

Seychelles warblers with silver spoons: juvenile condition is a lifelong predictor of annual survival, but not annual reproduction or senescence

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Abstract

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

Introduction

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

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

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

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

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

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

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

Methods

Study species and data collection

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

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

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

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

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

Statistical analysis

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

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

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

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

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

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

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

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

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

Results

Juvenile survival

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

Adult Body mass

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

Telomere length

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

Annual adult survival

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

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

Annual reproductive success

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

Discussion

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

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

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

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

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

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

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

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

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

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

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Author contributions

The study was conceived by T.J.B and D.S.R. Data was collected by all authors. Statistical analyses were 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 authors critiqued the output with important intellectual content. All authors gave their final approval for publication.

Conflict of interests

None declared.

Data availability Statement

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

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Tables

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 × 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

773

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		

Figures

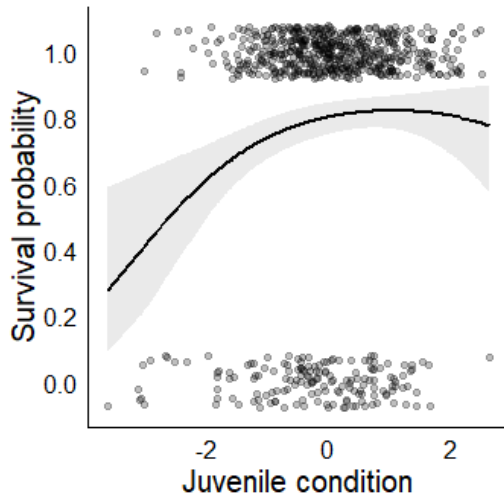


Figure 1: The probability of juvenile Seychelles warblers surviving to adulthood (>1 year of age) relative to their juvenile condition index. The solid line is a binomial regression between survival (Y/N) and condition with 95% confidence limits. Raw data points depict the distribution of jittered observed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

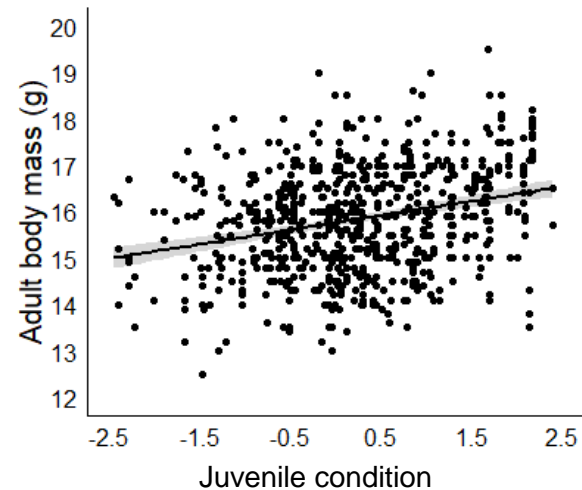


Figure 2: The relationship between juvenile condition and adult (>1 year of age) body mass in the Seychelles warbler. The fit-line is a linear regression with 95% confidence limits. Points depict raw data.

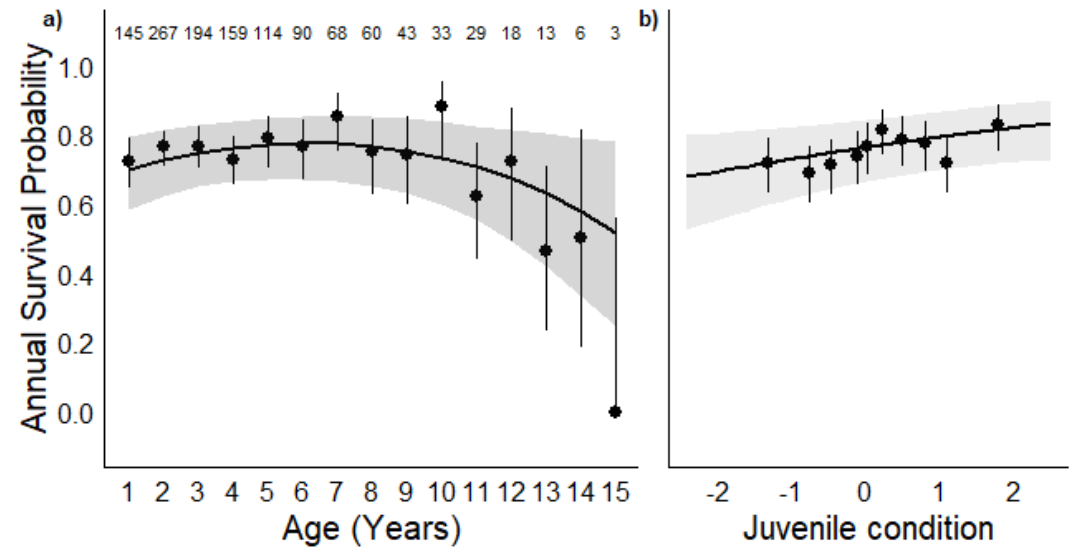


Figure 3: The probability of adult Seychelles warblers surviving to the next year relative to (a) age and (b) juvenile condition. The fit-lines are model-predicted survival curves with 95% confidence limits. Points with error bars are mean survival and binomial 95% confidence intervals of raw data, grouped 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.

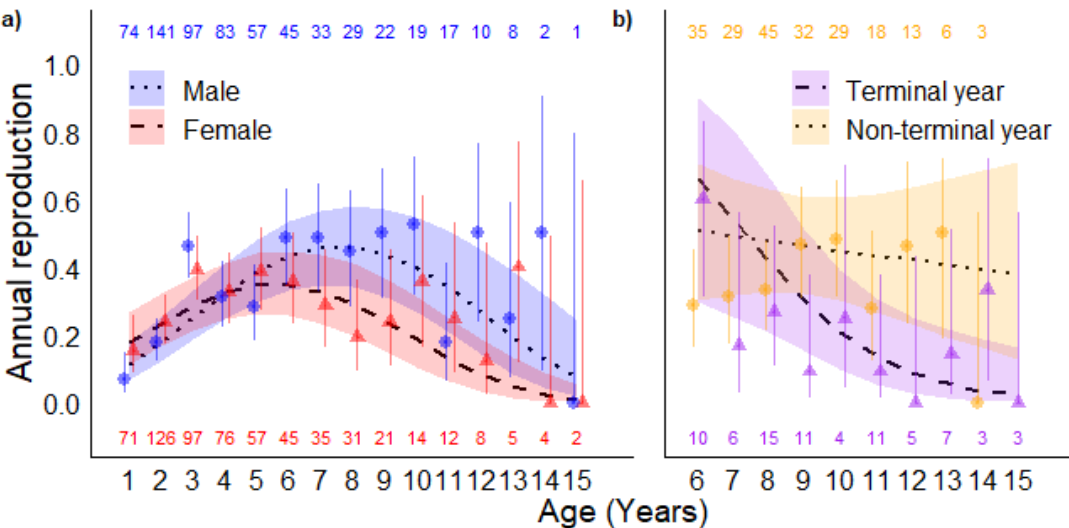


Figure 4: The probability of adult Seychelles warblers producing an independent offspring in a year relative to age and (a) sex and (b) terminal year (yes/no). The fit-lines are model-predicted probability curves with 95% confidence limits. Points with error bars are mean offspring and binomial 95% confidence 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).