; Williams, 1957). The logic for
57 this was based on the idea that senescence was caused by generalized deterioration, not from
58 major changes in any one system (Williams, 1957). It was argued that selection should act to
59 improve (delay onset) the first senescing trait that impairs fitness and function, thus
60 synchronizing the onset and rate of senescence (Maynard Smith, 1962; Moorad & Ravindran,
61 2022; Williams, 1957). There are more recent interpretations of the verbal theory. Hayward
62 (2015) hypothesized that there was a critical threshold for each trait value which if crossed,

will result in death. Thus, selection will be strongest on traits closest to the threshold value (Hayward et al., 2015). In contrast, Gaillard and Lemaître (2017) suggested that selection pressures on traits should differ according to their early life survival, thus aligning ageing trajectories. Regardless of the importance of traits to survival and reproduction, these interpretations of the original idea indicate that since selection does not act on all traits uniformly, ageing should be synchronous. However, selection pressures should be trait-specific (Gaillard & Lemaître, 2017). It, therefore, seems logical that traits more closely linked to fitness should age later and slower. Similarly, weaker selection on traits less important to fitness components would lead to comparatively earlier ageing in those traits, since optimal resource allocation would delegate less resources to repair that trait, leading to asynchronous ageing (Rodríguez-Muñoz et al., 2019).

More recent theories on (a)synchrony of ageing have hypothesized that ageing trajectories (rate, onset and shape) are determined by the correlation between the trait and fitness (Boonekamp, Mulder & Verhulst, 2018; Briga & Verhulst, 2021). Traits contributing most to fitness are predicted to be under the strongest selection pressures, and thus have the slowest ageing rates since fitness costs from senescence of these traits will be the highest (Rodríguez-Muñoz et al., 2019). Counterintuitively, a theoretical study found that traits under strongest selection in early life have the fastest rate of decline of age-specific selection, which leads to faster ageing rates for these traits (Moorad & Ravindran, 2022). While the difference in selection pressure has been the most reviewed cause, genetic correlations among traits between and within age classes may also impact asynchrony of ageing, depending on the selection pressures on respective traits (Hayward et al., 2015; Moorad & Ravindran, 2022). Non-evolutionary factors may also contribute to apparent asynchrony of senescence. Traits

may vary in the extent of damage they accumulate from environmental factors over time, causing differing rates of senescence (Moorad & Ravindran, 2022).

There is considerable empirical work providing evidence for the asynchrony of ageing across traits (Moullec, Reichert & Bize, 2023) but, to the best of our knowledge, none supporting William's theory of synchronous senescence. Health and lifespan are commonly found uncoupled in humans and laboratory model organisms (Bansal et al., 2015; Christensen et al., 2009). Studies have also demonstrated that traits differ in onset and rate of ageing in various taxa under both wild and captive conditions, such as plants, *Caenorhabditis elegans*, mammals, birds and snakes (Briga & Verhulst, 2021; Boonekamp, Mulder & Verhulst, 2018; Cayuela et al., 2020; Cooper et al., 2021; Herndon et al., 2002; Hayward et al., 2015; Moullec, Reichert & Bize, 2023; Rodríguez et al., 2017). Most studies showed asynchrony of senescence in reproductive and survival traits (e.g. Cayuela et al., 2020; Cooper et al., 2021; Fay et al., 2021), while two found asynchrony in physiological traits (Briga & Verhulst, 2021; Boonekamp, Mulder & Verhulst, 2018). Additionally, Hayward et al (2015) studied whether traits within a functional grouping (e.g., reproductive, survival, behavioural) senesced more similarly in Soay Sheep (*Ovis aries*), but did not detect any synchrony of ageing. However, only a few studies have investigated the synchrony of senescence across a broad range of traits. Here we address this gap by testing asynchrony of senescence across a wide range of traits in a longitudinal wild bird population.

The Seychelles warbler (*Acrocephalus sechellensis*) (here after SW) population on Cousin Island provides an exceptional longitudinal study system. Owing to bi-annual sampling for c.a. 30 years, the lack of (im)migration (<0.1%) (Komdeur et al., 2004) and high mean resighting probability (Brouwer et al., 2010), we have comprehensive life history data for individuals from birth to death, accurate survival data, and longitudinal measures of numerous traits

(Sparks et al., 2022). Importantly, these repeated individual measures allow us to account for selective disappearance by statistically separating within- and between-individual trait variation (van de Pol & Verhulst, 2006). Given the lack of predators of adults on the island, there are low levels of adult extrinsic mortality contributing to annual mortality (van de Crommenacker et al., 2017). Consequently, the SW is relatively long-lived with a mean lifespan of *ca.* 4.4 years post fledgling (Figure s1), and a maximum of 19 years (Hammers & Brouwer, 2017).

The warblers exhibit actuarial, reproductive and telomere length senescence (Barrett et al., 2013; Hammers et al., 2013, 2015), and ageing in provisioning rate (Hammers et al., 2021). Reproductive senescence begins at 6 years for females without helpers (Hammers et al., 2012) and 7.8 years for males (Raj Pant et al., 2020) respectively. These features make this population an excellent study system for investigating (a)synchronous ageing. In this study, we aim to 1) quantify the ageing trajectories of 13 traits in the SW including morphological, physiological behavioural and fitness related traits, and 2) test for their (a)synchrony of ageing. This study will help us identify wider patterns in variation in ageing between traits, and enable us to further understand the drivers of evolution of asynchronous ageing.

127 Methods

128 *Study system*

129 Seychelles warblers are small (13-14cm) passerine birds endemic to the Seychelles. On Cousin
130 island (4.3315° S, 55.6620° E) the population of this facultatively cooperative breeder is
131 structured into *ca.* 115 territories each containing 1 breed group that consists of a dominant
132 breeding pair, offspring, and may include helper or non-helper subordinates (Richardson,
133 Burke & Komdeur, 2002). The Cousin population of c.a. 320 individuals has been monitored
134 more intensively since 1985 (Komdeur, 1992, Komdeur & Daan 2005). Since 1997, ~ 96% of
135 the individuals have been ringed with a unique British Trust for Ornithology (BTO) ring and
136 colour ring combination (Richardson et al., 2001; Sparks et al., 2022).

137 Fieldwork occurs twice a year, in the minor (Jan-Mar) and major (Jun-Oct) breeding seasons.
138 Individuals were captured using mistnets and playback. Unringed birds were ringed with a
139 British Trust for Ornithology metal ring and a unique colour ring combination. Ca 70 µl of
140 blood was collected via brachial venipuncture (Brown et al., 2021b). These blood samples
141 have previously been used for molecular sexing and genetic parentage assignment (Sparks et
142 al., 2022; Richardson et al., 2001), measuring malaria presence (Hammers et al., 2016), buffy
143 coat (Brouwer, 2007), telomere length (Barrett et al., 2013; Brown et al., 2022), haematocrit
144 (Brown et al., 2021b), oxidative stress and antioxidant capacity (van de Crommenacker et al.,
145 2011). Unringed individuals were aged according to eye colour (Komdeur, Bullock & Rands,
146 1991). Morphological traits were measured including body mass ($\pm$ 0.1g), wing length ($\pm$
147 0.1mm), right tarsus length ($\pm$ 0.1mm) and fat score (0-5).

148

149 Individual territories were visited every two weeks to carry out a population census. Survival
150 and social status were determined by observing colour-ringed birds and following the

dominant female of each territory for 15 minutes (Crommenacker, Komdeur & Richardson, 2011; van Boheemen et al., 2019). The dominant breeders were defined as the pair-bonded male and female in a territory according to interactions and nesting behaviour, while subordinates were defined as helpers or non-helpers depending on whether they displayed brooding or offspring provisioning (Richardson, Burke & Komdeur, 2002). If a nest was found in the territory, the nest was checked every week to determine nest stage (Komdeur & Daan, 2005). 60-90 min nest watches were carried out during the incubation and provisioning stage of nesting (van Boheemen et al., 2019). Provisioning rates of individuals were calculated as the total number of provisioning events per bird over the duration of the watch. Watches where more than 10% of provisions were by unidentified birds were excluded (van Boheemen et al., 2019).

Food (insect prey) abundance was measured according to Komdeur (1996), and mean insect availability was calculated from averaging insect abundance across the island in a year or season. Territory quality was defined as the insect availability within a territory (Hammers et al., 2015), and was calculated as $\alpha \cdot \sum(c_x i_x)$, where α is the territory size (hectares), c_x is the foliage cover for broad-leaved tree species x , and i_x is the mean monthly insect count for tree species x per unit leaf area dm^2 (Komdeur, 1992, 1996).

174 Table 1. Rationale for phenotypic trait inclusion in the analysis and predictions of their ageing
175 trajectory.

Trait	Rationale for inclusion	Predicted (direction)
Body mass	Body mass is the most simple and common indicator of body condition (Labocha & Hayes, 2012). Many studies attributed body mass ageing to senescence in function and condition (Nussey et al., 2011).	Declines
Wing length	Indicator of flight ability and feather quality, may affect a bird's foraging ability and thermoregulation (Kiat & Sapir, 2018).	Declines
Right tarsus	Treated as a control of ageing trajectory as tarsus length is developmentally determined and not known to senesce (Tjørve & Tjørve, 2010).	No change
Fat score	Fat score indicates energy reserves and condition in birds (Labocha & Hayes, 2012).	Declines
Oxidative stress (ROMs)	Damages biological macromolecules which may cause accelerated ageing and degenerative diseases (Beckman & Ames, 1999; Finkel & Holbrook, 2000).	Increases
Antioxidant capacity (OXYs)	Buffers against oxidative stress which may help individuals avoid the harmful consequences of oxidative stress (Felton & Summers, 1995).	Declines
Haematocrit	Reflects haemoglobin concentration. An indicator of aerobic capacity, which is important in endurance and performance in SW (Brown et al., 2021b).	Declines
Buffy coat	Refers to the white blood cell layer after centrifugation. Measure of leucocyte content in blood, which may be indicator of immune function and survival (Mondragão-Rodrigues & Macedo, 2023; Møller & Saino, 2004).	Declines
Malaria presence	Potential indicator of immune response against infection in SW (Hammers et al., 2016).	Decreases then increases
Telomere length	Biomarker of senescence that declines with age and predicts survival in SW (Barrett et al., 2013)	Declines
Provisioning rate	Declines in female, but not male SWs, with age and offspring first year survival declines with parent age (Hammers et al., 2021)	Increases then decreases
Annual reproductive success (ARS)	Senesces in SW (Hammers et al., 2012; Raj Pant et al., 2020).	Increases then declines
Annual survival	Senesces in the SW (Hammers et al., 2013).	Declines after age 6

176 *Measurement of physiological and fitness traits:*

177 *Oxidative stress (ROMs) and Antioxidant capacity (OXYs):* Undertaken as part of a previous
178 study (Brown et al., 2021b; van de Crommenacker et al., 2011). Plasma from each blood
179 sample was separated by centrifugation (9889 *g* for 8 minutes) and frozen. The oxidative
180 damage and antioxidant compounds were quantified using d-ROMs test kit (Diacron,
181 Grosseto, Italy) and OXY-Adsorbent test kits (Diacron) respectively (van de Crommenacker et
182 al., 2011). Full assay details can be found in van de Crommenacker et al., (2011b). ROMs were
183 calculated as the sum of oxidative damage compounds while OXYs were calculated as the sum
184 of antioxidant compounds.

185 *Haematocrit and Buffy coat:* Within ca. 3 hours of bleeding, the heparinized capillary tube
186 was centrifuged for 8 minutes at 6000 *g* (Brown et al., 2021b). Haematocrit was measured as
187 the proportion of erythrocytes to the whole blood volume in the capillary tube with calipers
188 to the nearest 0.01mm. Buffy coat was measured under a 10x magnifying glass as the
189 proportion of leukocytes and platelets to the whole blood volume.

190 *Malaria:* Blood samples were tested for the presence or absence of haemosporidian parasite
191 infection using a nested PCR technique (Hellgren, Waldenström & Bensch, 2004; Hammers et
192 al., 2016) run twice per sample. Individuals with conflicting test results from the test
193 consensus were removed from the dataset. 87% of samples had consistent test results across
194 both PCR runs (Fairfield et al., 2016).

195 *Telomere length:* We used the telomere dataset from Spurgin et al (2018) for samples
196 collected between 1995-2014. A qPCR method was used to estimate Relative Telomere
197 Length (RTL; Barrett et al., 2013). Within and between plate repeatability for all samples
198 screened over different years was 0.74 (95% CI = 0.74 - 0.75) and 0.68 (95% CI = 0.65 - 0.70)

respectively (Sparks et al., 2022). There were no detected blood sample storage time effects on telomere length (Spurgin et al., 2018).

Annual reproductive success (ARS): Blood samples were genotyped and parentage was assigned using package *MasterBayes 2.52*, from which a pedigree was constructed (Hadfield, Richardson & Burke, 2006). Details of the parentage analysis and pedigree construction can be found in Sparks et al (2022). ARS was quantified as the number of offspring in the genetic pedigree assigned to a parent with $\geq 80\%$ genetic confidence in a year (Sparks et al., 2022).

Survival: Given the high resighting probabilities in this population (of 0.92 ± 0.02 for individuals ≤ 2 years and 0.98 ± 0.01 for older individuals) (Brouwer et al., 2010), birds not seen for two consecutive field seasons were assumed dead unless resighted thereafter.

Statistical analysis

Statistical analyses were conducted in R 4.2.2 (R development Core Team 2022). We analysed ageing trajectories of 13 traits (Table 1) with data collected between the years 1981-2022, using mixed Generalised Additive Models (GAMs) using the package *mgcv 1.9* (Wood, 2017). GAMs allowed us to fit non-parametric smoothing terms between a trait and age, which were more suitable as it allowed for combined testing of gradual and threshold changes with age due to its flexible nature, as observed e.g. in body mass and metabolism (Nussey et al., 2011, Douhard et al., 2017, Briga et al., 2019, Briga et al., 2021). All models were fitted with a smoothing term for age (main effect). Selective appearance and/or disappearance can obscure apparent senescence patterns if the relationship between trait values in older age and lifespan are stronger in certain traits, and the between- and within-individual differences are not distinguished (van de Pol & Verhulst, 2006). We controlled for selective disappearance by fitting lifespan as fixed effect and bird identity as random effect (van de Pol & Verhulst,

2006). Age of first and last reproduction was fitted in the ARS trait model to account for selective disappearance. Lifespan was not fitted in the survival model as individuals only die once. We fitted annual insect abundance, social status (dominant or subordinate) and sex as control variables for all models. Food abundance is an indicator of available resources on the island and energy acquisition in the warblers (Hammers et al., 2012), and social status may affect a bird's energy allocation and usage. Individual differences in the availability and allocation of these resources may influence senescence trajectories (Kirkwood, 1977). Sex was included to account for possible sex differences in ageing (Brouwer et al., 2006). We compared model fit for each trait using Akaike's Information Criterion (AIC) to determine whether an age by sex interaction should be fitted. The model with the lowest AIC was considered as the best fit ($\Delta AIC < 4$) (Burnham, Anderson & Huyvaert, 2011). Tarsus length was fitted in the body mass and wing length trait models to control for body size. Birth cohort was fitted as a random effect in all models. For all morphological traits, haematocrit, buffy coat, and provisioning rate models, observer identity was fitted as a random effect. Technician identity was fitted as a random effect for RTL. All response variables with a Gaussian distribution were z-transformed. All models were checked for convergence and tested for concurvity with the *mgcv* package. The full results of the ageing models, including all fixed and random effects for each trait can be found in the supplementary material (Tables S1-S13).

As GAMs do not produce interpretable or meaningful effect sizes or p values for smooth terms, we calculated the first order derivatives of the age smooth term to determine which traits demonstrated ageing. Positive derivative values indicate a positive slope, suggesting improvements with age, vice versa for negative derivative values, while value of 0 indicates maxima or minima. Traits reach maximum values when their first-order derivative is zero.

Hence, we defined a trait's ageing as statistically significant when the upper 95% confidence of the derivative crossed zero.

There are currently three main approaches to quantifying asynchrony of ageing. Hayward et al's (2015) quantitative method works well to quantify features of ageing trajectories. However, by normalizing age-specific means, this approach may miss variation in ageing rates. Cooper et al's (2021) quantitative approach also identifies whether ageing onset and ageing rates are determined by biologically meaningful trait values. However, this method may find asynchrony of senescence in traits with differing age-specific variances that have the same age-specific means. Results may therefore differ according to the methodology used to detect asynchrony of senescence or compare ageing rates (Moorad & Ravindran, 2022). The two methods outlined above both make indirect comparisons of ageing trajectories which do not estimate synchrony of ageing. Differently, Briga and Verhulst (2021) directly quantifies synchrony of ageing by estimating within-individual correlation of ageing rates between traits.

We tested for asynchrony of ageing according to the methods outlined in Briga and Verhulst (2021). Trait ageing trajectories were visually compared first. If trait GAMs showed different ageing trajectory shapes between traits, they were considered to have asynchronous ageing. If ageing traits showed visually similar ageing trajectory shapes, a bivariate model was run between the traits to estimate the covariance between the two traits to compare within individual ageing rates (Briga & Verhulst, 2021).

Visual comparison produced three groups of traits with similar ageing trajectories. We restricted the bivariate models to traits with age-related declines, which resulted in two groups. Bivariate models were run on traits in group 1 (traits ageing quadratically) and group

2 (traits ageing linearly). The package *mcgv* was used for models with only Gaussian responses, while *MCMCglmm* 2.36 was used for the models including non-Gaussian responses. Bivariate models were not run between survival and the other two traits in group 1 as comparing a within-individual ageing trajectory (body mass and provisioning rate) and a between-individual ageing trajectory (survival) is not biologically meaningful. Bivariate models from group 2 containing buffy coat (F) as one of the responses can only be compared among female warblers since the males showed a non-linear ageing trajectory and bivariate models require data from the same individual at the same age for both traits to estimate a covariance. We used uninformative priors with an Inverse Wishart distribution in the *MCMCglmm* bivariate models. For each *MCMCglmm* model, we checked convergence by ensuring autocorrelation was lower than 0.1, visual inspection of posterior trace plots and effective sample size being greater than 1000. The table of the full model and variables included can be found in the supplementary material (Tables S14-17).

Results

Ageing trajectories

Seven out of thirteen traits, one of which was sex-specific, showed age-related declines: Body mass, fat score, telomere length, buffy coat in females, provisioning rate, annual reproductive success (ARS) and annual survival probability (Figure 1 & 2 a, d, h, j, l, m, n respectively; Tables S1, S4, S8, S10, S11, S12 & S13 respectively). Body mass and provisioning rate showed a quadratic relationship with age, initially increasing then decreasing post-peak from c.a. 8.5 and 6 years, respectively (Fig. 1 & 2 a, l ; Table 2). Similarly, annual survival probability displayed an increase until the age of significant decline – 8.5 years (Fig 1 & 2 n; Table 2). Fat score and telomere length for both sexes, and buffy coat in females decreased linearly with

age (Figures 1 & 2 d, h, j, respectively; Table 2). ARS increased until age 3 then remains roughly constant from age 3 to 11, except displaying a small significant decrease at age 7, followed by a plateau, then a larger significant decrease after age 11 (Fig 1 & 2 m; Table 2).

Wing length and oxidative stress did not show statistically significant ageing, but showed a slight quadratic relationship (Figures 1 & 2b,e). Antioxidant capacity and haematocrit also did not show significant ageing, and had a linear relationship. As expected, tarsus length is developmentally determined, thus was constant throughout life (Fig 1 & 2 c). Buffy coat in males, and malaria presence showed an initial decrease (until ages 3 and 5, respectively) and then levelled out (Fig 1 & 2 i and j), thus there was no age-related decline as both traits remained steady with age after the initial decline.

Table 2. Age of onset of decline for seven phenotypic traits in the Seychelles warbler population on Cousin island (dates differ per dataset, minimum date 1981, maximum date 2022) based on the derivatives of the curves obtained from the Generalized Additive Models for each trait with significant ageing trajectories (Fig 2 a, d, h, k, l, m & n). The mean of the derivative of the slope indicates the estimated population mean age of ageing. The upper and lower 95% confidence intervals where the derivative of the slope crosses 0 estimates the variation around the mean age of ageing. NA indicates instances where the onset of ageing is not a biologically meaningful age, as the trait declines from early-life, thus onset will be negative. F= female. RTL = relative telomere length.

Trait mean & 95% CI	Body mass	Fat score	RTL	Provisioning rate	Buffy coat F	Survival	Annual Reproductive Success
Upper	8.5	0	0	6	0	8.5	7 and 11
Mean	4.7	NA	NA	NA	NA	6.2	6 and 10
Lower	1	NA	NA	NA	NA	3.8	2.8

311 Of the traits that showed significant age-related changes, three different age-specific
312 trajectories were observed. Group 1: Body mass, provisioning rate and annual survival had a
313 quadratic ageing trajectory (Fig 2a, l and n). Group 2: Buffy coat (Female), fat score and
314 relative telomere length showed a linear decline (Fig 2d, h, and k). Group 3: Male buffy coat,
315 and malaria prevalence decreased in early life and then stabilized in later life (Fig 2i & j).
316 Annual reproductive success (ARS) did not show a similar age-trajectory with any other
317 traits (i.e. ages asynchronously to other traits, Fig 2m). The traits within these 'similar
318 trajectory' groups do not belong to the same functional grouping (e.g., morphological,
319 physiological, fitness traits) except for group 3 being immune traits.

320

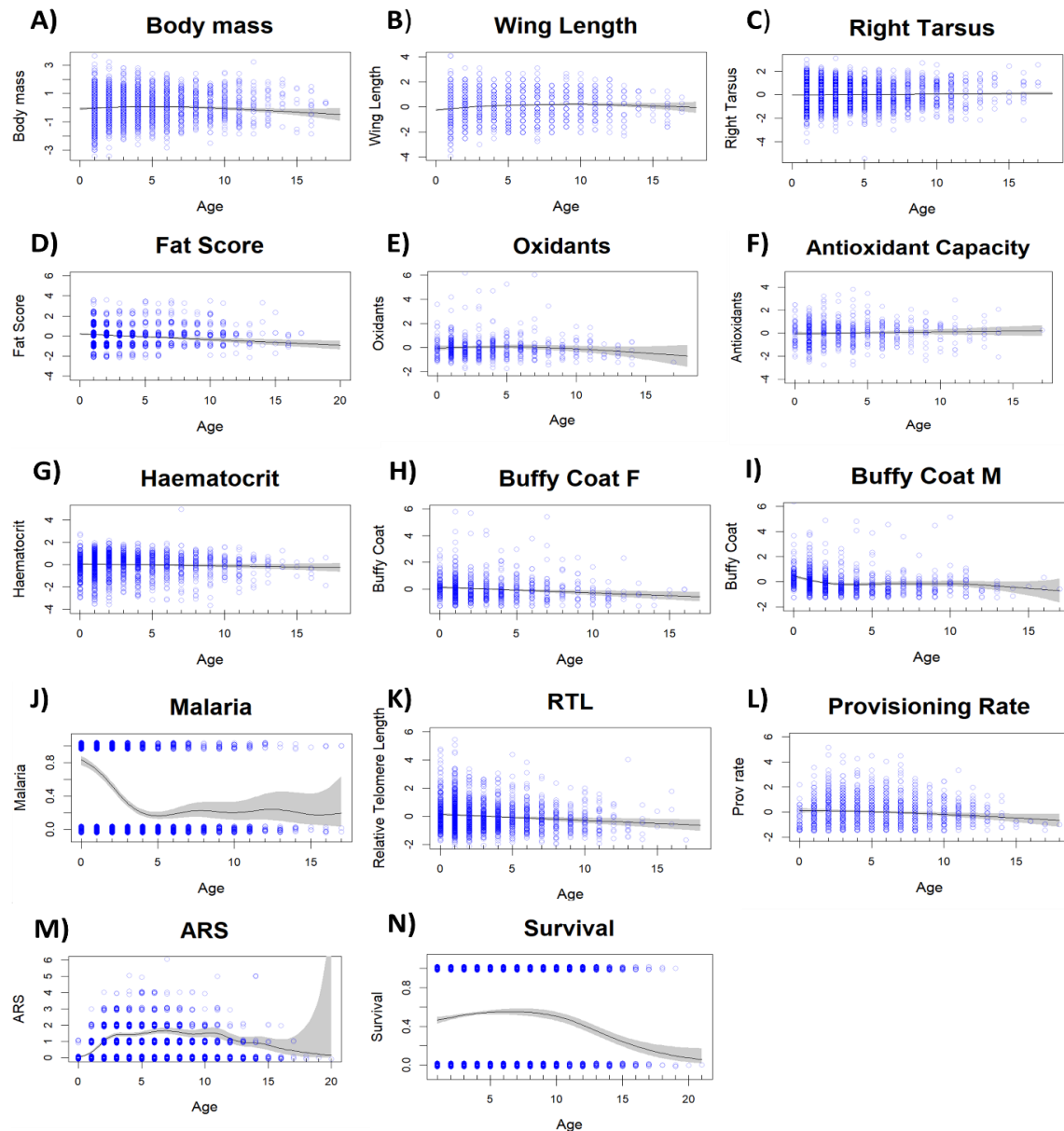


Figure 1. The age-specific trajectories of 13 phenotypic traits in individuals the Seychelles warbler population of Cousin Island (dates differ per dataset, minimum date 1981, maximum date 2022) identified through Generalized Additive Models. The x-axis is age in years, and the y-axis is the trait value; all traits, except for annual reproductive success, survival and malaria, are z-transformed. The solid black line depicts the model-predicted curve and the grey shaded areas depict the standard error. Blue points are raw data points. RTL = relative telomere length. ARS = Annual Reproductive Success. For buffy coat (Fig 1h & i), F indicates female, M indicates male.

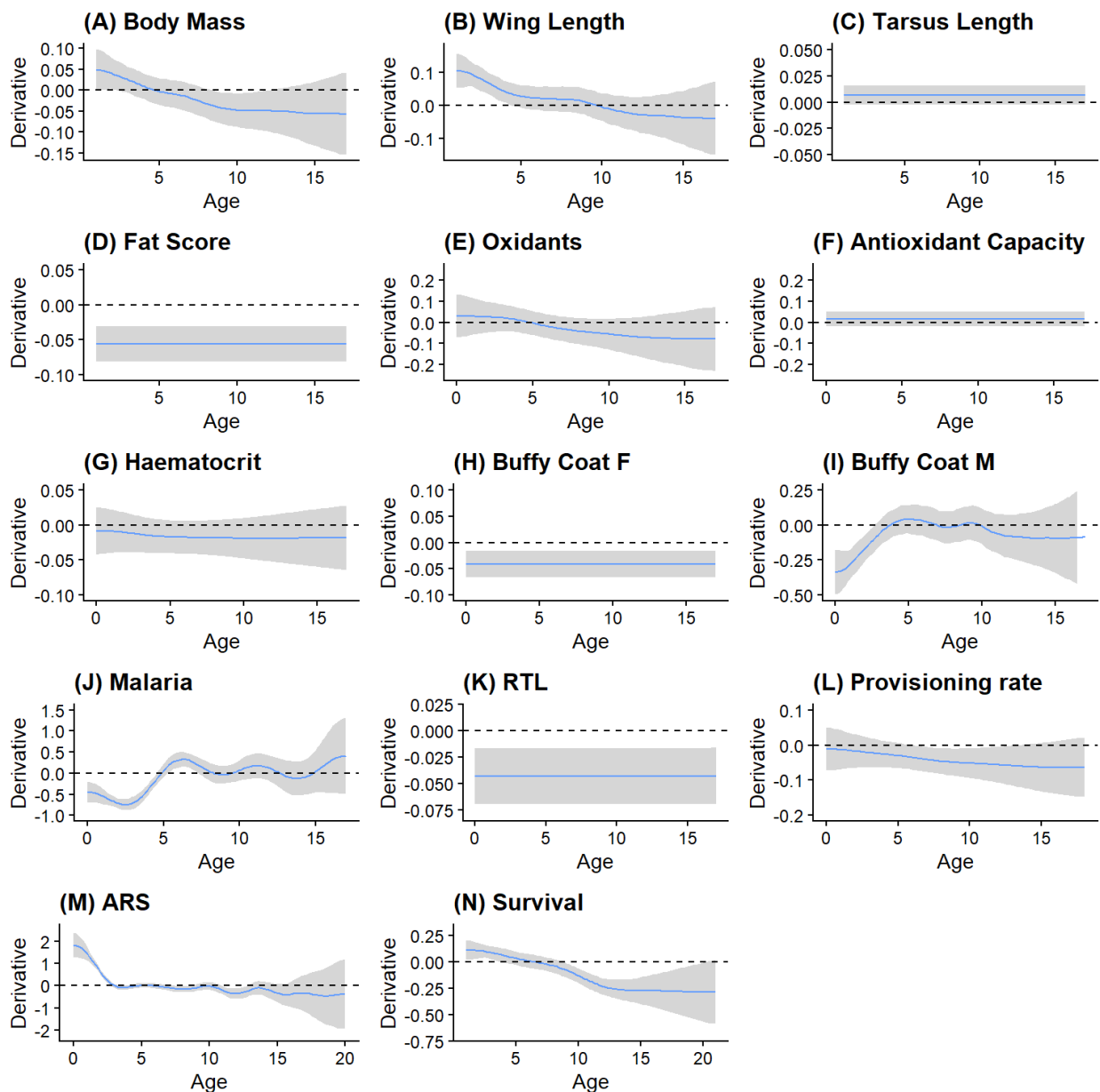


Figure 2. The ageing rates of the 13 phenotypic traits in individuals of the Seychelles warbler population of Cousin Island (dates differ per dataset, minimum date 1981, maximum date 2022). The rate of ageing of each trait was calculated by obtaining first-order derivatives (solid blue line) of the model-predicted curve of the age term in each Generalized Additive Model. On the y-axis is the derivative of the curve, with age (years) on the x-axis. The solid blue line depicts the ageing rate and the grey shaded areas around the blue line depict the 95% confidence intervals. A derivative value above 0 indicates the slope is positive, and vice versa.

Traits with 95% upper confidence intervals that cross the dotted zero line demonstrate significant trait ageing. This includes A) body mass, D) fat score, H) female buffy coat, K) RTL (relative telomere length), L) Provisioning rate, M) ARS (annual reproductive success) and N) survival.

Within individual covariance of senescence rate between traits

Only traits in group 1 and group 2 showed age-related declines. Thus bivariate models were run on pairs of traits within groups 1 and 2. Survival was not included as a response variable in any of the group 1 bivariate models as survival ageing is a between individual estimate. The degree of synchrony of ageing between traits was low ($<|0.13|$). Most trait pairs show a negative covariance with the exception of RTL and buffy coat F (Table 3 a & b). The full model output for the bivariate models are in the supplementary material (S14-17)

Table 3. Covariances between pairs of SW traits that visually had similar ageing trajectories estimated from bivariate Generalized Additive Models and bivariate MCMCglmm models. Table 3a contains covariances of traits ageing with a negative quadratic pattern (Group 1). Table 3b contains covariances of traits that showed a linear decline with age (Group 2). Results for bivariate models containing buffy coat are only pairwise comparisons between female SW individuals, as buffy coat only declined in later-life for females. The covariances are reported on the latent scale. RTL = relative telomere length

359 3a

Trait	Body Mass	Provisioning rate
Body mass	---	-0.03178245
Provisioning rate	---	---

3b

Trait	Fat Score	Buffy Coat F	RTL
Fat Score	---	-0.1283	-0.016682
Buffy Coat F	---	---	0.01222042
RTL	---	---	---

360

361 Discussion

362 We quantified ageing trajectories, and tested for asynchrony of ageing, across 13 phenotypic
363 traits in the Seychelles warbler. We found age-related declines in seven traits: body mass, fat
364 score, buffy coat (female), relative telomere length, provisioning rate, ARS and annual survival
365 probability. There were three groups of traits sharing similar ageing trajectories; 1) Quadratic
366 with age: Body mass, provisioning rate and survival, 2) Linear decline with age: Buffy coat
367 (female), fat score and telomere length, 3) Improves in early life and stabilizes in late life:
368 Buffy coat (male) and malaria infection. However, the onset of ageing often differed between
369 those traits that aged (Table 2), and the degree of synchrony of ageing was low between traits
370 that shared similar trajectories (Tables 3a & b). Additionally, there were sex differences in
371 asynchrony of ageing due to sex differences in ageing of buffy coat (white blood cell
372 abundance). Among the groupings of traits that shared similar trajectories, there was no
373 pattern of similarities in ageing in functional grouping (morphological, physiological, immune,
374 behavioural, fitness traits) aside from group 3 where both traits were immune traits. Overall,
375 our study showed asynchrony of ageing in the SW.

376

377 *Phenotypic trait ageing in the Seychelles Warbler*

378 *i. Morphological trait ageing (Body mass, wing length, Right tarsus length, fat score)*

Ageing of morphological traits has not been previously studied in the SW, but the present study revealed key patterns. First, the observed decline of both body mass (accounting for tarsus length) and fat score indicated body condition ageing in the SW. Most studies on body mass senescence in other species support our findings (Beirne, Delahay & Young, 2015; Douhard et al., 2017; Nussey et al., 2011; Kroeger et al., 2018), while a couple do not (Hämäläinen et al., 2014; Moullec, Reichert & Bize, 2023). In contrast, the only study (to our knowledge) using fat score did not report ageing (Milenkaya et al., 2013). Wing length did not show significant ageing in SW, unlike previous findings in other species (Piliczewski & Wysocki, 2018; Moullec, Reichert & Bize, 2023; Šliž, 2022). SW often prefer to hop or do short flights for foraging and do not disperse across islands (Komdeur et al., 2004), thus rely less on flight ability. This potentially results in negligible trade-offs between feather quality and other traits if the cost to maintain feather quality is lower than expected (Buttemer, Addison & Klasing, 2020; Kiat & Sapir, 2018), explaining the lack of ageing. Overall, our findings suggested body condition ageing in the warblers, but not ageing in other morphological traits.

ii. Physiological trait ageing (Oxidative stress, antioxidant capacity, telomere length, haematocrit)

Telomere length was the only physiological trait that showed ageing, which aligns with previous studies in the SW (Barrett et al., 2013; Brown et al., 2022), and many other species (Le Clercq et al., 2023; Remot et al., 2022). Additionally, telomere length senescences in the SW as short telomere length and higher telomere attrition rates predicted survival in the SW (Barrett et al., 2013; Brown et al., 2022).

The non-significant ageing of oxidative stress traits, i.e. ROMs and OXYs is consistent with past studies finding oxidative stress markers to be stable with age (Hindle et al., 2010; Hübner-Woźniak et al., 2011; Nussey et al., 2009), although another study found the opposite

(Williams, Roberts & Elekonich, 2008). As oxidative stress had the shortest timeframe of data collection (2006-2013), a lack of older individuals (age > 6, N=114) may have led to a reduced power to detect ageing.

Although non-significant, the trend of haematocrit decreasing with age found in the present study aligned with previous research on this species, which found a significant decline with age (Brown et al., 2021). Studies in other species also found age-related declines in haematocrit content (Elliott et al., 2015; Hickmott et al., 2024; Goldberg et al., 2023). Since haematocrit does not predict survival in later life in the SW (Brown et al., 2021b), it likely does not senesce in this species. Overall, there was therefore little evidence of ageing in physiological traits in SW aside from RTL.

iii. Immune trait ageing (Malaria presence, Buffy coat)

There was no evidence for age-related declines in immune traits in male SW. Although previously thought to be attributed to selective disappearance (van Oers et al., 2010), the results from the present study and Hammers et al (2016) refuted this. This suggests SW maintain immune function in late life (Hammers et al., 2015). The lack of ageing in male buffy coat that our results showed further supports the lack of immune trait ageing in male warblers, which differed to that found in the Soay sheep (Froy et al., 2019). We observed sex differences in ageing of buffy coat (Figure 2h & i). SW are hypothesized to show no differences in energy expenditure between sexes since they exhibit biparental care and share costs of breeding (Williams, 1957; Hammers et al., 2013; Komdeur, 1994, van Boheemen et al., 2021), which should suggest no sex differences in ageing. Coupled with no sex differences in lifespan in the SW, our results were not expected. Nonetheless, studies in other species often found sex differences in the ageing of immune parameters (Hickmott et al., 2024; Klein & Flanagan, 2016; van Lieshout et al., 2020). More generally, the evidence for immunosenescence / ageing

is mixed; with some finding ageing in immune traits (Cheynel et al., 2017; Peters et al., 2019) and others not (Bichet et al., 2022; Peters et al., 2019; Roast et al., 2022). This may be due to studies failing to quantify within-individual change (Peters et al., 2019). Although there is currently no consensus in wider immune trait ageing research, potential differences in selection pressure between sexes (Metcalf, Roth & Graham, 2020) may explain the observed sex differences in immune function senescence in SW, leading to sex differences in asynchrony of senescence.

iv. Behavioural trait ageing (Provisioning rate)

The ageing trajectory of provisioning rate identified in the current study was similar to previous results in the SW, showing a decline in provisioning rate with age (Hammers et al., 2021). This aligns with results in another bird species (Krist et al., 2024), but contrasted other studies (Cansse et al., 2024; Wilcoxon, Boughton & Schoech, 2010). In terms of implications for senescence of provisioning rate in the SW, although offspring first-year survival declines with breeder age in the SW (Hammers et al., 2021), it remains unclear whether this results specifically from age-related declines in provisioning rate, as breeder age may also affect offspring survival through factors like egg quality (Beamonte-Barrientos et al., 2010).

v. Fitness related trait ageing (ARS and survival).

Finding senescence in annual reproductive success (ARS) and survival in the SW was expected based on previous results in SW (Hammers et al 2015) and studies across a range of taxa (Jones et al., 2014; Lemaître & Gaillard, 2017; Tidière et al., 2018; Torres, Drummond & Velando, 2011; Vágási et al., 2021; Vrtílek, Žák & Reichard, 2022). The stability in ARS may partially be due to SW producing single-egg clutches in 91% of breeding attempts (Komdeur, 1996). Only 3% of SW had an ARS larger than two in our data, resulting in little variation in the cost of reproduction between breeders. Differences in estimated onset of reproductive senescence

(age 11 here vs. 6 for females and 7.7 for males in earlier studies: Hammers et al., 2012; Raj Pant et al., 2020), likely stem from dataset differences, as prior work excluded significant amounts of reproductive data gained in minor seasons and subordinates (Hammers et al 2012).

Survival probability ageing in our study shared the same trajectory shape with a previous SW study (Hammers et al., 2015), and is consistent with previous research across various taxa (Cooper et al., 2021; Hammers et al., 2015; Gaillard & Lemaître, 2020; Jones et al., 2014; Nussey et al., 2013). Unfortunately, survival senescence is a cross-sectional measure, since it is not possible to separate within and between individual heterogeneity in survival probability with a linear mixed model or GAM. To quantify survival senescence accurately, different approaches such as capture-mark-recapture models are required to account for individual variation in survival probability (Gimenez, Cam & Gaillard, 2018). Nonetheless, survival senescence is very well documented across taxa (Jones et al., 2014; Nussey et al., 2013). Overall, the ageing trajectories studied in the warbler largely aligned with past findings, demonstrating that the SW represents an excellent system to study ageing in the wild.

Asynchrony of senescence

The asynchronous ageing of traits in the SW demonstrate that the original verbal theories on synchronous ageing by Williams (1957) and Maynard Smith (1962) are erroneous, and add to growing evidence of asynchrony of senescence in a wide range of taxa e.g. (Briga & Verhulst, 2021; Cayuela et al., 2020; Cooper et al., 2021; Hayward et al., 2015; Herndon et al., 2002; Tully, Le Galliard & Baron, 2020; Tully, 2023). Apart from the similar ageing trajectory of immune related traits in male SW (Group 3), there is little evidence for functional grouping

patterns in ageing across traits in the Seychelles warbler. This is consistent with the findings of Hayward et al (2015) in the Soay sheep.

In terms of the evolutionary theory behind the asynchrony of senescence, this study provides weak evidence for the theoretical study that traits more associated with fitness undergo more rapid ageing (Briga & Verhulst, 2021; Moorad & Ravindran, 2022). We found age-related declines in direct fitness indices— i.e. survival and reproduction but not in traits less important to fitness such as wing length, tarsus length, antioxidant, and oxidant capacity. However, the role of selection pressure as a driver of patterns of senescence in traits less consequential to fitness still remains unknown. Considering the ageing trajectory of body mass and immune traits (e.g. malaria presence) as examples, ageing was significant in the first trait but not in the latter. Two predictions can arise according to the newer theories suggesting trait-specific selection pressure explains ageing trajectories: 1) body mass ages faster because body mass is under stronger selection than immune traits, 2) immune traits don't age because they are under stronger selection than body mass. We can envision prediction one to be plausible; Body mass as important indicator of condition (Gaillard et al., 2000; Nussey et al., 2011), may experience strong selection pressure both in early life and late life (Jebb et al., 2021; Merilä, Kruuk & Sheldon, 2001; Ronget et al., 2018). In SW, juvenile body mass predicts survival till adulthood (Brown et al., 2021a), i.e. strong selection on body mass. Thus, body mass is hypothesised to experience a more rapid waning of selection pressure and ageing rate according to Moorad and Ravindran (2022). Yet, prediction two is equally plausible. We can expect immune traits to experience strong selection, as the benefit of an optimized immune function for survival and fitness is extremely apparent (Sheldon & Verhulst, 1996; McKean & Lazzaro, 2011; Seppälä, 2015).

Nevertheless, the strength of selection pressure on traits in specific populations can be difficult to predict. Although most studies suggest that body mass is under strong selection, there is also evidence suggesting low association between fitness and body mass (Boratyński & Koteja, 2010; Cox & Calsbeek, 2015; Warkentin et al., 2016). Likewise, the strength of selection on immune traits may depend on the environment and the strength of the immune challenge (Seppälä, 2015; Langeloh et al., 2023, Roast et al., 2020). In the SW, there was no evidence that avian malaria presence affected adult warbler survival (Hammers et al., 2016), which may indicate low strength of immune challenge, hence low covariation between immunity and fitness in warblers. Widely speaking, selection on a trait can be dependent on population dynamics and environment (Wright et al., 2019), making it difficult to draw broader conclusions. We currently lack understanding of trait-specific selection to definitively predict how selection determines the rate and onset of senescence or ageing patterns across traits. Nonetheless, we can predict that the trait with similar ageing trajectories may share age-specific selection pressure patterns and vice versa.

Caveats and future directions

Senescence refers to a decline in a function in an organism that results in a decline in survival and reproductive success (Ricklefs, 2008). Therefore, inference of trait senescence is limited in our present study as for 4 out of the 7 traits that showed ageing, we have no evidence of a causative link between trait ageing and survival/reproduction decreases.

Further studies are needed to test how age-specific selection pressure on traits explains the asynchrony of ageing (Moorad & Ravindran, 2022). Additionally, genetic correlations within and between age classes, differential energy allocation and trade-offs may affect the evolution of asynchrony of senescence (Charlesworth, 2001; Hayward et al., 2015; Moorad & Ravindran, 2022). Testing for presence of genetic correlations between traits may elucidate

the genetic architecture of asynchrony of senescence. Understanding potential non-evolutionary causes of asynchrony of senescence is also instrumental in providing insight to asynchronous ageing (Moorad & Ravindran, 2022). For example, since telomere senescence rates in the SW are affected by the environment (Brown et al., 2022), this study could be extended to test the environmental effects on senescence rates across various traits to examine whether environmental damage leads to differences in trait ageing. Additionally, a path analysis or structural equation modelling how individual trait ageing contributes to the timing of actuarial senescence would provide insight on the mechanistic explanation of individual senescence (Lemaître & Gaillard, 2017).

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Author Contributions

This study was conceived by H.L.D. and developed by C.L.S.T. and D.S.R.. C.L.S.T. conducted statistical analyses with input from H.L.D., D.S.R. and M.B.. H.L.D., D.S.R., J.K., and TB manage the long-term Seychelles warbler study system including gaining the relevant funding. The genetic pedigree was constructed by H.L.D.. C.L.S.T wrote the paper with the help of H.L.D and D.S.R.. all co-authors provided comments on the manuscript and gave final approval for publication.

553 Declaration of Interest

554 The authors declare no conflicts of interest.

555

556 Data Availability

557 The data and code are available on github: [https://github.com/ClairetIs/Asynchrony-of-](https://github.com/ClairetIs/Asynchrony-of-ageing-code.git)
558 [ageing-code.git](https://github.com/ClairetIs/Asynchrony-of-ageing-code.git)

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560 References

561 Bansal, A., Zhu, L.J., Yen, K. & Tissenbaum, H.A. (2015) Uncoupling lifespan and healthspan in
562 *Caenorhabditis elegans* longevity mutants. *Proceedings of the National Academy of Sciences*. 112 (3),
563 E277–E286. doi:10.1073/pnas.1412192112.

564 Barrett, E.L.B., Burke, T.A., Hammers, M., Komdeur, J. & Richardson, D.S. (2013) Telomere length and
565 dynamics predict mortality in a wild longitudinal study. *Molecular Ecology*. 22 (1), 249–259.
566 doi:10.1111/mec.12110.

567 Beamonte-Barrientos, R., Velando, A., Drummond, H. & Torres, R. (2010) Senescence of Maternal
568 Effects: Aging Influences Egg Quality and Rearing Capacities of a Long-Lived Bird. *The American*
569 *Naturalist*. 175 (4), 469–480. doi:10.1086/650726.

570 Beckman, K.B. & Ames, B.N. (1999) Endogenous oxidative damage of mtDNA. *Mutation*
571 *Research/Fundamental and Molecular Mechanisms of Mutagenesis*. 424 (1–2), 51–58.

572 Beirne, C., Delahay, R. & Young, A. (2015) Sex differences in senescence: the role of intra-sexual
573 competition in early adulthood. *Proceedings of the Royal Society B: Biological Sciences*. 282 (1811),
574 20151086. doi:10.1098/rspb.2015.1086.

575 Bichet, C., Moiron, M., Matson, K.D., Vedder, O. & Bouwhuis, S. (2022) Immunosenescence in the
576 wild? A longitudinal study in a long-lived seabird. *Journal of Animal Ecology*. 91 (2), 458–469.
577 doi:10.1111/1365-2656.13642.

578 van Boheemen, L.A., Hammers, M., Kingma, S.A., Richardson, D.S., Burke, T., Komdeur, J. & Dugdale,
579 H.L. (2019) Compensatory and additive helper effects in the cooperatively breeding Seychelles
580 warbler (*Acrocephalus sechellensis*). *Ecology and Evolution*. 9 (5), 2986–2995.
581 doi:10.1002/ece3.4982.

582 Boonekamp, J.J., Mulder, E. & Verhulst, S. (2018) Canalisation in the wild: effects of developmental
583 conditions on physiological traits are inversely linked to their association with fitness. *Ecology*
584 *Letters*. 21 (6), 857–864. doi:10.1111/ele.12953.

585 Boratyński, Z. & Koteja, P. (2010) Sexual and natural selection on body mass and metabolic rates in
586 free-living bank voles. *Functional Ecology*. 24 (6), 1252–1261. doi:10.1111/j.1365-
587 2435.2010.01764.x.

588 Briga, M., Jimeno, B. & Verhulst, S. (2019) Coupling lifespan and aging? The age at onset of body
589 mass decline associates positively with sex-specific lifespan but negatively with environment-specific
590 lifespan. *Experimental Gerontology*. 119, 111–119. doi:10.1016/j.exger.2019.01.030.

591 Briga, M. & Verhulst, S. (2021) Mosaic metabolic ageing: Basal and standard metabolic rates age in
592 opposite directions and independent of environmental quality, sex and life span in a passerine.
593 *Functional Ecology*. 35 (5), 1055–1068. doi:10.1111/1365-2435.13785.

594 Brouwer, L. (2007) *Cooperative breeding and density regulation in small island populations of the*
595 *Seychelles warbler*. s.n.

596 Brouwer, L., Barr, I., Van De POL, M., Burke, T., Komdeur, J. & Richardson, D.S. (2010) MHC-
597 dependent survival in a wild population: evidence for hidden genetic benefits gained through extra-
598 pair fertilizations. *Molecular Ecology*. 19 (16), 3444–3455. doi:10.1111/j.1365-294X.2010.04750.x.

599 Brouwer, L., Richardson, D.S., Eikenaar, C. & Komdeur, J. (2006) The role of group size and
600 environmental factors on survival in a cooperatively breeding tropical passerine. *Journal of Animal*
601 *Ecology*. 1321–1329.

602 Brown, T., Dugdale, H., Hammers, M., Komdeur, J. & Richardson, D. (2021a) *Seychelles warblers with*
603 *silver spoons: juvenile condition is a lifelong predictor of annual survival, but not annual reproduction*
604 *or senescence*. doi:10.22541/au.163664637.70605525/v1.

605 Brown, T.J., Hammers, M., Taylor, M., Dugdale, H.L., Komdeur, J. & Richardson, D.S. (2021b)
606 Hematocrit, age, and survival in a wild vertebrate population. *Ecology and Evolution*. 11 (1), 214–
607 226. doi:10.1002/ece3.7015.

608 Brown, T.J., Spurgin, L.G., Dugdale, H.L., Komdeur, J., Burke, T. & Richardson, D.S. (2022) Causes and
609 consequences of telomere lengthening in a wild vertebrate population. *Molecular Ecology*. 31 (23),
610 5933–5945. doi:10.1111/mec.16059.

611 Burnham, K.P., Anderson, D.R. & Huyvaert, K.P. (2011) AIC model selection and multimodel
612 inference in behavioral ecology: some background, observations, and comparisons. *Behavioral*
613 *Ecology and Sociobiology*. 65 (1), 23–35. doi:10.1007/s00265-010-1029-6.

614 Buttemer, W.A., Addison, B.A. & Klasing, K.C. (2020) The energy cost of feather replacement is not
615 intrinsically inefficient. *Canadian Journal of Zoology*. 98 (2), 142–148. doi:10.1139/cjz-2019-0170.

616 Cansse, T., Vedder, O., Kürten, N. & Bouwhuis, S. (2024) Feeding rate reflects quality in both parents
617 and offspring: a longitudinal study in common terns. *Animal Behaviour*. 214, 111–120.
618 doi:10.1016/j.anbehav.2024.06.010.

619 Cayuela, H., Lemaître, J.-F., Rugiero, L., Capula, M. & Luiselli, L. (2020) Asynchrony of actuarial and
620 reproductive senescence: a lesson from an indeterminate grower. *Biological Journal of the Linnean*
621 *Society*. 131 (3), 667–672. doi:10.1093/biolinnean/blaa127.

622 Charlesworth, B. (1994) *Evolution in age-structured populations*. Cambridge University Press
623 Cambridge. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1685027/pdf/ajhg00363-0169.pdf>.

624 Charlesworth, B. (2001) Patterns of Age-specific Means and Genetic Variances of Mortality Rates
625 Predicted by the Mutation-Accumulation Theory of Ageing. *Journal of Theoretical Biology*. 210 (1),
626 47–65. doi:10.1006/jtbi.2001.2296.

627 Cheynel, L., Lemaître, J.-F., Gaillard, J.-M., Rey, B., Bourgoïn, G., Ferté, H., Jégo, M., Débias, F.,
628 Pellerin, M., Jacob, L. & Gilot-Fromont, E. (2017) Immunosenescence patterns differ between
629 populations but not between sexes in a long-lived mammal. *Scientific Reports*. 7 (1), 13700.
630 doi:10.1038/s41598-017-13686-5.

631 Christensen, K., Doblhammer, G., Rau, R. & Vaupel, J.W. (2009) Ageing populations: the challenges
632 ahead. *The Lancet*. 374 (9696), 1196–1208. doi:10.1016/S0140-6736(09)61460-4.

633 Cooper, E.B., Bonnet, T., Osmond, H.L., Cockburn, A. & Kruuk, L.E.B. (2021) Aging and Senescence
634 across Reproductive Traits and Survival in Superb Fairy-Wrens (*Malurus cyaneus*). *The American*
635 *Naturalist*. 197 (1), 111–127. doi:10.1086/711755.

636 Cox, R.M. & Calsbeek, R. (2015) Survival of the fattest? Indices of body condition do not predict
637 viability in the brown anole (*nolis sagrei*). *Functional Ecology*. 29 (3), 404–413. doi:10.1111/1365-
638 2435.12346.

639 van de Crommenacker, J., Hammers, M., van der Woude, J., Louter, M., Santema, P., Richardson,
640 D.S. & Komdeur, J. (2017) Oxidative status and fitness components in the Seychelles warbler.
641 *Functional Ecology*. 31 (6), 1210–1219. doi:10.1111/1365-2435.12861.

642 van de Crommenacker, J., Komdeur, J., Burke, T. & Richardson, D.S. (2011) Spatio-temporal variation
643 in territory quality and oxidative status: a natural experiment in the Seychelles warbler
644 (*Acrocephalus sechellensis*). *Journal of Animal Ecology*. 80 (3), 668–680. doi:10.1111/j.1365-
645 2656.2010.01792.x.

646 Crommenacker, J. van de, Komdeur, J. & Richardson, D.S. (2011) Assessing the Cost of Helping: The
647 Roles of Body Condition and Oxidative Balance in the Seychelles Warbler (*Acrocephalus*
648 *sechellensis*). *PLOS ONE*. 6 (10), e26423. doi:10.1371/journal.pone.0026423.

649 Douhard, F., Gaillard, J.-M., Pellerin, M., Jacob, L. & Lemaître, J.-F. (2017) The cost of growing large:
650 costs of post-weaning growth on body mass senescence in a wild mammal. *Oikos*. 126 (9), 1329–
651 1338. doi:10.1111/oik.04421.

652 Elliott, K.H., Hare, J.F., Le Vaillant, M., Gaston, A.J., Ropert-Coudert, Y. & Anderson, W.G. (2015)
653 Ageing gracefully: physiology but not behaviour declines with age in a diving seabird. *Functional*
654 *Ecology*. 29 (2), 219–228. doi:10.1111/1365-2435.12316.

655 Fairfield, E.A., Hutchings, K., Gilroy, D.L., Kingma, S.A., Burke, T., Komdeur, J. & Richardson, D.S.
656 (2016) The impact of conservation-driven translocations on blood parasite prevalence in the
657 Seychelles warbler. *Scientific Reports*. 6 (1), 29596. doi:10.1038/srep29596.

658 Fay, R., Ravussin, P.-A., Arrigo, D., von Rönne, J.A.C. & Schaub, M. (2021) Age-specific reproduction in
659 female pied flycatchers: evidence for asynchronous aging. *Oecologia*. 196 (3), 723–734.
660 doi:10.1007/s00442-021-04963-2.

661 Felton, G.W. & Summers, C.B. (1995) Antioxidant systems in insects. *Archives of Insect Biochemistry*
662 *and Physiology*. 29 (2), 187–197. doi:10.1002/arch.940290208.

663 Finkel, T. & Holbrook, N.J. (2000) Oxidants, oxidative stress and the biology of ageing. *Nature*. 408
664 (6809), 239–247. doi:10.1038/35041687.

665 Froy, H., Sparks, A.M., Watt, K., Sinclair, R., Bach, F., Pilkington, J.G., Pemberton, J.M., McNeilly, T.N.
666 & Nussey, D.H. (2019) Senescence in immunity against helminth parasites predicts adult mortality in
667 a wild mammal. *Science*. 365 (6459), 1296–1298. doi:10.1126/science.aaw5822.

668 Gaillard, J.-M., Festa-Bianchet, M., Delorme, D. & Jorgenson, J. (2000) Body mass and individual
669 fitness in female ungulates: bigger is not always better. *Proceedings of the Royal Society of London.*
670 *Series B: Biological Sciences*. 267 (1442), 471–477. doi:10.1098/rspb.2000.1024.

671 Gaillard, J.-M. & Lemaître, J.-F. (2020) An integrative view of senescence in nature. *Functional*
672 *Ecology*. 34 (1), 4–16. doi:10.1111/1365-2435.13506.

673 Gaillard, J.-M. & Lemaître, J.-F. (2017) The Williams’ legacy: A critical reappraisal of his nine
674 predictions about the evolution of senescence. *Evolution*. 71 (12), 2768–2785.

675 Gimenez, O., Cam, E. & Gaillard, J.-M. (2018) Individual heterogeneity and capture–recapture
676 models: what, why and how? *Oikos*. 127 (5), 664–686. doi:10.1111/oik.04532.

677 Goldberg, I., Cohen, E., Gaftor-Gvili, A., Shochat, T., Kugler, E., Margalit, I., Goldberg, E., Raanani, P. &
678 Krause, I. (2023) A Longitudinal Assessment of the Natural Change in Haemoglobin, Haematocrit,
679 and Mean Corpuscular Volume with Age. *Acta Haematologica*. 146 (3), 206–213.
680 doi:10.1159/000529356.

681 Hadfield, J.D., Richardson, D.S. & Burke, T. (2006) Towards unbiased parentage assignment:
682 combining genetic, behavioural and spatial data in a Bayesian framework. *Molecular Ecology*. 15
683 (12), 3715–3730. doi:10.1111/j.1365-294X.2006.03050.x.

684 Hämäläinen, A., Dammhahn, M., Aujard, F., Eberle, M., Hardy, I., Kappeler, P.M., Perret, M.,
685 Schliehe-Diecks, S. & Kraus, C. (2014) Senescence or selective disappearance? Age trajectories of
686 body mass in wild and captive populations of a small-bodied primate. *Proceedings of the Royal*
687 *Society B: Biological Sciences*. 281 (1791), 20140830. doi:10.1098/rspb.2014.0830.

688 Hammers, M. & Brouwer, L. (2017) *Rescue behaviour in a social bird: removal of sticky ‘bird-catcher*
689 *tree’ seeds by group members*. doi:10.1163/1568539X-00003428.

690 Hammers, M., Kingma, S.A., Bebbington, K., van de Crommenacker, J., Spurgin, L.G., Richardson,
691 D.S., Burke, T., Dugdale, H.L. & Komdeur, J. (2015) Senescence in the wild: Insights from a long-term
692 study on Seychelles warblers. *Experimental Gerontology*. 71, 69–79.
693 doi:10.1016/j.exger.2015.08.019.

694 Hammers, M., Kingma, S.A., Boheemen, L.A., Sparks, A.M., Burke, T., Dugdale, H.L., Richardson, D.S.
695 & Komdeur, J. (2021) Helpers compensate for age-related declines in parental care and offspring
696 survival in a cooperatively breeding bird. *Evolution Letters*. 5 (2), 143–153.

697 Hammers, M., Komdeur, J., Kingma, S.A., Hutchings, K., Fairfield, E.A., Gilroy, D.L. & Richardson, D.S.
698 (2016) Age-specific haemosporidian infection dynamics and survival in Seychelles warblers. *Scientific*
699 *Reports*. 6 (1), 29720. doi:10.1038/srep29720.

700 Hammers, M., Richardson, D.S., Burke, T. & Komdeur, J. (2012) Age-Dependent Terminal Declines in
701 Reproductive Output in a Wild Bird. *PLOS ONE*. 7 (7), e40413. doi:10.1371/journal.pone.0040413.

702 Hammers, M., Richardson, D.S., Burke, T. & Komdeur, J. (2013) The impact of reproductive
703 investment and early-life environmental conditions on senescence: support for the disposable soma
704 hypothesis. *Journal of Evolutionary Biology*. 26 (9), 1999–2007. doi:10.1111/jeb.12204.

705 Hayward, A.D., Moorad, J., Regan, C.E., Berenos, C., Pilkington, J.G., Pemberton, J.M. & Nussey, D.H.
706 (2015) Asynchrony of senescence among phenotypic traits in a wild mammal population.
707 *Experimental Gerontology*. 71, 56–68. doi:10.1016/j.exger.2015.08.003.

708 Hellgren, O., Waldenström, J. & Bensch, S. (2004) A NEW PCR ASSAY FOR SIMULTANEOUS STUDIES
709 OF LEUCOCYTOZON, PLASMODIUM, AND HAEMOPROTEUS FROM AVIAN BLOOD. *The Journal of*
710 *Parasitology*. 90 (4), 797–802.

711 Herndon, L.A., Schmeissner, P.J., Dudaronek, J.M., Brown, P.A., Listner, K.M., Sakano, Y., Paupard,
 712 M.C., Hall, D.H. & Driscoll, M. (2002) Stochastic and genetic factors influence tissue-specific decline
 713 in ageing *C. elegans*. *Nature*. 419 (6909), 808–814. doi:10.1038/nature01135.

714 Hickmott, A.J., Cervantes, L., Arroyo, J.P., Brasky, K., Bene, M., Salmon, A.B., Phillips, K.A. & Ross,
 715 C.N. (2024) Age-related changes in hematological biomarkers in common marmosets. *American*
 716 *Journal of Primatology*. 86 (4), e23589. doi:10.1002/ajp.23589.

717 Hindle, A.G., Lawler, J.M., Campbell, K.L. & Horning, M. (2010) Muscle aging and oxidative stress in
 718 wild-caught shrews. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular*
 719 *Biology*. 155 (4), 427–434. doi:10.1016/j.cbpb.2010.01.007.

720 Hübner-Woźniak, E., Okecka-Szymańska, J., Stupnicki, R., Malara, M. & Kozdroń, E. (2011) Age-
 721 Related Blood Antioxidant Capacity in Men and Women. *Journal of Medical Biochemistry*. 30 (2),
 722 103–108. doi:10.2478/v10011-011-0008-4.

723 Jebb, A.H.M., Blumstein, D.T., Bize, P. & Martin, J.G.A. (2021) Bigger is not always better: Viability
 724 selection on body mass varies across life stages in a hibernating mammal. *Ecology and Evolution*. 11
 725 (7), 3435–3445. doi:10.1002/ece3.7304.

726 Jones, O.R., Scheuerlein, A., Salguero-Gómez, R., Camarda, C.G., Schaible, R., Casper, B.B., Dahlgren,
 727 J.P., Ehrlén, J., García, M.B., Menges, E.S., Quintana-Ascencio, P.F., Caswell, H., Baudisch, A. &
 728 Vaupel, J.W. (2014) Diversity of ageing across the tree of life. *Nature*. 505 (7482), 169–173.
 729 doi:10.1038/nature12789.

730 Kiat, Y. & Sapir, N. (2018) Life-history trade-offs result in evolutionary optimization of feather quality.
 731 *Biological Journal of the Linnean Society*. 125 (3), 613–624. doi:10.1093/biolinnean/bly135.

732 Kirkwood, T.B.L. (1977) Evolution of ageing. *Nature*. 270 (5635), 301–304. doi:10.1038/270301a0.

733 Kirkwood, T.B.L. & Austad, S.N. (2000) Why do we age? *Nature*. 408 (6809), 233–238.
 734 doi:10.1038/35041682.

735 Klein, S.L. & Flanagan, K.L. (2016) Sex differences in immune responses. *Nature Reviews*
 736 *Immunology*. 16 (10), 626–638. doi:10.1038/nri.2016.90.

737 Komdeur, J. (1994) Conserving the seychelles warbler *Acrocephalus sechellensis* by translocation
 738 from Cousin Island to the islands of Aride and Cousine. *Biological Conservation*. 67 (2), 143–152.
 739 doi:10.1016/0006-3207(94)90360-3.

740 Komdeur, J. (1992) Importance of habitat saturation and territory quality for evolution of
 741 cooperative breeding in the Seychelles warbler. *Nature*. 358 (6386), 493–495.
 742 doi:10.1038/358493a0.

743 Komdeur, J. (1996) Seasonal Timing of Reproduction in a Tropical Bird, the Seychelles Warbler: A
 744 Field Experiment Using Translocation. *Journal of Biological Rhythms*. 11 (4), 333–346.
 745 doi:10.1177/074873049601100407.

746 Komdeur, J., Bullock, I.D. & Rands, M.R.W. (1991) Conserving the Seychelles Warbler *Acrocephalus*
 747 *sechellensis* by translocation: a transfer from Cousin Island to Aride Island. *Bird Conservation*
 748 *International*. 1 (2), 177–185. doi:10.1017/S0959270900002045.

749 Komdeur, J. & Daan, S. (2005) Breeding in the monsoon: semi-annual reproduction in the Seychelles
 750 warbler (*Acrocephalus sechellensis*). *Journal of Ornithology*. 146, 305–313.

751 Komdeur, J., Piersma, T., Kraaijeveld, K., Kraaijeveld-Smit, F. & Richardson, D.S. (2004) Why
 752 Seychelles Warblers fail to recolonize nearby islands: unwilling or unable to fly there? *Ibis*. 146 (2),
 753 298–302. doi:10.1046/j.1474-919X.2004.00255.x.

754 Krist, M., Edme, A., Höchsmannová, A., Janča, M., Lisická-Lachnitová, L., Ringlová, H. & Stříteský, J.
 755 (2024) Parental provisioning is weakly age-dependent and heritable in a small passerine. *Ibis*. 166
 756 (3), 857–870. doi:10.1111/ibi.13307.

757 Kroeger, S.B., Blumstein, D.T., Armitage, K.B., Reid, J.M. & Martin, J.G.A. (2018) Age, state,
 758 environment, and season dependence of senescence in body mass. *Ecology and Evolution*. 8 (4),
 759 2050–2061. doi:10.1002/ece3.3787.

760 Labocha, M.K. & Hayes, J.P. (2012) Morphometric indices of body condition in birds: a review.
 761 *Journal of Ornithology*. 153 (1), 1–22. doi:10.1007/s10336-011-0706-1.

762 Langeloh, L., Jokela, J., Seppälä, K. & Seppälä, O. (2023) Ecological determinants of variation in
 763 phenotypic selection on quantitative immune defence traits. *Oikos*. 2023 (2), e09506.
 764 doi:10.1111/oik.09506.

765 Le Clercq, L.-S., Kotzé, A., Grobler, J.P. & Dalton, D.L. (2023) Biological clocks as age estimation
 766 markers in animals: a systematic review and meta-analysis. *Biological Reviews*. 98 (6), 1972–2011.
 767 doi:10.1111/brv.12992.

768 Lemaître, J.-F. & Gaillard, J.-M. (2017) Reproductive senescence: new perspectives in the wild.
 769 *Biological Reviews*. 92 (4), 2182–2199. doi:10.1111/brv.12328.

770 van Lieshout, S.H.J., Badás, E.P., Mason, M.W.T., Newman, C., Buesching, C.D., Macdonald, D.W. &
 771 Dugdale, H.L. (2020) Social effects on age-related and sex-specific immune cell profiles in a wild
 772 mammal. *Biology Letters*. 16 (7), 20200234. doi:10.1098/rsbl.2020.0234.

773 Maynard Smith, J. (1962) Review lectures on senescence. I. The causes of ageing. *Proceedings of the*
 774 *Royal Society of London Series B*. 157 (966), 115–127.

775 McKean, K.A. & Lazzaro, B.P. (2011) The costs of immunity and the evolution of immunological
 776 defense mechanisms. *Mechanisms of life history evolution*. pp.299–310.
 777 https://lazzaro.entomology.cornell.edu/files/2023/06/2011-McKean_LifeHistEvolCh23.pdf.

778 Merilä, J., Kruuk, L.E.B. & Sheldon, B.C. (2001) Natural selection on the genetical component of
 779 variance in body condition in a wild bird population. *Journal of Evolutionary Biology*. 14 (6), 918–929.
 780 doi:10.1046/j.1420-9101.2001.00353.x.

781 Metcalf, C.J.E., Roth, O. & Graham, A.L. (2020) Why leveraging sex differences in immune trade-offs
 782 may illuminate the evolution of senescence. *Functional Ecology*. 34 (1), 129–140. doi:10.1111/1365-
 783 2435.13458.

784 Milenkaya, O., Weinstein, N., Legge, S. & Walters, J.R. (2013) Variation in body condition indices of
 785 crimson finches by sex, breeding stage, age, time of day, and year. *Conservation Physiology*. 1 (1),
 786 cot020. doi:10.1093/conphys/cot020.

787 Møller, A.P. & Saino, N. (2004) Immune response and survival. *Oikos*. 104 (2), 299–304.
 788 doi:10.1111/j.0030-1299.2004.12844.x.

789 Monaghan, P., Charmantier, A., Nussey, D.H. & Ricklefs, R.E. (2008) The Evolutionary Ecology of
 790 Senescence. *Functional Ecology*. 22 (3), 371–378.

791 Mondragão-Rodrigues, I. & Macedo, M.F. (2023) Buffy Coat Processing Impacts on Monocytes'
792 Capacity to Present Lipid Antigens. *Biomedicines*. 11 (3), 833. doi:10.3390/biomedicines11030833.

793 Moorad, J.A. & Ravindran, S. (2022) Natural Selection and the Evolution of Asynchronous Aging. *The*
794 *American Naturalist*. 199 (4), 551–563. doi:10.1086/718589.

795 Moullec, H., Reichert, S. & Bize, P. (2023) Aging trajectories are trait- and sex-specific in the long-
796 lived Alpine swift. *Frontiers in Ecology and Evolution*. 11.
797 <https://www.frontiersin.org/articles/10.3389/fevo.2023.983266>.

798 Nussey, D.H., Coulson, T., Delorme, D., Clutton-Brock, T.H., Pemberton, J.M., Festa-Bianchet, M. &
799 Gaillard, J.-M. (2011) Patterns of body mass senescence and selective disappearance differ among
800 three species of free-living ungulates. *Ecology*. 92 (10), 1936–1947. doi:10.1890/11-0308.1.

801 Nussey, D.H., Froy, H., Lemaitre, J.-F., Gaillard, J.-M. & Austad, S.N. (2013) Senescence in natural
802 populations of animals: Widespread evidence and its implications for bio-gerontology. *Ageing*
803 *Research Reviews*. 12 (1), 214–225. doi:10.1016/j.arr.2012.07.004.

804 Nussey, D.H., Pemberton, J.M., Pilkington, J.G. & Blount, J.D. (2009) Life History Correlates of
805 Oxidative Damage in a Free-Living Mammal Population. *Functional Ecology*. 23 (4), 809–817.

806 van Oers, K., Richardson, D.S., Sæther, S.A. & Komdeur, J. (2010) Reduced blood parasite prevalence
807 with age in the Seychelles Warbler: selective mortality or suppression of infection? *Journal of*
808 *Ornithology*. 151 (1), 69–77. doi:10.1007/s10336-009-0427-x.

809 Peters, A., Delhey, K., Nakagawa, S., Aulsebrook, A. & Verhulst, S. (2019) Immunosenescence in wild
810 animals: meta-analysis and outlook. *Ecology Letters*. 22 (10), 1709–1722. doi:10.1111/ele.13343.

811 Piliczewski, P., Jankowiak, Łukasz & Wysocki, D. (2018) Age-dependent changes in biometrics
812 indicate senescence in the European Blackbird *Turdus merula*. *Bird Study*. 65 (2), 219–224.
813 doi:10.1080/00063657.2018.1451821.

814 van de Pol, M. & Verhulst, S. (2006) Age-Dependent Traits: A New Statistical Model to Separate
815 Within- and Between-Individual Effects. *The American Naturalist*. 167 (5), 766–773.
816 doi:10.1086/503331.

817 Raj Pant, S., Hammers, M., Komdeur, J., Burke, T., Dugdale, H.L. & Richardson, D.S. (2020) Age-
818 dependent changes in infidelity in Seychelles warblers. *Molecular Ecology*. 29 (19), 3731–3746.
819 doi:10.1111/mec.15563.

820 Remot, F., Ronget, V., Froy, H., Rey, B., Gaillard, J.-M., Nussey, D.H. & Lemaitre, J.-F. (2022) Decline in
821 telomere length with increasing age across nonhuman vertebrates: A meta-analysis. *Molecular*
822 *Ecology*. 31 (23), 5917–5932. doi:10.1111/mec.16145.

823 Richardson, D.S., Burke, T. & Komdeur, J. (2002) Direct Benefits and the Evolution of Female-Biased
824 Cooperative Breeding in Seychelles Warblers. *Evolution*. 56 (11), 2313–2321. doi:10.1111/j.0014-
825 3820.2002.tb00154.x.

826 Richardson, D.S., Jury, F.L., Blaakmeer, K., Komdeur, J. & Burke, T. (2001) Parentage assignment and
827 extra-group paternity in a cooperative breeder: the Seychelles warbler (*Acrocephalus sechellensis*).
828 *Molecular Ecology*. 10 (9), 2263–2273. doi:10.1046/j.0962-1083.2001.01355.x.

829 Ricklefs, R.E. (2008) The Evolution of Senescence from a Comparative Perspective. *Functional*
830 *Ecology*. 22 (3), 379–392.

831 Ricklefs, R.E. & Finch, C.E. (1995) *Aging: A natural history*. Aging: A natural history. New York, NY,
832 US, Scientific American Library/Scientific American Books.

833 Roast, M.J., Aranzamendi, N.H., Fan, M., Teunissen, N., Hall, M.D. & Peters, A. (2020) Fitness
834 outcomes in relation to individual variation in constitutive innate immune function. *Proceedings of*
835 *the Royal Society B: Biological Sciences*. 287 (1938), 20201997. doi:10.1098/rspb.2020.1997.

836 Roast, M.J., Hidalgo Aranzamendi, N., Teunissen, N., Fan, M., Verhulst, S. & Peters, A. (2022) No
837 Evidence for Constitutive Innate Immune Senescence in a Longitudinal Study of a Wild Bird.
838 *Physiological and Biochemical Zoology*. 95 (1), 54–65. doi:10.1086/717937.

839 Rodríguez, J.A., Marigorta, U.M., Hughes, D.A., Spataro, N., Bosch, E. & Navarro, A. (2017)
840 Antagonistic pleiotropy and mutation accumulation influence human senescence and disease.
841 *Nature Ecology & Evolution*. 1 (3), 1–5. doi:10.1038/s41559-016-0055.

842 Rodríguez-Muñoz, R., Boonekamp, J.J., Liu, X.P., Skicko, I., Haugland Pedersen, S., Fisher, D.N.,
843 Hopwood, P. & Tregenza, T. (2019) Comparing individual and population measures of senescence
844 across 10 years in a wild insect population. *Evolution*. 73 (2), 293–302. doi:10.1111/evo.13674.

845 Ronget, V., Gaillard, J.-M., Coulson, T., Garratt, M., Gueyffier, F., Lega, J.-C. & Lemaître, J.-F. (2018)
846 Causes and consequences of variation in offspring body mass: meta-analyses in birds and mammals.
847 *Biological Reviews*. 93 (1), 1–27. doi:10.1111/brv.12329.

848 Seppälä, O. (2015) Natural selection on quantitative immune defence traits: a comparison between
849 theory and data. *Journal of Evolutionary Biology*. 28 (1), 1–9. doi:10.1111/jeb.12528.

850 Sheldon, B.C. & Verhulst, S. (1996) Ecological immunology: costly parasite defences and trade-offs in
851 evolutionary ecology. *Trends in Ecology & Evolution*. 11 (8), 317–321. doi:10.1016/0169-
852 5347(96)10039-2.

853 Śliż, M. (2022) *The effect of progressing age on feather renewal in zebra finches*.
854 <https://ruj.uj.edu.pl/xmlui/handle/item/302725>.

855 Sparks, A.M., Spurgin, L.G., van der Velde, M., Fairfield, E.A., Komdeur, J., Burke, T., Richardson, D.S.
856 & Dugdale, H.L. (2022) Telomere heritability and parental age at conception effects in a wild avian
857 population. *Molecular Ecology*. 31 (23), 6324–6338. doi:10.1111/mec.15804.

858 Spurgin, L.G., Bebbington, K., Fairfield, E.A., Hammers, M., Komdeur, J., Burke, T., Dugdale, H.L. &
859 Richardson, D.S. (2018) Spatio-temporal variation in lifelong telomere dynamics in a long-term
860 ecological study. *Journal of Animal Ecology*. 87 (1), 187–198. doi:10.1111/1365-2656.12741.

861 Tidière, M., Thevenot, X., Deligiannopoulou, A., Douay, G., Whipple, M., Siberchicot, A., Gaillard, J.-
862 M. & Lemaître, J.-F. (2018) Maternal reproductive senescence shapes the fitness consequences of
863 the parental age difference in ruffed lemurs. *Proceedings of the Royal Society B: Biological Sciences*.
864 285 (1886), 20181479. doi:10.1098/rspb.2018.1479.

865 Tjørve, K.M. & Tjørve, E. (2010) Shapes and functions of bird-growth models: how to characterise
866 chick postnatal growth. *Zoology*. 113 (6), 326–333.

867 Torres, R., Drummond, H. & Velando, A. (2011) Parental Age and Lifespan Influence Offspring
868 Recruitment: A Long-Term Study in a Seabird. *PLOS ONE*. 6 (11), e27245.
869 doi:10.1371/journal.pone.0027245.

870 Tully, T. (2023) Diversity, plasticity and asynchrony of actuarial and reproductive senescence in the
871 Collembola *Folsomia candida* (Willem, 1902). *Frontiers in Ecology and Evolution*. 11.
872 doi:10.3389/fevo.2023.1112045.

873 Tully, T., Le Galliard, J. & Baron, J. (2020) Micro-geographic shift between negligible and actuarial
874 senescence in a wild snake *R. Salguero-Gómez* (ed.). *Journal of Animal Ecology*. 89 (11), 2704–2716.
875 doi:10.1111/1365-2656.13317.

876 Vágási, C.I., Vincze, O., Lemaître, J.-F., Pap, P.L., Ronget, V. & Gaillard, J.-M. (2021) Is degree of
877 sociality associated with reproductive senescence? A comparative analysis across birds and
878 mammals. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 376 (1823),
879 20190744. doi:10.1098/rstb.2019.0744.

880 Vrtílek, M., Žák, J. & Reichard, M. (2022) Evidence for reproductive senescence across ray-finned
881 fishes: A review. *Frontiers in Ecology and Evolution*. 10. doi:10.3389/fevo.2022.982915.

882 Walker, L.C. & Herndon, J.G. (2010) Mosaic aging. *Medical Hypotheses*. 74 (6), 1048–1051.
883 doi:10.1016/j.mehy.2009.12.031.

884 Warkentin, I.G., Espie, R.H.M., Lieske, D.J. & James, P.C. (2016) Variation in selection pressure acting
885 on body size by age and sex in a reverse sexual size dimorphic raptor. *Ibis*. 158 (3), 656–669.
886 doi:10.1111/ibi.12369.

887 Wilcoxon, T.E., Boughton, R.K. & Schoech, S.J. (2010) Older can be better: physiological costs of
888 paternal investment in the Florida scrub-jay. *Behavioral Ecology and Sociobiology*. 64 (10), 1527–
889 1535. doi:10.1007/s00265-010-0966-4.

890 Williams, G.C. (1957) Pleiotropy, Natural Selection, and the Evolution of Senescence. *Evolution*. 398–
891 411.

892 Williams, J.B., Roberts, S.P. & Elekonich, M.M. (2008) Age and natural metabolically-intensive
893 behavior affect oxidative stress and antioxidant mechanisms. *Experimental Gerontology*. 43 (6), 538–
894 549. doi:10.1016/j.exger.2008.02.001.

895 Wood, S.N. (2017) *Generalized Additive Models: An Introduction with R, Second Edition*. 2nd edition.
896 New York, Chapman and Hall/CRC. doi:10.1201/9781315370279.

897 Wright, J., Bolstad, G.H., Araya-Ajoy, Y.G. & Dingemanse, N.J. (2019) Life-history evolution under
898 fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes.
899 *Biological Reviews*. 94 (1), 230–247. doi:10.1111/brv.12451.

900