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Age-dependent changes in infidelity in Seychelles warblers

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Abstract

Extra-pair paternity (EPP) is often linked to male age in socially monogamous vertebrates; that is, older males are more likely to gain EPP and less likely to be cuckolded. However, whether this occurs because males improve at gaining paternity as they grow older, or because “higher quality” males that live longer are preferred by females, has rarely been tested, despite being central to our understanding of the evolutionary drivers of female infidelity. Moreover, how extra-pair reproduction changes with age within females has received even less attention. Using 18 years of longitudinal data from an individually marked population of Seychelles warblers (*Acrocephalus sechellensis*), we found considerable within-individual changes in extra-pair reproduction in both sexes: an early-life increase and a late-life decline. Furthermore, males were cuckolded less as they aged. Our results indicate that in this species age-related patterns of extra-pair reproduction are determined by within-individual changes with age, rather than differences among individuals in longevity. These results challenge the hypothesis—based on longevity reflecting intrinsic quality—that the association between male age and EPP is due to females seeking high-quality paternal genes for offspring. Importantly, EPP accounted for up to half of male reproductive success, emphasizing the male fitness benefits of this reproductive strategy. Finally, the occurrence of post-peak declines in extra-pair reproduction provides explicit evidence of senescence in infidelity in both males and females.

KEYWORDS

age, extra-pair paternity, selective appearance and disappearance, senescence, within-individual effect

1 | INTRODUCTION

Across socially monogamous species, levels of extra-pair paternity (EPP) show that infidelity (i.e., extra-pair mating) occurs frequently, yet the evolution of this behaviour remains enigmatic (Griffith, Owens, & Thuman, 2002; Taylor, Price, & Wedell, 2014; Westneat

& Stewart, 2003). Despite being associated with costs, extra-pair mating is expected to benefit males by increasing their reproductive success (Jennions & Petrie, 2000). However, in females, extra-pair fertilizations do not necessarily increase immediate reproductive success, so if and how females benefit from infidelity is still unclear, despite considerable research and debate (Forstmeier, Nakagawa,

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Griffith, & Kempnaers, 2014; Griffith et al., 2002; Jennions & Petrie, 2000). Determining patterns of EPP within natural populations, and how they change over time in response to key variables (e.g., individual traits and socio-ecological factors), is important if we are to fully understand the evolutionary significance of extra-pair reproduction.

Age is a key phenotypic trait that appears to underlie considerable individual variation in extra-pair reproduction (Hamilton & Zuk, 1982; Hsu, Schroeder, Winney, Burke, & Nakagawa, 2015; Morton, Forman, & Braun, 1990; Westneat & Stewart, 2003). Numerous single-species studies have shown a positive association between male age and within- or extra-pair paternity success, or both (e.g., Edme, Munclinger, & Krist, 2016; Kempnaers, Verheyen, & Dhondi, 1997; Richardson & Burke, 1999; Westneat, 1990). Furthermore, meta-analyses have shown that, across species, extra-pair sires are often older than the males they cuckold (Ackay & Roughgarden, 2007; Hsu et al., 2015) and that EPP success is positively related to male age (Cleasby & Nakagawa, 2012). However, the vast majority of studies (individual studies and meta-analyses) have assessed population-level associations between age and EPP, whereas little is known about how the rate of extra-pair reproduction changes within individuals with age, even though this may be key to understanding the benefits of infidelity for females.

According to the influential “good genes” hypothesis, extra-pair reproduction enables socially constrained females to acquire higher quality paternal genes for their young (Hamilton & Zuk, 1982). Furthermore, if male age reflects good genes via demonstrated viability (Kokko, 1998; Trivers, 1972), females should seek extra-pair fertilizations from older males, especially when paired with young males. This should result in between-male differences in paternity gain and loss in relation to age (i.e., higher EPP success and lower within-pair paternity loss in older males). Alternatively, the “competitive ability” hypothesis (Nakagawa, Schroeder, & Burke, 2015) posits that males increase their ability to gain paternity as they age. This may be due to physiological changes (e.g., improved body/ejaculate condition) or experience-enhanced behavioural changes (e.g., improved mate-guarding, timing of copulations, increased ability to force copulations; Curio, 1983; Hsu et al., 2015; Morton et al., 1990; Westneat & Stewart, 2003). Contrary to the good genes hypothesis, the competitive ability hypothesis predicts a within-male age effect and does not imply any indirect genetic benefits for females. However, these two hypotheses are not mutually exclusive because both within- and between-individual differences in EPP in relation to age may occur at the same time.

Most research on EPP so far has relied on cross-sectional analyses, which can capture population-level associations between age and EPP, but cannot distinguish the processes that may underlie such associations, namely: (a) within-individual changes in EPP with advancing age and (b) between-individual changes, driven by the selective appearance/disappearance (i.e., the age of entry into/exit from the reproductive population, respectively) of individuals with consistently different ability to gain EPP (van de Pol & Verhulst, 2006). Indeed, very few studies have attempted to disentangle within- from

between-individual effects on EPP (Hsu et al., 2017; Schroeder et al., 2016). Clearly, more longitudinal studies are needed if we are to understand the factors that shape male age-dependent variation in EPP and, therefore, better understand the evolution of infidelity.

The relationship between age and extra-pair reproduction in females remains markedly understudied and unclear. Many reasons have been suggested as to why females may seek extra-pair copulations, including the acquisition of direct benefits (e.g., fertility insurance; Sheldon, 1994) or indirect genetic benefits (e.g., high-quality or compatible genes in offspring; Brown, 1997; Hamilton & Zuk, 1982; Zeh & Zeh, 1996). Older females may have fewer extra-pair offspring because they are more capable of obtaining a better quality social male (Wagner, Schug, & Morton, 1996), and thus do not need to seek extra-pair copulations. Alternatively, they may be more experienced at avoiding or resisting unwanted copulation attempts (Morton & Derrickson, 1990). On the other hand, older females may have more extra-pair offspring because they are better at avoiding mate-guarding, and at obtaining copulations with other males—for “good genes” or other reasons (Bouwman & Komdeur, 2005). Additionally, older females may be more likely to produce extra-pair offspring because they are better at overcoming constraints imposed by male retaliation to perceived paternity loss (the “constrained female” hypothesis; Dixon, Ross, O'Malley, & Burke, 1994; Gowaty, 1996). The few studies that have investigated the relationship between female age and the production of extra-pair offspring have provided contrasting results, showing a positive relationship (Bouwman & Komdeur, 2005; Dietrich, Schmoll, Winkel, Epplen, & Lubjuhn, 2004; Kempnaers, Congdon, Boag, & Robertson, 1999), a negative relationship (Moreno et al., 2015; Ramos et al., 2014; Stutchbury et al., 1997) or no relationship (Lubjuhn, Gerken, Brün, & Schmoll, 2007; Wagner et al., 1996). However, none of these studies distinguished within- and between-individual age effects.

Senescence—the progressive deterioration in performance in late life (Medawar, 1952; Williams, 1957)—is an interesting and important within-individual process related to age. There have been numerous studies assessing the fitness consequences of senescence, most of which have focused on declines in survival and reproduction with age (reviewed by Nussey, Froy, Lemaitre, Gaillard, & Austad, 2013). However, to our knowledge only one study has addressed, albeit not explicitly, senescence in EPP (Hsu et al., 2017), and has focused only on males.

A within-individual senescent decline in EPP success in late life is compatible with both the good genes and the competitive ability hypotheses. Specifically, in a good genes scenario, the oldest males are the most attractive because they are of highest intrinsic quality (as evidenced by highest longevity) and thus are preferred by females; however, if senescence causes lower fertilization ability (e.g., because of lower sperm competitiveness; Dean et al., 2010), very old males may gain less extra-pair (and total) paternity than younger (less attractive) males. In this case, annual EPP success would be impacted by both a between-individual age effect, represented by a positive association between annual EPP and longevity (because males that live longer are preferred by females),

and by a within-individual age effect, resulting in a decline in EPP in all males in late life (because at very old ages males are in lower physical condition). According to the competitive ability hypothesis, all males initially increase their reproductive success as they age (due to increasing experience and/or body condition) but, if senescence occurs, this initial increase in reproduction with age is expected to turn into a decline in late life. In this case, annual EPP would be predicted only by a within-individual age effect, resulting in an increase in EPP at young ages followed by a decline at old ages (while in the absence of senescence EPP should asymptote when added experience, or condition, does not lead to further improvements in the ability to gain EPP). Given that the acquisition of EPP may change with age and/or experience, and also show senescence, it is likely that the contribution of EPP to total reproductive success will vary considerably with age. Numerous studies have investigated how EPP alters male reproductive success (e.g., Albrecht et al., 2007; Lebigre, Arcese, Sardell, Keller, & Reid, 2012), but only a few have done so in relation to age (e.g., Girndt, Chng, Burke, & Schroeder, 2018; Hsu et al., 2017). To our knowledge, only one of these studies disentangled within- and between-individual age effects (Hsu et al., 2017), although this study did not explicitly test for post-peak senescence in EPP.

Here, we investigate extra-pair offspring production in relation to male and female age in the Seychelles warbler (*Acrocephalus sechellensis*). This long-lived passerine has a mean life expectancy of 5.5 years after fledgling (Komdeur, 1991) and a maximum observed lifespan of 19 years (Hammers & Brouwer, 2017). Seychelles warblers display facultative cooperative breeding (Komdeur, 1992; Richardson, Burke, & Komdeur, 2007): dominant pairs occupy a territory on their own or (in ~30% of territories) are joined by subordinates of either sex (Hammers et al., 2019). Clutches typically consist of one egg, but ~13% of nests contain one or two additional eggs, often laid by subordinate females (Richardson, Burke, & Komdeur, 2002; Richardson, Jury, Blaakmeer, Komdeur, & Burke, 2001). Individuals are socially monogamous, but ~44% of young are sired by males other than the social male (Hadfield, Richardson, & Burke, 2006; Richardson et al., 2001). Over 97% of all paternity is gained by dominant males (Hadfield et al., 2006; Raj Pant, Komdeur, Burke, Dugdale, & Richardson, 2019; Richardson et al., 2001) either in their own territory (within-group paternity: WGP) or with females from another territory (extra-group paternity: EGP). Thus, in this species EGP is virtually the equivalent of EPP.

In the Seychelles warbler, females that live in larger groups are more likely to produce extra-group offspring (EGO, i.e., offspring sired by extra-group males; Raj Pant et al., 2019). In subordinate mothers, but not in dominant mothers (which account for over 85% of offspring), the likelihood of producing EGO is positively linked to the genetic relatedness to the dominant male in the group (Raj Pant et al., 2019). However, this potential inbreeding avoidance mechanism in subordinate females does not prevent the occurrence of inbreeding in the population (Richardson, Komdeur, & Burke, 2004). In Seychelles warblers, there is evidence that dominant males actively seek EGP during extra-territorial forays (Komdeur, Kraaijeveld-Smit,

Kraaijeveld, & Edelaar, 1999). Past research has also shown that females initiate successful copulations, are able to resist mating attempts (Komdeur et al., 1999) and are more likely to gain extra-group fertilizations from more MHC (major histocompatibility complex)-diverse males when paired with males of low MHC diversity (Richardson, Komdeur, Burke, & von Schantz, 2005), which suggests that female choice plays an active role in EGP. However, the relative role of female choice (pre- or post-copulatory) and male-male competition (including sperm competition) in determining patterns of extra-group fertilizations remains unknown in this system.

We use an 18-year longitudinal data set from the Seychelles warbler to determine the patterns of extra-group reproduction in relation to age in males (dominant) and females (dominant or subordinate). Our isolated study population on Cousin Island provides an excellent system for such investigations: inter-island migration is virtually absent (Komdeur, Burke, Dugdale, & Richardson, 2016; Komdeur, Piersma, Kraaijeveld, Kraaijeveld-Smit, & Richardson, 2004), extrinsic mortality is low (Hammers et al., 2015) and >96% of individuals have been DNA-sampled and individually colour-ringed since 1997 (Brouwer et al., 2010). Accurate parentage assignment and precise estimates of survival and individual reproductive output (throughout life) are therefore available. We assess how patterns of extra-group reproduction are affected by within-individual changes with age and between-individual selective appearance and disappearance effects. We also test for declines in extra-group reproduction in late life (senescence). Finally, we quantify the relative contribution of EGP and WGP success to annual reproductive success in males. By undertaking the analyses outlined above, we provide evidence to distinguish between different hypotheses as to why females engage in extra-pair mating and improve our understanding of the factors driving the evolution of infidelity.

2 | MATERIALS AND METHODS

2.1 | Study system

The Seychelles warbler is an insectivorous passerine endemic to the Seychelles archipelago. The population on Cousin Island (29 ha, 04°20'S, 55°40'E) has been monitored as part of a long-term study, which started in 1981 and intensified in 1997 (Hammers et al., 2019; Komdeur, 1992; Richardson, Komdeur, & Burke, 2003). Since then, virtually all breeding attempts have been followed each year during the main breeding season (June–September). As many birds as possible were captured every year, either using mist-nets or as nestlings. Newly caught individuals were assigned a unique combination of three colour rings and a British Trust for Ornithology metal ring.

All caught individuals were blood sampled (~25 µl) using brachial venipuncture and DNA from these samples was used for molecular sexing (following Griffiths, Double, Orr, & Dawson, 1998) and genotyping based on 30 microsatellite loci (see: Richardson et al., 2001; Spurgin et al., 2014). Parentage was assigned to 1,554 offspring (1991–2015) using MASTERBAYES 2.52 and used to build a

genetic pedigree (see: Edwards, Dugdale, Richardson, Komdeur, & Burke, 2018; Sparks et al., 2020).

Inter-island dispersal is virtually absent (<0.1%) in the Seychelles warbler (Komdeur et al., 2004, 2016) and individual resighting probability per season on Cousin Island is very high (~92–98%, Brouwer et al., 2010); therefore individuals not seen over two consecutive seasons can safely be assumed to be dead (Hammers, Richardson, Burke, & Komdeur, 2013).

During each breeding season, group membership, social status and territory boundaries were assigned for all birds using observations of foraging and singing locations, non-aggressive social interactions, and aggressive territorial interactions (e.g., Bebbington et al., 2017). Within groups, dominant pairs were identified via pair and courtship behaviours. Subordinate birds, which are often offspring that have delayed dispersal (Kingma, Bebbington, Hammers, Richardson, & Komdeur, 2016), are classified as “helpers” or “non-helpers” based on their participation in incubation (females only) and in feeding offspring (both males and females; Hammers et al., 2019; Komdeur, 1994).

Reproduction is seasonally constrained by invertebrate prey availability and offspring are fed for up to three months after fledging (Komdeur, 1991). We refer to the dominant male in a group as the “social male” of any reproductively mature females in his group (dominant and subordinate), as males can fertilize both dominant and subordinate females in their territory.

2.2 | Data selection

We gathered previously generated parentage data for 934 Seychelles warblers that were assigned parentage with high confidence ($\geq 80\%$) and that hatched on Cousin Island during main breeding seasons in the period 1997–2014 (Edwards et al., 2018; Hadfield et al., 2006; Richardson et al., 2001; Sparks et al., 2020). We used these data to assess the age-dependent production of EGO by females and the age-dependent risk of cuckoldry for their social male partner (the dominant male in the group). We first tested if the likelihood that an offspring was sired by a male outside the breeding group (“EGP likelihood”) was related to the age of the mother (dominant or subordinate) and/or the age of the dominant male. The ages of dominant males and females are only weakly correlated in the Seychelles warbler ($r = 0.16$; Hammers et al., 2019). Given that Seychelles warbler females do not lay eggs in nests outside their own territory (Richardson et al., 2002), EGP likelihood will capture female infidelity.

We compiled 1,364 annual records of all dominant males alive between 1997 and 2014 that were genetically assigned at least one offspring across the whole data period (including entries of males siring no young in single years, $n = 237$ males). For each male, we determined the annual number of EGO (i.e., EGP success) and within-group offspring (i.e., WGP success). We then estimated the annual proportion of EGO sired by each dominant male (535 annual records from 233 males, excluding cases in which a male had an

annual reproductive success of zero). In our paternity measures, we included only offspring that survived for at least three months to remove any potential bias on annual reproductive estimates resulting from differing catching efforts across years (which cause offspring to be caught at different ages in different years). Using these data, we assessed the relationship between male age and WGP, EGP, and the annual proportion of EGO sired by each male (i.e., the contribution of EGP to annual reproductive success).

2.3 | Statistical analyses

We quantified within-individual effects of age on the production of EGO (i.e., longitudinal changes throughout an individual's lifetime). To separate out between-individual (population-level cross-sectional) effects of age (i.e., due to selective appearance and disappearance), we employed the method developed by van de Pol and Verhulst (2006). By including age of first reproduction and age of last reproduction (or longevity) in addition to age in the same mixed model, this approach allows us to quantify the within-individual effect of age (expressed by the age term) while controlling for selective appearance and disappearance (expressed by age of first and last reproduction/longevity, respectively). Here, we modelled selective appearance using the age of first dominance for males, to account for when they could potentially start breeding (virtually all paternity is obtained by dominant males in the Seychelles warbler; Raj Pant et al., 2019). Because females can reproduce before gaining dominance, we used the age at which females were first assigned an offspring as subordinates or the age of first dominance—whichever came first (subsequently termed “age of first dominance” for simplicity). Age at death (longevity) was used to model selective disappearance for both males and females. Individuals of unknown longevity (i.e., birds translocated to other islands or those that had not died by the end of 2018) were excluded from the analyses. The chronological age of individuals was always included as a fixed effect alongside age of first dominance and longevity so that it represents the within-individual effect of age on EGP. Chronological age, age of first dominance and longevity were all measured in years (integers).

Reproductive performance can change shortly before death, independently of age (Bowers et al., 2012; Coulson & Fairweather, 2001). Therefore, to avoid confounding any age-related effects with an age-independent terminal effect, we included a binary variable in models indicating whether a bird died before the subsequent breeding season.

We performed statistical analyses in R (3.6.3) with generalized linear mixed models (GLMMs) fitted using the `LME4` (1.1–20) package (Bates, Mächler, Bolker, & Walker, 2015). We built separate GLMMs to analyse the following variables (summarized in Table 1): (1) offspring EGP likelihood—i.e., the likelihood that the offspring was sired by a male outside the group (yes/no binary variable), in relation to the age of the mother ($n = 852$ offspring) or the age of the dominant male in the group ($n = 848$ offspring); (2) annual paternity obtained by each male ($n = 1,364$ male/years) split into (2a)

TABLE 1 Summary of the response variables addressed in our analyses of age-related changes in the reproduction of the Seychelles warbler, highlighting the age-effects we detected

Variable name	Description	Age-effects assessed for	Detected age-effects
Extra-group paternity (EGP) likelihood	The likelihood that the offspring is sired by an extra-group male (yes/no binary variable)	Females (the mothers)	Within-individual: increase in early life, senescent decline
		The dominant male in the natal group	Within-individual: decrease in early life (before levelling off)
EGP success	The annual number of extra-group offspring (EGO) sired	Males	Within-individual: increase in early life, senescent decline
WGP success	The annual number of within-group offspring (WGO) sired	Males	Within-individual: increase in early life, senescent decline
Annual reproductive success (ARS)	The annual number of offspring sired (EGO + WGO)	Males	Within-individual: increase in early life, senescent decline
Proportion of EGO	Annual EGP success over ARS	Males	Within-individual: increase in early life (before levelling off)

EGP success (number of EGO sired), (2b) WGP success (number of within-group offspring sired) and (2c) total reproductive success (i.e., extra-group + within-group young sired); and (3) annual proportion of EGO (i.e., the number of EGO over the number of total offspring per male per year) sired by each dominant male that was assigned at least one offspring in a given year ($n = 535$). Models analysing EGP likelihood and the annual proportion of EGO sired by each male were constructed with a binomial error structure and logit link function, while models of paternity success (EGP/WGP/annual reproductive success) were built with a Poisson error structure and log link function. Furthermore, we built a GLMM to perform a population-level comparison between the age of the social father (i.e., the cuckolded male) and the age of the genetic father (i.e., the extra-group sire) of each EGO ($n = 395$). The GLMM was built with a Poisson error structure and log link function. We checked for collinearity between fixed effects using the variance inflation factor (VIF) and found none ($VIF \leq 3$). We standardized (mean-centred and scaled to one standard deviation) continuous predictors and used the “BOBYQA” nonlinear optimization (Powell, 2009) to aid convergence of models. The statistical significance of model terms was assessed using parametric bootstrap p -values ($n_{sim} = 3,000$) from full models containing all biologically meaningful predictors of interest.

We assessed female and social male age effects on offspring EGP likelihood in separate models to avoid any potential bias caused by the non-independence of female and social male age over time (within our data set, 51% of females that reproduced in multiple years and 53% of social males that raised offspring in multiple years had more than one social partner). Both female and social male models contained four random effects (random intercepts): year, territory, mother's identity and social male's identity (pair identity explained zero variance and was not included as an additional random effect). Female and social male models also included two fixed effects in common: the age difference between the mother and her social male and the offspring's natal group size (offspring EGP likelihood is higher in larger groups; Raj Pant et al., 2019).

The model analysing female age effects on EGP likelihood included as additional fixed effects the mother's age (linear and quadratic), age of first dominance, longevity and terminal effect. To check for any potential bias caused by inbreeding avoidance effects occurring in subordinate females (Raj Pant et al., 2019), we re-ran this model on offspring produced only by dominant females ($n = 759$) and compared results with those from the model run on the full data set (i.e., offspring produced by dominant and subordinate females, $n = 852$).

The model analysing social male age effects on EGP likelihood contained the corresponding additional fixed effects of social male instead of female age traits (i.e., a social male's age, age of first dominance, longevity and terminal effect). Furthermore, we built a model to test for any differences between the age of cuckolded males and the age of the extra-group sires that cuckolded them (population-level analysis). This model featured male age as the response variable, male status (i.e., extra-pair or cuckolded male) as a fixed effect and three random effects (random intercepts: social father, genetic father and mother identity).

Models analysing annual paternity success (EGP/WGP/reproductive success) per male and the annual proportion of EGO sired by each male included five fixed predictors—male age (linear and quadratic), age of first dominance, longevity and a terminal effect—and three random effects (random intercepts)—year, territory and male identity. Because annual EGP and WGP may affect one another, when analysing EGP and WGP, we also included as fixed effects either WGP or EGP respectively, and the interaction between WGP/EGP and male age.

A negative quadratic relationship between reproductive components and age does not necessarily indicate that a late-life decline in these components exists but may just represent that an increase early in life levels off at later ages (Bouwhuis, Sheldon, Verhulst, & Charmantier, 2009). To determine whether EGP likelihood and paternity success exhibit true late-life declines consistent with senescence, we tested for linear age effects after the peak age for each of these components. We estimated peak ages from the linear and

quadratic coefficients of age, as $(-\beta_{\text{linear}})/(2 \times \beta_{\text{quadratic}})$, from models we built with non-standardized data. We compiled subsets of individuals with ages \geq the peak age for offspring EGP likelihood (female age effects: $n = 319$; social male age effects: $n = 346$), paternity success (within-group: $n = 598$; extra-group and total: $n = 360$), or the proportion of EGO sired ($n = 97$) per male. We ran models regressing EGP likelihood, paternity success (extra-group/within-group/total) or the proportion of EGO sired over the linear age (post-peak) of individuals and other predictors included in previous models, except the quadratic age term. For simplicity, when analysing EGP/WGP in the post-peak subsets we also excluded WGP/EGP and the interaction between WGP/EGP and male age, which were all nonsignificant predictors in full data set analyses (see Table 4).

3 | RESULTS

3.1 | Offspring EGP likelihood and female age

The proportion of offspring sired by an extra-group male was 42% in the population. There was a negative quadratic effect of maternal age on offspring EGP likelihood, which increased from a predicted ~29% for mothers in their first year to ~46% when the mother was 5.6 years old, after which it decreased to ~10% for the oldest mothers (Figure 1 and Table 2). Furthermore, the older a female was relative to the dominant male in her group, the higher the likelihood was

that she produced an EGO (Table 2). Regarding senescent effects, the EGP likelihood of offspring produced by females ≥ 6 years old (i.e., past the peak age of EGP likelihood) declined with female age ($\beta \pm SE = -0.41 \pm 0.20$, $p = .039$; Table S1). EGP likelihood was not affected by the mother's age of first dominance, longevity or a terminal effect (Table 2). EGP likelihood was positively related to group size (Table 2). All results remained quantitatively similar when repeating the analysis of EGP likelihood using only offspring produced by dominant mothers ($n = 759$; Table S2). This indicates that any inbreeding avoidance effect occurring via extra-group reproduction by subordinate females does not bias our results on age-dependent production of EGO by females.

3.2 | Offspring EGP likelihood and social male age

When analysing offspring EGP likelihood—i.e., the probability that a male was cuckolded (on an offspring by offspring case)—in relation to male age, we found a positive quadratic effect of male age. The likelihood of being cuckolded decreased within individuals, from a predicted ~44% in young males to ~34% in males of 6.2 years of age (Figure 2 and Table 3). Despite the positive quadratic effect of age there was no post peak senescent effect—i.e., that males were increasingly more likely to be cuckolded when they were ≥ 6 years old ($\beta \pm SE = 0.05 \pm 0.19$, $p = .808$; Table S3). Males that lost WGP were on average 1 year younger than the extra-group

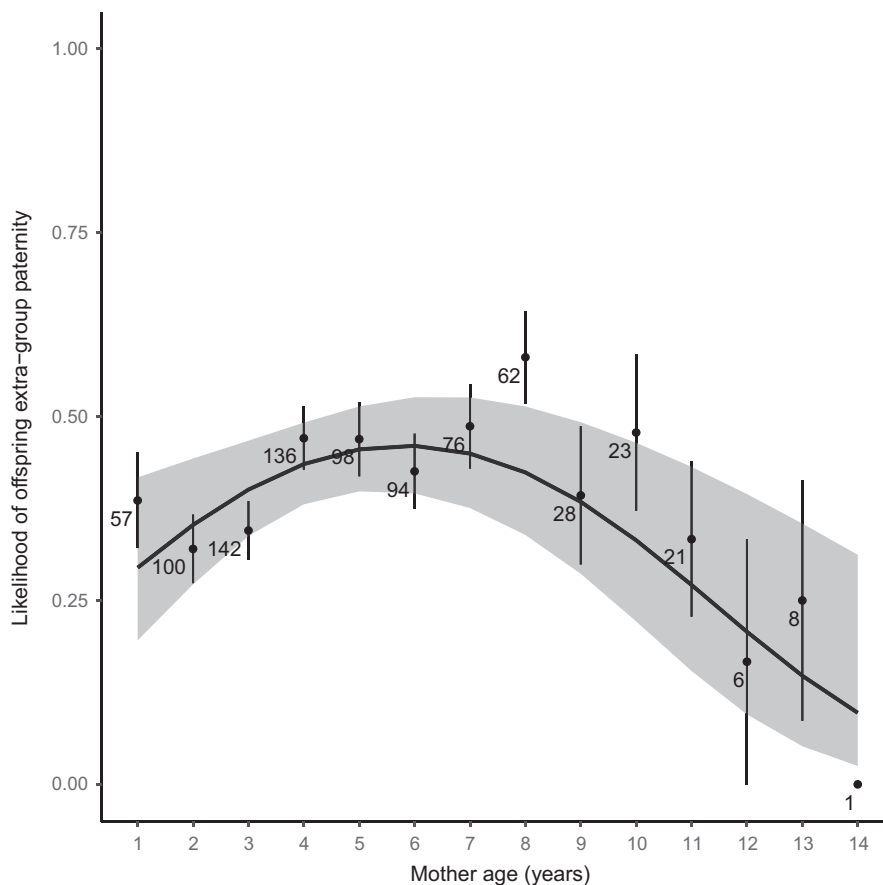


FIGURE 1 The likelihood of offspring extra-group paternity (EGP) in relation to maternal age in the Seychelles warbler ($n = 852$ offspring). Means of raw data (points) and their standard error (bars) are shown with associated sample sizes. The black line represents the prediction from the GLMM (Table 2) and the area shaded in grey indicates the 95% confidence interval (estimated with the *predict* function in R package *GGPLOT2*, version 3.3.0)

TABLE 2 Parameter estimates from a GLMM of offspring extra-group paternity (EGP) likelihood in relation to the age of mothers in the Seychelles warbler ($n = 852$ offspring)

Fixed effects	EGP likelihood ($n = 852$)		
	β	SE	p
Intercept	11.00	0.12	.098
Mother age	0.12	0.15	.451
Mother age²	-0.22	0.07	.002
Mother AFD	-0.05	0.09	.593
Mother longevity	-0.15	0.13	.260
Mother terminal effect	0.25	0.30	.401
Female-male age difference	0.39	0.12	.001
Group size	0.39	0.09	<.001
Random effects	σ^2	n	
Mother ID	0.22	298	
Social male ID	0.55	308	
Territory	0.00	138	
Year	0.00	18	

Note: Coefficient estimates (β), standard errors (SE) and p -values (p) are shown for each fixed effect. Variance (σ^2) and number of observations (n) are shown for each random effect. Significant ($p < .05$) terms are shown in bold.

Abbreviation: AFD, age of first dominance.

males that cuckolded them; this difference was significant (GLMM: $\beta_{\text{Male status (extra-group sire)}} = 0.23 \pm 0.03$, $p < .001$; Figure S1). The positive relationship between the probability of WGP loss and the female-social male age difference did not reach statistical significance ($p = .067$). The probability of being cuckolded was not associated with male age of first dominance or a terminal effect, and only showed a non-significant tendency to decrease with male longevity ($p = .063$). The probability of WGP loss was positively associated with group size (Table 3).

3.3 | Annual paternity success and male age

When analysing annual paternity success (extra-group, within-group and total) in relation to male age, we found an early-life increase and a late-life decline within individuals (Table 4). Specifically, there was a negative quadratic effect of male age on EGP success; the predicted number of extra-group offspring sired per annum increased from ~ 0.06 in males in their first year to peak at ~ 0.24 at 7.8 years and decreased thereafter to ~ 0.03 in the oldest males (Figure 3 and Table 4). There was also a negative quadratic effect of male age on annual WGP gained; the predicted number of within-group offspring sired increased from ~ 0.23 per annum in males in their first year to ~ 0.32 at 6.1 years and declined to ~ 0.09 in the oldest males (Figure 3 and Table 4).

As a result of the age-related changes in EGP and WGP outlined, total predicted annual reproductive success increased with male age from ~ 0.29 offspring in first-year males up to ~ 0.58 at 7.7 years, before declining to ~ 0.14 in the oldest males (Figure 3 and Table 4). The post-peak reduction in male reproduction in late life was confirmed

by the significant negative linear relationships between age and annual EGP in males ≥ 8 years ($\beta \pm SE = -0.32 \pm 0.16$, $p = .046$), WGP in males ≥ 6 years ($\beta \pm SE = -0.27 \pm 0.10$, $p = .013$) and total paternity success in males ≥ 8 years ($\beta \pm SE = -0.25 \pm 0.11$, $p = .021$; Table S4). Male annual extra-group, within-group and total reproductive success were not affected by male longevity, age of first dominance or a terminal effect (Table 4). We found no evidence of a trade-off between EGP and WGP: WGP and its interaction with male age were not related to EGP success, and EGP and its interaction with male age did not predict WGP success (Table 4). When analysing the proportion of a male's annual reproductive output obtained outside his own group, this increased with age, from a predicted $\sim 19\%$ in first-year males to a peak of $\sim 49\%$ at 8.6 years (Figure 4 and Table 5). Despite finding a significant negative quadratic effect of age, there was no significant senescent decline in the proportion of reproductive success resulting from EGP with age in males ≥ 9 years old ($\beta \pm SE = -0.23 \pm 0.25$, $p = .343$; Table S5). This suggests that the proportion of EGO sired remained relatively stable after peaking, probably as the decline in the amount of extra- and within-group offspring sired were similar in late life. The annual proportion of EGO sired was not influenced by male longevity, age of first dominance or a terminal effect (Table 5).

4 | DISCUSSION

Our results show that in both male and female Seychelles warblers, extra-group reproduction changed in relation to age within individuals, increasing in early life and declining in late life. In males, there were similar within-individual changes with age in WGP gained

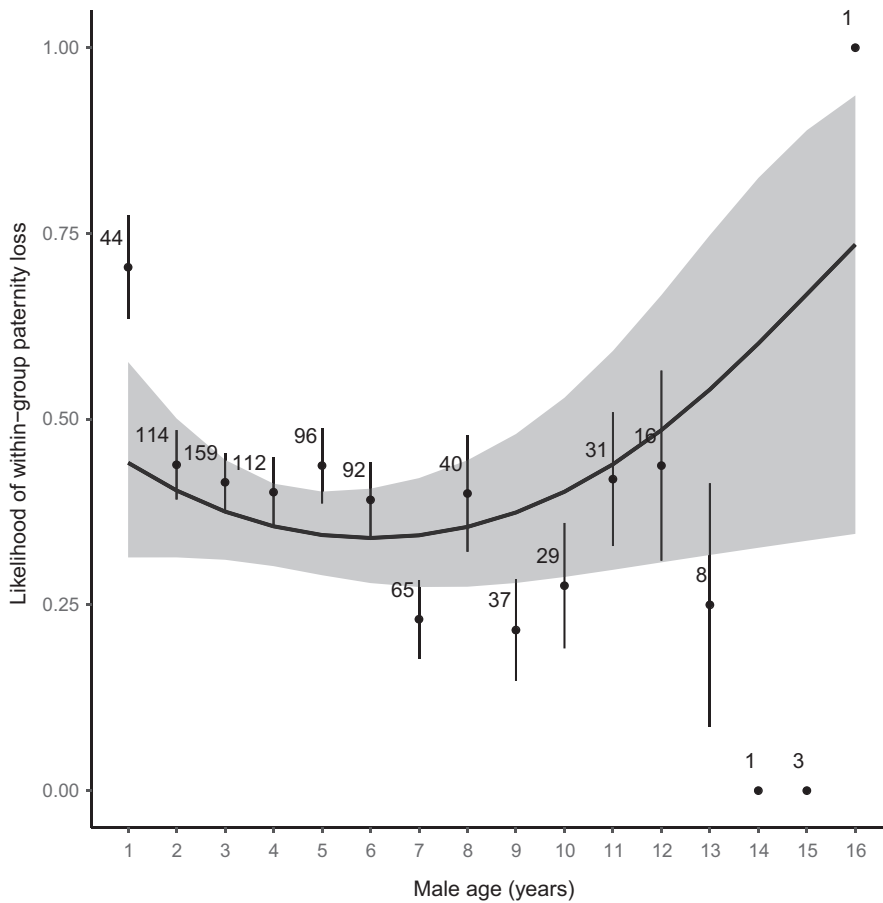


FIGURE 2 The likelihood of within-group paternity loss in relation to male age in the Seychelles warbler ($n = 848$ offspring). Means of raw data (points) and their standard error (bars) are shown with associated sample sizes. The black line represents the prediction from the GLMM (Table 3) and the area shaded in grey indicates the 95% confidence interval (estimated with the *predict* function in R package GGLOT2, version 3.3.0)

Fixed effects	EGP likelihood ($n = 848$)		
	β	SE	p
Intercept	-0.67	0.13	<.001
Social male age	-0.11	0.16	.502
Social male age²	0.15	0.07	.049
Social male AFD	-0.09	0.10	.371
Social male longevity	-0.25	0.13	.063
Social male terminal effect	0.18	0.31	.559
Female-male age difference	0.23	0.13	.067
Group size	0.37	0.09	<.001
Random effects	σ^2	n	
Mother ID	0.33	311	
Social male ID	0.41	287	
Territory	0.00	137	
Year	0.00	18	

TABLE 3 Parameter estimates from a GLMM of offspring extra-group paternity (EGP) likelihood in relation to the age of the dominant male in the offspring's natal group (i.e., the social male of the offspring's mother) in the Seychelles warbler ($n = 848$ offspring)

Note: Coefficient estimates (β), standard errors (SE) and p -values (p) are shown for each fixed effect. Variance (σ^2) and number of observations (n) are shown for each random effect. Significant ($p < .05$) terms are shown in bold.

Abbreviation: AFD, age of first dominance.

and—as a result of EGP and WGP patterns—in total reproductive success. Moreover, the likelihood of being cuckolded decreased within males from early to midlife. Extra-group reproduction accounted for ~50% of annual reproduction for males at their reproductive

peak. No age-dependent differences among individuals, due to selective appearance or disappearance, were detected in relation to extra-group reproduction in either males or females, or in relation to within-group and total reproductive success in males. We detected

FIGURE 3 Extra-group paternity (EGP, top panel), within-group paternity (WGP, middle panel) and total paternity (bottom panel) gained by dominant male Seychelles warblers per year in relation to their age ($n = 1,364$ annual observations from 237 males). Means of raw data (points) and their standard error (bars) are shown with associated sample sizes. Black lines represent the predictions from the GLMMs (Table 4) and the areas shaded in grey indicate the 95% confidence intervals (estimated with the *predict* function in R package GGLOT2, version 3.3.0)

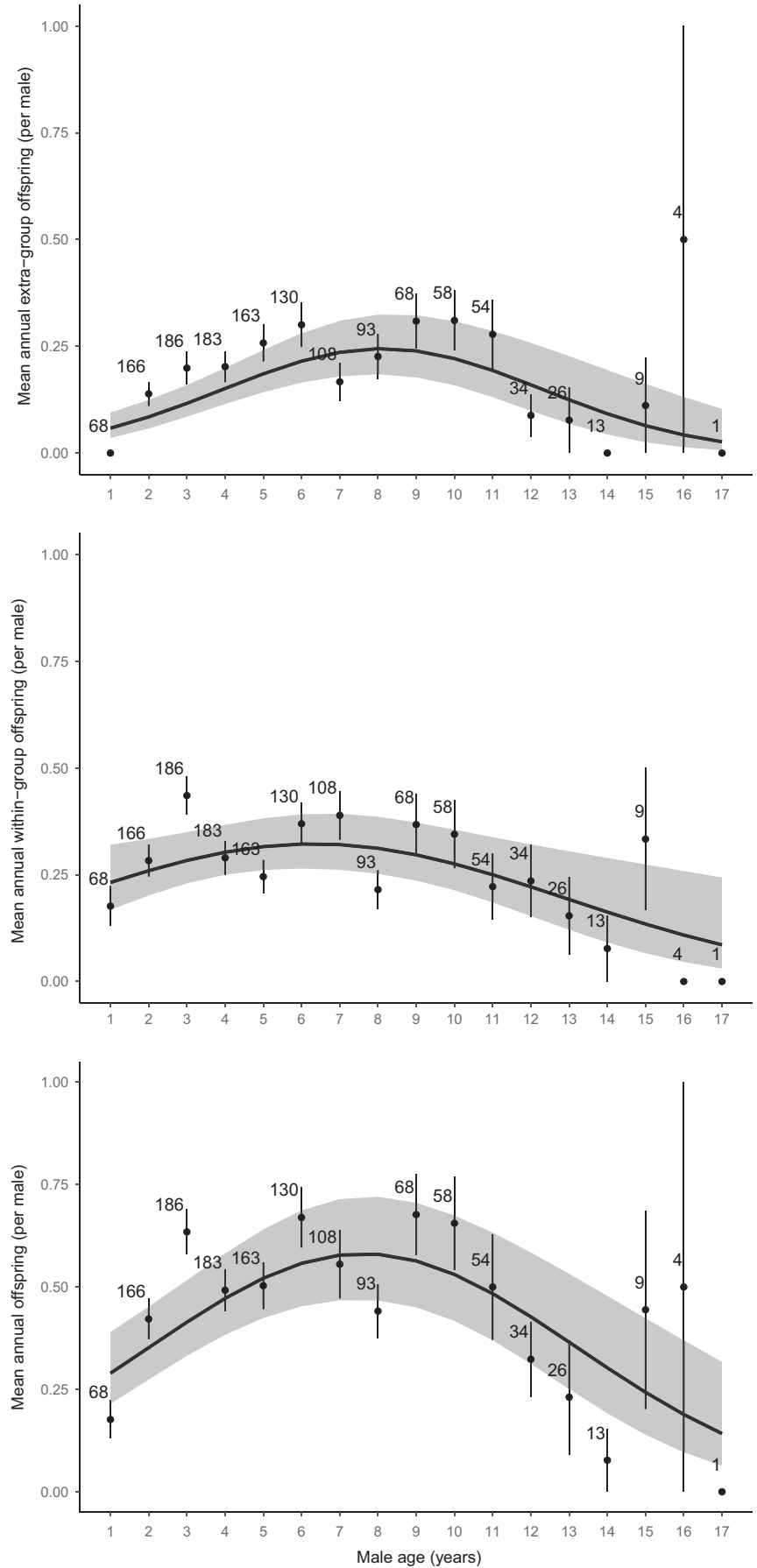


TABLE 4 Parameter estimated from GLMMs of annual (A) extra-group paternity (EGP) success, (B) within-group paternity (WGP) success and (C) total reproductive success (RS) in relation to male age in the Seychelles warbler ($n = 1,364$).

Fixed effects	(A) EGP success			(B) WGP success			(C) Total RS		
	β	SE	<i>p</i>	β	SE	<i>p</i>	β	SE	<i>p</i>
Intercept	-1.60	0.14	<.001	-1.11	0.10	<.001	-0.60	0.11	<.001
Male age	0.43	0.11	<.001	0.09	0.08	.239	0.22	0.06	<.001
Male age ²	-0.30	0.07	<.001	-0.12	0.05	.009	-0.17	0.04	<.001
Male AFD	-0.04	0.08	.574	0.00	0.05	.941	-0.01	0.04	.697
Male longevity	-0.13	0.11	.229	-0.10	0.07	.151	-0.10	0.06	.068
Male terminal effect	0.15	0.21	.500	-0.27	0.19	.149	-0.07	0.14	.571
WGP success	0.02	0.07	.808	-	-	-	-	-	-
EGP success	-	-	-	<0.001	0.05	.978	-	-	-
WGP success X male age	0.10	0.08	.271	-	-	-	-	-	-
WGP success X male age ²	0.02	0.07	.840	-	-	-	-	-	-
EGP success X male age	-	-	-	0.10	0.07	.139	-	-	-
EGP success X male age ²	-	-	-	0.02	0.04	.883	-	-	-
Random effects	σ^2	<i>n</i>		σ^2	<i>n</i>		σ^2	<i>n</i>	
Male ID	0.22	237		0.00	237		0.02	237	
Territory	0.16	138		0.00	138		0.00	138	
Year	0.12	18		0.09	18		0.15	18	

Note: Coefficient estimates (β), standard errors (SE) and *p*-values (*p*) are shown for each fixed effect.

Variance (σ^2) and number of observations (*n*) are shown for each random effect.

Significant ($p < .05$) terms are shown in bold.

Abbreviations: AFD, age of first dominance; X, interaction between two terms.

significant post-peak senescent declines in extra-group reproduction for both sexes, and in within-group and total paternity success for males.

4.1 | Age-dependent female extra-group reproduction

The likelihood of producing EGO changed with age within females, increasing until females were 5.6 years old and declining thereafter (Figure 1), but there were no selective appearance or disappearance effects (between-female age effects). Our findings are consistent with some cross-sectional studies that have found a positive association between female age and infidelity (Bouwman & Komdeur, 2005; Dietrich et al., 2004; Kempnaers et al., 1999), while other cross-sectional studies have shown a negative relationship (Moreno et al., 2015; Ramos et al., 2014; Stutchbury et al., 1997) or no relationship with age (Cordero, Wetton, & Parkin, 1999; Li & Brown, 2000; Lubjuhn et al., 2007; Veiga & Boto, 2000; Wagner et al., 1996). To our knowledge, no other studies have separated within- from between-individual age effects on the production of EGO by females.

The age-related increase in female extra-group reproduction we observed may be due to increases in experience and/or body condition of females with age (until they approach 6 years).

In female Seychelles warblers, breeding and helping experience, which accrue with age, enhance the number of offspring raised to independence (Komdeur, 1996). Moreover, female reproductive success increases until they reach 6.5 years of age (Hammers, Richardson, Burke, & Komdeur, 2012), suggesting that a female's physical condition (and experience) improves until this point. It is possible that females at this peak of reproduction are more attractive to males seeking EGP (which may perceive them as successful reproducers) and that they are targeted for extra-group fertilizations. In that case, the detected within-female change in reproduction may be mostly, or even entirely, male-driven. Another possibility is that, as they grow older, females improve their ability to avoid mate-guarding and engage in extra-group copulations, thanks to experience or improved body condition (Bouwman & Komdeur, 2005). Additionally, greater experience and/or condition may allow older females to cope better with any reduction in paternal investment that may occur when males perceive a loss of paternity, thus allowing females to gain more extra-group fertilizations (the constrained female hypothesis; Gowaty, 1996). However, indirect evidence suggests that female extra-group reproduction is not constrained by male retaliation in the Seychelles warblers. In territories with cooperative breeding, helpers provide load-lightening to the dominant pair (van Boheemen et al., 2019; Hammers et al., 2019) and this might liberate dominant females from the costs imposed by male retaliation (Mulder, Dunn,

FIGURE 4 The proportional contribution of extra-group paternity (EGP) to the annual reproductive success of dominant male Seychelles warblers (siring ≥ 1 offspring), in relation to age ($n = 535$ annual observations from 233 males). The means of raw data (points) and their standard error (bars) are shown with associated sample sizes. The black line represents the prediction from the GLMM (Table 5) and the area shaded in grey indicates the 95% confidence interval (estimated with the *predict* function in R package GGPLOT2, version 3.3.0)

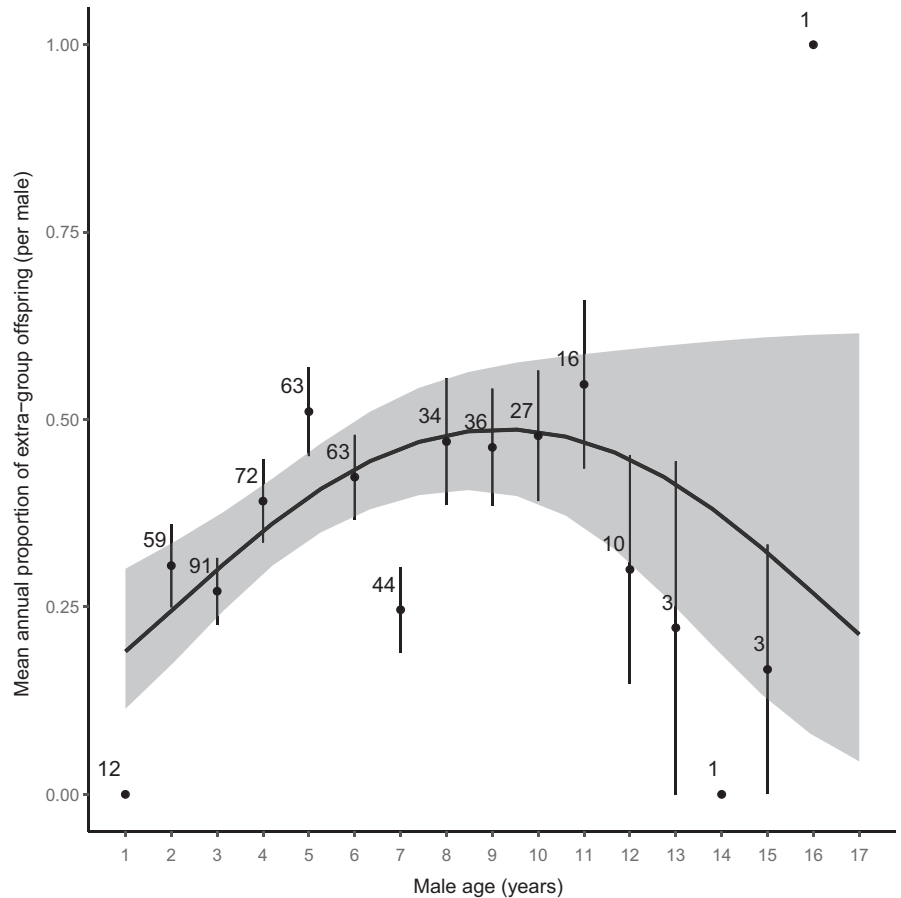


TABLE 5 Parameter estimates from a GLMM of the proportional contribution of extra-group paternity (EGP) to the annual reproductive success of dominant male Seychelles warblers (siring ≥ 1 offspring), in relation to male age ($n = 535$)

Fixed effects	Proportion of EGP ($n = 535$)		
	β	SE	p
Intercept	-0.37	0.13	.005
Male age	0.38	0.14	.005
Male age²	-0.18	0.07	.012
Male AFD	-0.02	0.10	.835
Male longevity	-0.01	0.13	.941
Male terminal effect	0.50	0.30	.117
Random effects	σ^2	n	
Male ID	0.00	233	
Territory	0.51	131	
Year	0.00	18	

Note: Coefficient estimates (β), standard errors (SE) and p -values (p) are shown for each fixed effect. Variance (σ^2) and number of observations (n) are shown for each random effect. Significant ($p < .05$) terms are shown in bold.

Abbreviation: AFD, age of first dominance.

Cockburn, Lazenby-Cohen, & Howell, 1994). Contrary to the expectation based on this logic, the presence of helpers is not associated with higher dominant female extra-group reproduction in the Seychelles warbler (Raj Pant et al., 2019).

When analysing female age effects, we also found that the older a female was compared to the dominant male in her group, the higher the likelihood was that she would produce an EGO. This is in

accordance with other studies in which the production of extra-pair offspring was based on the combination of the female's age and that of her social male (Bouwman & Komdeur, 2005; Dietrich et al., 2004; Ramos et al., 2014; Rätti, Lundberg, Tegelström, & Alatalo, 2001)—but see Lubjuhn et al. (2007) and Moreno et al. (2015). This result further suggests that females may be targeted more by extra-group males—and/or more easily avoid mate-guarding—when socially

paired with a male that is considerably younger than the female (i.e., a young male that is not skilled at mate-guarding and/or defending his territory from intruders).

4.2 | Female benefits of infidelity

One key hypothesis suggests that females may seek extra-group fertilizations to obtain good paternal genes for their offspring (Hamilton & Zuk, 1982) and age is expected to reflect individual quality via viability (Trivers, 1972). Consequently, the fact that many (cross-sectional) studies have shown that older males gain more paternity through extra-pair reproduction than younger males (Ackay & Roughgarden, 2007; Hsu et al., 2015) has often been put forward as support for the good genes hypothesis (Forstmeier et al., 2014). In the Seychelles warbler, we found that male paternity gain (and loss) varied with age within individuals, and that age-related changes were not explained by selective appearance or disappearance effects. Similar results were found in the two other studies that have separated within- from between-individual age effects on EPP success and within-pair paternity loss (Hsu et al., 2017; Schroeder et al., 2016). This lack of any between-individual male age effect on EPP success is important because it undermines key evidence put forward to support the good genes model, as preferred or more successful sires do not appear to be of higher quality, at least as evidenced through greater longevity.

At first glance, this finding may appear to be in contrast to previous studies on the Seychelles warbler, which have provided evidence that extra-pair mating can offer genetic benefits. Those studies showed that dominant female Seychelles warblers paired with males exhibiting low MHC diversity gain extra-pair fertilizations (with males of higher MHC diversity) to produce more MHC-diverse offspring, with improved juvenile survival (Brouwer et al., 2010; Richardson et al., 2005). However, any female (pre-/post-copulatory) preference for more MHC-diverse extra-pair males would not cause a between-individual effect of male age on EPP in the Seychelles warbler, because the survival benefit of higher MHC diversity is only observed in juveniles. In adult males, there is no differential survival linked to MHC diversity (older adult males are not more MHC-diverse than younger adult males).

Further work is now required to understand the mechanisms through which males improve their ability to gain EGP with age, and whether this also provides any benefits to females. Females may also engage in extra-pair mating to gain other types of benefits (Forstmeier et al., 2014), such as fertilization assurance (Sheldon, 1994) in case they are socially paired with truly infertile males (Hasson & Stone, 2009). In the Seychelles warbler, individual males both gain EGP and lose WGP. This indicates that males that become cuckolded are not infertile but does not rule out that extra-group copulations could have evolved to guard against any rare cases of infertility (although totally infertile males have never been identified in the Seychelles warbler). Another reason why females may seek extra-pair fertilizations is to

acquire indirect genetic non-additive benefits (e.g., compatible genes in offspring; Brown, 1997; Zeh & Zeh, 1996). However, unlike “good genes” benefits, other benefits are not normally expected to be signalled by male viability.

Alternatively, it is possible that infidelity may not provide any benefits for females and instead may have evolved as a by-product of positive selection on genetically correlated traits in males (between-sex correlation) or in females themselves (Arnqvist & Kirkpatrick, 2005; Forstmeier, Martin, Bolund, Schielzeth, & Kempenaers, 2011; Forstmeier et al., 2014; Halliday & Arnold, 1987). This idea, which has received little attention so far, may constitute a promising avenue in unveiling the evolution of infidelity in socially monogamous species, but assessing this hypothesis is beyond the scope of the current study.

4.3 | Male age-dependent paternity gain and loss

Both extra-group and within-group paternity success increased within individual male Seychelles warblers in early life and declined in late life. Moreover, the likelihood of being cuckolded decreased within males at young ages and remained stable from midlife onward. These within-male changes in reproduction and cuckoldry, coupled with the lack of between-male differences due to selective appearance and disappearance, do not provide evidence for the good genes hypothesis (Hamilton & Zuk, 1982) but support the competitive ability hypothesis (Nakagawa et al., 2015). This hypothesis argues that the improvement in male paternity success with age is due to increasing experience (Hsu et al., 2015; Morton et al., 1990; Westneat & Stewart, 2003) or body condition (Nakagawa et al., 2015) causing, for instance, improvements in ejaculate competitiveness, timing of copulations, mate-guarding ability, and effectiveness in finding and copulating with fertile extra-pair females. Even though EGP success changed within individuals with age and was unrelated to longevity (which is expected to reflect an individual's intrinsic quality through viability), the correlative nature of our study calls for further work to distinguish between effects arising due to age per se and effects caused by the difference in genetic or phenotypic quality among individuals. A starting point would be to determine which variables improve with age in the Seychelles warbler.

Gaining EPP enables males to increase their reproductive output without suffering costs associated with rearing additional offspring. In the Seychelles warbler, this ability showed marked changes with age in males. EGP success increased in males up to 7.8 years, before displaying a decline consistent with senescence in the oldest males. The relative contribution of EGP to total paternity increased until 8.6 years of age, with no evidence for a post-peak decline (i.e., both EGP and WGP declined similarly in late life, so the proportion of paternity explained by EGP remained constant). Consequently, EGP is a very important source of total paternity gain, contributing ~49% of annual reproductive success in older males. These results concur with those from numerous cross-sectional studies that have shown a

positive correlation between EPP success and male age (reviewed by Cleasby & Nakagawa, 2012) and with a longitudinal study on house sparrows which identified age-dependent increases in EPP and within-pair paternity success (Hsu et al., 2017). However, our results are particularly insightful because they clearly show that these age-related changes in extra- and within-group paternity occur within individuals and not as a result of preferred males living longer.

There was no evidence of a trade-off between WGP and EGP gain in Seychelles warblers and both WGP and EGP success increased in early life and declined in late life (Figure 3); this indicates that when males obtain more WGP success, they do not do so at the expense of EGP gains, and vice versa. The combined result of EGP and WGP is that annual reproductive success changes with male age, increasing until 7.7 years and declining thereafter (Figure 3). Such within-individual variation in reproductive success (an increase in early life followed by a decline in late life) is common in vertebrates (Nussey et al., 2013). In the Seychelles warbler, annual EGP success displayed a particularly steep increase at young ages, thus strongly intensifying the spike in annual male reproductive success at 7.7 years of age (Figure 3).

Age-dependent changes in the contribution of EPP to male reproductive success have been shown in several species. Most of these (largely cross-sectional) studies have found an increase in the contribution of EPP to reproductive success with male age (e.g., Brekke, Ewen, Clucas, & Santure, 2015; Girndt et al., 2018; Richardson & Burke, 1999) (but see e.g., McDonald, Spurgin, Fairfield, Richardson, & Pizzari, 2017). To our knowledge, the only study that has disentangled within- from between-individual age effects found that the contribution of EPP to reproductive success increased within males until midlife (in agreement with our findings), but that it also varied between individuals with age (Hsu et al., 2017). Our results are important because they show that EGP may play a very substantial role in male fitness, especially later in life. More longitudinal studies across a diversity of taxa are needed to fully understand how important EPP is in terms of overall reproductive success and, in particular, how that may change in relation to age.

It is widely recognized that senescence is an important age-related process occurring in the wild. Numerous studies have assessed senescence in multiple traits (Hayward et al., 2015), including survival (e.g., Cameron & Siniff, 2004) and reproductive output (e.g., Dugdale, Pope, Newman, MacDonald, & Burke, 2011), across a number of species. In the Seychelles warbler, senescence in female reproductive success has been detected in the past (Hammers et al., 2012). To our knowledge, however, no studies have assessed senescence in extra-pair reproduction in females, and only one study has addressed (and found) senescence in extra-pair reproduction in males (Hsu et al., 2017), although this study did not explicitly test for senescent post-peak declines in EPP. Here, we analysed senescent post-peak declines in extra-group reproduction and found these to occur in both male and female Seychelles warblers. In males, we also assessed and found evidence for senescence in WGP and total paternity success. Our results

highlight the importance of the role that senescence plays in the alternative pathways to reproductive success in this and possibly other species.

5 | CONCLUSIONS

The lack of between-male age effects on extra-group reproduction emerging from our study undermines the often cited suggestion that male age-dependent patterns of EPP success support the good genes hypothesis for the evolution of female infidelity. Our results provide support for the idea that infidelity may be important to females for other reasons, such as the acquisition of compatible genes in offspring, or that infidelity evolved because of genetic constraints (i.e., genetic correlation between infidelity and traits under positive selection). Our analyses also provide, to our knowledge, the first explicit evidence that senescence in extra-group reproduction occurs not only in males, but also in females. Finally, our work shows that EGP explains a large proportion of the annual reproductive success of males, and that age-specific changes in EGP amplify age-dependent patterns of reproduction. Further work is now needed to understand how this affects male variance of reproductive success and therefore selection for infidelity.

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AUTHOR CONTRIBUTIONS

D.S.R., H.L.D., S.R.P. and M.H. conceived and designed the study. D.S.R., M.H. and S.R.P. contributed significantly to fieldwork, and H.L.D. performed parentage assignment. S.R.P. undertook the analysis (with substantial input from M.H.) and wrote the manuscript. S.R.P., M.H., D.S.R. and H.L.D. contributed to the interpretation of results and conclusions. All authors discussed the results and contributed to the manuscript. D.S.R., J.K., T.B. and H.L.D. manage the

long-term warbler project and data set. D.S.R. and J.K. raised the PhD studentship funding for S.R.P.

DATA AVAILABILITY STATEMENT

Analyses reported in this article can be reproduced using the data provided by Raj Pant, Komdeur, Burke, Dugdale, and Richardson (2020). The data used in this study are available in DRYAD (<https://doi.org/10.5061/dryad.3j9kd51fs>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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