Article title:

Sex-dependent effects of parental age on offspring fitness in a cooperatively breeding bird

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Abstract

Parental age can have considerable effects on offspring phenotypes and health. However, intergenerational effects may also have longer-term effects on offspring fitness. Few studies have investigated parental age effects on offspring fitness in natural populations while also testing for sex- and environment-specific effects. Further, longitudinal parental age effects may be masked by population-level processes such as the selective disappearance of poor quality individuals. Here, we used multi-generational data collected on individually marked Seychelles warblers (*Acrocephalus sechellensis*) to investigate the impact of maternal and paternal age on offspring lifespan and lifetime reproductive success. We found negative effects of maternal age on female offspring lifespan and lifetime reproductive success which was likely driven by within-mother effects. There was no difference in annual reproductive output of females born to older versus younger mothers, suggesting that the differences in offspring lifetime reproductive success are driven by offspring lifespan. In contrast, the lifetime reproductive success of male offspring increased with maternal age, but this was driven by between-mother effects. No within- or between-individual paternal age effects were found for female offspring, but fathers that reached old age produced male offspring with higher lifetime reproductive success. We did not find strong evidence for environment-dependent parental age effects. Our study provides evidence for parental age effects on the lifetime fitness of offspring and shows that such effects can be sex-dependent. These results add to the growing literature indicating the importance of intergenerational effects on long-term offspring performance and highlights that these effects can be an important driver of variation in longevity and fitness in the wild.

Impact summary

In virtually all animals an individual’s health and condition deteriorates with age (senescence), which impacts their survival and the number of offspring produced in later life. Importantly, the quality of offspring produced, as measured through their physiological condition, survival and reproductive success, may also be impacted by their parent’s ageing. This may have considerable health and evolutionary implications. However, most of the evidence comes from studies on laboratory animals where artificial conditions exist. Little is known about how, if, and why such effects exist in natural populations where a myriad of different stresses and strains act upon individuals. Furthermore, it remains unclear whether parental age effects on offspring fitness are sex-specific and affected by environmental conditions. Our study reveals that, in wild-living birds, parental age effects on offspring lifespan and lifetime fitness depend on both the sex of the parent and the sex of the offspring. Cross-sectionally, we found negative effects of maternal age on offspring lifespan and lifetime reproductive success of female offspring, which was likely driven by within-maternal age effects. In contrast, there were positive effects of maternal age on the lifetime reproductive success of male offspring. Our study highlights that not including such intergenerational age effects, not separating within- and between-individual effects and not testing for sex-specific effects, may underestimate or obscure important components of senescence in wild populations. These intergenerational effects could have important implications for population dynamics, particularly in age-structured populations, for example in terms of conservation management and evolutionary dynamics.

Introduction

Early-life environmental conditions can have considerable consequences for later-life individual fitness. Parental effects, whereby an offspring's phenotype is influenced by their mother's or father's phenotype, above and beyond the genes they inherit, are widespread in natural populations (Mousseau & Fox 1998) and have important consequences for ecological and evolutionary dynamics (Kirkpatrick & Lande 1989; Wolf *et al.* 1998). For instance, a recent synthesis of studies found that maternal effects explained half as much phenotypic variance as additive genetic effects across all traits, while for morphological and phenological traits maternal effects are comparable to additive genetic effects (Moore *et al.* 2019). While the impact of parental effects are typically largest in early life (Moore *et al.* 2019; Gauzere *et al.* 2020), a growing number of studies have indicated that parental effects can have long-term effects on offspring survival and fitness (Arslan *et al.* 2017; Bock *et al.* 2019).

Due to the deterioration of individuals with age in a process known as senescence, parental age is an important component of parental effects with the potential to have large negative consequences on offspring phenotype and performance. For instance, a negative effect of parental age on offspring lifespan has been reported across a range of taxa in both laboratory and field studies ('Lansing effect'; (Plaistow *et al.* 2015; Wylde *et al.* 2019; Monaghan *et al.* 2020), however this effect is not universal (Fox *et al.* 2003; Yilmaz *et al.* 2008; Krishna *et al.* 2012). Age-dependent declines in parental gamete quality (Monaghan & Metcalfe 2019) and declines in parental care (Hammers *et al.* 2021) are predicted to cause reduced fitness in offspring of elderly parents. Indeed, there is increasing evidence in wild populations that elderly parents produce offspring with lower birth weights, reduced neonatal survival and lower recruitment rates (Hadley *et al.* 2006; Descamps *et al.* 2008; Nussey *et al.* 2009; Hoffman *et al.* 2010; Hayward *et al.* 2015; Fay *et al.* 2016; Hammers *et al.* 2021). However, due to the necessity for long-term longitudinal studies with accurate lifetime reproductive success and survival data, the number of studies that have investigated the impact of parental age on the lifespan and lifetime fitness of offspring in natural populations remains limited (Rödel *et al.* 2009; Bouwhuis *et al.* 2010, 2015; Schroeder *et al.* 2015; Reichert *et al.* 2019; Kroeger *et al.* 2020). Results from these studies have been mixed, finding for maternal age on offspring lifetime reproductive success: no difference (Bouwhuis *et al.* 2010), an optimal middle-age effect (Rödel *et al.* 2009), a lower middle-aged effect (Reichert *et al.* 2019), or a positive effect (Kroeger *et al.* 2020). In contrast, other studies have found negative effects of parental age and that older parents produced offspring with shorter lifespans (Bouwhuis *et al.* 2015) and lower lifetime reproductive success (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015). Further, longitudinal parental age effects may be obscured by population-level processes such as the selective (dis)appearance of poor quality individuals, but these can be separated into within and between-parental age effects using within-subject centering (van de Pol & Wright 2009). However, of these studies in natural populations, only two have separated within from between parental age effects to account for the effects of selective (dis)appearance (Bouwhuis *et al.* 2015; Reichert *et al.* 2019) and only two have investigated both maternal and paternal age effects on offspring of both sexes (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015).

Parental age studies typically focus on maternal age effects, since these are expected to be more important in most species where mothers invest more in offspring than fathers. However, an increasing number are documenting paternal age effects on offspring performance (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015; Fay *et al.* 2016). In addition, offspring sex-dependent effects of parental age have been observed (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015). These may be due to differences between the sexes in their responses to their early life environment or sex-specific epigenetic inheritance or investment (Bouwhuis *et al.* 2015). Although the underlying mechanisms are unknown, documented offspring sex-specific parental age effects are typically found in offspring of the same sex as the parent (Priest *et al.* 2002; Carnes *et al.* 2012; Bouwhuis *et al.* 2015; Lind *et al.* 2015; Schroeder *et al.* 2015). Further, while early-life environmental conditions affect offspring fitness (Monaghan 2008), only one study has investigated how such conditions may interact with parental age (Kroeger *et al.* 2020). More longitudinal studies investigating both maternal and paternal age effects and testing whether these effects are dependent on offspring sex, or the environment, are needed to fully assess the importance of parental age effects.

Here, we examine the relationships between parental age and offspring lifespan and lifetime fitness in the facultatively cooperative-breeding Seychelles warbler (*Acrocephalus sechellensis*). The entire population on Cousin Island has been the subject of a long-term individual-based monitoring project since 1985. Seychelles warblers live in and defend territories in which a dominant male and female reside. Around half of these territories may also contain subordinate individuals, of which approximately one third help with parental care in any given year (Hammers *et al.* 2019). A combination of high annual resighting rates (Brouwer *et al.* 2006), virtually no inter-island dispersal (Komdeur *et al.* 2004) and low extrinsic mortality means that the birds live long lives (up to 19 years) and accurate birth and death years can be estimated (Hammers *et al.* 2015). High levels of extra-pair paternity and subordinate female breeding occur (Raj Pant *et al.* 2019; Sparks *et al.* 2021), but a genetically verified pedigree allows accurate estimation of lifetime reproductive success (Sparks *et al.* 2021). Furthermore, the high extra-pair paternity allows us to separate the effects of the age of the genetic father (e.g. germline deterioration) from that of the social father (deterioration in parental care).

Senescence has been well documented in the Seychelles warbler (Hammers *et al.* 2015) with age-dependent declines in both survival and reproduction (Hammers *et al.* 2012, 2013; Raj Pant *et al.* 2020). Mothers provide more parental care to the offspring than fathers (Hammers *et al.* 2019) and the amount of provisioning declines with maternal, but not paternal age (Hammers *et al.* 2021). Further, the first-year survival of offspring declines with maternal, but not paternal age (Hammers *et al.* 2021). The presence of helpers, however, does compensate for age-related declines in parental care and first year survival with dominant female age (Hammers *et al.* 2021), providing a means by which social conditions in early life could influence offspring fitness. However, the long-term effects of parental age on offspring lifespan and lifetime reproductive success remain unknown.

In this study, we use a 24-year dataset on individually-marked Seychelles warblers to investigate whether maternal and paternal age are associated with the lifespan and lifetime reproductive success of offspring. We investigate how offspring fitness is associated with maternal age as well as separately testing the effect of the age of the genetic and social father and for offspring-sex-specific effects on offspring performance. We also investigate whether parental age effects were dependent on the offspring's early-life environment. We predict that beneficial early-life environments may counteract the negative impacts of parental age effects on offspring fitness, whereas negative early-life environments may amplify these effects. Finally, we separate out parental age effects into within-individual versus between-individual effects to test for longitudinal versus population-level processes, such as selective disappearance of poor quality individuals.

Methods

Study system

The Seychelles warbler is a small insectivorous passerine bird endemic to the Seychelles archipelago. Since 1985, the entire population (ca. 320 adult individuals) on Cousin island (04′20′S, 55′40′E) has been monitored intensively (Komdeur 1992; Richardson *et al.* 2007; Hammers *et al.* 2019; Raj Pant *et al.* 2019). Seychelles warblers live in and defend territories (ca. 115 territories) in which a dominant male and female and any subordinates, if present, reside all year round (Komdeur 1994; Richardson *et al.* 2001). The dominant breeding pair in each territory is determined by behavioural observations of contact calls and mate guarding (Komdeur 1992; Richardson *et al.* 2002). The main breeding season runs from June to September and coincides with the peak of insect abundance (Komdeur *et al.* 1991). However, a smaller proportion of individuals also breed between January and March. On Cousin most clutches contain 1 egg, though clutches of up to 3 eggs can occur (Komdeur *et al.* 1991; Richardson *et al.* 2001). While one female can lay more than one egg the presence of multiple eggs in a nest is often indicative of subordinate females breeding (Richardson *et al.* 2002).

Subordinate female cobreeding contributes to 11% of maternities (Raj Pant *et al.* 2019; Sparks *et al.* 2021), and it is always by subordinate females within the territory, with no evidence of egg dumping by females from other territories (Richardson *et al.* 2001). Extra-group paternity accounts for 41% of paternities (Raj Pant *et al.* 2019). Only 0.6% of paternities are gained by (within-group or extra-group) subordinate males (Sparks *et al.* 2021).

Fieldwork is carried out during the breeding seasons, when as many birds as possible are caught using mist nests or captured in the nest. The age of unringed birds is estimated based on lay, hatch or fledge dates and/or using eye colour (Komdeur *et al.* 1991). Since 1995 blood samples have been collected by brachial venepuncture from all birds captured and stored at room temperature in 1 ml of absolute ethanol for molecular sexing and genetic pedigree construction. From 1997 onwards, >96% of individuals in the population have been individually marked with a unique combination of a British Trust for Ornithology metal ring and three colour rings (Brouwer *et al.* 2010). Extrinsic mortality is low due to the absence of predation on adults and individuals have long lifespans (mean = 5.5 years, max= 19 years; (Hammers *et al.* 2015)). Since the population is virtually closed (Komdeur *et al.* 2004), and annual resighting probability is high (ca. 0.92±0.02 for individuals ≤2 years and 0.98±0.01 for older birds, (Brouwer *et al.* 2010)), individuals can be followed from birth until death (Hammers *et al.* 2015).

To investigate the influence that early-life conditions have on parental age effects we investigated the effect of natal territory quality, group size and helper presence in the offspring's natal territory. We used an index of insect abundance as a measure of territory quality as warblers are almost entirely insectivorous (Komdeur & Daan 2005). Territory quality was calculated using $A*\sum(Cx*Ix)$, where A is the territory size (in hectares), Cx is the amount of foliage cover for tree species x, and Ix is the mean monthly insect density for tree species x per unit leaf area in dm^2 (following (Komdeur 1992; van de Crommenacker *et al.* 2011)). Where territory quality was not available for that field season, we used the mean territory quality of the previous and next field season (Brouwer *et al.* 2012).

We used natal group size and helper presence as proxies for the early-life social environment. Natal group size was the number of independent individuals (i.e. two breeders and any subordinates) in the natal territory (range: 2–6). Helpers are subordinates observed to help incubate or provision offspring in a specific breeding season (0–3 per territory). Due to few instances of >1 helper in the dataset (N=56 of 1643), helper presence in the natal territory was included as a binary variable (present/absent; (Hammers *et al.* 2019)).

Statistical analyses

We included all individuals that were born 1995–2018 with assigned parentage (1643 offspring from 464 mothers and 440 fathers). All statistical analyses were performed in R v3.6.3 (R Core Team 2019) and all models were run separately for male and female offspring to allow for differences in lifetime reproductive success and lifespan between the sexes (Figure S1) and to improve interpretability of interactions.

We investigated parental age effects with genetic parents identified using MasterBayes v2.5.2 (Hadfield *et al.* 2006) following Sparks et al. (2021). Parentage was assigned where $p \geq 0.8$. The Seychelles warbler pedigree includes parentage assignments for individuals born 1992-2018 and contained 1980 individuals with 1708 maternities and 1776 paternities (calculated using Pedantics v1.7 (Morrissey & Wilson 2010)). Although 11% of maternities are from subordinate females, there is no difference in the provisioning rates of subordinate or dominant females at nests where a subordinate offspring is present (Table S1). Hence, in this dataset we take the genetic mother as the social mother. In addition to the genetic father, we also included the age of the dominant male in models. Correlations between age of the mother and the age of the genetic and/or social father were weak, which allowed them to be included in the same model (maternal age and paternal age: Pearson's correlation; $r=0.091$, $t_{1641}=3.695$, $p<0.001$; Figure S2; maternal age and dominant male age: Pearson's correlation; $r=0.081$, $t_{1618}=3.288$, $p<0.001$). The correlation between the age of the genetic father and dominant male was moderate (Pearson's correlation; $r=0.545$, $t_{1618}=26.141$, $p<0.001$) which was unsurprising given that 59% of offspring are sired by the dominant male within the territory (Raj Pant *et al.* 2019). We checked for collinearity between fixed effects by calculating Variance Inflation Factors (VIF), as well as overdispersion in all models. To help with model convergence and aid interpretation of the model coefficients, continuous predictor variables were standardised by subtracting the mean and dividing by two standard deviations in arm v.1.11-2 (Gelman & Su 2018). Significance of fixed effects was determined by likelihood ratio tests comparing a model with and without the fixed effect of interest. Non-significant (i.e. $P>0.05$) age^2 effects and interactions were removed from the models sequentially, in order of least significance, to ensure their inclusion did not affect interpretation of the first-order effects. All dropped terms were retested against the base model using likelihood ratio tests.

Lifespan was calculated for all individuals who survived until at least one year of age. Since the resighting probability is high, an individual's death year was assigned as the last sighting year. Lifespan analyses were performed using generalised linear mixed models (GLMM) in glmmTMB v1.0.2.1 (Brooks *et al.* 2017) for all individuals who were not translocated as part of a conservation programme (Richardson *et al.* 2006; Wright *et al.* 2014) and whose last seen year was before 2019. We included the ages of the genetic mother, genetic father and dominant male as fixed effects (linear and squared covariates), in addition to hatch year (linear covariate), the natal group size (linear covariate), presence of helpers in the natal territory (binary factor), natal territory quality (linear covariate), and the presence of siblings in the nest (binary factor). Offspring hatch year was included to account for the fact that individuals born more recently in the dataset lived short lives (following (Bouwhuis *et al.* 2015)). Cohort (hatch year), maternal, paternal, and dominant male identity were included as random effects. To calculate a hazards ratio for parental age on offspring survival we also ran these models using Cox mixed effects proportional hazards models in package coxme v2.2-16 (Therneau 2019) using the same model structure but without standardising variables and without hatch year as a covariate as some individuals in these models were still alive. In these models, individuals (130 females, 141 males) that were still alive (i.e. observed in 2019 or 2020), or translocated to other islands (30 females, 44 males) were right-censored. In both models, we subsequently tested for environment-dependent parental age effects by testing for two-way interactions of natal territory quality, group size and helper presence with maternal and genetic father and dominant male age.

We next tested whether any parental age effects on lifespan translated to differences in reproductive lifespan. We calculated reproductive lifespan as the difference between age at last and first breeding defined by the first and last year an individual had offspring in the genetic pedigree. We included all individuals who survived to one year of age, were not translocated, and whose last seen year was before 2018 (last year of the pedigree). Analyses were performed using a zero-inflated poisson GLMM in glmmTMB with the same model structure as for the lifespan GLMM.

Lifetime reproductive success (LRS), calculated as the sum of offspring produced who survived to at least one year of age, was calculated for individuals following the same criteria as for reproductive lifespan. Analyses were performed using a zero-inflated poisson GLMM in glmmTMB. We included the same fixed and random effects as the lifespan and reproductive lifespan models. To test whether any effects of parental age may be mediated by offspring lifespan, we included offspring lifespan in our models. Similar to the analyses of lifespan, we subsequently tested for environment-dependent parental age effects by including interactions between parental age and natal group size, helper presence and natal territory quality.

We subsequently investigated whether any parental age effects on offspring lifespan and lifetime reproductive success were driven by within-individual parental age effects rather than between-individual parental age effects, using the within-subject centering method (van de Pol & Wright 2009). We included mean age per parent (between-individual parental age effects, e.g. testing for selective disappearance of lower-quality individuals) and the deviation from the mean age of the parent (testing for within-individual parental age effects) in the GLMMs of LRS and lifespan. To test whether the within- and between-individual parental age slopes were significantly different from each other, we included age of the parent (within-parent age effects) and mean age of the parent (difference between the within- and between-individual slopes) as predictors in a second model. Using this parameterisation of the model, the significance of mean age indicates that the within and between slopes in the first model are significantly different from each other (van de Pol & Wright 2009).

Finally, in addition to lifespan, parental age effects on offspring lifetime reproductive success may be caused by differences in the annual reproductive output of offspring. Annual reproductive success of offspring was calculated as the number of offspring produced in a year who survived to one year of age. This was calculated for all individuals which had LRS data. Analyses were performed using a poisson GLMM in glmmTMB. We included age (linear and squared), lifespan, ages of the mother, father, and dominant male, birth year, territory quality, group size and the presence of helpers (factor) as fixed effects and individual identity and year as random effects.

Results

Parental age and offspring lifespan

The association between maternal age and offspring lifespan was sex-dependent. Older mothers produced female offspring with shorter lifespans (Table 1 & S2, Figure 1). This effect translated into a 3% increase in mortality risk for female offspring for each year that the mother was older (Table S2). There was no significant association between maternal age and lifespan for male offspring (Table 1 & S2). Further, there was no effect of paternal age on offspring lifespan of either sex (Table 1 & S2). Similar results were found for offspring reproductive lifespans; older mothers produced female offspring with shorter reproductive lifespans (Table S3).

We found no interactions between parental ages and early-life conditions on offspring lifespan, suggesting no evidence for environment-dependent parental effects (Tables S4 & S5). However, there was a positive association between natal territory quality and female offspring lifespan in the Cox proportional hazards model only (Table S2). There was no effect of helper presence, sibling presence or group size on the lifespan of offspring of either sex.

When parental age effects on offspring lifespan were separated into within- versus between-individual parental age effects there was a significant negative within-individual maternal age effect on female offspring lifespan (Table 2, Figure 2). As individual mothers aged, the female offspring they produced had shorter lifespans (Table 2, Figure 2). The within-individual maternal age slope was significantly more negative than the between-individual maternal age slope (Table 2, Table S6). There were no within- or between-individual maternal age effects on male offspring lifespan, and no within- or between-individual paternal age effects on offspring lifespan of either sex (Table 2).

Parental age and offspring lifetime reproductive success

Cross-sectionally, females with older mothers at birth had lower lifetime reproductive success (Table 3, Figure 3A). In contrast, there was a weaker but positive association between maternal age and the lifetime reproductive success of male offspring (Table 3, Figure 3B). There was no effect of paternal age, or age of the dominant male, on the lifetime reproductive success of offspring of either sex (Tables 3). There was a strong positive correlation between lifespan and lifetime reproductive success (Pearson's correlation; $r=0.780$, $t_{923}=37.825$, $p<0.001$; Figure S3). When we added longevity as a covariate to the model, the association between maternal age and female offspring LRS was no longer significant (maternal age $\beta=0.031 \pm 0.131$ SE, $\chi^2_{(1)}=0.057$, $p=0.812$; lifespan $\beta=1.743 \pm 0.117$ SE, $\chi^2_{(1)}=204.930$, $p<0.001$), which suggests that differences in lifetime reproductive success between female offspring born to different age mothers were driven by differences in longevity rather than by differences in annual reproductive output.

There was no strong evidence for environment-dependent parental age effects (Tables S7). There was a marginally significant paternal age by territory quality and dominant male age by territory quality interaction. It appeared that older males in higher quality territories produced female offspring with lower LRS than older males in lower quality territories (Figure S4-7). However, this interaction was driven by a few outliers and the errors around these effects were large (Figure S4-7). In terms of offspring early-life effects, there was a negative effect of helper presence in the natal territory on female offspring lifetime reproductive success (Table 3), but no effect on male offspring or effects of group size, sibling presence or territory quality on either sex.

Parental age effects on offspring LRS were separated into within- versus between-individual parental age effects. There was a significant negative within-individual maternal age effect on female offspring lifetime reproductive success (Table 4, Figure 4A). As individual mothers aged, the female offspring they produced had lower lifetime reproductive success (Table 4, Figure 4A). The within- versus between-individual maternal age slopes were not significantly different from each other (Table S8). There was also a significant positive between-individual maternal age effect and a marginally significant positive between-individual paternal age effect on male offspring lifetime reproductive success (Table 4, Figure 4B-C). This shows that, cross-sectionally, mothers and fathers that survived to, or started to breed at, older ages had male offspring with higher lifetime reproductive success (Table 4, Figure 4B-C). However, there was no difference in the within versus between slopes for either maternal or paternal age for male offspring (Table S8).

Parental age and annual reproductive success

We found no association between maternal, paternal or dominant male age on offspring annual reproductive success (Table S9). This suggests that any parental age effects on offspring lifetime reproductive success are driven by differences in lifespan rather than annual reproductive output. There was a negative effect of helper presence at the nest in which the individual was hatched on the annual reproductive success of female offspring. This suggests that the lower lifetime reproductive success of female offspring from nests with a helper were driven by a reduction in annual reproductive output.

Discussion

We found evidence for sex-dependent parental age effects on offspring fitness in the Seychelles warbler, with negative within-individual maternal age effects for female offspring but positive between-individual maternal age effects for male offspring (summarised in Table 5). Female offspring born to older mothers had shorter lifespans and lower lifetime reproductive success than females born to younger mothers, which appeared to be driven by within-maternal age effects. Male offspring born to older mothers had higher lifetime reproductive success than males born to younger mothers, which appeared to be driven by between-maternal age effects. Although there were no cross-sectional paternal age effects, there was a positive between-paternal age effect on male offspring lifetime reproductive success.

The mechanisms by which parental age impacts offspring quality or lifespan are not well resolved, especially in wild populations. Direct effects of ageing parents on offspring phenotypes could be caused by age-dependent declines in parental gamete quality (Monaghan & Metcalfe 2019), declines in the quality of parental care (Hammers *et al.* 2021) or age-dependent increases in the costs of inbreeding depression (Charlesworth & Hughes 1996). In our study, we tested for effects of the ages of the mother, genetic father and the dominant male on offspring lifespan and lifetime reproductive success. While 11% of maternities are due to subordinate females (Sparks *et al.* 2021), both dominant and subordinate females provide parental care to offspring (Table S1). Consequently, effects of the age of the genetic mother on offspring phenotype may be caused by age-dependent changes in gamete quality, incubation of the egg, parental care of the nestling, or epigenetic inheritance. In contrast, 41%

of paternities are sired by an extra group dominant male who provides no parental care to the offspring (Raj Pant *et al.* 2019). This allowed us to compare the effects of the age of the genetic father and the dominant male on offspring phenotype. While age of the genetic father could be associated with changes in gamete quality or epigenetic inheritance, the age of the dominant male may be important as they provision and defend the offspring. However, we only found within-individual maternal age effects on offspring, and no paternal age effects, of either the genetic father or dominant male. The greater impact of maternal age on offspring performance is perhaps unsurprising given that only females incubate and females provision more than males (Hammers *et al.* 2019; van Boheemen *et al.* 2019). Further, age-dependent declines in provisioning rates occur for dominant females but not males, which also suggests that maternal rather than paternal age should be more important for offspring quality in this population (Hammers *et al.* 2021).

While negative effects of maternal age on early-life offspring survival have been widely reported (Descamps *et al.* 2008; Nussey *et al.* 2009; Reid *et al.* 2010; Torres *et al.* 2011; Cooper *et al.* 2020), our study adds to the growing evidence of sex-specific parental age effects on long-term offspring fitness in natural populations (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015). So far only two studies have investigated both maternal and paternal age effects on the lifespan and lifetime reproductive success of female and male offspring. In both wild house sparrows (*Passer domesticus*) and common terns (*Sterna hirundo*) female, but not male, offspring born to older mothers had lower lifetime reproductive success (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015). While differences in lifespan appear to be driving the lower LRS of female offspring born to older mothers in the Seychelles warbler, in these previous studies differences in annual reproductive success appeared to cause the effect; i.e. there was no association between maternal age and lifespan (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015). In contrast to our positive between-individual maternal age effect observed on the lifetime reproductive success of male offspring, the two previous studies found no maternal age effects on males. However, they did find a negative effect of paternal age on male annual reproductive success in the house sparrow and a negative effect of paternal age on male offspring lifespan in the common tern. Both of these effects translated to reduced lifetime reproductive success of male offspring born to older fathers (Bouwhuis *et al.* 2015; Schroeder *et al.* 2015). In contrast, our study found a positive between-individual paternal age effect on lifetime reproductive success of male offspring.

The majority of studies in natural populations have found negative effects of increased maternal or paternal age on offspring lifespan and lifetime reproductive success (Rödel *et al.* 2009; Bouwhuis *et al.* 2015; Schroeder *et al.* 2015), or in one case no effect (Bouwhuis *et al.* 2010). However, there is also some evidence for positive effects. In yellow-bellied marmots (*Marmota flaviventer*), daughters born to older mothers had greater annual reproductive success, which translated to higher lifetime reproductive success (Kroeger *et al.* 2020). The authors suggested that maternal restraint (due to residual lifespan; (Williams 1966; Pianka 1976)) or constraint (e.g. constrained skills or physiological condition; (Curio 1983)) of younger mothers and increased experience or terminal investment in older mothers may explain this (Kroeger *et al.* 2020). In a population of semi-captive Asian elephants (*Elephas maximus*) a complex pattern was observed (Reichert *et al.* 2019); female offspring survival decreased with increasing maternal age, but daughters from younger and older mothers had higher lifetime reproductive success than daughters from middle-aged mothers. The authors suggest that as middle-aged mothers have the highest annual reproductive rate and working activity in the timber industry, they may invest less in each offspring (Reichert *et al.* 2019). In our warbler population, the cross-sectional positive effect of maternal age on male lifetime reproductive success appeared to be driven by between-maternal age effects. While we found no cross-sectional effect of paternal age, we did find a positive between-paternal age effect on male offspring lifetime reproductive success. Overall, these results show that mothers and fathers breeding at older ages have male offspring with higher lifetime reproductive success.

Associations between parental age and offspring lifespan could, potentially, be linked to telomere dynamics. Telomeres, the protective caps at the ends of chromosomes, tend to shorten with age and shorter telomeres are associated with increased mortality risk (Salomons *et al.* 2009; Aubert *et al.* 2012; Wilbourn *et al.* 2018) including in Seychelles warblers (Barrett *et al.* 2013; Spurgin *et al.* 2018). In humans, there is cross-sectional evidence that sperm telomere length is positively correlated with age and older fathers have offspring with longer telomeres (Unryn *et al.* 2005; Kimura *et al.* 2008; Aston *et al.* 2012; Eisenberg *et al.* 2012; Broer *et al.* 2013). However, evidence from natural vertebrate populations is mixed (Eisenberg 2019). In the Seychelles warbler, there is a weak negative within-paternal age at conception effect on offspring telomere length (Sparks *et al.* 2021). Additionally, there is no evidence for within-maternal age at conception effects on offspring telomere length, which might be expected if there is selection for higher-quality oocytes with longer telomeres to be used first (Monaghan *et al.* 2020). Therefore, the parental age effects on offspring fitness observed in our study are unlikely to be due to parental age at conception effects on offspring telomere length.

While there is growing evidence of sex-specific parental age effects on offspring lifespan and fitness, the mechanisms through which these occur are unknown. Studies have reported different sensitivities between the sexes to poor early-life environments (Jones *et al.* 2009). For example, in great tits (*Parus major*) natal environmental conditions impacted the lifespan and breeding success of males but not females (Wilkin & Sheldon 2009). This may be because the sexes respond differently to, or require different levels, of early-life investment (Jones *et al.* 2009; Wilkin & Sheldon 2009). An early comparative study showed that juvenile mortality was proportional to sexual size dimorphism (Clutton-Brock *et al.* 1985). Further work suggested that sex differences in mortality may be due to sex-linked deleterious alleles in the heterogametic sex (Myers 1978), and the effects of these deleterious alleles may be dependent on the environment (e.g. (Marr *et al.* 2006)). However, a more recent meta-analyses found that sex differences in environmental sensitivities in birds could not be explained by sex or size-dependent vulnerabilities alone (Jones *et al.* 2009). Further explanations could include sex-specific epigenetic inheritance (Hager *et al.* 2008; Broer *et al.* 2013), age- and sex-specific differences in foraging, offspring provisioning (Weimerskirch 2018), or differential investment in eggs, which could result in complex sex-specific parental age effects on offspring condition (Bouwhuis *et al.* 2015).

Despite ample evidence that early-life environments can affect offspring performance (Monaghan 2008), we found no evidence that parental age effects on offspring fitness differed with early-life conditions. In the warbler system, offspring early-life survival declines with dominant female age, but helpers may mitigate these declines, suggesting that the early-life social environment could impact parental age effects (Hammers *et al.* 2021). However, we found no evidence that helper presence, territory quality or group size, impacted the effects of parental age on the fitness of offspring that survived their first year of life (i.e. their most critical period). Only one study has examined the impact of the environment on long-term parental age effects (Kroeger *et al.* 2020). In yellow-bellied marmots, there was a positive association between maternal age and the lifetime reproductive success of daughters. However, daughters born to older mothers in favourable environments had greater declines in annual reproductive success with age. While contrary to predictions, this was driven by daughters of older mothers in harsher environments not living long enough to senesce. Further, natal litter size negatively affected daughters born to older but not younger mothers, indicating an offspring number and quality trade-off for older mothers (Kroeger *et al.* 2020). Although we did not find evidence for environment-dependent parental age effects in our study population, the marmot study indicates that future studies should also investigate whether parental age effects are dependent on early life environmental conditions.

In the Seychelles warbler, provisioning rates and subsequent juvenile survival decline with dominant female, but not male, age (Hammers *et al.* 2021). Further, female offspring are more likely to forgo dispersal and help as the dominant female ages (Hammers *et al.* 2019). This could explain the negative effect of maternal age on the fitness of female, but not male, offspring in our study. However further work is needed to determine the mechanisms by which these sex-specific parental age effects occur and whether being a helper reduces survival. While actuarial and reproductive senescence occur in this warbler population (Hammers *et al.* 2012, 2013; Raj Pant *et al.* 2020), our study indicates that parental age effects can have longer-term effects on offspring fitness. Not investigating such intergenerational effects, including sex-specific effects, may therefore miss important components of senescence.

Finally, a negative effect of increasing parental age on offspring lifespan may not necessarily have negative consequences for offspring fitness if the reproductive timing of offspring is altered (Monaghan *et al.* 2020). For instance, in great tits, offspring born to different age mothers had different age-specific reproductive success trajectories, but these equated to the same lifetime reproductive success (Bouwhuis *et al.* 2010). We found no difference in annual reproductive output in relation to parental age. However, females from older mothers had shorter reproductive lifespans and lower lifetime reproductive success than those from younger mothers. In cooperatively breeding species such as the Seychelles warbler, these parental age effects may reveal an additional cost to females of becoming a subordinate if it leads to delayed reproduction. Further, older dominant females are more likely to be displaced from their breeding position by a subordinate than are dominant males (Richardson *et al.* 2007), which may be adaptive if helping older females to reproduce is less beneficial.

In conclusion, the existence of complex, often sex-specific, intergenerational effects linked to parental age, will have consequences for our understanding of the fitness effects of senescence, and subsequently, evolutionary dynamics. Such effects will also have important ramifications for animal breeding and the conservation of species, particularly where populations are small or age-structured and when older individuals are used for breeding or translocations.

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Author Contributions

The idea to test the Lansing effect in this population was conceived by AMS, MH, HLD, DSR, TB and JK. AMS and MH conceived the specific study design, data selection and methodology. AMS performed all data analyses with input from MH and HLD. HLD, DSR, JK and TB manage the long-term Seychelles warbler study system including gaining the relevant funding. HLD constructed the genetic pedigree. AMS wrote the manuscript with input from MH, HLD and DSR. All authors gave final approval for publication.

Data Accessibility

Data will be deposited in the Dryad Digital Repository upon acceptance. All scripts for the analysis will be made available at https://github.com/Seychelle-Warbler-Project

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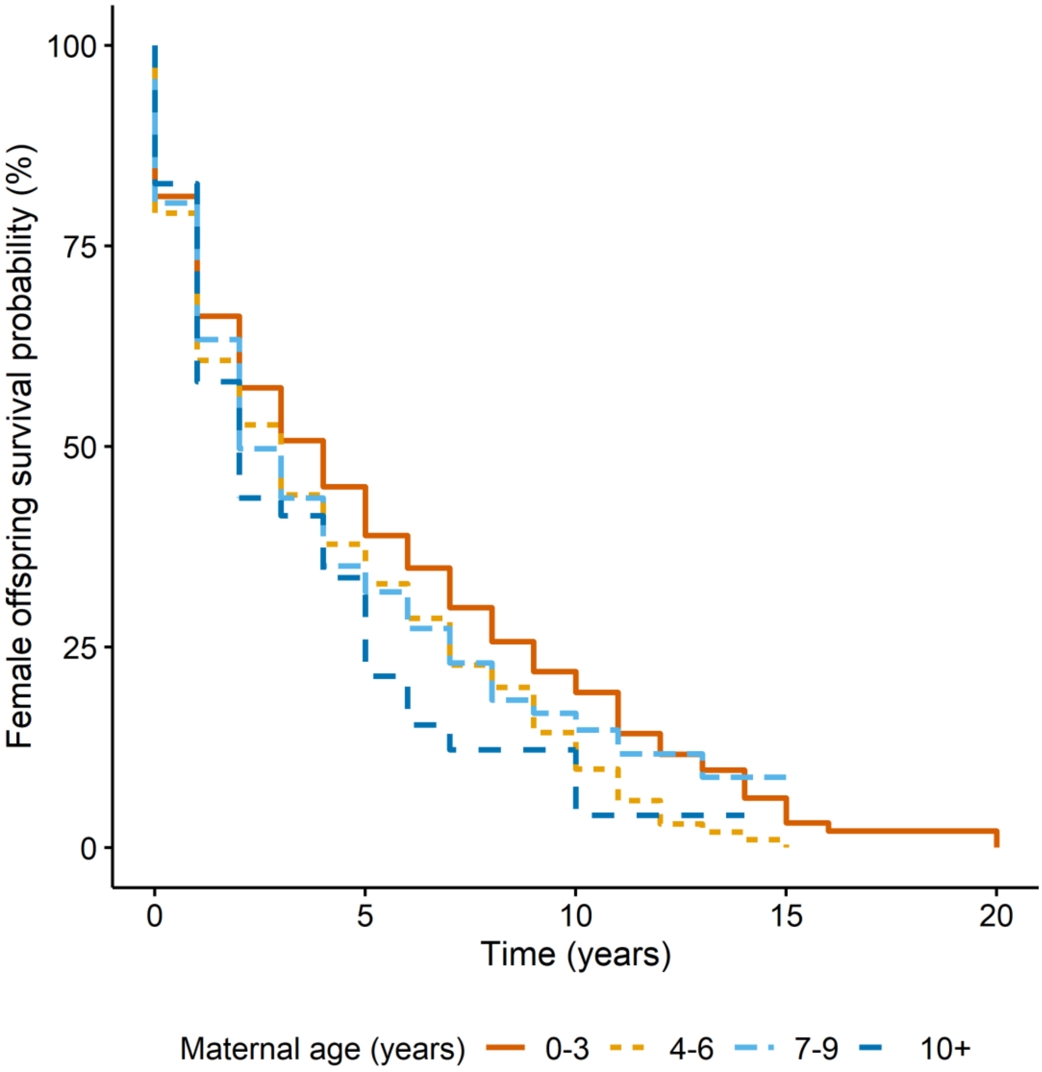

Figure 1. Survival probability of female Seychelles warbler offspring over time broken down by age of the mother in the cross-sectional analyses. Maternal age was treated as a continuous variable in our analyses, but for graphical purposes, here maternal age is grouped into four age classes 0-3 years, 4-6 years, 7-9 years, and 10+ years.

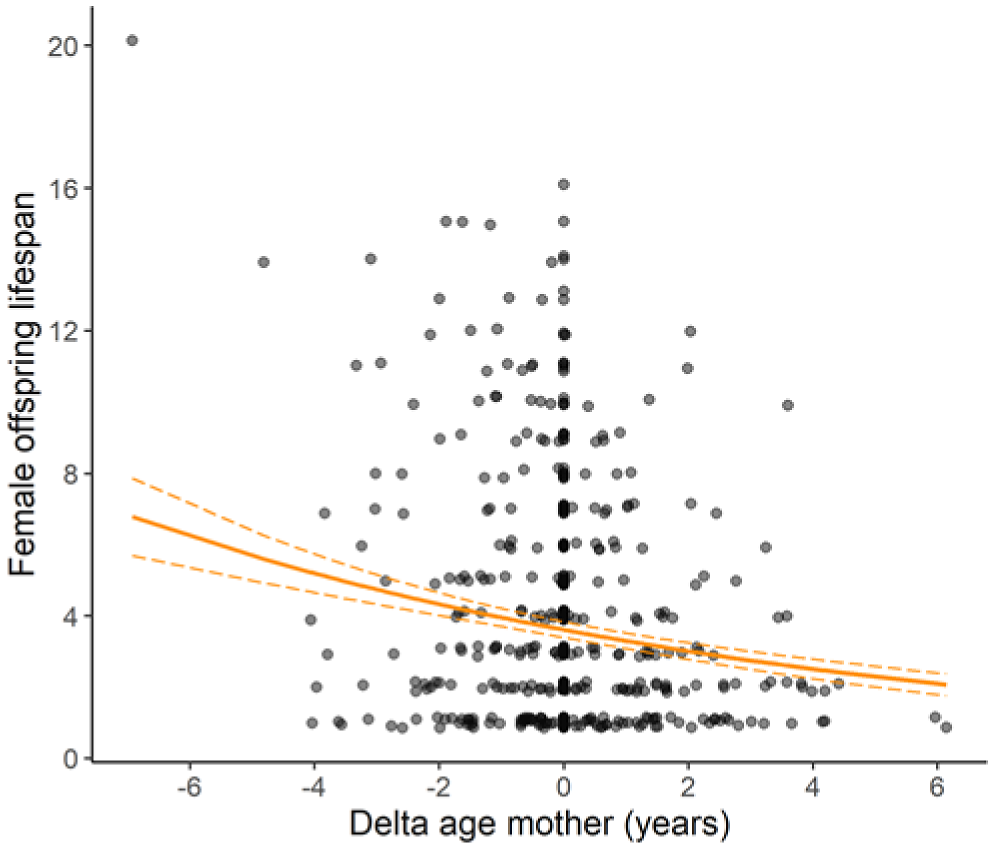

Figure 2. Within-individual maternal age effects ('Delta age mother') on the lifespan of female offspring in the Seychelles warbler, using within-subject centering (van de Pol & Wright 2009). The solid line is the GLMM prediction with mean values for all other continuous fixed effects in the model and the dashed lines indicate standard errors (Table 2). Dots show the raw data points. Lifespan values are integers but are jittered to show overlapping values. Model estimates (Table 2) are similar without the outlier (the offspring with a lifespan of 20 years) (Table S10).

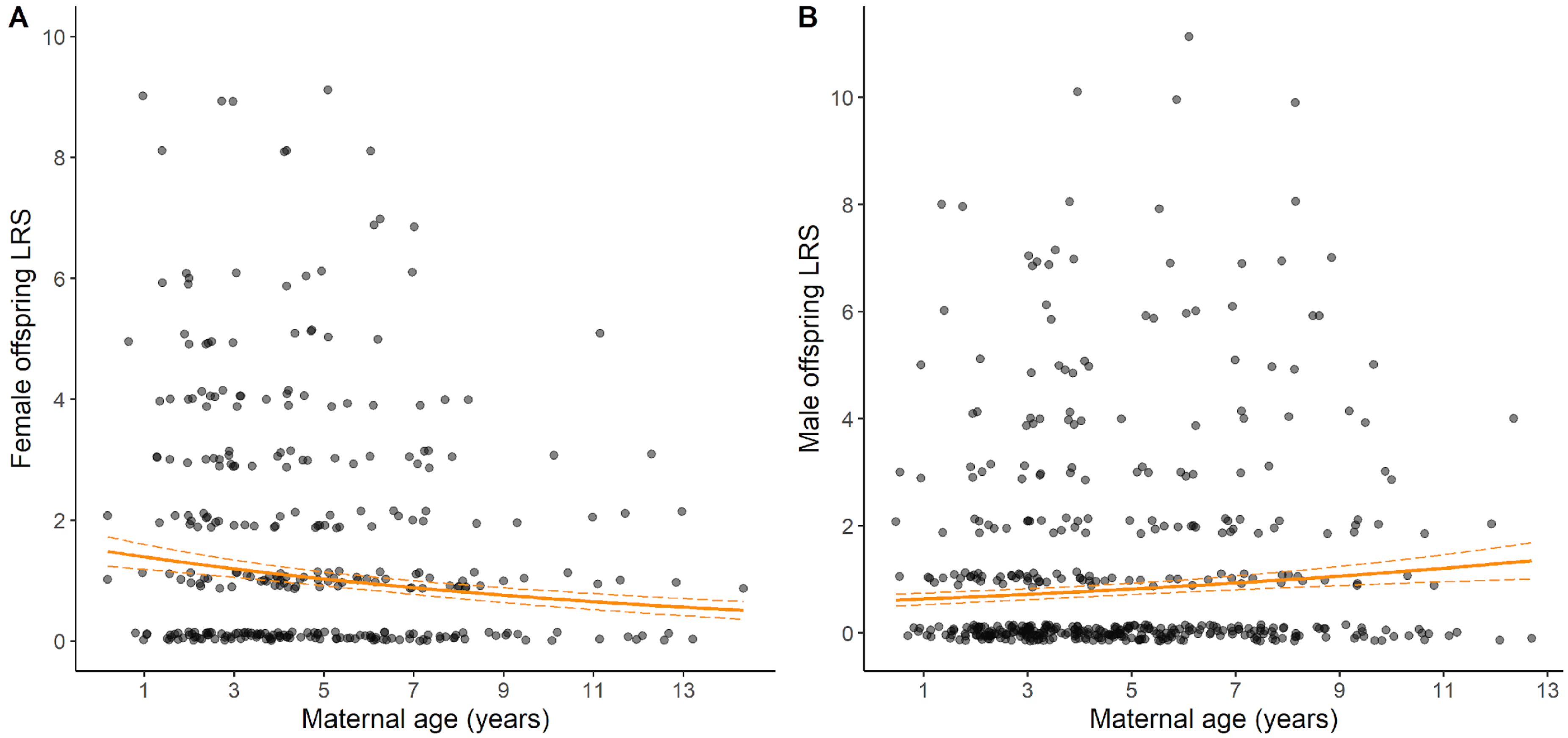

Figure 3. Cross-sectional maternal age (years) effects on the lifetime reproductive success of female (A) and male (B) offspring (based on genetically assigned offspring) in the Seychelles warbler. Solid lines indicate GLMM predictions with mean values for all other continuous fixed effects in the model and dashed lines indicate standard errors (Table 3). Dots show the raw data points. LRS values are integers but are jittered to show overlapping values.

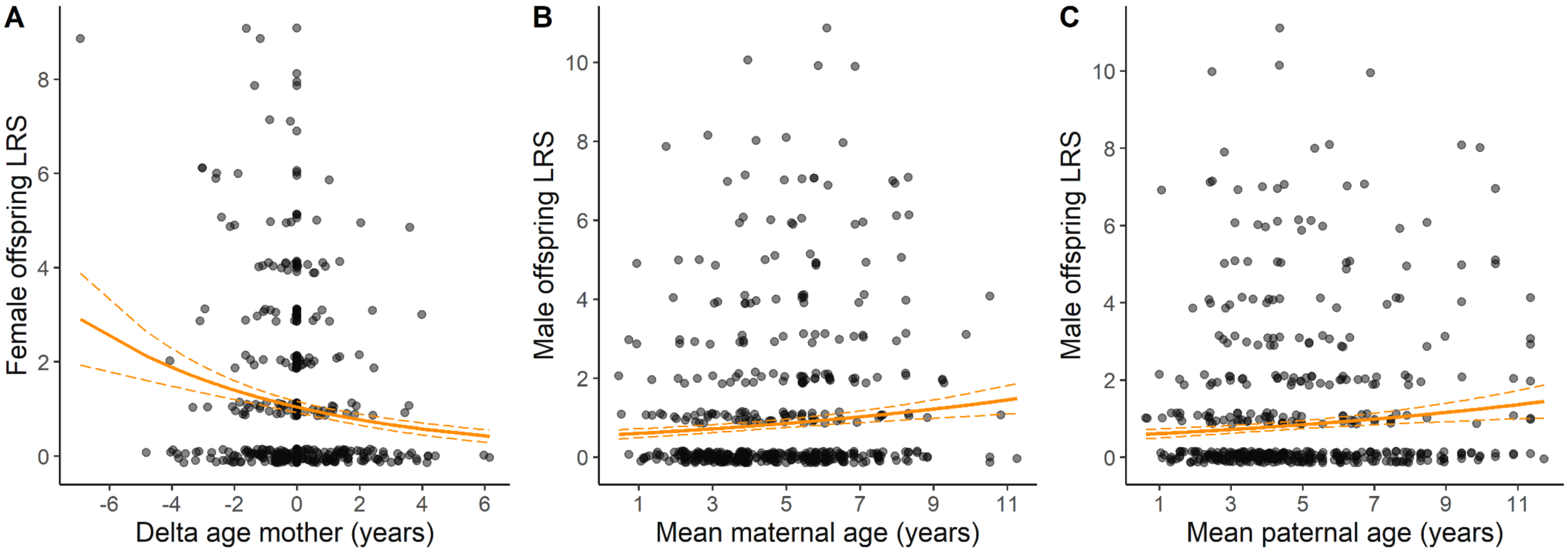

Figure 4. Within and between genetic parental age effects on the lifetime reproductive success (LRS) of female (A) and male (B-C) offspring in the Seychelles warbler using within-subject centering (van de Pol & Wright 2009). Lines indicate GLMM predictions with mean values for all other continuous fixed effects in the model and dashed lines indicate standard errors (Table 4). Dots show the raw data points. LRS values are integers but are jittered to show overlapping values. Model estimates (Table 4) are similar without the outlier in Figure 4A (Table S11).

Table 1. Generalised linear mixed model results investigating associations between parental age effects on offspring lifespan, for male and female offspring separately, in the Seychelles warbler (including all genetically assigned offspring who survived to one year of age). Included are the parameter estimates (estimate), their standard errors (SE), and the significance of fixed effects based on a likelihood ratio test (LRT, P) where d.f.=1. Significance of dropped squared parental ages, and environment by parental age interactions are shown in Table S4. Significant fixed effects are in bold.

	Female offspring lifespan				**Male offspring lifespan**			
	n=467				n=485			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	1.276	0.061			1.196	0.072		
age of mother	**-0.242**	**0.075**	**10.569**	**0.001**	0.098	0.068	2.098	0.148
age of father	-0.041	0.088	0.217	0.641	-0.062	0.085	0.545	0.460
age of dominant male	0.135	0.082	2.676	0.102	0.125	0.081	2.363	0.124
birth year	**-0.584**	**0.108**	**22.852**	**<0.001**	**-0.556**	**0.138**	**13.710**	**<0.001**
territory quality	0.019	0.081	0.054	0.816	0.149	0.093	2.598	0.107
group size	-0.109	0.077	1.994	0.158	-0.075	0.080	0.863	0.353
helper presence (y)	-0.153	0.092	2.787	0.095	-0.128	0.101	1.631	0.202
sibling presence (y)	-0.068	0.103	0.439	0.508	0.135	0.100	1.835	0.176
random effects								
maternal ID	0.085				0.086			
paternal ID	0.163				0.084			
dominant male ID	0.019				0.068			
birth year	0.021				0.068			

Table 2. Generalised linear mixed model results investigating between versus within maternal and paternal age effects on offspring lifespan, in each offspring sex separately, in the Seychelles warbler using the within-subject centering method (van de Pol & Wright 2009). Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P-value) where df=1. The model investigates within-parental age effects (deviation from the mean age of the parent) and between-parental age effects (mean age for each parent). Significant fixed effects are in bold.

	Female offspring lifespan				**Male offspring lifespan**			
	n=467				n=485			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	1.284	0.062			1.203	0.070		
between-maternal age	-0.097	0.090	1.140	0.286	0.127	0.095	1.793	0.181
within-maternal age	**-0.508**	**0.121**	**17.503**	**<0.001**	0.092	0.096	0.920	0.338
between-paternal age	0.004	0.110	0.001	0.973	0.045	0.104	0.189	0.664
within-paternal age	-0.157	0.134	1.361	0.243	-0.198	0.128	2.437	0.119
between-dominant male age	0.113	0.094	1.437	0.231	0.158	0.099	2.570	0.109
within-dominant male age	0.252	0.146	2.974	0.085	0.102	0.131	0.604	0.437
birth year	**-0.525**	**0.112**	**19.000**	**<0.001**	**-0.514**	**0.138**	**12.252**	**<0.001**
territory quality	0.022	0.080	0.075	0.784	0.150	0.093	2.645	0.104
group size	-0.104	0.077	1.825	0.177	-0.065	0.081	0.654	0.419
helper presence (y)	-0.153	0.092	2.806	0.094	-0.140	0.101	1.936	0.164
sibling presence (y)	-0.069	0.103	0.446	0.504	0.142	0.100	1.991	0.158
random effects								
maternal ID	0.089				0.088			
paternal ID	0.170				0.081			
dominant male ID	0.004				0.069			
birth year	0.022				0.054			

Table 3. Generalised linear mixed model results investigating associations between parental age effects on offspring lifetime reproductive success (LRS) for males and female offspring separately in the Seychelles warbler (including all genetically assigned offspring who survived to one year of age). Included are the parameter estimates (estimate), their standard errors (SE), and the significance of fixed effects based on a likelihood ratio test (LRT, P) where d.f.=1. Significance of dropped squared parental ages, and environment by parental age interactions are shown in Table S7. Significant fixed effects are in bold.

	Female offspring LRS				**Male offspring LRS**			
	n=441				n=466			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	0.506	0.128			0.298	0.143		
age of mother	**-0.427**	**0.152**	**7.817**	**0.005**	**0.323**	**0.140**	**5.297**	**0.021**
age of father	0.145	0.162	0.798	0.372	0.265	0.174	2.295	0.130
age of dominant male	-0.083	0.158	0.276	0.599	0.023	0.154	0.023	0.879
birth year	**-1.082**	**0.221**	**25.568**	**<0.001**	**-1.169**	**0.273**	**17.446**	**<0.001**
territory quality	-0.135	0.143	0.892	0.345	0.245	0.199	1.495	0.222
group size	-0.032	0.151	0.046	0.830	-0.144	0.172	0.708	0.400
helper presence (y)	**-0.635**	**0.203**	**10.055**	**0.002**	-0.220	0.215	1.069	0.301
sibling presence (y)	-0.078	0.191	0.167	0.683	0.081	0.205	0.156	0.693
random effects								
maternal ID	0.134				0.155			
paternal ID	0.104				0.265			
dominant male ID	0.030				<0.001			
birth year	0.050				0.105			

Table 4. Generalised linear mixed model results investigating between versus within maternal and paternal age effects on offspring lifetime reproductive success in each offspring sex separately in the Seychelles warbler, using the within-subject centering method (van de Pol & Wright 2009). Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P-value) where df=1. The model investigates within-parental age effects (deviation from the mean age of the parent) and between-parental age effects (mean age for each parent). Significant fixed effects are in bold.

	Female offspring LRS				**Male offspring LRS**			
	n=441				n=466			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	0.513	0.131			0.345	0.143		
between-maternal age	-0.298	0.166	3.197	0.074	**0.442**	**0.176**	**6.424**	**0.011**
within-maternal age	**-0.835**	**0.261**	**9.640**	**0.002**	0.139	0.219	0.402	0.526
between-paternal age	0.046	0.178	0.067	0.796	**0.461**	**0.220**	**4.383**	**0.036**
within-paternal age	0.291	0.278	1.103	0.294	-0.071	0.277	0.067	0.796
between-dominant male age	-0.140	0.170	0.690	0.406	-0.134	0.192	0.491	0.484
within-dominant male age	0.025	0.301	0.007	0.935	0.324	0.307	1.129	0.288
birth year	**-1.076**	**0.227**	**23.569**	**<0.001**	**-1.119**	**0.272**	**16.840**	**<0.001**
territory quality	-0.136	0.142	0.927	0.336	0.219	0.199	1.211	0.271
group size	0.004	0.151	0.001	0.981	-0.097	0.175	0.304	0.581
helper presence (y)	**-0.611**	**0.201**	**9.336**	**0.002**	-0.279	0.222	1.643	0.200
sibling presence (y)	-0.109	0.189	0.333	0.564	0.070	0.204	0.118	0.732
random effects								
maternal ID	0.100				0.153			
paternal ID	0.090				0.234			
dominant male ID	0.046				<0.001			
birth year	0.064				0.085			

Table 5. Summary of the models investigating parental age effects on offspring lifespan and LRS in the Seychelles warbler. Included are the cross-sectional effects, within-individual (w/n) and between-individual (b/n) parental age effects and whether there was a significant difference between the within- and between-individual parental age slopes (diff). Positive estimates are indicated by +ve, negative estimates are indicated by -ve, ns indicates non significant results, and Y and N indicate yes and no, respectively. Significant effects are highlighted in bold.

		Age of mother				Age of genetic father				Age of dominant male			
		cross-sectional	w/n	b/n	diff	cross-sectional	w/n	b/n	diff	cross-sectional	w/n	b/n	diff
Offspring lifespan	Females	**-ve**	**-ve**	ns	**Y**	ns	ns	ns	N	ns	ns	ns	N
	Males	ns	ns	ns	N	ns	ns	ns	N	ns	ns	ns	N
Offspring LRS	Females	**-ve**	**-ve**	ns	N	ns	ns	ns	N	ns	ns	ns	N
	Males	**+ve**	ns	**+ve**	N	ns	ns	**+ve**	N	ns	ns	ns	N

Supplemental information for:

Sex-dependent effects of parental age on offspring fitness in a cooperatively breeding bird

Alexandra M. Sparks, Martijn Hammers, Jan Komdeur, Terry Burke,
David S. Richardson, Hannah L. Dugdale

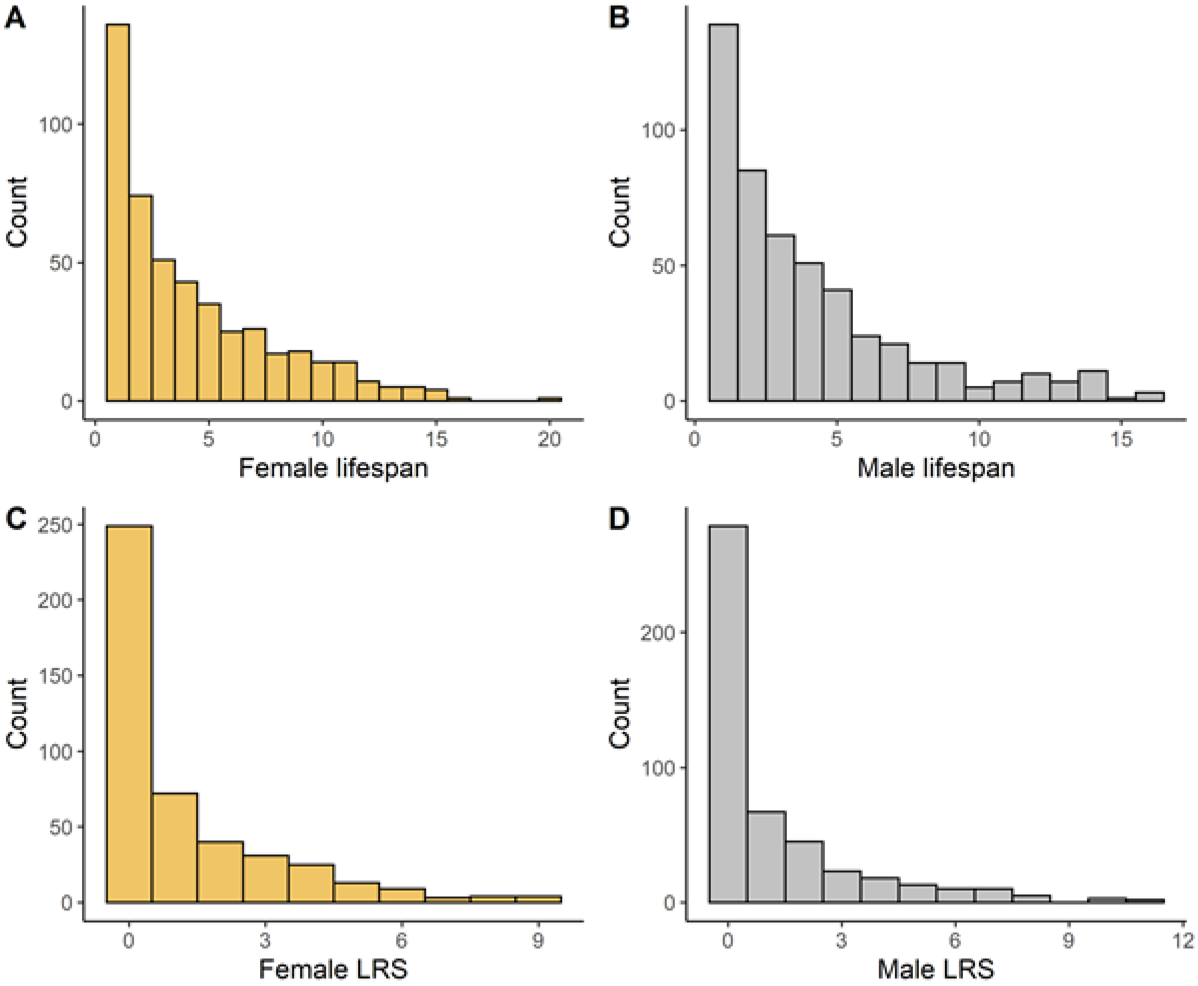

Figure S1. Histograms of the frequency of offspring lifespan (A-B) and lifetime reproductive success (measured as the number of assigned offspring in the pedigree who survived to 1 year, C-D) in the Seychelles warbler for females (A,C) and males (B,D) who survived to one year and had complete lifetime data (A: n=476; B: n=494; C: n=450; D: n=475).

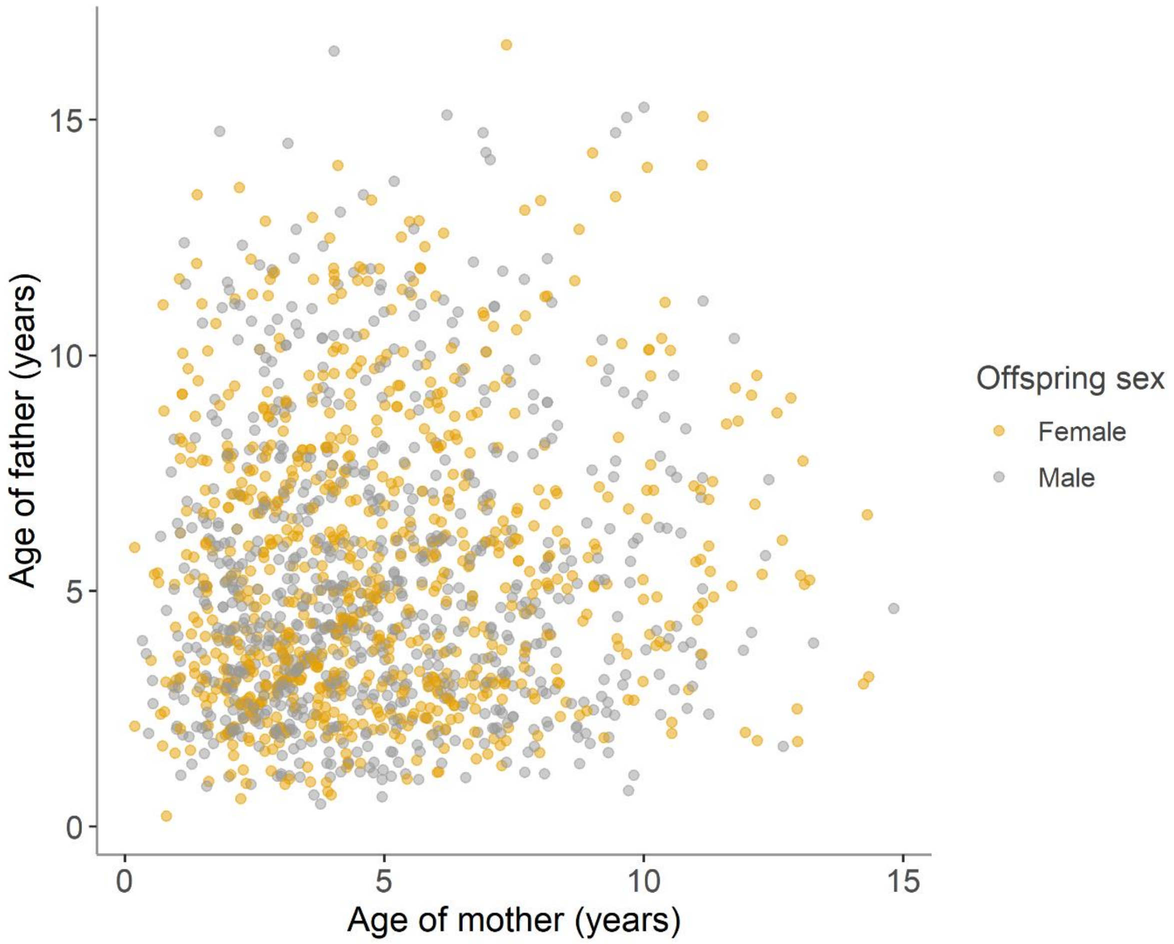

Figure S2. Scatterplot of raw data showing the correlation between (genetic) maternal and paternal ages of Seychelles warbler offspring at birth (n=1643 genetically assigned offspring, 464 mothers and 440 fathers).

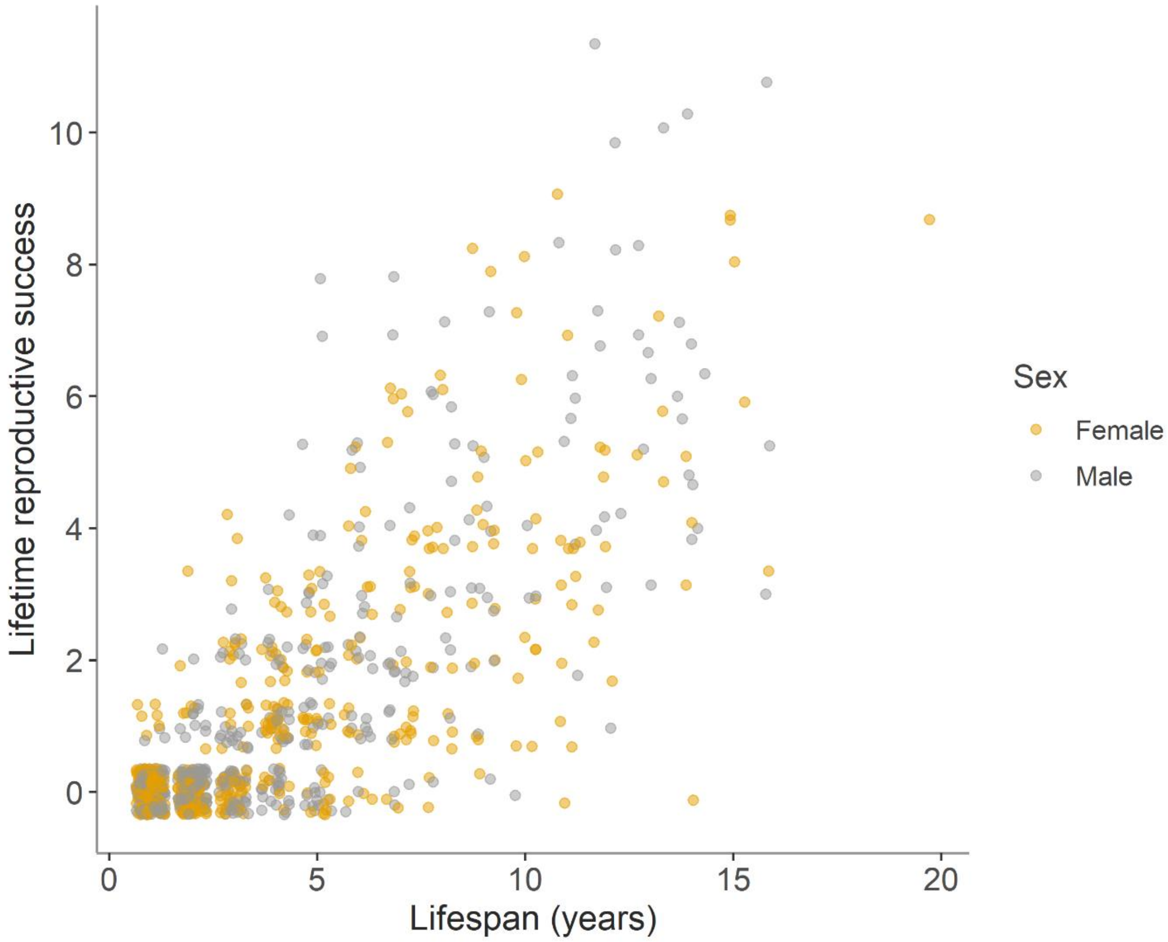

Figure S3. Scatterplot of raw data showing the correlation between lifespan and lifetime reproductive success (based on assigned offspring) in the Seychelles warbler for all individuals who survived to one year and had complete lifetime data (n=925). Lifespan and LRS are integers but jittered to minimise overplotting.

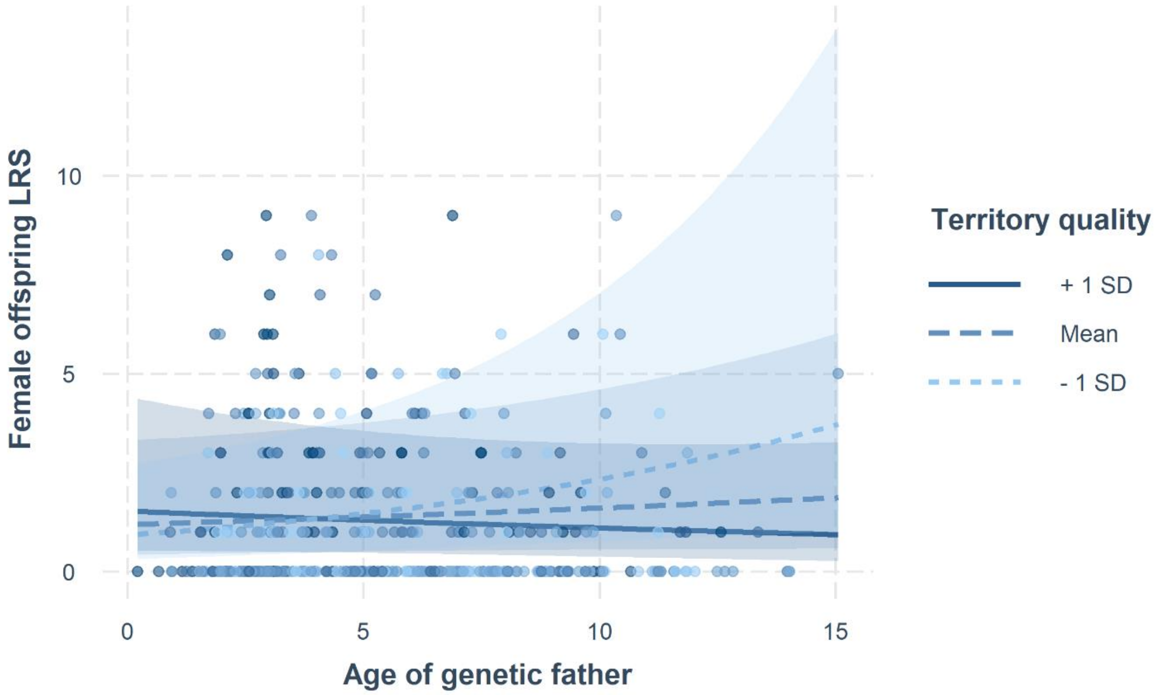

Figure S4. Interaction plot describing the marginally significant interaction between the age of the genetic father and territory quality on female offspring lifetime reproductive success (LRS) in the Seychelles warbler (Table S7). Dots show the raw data points, colour coded by territory quality (lighter = lower territory quality, darker = higher territory quality). Lines show model prediction lines and 95% confidence intervals for the relationship of the age of the genetic father and female offspring LRS on three different levels of territory quality (mean territory quality +/- 1 standard deviation from the mean, see legend). The interaction is based on limited data points (N=38) for older males (>10 years) so there are large error estimates around these values. The interaction plot between the age of the dominant male and territory quality on female offspring LRS showed a similar pattern (Figure S6).

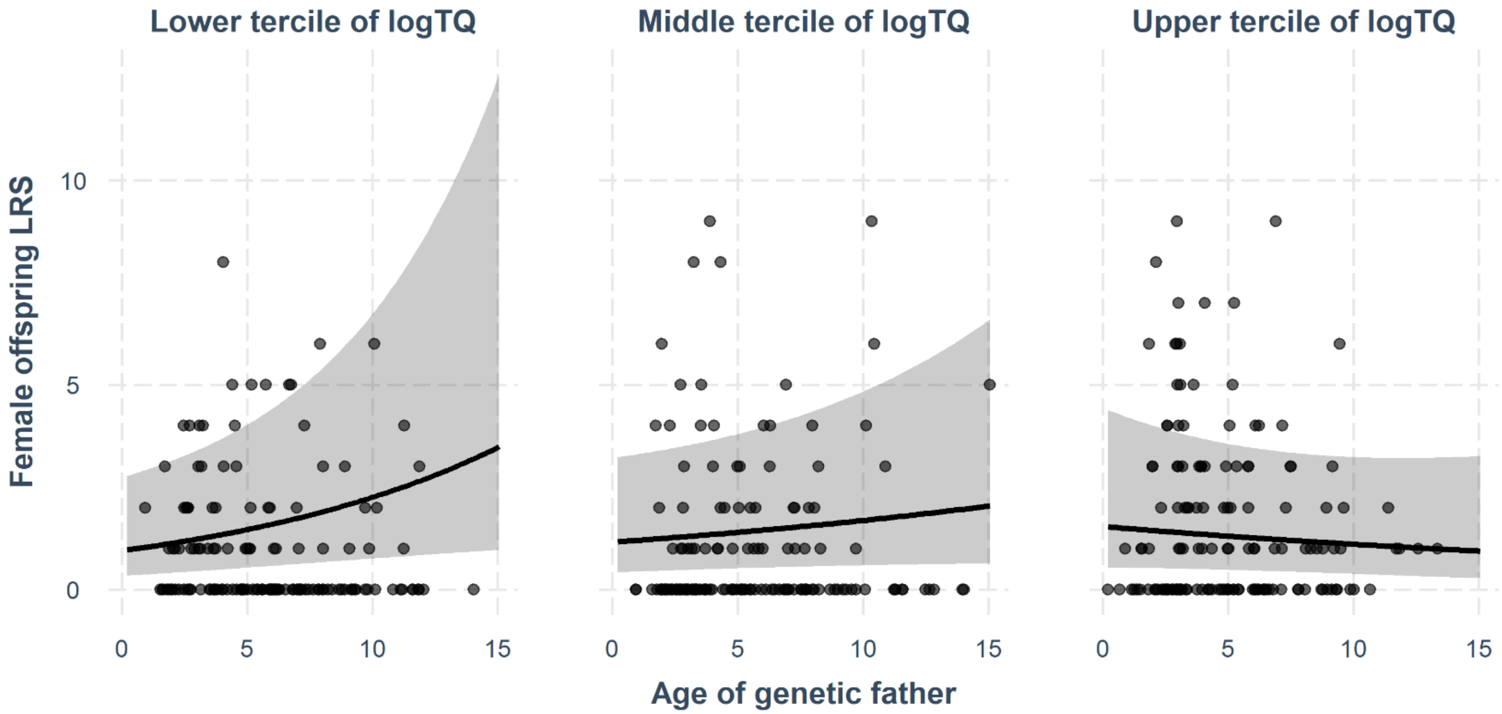

Figure S5. Interaction plot describing the marginally significant interaction between the age of the genetic father and territory quality on female offspring lifetime reproductive success (LRS) in the Seychelles warbler (Table S7). This multi-panel plot is split into three approximately equal-sized groups with the lowest third, middle third and highest third of the territory quality data accordingly. Dots show the raw data points. The lines show the estimated relationship between the age of the genetic father and female offspring LRS within each tercile of the territory quality data with the shaded area indicating the 95% confidence interval. The slopes of each line are based on a few points for older (>10 years) males (N=38) such that there are large error estimates around these values. The interaction plot between the age of the dominant male and territory quality on female offspring LRS showed a similar pattern (Figure S7).

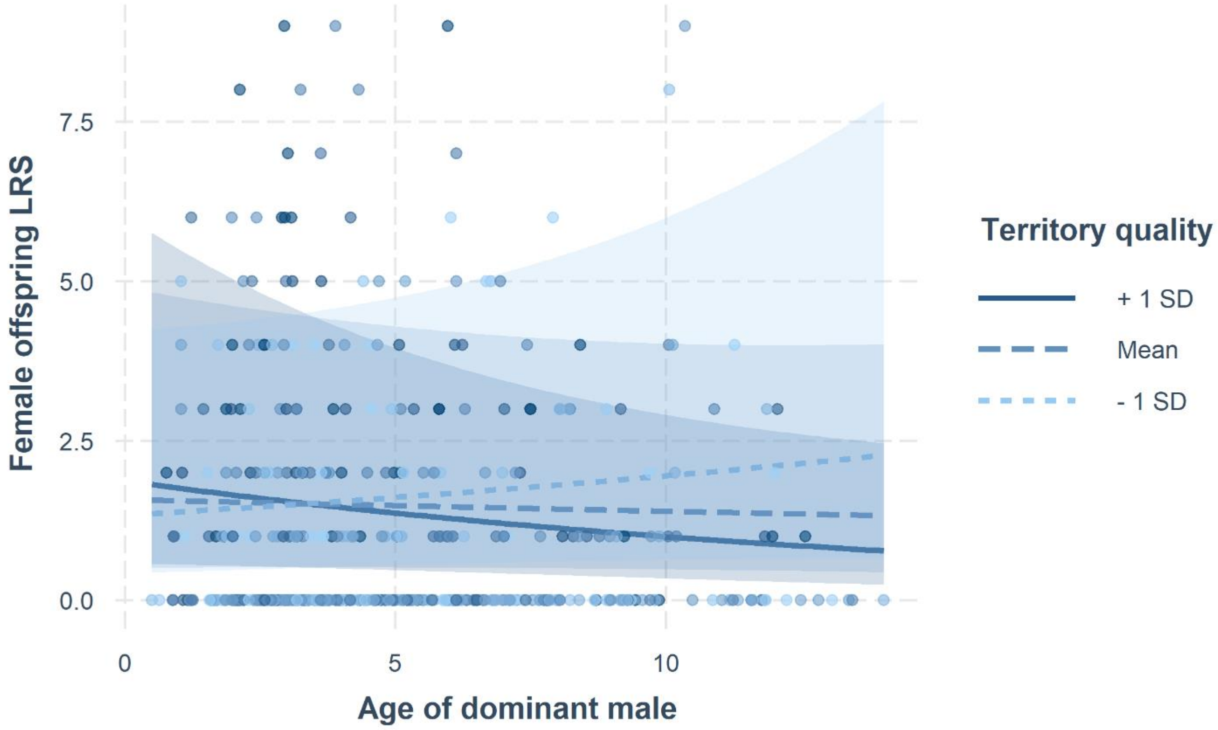

Figure S6. Interaction plot describing the marginally significant interaction between the age of the dominant male and territory quality on female offspring lifetime reproductive success (LRS) in the Seychelles warbler (Table S7). Dots show the raw data points, colour coded by territory quality (lighter = lower territory quality, darker = higher territory quality). Lines show model prediction lines and 95% confidence intervals for the relationship of the age of the dominant male and female offspring LRS on three different levels of territory quality (mean territory quality +/- 1 standard deviation from the mean, see legend). The interaction is based on limited data points (N=34) for older males (>10 years) so there are large error estimates around these values.

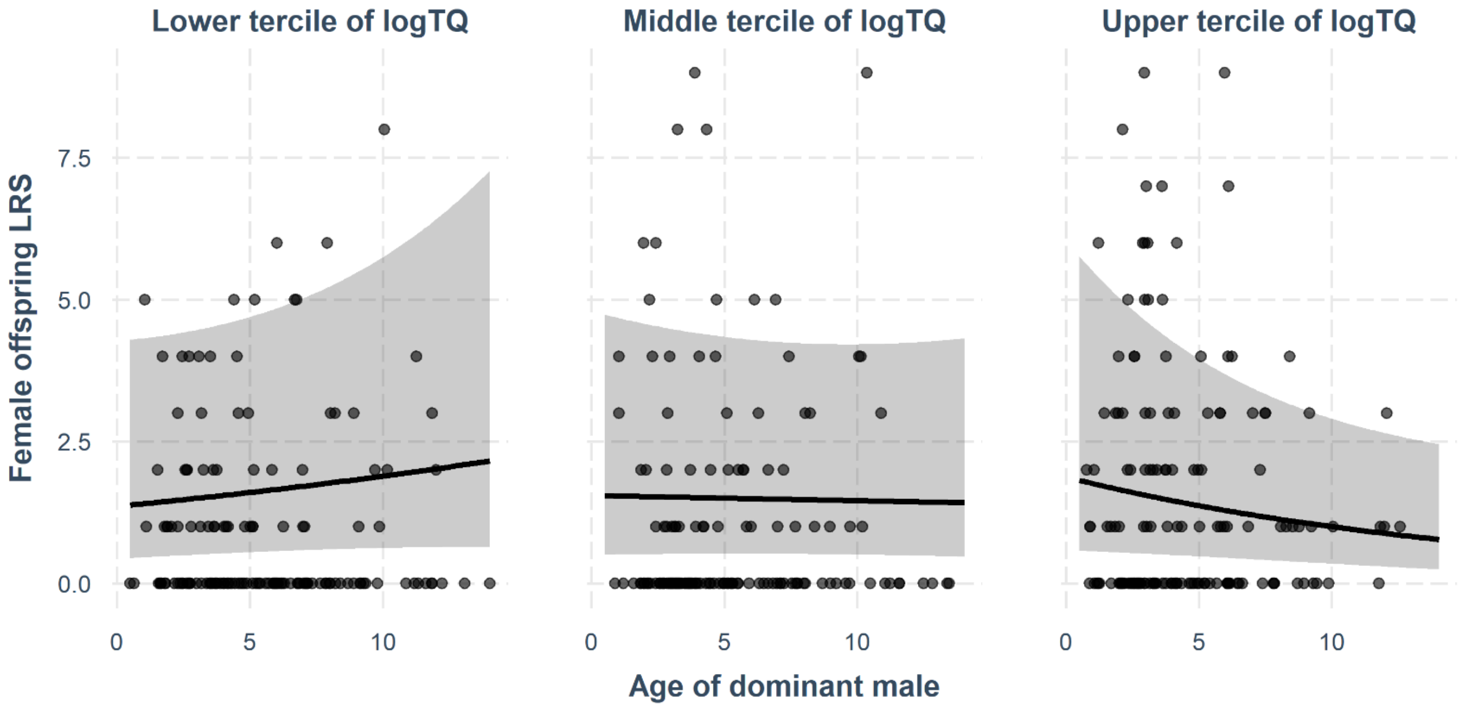

Figure S7. Interaction plot describing the marginally significant interaction between the age of the dominant male and territory quality on female offspring lifetime reproductive success (LRS) in the Seychelles warbler (Table S7). This multi-panel plot is split into three approximately equal-sized groups with the lowest third, middle third and highest third of the territory quality data accordingly. Dots show the raw data points. The lines show the estimated relationship between the age of the dominant male and female offspring LRS within each tercile of the territory quality data with the shaded area indicating the 95% confidence interval. The slopes of each line are based on a few points for older (>10 years) males (N=34) such that there are large error estimates around these values.

Table S1. Generalised linear mixed model (GLMM) results investigating associations between the status of the female and provisioning rate (feed counts), in the Seychelles warbler. The model included nest watch data from nests where at least one of the chicks (brood sizes 1-3) in the nest was from a subordinate female (using the pedigree) and included nest watches where there were ≥90% of birds identified. The response variable was the total number of feed counts of the subordinate and dominant female for each nest watch. To account for differences in length of nest watches (usually 60 minutes), an offset of the nest watch duration (logged) was added. The zero-inflated Poisson GLMM was run in glmmTMB v1.0.2.1 (Brooks et al. 2017). Included are the parameter estimates (estimate), their standard errors (SE), and the significance of fixed effects based on a likelihood ratio test (LRT, P) where d.f.=1. Reference levels for the female status was dominant and for the watch type was feeding. There was no significant difference in provisioning rates between the cobreeding subordinate female and dominant female. N=49 nest watch IDs, each with a provisioning count for the dominant female and subordinate female (N=98 rows). Significant fixed effects are highlighted in bold.

	Provisioning rate			
variables	estimate	SE	LRT	P
fixed effects				
intercept	-2.167	0.181		
status of female (subordinate female)	0.076	0.094	0.627	0.428
brood size	0.133	0.107	1.537	0.215
watch type (feeding and incubating)	**-0.431**	**0.120**	**12.124**	**<0.001**
random effects				
NestWatchID/NestID	0.052			
NestID	<0.001			
BirdID	0.034			
Observer	<0.001			
Year	0.073			

Table S2. Cox proportional hazards mixed model results for parental age effects on offspring lifespan, for males and females separately, in the Seychelles warbler. Included are the parameter estimates (estimate) and their standard errors (SE), the exponentiated coefficient (exp(est)) which represents multiplication effects on the hazard and the significance of fixed effects based on a likelihood ratio test (LRT, P) where d.f.=1. Significance of dropped squared parental age variables, and the environment by parental age interactions are shown in Table S5. Significant fixed effects are in bold.

	Female offspring lifespan					**Male offspring lifespan**				
	n=627					n=670				
variables	estimate	SE	exp(est)	LRT	P	estimate	SE	exp(est)	LRT	P
fixed effects										
age of mother	**0.034**	**0.017**	**1.035**	**3.871**	**0.049**	0.010	0.018	1.010	0.2791	0.597
age of father	0.001	0.018	1.001	0.013	0.909	0.003	0.020	1.003	0.023	0.880
age of dominant male	0.002	0.019	1.002	0.018	0.895	-0.037	0.020	0.963	3.6529	0.056
territory quality	**-0.265**	**0.122**	**0.767**	**4.707**	**0.030**	-0.136	0.144	0.872	0.8909	0.345
group size	0.109	0.069	1.115	2.360	0.125	0.140	0.072	1.150	3.651	0.056
helper presence (y)	0.222	0.130	1.248	2.866	0.090	-0.242	0.139	0.785	3.1135	0.078
sibling presence (y)	-0.011	0.151	0.989	0.006	0.941	-0.161	0.143	0.851	1.2858	0.257
random effects										
maternal ID	<0.001					<0.001				
paternal ID	<0.001					<0.001				
dominant male ID	<0.001					<0.001				
birth year	0.020					0.096				

Table S3. Generalised linear mixed model results investigating associations between parental age effects (in years) on female offspring reproductive lifespan in the Seychelles warbler. Included are the parameter estimates (estimate), their standard errors (SE), and the significance of fixed effects based on a likelihood ratio test (LRT, P) where d.f.=1. n refers to the number of female offspring with full LRS data. Significant fixed effects are highlighted in bold.

	Female offspring reproductive lifespan			
	n=441			
variables	estimate	SE	LRT	P
fixed effects				
intercept	0.722	0.125		
age of mother	**-0.467**	**0.147**	**9.932**	**0.002**
age of father	0.118	0.155	0.575	0.448
age of dominant male	-0.049	0.156	0.098	0.755
birth year	-1.353	0.233	32.013	<0.001
territory quality	-0.182	0.138	1.721	0.190
group size	**-0.277**	**0.140**	**3.978**	**0.046**
helper presence (y)	-0.372	0.195	3.590	0.058
sibling presence (y)	-0.182	0.181	1.002	0.317
random effects				
maternal ID	0.135			
paternal ID	0.109			
dominant male ID	0.147			
birth year	0.067			

Table S4. Significance of quadratic parental age effects (in years) and environment by parental age interactions on female offspring and male offspring lifespan, in the Seychelles warbler using a GLMM. Significance was determined by a likelihood ratio test (LRT, P) where df=1, by adding the variable to the minimal model (Table 1).

	Female offspring lifespan			**Male offspring lifespan**		
variables	LRT	df	P	LRT	df	P
age of mother^2	0.001	1	0.970	2.523	1	0.112
age of father^2	0.483	1	0.487	0.808	1	0.369
age of dominant male^2	1.547	1	0.214	1.347	1	0.246
territory quality*maternal age	0.407	1	0.524	0.290	1	0.590
territory quality*paternal age	0.052	1	0.820	0.295	1	0.587
territory quality*dominant male age	0.121	1	0.728	0.095	1	0.758
group size*maternal age	2.650	1	0.104	1.164	1	0.281
group size*paternal age	0.126	1	0.722	2.082	1	0.149
group size*dominant male age	1.407	1	0.236	1.563	1	0.211
helper*maternal age	0.002	1	0.968	0.057	1	0.812
helper*paternal age	2.163	1	0.141	0.838	1	0.360
helper*dominant male age	0.326	1	0.568	1.122	1	0.290

Table S5. Significance of quadratic parental age effects (in years) and environment by parental age interactions on female offspring and male offspring lifespan, in the Seychelles warbler, in the Cox proportional hazards mixed model. Significance was determined by a likelihood ratio test (LRT, P) where df=1, by adding the variable to the minimal model (Table S2).

	Female offspring lifespan		**Male offspring lifespan**	
variables	LRT	P	LRT	P
age of mother^2	0.008	0.929	0.105	0.746
age of father^2	1.954	0.162	0.152	0.697
age of dominant male^2	0.016	0.899	0.878	0.349
territory quality*maternal age	0.044	0.833	0.420	0.517
territory quality*paternal age	0.124	0.724	1.842	0.175
territory quality*dominant male age	0.063	0.802	0.147	0.702
group size*maternal age	0.748	0.387	0.032	0.859
group size*paternal age	1.311	0.252	0.011	0.916
group size*dominant male age	0.010	0.919	0.381	0.537
helper*maternal age	0.007	0.934	0.784	0.376
helper*paternal age	2.042	0.153	0.692	0.406
helper*dominant male age	0.076	0.783	0.020	0.889

Table S6. Generalised linear mixed model results investigating between- versus within- maternal and paternal age effects (in years) on offspring lifespan, in each sex separately, in the Seychelles warbler, using the within-subject centering method (van de Pol and Wright 2009). Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P-value) where df=1. The model investigates whether the within- and between-parental age slopes from Table 2 are significantly different from each other (mean age represents the difference between the slopes and is significant if the slopes are significantly different from each other). The age component is now equivalent to the within-parental age slope from Table 2. Significant fixed effects are highlighted in bold.

	Female offspring lifespan				**Male offspring lifespan**			
	n=467				n=485			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	1.284	0.062			1.204	0.070		
mean maternal age	**0.412**	**0.146**	**7.939**	**0.005**	0.035	0.134	0.069	0.794
maternal age	**-0.508**	**0.121**	**17.503**	**<0.001**	0.092	0.096	0.920	0.338
mean paternal age	0.161	0.166	0.928	0.335	0.244	0.154	2.503	0.114
paternal age	-0.157	0.134	1.361	0.243	-0.198	0.128	2.437	0.119
mean dominant male age	-0.139	0.169	0.675	0.411	0.056	0.158	0.126	0.723
dominant male age	0.252	0.146	2.974	0.085	0.102	0.131	0.604	0.437
birth year	**-0.525**	**0.112**	**19.000**	**<0.001**	**-0.514**	**0.138**	**12.252**	**<0.001**
territory quality	0.022	0.080	0.075	0.784	0.150	0.093	2.645	0.104
group size	-0.104	0.077	1.825	0.177	-0.065	0.081	0.654	0.419
helper presence (y)	-0.153	0.092	2.806	0.094	-0.140	0.101	1.936	0.164
sibling presence (y)	-0.069	0.103	0.446	0.504	0.142	0.100	1.991	0.158
random effects								
maternal ID	0.089				0.088			
paternal ID	0.170				0.081			
dominant male ID	0.004				0.069			
birth year	0.022				0.054			

Table S7. Significance of quadratic parental age effects and environment by parental age interactions on female offspring and male offspring lifetime reproductive success in the Seychelles warbler. Significance was determined by a likelihood ratio test (LRT, P), df = 1, by adding the variable to the minimal model (Table 3). Significant fixed effects are highlighted in bold.

	Female offspring LRS		**Male offspring LRS**	
variables	LRT	P	LRT	P
age of mother^2	0.646	0.421	0.187	0.666
age of father^2	0.456	0.500	0.078	0.780
age of dominant male^2	0.480	0.488	0.072	0.788
territory quality*maternal age	0.626	0.429	0.082	0.775
territory quality*paternal age	**6.085**	**0.014**	0.009	0.926
territory quality*dominant male age	**4.698**	**0.030**	0.010	0.922
group size*maternal age	0.951	0.330	0.090	0.764
group size*paternal age	0.046	0.831	0.714	0.398
group size*dominant male age	1.773	0.183	0.086	0.770
helper*maternal age	0.530	0.467	0.612	0.434
helper*paternal age	0.013	0.911	0.772	0.380
helper*dominant male age	1.996	0.158	0.001	0.972

Table S8. Generalised linear mixed model results investigating between- versus within- maternal and paternal age effects (in years) on offspring lifetime reproductive success, in each sex separately, in the Seychelles warbler using the within-subject centering method (van de Pol and Wright 2009). Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P-value) where df=1. The model investigates whether the within and between parental age slopes from Table 4 are significantly different from each other (mean age represents the difference between the slopes and is significant if the slopes are significantly different from each other). The age component is now equivalent to the within parental age slope from Table 4. Significant fixed effects are highlighted in bold.

	Female offspring LRS				**Male offspring LRS**			
	n=441 females				n=466 males			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	0.513	0.131			0.345	0.143		
mean maternal age	0.537	0.289	3.344	0.067	0.303	0.274	1.219	0.270
maternal age	**-0.835**	**0.261**	**9.640**	**0.002**	0.139	0.219	0.402	0.526
mean paternal age	-0.245	0.303	0.659	0.417	0.533	0.345	2.449	0.118
paternal age	0.291	0.278	1.103	0.294	-0.071	0.277	0.067	0.796
mean dominant male age	-0.164	0.322	0.260	0.610	-0.459	0.379	1.493	0.222
dominant male age	0.025	0.301	0.007	0.935	0.324	0.307	1.129	0.288
birth year	**-1.076**	**0.227**	**23.569**	**<0.001**	**-1.119**	**0.272**	**16.840**	**<0.001**
territory quality	-0.136	0.142	0.927	0.336	0.219	0.199	1.211	0.271
group size	0.004	0.151	0.001	0.981	-0.097	0.175	0.304	0.581
helper presence (y)	**-0.611**	**0.201**	**9.336**	**0.002**	-0.279	0.222	1.643	0.200
sibling presence (y)	-0.109	0.189	0.333	0.564	0.070	0.204	0.118	0.732
random effects								
maternal ID	0.100				0.153			
paternal ID	0.090				0.234			
dominant male ID	0.046				<0.001			
birth year	0.064				0.085			

Table S9. Generalised linear mixed model results investigating parental age effects (in years) on offspring annual reproductive success (measured as the number of offspring in the pedigree who survived to 1 year), in each sex separately, in the Seychelles warbler. Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P) where df=1. Significant fixed effects are highlighted in bold.

	Female offspring ARS				**Male offspring ARS**			
	n=2287 observations of 441 IDs				n=2341 observations of 466 IDs			
variables	estimate	SE	LRT	P	estimate	SE	LRT	P
fixed effects								
intercept	-1.912	0.118			-1.961	0.108		
age	4.983	0.399	-	-	4.870	0.356	-	-
age^2	**-4.935**	**0.435**	**211.530**	**<0.001**	**-4.043**	**0.331**	**213.390**	**<0.001**
lifespan	**0.392**	**0.134**	**8.407**	**0.004**	**0.350**	**0.132**	**7.017**	**0.008**
age of mother	-0.039	0.107	0.130	0.718	0.117	0.096	1.461	0.227
age of father	-0.015	0.119	0.016	0.900	0.128	0.114	1.256	0.263
age of dominant male	-0.139	0.117	1.416	0.234	0.161	0.113	2.032	0.154
birth year	-0.036	0.207	0.030	0.863	-0.207	0.201	1.062	0.303
territory quality	-0.107	0.114	0.878	0.349	0.129	0.126	1.035	0.309
group size	0.090	0.111	0.634	0.426	-0.193	0.115	2.878	0.090
helper presence (y)	**-0.342**	**0.153**	**5.109**	**0.024**	0.010	0.147	0.005	0.944
sibling presence (y)	0.043	0.151	0.082	0.775	-0.058	0.136	0.183	0.669
random effects								
ID	0.070				0.066			
Year	0.153				0.120			

Table S10. Generalised mixed model results investigating between- versus within- maternal and paternal age effects on female offspring lifespan in the Seychelles warbler, using the within-subject centering method (van de Pol and Wright 2009). This model excludes the outlier seen in Figure 2, but model estimates are very similar with this outlier included (Table 2). Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P-value) where df=1. The model investigates within-parental age effects (deviation from the mean age of the parent) and between-parental age effects (mean age for each parent). Significant fixed effects are in bold.

	Female offspring lifespan			
	n=466			
variables	estimate	SE	LRT	P
fixed effects				
intercept	1.281	0.062		
between-maternal age	-0.104	0.090	1.309	0.253
within-maternal age	**-0.470**	**0.126**	**14.046**	**<0.001**
between-paternal age	0.012	0.110	0.011	0.916
within-paternal age	-0.162	0.134	1.460	0.227
between-dominant male age	0.111	0.094	1.383	0.240
within-dominant male age	0.240	0.147	2.680	0.102
birth year	**-0.522**	**0.113**	**18.460**	**<0.001**
territory quality	0.021	0.081	0.067	0.796
group size	-0.100	0.077	1.704	0.192
helper presence (y)	-0.149	0.092	2.678	0.102
sibling presence (y)	-0.063	0.103	0.375	0.540
random effects				
maternal ID	0.086			
paternal ID	0.168			
dominant male ID	0.007			
birth year	0.024			

Table S11. Generalised mixed model results investigating between- versus within- maternal and paternal age effects on female offspring lifetime reproductive success in the Seychelles warbler using the within-subject centering method (van de Pol and Wright 2009). This model excludes the outlier seen in Figure 4A, but model estimates are very similar with this outlier included (Table 4). Included are the estimated effects (estimate), standard errors (SEs), and significance of fixed effects based on a likelihood ratio test (LRT; P-value) where df=1. The model investigates within-parental age effects (deviation from the mean age of the parent) and between-parental age effects (mean age for each parent). Significant fixed effects are in bold.

	Female offspring LRS			
	n=440			
variables	estimate	SE	LRT	P
fixed effects				
intercept	0.509	0.131		
between-maternal age	-0.296	0.168	3.079	0.079
within-maternal age	**-0.847**	**0.298**	**7.695**	**0.006**
between-paternal age	0.044	0.178	0.061	0.806
within-paternal age	0.295	0.281	1.109	0.292
between-dominant male age	-0.141	0.171	0.689	0.407
within-dominant male age	0.027	0.303	0.008	0.928
birth year	**-1.079**	**0.228**	**23.354**	**<0.001**
territory quality	-0.135	0.142	0.898	0.343
group size	0.003	0.154	<0.001	0.986
helper presence (y)	**-0.613**	**0.202**	**9.347**	**0.002**
sibling presence (y)	-0.110	0.190	0.338	0.561
random effects				
maternal ID	0.101			
paternal ID	0.094			
dominant male ID	0.049			