

1 Seychelles warblers with silver spoons:
2 juvenile condition is a lifelong predictor of
3 annual survival, but not annual
4 reproduction or senescence
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28 Abstract

- 29 1) The environment experienced during development, and its impact on intrinsic condition, can
30 have lasting outcomes for adult phenotypes and could contribute to the individual variation
31 in senescence trajectories.
- 32 2) However, the nature of this relationship in wild populations remains uncertain, owing to the
33 difficulties in summarizing environmental complexity and long-term monitoring of individuals
34 from free-roaming long-lived species.
- 35 3) In this study, we determine whether juvenile condition (derived from measures of body mass
36 and size) is associated with senescence-related traits of a closely monitored population of
37 Seychelles warblers (*Acrocephalus sechellensis*).
- 38 4) Juveniles with a higher condition index were more likely to survive to adulthood – suggesting
39 these juveniles experienced better developmental conditions. Furthermore, these juveniles
40 as adults were in better condition and had higher rates of annual survival, independently of
41 age. In contrast, there was no association between juvenile condition and declines in adult
42 telomere length (a measure of somatic stress) nor annual reproduction.
- 43 5) These results indicate that juvenile condition, while not associated with senescence
44 trajectories, can influence the likelihood of surviving to old age due to silver-spoon effects.
45 This study shows that measures of intrinsic condition in juveniles can provide important
46 insights into long-term fitness of individuals in wild populations.

47 Introduction

48 Senescence – defined as the decline in fitness-related traits with advancing age - is widespread across
49 the tree of life (Jones et al, 2014). However, longitudinal studies have demonstrated that, even within
50 the same species, individuals can show considerable variation in their onset and rate of senescence in
51 natural environments (Williams *et al.*, 2006; Nussey *et al.*, 2013). Identifying drivers of this individual
52 variation is vital for understanding the causes and evolution of senescence. Environmental factors can
53 play a crucial role in shaping individual senescence (Monaghan *et al.*, 2008). For example, elderly
54 individuals have been shown to be more vulnerable to harsh environments than prime-aged
55 individuals (Reichert *et al.*, 2010; Oro *et al.*, 2014). Furthermore, the onset and rate of senescence can
56 be affected by the environment experienced during early-life. The developmental period – the time
57 from conception to sexual maturity – is of particular importance in modulating the adult phenotype
58 (Lindström, 1999; Taborsky, 2006; Vaiserman, Koliada and Lushchak, 2018). However, there remains
59 uncertainty on how the developmental environment affects senescence.

60 There is abundant evidence that beneficial (or benign) environmental conditions during development,
61 such as a high nutrition diet, have positive effects on multiple aspects of individual fitness (Lindström,
62 1999; Cooper and Kruuk, 2018a); a phenomenon referred to as the “silver-spoon effect” (Monaghan,
63 2008a). The silver-spoon effect may result in delayed (or reduced rate of) senescence when the fitness
64 benefits of beneficial conditions during development persist into late-life (Nussey *et al.*, 2007; Pigeon,
65 Festa-Bianchet and Pelletier, 2017; Cooper and Kruuk, 2018). However, silver-spoon effects may also
66 lead to earlier and accelerated senescence (e.g. Hunt *et al.*, 2004; Spagopoulou *et al.*, 2020), for
67 example when a greater allocation of resources into growth and reproduction during early-life - as a
68 result of beneficial early-life conditions - negatively affects somatic maintenance and, consequently,
69 later-life fitness (Hammers *et al.*, 2013; Lemaitre *et al.*, 2014, Kirkwood, 1977). A recent meta-analysis
70 found that good developmental environments are more often associated with slower rates of
71 reproductive (but not survival) senescence in wild populations; suggesting persistent silver-spoon
72 effects are more prevalent (or detectable) than early- versus late-life fitness trade-offs (Cooper and
73 Kruuk, 2018).

74 While development environments clearly act as a constraining force on an individual’s age-specific
75 fitness (and hence senescence), this may also interact with the responses of juveniles to those
76 environments. For example, harsh developmental environments can generate more resilient adult
77 phenotypes (‘thrifty phenotype hypothesis’; Hales and Barker 2001) or remove individuals with less-
78 resilient phenotypes at younger ages (selection hypothesis; Nol and Smith, 1987), resulting in
79 individuals that are more resistant to fitness declines in late-life (Marshall *et al.*, 2017). Additionally,
80 the developmental environment, whether good or bad, may be less important for senescence than
81 whether or not the same environment persists into adulthood, with environmental mismatches
82 resulting in poorly-adapted, faster senescing individuals (Gluckman, Hanson and Spencer, 2005;
83 Monaghan, 2008). Thus, while there is agreement that developmental environments can explain
84 between-individual variation in senescence, there is yet little consensus on the reason for, or direction
85 of, the effect.

86 Determining the relationship between a developmental environment and senescence is not
87 straightforward, not least because of the multi-faceted nature of environment. Most previous studies
88 have measured characteristics of the environment directly, with proxies of food availability or closely
89 related factors e.g. population density and weather (Cooper and Kruuk, 2018a). However, such
90 measures often lack the resolution to determine local individual-level environments, nor do they
91 reflect the developmental decisions occurring within juveniles in response to environmental stimuli.
92 This difficulty can be addressed by measuring metrics of intrinsic condition that reflect the
93 developmental environment.

94 Body mass and derived indices (e.g. size-adjusted mass) are commonly used measures of individual
95 condition in ecological studies. Body mass is strongly positively correlated with body fat content – the
96 main component of energy storage – and the structural size of individuals (Schulte-Hostedde *et al.*,
97 2005; Hayes and Shonkwiler, 2010; Labocha and Hayes, 2012a). In juveniles, being heavier or larger
98 often reduces vulnerability to predation (at least in non-flying organisms – see below), food-shortages
99 and cold-weather events, and can provide a competitive advantage over peers (Arendt, 1997). As a
100 result, juvenile body mass is generally positively associated with survival to adulthood in birds and
101 mammals (Tinbergen and Boerlijst, 1990; Ronget *et al.*, 2018a). However, there has been extensive
102 debate concerning the quantification of condition (Green, 2001; Speakman, 2001; Stevenson and
103 Woods, 2006; Labocha and Hayes, 2012b; Labocha, Schutz and Hayes, 2014; Wilder, Raubenheimer
104 and Simpson, 2016; Frauendorf *et al.*, 2021), which agree that simple positive correlations between
105 body mass, condition and fitness cannot be assumed without validation. For example, excessive fat
106 deposition (i.e. high body mass relative to size) can reduce an individual’s ability to evade predators,
107 especially for flying organisms (Gosler, Greenwood and Perrins, 1995; Covas *et al.*, 2002). Therefore,
108 the optimal body mass is expected to be less than the maximum achievable body mass (Barnett *et al.*,
109 2015).

110 Juvenile body mass and derived condition indices may also have lasting associations with fitness-
111 related traits (e.g. Merilä and Svensson, 1997). The growth and fat deposition of juveniles can be
112 constrained or delayed by poor (e.g. nutrient-limited) environments, with long-lasting consequences
113 for physiological development and fitness (Metcalf and Monaghan, 2001; Hsu, Dijkstra and
114 Groothuis, 2017; Seress *et al.*, 2020). For example, in captive zebra finches (*Taeniopygia guttata*)
115 juveniles reared on poor-quality diets had lower body mass, but also lower reproductive success
116 (Haywood and Perrins, 1992; Blount *et al.*, 2006) and shorter adult life-spans (Birkhead, Fletcher and
117 Pellatt, 1999). Therefore, juvenile body mass can reflect a silver-spoon effect of early-life environment
118 on adult fitness. Conversely, due to trade-offs between early and late-life fitness, individuals which
119 are larger (and thus heavier) or grow at faster rates can have reduced fitness in late-life (Miller *et al.*,
120 2002; Metcalfe and Monaghan, 2003; Kraus, Pavard and Promislow, 2013; Vaiserman, Koliada and
121 Lushchak, 2018). Achieving larger absolute size, or attaining adult size earlier, reflects a greater
122 investment in growth, which may incur costs in terms of late-life fitness i.e. a ‘live-fast-die-young’
123 phenotype. Likewise, individuals reared in poor-nutrition environments may prioritize energy
124 retention (i.e. fat content) over growth and size i.e. a ‘thrifty’ phenotype. Therefore, the initial benefits
125 of high body mass, large size or a beneficial early-life environment (e.g. high food abundance) can
126 result in accelerated senescence.

127 Our current understanding of the relationships between juvenile body mass, size and senescence is
128 mainly restricted to studies that have manipulated body mass or growth rates of laboratory and
129 captive populations (but see Spagopoulou et al., 2020). In wild populations, body mass and derived
130 condition indices are more often related to immediate fitness (i.e. annual measures of survival and
131 reproductive success) rather than lifetime or late-life fitness; owing to the difficulty of monitoring
132 individuals across their entire life course in many wild populations (but see Lewin *et al.*, 2017).
133 Therefore, it is not certain whether natural variation in juvenile body mass and size can explain
134 variation in senescence trajectories observed in wild populations. In this study, we determine whether
135 the body mass of juveniles predicts fitness-related traits in adult Seychelles warblers, *Acrocephalus*
136 *sechellensis* – a small insectivorous passerine endemic to the Seychelles. The closely monitored
137 population on Cousin Island is uniquely suited for this study; each individual has annual measures of
138 survival and reproduction, and repeated measures of condition starting from juvenile age. This study
139 will contribute to our understanding of the role that early-life condition plays on variable senescing
140 phenotypes in wild populations.

141 Methods

142 Study species and data collection

143 The Seychelles warbler is a small insectivorous passerine endemic to the Seychelles. The population
144 on Cousin Island (29 ha; 4°20' S, 55°40' E) – containing *ca.* 320 adult individuals at any given point
145 (Brouwer et al 2009) – has been extensively monitored since 1985 (Komdeur, 1992; Hammers *et al.*,
146 2015; Sparks *et al.*, 2020a). Since 1997, nearly all individuals (>96%) have been ringed with a unique
147 combination of a British Trust for Ornithology (BTO) metal ring and three colour rings for easy
148 identification (Richardson *et al.*, 2001; Raj Pant *et al.*, 2020a). Individuals are usually first caught as
149 nestlings, or as dependent juveniles (<5 months old) in their natal territory using mist nets (see Kingma
150 *et al.*, 2016 for details). Juveniles are aged as fledglings (1–3 months), old fledglings (3–5 months) or
151 sub-adults (5–12 months) based on behaviour and eye colour (Komdeur, 1992). In addition to
152 capturing unringed juveniles, as much of the ringed adult population as possible (normally *ca.* 35%) is
153 re-captured and sampled during the major breeding season (June–September) each year.

154 The population is structured into *ca.* 115 clearly defined territories (Kingma *et al.*, 2016), each
155 containing a socially monogamous dominant pair. However, the Seychelles warbler is a facultative
156 cooperative breeder; thus, *ca.* 50% of territories contain 1-5 sexually mature subordinates (usually,
157 but not always, past offspring of the dominant pair), of which *ca.* 20% of males and *ca.* 42% of females
158 engage in helping behaviour and cobreeding (Richardson, Burke and Komdeur, 2002; Hammers *et al.*,
159 2019). Each year, during the major breeding season, each territory is visited at least every two weeks

160 to identify all individuals present and determine their status through behavioural observations
161 (Richardson, Burke and Komdeur, 2003). During visits, the dominant female is followed for ≥ 15
162 minutes to assess breeding activity (Richardson, Burke and Komdeur, 2007). The majority of breeding
163 activity (94% of territories) occurs from June to August, but a minor breeding season also occurs from
164 January to March (Komdeur and Daan, 2005). Most breeding attempts involve one-egg clutches
165 (Komdeur, 1994a) but clutches of two or three eggs occur (Richardson *et al.*, 2001). The extensive
166 duration of parental care (ca. three months post fledging), relative to the length of breeding seasons,
167 limits the opportunity for multiple successful breeding attempts (Komdeur, 1996b). As a result, the
168 vast majority of successful territories produce just one offspring per breeding season.

169 In both males and females, annual reproductive success follows a bell-shaped relationship with age;
170 increasing until 7–8 years-of-age before declining in older age (Hammers *et al.*, 2012; Raj Pant *et al.*,
171 2020a). The resighting probability of adults during the major breeding season is close to one ($0.98 \pm$
172 0.01 SE; Brouwer *et al.*, 2010) and dispersal from the island is virtually absent (Komdeur *et al.*, 2004).
173 Therefore, individuals that are not observed during the major breeding season can be confidently
174 assumed dead. First year survival is 0.61 ± 0.09 SE, increasing to a relatively stable 0.84 ± 0.04 SE
175 annual survival in adults (Brouwer *et al.*, 2006), before declining from ca. 7 years of age i.e. the onset
176 of survival senescence (Hammers *et al.*, 2013; 2015). In elderly females, reproductive success is also
177 lower in the last year of life (“Terminal year effect”), suggesting that elderly females are in poorer
178 physiological condition prior to death (Hammers *et al.*, 2012).

179 During capture events, body mass is measured using either a Pesola or electronic scale (± 0.1 g) and
180 structural size is measured using sliding callipers (± 0.1 mm) as the length of the right tarsus. Ca 25 μ l
181 of blood is taken from the brachial vein and stored in 100% ethanol (Richardson *et al.*, 2001). DNA
182 extracted from blood samples (following Richardson *et al.*, 2001) is used to confirm sex, using up to
183 three sexing markers, and assign parentage using MasterBayes 2.52 (Hadfield *et al.* 2006) based on
184 genotypes derived from 30 microsatellite loci (for details see Sparks *et al.*, 2020). Relative Telomere
185 Length (RTL; the concentration of amplified telomeric DNA relative to that amplified at GAPDH – a
186 single copy gene) has also been measured as part of a previous study (for details see Spurgin *et al.*,
187 2017). In many species, including the Seychelles warbler, telomere length declines with age and with
188 increased exposure to various stressors (Barrett *et al.*, 2013; Spurgin *et al.*, 2017; Young, 2018). Thus,
189 telomere length has been advocated as a marker of accumulated somatic stress and survival prospects
190 (Wilbourn *et al.*, 2018).

191 Statistical analysis

192 All analyses were performed in Rstudio (version 1.2.5033 and R version 4.0.3, Rstudio Team, 2020).
193 We selected all individuals with biometric data at post-fledging juvenile age (3 weeks to 5 months
194 after hatching). This is just after the developmental period when skeletal growth is complete
195 (Komdeur, 1991), when juveniles are still dependent on the adults from the natal territory, and before
196 sexual maturity (ca. 8 months; Komdeur, 1997). The Seychelles warbler is sexually dimorphic, with
197 males being larger than females (Richardson 2013). Body mass, as well as being higher in males than
198 females, is also positively correlated with structural size (tarsus length) and the time of day of capture
199 (Fig. S1, Table S1, Kingma *et al.*, 2016). Using linear mixed effect models, which predicted the mass of
200 an individual for a given tarsus length, measured at a given time of day, we calculated residual mass
201 (i.e. the difference between observed and predicted mass) separately for males and females. Observer
202 was included as a random effect to control for possible observer bias in measurements. This approach
203 eliminates the dependency of body mass on other predictors, namely tarsus length and sex, in multiple
204 regression models; thus, giving the “true” effect of body mass on the response variable beyond that
205 caused by size- or sex- related differences in body mass (e.g. Ross *et al.*, 2021). Residual mass
206 (hereafter, “condition”) is a widely used condition index that is highly correlated with fat content in
207 other species (Schulte-Hostedde *et al.*, 2005; Labocha and Hayes, 2012a). However, condition can also
208 reflect differences in bodily components other than fat content, such as muscle and organ mass
209 (Labocha and Hayes, 2012b; Frauendorf *et al.*, 2021). For a subset of juveniles ($N = 364$), we had visual
210 estimates of abdominal fat (hereafter, “fat scores”) which, although positively correlated ($\beta = 0.105 \pm$
211 0.050 , $t = 2.088$, $P = 0.038$; Fig. S1), explained a negligible amount of variation in condition (adjusted
212 $R^2 = 0.009$). Since we lack the data to test the degree to which condition and/or fat scores correlate
213 with actual fat content in this species, condition is more broadly defined as the mass of an individual
214 that is independent of structural size, sex and capture time. All analyses were repeated with raw body
215 mass instead of condition, which produced qualitatively similar results (not shown).

216 We first determined whether juvenile condition influenced survival to adulthood (>1 year of age).
217 Survival to adulthood (yes/no) was fitted as a binomial response with log link function in a generalized
218 linear mixed model (GLMM) using lme4 1.1-25 (Bates *et al.*, 2015). Condition was entered as main
219 effect and as a quadratic (i.e. squared) function (see Barnett *et al.*, 2015). To confirm the fit suggested
220 by the quadratic function, we repeated the analyses using a Generalized Additive Mixed Model
221 (GAMM) using gamm4 (v0.2-6; Wood, 2017) with a non-parametric smoothing spline for juvenile
222 condition. Additional predictors included sex, age (months) of measurement and tarsus length (mean-
223 centered by sex) - to determine whether skeletal size influences survival independently of condition.
224 Year was included as a random factor to account for annual differences in juvenile survival.

225 In subsequent juvenile survival models, we included information on the individual's overall and
226 immunological genetic diversity (for which we had a reduced dataset). Heterozygosity, MHC diversity
227 (log transformed) and the presence of TLR3^A and MHC *Ase-ua4* alleles (yes/no) have been positively
228 associated with juvenile survival in earlier studies on this species (Richardson, Komdeur and Burke,
229 2004; Brouwer *et al.*, 2010; Davies *et al.*, 2021). Therefore, by including these additional predictors
230 into our model, we determined whether the juvenile survival-condition relationship occurred
231 independently of these genetic effects.

232 Secondly, for juveniles that survived to adulthood, we tested whether juvenile condition was
233 associated with two measures of adult condition – body mass and RTL – to assess physiological
234 senescence. Both traits were fitted as responses in two Linear Mixed Models (LMM). Juvenile
235 condition, adult tarsus length and sex were included as main effects. In the body mass model, capture
236 time was included as an additional predictor. We opted to use raw body mass as a measure of adult
237 condition, rather than the residual condition index used in juveniles, since these measures are
238 equivalent in a model controlling for the effects of sex, tarsus length and capture time on adult body
239 mass in a LMM (Freckleton 2002). In the RTL model, we included technician as a two-level factor to
240 account for technician-related differences in RTL (Sparks *et al.*, 2020b). We used within-subject
241 centering (van de Pol and Wright, 2009) to separate the role of between- versus within-individual
242 variation with age, i.e. cross-sectional from longitudinal effects. In this way, the individual's age (at
243 measurement of body mass/telomere length) was split into two predictors, (i) mean age across all
244 sampling events for a given individual (mean age), and (ii) within-individual deviation from mean age
245 (Δ age). An interaction term between juvenile condition and Δ age tested whether juvenile condition
246 alters the within-individual slope of adult body mass/telomere length. Since individuals often had
247 multiple measures of adult body mass and telomere length, individual identity was included as a
248 random effect. In the body mass model, observer was also included as a random effect to control for
249 possible observer bias in measurements. In the telomere length model, PCR plate identity was
250 included as a random effect to control for possible inter-plate variation in telomere length (Sparks *et*
251 *al.*, 2020b).

252 Thirdly, we tested whether juvenile condition was associated with two fitness components shown to
253 senesce in later adult life in the Seychelles warbler; annual survival and annual reproduction
254 (Hammers *et al.*, 2012, 2013, 2015; Raj Pant *et al.*, 2020a). For this analysis, we excluded individuals
255 that had not died by the end of the study period (2019). Furthermore, we excluded the first year of
256 the individual's life, since first year survival was covered in our survival to adulthood analysis (see
257 above) and individuals rarely reproduce before one year of age (Komdeur, 1991, 1992). Annual
258 survival was defined as whether or not the individual died before the subsequent main breeding

259 season. Annual reproduction indicated whether the individual produced at least one independent
260 offspring (i.e. surviving to at least 5 months of age) during that year. These fitness traits were fitted as
261 binomial responses (yes versus no) with a log link function in GLMMs. Juvenile condition was entered
262 as a main effect and as an interaction term with age. A significant main effect would indicate that
263 juvenile condition influences the fitness component overall, independently of age, while a significant
264 interaction would indicate that juvenile condition modifies the age-dependent change in the fitness
265 component. Age (at the end of the main breeding season) was included as a linear and squared term,
266 (Hammers *et al.*, 2012, Raj Pant *et al.*, 2020a). To confirm the presence of late-life declines in survival
267 and reproduction, we repeated analyses including only data above the age of onset of declines;
268 determined visually from non-standardized squared functions of age (Fig. 3a and 4a). Sex and tarsus
269 length were included as additional predictors. Since individuals had multiple measures of fitness,
270 individual identity was included as a random factor. Year was also included as a random factor to
271 control for annual differences in fitness (Brouwer *et al.*, 2006).

272 In the annual reproduction model, additional predictors were included due to their previously
273 reported associations with annual reproduction and fledging success in this system. An interaction
274 term between sex and age was included due to sex-specific differences in the onset of reproductive
275 senescence (Hammers *et al.*, 2012; Raj Pant *et al.*, 2020b). Year quality (i.e. island-wide mean insect
276 abundance during the years main breeding season) and territory quality (i.e. the difference between
277 year quality and insect abundance within the individual's territory) data were available for some years
278 (all except 2000 – 2002 and 2005) and were included due to positive associations with fledging success
279 (Hammers *et al.*, 2012). Whether or not the year in question was the last year of an individual's life
280 (terminal year, yes/no) was included, since fledging success was found to be lower in the terminal
281 year of old (≥ 6 years) females (Hammers *et al.*, 2012). We also included age-at-death, to quantify the
282 within-individual effect of age on reproductive success while controlling for selective disappearance
283 (van de Pol and Verhulst, 2006, Hammers *et al.* 2012).

284 In all models, non-significant interaction terms were removed sequentially (in order of least
285 significance), so that the first order effects could be interpreted, and were only reported if of specific
286 interest. All fixed effects remained in final models (regardless of significance) except for squared
287 functions of continuous variables, which were removed when non-significant (see Whittingham *et al.*,
288 2006). Parameter estimates and significance of removed effects were determined by re-entering them
289 into final models. Continuous fixed effects involved in squared effects and interactions were mean
290 centered to reduce collinearity and aid interpretation (Schiegg, 2010). Where model singularity
291 errors occurred, we applied maximum a posteriori estimation using *blme* (v1.0-5; Dorie, 2013). To aid

292 model convergence of GLMMs, we used the “BOBYQA” nonlinear optimization (Powell, 2009). Model
293 fit was calculated as conditional R^2 using MuMin (v1.43.17; Bartoń, 2019).

294 Results

295 Juvenile survival

296 Of the 711 juveniles included in our analysis, 545 survived to adulthood (>1 year-of-age). Juveniles
297 with a higher condition index were more likely to survive to adulthood (Table 1; Fig. 1). The squared
298 condition term revealed a ‘ceiling effect’; juvenile survival increased with condition at values < 0,
299 above which juveniles shared the highest survival prospects (ca. 80%; Fig. 1). The non-parametric
300 smoothing function for condition from the GAMM showed a very similar pattern compared to the
301 quadratic condition term shown in Fig.1 ($df = 2.618$, $F = 5.38$, $P = 0.001$; Fig. S3). Juvenile survival also
302 increased with tarsus length, but was not associated with age or sex (Table 1). Complete data for
303 genetic factors (heterozygosity, MHC diversity, TLR3^A and MHC *Ase-ua4* allele presence), previously
304 shown to influence juvenile survival, were available for 240 juveniles. In our model, none of these
305 genetic factors were associated with survival (Table S2) and the observed juvenile survival-condition
306 relationship remained significant while controlling for these genetic factors (Table S2).

307 Adult Body mass

308 As expected, adult body mass was higher in males and, in both sexes, increased with tarsus length and
309 time of capture; in a similar manner to that observed with juvenile body mass (Table S1). While
310 controlling for these factors, adult body mass was positively correlated with juvenile condition (Table
311 2a; Fig. 2). This indicated that relatively heavier or lighter juveniles tended to remain relatively heavier
312 or lighter, respectively, as adults. Adult body mass increased with age between individuals (i.e. cross-
313 sectional) and not within-individuals (longitudinal), but these slopes did not significantly differ ($t =$
314 1.776 , $P = 0.076$), indicating that the between-individual rate of increase was not greater than the
315 within-individual lack of change. (Table 2a).

316 Telomere length

317 RTL tended to decreased both within and between individuals with increasing age (Table 2b). The
318 within- and between individual rate of change in RTL did not significantly differ ($t = -1.770$, $P = 0.078$).
319 Juvenile condition was not associated with overall adult RTL (Table 2b) nor the within-individual
320 decline in RTL (Table 2b; Δ age \times Juvenile condition). Telomere length was not associated with sex or
321 tarsus length (Table 2b).

322 Annual adult survival

323 Annual survival remained relatively stable at ca. 80% from one to seven years-of-age, beyond which
324 annual survival declined with age (Fig. 3a). This decline in annual survival was confirmed by re-running

325 the analysis with data ≥ 7 years-of-age ($\beta = -0.2523 \pm 0.086$, $z = -2.954$, $P = 0.003$). Juvenile condition
326 was positively associated with annual survival, independent of age (Table 3a; Age \times Juvenile condition,
327 Fig. 3b). Therefore, individuals with higher condition index as juveniles had higher annual survival
328 throughout adult life. Annual survival was not influenced by sex or tarsus length (Table 3a)

329 Annual reproductive success

330 Neither year quality nor territory quality were associated with annual reproduction and so were
331 removed as predictors to maximize sample size ($N = 1034$ versus $N = 1242$). Annual reproduction
332 exhibited a humped relationship with age; increasing in early-life before peaking and declining from
333 mid- to late-life (Fig. 4a). The age of the peak in annual reproduction (and thus the onset of
334 reproductive senescence) differed between sexes (Fig. 4a), with female and male annual reproduction
335 peaking at ca. 6 and 8 years-of-age. Annual reproduction was also lower in the terminal year (Table
336 3b). Re-running the analysis on ages from the onset of reproductive senescence (≥ 6 years for females,
337 ≥ 8 years in males) confirmed that annual reproduction declined with advanced age, and that the slope
338 of the decline was greatest in the terminal year (Age \times Terminal year: $\beta = 0.442 \pm 0.180$, $z = 2.459$, P
339 $= 0.014$, Fig. 4b). Juvenile condition was not associated with annual reproduction, nor with the age-
340 dependent change in annual reproduction (Table 3b; Age \times Juvenile condition). Annual reproduction
341 was not influenced by tarsus length (Table 3b).

342 Discussion

343 Juvenile condition (size-, sex- and time- corrected mass) was positively associated with survival to
344 adulthood, independently of specific genetic factors. For individuals that survived to adulthood,
345 juvenile condition was positively associated with adult body mass - indicating that individual
346 differences in condition are maintained from the juvenile period to throughout adulthood. More
347 importantly, the survival benefit of high juvenile condition persisted throughout adult-life. Therefore,
348 juveniles that reached adulthood despite a low condition index still had poorer survival in a given year
349 compared to adults that had a high juvenile condition index. The effect of juvenile condition on annual
350 survival was constant with age, i.e. the age-dependent decline in survival from 7 years-of-age observed
351 in this species did not change in respect to juvenile condition. So while juveniles in better condition
352 are more likely to reach older ages (i.e. have greater longevity), they still exhibit the same pattern of
353 survival senescence as those individuals that had poor condition as juveniles. There was no effect of
354 juvenile condition on annual reproductive success, nor the maintenance of adult telomere length.

355 That condition is positively associated with a juvenile's likelihood of surviving to adulthood in the
356 Seychelles warbler is consistent with findings across birds and mammals (reviewed in Ronget *et al.*,
357 2018). It is likely that a high condition index is indicative of a good natal environment, which

358 subsequently leads to higher survival. Indeed, juvenile Seychelles warblers receiving cooperative nest
359 care have higher provisioning rates and, consequently, higher mass than juveniles without helpers
360 (Komdeur, 1994b; van Boheemen *et al.*, 2019). Furthermore, the presence of helpers and higher food
361 abundance have been associated with higher juvenile survival (Komdeur, 1992; Brouwer *et al.*, 2006;
362 Hammers *et al.*, 2021). While these findings are correlative, experimental studies demonstrate that
363 manipulations of natal/early-life environments have similar outcomes for juvenile mass/condition and
364 survival in other species (e.g. Le Galliard, Ferrière and Clobert, 2005; Grace *et al.*, 2017). Direct benefits
365 of high condition also occur where this reflects more abundant energy stores (i.e. fat and protein),
366 since newly independent juveniles lacking experience can be more vulnerable to starvation and
367 exposure (e.g. Jones *et al.*, 2017). In other systems, the benefits of energy storage may be traded
368 against increased predation risk, resulting in a condition-survival relationship that becomes negative
369 with increasing condition (Adriaensen *et al.*, 1998; Blums *et al.*, 2005). In contrast to these systems,
370 we found a condition-survival relationship did not become negative, which was expected given that
371 post-fledging predation does not occur in this population (Komdeur, 1996a). In fact, previous work in
372 this species suggests that individual condition (size-adjusted mass) is primarily constrained by food
373 availability and population density (Brouwer *et al.*, 2009). Therefore, mass-derived condition is
374 indicative of intrinsic condition in juveniles of this system.

375 Juvenile condition was positively correlated with adulthood body mass in the Seychelles warbler,
376 independently of permanent mass constraints such as sex and structural size. This indicates that
377 between-individual differences in the variable component of juvenile mass (e.g. fat, muscle) is partially
378 maintained across an individual's lifetime. Similar within-individual consistencies between juvenile
379 and adult condition have been observed in other bird species (Merilä and Svensson, 1997; Guillemain
380 *et al.*, 2013). Previous studies on adult Seychelles warblers have shown that mass is lost during energy-
381 demanding reproductive behaviors (Komdeur, 2001; van de Crommenacker, Komdeur and
382 Richardson, 2011; Bebbington *et al.*, 2017). Therefore, heavier juveniles may be better able to
383 maintain or recover lost energy reserves (i.e. mass) in adult-life, perhaps contributing to heavier
384 juveniles also having higher rates of annual survival observed in this study. Conversely, achieving high
385 juvenile condition at the expense of other physiological components could have negative
386 consequences for adult condition. One potential trade-off is a greater rate of telomere shortening in
387 early-life, resulting in shorter telomere lengths in adulthood (Monaghan and Ozanne, 2018). In many
388 systems, including the Seychelles warbler, short telomeres and/or greater telomere shortening in
389 adulthood also reflects more stressful life-histories and reduced survival prospects (Barrett *et al.*,
390 2013; Monaghan and Ozanne, 2018; Wilbourn *et al.*, 2018; Hammers *et al.*, 2019). However, we found
391 no association between juvenile condition and adult telomere length, which suggests that the initial

392 benefit of high juvenile condition does not have long-term physiological costs, at least when measured
393 with telomere length.

394 We found that the survival benefits associated with high juvenile condition were not limited to the
395 first year of life in the Seychelles warbler, with heavier juveniles also having higher annual survival
396 throughout adulthood. This is consistent with our adult body mass analysis, which showed that
397 individuals in better condition survived to older ages. Silver-spoon effects of early-life environment on
398 adult survival have been observed in many wild populations (Reid *et al.*, 2003; Van De Pol *et al.*, 2006;
399 Cartwright *et al.*, 2014; Alberts, 2019). Such effects may occur because juveniles that are heavier
400 and/or reared in better natal environments have a competitive advantage that leads to them
401 occupying better quality habitat as adults (Verhulst, Perrins and Riddington, 1997; Both, Visser and
402 Verboven, 1999; Van De Pol *et al.*, 2006). Similarly, juveniles that survive to adulthood despite poor-
403 natal environments, and hence poor condition, may have required compensatory physiological
404 mechanisms that have delayed survival costs (Metcalf and Monaghan, 2001; Briga *et al.*, 2017).

405 The silver-spoon effect of juvenile condition also contributes to lifetime reproductive success, since
406 this is strongly correlated with longevity in this species (Davies *et al.* 2021). However, juvenile
407 condition did not affect the probability of producing offspring in a given year (after controlling for age-
408 effects), which is in contrast to studies that have measured the effect of the natal-environment on
409 reproductive success (e.g. Nussey *et al.*, 2007; Douhard *et al.*, 2014). In this system, individual breeding
410 attempts are strongly constrained by population density (i.e. limited availability of breeding positions)
411 and seasonal food availability (Komdeur, 1992, 1996c). Additionally, the success of breeding attempts
412 is likely to depend on fine-scale environmental variation, which was not accounted for in this study.
413 Therefore, ecological constraints and confounds may limit the detectable influence of juvenile
414 condition on annual reproductive success. Furthermore, the strong decline of annual reproduction in
415 the terminal year likely means that poor-condition and/or illness in the current year outweighs the
416 effect of past condition (Hammers *et al.*, 2012).

417 The effect on juvenile condition on annual survival was constant with age, and did not affect the onset
418 or rate of survival senescence. This is consistent with a recent meta-analysis that found that the quality
419 of early-life environments was not associated with survival senescence across 18 wild populations
420 (Cooper and Kruuk, 2018). One explanation is that the majority of individuals that experience poor
421 early-life conditions, or are themselves in poor condition, die before reaching senescent age (the age
422 at which a population exhibits reduced survival), while the few individuals that reach old age share
423 traits that mask the effects of early-life factors (“selection hypothesis”; Nol and Smith, 1987; Dugdale
424 *et al.*, 2011). Another possibility is that the silver-spoon effect of juvenile condition is not associated

425 with early-life investments (e.g. growth, reproductive effort) that have delayed costs for late-life
426 performance (Hunt et al., 2004; Spagopoulou et al., 2020). For example, Hammers *et al.* 2013
427 identified in this species a trade-off between early-life reproductive effort and late-life survival;
428 individuals that start breeding at earlier ages had an earlier onset of survival senescence. In contrast,
429 our findings suggest that investments in early adult-life (in terms of age-specific annual reproduction)
430 are not associated with juvenile condition. Therefore, juvenile condition may fail to generate such
431 resource allocation trade-offs (i.e. between early-life reproductive effort and somatic maintenance)
432 that influence senescence patterns.

433 Our study shows that a juvenile's mass-derived condition can be a marker of persistent individual
434 differences in adult condition and performance. This finding reinforces the hypothesis that natal-
435 environmental factors that influence juvenile mass can have individual fitness consequences beyond
436 juvenile survival. While juvenile mass was not found to predict individual differences in senescence
437 rates, either directly or via associations with early-life investments, juvenile condition is positively
438 associated with longevity, and thus the likelihood of reaching the age at which senescence occurs in
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450 Author contributions

451 The study was conceived by T.J.B and D.S.R. Data was collected by all authors. Statistical analyses were
452 conducted by T.J.B with input from D.S.R and H.L.D. The manuscript was written by T.J.B and all
453 authors critiqued the output with important intellectual content. All authors gave their final approval
454 for publication.

455 Conflict of interests

456 None declared.

457 Data availability Statement

458 The data that support the findings of this study will be made openly available in Dryad Digital
459 Repository.

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761 Tables

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Table 1: General linear mixed effects exploring predictors of juvenile survival to adulthood in Seychelles warblers. Significant effects are in bold.

<i>Juvenile survival</i> ; conditional $R^2 = 0.061$				
Predictor	Estimate	SE	z	P
(Intercept)	1.159	0.307	3.769	<0.001
Condition	0.243	0.093	2.613	0.009
Condition²	-0.115	0.058	-1.989	0.047
Age (months)	0.996	1.077	0.925	0.355
Sex (female)	-0.086	0.184	-0.469	0.639
Tarsus length	0.208	0.095	2.195	0.028
Random	699 individuals	Variance		
Catch year	22 years	0.048		

Table 2: Linear mixed effects models explaining variation in a) Adult body mass, and b) Relative telomere length in the Seychelles warbler. Significant effects are in bold.

<i>a) Adult body mass</i> ; conditional $R^2 = 0.612$				
Predictor	Estimate	SE	t	P
(Intercept)	7.107	1.288	5.520	<0.001
Juvenile condition	0.199	0.036	5.573	<0.001
Sex (female)	-0.848	0.102	-8.315	<0.001
Tarsus length	0.338	0.050	6.800	<0.001
Time of capture	0.001	0.000	4.769	<0.001
Mean age	0.041	0.018	2.264	0.024
Δ age	-0.003	0.016	-0.191	0.848
Δ age \times Juvenile condition	-0.002	0.016	-0.105	0.917

Random	704 observations	Variance
Bird Identity	311 individuals	0.114
Observer	41 observers	0.040
Residual		0.490

b) Relative telomere length; conditional $R^2 = 0.178$

Predictor	Estimate	SE	t	P
(Intercept)	0.933	0.025	37.666	<0.001
Juvenile condition	0.009	0.010	0.933	0.353
Sex (female)	<0.001	0.019	0.000	1.000
Tarsus length	-0.002	0.010	-0.185	0.854
Δ age	-0.011	0.006	-1.770	0.078
Mean age	-0.009	0.005	-1.987	0.049
Technician	0.081	0.022	3.709	<0.001
Δ age \times Juvenile condition	0.007	0.006	1.163	0.246

Random	427 observations	Variance
Bird Identity	207 individuals	0.001
qPCR plate	70 PCR plates	0.004
Residual		0.032

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Table 3: General linear mixed effects models explaining variation in a) annual survival and b) annual reproductive success in adult Seychelles warblers. Significant effects are in bold.

a) Annual survival; conditional $R^2 = 0.245$

Predictor	Estimate	SE	z	P
(Intercept)	1.176	0.252	4.674	0.000
Age	0.148	0.117	1.260	0.208
Age²	-0.132	0.059	-2.239	0.025
Juvenile condition	0.175	0.080	2.185	0.029
Sex (female)	0.066	0.147	0.449	0.653
Tarsus length	0.112	0.076	1.477	0.140
Age \times juvenile condition	0.079	0.103	0.763	0.445
Age ² \times Juvenile condition	-0.077	0.065	-1.186	0.236
Random	1242 observations	Variance		
Bird Identity	306 individuals	0.110		
Year	21 years	0.897		

b) Annual Reproductive success; conditional $R^2 = 0.287$

Predictor	Estimate	SE	z	P
(Intercept)	-1.136	0.261	-4.350	0.000
Age	0.855	0.173	4.935	<0.001

Age²	-0.417	0.093	-4.501	<0.001
Juvenile condition	0.114	0.095	1.197	0.231
Sex (female)	-0.143	0.210	-0.680	0.496
Tarsus length	-0.026	0.090	-0.289	0.773
Terminal year (no)	0.718	0.210	3.415	0.001
Age at death	0.052	0.131	0.398	0.691
Age × Sex (female)	-0.597	0.205	-2.913	0.004
Age ² × Sex (female)	0.070	0.134	0.523	0.601
Age × Juvenile residual mass	0.094	0.113	0.828	0.408
Age ² × Juvenile residual mass	-0.129	0.072	-1.794	0.073
Random	1242 observations	Variance		
Bird Identity	306 individuals	0.485		
Year	21 years	0.359		

774 **Figures**
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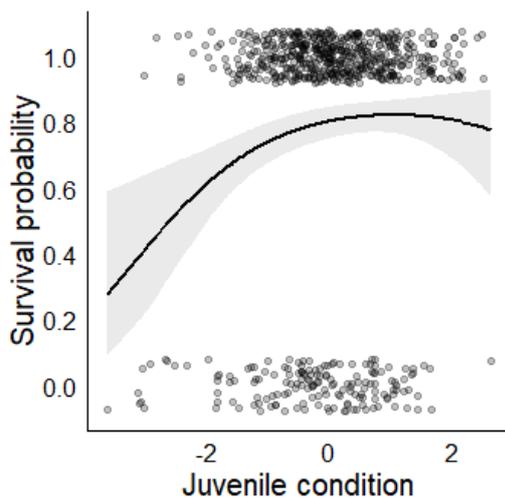


Figure 1: The probability of juvenile Seychelles warblers surviving to adulthood (>1 year of age) relative to their juvenile condition index. The solid line is a binomial regression between survival (Y/N) and condition with 95% confidence limits. Raw data points depict the distribution of jittered observed survival counts (1 = survived, 0 = deceased).

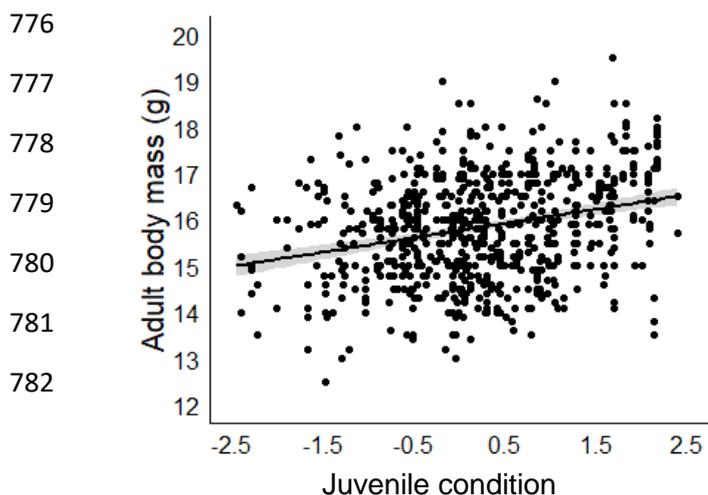


Figure 2: The relationship between juvenile condition and adult (>1 year of age) body mass in the Seychelles warbler. The fit-line is a linear regression with 95% confidence limits. Points depict raw data.

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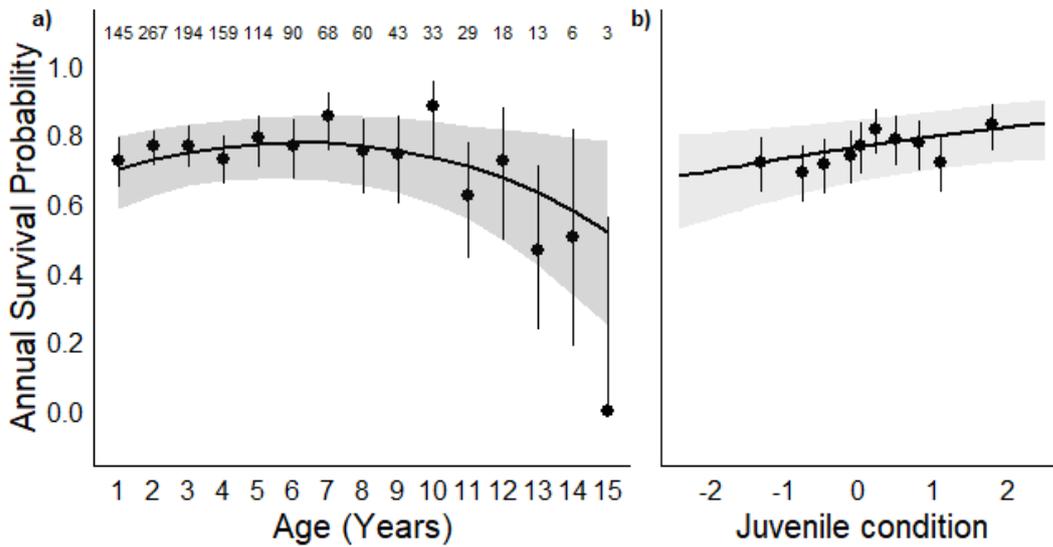


Figure 3: The probability of adult Seychelles warblers surviving to the next year relative to (a) age and (b) juvenile condition. The fit-lines are model-predicted survival curves with 95% confidence limits. Points with error bars are mean survival and binomial 95% confidence intervals of raw data, grouped by (a) age and (b) percentiles of juvenile condition; note that the x-axis position of points corresponds to the percentile distribution of juvenile condition. In text numbers in panel (a) refer to sample sizes per age.

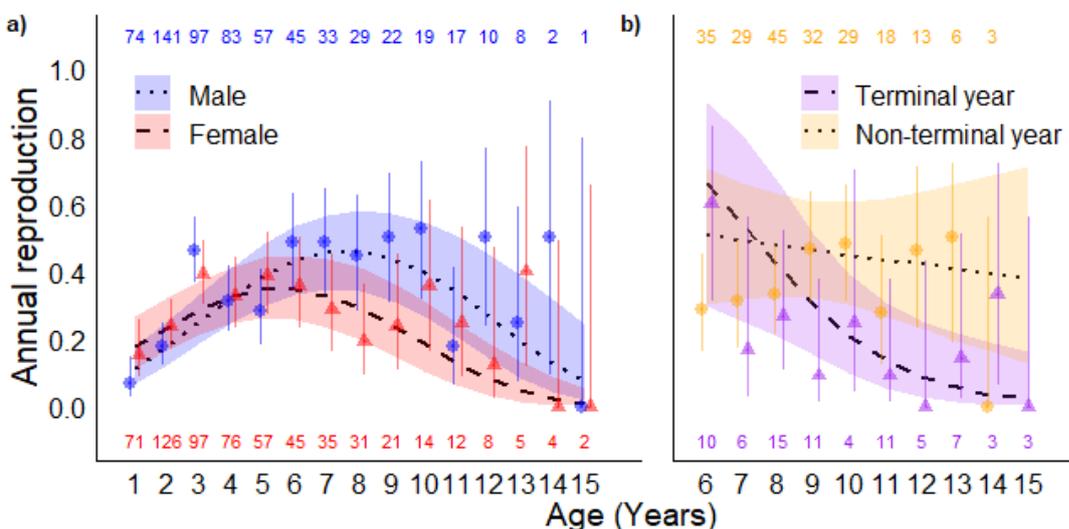


Figure 4: The probability of adult Seychelles warblers producing an independent offspring in a year relative to age and (a) sex and (b) terminal year (yes/no). The fit-lines are model-predicted probability curves with 95% confidence limits. Points with error bars are mean offspring and binomial 95% confidence intervals of raw data, grouped by age per sex (a) and age per terminal year (b). In text numbers refer to the sample sizes per age per grouping variable. Males and females had differing onsets of decline in annual reproduction (a), and the rate of decline was greatest in the terminal year (b).